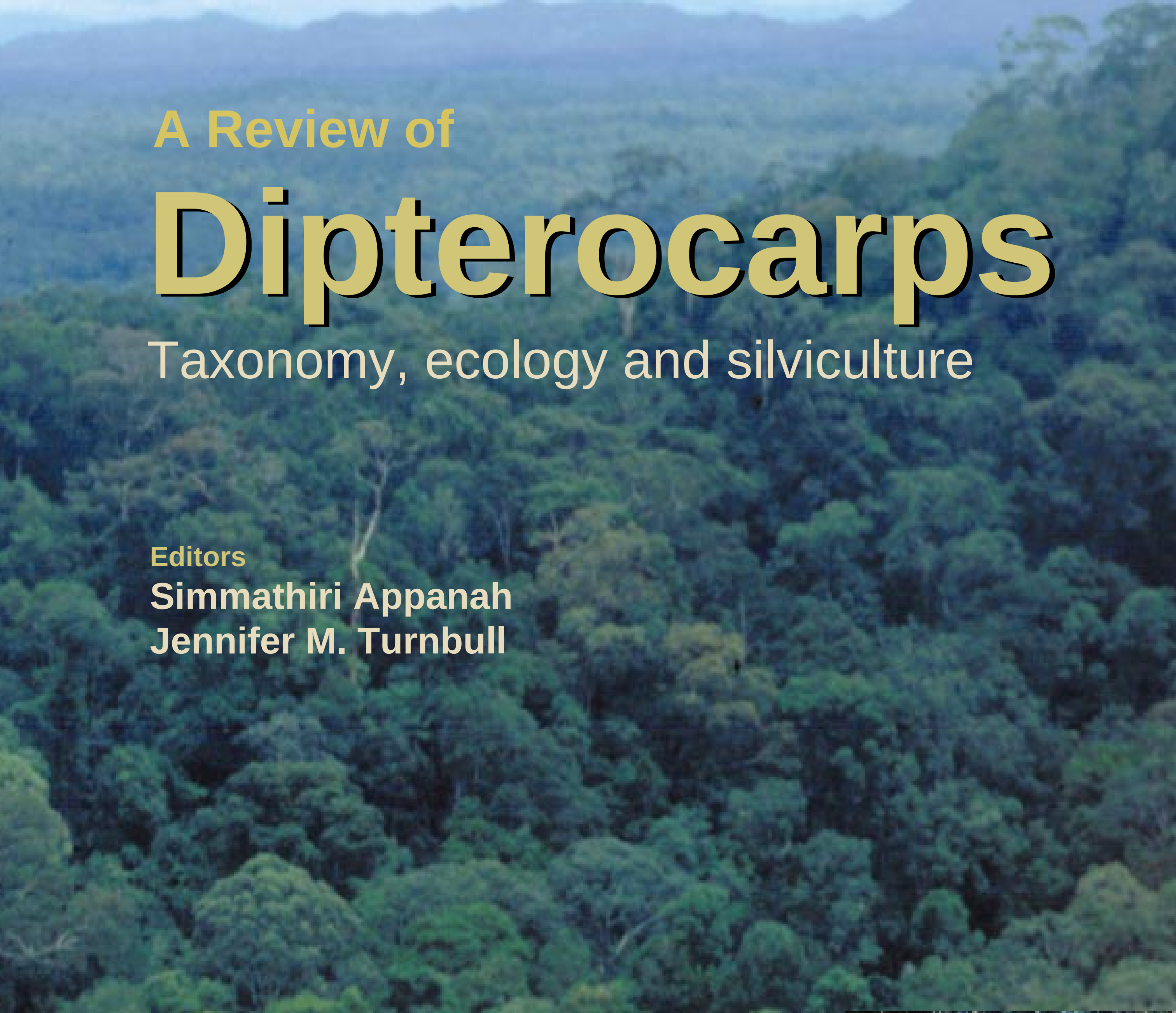

A Review of

Dipterocarps

Taxonomy, ecology and silviculture

Editors

Simmathiri Appanah

Jennifer M. Turnbull

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Abbreviations

ABA	Abscisic acid
ACOM	Asian Conference on Mycorrhizae
AFTSC	ASEAN Forest Tree Seed Centre
ASEAN	Association of Southeast Asian Nations
ASTAG	Agriculture Division in the Asian Technical Department, World Bank (ceased January 1993)
BHC	Benzene hexachloride
BIO-REFOR	Biotechnology assisted Reforestation
BIOTROP	See SEAMEAO-BIOTROP
CIFOR	Center for International Forestry Research
DABATTS	Database of tropical tree seed research
DENR	Department of Environment and Natural Resources, Philippines
DFID	Department for International Development (United Kingdom)
DNA	Deoxyribonucleic acid
EEC	European Economic Community
FAO	Food and Agriculture Organization of the United Nations
FD	Forest Department of Peninsular Malaysia
FORSPA	Forestry Research Support Program for the Asia-Pacific
FRIM	Forest Research Institute Malaysia
GTZ	Deutsche Gesellschaft für Technische Zusammenarbeit
IBPGR	International Board for Plant Genetic Resources (now IPGRI)
ICFRE	Indian Council of Forestry Research and Education
IIED	International Institute for Environment and Development
IPGRI	International Plant Genetic Resources Institute
ITTO	International Tropical Timber Organisation
IUCN	The World Conservation Union
IUFRO	International Union of Forestry Research Organizations
IWGD	International Working Group on Dipterocarps
JICA	Japan International Cooperation Agency
JIRCAS	Japan International Research Centre
LN	Liquid nitrogen
LSMC	Lowest-safe moisture content
MC	Moisture content
MP	Melting point
MTC	Malaysian Timber Council
MUS	Malayan Uniform System
NCT	Non-crop trees
NTFPs	Non-timber forest products
ODA	Overseas Development Authority (United Kingdom) (now DFID)
OLDA	Orthodox with limited desiccation ability
OTA	Office of Technology Assessment
PAR	Photosynthetically active radiation
PCARRD	Philippine Council for Agriculture, Forestry and Natural Resources Research and Development
PCT	Potential final crop trees
PEG	Polyethylene glycol
PSLS	Philippine Selective Logging System
RAPA	Regional Office for Asia and Pacific (FAO)
RAPD	Random Amplified Polymorphic DNAs
RIF	Regeneration Improvement Fellings
RIL	Reduced Impact Logging
ROSTSEA	Regional Office for Science and Technology for South East Asia (UNESCO)
SEAMEO-BIOTROP	South-East Asian Regional Centre for Tropical Biology
SMS	Selective Management System
SPDC	Special Programme for Developing Countries (IUFRO)

SPINs	Species Improvement Network
TPI	Tebangan Pilih Indonesia (Indonesian Selective Cutting System)
TPTI	Tebang Pilih Tanam Indonesia (Modified Indonesian Selective Cutting System)
TROPENBOS	The Tropenbos Foundation, Netherlands
TSI	Timber Stand Improvement
UNESCO	United Nations Educational, Scientific and Cultural Organization
UPM	Univesiti Pertanian Malaysia (Agriculture University of Malaysia)
USDA	United States Department of Agriculture
VAM	Vesicular arbuscular mycorrhizas

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The dedication and enthusiasm of the authors have contributed to make this book what it is. Our special thanks go to Christian Cossalter of the Center for International Forestry Research for his major role at the start of the project deciding content, general structure and authorships and later in arranging external reviewers. His attention and support has freed us from the day-to-day problems of bringing such a book to completion and allowed us to concentrate on editorial tasks. We would also like to thank those who reviewed the various chapters: they are P.S. Ashton (Harvard Institute for International Development), Peter Becker (Universiti Brunei Darussalam), Tim Boyle (Center for International Forestry Research), P. Burgess, P. Moura-Costa (Innoprise), K.S.S. Nair (Kerala Forest Research Institute), F.E. Putz (Center for International Forestry Research), Manuel Ruiz-Perez (Center for International Forestry Research), Willie Smits (The International MOF TROPENBOS – Kalimantan Project), Paul B. Tompsett (Royal Botanic Gardens Kew), Ian Turner (National University of Singapore) and T.C. Whitmore (Cambridge University). Our warm thanks go also to Rosita Go and Meilinda Wan for secretarial assistance, Gideon Suharyanto for the layout, Paul Stapleton for the cover design, Patrick Robe for the scientific index and Michael Harrington for the general index. The photographs used in this book have been supplied by Christian Cossalter.

The editors
Simmathiri Appanah and Jennifer M. Turnbull

Foreword

The Center for International Forestry Research (CIFOR) was established in 1993 at a time when there was a resurgence of interest in the sustainable management of the world's tropical rain forests. At that time it was evident that a particular focus for CIFOR's research should be in the moist tropical forests of Asia. Trees in the family Dipterocarpaceae, "the dipterocarps" are a major component of southeast Asia's tropical forests. Their wood is pre-eminent in the international tropical timber trade and they play a key role in the economies of several countries.

A considerable research effort had already been devoted to the management and utilisation of dipterocarp forests starting with the British in India last century and continuing throughout the 20th century, especially in Malaysia. A vast amount of information has been gathered, but unfortunately it has not been consolidated and no readily accessible compilation of results has been available. This has reduced the impact of the research and has almost certainly resulted in the duplication of efforts by national and international bodies.

As a new international research centre it was appropriate that CIFOR should take the initiative and commission a general review of the current state of knowledge of dipterocarp taxonomy, ecology and silviculture, to identify gaps in this knowledge and to spell out priority areas for new research. This action accorded with the views of many members of the informal Round Table on Dipterocarps who had been meeting on a regular basis to share information on the family . A draft outline of the book was endorsed by the Fifth Round Table on Dipterocarps at its meeting in Chiang Mai, Thailand late in 1994. Since then, under the direction of Christian Cossalter at CIFOR and Dr S. Appannah at Forest Research Institute Malaysia (FRIM), 13 authors have prepared and revised the 10 chapters of the book. With authors located in Asia, Europe and the United States this has been a major undertaking and the efforts of all concerned to bring this work to a successful conclusion are very much appreciated.

I anticipate that this book will be especially beneficial to those planning research on dipterocarps in Asia. I hope it will assist university graduate and post-graduate researchers, and especially scientists in national and international organisations to re-orient their research to meet priority needs. The review should also be useful to forest managers in both public and private sectors who must make decisions based on whatever information is available to them and who have neither the time nor the resources to delve into the highly dispersed literature on dipterocarps.

CIFOR is very grateful to many people for their assistance with this book; to all the contributing authors for their commitment and for their patience with demands made on them by the editors; to the reviewers who provided critical appraisals of the chapters and made valuable inputs; to the editors who brought all the contributions together and completed endless checking and cross-checking of the information: to the CIFOR Communications Group for typesetting and layout; and finally to the staff of the Forest Research Institute Malaysia and its Director General Dr. M.A.A. Razak for their unflagging support and cooperation in producing this book. I thank all who contributed in so many ways.

Prof. Jeffrey Sayer
Director General of CIFOR

Introduction

S. Appanah

As a family of plants, Dipterocarpaceae may perhaps hold the distinction of being the most well known trees in the tropics. This famed family of trees stand tall in some of the grandest forest formations the earth has ever witnessed. Their overwhelming presence has led us to call these vegetation zones dipterocarp forests. Currently the dipterocarps predominate the international tropical timber market, and therefore play an important role in the economy of many of the Southeast Asian countries (Poore 1989). The dipterocarps also constitute important timbers for domestic needs in the seasonal evergreen forests of Asia. In addition, these forests are sources of a variety of minor products on which many forest dwellers are directly dependent for their survival (Panayotou and Ashton 1992). Despite such eminence in the plant world, there has never been an attempt to assemble under one cover all the principal aspects of this exceptional family of trees. This is a serious lack which we hope to start redressing and thus pay fitting tribute to this great family of trees.

A greater concern however belies this slim effort. The very existence of these trees and the forests they stand in is at stake today because of the unrelenting pace at which we are chopping down these forest giants and converting their forests to other forms of landuse (FAO 1989). If present trends persist, not only will nations and people become impoverished, but mankind will stand to lose many species of plants and animals forever. These dipterocarp forests, especially those everwet formations of West Malesia, are among the richest worldwide in terms of flora and fauna (Whitmore 1975).

Much of the knowledge on the species within the Dipterocarpaceae exists in a disparate form even though research on dipterocarps extends for about a century, almost since the beginning of tropical forestry in British India. Apart from some classical work on their taxonomy (e.g. Symington 1943) and silviculture (Troup 1921, Wyatt-Smith 1963), most other studies remain fragmented. A uniform and comparative body of information on dipterocarps did not develop. Studies equivalent to those on acacias or eucalypts in Australia never resulted (e.g. Jacobs 1981). This situation is the result of a number of factors including:

1. The dipterocarps that comprise timber species are distributed over a very wide range throughout tropical Asia, covering several climatic zones and geographies. The number of species in each country varies from 1 to over 200 (Ashton 1982). Consequently the depth of interest differs from country to country.
2. The historical emphasis upon forest management differs between countries, and this is reflected in differences in institutional strengths and development in research. While the dipterocarps are managed in some countries, in other locales they are simply exploited. A quick glance at the status of knowledge on the dipterocarps in the region confirms this unevenness. In some locations, the Indian continent for example, the knowledge on many aspects of dipterocarps is comprehensive. In others like Laos and Cambodia, it varies from fragmentary to cursory.
3. Whatever scientific links that existed during the colonial period have broken down. In fact, the first forester brought in to attend to Malayan forest needs was from British India (Wyatt-Smith 1963). Today, scientific links between countries sharing the dipterocarps have become desultory.
4. A considerable amount of information is sitting in national institutes either in unprocessed form in departmental files, or as internal reports, unpublished theses, etc. Some reports are written in the local language. Thus, a substantial wealth of knowledge is simply not available to the vast majority of scientists.

As a consequence, much of the knowledge on dipterocarps appears to be accessible only to specialists. The potential benefits of this family have not been fully recognised, and if the present situation is allowed to proceed, mankind may lose important opportunities. The following examples affirm this view. Few realise that the only moist tropical forests in the world where sustainable forest management has been demonstrably practiced are the dipterocarp forests (FAO 1989). The best silvicultural system that was ever formulated for a tropical forest is perhaps the Malayan Uniform System which is based on the exceptional regeneration properties of dipterocarps (Wyatt-Smith 1963). In fact dipterocarp forests are the envy of foresters and silviculturists toiling in the African and neotropical areas. However, these facts are seldom if ever highlighted.

The general lack of comprehension about the family has led to a tide of opinion that it is not possible to manage tropical forests, an opinion strongly contested by those involved in dipterocarp forest management. Few realise that the apparent failures in establishing sustainable yields were more the result of changes in landuse patterns and economic restructuring than from an inherent inability of the forest to respond to appropriate silvicultural interventions (Appanah and Weinland 1990). To a degree, this lack of understanding has led us to exploit the forests somewhat carelessly without considering the wonderful opportunities they offer for practicing sustainable forestry.

This ignorance of the qualities of dipterocarps has also led us to search elsewhere for usable tree species when interest in timber plantations for the moist tropics developed (e.g. Spears 1983). The general impression was that dipterocarps, as a group, are slow growing and planting material difficult to procure. Such over-generalisations made us miss some important opportunities with dipterocarps. There are dipterocarps which make excellent plantation species (Appanah and Weinland 1993), and several have growth rates that are acceptable or superb for this purpose (Edwards and Mead 1930). Few recognise the potential of dipterocarps with their mycorrhizal associations to grow under poorer soil conditions. Nor has attention been focused on the variety of dipterocarp species available that are adapted to a wide range of habitats and edaphic conditions making it possible to match species to specific conditions in plantations.

Now that attempts to establish fast growing hardwood plantations based on exotic timber species in moist forests of Asia have met with many difficulties, there is a resurgence of interest in indigenous species for this purpose. Many of the species under consideration are dipterocarps (Anon. 1991). Throughout Southeast Asia, plans for planting dipterocarps are regularly announced while major reforestation activities are often based on the use of species from this family. Meanwhile, forest scientists and managers from all over the world are looking to dipterocarp forests to provide models for sustainable forest management for the moist tropics and ensure a steady supply of industrial wood in the future.

Currently, numerous initiatives, both national and international, are underway to address the variety of issues related to dipterocarps and dipterocarp forests. These issues under investigation cover a very wide spectrum, from basic management issues (e.g. National Institutes, Food and Agriculture Organization (FAO), International Tropical Timber Organisation (ITTO), Department for International Development (DFID)), to producing quick field identification guides (DFID)**,** and biodiversity (DFID), ecology and economics (National Science Foundation, Center for Tropical Forest Science), vegetative propagation (TROPENBOS, Japanese International Cooperation Agency), mycorrhiza (TROPENBOS, National Institute for Environmental Studies, European Commission), non-timber forest products, plantations (ITTO, TROPENBOS, Forestry Research Support Programme for Asia and the Pacific), and so on. In addition to the interest in planting dipterocarps, there is also a general surge of excitement over all other aspects of this family. Some major studies currently underway include sustainable management of dipterocarp forests (Sabah Forest Department/Deutsche Gesellschaft Fuer Technische Zusammenarbeit MbH) and carbon sequestration and reduced impact logging (Forest Absorbing Carbon-dioxide Emissions Foundation).

While the above endeavours are laudable, and bear testimony to the value of dipterocarps, we view this proliferation of apparently uncoordinated initiatives with some concern. Undoubtedly, these undertakings are going to vastly increase our knowledge of the trees and the ecosystem, so that in the final analysis we get closer to our ultimate goal – the ability to manage these forests on a sustainable basis. But at what price in terms of efficient use of resources? Several issues require further reflection:

1. While dipterocarps may seem to hold better prospects, one should not be trapped into the notion that they are the solution to our present problems. The difficulties encountered with planting of exotics are not limited to biological constraints (e.g. Evans 1982, Appanah and Weinland 1993). Management and economic issues played just as big a role in these difficulties. The same difficulties could be encountered with planting of dipterocarps. Therefore, past experiences should be analysed and/or new work started in areas like species trials, provenance testing, seed orchards, selection of plus trees, vegetative propagation, etc.
2. There is a general lack of coordination between and among external agencies and international donors for most of the initiatives. While duplication of activity is common, experiences are rarely shared, leading to adoption of practices that have been proven to have no potential. Furthermore, if such duplication of research had been avoided, perhaps funds and resources could have been applied more optimally.
3. The lack of a common and easily accessible body of information on dipterocarps has had unfortunate impact on the development of moist forest management techniques. Many a trial, effectively proven unworkable, is repeatedly tried out elsewhere in blissful ignorance, sometimes even in the same locale by a fresh generation of researchers and managers, while documentation of the previous experiences remained locked away in dusty filing cabinets. Lessons learned in the past have been misunderstood, forgotten or simply not recognised. One notorious example is the case of underplanting with dipterocarps. Despite ample proof that dipterocarps will need a reasonable amount of direct light for fast growth, even today hundreds (or even thousands) of hectares of exotic plantations have been underplanted with dipterocarps in several countries. Such trials are doomed to fail.
4. Even the practice of silviculture has not been free of this repetition of mistakes. Here there appears to be a tendency to start at the bottom when it comes to research. Seldom research is initiated that follows through findings of previous researchers. A thorough understanding of past research seems to elude the next generation of scientists. Examples of such cases are disconcertingly numerous. For example, in the 1930s the classic Departmental Improvement Fellings in Malaya were found incapable of releasing the bigger poles and residuals, unless the fellings were repeated several times at a high cost (Barnard 1954). Instead, such fellings released the young regeneration. In the 1970s, the same approach under a different name, called Liberation Felling was adopted in Sarawak (see FAO 1981). The results were the same. However, the recognition that both these systems are the same in principle has not yet been appreciated by most forest scientists.
5. Research on dipterocarps is still being carried out within the confines of narrow disciplines, and problem-oriented, multi-disciplinary approaches are indeed rare. Notable cases exist even within the same research institutions with their silviculturists and forest managers carrying out reforestation programs without the benefits of inputs from tree breeders and geneticists, while the latter appear more interested in theoretical, evolutionary issues.

In conclusion, we can state that our efforts to manage dipterocarp forests is pitted with difficulties: missed opportunities, workable schemes arriving too late, and mistakes repeated time and again. There is no guarantee that this situation will not perpetuate unless we rethink our approach to the whole research and development question. Otherwise more mistakes will be made, more trials and management systems will fail, and the conclusions will point in the most negative direction – that it is not possible to manage tropical rain forest. This, we have to avoid. Time is also against us, considering the rate at which these forests are being logged.

1. In the first instance, there is a need for thorough reviews of former research as well as application trials, both at country and regional levels. Agencies such as Center for International Forestry Research (CIFOR), FAO and Asian Development Bank are well placed to initiate these reviews. These, while pointing out the successful methods, should at the same time identify the unsolved problems and gaps in research for which urgent work is needed.
2. Armed with these reviews, national and international agencies can approach donor agencies for funding. Agencies like the International Working Group on Dipterocarps could assist national and international institutions in identifying relevant projects. If several of these big projects are placed in one basket and handed to donor agencies, they could then select

each project that is most needed for specific countries, and identify the specific groups that are in the best position to carry out the work. It is time dipterocarp forest scientists emulate the manner of astronomers. They are few in number, but collectively were able to put the billion dollar Hubble Space Telescope into space.

3. Another possibility is to set up research centres exclusively devoted to research on dipterocarps. Interest has been expressed in setting up a Dry Dipterocarp Centre in Thailand and a Moist Dipterocarp Forest Centre in Kalimantan.

For things to start moving in the right direction, it seems opportune to provide a general overview of what is already known about dipterocarps, and to identify the priority areas for further research, including what is needed to achieve the optimal use of dipterocarps. CIFOR has, therefore, undertaken to make this rapid overview of the family, from its systematics, ecology, management, end-uses, etc. This publication must be regarded as a first attempt to broadly cover several aspects of the dipterocarps. We take a broad look at the forests and the trees, and reexamine the way we manage them, and the opportunities awaiting their fullest development. Beyond that, we also touch on the research and development activities currently ongoing, and the future research and development needs. While the principal findings are stated, the document goes further to point out the important gaps in our knowledge and the kind of initiatives, both at international and national levels, that are needed. Finally, we hope this overview will form a precursor for a grander and more comprehensive coverage of this family of trees in the future.

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Chapter 1

Biogeography and Evolutionary Systematics of Dipterocarpaceae

G. Maury-Lechon and L. Curtet

The history of Dipterocarpaceae botany, as understood in modern terms, started more than two centuries ago when Rumphius first mentioned the family in 1750. At that time dipterocarp forests were considered to be inexhaustible sources of wild products. The dipterocarps were thought to dominate extensively throughout southeast Asia. As soon as the high value of their products (camphor, resins, timber) was perceived funds were made available for botanists to conduct expeditions and laboratory research. A considerable amount of information has thereby been collected, and we now can recognise the valuable timber species in the forests and their natural distribution. The quality of market products thereby has become more uniform and predictable, thus favouring trade. At present, underestimated and unrestricted exploitation has encouraged excessive harvesting of dipterocarps and together with modern technologies and economics, has finally endangered the future of dipterocarp forests.

As early as 1824 and 1868 de Candolle emphasised the importance of the number of stamens and their position in relation to petals to separate dipterocarp genera (*Pentacme* from *Vateria*, *Petalandra* from *Hopea*). These characters may affect the quantity of pollen produced and its availability for eventual pollinators. Similarly fruit and seed structures and shapes used in systematics also affect fruit-seed dispersal, germination and plant establishment.

Present geographical distribution and the structures and functions of tropical plants are the results of past adaptations to environmental constraints. These features were produced in geological time under the influence of ancient climatic variation (Muller 1972, 1980). During the last decades, the intensification of human pressure on valuable trees has become the predominant factor of transformation for tropical forests (Maury-Lechon 1991). Excessive canopy openings provoke the rise of ambient temperature and desiccation. Faced with these new drastic conditions, past adaptations may no longer be suitable. If so, the definition of biological plasticity of well defined taxa according to their phylogenetic and ecological relations with the congeners will provide useful tools for forest managers (Maury-Lechon 1993).

Such knowledge in systematics may have value in rehabilitation and sustainable management of forests. Understanding events such as pollination, fruit dispersal, seedling mycorrhization and survival, coupled with biogeographic distribution and evolutionary systematics may help to define lines of lesser phylogenetic resistance (Stebbins 1960, Maury-Lechon 1993). Such an approach provides the boundaries and physical limitations in which a species is able to survive and can be used to identify species most suitable for rehabilitation in the changing conditions that man has introduced into the environment.

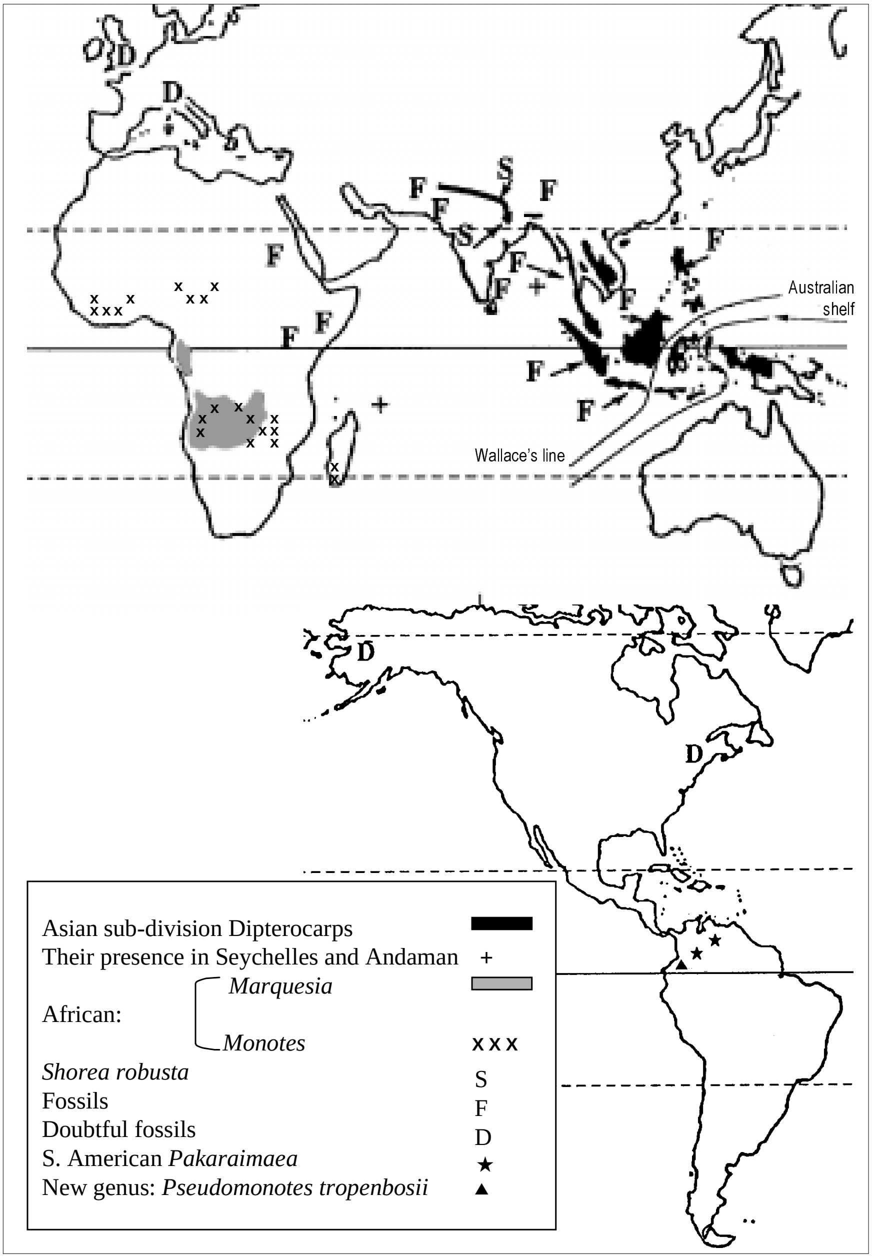
In this chapter, the present understanding of biogeography and evolutionary systematics of the family Dipterocarpaceae is reviewed and whenever possible there are attempts to link this knowledge to its use in the development sector. Finally, there are some notes on further research needs and expertise in the field.

Presentation of the Family Dipterocarpaceae

Taxonomy

All Dipterocarpaceae species are arborescent and tropical (Fig. 1). The family type genus is the Asian *Dipterocarpus* Gaertn.f. Dipterocarps are trees with alternate entire leaves and pentamerous flowers. The family Dipterocarpaceae *sensu stricto* is homogeneous for only Asian plants while the Dipterocarpaceae *sensu lato* include three subfamilies: Dipterocarpoideae in Asia; Pakaraimoideae in South America; and

Figure 1. Distribution of Dipterocarpaceae (adapted from Meher-Homji V.M. 1979).



Monotoideae in Africa and South America. The position of the African and South-American taxa relative to the Asian group varies with authors (Table 1).

Consequently the family contains either 15, 16 or 19 genera (Table 2) and 470 to 580 or more species (plus the newly found South American taxon, the monospecific genus called *Pseudomonotes tropenbosii* which has been attributed to the Monotoideae by its authors (Londoño *et al.* 1995, Morton 1995). During the past decade the numbers have reduced with the increase in collections and systematic expertise. However, uncertainties remain in Asia and Africa, underlining the necessity of an exhaustive and detailed review.

Diversity of opinions also exists for generic divisions, especially with the genus *Shorea* and the group of genera *Vatica* and *Cotylelobium*. A synthetic classification is thus needed. It could be produced from

Table 1. Recent content of Dipterocarpaceae family.

Families	Sub families	Genera
Maguire *et al.* 1977, Maguire and Ashton 1980		
Dipterocarpaceae	Monotoideae	Monotes
		Marquesia
	Pakaraimoideae	Pakaraimaea
	Dipterocarpoideae	see table 2
Maury 1978, Maury-Lechon 1979a, b*		
Monotaceae	Monotoideae	Monotes
		Marquesia
	Pakaraimoideae	Pakaraimaea
Dipterocarpaceae	see table 2	see table 2
Kostermans 1978, 1985, 1989		
Monotaceae		Monotes
		Marquesia
		Pakaraimaea
Dipterocarpaceae	see table 2	see table 2
Londoño *et al.* 1995		
	Monotoideae	Pseudomonotes
		Monotes
		Marquesia

* presented 1977, no formal status for taxonomic ranks, emphasis on greater affinities among taxa.

the data now available, and the collaboration of still active workers, to define a solution acceptable to all in the laboratory, herbaria and field and the timber markets. First, however, more collections are needed of what appear to be key characters, in order to test their validity, particularly among species currently difficult to assign to supraspecific groupings.

Botany

Pakaraimaea are relatively small trees or sometimes even shrubs with alternate leaves (Table 3), conduplicate in aestivation, triangular stipules tomentulose outside and glabrous within, early fugaceous, glabrescent petioles, inflorescences axillary, racemi-paniculate, flowers 5-merous, petals shorter than sepals, neither connate at the base nor forming a cup and not winged at all, all 5 sepals become ampliate and none alate, calyx persistent, anthers deeply basi-versatile, connective conspicuously projected as an apical appendage, pollen grains tricolporate, exine 4-layered, ovary 5-locular (rarely 4), each loculus 2-ovulate (rarely 4), fruit with 5 aliform short sepals, capsule at length dehiscent or splitting along dorsal line of carpel, wood, leaves and ovary devoid of resin or secretory canals, wood rays dominantly biseriate. No economic use is known (Maguire *et al.* 1977, Maguire and Steyermark 1981).

Monotoideae are of three genera, *Monotes*, *Pseudomonotes* and *Marquesia*, and are trees or shrubs (Table 3). They have alternate leaves presenting an extra-floral nectary at the base of the midrib above (Verdcourt 1989), small caducous stipules papyraceous, inflorescences in simple panicles, flowers 5-merous, 5 sepals equally accrescent, petals longer than sepals and variously pubescent, calyx persistent, anthers basi-versatile with apical connective-appendage scarcely to somewhat developed, pollen grains tricolporate, exine 4-layered; ovary 1 to 3 locular (rarely 2, 4 or 5) with generally 2 ovules in each locule (rarely 4) except in *Pseudomonotes* (1 only), wood, ovary and commonly leaves without resin ducts, fruit sepals aliform and neither connate at the base nor forming a cupule, wood rays dominantly uniseriate.

In *Marquesia*, trees are tall to medium-sized and buttressed, leaves evergreen and acuminate, nerves prominent with tertiary venation densely reticulate, indumentum of simple hairs and minute spherical glands on nerves and venation; flowers are small in terminal and axillary panicles; ovary 3-locular becoming 1-locular above parietal placentation, 6 ovules; fruit is ovoid with 5 wings derived from the accrescent calyx, often 1-seeded and apically 2, 3 or 4-dehiscent.

Monotes are shrubs to medium-sized trees without buttresses, with leaves mostly rounded or retuse at apex, rarely acuminate, with more or less rounded extra-floral nectary at the base of the midrib above and sometimes additional ones in lower nerve-axils, with very varied indumentum and small spherical glands sparse or dense on both surfaces which often make the blades viscid, flowers in axillary small or compound panicles, ovary ovoid and hairy completely divided in 1, 2 or 3 (sometimes 4: Maury 1970b, or 5: Verdcourt 1989) locules with 2 ovules in each locule, fruit subglobose presenting 5 equal minutely hairy wings derived from accrescent calyx, fruit normally 1-seeded and indehiscent (often 2, sometimes 3 or 4, rarely 5; in Maury 1970b).

Pseudomonotes trees are 25-30 m tall with a 70-80 cm diameter, with poorly developed buttresses. This species forms entire alternate leaves conduplicate in

Table 2. Recent (1994) genera, sections and sub-sections related to Dipterocarpaceae and authors. (Londoño *et al*. 1995: new genus *Pseudomonotes* included, into Monotoideae *sensu* Maguire *et al*.)

Ashton 1964, 68, 77, 80, 82	Meijer and Wood 1964, 76	Maury 1978 Maury-Lechon 1979a, b	Kostermans 1978, 81a, b, c, 82a, b, 83, 84, 85, 87, 88, 92
1 Hopea	**1 Hopea**	**1 Hopea**	**1 Hopea**
s.Hopea		s.Hopea	
s.s.Hopea		s.s.Hopea	
s.s.Pierrea		s.s.Pierrea	
s.Dryobalanoides		s.Dryobalanoides	
s.s.Dryobalanoides		s.s.Dryobalanoides	
s.s.Sphaerocarpae		s.s.Sphaerocarpae	
2 Neobalanocarpus		not yet created	**2 Neobalanocarpus**
		2 Balanocarpus heimii	**3 Balanocarpus**
3 Shorea	**2 Shorea**	**3 Shorea**	**4 Shorea**
s.Shorea		s.Shoreae	Shorea including
s.s.Shoreae	s.g.Eushorea= Shorea	s. Barbatae	Pentacme genus
s.s.Barbata			(1992: p.60)
s.Richetioides		**4 Richetia**	
s.s.Richetioides	s.g.Richetia	s.Richetioides	
s.s.Polyandrae		s.Maximae	
s.Anthoshorea	s.g.Anthoshorea	**5 Anthoshorea**	
	s.g.Rubroshorea	**6 Rubroshorea**	
s.Mutica	subgr.Parvifolia	s.Muticae	
s.s.Mutica		s.s.Muticae	
s.s.Auriculatae		s.s.Auriculatae	
s.Ovalis	subgr.Ovalis	s.Ovalis	
s.Neohopea		s.Rubellae	
s.Rubella		s.Neohopeae	
s.Brachypterae		s.Brachypterae	
s.s.Brachypterae	subgr.Pauciflora	s.s.Brachypterae	
s.s.Smithiana	subgr.Smithiana	s.s.Smithianeae	
s.Pachycarpae	subgr.Pinanga	s.Pachycarpae	
s.Doona		**7 Doona**	**5 Doona**
s.Pentacme		**8 Pentacme**	
4 Parashorea	**3 Parashorea**	**9 Parashorea**	**6 Parashorea**
5 Dryobalanops	**4 Dryobalanops**	**10 Dryobalanops**	**7 Dryobalanops**
6 Dipterocarpus	**5 Dipterocarpus**	**11 Dipterocarpus**	**8 Dipterocarpus**
7 Anisoptera	**6 Anisoptera**	**12 Anisoptera**	**9 Anisoptera**
s.Anisoptera	s.Pilosae	s.Anisoptera	
s.Glabrae	s.Glabrae	s.Glabrae	
8 Upuna	**7 Upuna**	**13 Upuna**	**10 Upuna**
9 Cotylelobium	**8 Cotylelobium**	**14 Cotylelobium**	
10 Vatica	**9 Vatica**	**15 Sunaptea**	**11 Sunaptea (+Coty.)**
s.Sunaptea	s.g.Synaptea	**16 Vatica**	**12 Vatica**
s.Vatica	s.g.Isauxis	s.Vatica	
(s.Pachynocarpus 1964)	s.g.Pachynocarpus	s.Pachynocarpus	
11 Stemonoporus		**17 Stemonoporus**	**13 Stemonoporus**
12 Vateria		**18 Vateria**	**14 Vateria**
13 Vateriopsis		**19 Vateriopsis**	**15 Vateriopsis**
14 Monotes			
15 Marquesia			
16 Pakaraimaea			

s.: section; s.s.: sub-section; s.g.: sub-genus; subgr.: sub-group.

Table 3. Affinities between Dipterocarpaceae *sensu lato* and other close angiosperm families.

BOTANICAL CHARACTERS		*Dipterocarpaceae* sensu lato*			*Guttiferae*	*Theaceae*	*Tiliaceae*	*Elaeocarpaceae*	*Ochnaceae*	*Sarcolaenaceae*
		Dipterocarpoideae	*Monotoideae*	*Pakaraimoideae*						
inflorescence	paniculate (compound raceme)	+	+		±					
	racemi-paniculate	(+)	+	+						+
	cyme appearance	(+)								
bisexual flower		+	+	+	+	+	+	+	+	+
unisexual flower		-	-	-	+		(-)	(-)		
5-merous perianth		+	+	+		±	±	±	-	±
bud-flower sepals	imbricate	+	-	+		+	-	+	+	+
	valvate	+	+	-		-	+	-	-	-
open-flower sepals	imbricate	+	-	+						
	valvate	+	+	-						
contorted corolla		±			±	-	±	-	+	+
persistent sepals and calyx		+	+	+	+	+				
fruit-sepals	imbricate	+	+	±	±	+			+	+
	valvate	+	+	+		+	+	+		
centrifugal stamens		+	+	+	+	+	+			
hypogynous stamens	numerous	+	+	+	+	+				
	many	+	+	+	+					
2-celled anthers generally dehiscing longitudinally		±	+	+		+				
subversatile anthers		+	+	+			+			
connectival appendage		±			-	-		+		
pollen	tricolporate	-	+	+			+			+
	tricolpate	+								
exine pollen	2-3 layers	+								
	4 layers	-	+	+			+			
ovary	(2)-3-locular	+				+				
	(2)-3-(5)-locular		+							
	4-5-locular			+						
	superior	+	+	+						
	semi-inferior	(+)	(+)							
	generally 2 ovules/ cell	+	(+)							+
placentation axile		+	+	+		+				
aliform fruit sepals		+	+	+	-					
short-sepal fruit calyx		+				-				
possibility of peltate scales on the twig		+								
seeds with scanty endosperm		+				+				

Table 3. (continued) Affinities between Dipterocarpaceae *sensu lato* and other close angiosperm families.

BOTANICAL CHARACTERS		*Dipterocarpaceae* sensu lato*			*Guttiferae*	*Theaceae*	*Tiliaceae*	*Elaeocarpaceae*	*Ochnaceae*	*Sarcolaenaceae*
		Dipterocarpoideae	*Monotoideae*	*Pakaraimoideae*						
leaves	opposite	-	-	-	+					
	alternate	+	+	+		+	+	+	+	+
leaf venation	prominent pinnate	+	+	+				+		
	vertically transcurrent	+	+	+	+					
	entirely transcurrent and	+	+	+	+		+		+	
	presence of columns of sclerenchyme									-
	indistinct leaf venation	+		+		±				
	dentate leaves					±				
paired basal leaf nerves		-	-							+
stipule		±	±	±	-	-	+	+	+	+
hypodermis (+papillose lower epiderms)		-			+					
1-2 layered hypodermis		±		+						+
hair (various within a section)	stellate	±			-	-				
	tufted	±				-				+
	glandules	±			-	-				
complex indumentum		+	+	+			+			
geniculate petiole		+	+	+				+		
indumentum + complex anatomy petiole (Malvales type)		+	+	+						
rays	uniseriate	-	+	-			-			
	biseriate		-	+						
	multiseriate	+	-	-			-			
	mixed uni/multiseriate	+					+			
presence of resins		+	+	+			-			
intercellular resin canals		+	-	-	+		-			
mucilage canals in cortex and cells in the epidermis		+		+			+	-		+
elongate medullary mucilage cells			+	+		-	+			+
arrangement of bast fibres *	into outwardly tapering wedges	+	+	+				+		
pith and primary cortex with indumentum		+	+	+			+			
anomocytic stomata		+	+	+			+			
complex petiolar vascular supply		±	-	-			-			
chromosomes	n=7	+	+		(+)	(+)	(+)	-	-	
	n=11	+			-		-	-	-	

±: present and other possibilities;
+: present;
-: absent;

(-) or (+): exceptions;
* : adapted from Ashton 1982, Maury-Lechon 1979, and other works (see in text: Classification).

vernation, oblong-ovate and chartaceous, with a vestigial gland on the midrib at the base of the blade, triangular, glabrous and caducous stipules. Inflorescences are axillary, subcymose, with bisexual 5-merous flowers, showing a glabrous calyx with 5 lobes which form a shallow cup at the base, a glabrous corolla with contorted petals, the petals longer than sepals, the stamens numerous, cyclic, hypogynous, the anthers basi-versatile, the connective broad and very expanded, continued into a triangular appendage one-fourth to one-half as long as the body of the anther, the pollen grains tricolporate, rarely tetracolporate, sometimes trisyncolpate, exine minutely reticulate to foveolate, columellate, tectateperforate, the ovary glabrous, 3-locular, one ovule per loculus. The fruit is a dry nut, glabrous with a woody pericarp, a persistent calyx with 5-winged accrescent sepals, thinly papyraceous, and 1 seed per fruit. As in African monotoids the wood anatomy of *Pseudomonotes* shows solitary vessels (occasionally in radial pairs), rays mainly uniseriate with infrequent biseriate portions, heterocellular rays, resinous contents present in vessel, rays and parenchyma cells, and presence of secretory cavities in the pith. No economic use is known but the local name (Nonuya Indians) means (in Spanish) 'arbol de madera astillosa', thus wood is probably used by native people.

Pseudomonotes, *Monotes* and *Marquesia* may share solitary vessels or vessels in radial pairs, simple perforation plates, resinous content present in the vessels, rays and parenchyma cells, wood rays, presence of secretory cavities in the pith, lack of resin canals, single gland on the upper surface of the lamina at the base of the midrib, basi-versatile anthers and tricolporate pollen grains. *Pseudomonotes* differs from the Asian dipterocarps in the absence of fasciculate trichomes, multiserate rays, wood, ovary and leaves resin canals and tricolpate grains, and having one ovule per locule with nearly basal placentation.

Dipterocarpoideae, the Asian dipterocarps are small or large, resinous, usually evergreen trees, often buttressed and usually developing scaly or fissured bark on large trees. Some or most parts present a tomentum, with alternate simple leaves, margin entire or sinuate, not crenate, penninerved, with a more or less geniculate petiole, stipules paired, large or small, persistent or fugaceous and leaving small to amplexical scars, inflorescence in panicles with racemose branches usually with flowers secund, i.e. turned to one side, except in *Upuna* (cymose appearance perhaps due to reduction of a panicle of the *Shorea* type, and an even stronger reduction in some *Stemonoporus* and *Dipterocarpus rotundifolius*, whose flowers are solitary; in Kostermans 1985). Extra-floral nectaries were recently found in many genera (Ashton, personal communication). In the 5-merous flower, petals are longer than sepals and variously pubescent, calyx persistent with 0, 2, 3 or 5 sepals enlarged into wing-like lobes in fruit, either free down to the base, forming a cup or a tube more or less enclosing the fruit, adnate to or free from it; when free to the base they are mostly imbricate. The basifixed erect anthers bear mainly 2 pollen sacs (rarely 4) on the connective terminated by a short or prominent appendage. Pollen grains are tricolpate with a 2 or 3-layered exine. The ovary is superior or semi-inferior, 3 (rarely 2) locular, each loculus contains 2 ovules. The fruit is loculicidally indehiscent, or at length splitting irregularly, or opening at staminal pore at germination, normally 1-seeded (sometimes 2, exceptionally up to 12 or 18), with woody pericarp and persistent more or less aliform sepals. The stipules are often conspicuously large. Wood, ovary and leaves contain resin secretory canals. Wood rays are multiseriate (Maguire *et al.* 1977).

Ecology

Monotes grows in deciduous formations, and most *Marquesia* species form dry deciduous forests or savanna woodlands. One species, *M. excelsa*, grows in Gabonese rain forest and resembles the Malaysian rain forest dipterocarps. *Pseudomonotes* is found in wet, evergreen rain forest and *Pakaraimaea* in evergreen associations.

Pakaraimaea dipterocarpacea may dominate in dry seasonal evergreen forests on a variety of topographical situations, at altitudes of 450 to 600 m, on weakly ferralitic sandstones. The tallest tree recorded is 20 m with a diameter of 50 cm. Older or damaged trees freely coppice from the base as do some savanna dipterocarps in Asian seasonal regions.

Pseudomonotes tropenbosii develops at 200-300 m, on clayey to sandy sediments, on summits of hills and along shoulders of slopes. These trees constitute the most ecologically important species in the rain forest a few kilometres south of Araracuara (Colombia).

Asian dipterocarps deeply imprint the forest ecology and economy of the places where they grow. They constitute prominent elements of the lowland rain forest (Whitmore 1988) and are also well represented in the understorey. As a family they dominate the emergent stratum. Most belong to the mature phase of primary forest, which contains most of the entire genetic stock (Jacobs 1988). All species can colonise secondary forests during the succession phases provided there is a seed source; seed dispersal is limited, except among water dispersed species. However, none seems presently confined to secondary formations. Certain dipterocarps of the seasonal regions dominate the fire-climax deciduous forests of northeast India and Indo-Burma.

In Asia, dipterocarps occupy a large variety of habitats (Symington 1943, Wyatt-Smith 1963) from coastal to inland, riverine to swampy and to dry land, undulating to level terrain, ridges, slopes, valley bottoms, soils deeply weathered to shallow, well-drained to poorly drained, and rich to poor in nutrients. In Peninsular Malaysia the altitudinal zonation of their main habitat types ranges from 0-300 m (low-undulating dipterocarp forest), 300-750 m (hill dipterocarp forest), and 750-1200 m (upper dipterocarp forest). Zonation however, differs in Borneo and Sri Lanka. The freshwater swamps, especially in drier parts, are rich in species (Corner 1978, in Jacobs 1988) while true peat-swamp is relatively poor. The dipterocarp flora is also poor on limestone and riverine fringes.

Asian dipterocarps are limited altitudinally (Symington 1943) by climatic conditions, and the conjunction of altitude and other natural barriers, such as large rivers and watersheds, have obstructed the distribution of species in Borneo. For example, the northwest and northeast of Kalimantan, Sarawak, Brunei and Sabah are much richer in species than the rest of Kalimantan. The everwet areas are also richer in species than the seasonal ones as shown in Sri Lanka by the concentration of species in the southwest quarter, or in the Thai-Malaysian transition belt, or from Java to the Lesser Sundas (Jacobs 1988).

Distribution of Dipterocarps and Related Taxa

The present distribution patterns of dipterocarps are thought to reflect routes of colonisation and past climatic conditions (Fig. 1). Living dipterocarps *sensu lato* are spread over the tropical belt of three continents of Asia, Africa and South America. They occupy several phytogeographical zones that mainly conform to climatic and ecological factors. However, in southeast Asia, Wallace's line where it runs east of the Philippines and between Borneo and Celebes, is a major phytogeographic boundary for dipterocarps. It cannot be explained in terms of climatic differences but requires the intervention of continental shelf drift.

Phytogeographical Regions of Living Taxa

The South American region (Fig. 1, Table 4) corresponds to Guyana, Venezuela and the part of Colombian Amazon which overlies the Guyana shield.

The African region (Fig. 1, Table 4) includes a continental area and an insular part in Madagascar. The former is in two disjunct areas (Aubreville 1976): a) a narrow strip in the northern hemisphere from Mali on the west, to Sudan on the east, neither reaching the Atlantic nor the Indian Ocean; and b) in the southern hemisphere the *Monotes*-*Marquesia* area covers a semi-dry region between the two oceans, south of the Congolese rain forest, most of which is essentially central and does not reach the Atlantic or Indian Oceans.

The Asian region (Fig. 1, Table 4) corresponds to the Indo-Malesian area, which concentrates a high number of genera and species in the equatorial forests. This area is limited northward by the Himalayan foothills, then approximately by the borders of Assam, Arunachal Pradesh (India), Burma, Laos and Vietnam, and penetrating into south China including Hainan Island. On the extreme southwest the large belt of Asian dipterocarps reaches the Seychelles (1 sp. *Vateriopsis seychellarum*), and covers India and Sri Lanka. Its eastern border corresponds to New Guinea. The Sundalands delimit the most southern part. No dipterocarp species is found in Australia.

Five main phytogeographical regions are classically recognised within this distribution area: 1) Malesia: Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands, Borneo, the Philippines, Celebes, the Moluccas, New Guinea and the Bismarks. The northern frontier of Peninsular Malaysia delimits this part; 2) Mainland southeast Asia: Burma, Thailand, Cambodia, Laos, Vietnam and south China (Smitinand 1980, Smitinand *et al.* 1980, 1990); 3) south Asia: India, Andaman islands, Bangladesh, Nepal; 4) Sri-Lanka; and 5) Seychelles. In these Asian phytogeographical areas each dipterocarp group manifests a more or less distinctive pattern of variation at the species level (Ashton 1982).

Table 4. Phytogeographical regions and distribution of numbers of genera and species.

Area Country	Number of genera		Number of species		Authors
	area	country	area	country	
Malesia	10		465*		*Ashton 1982
Malaya		14		155* 168	Symington 1943
Borneo		13		267* 276	"
Sumatra		?		106*	*Ashton 1982
Philippines**		11		50* 52	" W. Wallace's line
Sulawesi		4		7	*Ashton 1982
Moluccas		3		6	*Ashton 1982
New Guinea		3		15	" E. Wallace's line
Mainland					
Southeast Asia	8		76		Smitinand 1980
					Smitinand *et al.*1990
Burma		6		33	"
Thailand		8		66	"
Laos		6		20	"
Cambodia		6		28	"
Vietnam		6		36	"
China	5		24		Huang 1987
			11		Xu and Yu 1982
Sri Lanka	7		44-45		Ashton 1977
South Asia:	9		58		Kostermans1992
India+Andamans	5 (6)		31		Tewary 1984
North India		4		10	Jacobs 1981
South India		5		14	"
Andamans		2		8	"
Seychelles	1		1		Parkinson 1932
Africa			37*		* Ashton 1982
plus Madagascar	3		49°		° Shaw 1973
Africa	2		48		Shaw 1973
			36		Ashton 1982
			≈30		Verdcourt 1989
Madagascar	1		1		
South America	1		1		Maguire *et al.*1977
					Maguire and Ashton 1980

*: numbers in Ashton's 1982 publication;

°: Shaw's numbers in Jacobs 1981;

Philippines**: east of Wallace's line only 3 genera and 13 species.

NB:
- Number of genera in China assumes China's view of the China-India border, not accepted by India or internationally (*Shorea* probably does not occur in China).
- Symington included undescribed entities, most of which were later absorbed in described entities by Ashton, which explains the difference between numbers.

Present Distribution in the Phytogeographical Regions

The South American region possesses now two monospecific genera related to Dipterocarpaceae *sensu lato*, and belonging to the two different non-Asian main groups: *Pseudomonotes* attributed by its authors to *Monotoideae*, and *Pakaraimaea* in *Pakaraimoideae sensu* Maguire *et al.* (1977).

Pseudomonotes tropenbosii appears to be confined to a small area in the southwesternmost limit of the Guyana Highland and the superposed Roraima Formation sediments in Amazonian Colombia (Fig. 1: nov. gen.). In spite of being found near the distribution area of *Pakaraimaea, Pseudomonotes* has stronger affinities with the African species. Such affinities recall the remote Gondwanan connection between Africa and South America.

Pakaraimaea dipterocarpacea contains two subspecies: *P. dipterocarpacea* ssp. *dipterocarpacea* in Imbaimadai savannas, Pakaraima Mountains, Guyana, and *P. dipterocarpacea* ssp. *nitida* in Gran Sabana and Guaiquinima, Venezuela (Maguire and Steyermark 1981). The new genus *Pseudomonotes* from Colombia (Fig. 1) in most respects seems to be a Monotoideae (*sensu* Maguire and Ashton in Maguire *et al.* 1977), not a Pakaraimoideae (Londoño *et al.* 1995).

African dipterocarps need a reassessment to reduce over-estimations in the Angolan flora. All *Monotes* (about 26 instead of 32 (Verdcourt 1989)) and *Marquesia* (3 or 4 species) grow in the southern hemisphere. Only *Monotes kerstingii* occurs in both hemispheres (Fig. 1). It occurs in the northern hemisphere as an isolated species in a narrow strip, and in the southern hemisphere in the main distribution area of the Monoitoideae. Some species exist through Katanga, Zambia and Mozambique up to the Indian Ocean. Only one species (*Monotes madagascariensis*) reaches south Madagascar.

Marquesia may form monospecific open forests along the fringe of the Congolese rain forest, at the limit of Zaire, Angola and northern Zambia.

The numbers of genera and species in Asia (Table 4: * indicates Ashton's 1982 numbers) show much greater diversity compared to Africa and South America. As expected the higher numbers clearly occur in the everwet regions. The same trend exists from the Malesian region (10 or 14 genera, 465* species) and particularly from Borneo (13 genera, 267* species) and Peninsular Malaysia (14 genera, 155* species), westwards to mainland southeast Asia (8 genera, 76 species) to Sri Lanka (7 or 9 genera, 44-58 species), India (5 or 6 genera, 31 species) and the Seychelles (1 genus, 1 species). The same situation appears eastwards inside the Malesian region from Borneo to Peninsular Malaysia or to the Philippines (11 genera, 50* species) and from Malesia to China (5 genera, 11 or 24 species). The number of taxa strongly decrease on the east side of the Wallace's line in the Philippines (3/11* genera, 13/50* species) and New Guinea (3* genera, 15* species).

Particular needs for a new synthesis concern the Chinese taxa (Yunnan, South China, Hainan Island), using both the published literature (Wang *et al.* 1981, Tao and Tong 1982, Tao and Zhang 1983, Tao and Dunaiqiu 1984, Huang 1987, Zhu and Wang 1992), the on-going works (Yang Yong Kang 1994 personnal communication) and new collections to be done. Dipterocarps in New Guinea and the Philippines have been identified (Revilla 1976) but some biological aspects have to be specified.

Cotylelobium Pierre and *Pentacme*, are the only Asian dipterocarps with a present disjunct distribution area (Table 5). *Cotylelobium* grows in Sri Lanka, mainland Southeast Asia and Sundaland, both under seasonal and aseasonal evergreen forests. *Pentacme* develops in mainland Southeast Asia and also in the Philippines and Papua-New Guinea. Only five genera develop east of Wallace's line (Ashton 1979a) if *Pentacme* is not merged into *Shorea* genus: *Dipterocarpus*, *Vatica* (including *Sunaptea*), *Hopea* (section *Hopeae*) and *Shorea* (*Anthoshorea* and *Brachypterae* groups) and *Pentacme*. Apart from *Pentacme*, the other four genera presently exist in India and occur in Indian fossils (Table 5) as does the genus *Anisoptera* (presently extinct). *Anthoshorea* Heim extends from India to east of Wallace's line. Section *Shorea* Ashton is mainly centered in southeast Asia but is well represented in Sri Lanka; it contains two fire-resistant species in the Indian and Indo-Burmese dry dipterocarp forests. The other genera or sections have more restricted areas (Table 5). The south Asian endemic taxa are *Vateria* genus represented in south India and Sri Lanka, and *Stemonoporus* and *Doona* confined to Sri Lanka. In the southeast part *Upuna* is endemic in Borneo.

Two genera, *Vatica* (*sensu* Kostermans) and *Hopea*, show the largest distribution from India to east of Wallace's line. This is an important fact.

Table 5. Distribution of living and fossil dipterocarp genera or section.

Taxa	S.Am	Afri	Mada	Seyc	India	Sri-L	Chin	Burm	InCh	Thai	Mal	Born	Indo	Phil	N.Gu
Pakaraimaea	O														
Marquesia		O													
Monotes		O	O												
Vateriopsis				O											
Vateria					O*	O									
Stemonoporus						O									
Doona						O									
Balanocarpus K.					O	O									
Vatica Kosterm.					O*	O	O	O	O	O	O	O	O*	O	O
Dipterocarpus		* (?)			O*	O		O*	O*	O	O	O	O*	O	
Anisoptera					*			O	O	O	O	O	O	O	O
Anthoshorea					O	O	O?	O	O	O	O	O	O	O	
s.Shorea (*°)					O*°	O	O?	O*°	O*°	O	O	O	O*°	O	
s.Hopea					O*	O	O	O	O	O	O	O	O	O	O
s.Dryobalanoides								O	O	O	O	O	O	O	O
Parashorea							O	O	O	O	O	O	O	O	
Pentacme					*(?)			O	O	O	(O)			O	O
Sunaptea							O	O	O	O	O	O	O	O	O
Cotylelobium						O				O	O	O	O		
Neobalanocarpus										(O)	O				
Dryobalanops					*				*		O	O*	O*		
s.Richetioides										(O)	O	O	O	O	
s.Rubroshoreae										(O)	O	O	O	O	
s.Brachypterae											O	O	O	O	
s.Pachycarpae												O	O		
s.Rubellae												O		O	
s.Neohopea												O			
Upuna												O			

S.Am: South America; Afri: Africa; Mada: Madagascar; Seyc: Seychelles; Sri-L: Sri-Lanka; Burm: Burma; Chin: China; InCh: Indo-China; Thai: Thailand; Mal: Peninsular Malaysia; Born: Borneo; Indo: Sumatra, Java and other Indonesian islands but Borneo; Phil: Philippines; N.Gu: New Guinea; (O): extreme geographic position (Langkawi island for Malaysia, extreme S-W Thailand); O: living species; *: fossils; O*: living species and fossils; s.Shorea(*°): both section Shorea, and *Shorea sensu lato* for fossils; O*°: both section Shorea and *Shorea sensu lato* when precise taxonomic level not specified, particularly for fossils.

Potential Taxa for Differentiation

The preceding facts suggest that *Dipterocarpus*, *Vatica*, *Hopea* section *Hopeae* and *Shorea* (sections *Anthoshorea* and *Shorea*) could be the main Dipterocarpoideae taxa from which new forms could arise by diversification during periods of isolation of Indian and East Asian lands. This is supported by certain highly variable species which, in a single species, may contain much of the whole set of variations of the other species in their own genus, or even that of different other genera for example, *Shorea roxburghii* and *Vatica pauciflora* (respectively *S. talura* and *V. wallichii*: in Maury 1978, Maury-Lechon 1979 a, b, Maury-Lechon and Ponge 1979). The new taxa should probably correspond to groups of species such as *Hopea* s. *Dryobalanoides* and all the *Shorea* of the 'red-meranti' group in the Malesian area, and perhaps also *Balanocarpus* Kosterm. in the Indo-Sri Lankan part. The limited taxa *Vateriopsis*, *Vateria* in the west and *Upuna* in the east, are residual genus with limited potential for differentiation. *Anisoptera*, with the fossil and present distribution area, perhaps partly shares this lack of evolutionary potential and could be a regressing group. With more limited areas, *Parashorea* and *Pentacme* from one part, and *Dryobalanops* from the other, could also enter this evolutionary-limited-potential group.

Sunaptea, having been several times merged into *Vatica*, requires fossil and living distributions. The *Sunaptea* morphological and anatomical characters in embryos, fruit-seeds and seedlings could have had a much larger distribution. The same remarks concern *Cotylelobium*. Kostermans (1992) changed *Cotylelobium scabriusculum* (Thw.) Brandis into *Sunaptea scabriuscula* (Thw.) Brandis. Perhaps information on living and fossil dipterocarps from China, Indo-China and Burma could modify the present perception of their extension. It is also unknown whether the *Vaticoxylon* were of the *Vaticae*, *Pachynocarpus* or *Sunaptea* types. The absence of *Cotylelobium* among fossil forms results from a lack of detailed criteria in wood anatomy that prevents assessment of its presence.

Close cooperative works between paleobotanists, wood anatomists of living forms and systematicists are needed to consolidate present conclusions on the mixed taxa of *Vatica* and *Cotylelobium*. Future work should particularly consider separately the *Sunaptea*, *Vaticae* and *Pachynocarpus*. The same treatment is necessary for the *Shorea* and *Hopea* sections. These remarks are especially pertinent for the new molecular approaches being rapidly developed, and which have been applied in a few instances to dipterocarps (e.g. Chase *et al.* 1993, Wickneswari 1993). Some of the diverse opinions, in all disciplines, are due to the studies being limited to a restricted number of species. It is therefore necessary to examine the whole set of species instead, with particular attention to intermediate ones such as *Vatica heteroptera* and *V. umbonata* group. The *V. pauciflora* (ex *V. wallichii*) case has already been mentioned above, together with *Shorea roxburghii* (ex *S. talura*). Maury-Lechon's previous conclusions (Maury 1978, Maury-Lechon 1979a, b: Fig. 16, p.100) based on cotyledonary shapes and structures have been vindicated by Wickneswari's results (1993: Fig. 1). These conclusions concern affinities between the *Sunaptea* group and *Cotylelobium* and their joint affinities with *Upuna*, as well as the connection of these three taxa with the closely related group of *Anisoptera* first, and then *Dipterocarpus* and *Dryobalanops*. *Shorea bracteolata*, the only *Anthoshorea* in Wickneswari's study, has cotyledonary characters that are distinct from species such as *S. roxburghii* and *S. resinosa* (Maury 1978, Maury-Lechon 1979 a, b, Maury-Lechon and Ponge 1979). Consequently, the position of *S. bracteolata* reflects perhaps only partially the position of the whole group of species presently included within the *Anthoshorea*. *Shorea resinosa* and *S. roxburghii* cotyledonary shapes locate the *Anthoshorea* close to *Doona* and to *Dryobalanops*, *Dipterocarpus* and *Cotylelobium*. The present heterogeneity of *Anthoshorea* suggests the need for a re-examination both by DNA analysis and other approaches.

The *Dipterocarpus* genus should also be examined for eventual correspondence between chemotaxonomic groups (Ourisson 1979) and biological characters such as seed sensitivity to desiccation and cold temperatures, seed and seedling resistance to pathogens by defensive secretions, and chemical type of root exudates for mycorrhizal fungi association. The statement that there is no relation between chemical groups and morphological features should be re-examined in considering flower characters, particularly stamen shapes, pollen and pollination, sexual and non-sexual reproduction, the fruit-seed-embryo-seedling sequence and the habitat.

Phytogeographical Regions of Extinct Dipterocarps or Related Taxa

No living or extinct monotoid (Tables 5 and 6) has been reported in Asia while diverse supposed dipterocarpoid fossils are described from Europe: *Woburnia porosa* wood from Bedfordshire Lower Cretaceous, U.K. (Stopes 1912, Kraüsel 1922, Schweitzer 1958, all in Aubréville 1976), flowers of *Monotes oeningensis* (Heer) Weyland from Upper Eocene in Hungary (Boureau 1957, Boureau and Tardieu-Blot 1955), and Tertiary fruits of west Germany, Switzerland and Austria (Gothan and Weyland 1964, in Aubréville 1976). Doubts were cast on these identifications (Bancroft 1933, Harris 1956 and Hughes 1961 in Aubréville 1976, Gottwald and Parameswaran 1966, 1968). Other doubtful fruits of *Monotes* type have even been reported from New York (USA) and from the Alaska Eocene putative but unlikely tropical forest (Wolffe 1969, 1977).

Boureau (in Boureau and Tardieu-Blot 1955) doubted this sequence but he remained convinced of the real presence of *Monotes* in the European Cretaceous and Tertiary. Huge distances would then separate the living Monotoideae from the extinct ones, and the Asiatic-Malesian Dipterocarpaceae from the European fossils, without any fossils in between, notably in North Africa.

Tertiary dipterocarp fossils have been reported from the African Miocene of Ethiopia (Beauchamp *et al.* 1973, Lemoigne 1978, Laveine *et al.* 1987) and from the putative (but probably earlier) Plio-Pleistocene of Somalia (Chiarugi 1933). That is in a continent where not a single living dipterocarpoid has been found, and where present monotoids are living. Lemoigne (1978, p.123) specifies 'c'est avec des bois de la famille des Dipterocarpaceae, notamment ceux du genre *Monotes* que notre echantillon parait avoir le plus d'affinites... Certes les affinites avec la famille des Lauraceae sont aussi remarquables'. In spite of its name *Dipterocarpoxylon*, this fossil is thus of a Monotoid type (not Dipterocarpoid). In this case, is the African rain forest species *Marquesia excelsa* derived from a common ancestor with *Monotes* and adapted to a more humid climate, or is it the only surviving species of some Dipterocarpoid ancestor which could have fossilised in Ethiopia and Somalia (and Egypt?)? A study of the pollen exine structure in *Marquesia* is needed to clarify this genus situation, as well as a critical re-examination of all dipterocarpoid fossils (doubtful or not).

Numerous accepted fossils from Asia (Awasthi 1971) testify that the present great species richness of the Asian flora (Table 6) probably existed since the Miocene and persists through the Pliocene and Pleistocene, up to the Quaternary (*Anisopteroxylon*, *Dipterocarpoxylon*, *Dryobalanoxylon*, *Hopenium*, *Shoreoxylon*, *Vaticoxylon*, *Vaterioxylon*).

These fossils demonstrate a reduction of dipterocarp distribution area both in Africa (Fig. 1, Tables 5 and 6) and Asia (extinction of *Anisoptera* and *Dryobalanops* in India, and of the latter in Indo-China), and total extinction in Europe and North America (doubtful fossils?). Could thus the Tertiary distribution area of dipterocarps *sensu stricto* include Africa and Asia (and Europe?)?

Hypotheses on the Geographical Origin of Dipterocarpaceae

If Monotoideae and *Pakaraimaea* are to be connected to Asian dipterocarps (by a single family or into different families), a common ancestor and its migration path have to be found. During the transition from the later Cretaceous to the very early Eocene the paleogeographic changes, in combination with other effects, could have produced the present geography. Thus dipterocarp ancestors should have been present when land connections still existed between South America, Africa and India and between them and southeast Asia (and probably with the European and north American Laurasia block with its intermittent 'Grande coupure'). This situation occurred (Figs. 2 (A, B), 3) in the Permo-Triassic period. Later, parts of the northeastern Gondwana land detached from the Gondwana shelf, crossed the Tethys and joined southeast Laurasia (just as India would do later). These changes would have happened during the Permo-Triassic, Jurassic and Cretaceous times according to recent works on Cathaysian floras (Kovino 1963, 1966, 1968, all in Vozenin-Serra and Salard-Cheboldaeff 1994, Lemoigne 1978, Jaeger *et al.* 1983, Vozenin-Serra 1984, Vozenin-Serra and Taugourdeau-Lantz 1985, Laveine *et al.* 1987, Taugourdeau and Vozenin-Serra 1987, Renous 1989, Scotese and McKerrow 1990 in Vozenin-Serra and Salard-Cheboldaeff 1994), and on the Tethys Sea (Dercourt *et al.* 1992).

Croizat (1964, 1952 in Aubréville 1976) and Ashton (1969) expressed the view of a dipterocarp Gondwanan origin of the present distribution area and to a further migration towards Indo-Malesia. Aubréville (1976) considered that Dipterocarpaceae probably occupied two main areas before the Cretaceous general drift of Gondwanan shelves: one in Asia and one in the joined Africa-India-Seychelles-Sri Lanka complex. He believed that the origin was in Europe from where ancestors of monotoids would have migrated towards Africa and further from there to India. He suggested two Tertiary centres of dipterocarps: one Indo-Malesian from Laurasian origin; and one Africano-Indian from a Gondwanan origin, on both sides of the Tethys Sea. More recent studies (Renous 1989, Dercourt *et al.* 1992, Vozenin-Serra and Salard-Cheboldaeff 1994) identify direct land connections between southeast Asia and Laurasia lands. These authors consider a possible series of small blocks detached from the northeastern part of Gondwana, moving through the Tethys, and forming an archipelago (Fig. 3: Tazrim-Sino-Korean block (1), north China block (2), north Tibet block (3), Khorat-Kontum block: east Thailand and most parts of Laos, Cambodia and Vietnam (4), south Tibet block (5), Kashmir block (6), Iran-Afghanistan block (7), Turkey block (8), Spain block (9)) together with the different southeast Asian plates. This putative archipelago would have served as a relay, perhaps owing to volcanism which would open routes for floral migration. Before the rise of the Himalayas, floristic exchanges would also have been possible around the Tethys (Dercourt *et al.* 1992).

Figure 2. Continental drifts concerning the area of Dipterocarps from Primary to Tertiary (adapted from Renous 1989).

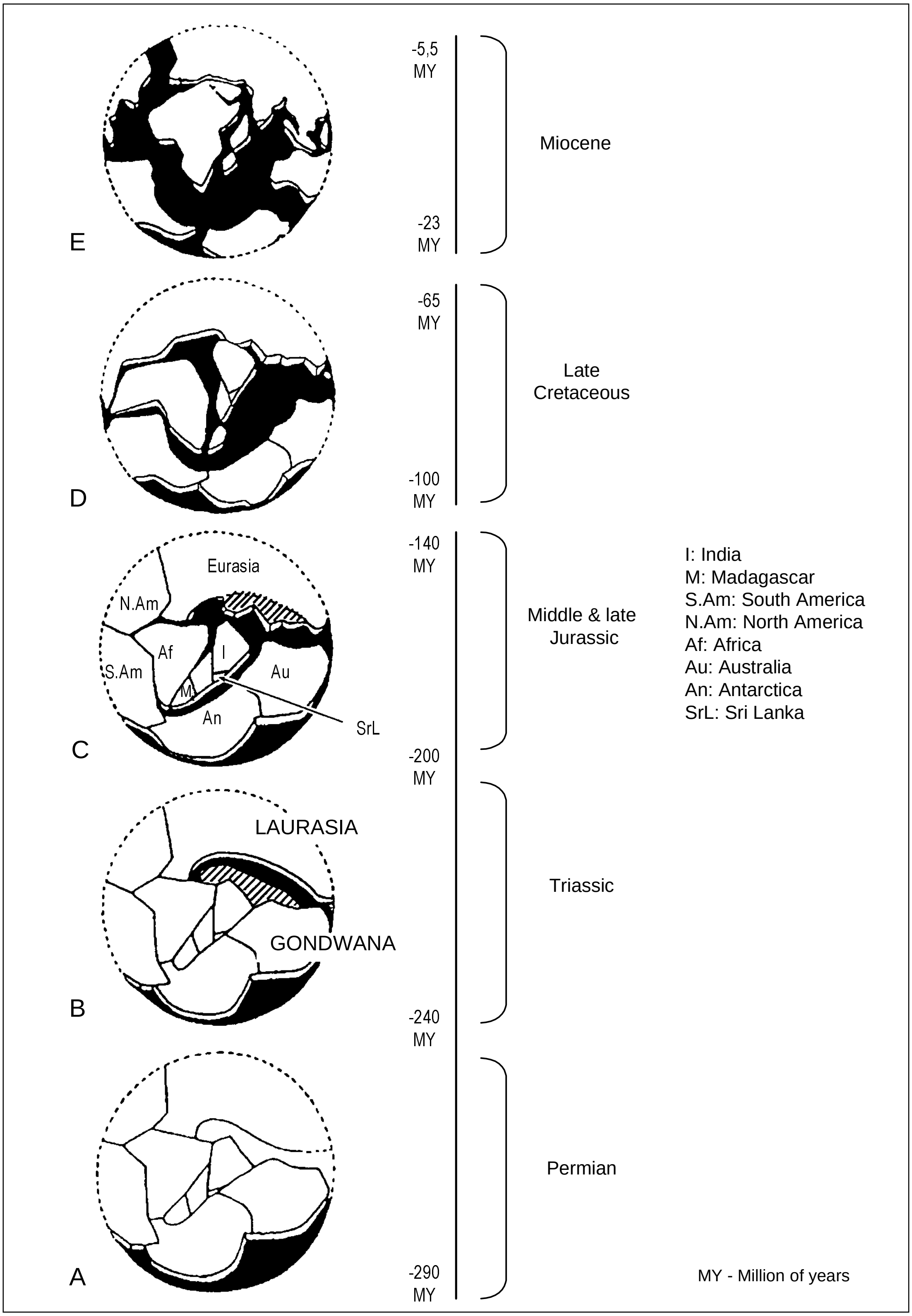


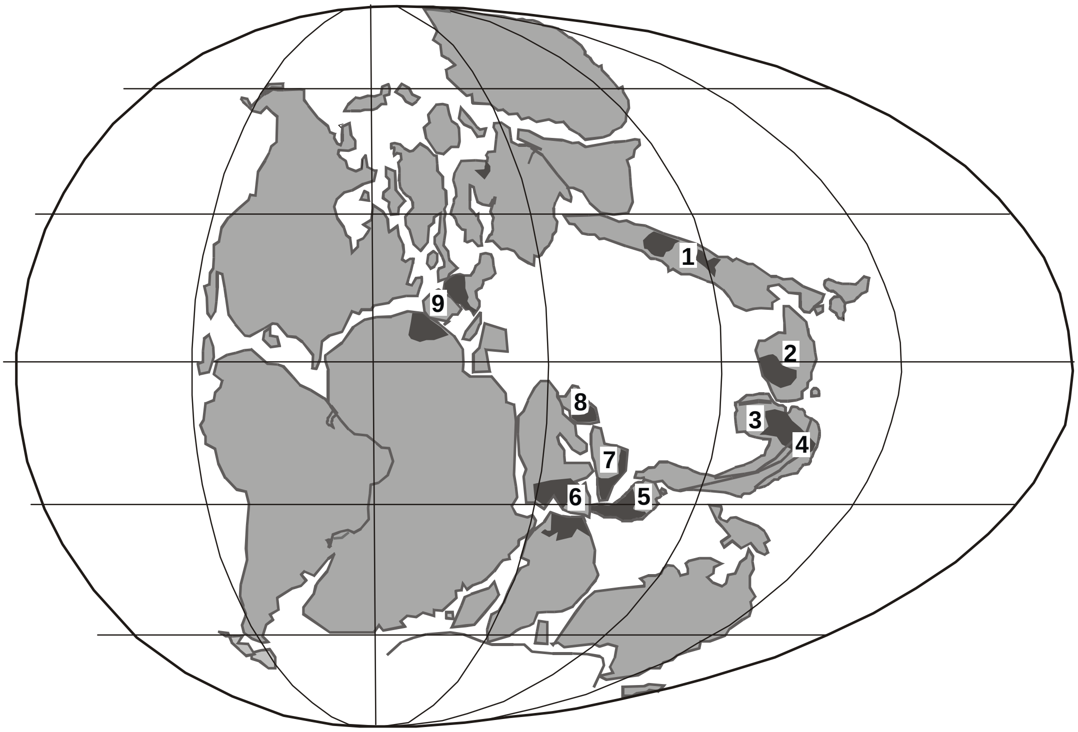
Table 6. Dipterocarp fossil distribution in time and space.

Fossil genera	Number of species			Geological	periods				
	total	country		II	III				IV
				Cret.	Eoc.	Olig.	Mio.	Plio.	Plei.
Monotes oeningensis flower?	1	1	Hungary		*				
Monotoid fruit remants?		1	Germany, Austria Switzerland		*				
Monotoids?? :	3			&					
Calicites alatus, C.obovatus	2	2	New-York USA	&					
Monotoid fossil?	1	1	Alaska	&					
Dipterocarpoxylon? Woburnia	1	1	Great Britain	&					
Dipterocarpophyllum?	1	1	Egypt	&					
Dipterocarpophyllum	1	1	Nepal, N. India			*	*		
Dipterocarpus-type pollen	1	1	Nepal, N. India				*		
"	1	1	Vietnam			III			
Dipterocarpoxylon? Monotoid (Lemoigne 1978)	30	1	Ethiopia				#		
Dipterocarpoxylon? Monotoid?		2	Somalia					&	#
Dipterocarpoxylon		11	North India				+	#	
"		2	Burma			III			
"		2	Vietnam			III			
"		3	Sumatra			III			IV
"		7	Java			III			
Anisopteroxylon	7	5	N. and NW India				**	#	
"		2	India				**	#	
Vaticoxylon	2	1	Sumatra						IV
"		1	Java					*	
Vaterioxylon	2	2	North India				&	#	
Shoreoxylon	23	13 3	India-Assam				**	#	
"		1	Northwest India				**	#	
"		1	North India			III			
"		3	South India				**	#	
"		1	Assam-Cambodia						*
"		1	Burma			III			
"		1	Thailand					#	#
"		7	Sumatra				*	*	IV
Pentacmoxylon??	1	1	India			III?			
Hopenium	4	2	North India				*		
		2	South India				*		
Dryobalanoxylon	13	1	Cambodia						IV
"		1	South Vietnam				#	#	
"		1	Borneo				*		
Dryobalanops pollen		1	Borneo			*			
Dryobalanoxylon		6	Sumatra					*	*
"		5	Java					**	#

: early period; & : upper period; ** : mid+upper period.
* : mid period; + : early+mid-period;

The two successive hypotheses, of Aubréville's double-cradle areas, and of the Vozenin-Serra and Salard-Cheboldaeff's archipelago connection anterior to India's contact with Laurasia, could support a possible very remote common ancestor of American, African and Asian dipterocarps. They could explain the particularities of the Indian-Seychelles-Sri Lanka region, the existence of *Upuna* in Borneo and the post Cretaceous explosion of the dipterocarp family in the more humid and warm conditions found in southeast Asia.

Figure 3. Paleogeographical reconstitution of southeast Asian Permo-Triassic in conformity with paleobotanic data (from Vozenin-Serra and Salard-Cheboldaeff 1994).



1. Sinkiang block (Tarim) + Sino-Korean block (North China).
2. Yangtse block (North China).
3. North Tibet block (North Xizang + North-West Xunnan + Shan Plateau).
4. Khorat-Kontum block (East Thailand, most of Laos, Cambodia and Vietnam, South of Song Ba suture).
5. South Tibet block (Lhassa plate + lands located South of Yalu Tsangpo).
6. Kashmir.
7. Iran and Afghanistan (Helmand block).
8. Turkey.
9. Spain.

Be the origin in Europe or in Africa, both cases would have favoured dispersal and colonisation by the small, light, large-winged fruits over great distances and probably under drier conditions than those of the present rain forests. This could explain why certain present taxa suggest an ancestral form with these fruit characters and again brings forward the hypothesis (Maury *et al.* 1975a, Maury 1978, 1979, Maury-Lechon 1979b) of an origin in open (perhaps semi-dry) environment. Forms with wingless fruits would have had the only possibility to concentrate their evolutionary potential into the protective structures around the seed (e.g., *Vateria*, *Vateriopsis*, *Stemonoporus*, certain *Vatica* and other species with large wingless fruits), these structures could have favoured water dispersal. In the taxa possessing winged fruits the evolutionary potential might have remained available for new opportunities. *Upuna* and *Monotes kerstingii* are perhaps parallel in this respect, as they suggest the hypothesis that they represent similar situations developed in or near Laurasia (*Upuna*) and in Gondwana (*Monotes kerstingii*) during long periods of supposed separation.

Past Continental Changes and Floral Evolution

Past flora also underline a connection between large floristic-climatic changes and the main known collisions or ruptures of continental drifts: a) by lack of marine influence the Permian continental block (Fig. 2 (A), 3) would have been drier than the previous split continents of the Carboniferous with its luxurious Cryptogamic flora; b) the split of Gondwanaland during the Secondary would have permitted marine humidity to enter the fragmented lands (Fig. 2 (B, C) and probably the first Angiosperm ancestral forms to originate; c) the supposed late Cretaceous - early Eocene (Renous 1989, Dercourt *et al.* 1992) connection of India with Eurasia (Fig. 2 (D)), between -65 and -40 million years, and later that of Africa (Fig. 2 (E)), would have created new dry and humid zones and corresponded to the differentiation of Angiosperms (and dipterocarp ancestors?).

According to these reconstituted changes, the flora of past continents from Permian (Primary) to Miocene (Tertiary) times had a very ancient common history (land and climate). Later on the future southern part of the Eurasian southeast zone first separated from the rest of Eurasia (Fig. 2 (B): Triassic: hatched area, Fig. 3) and then (the upper Jurassic) connected with it (Fig. 2 (C, D, E)). Wallace's line corresponds to the separation between lands of different origins: the two Gondwanan shelves, the Indian on the west and the Australian on the east (Fig. 2 (C)).

For long geological periods (lower to extreme upper Cretaceous period, Secondary) the Indian-Seychelles-Sri Lanka part of the Gondwana shelf remained under an insular situation. For similar long periods the present regions of mainland southeast Asia, China and Malesia *pro-parte* remained separated from the Indian island, but perhaps intermittently connected to Eurasia. The Indian collision with Eurasia produced huge changes (land, climate, flora) as well as possibilities (or difficulties) of colonisation and species evolution for both types of flora (the insular-Indian flora and the continental-Asian flora) in the new territories.

Paths of Possible Flora Migrations

Four main land connections are thus suggested for eventual migrations of the ancestors of the dipterocarps, at different periods after the Gondwana split: a) India-Sri Lanka-Madagascar-Africa-America-Eurasia (Fig. 2 (C)); b) the putative eastern archipelago northeast of Gondwana to Eurasia (Fig. 3); c) later, India-Sri Lanka-Eurasia (Fig. 2 (C, D)); and d) finally northeast Africa - Southeast Eurasia (Fig. 2 (E)). Because of the distances, land dimensions and climate history, the first connection could have favoured the success and survival of species with small winged fruits, the second could have aided species with water dispersal, while the third could have permitted the persistence and establishment of more diverse biological types. Perhaps excessively dry climates did not favour dipterocarp migrations in the fourth case.

These geological events bring light to the present distribution over three continents and the paucity east of Wallace's line. They explain certain endemic aspects such as the *Monotes kerstingii* disjuncted area in Africa (survival at the periphery of the rain forest newly established in the previously drier area of *Monotes*). They could justify *Upuna* in Borneo, and localisation of *Vateriopsis*, *Vateria*, *Stemonoporus* and *Doona* in the Indian island zone. These events underline the existence of a very long past of successive modifications, and help to explain the real difficulty in finding primitive features in present flora. If characters evolved independently from each other, a single present taxon might have retained some primitive aspects and modified others; these latter preventing consideration as an ancestral form.

Endemicity of Dipterocarps *Sensu Lato*

As expected, the higher endemicity is located at the extremes of the geographical area of distribution. It is due to monospecific genera westward in south America (100%: 2 sp.), Madagascar (100%: 1 sp.) and Seychelles (100%: 1 sp.). Endemicity is of different intensity (Table 7) eastward in Sri Lanka (98%: 43/44 spp.), south India (85%: 11/13 spp.) and in New Guinea (73%: 11/15 spp.), and with a much lower proportion in Borneo (58 to 55%: 158 to 155/267 spp. of which 1 is a monospecific endemic genus), north Peninsular Malaysia (49%: 23/47 spp.) and the Philippines (47%: 21/45 spp.) and north India (40%: 4/13 spp.). A certain endemicity also exists in the other Malesian areas but the values rapidly decrease: Celebes (29%), Java (20%), Peninsular Malaysia (17-18%), Moluccas (16%). Peninsular Malaysia, Sumatra and Borneo only separated 10,000 years B.P. and, if taken as one biogeographic region, its endemicity is 293/345 species or 85% when the boundary is determined by the Kangar/Pattani line, 303/345 species or 87% when the boundary is the Isthmus of Kra.

Endemicity is very reduced on a country to country basis (Vietnam 9%, Laos 5%), or absent in the mainland southeast Asian phytogeographical area (Burma, Thailand, Cambodia; however, for Indo-Burma as one biogeographic region it is high), and totally absent from

Table 7. Distribution and importance of endemicity in Dipterocarpaceae family.

Geographical areas	Ashton 1982		Jacobs 1981		
	number of species	% of endemicity	total number of species	number of endemics	% of endemicity
Seychelles			1	1	100
Sri Lanka			44	43	98
South India			13	11	85
North India			13	4	40
Andamans			8	1	12
Burma			32	0	0
China mainland			5*	3	60 ?
Hainan			1	0	0
Vietnam			35	3	9
Laos			19	1	5
Cambodia			27	0	0
Thailand			63	0	0
Peninsular Malaysia	155	18	156	26	17
Sumatra	106	10	95	10	10
Java	10	20	10	2	20
Lesser Sundas			3	0	0
Lombok	3	0			0
Borneo	267	58	267	158	55
Philippines	50	47	45	21	47
Celebes	7	29	7	2	29
Moluccas	6	16	6	1	16
New Guinea	15	73	15	11	73
North Peninsular Malaysia (Malayan-Burmese floristics)			47	23	49

* at least total of 16-24 sp. in China (Huang 1987, Yang Y.K. Personal communication), perhaps about 38%.

Lesser Sundas and Lombok islands. In mainland China and Hainan Island data are too uncertain to draw any conclusion. More studies are needed in mainland southeast Asia and China.

Asian Dipterocarp Vicariance

Asian dipterocarps also present groups of twin vicariant species with similar function in different areas. Vicarious species (Ashton 1979a) have been noted in genera *Dipterocarpus*, *Anthoshorea* and *Hopea* (*Hopea* section) between Sri Lanka and either south India or Malesia, and between south India and Malesia or Indonesia.

All these features correlate with the history of the continents and the combined action of island isolation and two other major forces: a) the drier climates in the western lands which are accentuated in South America, Africa, Madagascar and lower for the Seychelles, south India, north India, and part of Sri Lanka; and b) the maintained humidity in the eastern extreme of the Eurasian lands. The Eurasian lands could have permitted the development and spread of winged, light-fruited dipterocarps for long periods of time. This would allow migrations and floristic exchanges first in the Eurasian and later into India on the west, as well as into recently emerged parts of Sunda and Malaysia regions, and the newly arrived parts of New Guinea.

The Sunda region has been (and is still) submitted for long periods to an intense geological activity which could have interfered with the great diversification of dipterocarps within the wet Malesian region and more particularly in Borneo (Maury 1978).

Geographical Patterns in Biological Characters

There is a relation between shapes and structures and the biological processes they permit. It is thus necessary to try to understand how the morphological or biological characters (which constitute the base of the taxonomic divisions and systematic affinities) are related to the survival of plants in a given habitat, particularly under eventual modifications. During the past geological time, climatic and/or geographic variations predominated, while presently the transformations by human beings predominate. This type of information is not yet available for the American and African putative dipterocarp taxa.

Most importantly, some characters (which are essential in establishing phylogenies and classifications) are ancestral and do indeed constrain the ecological range of species; but others are plastic, derived and adaptive to ecological circumstances. This distinction still requires classification among dipterocarps. For Ashton, the greater the number of correlated/independent character states, the more ancient, conservative and phylogenetically important they are, thus this point should be a major basis for assessment of phylogenetic generic delimitation. However, Kostermans strongly disagreed with this approach when presenting his case for *Sunaptea*.

Biological Groups

All the African taxa, except one, fit into monospecific formations of savanna woodland or dry deciduous forests, under seasonal climates. *Marquesia excelsa*, a residual species of the Gabonese rain forest is close to the other savanna species of the genus, and the new South American genus *Pseudomonotes* which appears closely related to *Marquesia*, present the opposite situation. *Pakaraimaea* is abundant but not monospecific and could multiply both through coppicing and sexual reproduction. However in the laboratory the germinative potential of seeds was low and the survival of young seedlings in USA and France nearly impossible (Maguire and Steyermark 1981, Maguire and Maury unpublished).

Most Asian dipterocarps remain in evergreen forests (some in seasonal regions, most in aseasonal areas). A few species of *Dipterocarpus* and *Shorea* live in fire-climax savanna woodlands, though closely allied to rain forest species.

There is a sharp discontinuity in Asian dipterocarps in ecological and geographical ranges of the family Dipterocarpaceae between the evergreen forest and the fire climax dry dipterocarp woodlands (Ashton 1979a). The species of the latter group present characters which are unusual within the family: thick, ruggedly fissured bark, some seed dormancy, cryptocotylar germination, easily coppicing, seedlings with prominent taproots as a result of frequent burning.

The dipterocarp flowering (and consequent fruiting) phenology also changes: in seasonal areas species flower annually with varied intensities each year; in aseasonal regions sporadic flowerings occur each year in riparian species for example, but large gregarious flowerings happen at intervals of 3 or 4 years (Sri Lanka) or 5 or 10 years (aseasonal Malesia) (Ashton 1988, 1989). The gregarious flowerings are synchronous within populations and occur over several months for the whole family (Ashton 1969, Chan 1977, 1980, 1981, Ng 1977). Certain understorey *Stemonoporus* and *Shorea* however, do not follow this timing. The climatic boundaries closely coincide with the boundaries of the regions of exceptional dipterocarp diversity. The abundance of species and gregarious flowerings both occur in aseasonal west Malesia.

Detailed information on these aspects is needed for the American and African taxa.

Morphological Trends Related to Biological Patterns

Deciduousness is mainly connected to seasonal areas while evergreen trees are more frequent in the aseasonal zones (Ashton 1979a). Degree of hairiness decreases from seasonal to aseasonal; the extreme expression of glabrousness is in understorey taxa such as certain *Vatica* and many *Hopea*. The tomentum disappears first from leaves, then from twigs, followed by the young shoots and finally the inflorescence and floral parts. Similar trends exist in Africa with *Marquesia* species from the open savanna forests and the only species from the rain forest, *Marquesia excelsa*.

Flower and fruit characters have strongly influenced dipterocarp classification. Flower size seems constant within genera and *Shorea sensu lato* subdivisions, except in *Dipterocarpus*. The larger flowered taxa have their crowns in or above the canopy. This is the case for *Vateria*, *Vateriopsis*, *Dipterocarpus*, *Anisoptera*, *Parashorea, Shorea* section *Shorea* (Ashton's sub-section *Shorea*), *Pentacme*, *Doona* and *Anthoshorea* which form a full complement of supraspecific taxa exclusively confined to canopy in the Asian seasonal tropics (Ashton 1979a). But many other emergent *Shorea*, especially the *Richetioides* group, have small flowers, whereas *Vatica* and *Stemonoporus* (many of which flower beneath the canopy) have large flowers (as big as *Parashorea* or *Anthoshorea*).

The anther and stamen sizes broadly follow the same trend: a) in the seasonal area the anthers are large, elongate and bright yellow for *Vateria*, *Vateriopsis*, *Dipterocarpus*, *Parashorea*, and *Pentacme*; and b) the same type of anthers also characterise certain taxa confined to aseasonal regions: *Dryobalanops*, *Cotylelobium*, *Neobalanocarpus*, *Stemonoporus*, Ashton's *Shorea* section *Rubellae*, and *Doona*. In the other taxa, such as *Anthoshorea* and *Ovalis*, anthers are smaller, white and subglobose to ellipsoid; *Richetioides* presents the smaller ones. The African taxa seem to possess numerous stamens of medium size (drawings of Verdcourt 1989).

The number of stamens (Ashton 1979a) is often 15: *Vateria*, *Vateriopsis*, most *Dipterocarpus* species, *Anisoptera* section *Anisoptera*, *Dryobalanops*, *Shorea* sections *Shorea* and *Rubellae*, 6 species of *Anthoshorea* all in seasonal sites, *Ovalis*, 1 species of *Brachypterae*, 1 species of *Richetioides*, and 3 species of *Hopea* (2 of which are in seasonal sites). Ten species have less than 15 stamens: 10 stamens in 6 species of *Hopea* and 3 species of *Richetioides*, 5 stamens in 2 species of *Stemonoporus* and 1 species of *Vatica*.

Large flowers produce large pollen grains (Muller 1979). Flower and pollen dimensions will interfere with potential pollinators. Clear relations have been demonstrated between ovary shapes and sizes within *Shorea sensu lato* subgroups and pollinator size or taxonomical group (Chan and Appanah 1980, Appanah and Chan 1981, Appanah 1990). Bees pollinate large yellow elongate anthers while thrips pollinate small, white anthers. Bees prevail in seasonal tropics and Sri Lanka. Pollination changes during geological to present times probably explain much of the present aspect of dipterocarps. This is an important point to consider when planting trees outside their original areas. Forest degradation may result in the absence of tree reproduction by extinction of pollinators.

The biggest fruits are in taxa with large flowers, and more frequently in species producing wingless-fruits than in species with winged fruits. There is also a relation between large dimensions and the development of a protective thickening of pericarp and/or calyx base to prevent dehydration of the embryo and sometimes permit floating of the fruit (Maury 1978, Maury-Lechon 1979b, Maury-Lechon and Ponge 1979). Thickened sepal bases are a defining character of *Shorea sensu* Ashton, but do not occur in *Anisoptera*, *Upuna*, *Cotylelobium* or *Sunaptea*. Pericarp thickenings characterise particularly the *Pachynocarpus* and *Vatica* groups of genus *Vatica* and genera *Stemonoporus* and *Vateria*. The thickening is of different type in Monotoideae and the case of *Dipterocarpus* remains apart because of the variously thickened calyx ornamentations (tubercules, simple or folded wings). The protective thickenings mainly develop in the group of taxa forming 15 elongate, large, yellow anthers. Large fruits are produced in smaller numbers, and they represent an investment which lowers risks in weakly lit places. The increased size of seed-embryo probably demonstrates a trial for better survival in unpredictable habitats with irregular supply of light and nutrients (and water) during the germination period of non-dormant seeds. However, fewer fruits are produced, so that investment is in fewer high-cost seeds bearing other risks of probably lower intensity. Animal predation is mainly by insects and seeds do germinate and develop normal seedlings in spite of insect larvae which continue their development within the fleshy cotyledonary limbs; human predation is more drastic and mainly corresponds to traditional and industrial oil extraction.

The 5-winged fruits of *Pakaraimaea*, *Monotes* and *Marquesia* clearly disperse in open and windy habitats, as probably do that of *Pseudomonotes* (detailed information not yet available). In these taxa pollen and nuts show evident adaptations to the dry conditions of their seasonal climates: thick layers and protected apertures, while the thin coriaceous pericarp of the ripe fruit of *Marquesia excelsa* is an exception (Maury *et al.* 1975a, b, Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979). In Asia the winged-light fruits of *Sunaptea* and *Cotylelobium*, of certain species of *Hopea*, *Shorea* (Ashton *sensu lato*) and *Upuna* present thin pericarps, even in seasonal regions.

Asian taxa have developed winged fruits in seasonal and aseasonal regions. In closed forests these fruit wings have limited possibilities for dispersal. However, over the canopy and at forest borders, storms and very strong winds at the beginning of the rainy season may transport them for several hundred metres and sometimes about one kilometre. In the open dry deciduous forest of the seasonal Asian regions the dispersal of dipterocarp winged fruits becomes much more efficient. However, occasional dispersal over long distances has probably succeeded, judging from the present high diversity of Asian dipterocarp habitats in aseasonal regions.

Classification

The full set of taxonomic and systematic works available has been reported and discussed in the more recent flora books, monographs, theses and other publications of Ashton (1962, 1963, 1964, 1967, 1969, 1972, 1977, 1979b, c, d, 1980, 1982), Bancroft (1933, 1934, 1935a, b, c, d, e, 1936a, b, 1939), Bisset *et al.* (1966, 1967, 1971), Damstra (1986), Diaz and Ourisson (1966), Diaz *et al.* (1966), Gottwald and Parameswaran (1964, 1966, 1968), Jacobs (1981), Jong and Lethbridge (1967), Jong and Kaur (1979), Jong (1976, 1978, 1979, 1980, 1982), Kochummen (1962), Kochummen and Whitmore (1973), Kostermans (1978, 1980, 1981a, b, c, 1982a, b, 1983, 1984, 1985, 1987, 1988, 1989, 1992), Maguire (1979), Maguire *et al.* (1977), Maguire and Ashton (1980), Maguire and Steyermark (1981), Maury *et al.* (1975a,b), Maury 1978, Maury-Lechon (1979a, b, 1982 in Ashton: p. 265-266 ripe embryo, germinating seedlings and 268 palynology, 1985 in FAO: palynology, Maury-Lechon and Ponge (1979), Meijer (1963, 1968, 1972, 1973, 1974a, b, 1979), Meijer and Wood (1964, 1976), Ourisson (1979), Parameswaran (1979a, b), Parameswaran and Gottwald (1979), Parameswaran and Zamuco (1979, 1985 in FAO), Rojo (1976, 1977, 1979, 1987), Rojo *et al.* (1992), Sidiyasa *et al.* (1986, 1989a, b), Smitinand (1958a, b, 1979, 1980), Smitinand and Santisuk (1981), Smitinand *et al.* (1980, 1990), Sukwong (1981), Sukwong *et al.* (1975), Tao and Tong (1982), Tao and Zhang (1983), Tao and Dunaiqiu (1984), Tewary (1984), Tewary and Sarkar (1987a, b), Verdcourt (1989), Vidal (1960, 62, 79), Whitmore (1962, 1963, 1976, 1979, 1988), Wildeman (1927), and Wildeman and Staner (1933).

Affinities of the Dipterocarpaceae Family

Hutchinson (1959, 1969 in Maury 1978) put the family in the order Ochnales and later suggested a phylogenetic location of the order at the end of a series whose progressive steps were ordered as follows: Magnoliales, Dilleniales, Bixales, Theales and Ochnales.

Cronquist (1968) moved Dipterocarpaceae into the order Theales and Takhtajan (1969) regrouped Ochnales, Theales and Guttiferales in Theales and placed Dipterocarpaceae under it near Lophiraceae and Ancistrocladaceae. Dalgren (1975) placed the dipterocarp family in the order Malvales under superorder Dilleniflorae.

After the description and detailed study of *Pakaraimaea dipterocarpacea* and its inclusion in Dipterocarpaceae, Ashton removed the family from Guttiferales and considered the imbricate calyx of Dipterocarpaceae and Sarcolaenaceae (Maguire *et al.* 1977) as an isolated and derived character among otherwise Malvalian features, and hence a justification for inclusion in Theales. From the study of *Pakaraimaea*, a closer affinity was underlined between the Dipterocarpaceae and Sarcolaenaceae families. Indeed, the affinities between these two families within the Malvales could be regarded as greater than with the Tiliaceae (Maguire and Ashton in Maguire *et al.* 1977: p. 359-361). The Tiliaceae relation is stronger with the African taxa while for the American *Pakaraimaea* the strong affinities are to be found with the Sarcolaenaceae (De Zeeuw, in Maguire *et al.* 1977). The Monotoideae could be a link between Tiliaceae and Dipterocarpaceae.

Previously Blume (1825), who first described the family Dipterocarpaceae, Pierre (1889-1891 in Maury 1978), Heim (1892) and Hallier (1912 in Ashton 1982) mentioned the close affinity of *Monotes* and Tiliaceae. Heim and Hallier had concluded that *Monotes* did not belong to Dipterocarpaceae (Kostermans 1985). The tilioid structure of the pollen exine (Maury *et al.* 1975a, b) in Asian and African taxa again called attention to these possible affinities with Tiliaceae.

Kostermans (1978) excluded Monotoideae and Pakaraimoideae from Asian Dipterocarpaceae and formally described the family Monotaceae (suggested by Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979) and recognised close relations between Monotaceae and Tiliaceae. By the structure of the pollen exine the Monotoideae strongly differ from Asian Dipterocarpaceae in spite of the similarities of the tilioid aspect of the exine surface.

Later Kostermans (1985) concluded that ‘it is very difficult to make a decision of alliance of the real Asiatic Dipterocarpaceae. They are not much allied to Guttiferae or Ternstroemiaceae’ (=Theaceae) ‘and apparently represent an ancient family, in which nowadays links with other families have disappeared.' Thus we can just 'resign ourselves to leave the Dipterocarpaceae *s.s.* near the Guttiferae and Ternstroemiaceae (=Theaceae). With the Malvales or Tiliales they have very little or nothing in common.'

However, with recent help of molecular techniques on two species of Dipterocarpoideae (*Shorea stipularis*, *Anthoshorea* section, and *S. zeylanica* = *Doona zeylanica*) (Chase *et al.* 1993), Dipterocarpaceae are placed as an outlier in the order of Malvales. Its relations with Malvales are with Bombacaceae (*Bombax*), Tiliaceae (*Tilia*), Sterculiaceae (*Theobroma*) and Malvaceae (*Thespesia*, *Gossypium*). This work on chloroplast plastid gene rbcL1 confirms several major lineages which correspond well with Dalgren (1975) taxonomic schemes for Angiosperms.

From the serology studies of John and Kolbe (1980) and Kolbe and John (1980) the further existence of the 'Theales' is not justified if it contains Guttifereae, Dipterocarpaceae and Ochnaceae.

In other works on DNA (Tsumura *et al.* 1993, Wickneswari 1993) parsimony analysis of molecular data revealed three major groups which resemble conclusions drawn from the anatomy of cotyledonary nodes (Maury 1978, Maury-Lechon 1979a,b). These are: an ancient group comprising *Upuna*, *Cotylelobium*, *Vatica* (*V. odorata* which is a *Sunaptea*), an intermediate group comprising *Dryobalanops* and *Dipterocarpus*, and an advanced group comprising *Shorea*, *Hopea* and *Neobalanocarpus*.

Characters Specific to Dipterocarpaceae

Among the numerous characters cited in the literature there is not a single character shared by all species of Dipterocarpaceae *sensu lato*. A detailed study is needed to verify the flower bud sepals in all species; a semi-quincuncial sepal arrangement is reported in *Pakaraimaea* and Monotoideae (Maguire *et al.* 1977), while this arrangement is imbricate (=semi-quincuncial) or valvate in Dipterocarpoideae.

On the contrary three biological characters exist in all species of Dipterocarpaceae *sensu stricto*: the stamen architecture (Kostermans 1985) and the pollen type (tricolpate grains, exine without endexine: Maury *et al.* 1975a, b), and the absence of real post-germinative growth of cotyledons (Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979).

The detailed aspects of stamens were underlined by Kostermans (1985): Asian Dipterocarpaceae 'without a single exception, have short, very much flattened, broadly (more rarely narrowly) triangular filaments, which terminate in a very short, thin, cylindrical part, which continues behind the pollen sacs as a cylindrical, often differently colored connectival part and often protrudes beyond the place of insertion of the pollen sacs, giving the impression of a sporophyllous 'leaf' to which the pollen sacs are attached at the interior surface. The anthers are actually dorsifixed, but they appear to be basifixed. It seems that the stamen architecture is one of the 'old' characteristics of Dipterocarpaceae *s.s.* which remained immutable (and hence defines the family, cf. Stebbins, 1974 and Melville 1983).' (Stebbins, 1974 and Melville 1983 in Kostermans 1985).

'In Monotoideae the filaments are very long, cylindrical, thin, the 2-celled anthers are dorsally attached, versatile, there is no extension of the filament behind the pollen sacs and there is no protruding part (this is sometimes also lacking in Dipterocarpoideae, but often replaced by this setae). The pollen sacs of Dipterocarpoideae are separately and rather loosely (not completely) tied to cylindrical dorsal connectival part; the 2 or 4 sacs are not much connected, their tips are free and pointed or very pointed; the tips have no connective tissue. C. Woon and Hsuan Keng (1979) have depicted numerous stamens of the Asiatic Dipterocarpaceae and all have the same form. In the Monotoideae, on the contrary, the 2 pollen sacs are united at their apex (not in *Marquesia*) by a thick, triangular-ovoid connectival tissue' (Kostermans 1985). Further investigation is thus needed in Asian, African and South American taxa (including the new Colombian taxon *Pseudomonotes*) to judge if these differences have been over-estimated.

Anatomically the presence of wood resin canals and multiseriate wood rays, also characterise the Asian taxa. Chemically the presence in the resins of the Asian dipterocarps of dammaranic triterpenes and sesquiterpenes, combined with the absence of monoterpenes is also common to all Asian species examined by Ourisson's team (Bisset *et al.* 1966, 1967, 1971, Diaz and Ourisson 1966, Diaz *et al.* 1966). The triterpenes derived from the skeleton 'epoxyde of squalene' (precursor of sterols) constitute a familial feature for Dipterocarpaceae *sensu stricto*. The distribution of the other resin compounds (particularly dipterocarpol) is considered of inferior rank (generic: for example, the hydroxydammarenon in genus *Dipterocarpus*; sub-generic: the sesquiterpenes derived from humulene at infrageneric rank).

From the study of pollen, fruit, embryo and young seedlings (Maury 1978, Maury-Lechon 1979a, b) biological characters of seed germination have been used together with pollen types and exine structure, at familial and sub-familial levels. Other characters of the anatomy of very young seedlings and the morphology of ripe fruit, the epidermis of seedling cotyledons and the two first leaves, have been hierarchically ordered. Thus a new classification was proposed, without formal descriptions, to serve as a base for further studies on the delimitation of natural groups of taxa inside Dipterocarpaceae *sensu lato* (*cf.* below: present classifications).

Supraspecific Taxa in Dipterocarpaceae

Apart from the above familial and sub-familial rank, four principal taxonomic criteria have been expressed (Ashton 1979c) for definition of supraspecific taxa in current revisions: 1) at least a pair of characters which are not functionally interrelated; 2) these characters should be common to all species in the taxon; 3) there should therefore be clear discontinuities in the variation between taxa; and 4) the prime goal of taxonomy should be to achieve nomenclatural stability. 'Given these criteria, genera must be regarded as essentially artificial groupings in the sense that they are defined by breaks in the total range of variation' (Ashton 1979b, p. 129).

In Asian Dipterocarpaceae most characters correspond to two main trends expressed in the tribes Dipterocarpi and Shoreae *sensu* Ashton (1979b), which are nearly equivalent to 'Valvate' and 'Imbricate' groups *sensu* Maury-Lechon (1979a) except the *Dryobalanops* genus, which in the latter is intermediary (certain characters of Imbricate type and others of Valvate type). In these groups the characters are greatly or weakly predominant but their presence (and intensity) is not systematic in all species of the group. This situation explains the difficulty of establishing clear deliminations or affinities. Chromosome numbers (n=7 in most Imbricate species and n=11 in Valvate taxa) illustrate these facts and provide some explanation.

The main differences between Ashton's and Maury-Lechon's two main groupings are:

1. in Ashton: presence (Shoreae) or absence (Dipterocarpi) of the incrassate fruit sepal base (as opposed to whole calyx tube), and in most cases the basic chromosome n-number is consistent for each of the two groups (7 in Shorea*e*, 11 in Dipterocarpi), as also are the scattered (Dipterocarpi) or tangential bands (Shoreae) of resin canals;
2. in Maury-Lechon: some consistent characters for each of the two groups (a), and most frequent expression of some other characters in each group (b);
   a) Three consistent characters:
   - fruit-sepal base arrangement in ripe fruit: imbricate (Imbricate group), valvate (Valvate group) or intermediary (mainly *Dryobalanops*, but also *Parashorea* or *Stemonoporus*) according to their development from flower-bud to open flower. Sepals are clearly imbricate before the petals develop out of the sepal bud and remain so after the petals have grown out of the sepal bud in the Imbricate group. The sepals are imbricate at first and then only retain some traces of imbrication in *Dryobalanops*, *Stemonoporus*, *Vateria*, *Marquesia*, *Monotes*; imbricate at first and then valvate in all *Vatica*, and valvate all along their development in *Dipterocarpus*;
   - number of strata in pollen exine (3 in Imbricate group or 2 in Valvate group, and 4 in Monotoideae and Pakaraimoideae); basic chromosome n-number (mostly 7 in Imbricate, 11 in Valvate, intermediary cases), tilioid structure of exine absent (Imbricate) or present (Valvate), and columellae shape-type T and Y (Imbricate) or V and U (Valvate),
   - in secondary wood: arrangement of vessels grouped (Imbricate) or solitary (Valvate), resin canals in bands (Imbricate) or scattered (Valvate) with cellular divisions of canal formation radial (Imbricate) or oblique (Valvate);

   b) Three most frequent expressions:
   - fruit: number of incrassate bases of sepals (and number of accrescent sepals) 2 or 3 (Imbricate) or 0 or 5 (Valvate), bases of fruit sepals free (Imbricate) or fused (Valvate), type of pericarp tissue rigid (Imbricate) or rigid to soft (Valvate), fruit equatorial section circular (Imbricate) or circular to 3-symmetric (Valvate);
   - embryo: cotyledons 'covering-piled' (Maury 1978) (Imbricate), neither covering nor piled (Valvate), hypocotyl inferior or median-inferior (Imbricate), not inferior but apical or median (Valvate);
   - seedling: cotyledons bilobed (Imbricate), or entire (Valvate), number of root-xylem poles 4 (Im-

bricate) or 6, 8 or 10 (Valvate), cotyledonary vascular bundles uni to trilacunar (Imbricate) or tri to multilacunar (Valvate), stomatal types in first leaves paracytic, or para-cyclocytic, or anomo-cyclocytic (Imbricate) versus cyclocytic or anomocytic or anisocytic (Valvate), stomata elongate and sunken in the epiderm (Imbricate) or round and raised above the epiderm (Valvate).

The overall pattern of infrageneric variation supports the establishment of the two Asian groups Dipterocarpi and Shoreae (tribes: Ashton 1979b) or Valvate and Imbricate (Maury 1979a). Wood anatomy (Parameswaran and Gottwald 1979), palynology and characters of fruit-embryo-seedling (Maury *et al.* 1975a, b, Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979) locate the genus *Dryobalanops* at an intermediary position between Shoreae-Imbricate and Dipterocarpi-Valvate groups. Its calyx in ripe fruit is subvalvate, thus close to the Valvate group, but the chromosome number is 7 as in the Imbricate group.

The basic distinctions of these two groups are:

1. Valvate- Dipterocarpi group: base of sepals in calyx of ripe fruit valvate, vessels solitary, resin canals scattered; basic chromosome number n=11: *Vateria*, *Vateriopsis*, *Stemonoporus*, *Vatica*, *Cotylelobium*, *Upuna*, *Anisoptera*, *Dipterocarpus*. and
2. Imbricate-Shoreae group: fruit sepals imbricate at the incrassate-cupped base of the ripe fruit, vessels always grouped, resin canals in tangential bands, basic number n=7; *Shorea*, *Parashorea*, *Hopea, Neobalanocarpus*.

Loosely associated genera such as *Vateria* L. and *Vateriopsis* Heim are distinguishable on many characters such as floral parts, bark, fruit, embryo, germination, and wood anatomy, as are *Stemonoporus* Thw., *Cotylelobium* Pierre and *Sunaptea* Griff. by the same features. The other taxa in *Vatica* L. show the same nervation type and rather comparable adult wood or bark anatomy. However, a high diversity occurs in vascular structures in the seedling cotyledonary-node (Maury 1978; Fig. 677-679, p. 309-313, Maury-Lechon 1979a, b; Fig. 16 p. 100). A certain diversity also exists in flower-bud development (Maury 1978; vol. II tables VI, VII, p. 51-52) or style-stigma and stamen shapes (Woon and Keng 1979; Fig. 30, p. 40). A high diversity is observed in fruit forms of sepal aestivation and wing-accrescence, and pericarp or sepal incrassatescence (Symington 1943, Ashton 1964; Fig. 10, 1968; Fig. 29, Maury 1978; Vol. II, Tables VI, VII, p. 51-52). *Stemonoporus* present a unique terminal bud set in a depression at the twig apex which is prolonged beyond the last leaf insertion. In *Anisoptera* the two sections are based on floral and bark aspects. *Parashorea* stands out on account of its flower and its 5 or non-winged fruit.

The infrageneric classification of the three genera *Shorea*, *Hopea* and *Neobalanocarpus* is more complex. *Shorea* and *Hopea* differ morphologically by the number of thickened bases of calyx (respectively 3 and 2) which eventually expand into wings; this is the sole consistent difference. Shoreas are mainly tall emergent or canopy trees while Hopeas mainly remain understorey or in the canopy. Flowers and leaf venation may distinguish the two genera but these characters also separate the sections within the two genera and are not constant for either genus as a whole (Ashton 1979b). *Hopea* sections differ by leaf characters only, while within each section the two subsections are principally classified by the shape of the floral ovary.

Heim (1892) first and Symington (1943) afterwards produced sound groupings of *Shorea* and later noticed that floral characters closely correlate with field characters of bark morphology and wood anatomy in defining groups. However, Symington never gave a formal nomenclature to his groups (Ashton 1979b). Floral characters also correlate with pollination biology (Chan 1977, 1981, Chan and Appanah 1980, Appanah and Chan 1981, Appanah 1990). For these reasons and in light of the Woon and Keng's (1979) results, additional emphasis has to be put on the importance of stamen shapes in the family Dipterocarpaceae.

Some of the characters by which the groups in *Shorea* are recognised are also those which distinguish *Cotylelobium*, *Vatica*, *Stemonoporus*, *Vateria* and *Vateriopsis* as genera. This evidence was stressed by Parameswaran and Gottwald (1979) from wood anatomy studies. They stated that groups *Anthoshorea*, *Shorea*, *Richetia*, and *Mutica* merited generic status. However, Ashton maintains a different status for these groupings in *Shorea.* On the contrary he gives generic rank to *Vatica* and its allies. He justifies this difference of treatment owing to the presence of species with intermediate character states between most of the flowers within the *Shorea* group, as opposed to their absence between the taxa of the *Vatica* group. This situation could result from different degrees of diversification potential, and merits further investigation.

Consistent Criteria for Definition of Species and Sub-species

Consistent criteria (Ashton 1979a) for definition of species and sub-species were expressed for Dipterocarpaceae as follows:

1. Size differences are not by themselves sufficient, neither are differences of leaf size and shape combined. Differences in fruit size are likewise unreliable and rarely correlate with other characters; collections from one tree in different years often exhibit great variation. A consistent discontinuity in leaf size, when correlated with differences in androecium or gynoecium, in qualitative (not quantitative) characters of indumentum, with qualitative characters of the twig or stipule or with a discontinuity in the range in the number of leaf nerves does constitute an adequate criterion for separating species.
2. Subspecies can be defined where discontinuities occur in the range of dimensions of parts, in tomentum distribution and in density. However, sometimes taxa which share a unique qualitative character, especially of fruit or flower, are recognised as subspecies even though they may differ qualitatively in vegetative parts.

Experience has shown that this definition of subspecies is sometimes too conservative (for example, *Shorea macroptera* ssp. *baillonii* and ssp. *macropterifolia* occur together in some forests, *Vatica oblongifolia* ssp. *multinervosa*, ssp. *crassilobata* and ssp. *oblongifolia* do seem at times to intergrade. This definition of subspecies, albeit consistent, is essentially arbitrary but may be useful when evidence of hybridisation in nature is unavailable.

Ontogenetic Aspects of Morphological and Anatomical Characters

In Dipterocarpaceae decisions on the primitiveness or derived conditions of characters are drawn from personal hypotheses on the evolutionary trends within and between angiosperm families. Ontogenic trends may follow evolutionary trends. Even in the absence of this relationship, study of the embryonic trends helps to understand taxonomic relations.

Chemotaxonomic studies have shown (Ourisson 1979) the existence of certain chemical directions for molecular construction in the family: from the epoxyde of squalene to the triterpenes of the resins, in all species of dipterocarps *sensu stricto*.

The embryogenesis from seed germination to young seedling in dipterocarps analysed by Maury-Lechon has demonstrated a unique direction for the construction of the vascular structures in cotyledon node and petiole, from simple to very complex (Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979). This trend exists in certain species at different developmental phases and morphological levels (node: base, mid-part, top of petiole) within a single plant (e.g. *Vateria copallifera* in Maury-Lechon 1979b; photographs Fig. 49). In other species the trend may be visible by comparing plants of a given species (most genera of the family: *Dipterocarpus*, *Dryobalanops*, *Parashorea*, *Vatica* sections *Vaticae* and *Pachynocarpus*, *Vateria*, *Hopea* and *Shorea*) or by comparison of different species at a given stage of development and morphological level as, for example, from the simple trilacunar vascular structures of cotyledonary petiole in *Shorea curtisii*, to the increasing complexity of *Stemonoporus affinis*, *S. reticulatus* and finally the trilacunar appearance of the very complex structure of *Vateria copallifera* (Maury 1978, Maury-Lechon 1979b). Simplest structures (unilacunar with a single resin canal in cotyledonary node) are remarkable in *Sunaptea*, *Cotylelobium*, *Upuna* and also exist in certain *Hopea*, *Anthoshorea*, *Richetioides* and *Muticae*. *Monotes* and *Marquesia* have different (no canals and different organisation of vascular bundles) and more complex structures than the Asian simplest forms.

These simplest structures correspond to the taxa with small winged fruits, well dispersed by wind, thus again with the open areas and long distance migrations. These structures allow a better putative relation with the African and American taxa (simple but of different type and devoid of resin canals). They could evoke ancestral dipterocarp migrations in more open, windy and perhaps drier environments than those of the present rain forest.

Polyploidy, Polyembryony, Apomixy and Variability of Dipterocarp Characters

The two basic chromosome numbers tend to remain constant within a single genus and between groups of genera even in heterogeneous genera like *Shorea* and *Hopea*. It is premature to say which of the numbers is derived or ancestral (Jong and Kaur 1979). There is a low frequency of polyploidy series and intraspecific polyploids in the Asian genera *Shorea* and *Hopea*, especially in cases where polyploidy is associated with agamospermy. Intraspecific polyploidy has been reported in *Hopea odorata* and *Dipterocarpus tuberculatus* (Jong 1976).

It has been demonstrated that certain species produce polyembryonic seeds (Maury 1968, 1970a, b, Kaur *et al.* 1978). *Shorea ovalis* ssp. *sericea* is tetraploid with frequent polyembryony. These polyembryos originate from nucellar cells at the micropilar end of the ovule (Jong and Kaur 1979). However, fruit formation in *S. ovalis* requires stimulation of pollination (Chan 1980), which is pseudogamous. Pollen tubes have been observed in some embryological preparations, thus the possibility exists that a zygotic embryo is sometimes formed. Some participation by embryo-sac cells other than the egg in the formation of pro-embryos, in addition to those derived from the nucellus (Jong and Kaur 1979), could also be possible.

On the basis of chromosome number (odd polyploidy) and other tentative evidence, it may be inferred that all triploids or near triploids (Kaur *et al.* 1978) may also be apomicts with polyembryony. The triploid condition may have arisen in some cases from hybridisation between diploid and tetraploid congeners. Agamospermy may indeed provide a mechanism for overcoming chromosome sterility, and/or for the stabilisation of a heterozygous combination favoured by natural selection (Grant 1971 in Jong and Kaur 1979).

A close association between agamospermy, polyploidy and hybridity has been demonstrated in a wide range of temperate angiosperms (Gustafsson 1947, Stebbins 1960). Even though much available evidence is indirect, such a pattern may also occur in *Shorea* and *Hopea*.

Apomictic plants are troublesome for taxonomists because of the multitude of biotypes or microspecies that result from agamospermous reproduction; the periodic occurrence of hybridisation involving facultative apomicts and related sexual species generate additional variant forms which add to the complexity of the variation pattern. Some classificatory difficulties in Dipterocarpaceae at the supraspecific level presented by *Shorea* and *Hopea* may well be attributable to the presence in each genus of species groups or agamic complexes in which sexual and related agamospermous taxa exist side by side. Agamospermy whether facultative or obligate could well be an important contributory factor to the floristic diversity of the lowland mixed dipterocarp rain forests of southeast Asia (Kaur *et al.* 1978).

Present Classifications

The four more recent classifications (Tables 1, 2, 8) of the family Dipterocarpaceae (Ashton 1964, 1968, 1982, Meijer 1963, 1979, Maury 1978, Maury-Lechon 1979a, b, Maury-Lechon and Ponge 1979, Kostermans 1978, 1992) have retained large parts of the previous classifications from Heim (1892) and Symington (1943).

Meijer has only taken into consideration the genera growing in Sabah and Kostermans has centered his works on Sri Lankan taxa and the three non-Asian genera.

Ashton had a taxonomical approach, while Maury-Lechon concentrated on the definition of natural groups and their phylogenetic trends. They both utilised the results of anatomy studies produced by Whitmore (1963) on bark, Gottwald and Parameswaran (1964) and Brazier (1979) on wood. Likewise, they used works on cytology from Jong and Kaur (1979), embryology, chemotaxonomy (Ourisson *et al.* 1965, Diaz and Ourisson 1966, Diaz *et al*. 1966, Ourisson 1979) and

Main aspects of Ashton's classification (see also Tables 1, 2, 8)

Taxonomical levels	
Family (1):	▪ Dipterocarpaceae (16 genera, 3 sub-families, 2 tribes)
Sub-families (3):	▪ Pakaraimoideae: 1 monospecific genus, 2 sub-species
	▪ Monotoideae: 2 genera *Monotes* (more than 24 species), *Marquesia* (about 3 species)
	▪ Dipterocarpoideae (2 tribes, 13 genera, 17 sections, 12 sub-sections):
Tribes (2):	▪ Dipterocarpi (8 genera, 4-5 sections): *Dipterocarpus*, *Anisoptera* (2 sections), *Upuna, Cotylelobium, Vatica* (2-3 sections), *Stemonoporus*, *Vateria*, *Vateriopsis*.
	▪ Shoreae (5 genera, 13 sections, 12 sub-sections): *Hopea* (2 sections, 4 subsections), *Shorea* (11 sections, 8 subsections), *Parashorea*, *Neobalanocarpus*, *Dryobalanops*.

the herbarium collections of Asia (Forest Research Institute Malaysia, Kepong including Symington's collection; Bogor in Indonesia, Peradeniya in Sri Lanka, Bangkok in Thailand) and Europe (Kew in U.K, Paris and Lyon in France, Leiden in Netherlands) where large collections including Ashton's, Meijer's, and Maury's, are preserved.

There is a certain complementarity in the above works, but a synthetic classification integrating all previous results is still not available. Traditional and modern approaches will have to be integrated, including DNA and mathematical analyses, as well as the use of computer systems for determination and treatment of the data.

Main aspects of Maury-Lechon's classification (see also Tables 1, 2, 8)

The taxonomical levels have intentionally been left without formal definition to serve as a base for further research. The relative position of these levels is much more important than their names. However, to facilitate the explanations, the more proximal names usually adopted for these divisions were used (Maury-Lechon 1979a).

The separation of Monotoid taxa from the Dipterocarpaceae underlines the differences that introduce heterogeneity when these taxa are put together with the Asian group in the same family. The grouping of Monotaceae and Dipterocarpaceae in a supra-familial joint division (order or suborder), reminds the greater affinities of these two families among the other angiosperms. All the other groups aim to underline the closer resemblances on the basis of living biological, morphological and anatomical characters of the successive ontogenic phases (mainly fruit-seed, embryo, seedling) and the pollen types and structures.

The characters of embryo-seedlings and pollens strongly emphasise the particular position of *Anthoshorea* close to *Doona* and partly to *Pentacme* within the Anthoshorinae group, and their position near *Hopea* and *Neobalanocarpus* in the Imbricate group.

Still stronger relations exist with the intermediary genus *Dryobalanops* leading directly to the Valvate group. Tighter connections of the latter genus occur within the Dipterocarpae subgroup (*Dipterocarpus* and *Anisoptera*) as well as with the Vaticae subgroup through *Sunaptinae* taxa first (*Cotylelobium* mainly, *Sunaptea* too), and then to *Stemonoporus*. Through *Dryobalanops* another line of similarities leads to *Anisoptera*, *Vateria* and *Vateriopsis*.

Taxonomical levels		
Supra-family level (1) (order or sub-order):	▪	Dipterocarpales (2 families)
Family level (2):	▪	Monotaceae (3 genera: *Pakaraimaea*, *Marquesia*, *Monotes*)
	▪	Dipterocarpaceae (2 infra-family groups: sub-families, 4 sub-groups: tribes, 9 sub-subgroups: sub-tribes, 19 genera)
Sub-family level (2):	▪	Imbricate [2 tribes (a & b), 3 sub-tribes, 9 genera, 19 sections]
	▪	Valvate [2 tribes (c & d), 7 sub-tribes, 10 genera, 8 sections]
Tribe level (4):	a)	Hopeae (2 genera, 4 sections): *Hopea* (4 sections), *Neobalanocarpus*
	b)	Shoreae (3 sub-tribes, 7 genera, 15 sections):
	▪	Anthoshorinae (3 genera): *Doona*, *Pentacme*, *Anthoshorea* (2 sections)
	▪	Shorinae (3 genera): *Shorea* (2 sections), *Richetia* (2 sections), *Rubroshorea* (7 sections)
	▪	Parashorinae (1 genera): *Parashorea* (2 sections)
	c)	Dipterocarpae (2 sub-tribes, 3 genera, 2 sections):
	▪	Dryobalanoinae (1 genus): *Dryobalanops*
	▪	Dipterocarpinae (2 genera): *Dipterocarpus*, *Anisoptera* (2 sections)
	d)	Vaticae (5 sub-tribes, 7 genera, 6 sections):
	▪	Upuninae (1 genera): *Upuna*
	▪	Sunaptinae (2 genera): *Cotylelobium, Sunaptea* (2 sections)
	▪	Vaticinae (1 genus): *Vatica pro parte* (2 sections)
	▪	Stemonoporinae (1 genera): *Stemonoporus* (2 sub-groups)
	▪	Vaterinae (2 genera): *Vateria, Vateriopsis*

Pollen, embryo and seedling characters, as well as parsimony analysis of molecular data (Tsumura *et al.* 1993, Wickneswari 1993), show similar conclusions. By the pollen surface *Anthoshorea* resemble *Dryobalanops*, *Doona*, *Neobalanocarpus heimii* and *Cotylelobium*, and a basic similarity exists between *Dryobalanops* and *Dipterocarpus*, as with cotyledonary shapes.

Table 8. Comparative classifications of Asian *Dipterocarpaceae*.

HEIM 1892		MAURY 1978		MEIJER 1964		ASHTON 1964-68-82	SYMINGTON 1943	
Hopea	IMBRICATE	Hopea	Hopeae	Hopea	SHOREA	Hopea	Hopea	
Euhopea, Hancea,		Hopeae		Group I		Hopea	Euhopea	
Dryobalanoides,		Pierreae		Group II		*Hopea, Pierrea*	Pierrea	
Petalandra		Dryobalanoides				Dryobalanoides	Dryobalanoides	
Pierrea		Sphaerocarpae				*Dryobalanoides*	Bracteata	
Duvallelia		Balanocarpus hemii				*Sphaerocarpae*		
Balanocarpus								
Eubalanocarpus						Neobalanocarpus	Balanocarpus	
Pachynocarpoides						hemii	hemii	
Microcarpae								
Sphaerocarpae								
Parahopea								
Doona		Doona	Anthoshorinae Shoreae	Doona				
						Shorea		
Pentacme		Pentacme		Pentacme		Pentacme	Pentacme	
		Antoshorea		Shorea		Doona	Shorea	
Isoptera		Anthoshoreae		Anthoshorea		Anthoshorea →	Meranti Pa'ang	
Richetia		Bracteolatae						
Shorea		Shorea	Shorinae	Shorea		Shorea →	Balau	
Eushorea		Shoreae		*Isoptera*		*Shorea, Barbata*		
Anthoshorea		Barbatae		*Barbata, Ciliata*		Neohopea		
Hopeoides		Richetia		Richetia		Richetioides →	Damar hitam	
Richetioides		Richetioides				*Richetioides*		
		Maximae				*Polyandrae*		
Rugosae		Rubroshorea		Rubroshorea				
		Muticae		*Parvifolia subgr.*		Mutica →	Parvifolia subgr.	Red Meranti
		Muticae				*Mutica*		
		Auriculatae				*Auriculatae*		
		Ovalis		*Ovalis subgr.*		Ovalis →	Ovalis subgr.	
		Rubellae				Rubellae		
Brachypterae		Brachypterae		*Pauciflora subgr.*		Brachypterae →	Pauciflora subgr.	
Brachypterae		*Brachypterae*				*Brachypterae*		
Smithianeae		*Smithianeae*		*Smithiana subgr.*		*Smithiana*		
Pachycarpae		Pachycarpae		*Pinanga subgr.*		Pachycarpae		
Parashorea		Parashorea	Parashorinae	Parashorea		Parashorea	Parashorea	
		Tomentellae						
		Smithianae						
Dryobalanops	SUB-VALVATE	Dryobalanops	Dipterocarpae	Dryobalanops		Dryobalanops	Dryobalanops	
Baillonodendron		(Dryobalanoinae)						
Dipterocarpus	VALVATE	Dipterocarpus	Dipterocarpinae	Dipterocarpus	DIPTEROCARPI	Dipterocarpus	Dipterocarpus	
Sphaerales,								
Angulati, Plicati,								
Alati, Tuberculati								
Anisoptera		Anisoptera		Anisoptera		Anisoptera	Anisoptera	
Pilosae, Glabrae,		Anisoptera,		Pilosae		Anisoptera	Pilosae	
Antherotriche		Glabrae		Glabrae		Glabrae	Glabrae	
		Upuna (Upuninae)		Upuna		Upuna		
Cotylelobium		Cotylelobium	Sunaptinae	Cotylelobium		Cotylelobium	Cotylelobium	
Sunaptea		Sunaptea						
Dyerella		Sunapteae						
		Vaticoides						
Vatica		Vatica	Vaticinae Vaticae	Vatica		Vatica	Vatica	
Euvatica, Isauxis		Vaticae		Synaptea		Sunaptea	Synaptea	
Retinodendron				Isauxis		Vatica	Isauxis	
Pachynocarpus		Pachynocarpus		Pachynocarpus		(Pachynocarpus*)	Pachynocarpus	
Stemonoporus		Stemonoporus	Stemonoporinae			Stemonoporus		
Eustemonoporus		Sphaerae						
Monoporandra		Ovoides						
Vesquella								
Vateriopsis		Vateriopsis	Vaterinae			Vateriopsis*		
Vateria		Vateria				Vateria		
Paenoe								
Hemiphractum								

*: Ashton 1964, 1968, spelling changes in and after 1982; subgr.: sub-group.

These features group together the living and fossil dipterocarps which have lived together in the same phytogeographical areas (Table 5). They also correspond to the subsequent hypothesis concerning their potential for differentiation (see above). They also suggest an eventual remote relation from *Anthoshorea* to *Marquesia* and then to *Monotes*.

In the Valvate division the Dipterocarpinae group underlines the relations between the 2 subgroups: 1) *Dryobalanops*, and 2) *Dipterocarpus* with *Anisoptera*.

Similarly the Vaticinae group emphasises the existence of 5 subgroups:

1. *Upuna* alone but near subgroup 2;
2. *Cotylelobium* close to *Sunaptea*;
3. *Vatica pro-parte* intermediate between groups 1 and 2, and 4 and 5;
4. *Stemonoporus* position between subgroups 2 and 5;
5. *Vateria*, and *Vateriopsis* with particular similarities (cotyledon position and shape, germination type) with *Vatica* and also *Anisoptera*, *Stemonoporus* and *Cotylelobium*.

Vatica genus (excluding *Sunaptea*) stands somewhat isolated within the family Dipterocarpaceae by the pollen characters principally, and much less so by some aspects of embryo shape and structure (particularly seedling vascular structure). As mentioned, the tilioid surface of the pollen exine could suggest a proximity with monotoid taxa, however, its structure is definitely different (Maury *et al.* 1975a, b). New investigations are needed on a great number of species of *Vatica* genus *sensu lato* (including *Sunaptea* and *Pachynocarpus*) to permit a clearer view on infra-generic variation of these characters.

Main lines of Kostermans' classification (See also Tables 1, 2)

Kostermans has mainly considered the Sri Lankan taxa so that, as in Meijer's work, only the Asian genera represented in this geographical area were analysed in detail. Contrary to Maury-Lechon's work he formally described the Monotaceae family, as well as genera *Doona* and *Sunaptea* (the latter including *Cotylelobium*). No publication remains on his views concerning the affinities of the genera inside his Dipterocarpaceae family, nor in eventual sections within the *Shorea* genus which includes *Pentacme* (Kostermans 1992). In *Stemonoporus* he suggests 2 sub-divisions based on the pericarp aperture at germination (character used in Maury 1978 and Maury-Lechon 1979a, b).

Taxonomical levels	
Family (2):	▪ Monotaceae (3 genera): *Pakaraimaea*, *Marquesia*, *Monotes* ▪ Dipterocarpaceae (15 genera): *Hopea*, *Neobalanocarpus*, *Balanocarpus*, *Shorea*, *Doona*, *Parashorea*, *Dipterocarpus*, *Anisoptera*, *Dryobalanops*, *Upuna*, *Sunaptea* (*Cotylelobium* included), *Vatica*, *Stemonoporus*, *Vateria*, *Vateriopsis*

Main Recent Taxonomic Changes:

They successively concerned the:

1. establishment of subgenera *Shorea, Anthoshorea, Richetia and Rubroshorea* (Meijer 1963, Meijer and Wood 1964);
2. establishment of 11 sections in genus *Shorea* including the previous genera *Doona* and *Pentacme* (Ashton 1964, 1968, 1980, 1982);
3. proposition to re-install some ancient genera such as *Doona* Thw., *Anthoshorea* Heim and *Richetia* Heim outside genus *Shorea* Gaertn., *Sunaptea* Griff. outside genus *Vatica* and *Vateriopsis* Heim out of genus *Vateria* L. (Maury 1978, Maury-Lechon 1979a, b);
4. acceptance of the re-establishment of *Vateriopsis* genus by Ashton (1982);
5. announcement of the discovery and description of *Pakaraimaea* (Maguire 1979, Maguire and Ashton 1980, Maguire and Steyermark 1981);
6. formal re-establishment of genus *Doona* Thw. outside *Shorea* (Kostermans 1984), genus *Banalocarpus* Beddome outside *Hopea* and independent from *Neobalanocarpus* (Kostermans 1981a) genus *Sunaptea* outside genus *Vatica* but including genus *Cotylelobium* (Kostermans 1987); and
7. discovery and description of *Pseudomonotes tropenbosii* (Londoño *et al.* 1995) which is included in Monotoideae *sensu* Maguire *et al.* (1977) close to the African *Monotes* and *Marquesia*.

Discussion and Conclusions

Morphology, as well as anatomy and ecophysiology, shows many characters tightly related to their biological functions, and these functions are connected to both the biotic associations and the climatic environmental features which influence flower pollination, seed dispersal and seedling survival. It has been shown that the species diversity of ovary and style sizes and shapes in the *Shorea sensu lato* subdivisions correspond to their pollinator insect groups (Appanah 1990). The successive ontogenic phases of flower aestivation and seed germination, and seedling construction, also reveal the existence of particular directions such as the change of sepal position from imbricate in the young flower to subvalvate or valvate in ripe fruit (not the reverse), the multiplication of vascular bundles and resin canals (never the reverse) and the presence/absence of a post-germinative growth of cotyledonary limbs (Maury 1978, Maury-Lechon 1979a, b).

The biological plasticity of ripe seeds and seedlings depends on their ability to maintain their biological functions (which are dependent on their structures). This plasticity determines the possibilities of survival in a changing environment or in new and different places. The exact knowledge of the present geographical distribution and the main ecological features of these places already allow useful speculations for the choice of species potentially able to adapt in more drastic conditions (Maury-Lechon 1993, 1996, Xu and Yu 1982). This is, for example, the case of species from the seasonal tropics, or from the aseasonal regions subjected to great changes (diurnal, seasonal or unpredictable climatic events) on dry sands of sea coastal areas, or temporary and alternatively flooded or dried areas. The evolutionary trends established by *Hopea* or *Shorea* allow a much wider range of possible future adaptations than do those established by *Vateria* or *Stemonoporus* (Maury-Lechon 1979b). Thus a second level of prediction for adaptability is possible.

Overall, the striking feature of the family is the high variability of characters within and between species, within and between individual trees in many cases, and even within a single seed in certain species. Furthermore, the present classification demonstrates a heterogeneity of levels between the two Asian subgroups Dipterocarpi and Shoreae *sensu* Ashton. A notable case is the 11 sections of the *Shorea* genus in the Shoreae subgroup. They have unequal hierarchic levels when comparisons are established between the two Asian subgroups. Sections such as Anthoshorea, Shoreae or Richetioides of the Shoreae tribe have much higher rank than sections Rubellae or Ovalis for example, and a similar level to *Doona*, *Pentacme*, and *Parashorea* in the Imbricate group (*sensu* Maury-Lechon). A similar situation appears for the *Vatica* genus in the Dipterocarpi subgroup (*sensu* Ashton). For this reason *Sunaptea* (*Vatica pro-parte* in certain cases) has again been raised to generic rank (Kostermans 1987). These difficulties underline the complexity of the family. However certain well defined genera exist, such as *Dryobalanops*, *Dipterocarpus*, *Anisoptera* and *Upuna*. It could thus be hoped that a more equal weighting of characters is still possible in building a more homogeneous classification in the complex parts of the family, and that criteria can be defined for Asian dipterocarps to determine generic rank.

Present supraspecific taxa are mainly defined by groups of characters concerning the morphological aspects of leaves, the sequence fruit-seed-embryo-seedling, flowers, bark and wood, and colour and consistency of resins. Anatomical structures (wood, bark, petioles, epidermis, germinating seeds and seedlings), stomatal types, and chemistry of resins, have historically clarified the definition of supraspecific taxa (but very few wood characters are specific) in Dipterocarpaceae. However anatomical or chemo-taxonomical groups are not yet totally integrated into the present taxonomic divisions. This is the case for genus *Dipterocarpus* for example, in which phytochemistry has recognised main groups without evident correspondence with the previous morphological divisions based on fruit characters (Meijer 1979). The main reason for this is that too few species have been studied in this way to permit a rigorous understanding of within group variability and thereby establish which characters provide useful criteria for defining groups and hierarchic levels.

The morphological variability in the seasonal tropics may be the result of the frequent great changes with time in distribution of habitats and geographical boundaries. These changes favoured variability but rarely provided prolonged isolation mechanisms for fertility barriers to evolve. The frequency of hybrids suggests the same conclusion. It is not really known to what extent competition eliminates these hybrids. In the aseasonal tropics dipterocarps appear to be outbreeding species. Many other species in aseasonal tropics present allopatric differentiation and clear discontinuities in variation. Facultative apomixis may produce successful genotypes and accelerate ecotypic differentiation and short term evolution. Apomixis could serve to maintain fecundity where sexual reproduction is inadequate, and perhaps allow rapid spread of favourable ecotypes in heterogeneous terrain. However apomixis should probably lead to lowered genetic variability within populations, and thus could still result in increased probability of extinction when unadapted to the environmental changes. Constant differences in habit, morphology and reproductive biology exist between emergent and understorey trees (Richards 1952, Hallé *et al*. 1978, Yap 1982 in Ashton 1984). Ontogenesis thus follows predictable patterns in the larger trees and selection acts on these characteristics, which include tree habit and leaf shape, irrespective of their systematic relationships. These species present an ecological complementarity. It is however, not certain that species sharing a common habitat and geography will identically respond from flower-bud initiation to sensitivity to light, mycorrhizal invasion, water stress, seed predation, or share the same pollinators and seed vectors (M.S. Ashton 1992, 1995). Ecological criteria such as seed water content and seed resistance to desiccation are expressions of the species' biological plasticity and the possible complementarity between species (Maury-Lechon 1993). Certain species are abundant and others rare. Detailed systematic and biosystematic comparisons between rare and abundant congeners should bring some answers (Ashton 1992). We need to confirm whether the means exist for gene flow, and then to directly measure the level and pattern of genetic variability. Amenable source of evidence could also be tested for the presence or absence of associations between population distributions in space, and demographic and population genetic studies are also required on the basis of repeated observations. These observations and the use of species' complementarity would reinforce the understanding of systematics and help the forest managers to make decisions in rehabilitation and conservation programmes (Maury-Lechon 1991, 1993, 1996).

Bearing in mind the economic value and the present status of Dipterocarpaceae, it is also urgent to relate phylogeny to comparative ecology within genera and sections by a combination of:

1. molecular phylogenic studies, concentrating on genera and below;
2. comparative demographic studies of groups of related species, especially those which co-occur:
   a) during the reproductive phase (bud to recruit, and including fecundity),
   b) during stand development and trough to mortality,
   c) population genetics of selected species under selected conditions;
3. comparative ecophysiological experiments on seeds and seedlings; and
4. competition experiments.

The teams exist within the frame of the International Working Group on Dipterocarps (IWGD-IUFRO S.07-17 Working Party) and contacts have already been taken between the authors of this paper and their direct commentators for this purpose. Field and laboratory works will be organised on the base of complementarity. Overall, a cooperative, integrated and detailed re-assessment is needed for the whole family Dipterocarpaceae *sensu lato*, with the establishment of an evolutionary classification based on a general consensus. Several groups around the world are currently working on projects that can lead to such a solution. They include: Forest Research Institute Malaysia, Kepong and Unité Mixte de Recherche 5558 du Centre National de la Recherche Scientifique with Lyon University (France), in association with Harvard University (USA), who are working on the genetic analysis of DNA sequences; Massachusetts University (USA) on genetic and breeding system studies (Murawski and Bawa 1994, Murawski *et al.* 1994); and Cambridge-Edinburgh (U.K.) on computer identification keys (Newman *et al.* 1995). Several more complementary works are needed in palynology (pollen and exine), stamen architecture and shape (the flower being observed from the pollination point of view), ontogenesis (structure and morphology of fruit-embryo-germination, anatomy of cotyledonary node and petiole, epidermis of primordial leaves), wood anatomy, chemotaxonomy and architecture of juvenile stage. These complementary works will require broad cooperation with colleagues and institutions from the Asian, African and South American zones. More effort is needed for the Asian dipterocarps from China, Burma and Indo-China. Likewise, there is a need for contact with African colleagues

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Chapter 2

Conservation of Genetic Resources in the Dipterocarpaceae

K.S. Bawa

Introduction

The biological and economic importance of Dipterocarpaceae lies in the extraordinary dominance of its members over vast areas in forests of southeast Asia. With approximately 510 species and 16 genera, the family may not be particularly large among tropical woody groups. Other families such as Euphorbiaceae, Myrtaceae, Rubiaceae, Annonaceae, and Lauraceae have more taxa than the Dipterocarpaceae, however, they are pantropical in distribution. Although members of Dipterocarpaceae are also found in the African and American tropics, 13 out of 16 genera and 470 out of 510 species are largely restricted to Asia, and there, restricted primarily to south and southeast Asia. In Malaysia, it is certainly among the six largest families that are predominantly woody, the others being Euphorbiaceae, Myrtaceae, Rubiaceae, Annonaceae, and Lauraceae. Moreover, the members of the family are exceedingly abundant in lowland forests of southeast Asia, for example, in many areas, 80% of the emergent individuals and 40% of understorey trees are dipterocarps (Ashton 1982). Thus, when one considers the relatively restricted distribution of the family, both diversity and abundance are its main attributes.

The diversity of the family is under assault from deforestation and habitat alteration. Effective in-situ and ex-situ conservation strategies are required to conserve the existing genetic resources. To conserve genetic resources, it is essential not only to maintain existing diversity, but also to understand the ecological and evolutionary processes that have been responsible for the origin, evolution, and maintenance of diversity at intraspecific and higher taxonomic levels. This chapter has two broad objectives. One is to review genetic mechanisms responsible for the origin and maintenance of diversity. The second is to identify areas of research that may elucidate patterns and processes of diversity and a more complete understanding of factors regulating diversity. It is assumed that a better understanding of diversity and the mechanisms maintaining diversity may be helpful in developing effective strategies for conservation of genetic resources. The chapter ends with a brief commentary on the institutions involved in research related to the conservation genetics of the family.

Diversity

Genetic mechanisms responsible for diversification at intraspecific and specific levels are considered and then patterns of genetic variation within and among populations are described.

Chromosomal Differentiation

Information about chromosome numbers is available for 9 out of 15 genera and 68 out of 510 species of the family (Jong and Kaur 1979, Ashton 1982). Species and genera are remarkably uniform with respect to chromosome number. Perhaps all species in the genera *Dryobalanops*, *Hopea*, *Neobalanocarpus*, *Parashorea*, and *Shorea* have $x=7$ as the basic number. *Anisoptera*, *Dipterocarpus*, *Upuna*, and *Vatica* seem to have $x=11$ as the basic number. Several species in the genera with $x=7$ as the basic number have a somatic chromosome number of 20, 21 and 22. Thus, $x=11$ may have been derived from $x=7$ through alloploidy.

Polyploid species are known in only two genera: *Hopea* and *Shorea*. In *Hopea*, polyploidy has been reported in 5 out of 9 species and in *Shorea* in 3 out of 36 species. Five of these polyploid species are triploids ($2n=21$; also $2n=20$ and 22) and one ($2n=20$) seems to be an aneuploid derivative of a triploid. Many of the triploids are apomictic (see below).

Table 1. Infraspecific variation in chromosome number (from Ashton 1982).

Species	Chromosome Number
Dipterocarpus alatus	20, 22
D. tuberculatus	20
D. tuberculatus var. *turbinatus*	30
Hopea beccariana	20, 21, 22
H. odorata	14, 20, 21, 22
H. subalata	20, 21, 22

Aneuploid series are common in *Anisoptera* and *Dipterocarpus*. Both genera have species with 2n=20 or 2n=22. In some taxa, both variants occur within the same species (Table 1).

Thus, both polyploidy and aneuploidy indicate the importance of chromosomal variation in diversification at the species level. However, the largest genus, *Shorea*, shows remarkable uniformity in chromosome number; 31 out of the 34 species, for which chromosome numbers are known, have the same diploid number, viz. 2n=14.

Intraspecific variation in chromosome number has been reported in several species, particularly in *Dipterocarpus* and *Hopea* (Table 1). Of the 68 species for which chromosome numbers are available, 6 species have been recorded to show intraspecific variation. Such variation has not been reported for species of *Shorea*, the largest genus of the family even though data are available for 34 species.

Inter and intraspecific variation in chromosome numbers is difficult to interpret for two reasons. First, more than one chromosome numbers for the same taxon have been reported by different rather than the same author. Second, much of the reported variation due to reports of a single author, Tixier (1960) and most of Tixier's counts have not been confirmed by others.

It should, also be kept in mind that information on chromosome number for large tropical trees is usually obtained from very small sample sizes. Often only one or two individuals in a population are examined and rarely is there data from more than one population. Thus, it is impossible from available data to determine the magnitude of intraspecific variation in chromosome number. Furthermore, even in these cases, where such variation has been reported, one cannot estimate the extent of variation and therefore its significance. For example, for species of *Dipterocarpus* as well as *Hopea* listed in Table 1, variation is in the form of either aneuploid or polyploid chromosomal series, but whether this variation is in the form of occasional aneuploid or polyploid populations is not known (Ashton 1982).

Breeding Systems

Breeding systems are one of the primary determinants of the pattern of genetic diversity in natural populations of plants (Hamrick 1982, Hamrick and Godt 1989). Outcrossing combined with extensive movement of pollen and seed can lead to a high degree of genetic variation within populations but reduce differentiation among populations. Selfing and limited mobility of pollen and seed can have the opposite effect of reducing variation within, but promoting differentiation among populations. Dipterocarpaceae have bisexual flowers which are pollinated by a variety of animal vectors (see below). Controlled pollinations have revealed the presence of self-incompatibility systems in a large number of species. At least 14 out of 17 species appear to be self-incompatible (Table 2.) The self-incompatibility system in several species is apparently weak, as is the case in many other tropical species. In most of the species subjected to controlled pollination so far, a certain proportion of self-pollinated flowers set fruits. Dayanandan *et al.* (1990) and Momose *et al.* (1994) suggest that fruit set in self and cross-pollinated flowers is initially high but during development, fruits from self-pollinated flowers suffer from higher abortion rates than fruits from cross-pollinated flowers. T. Inoue (personal communication) has implicated the existence of a post-zygotic incompatibility system in *Dryobalanops lanceolata*. Such systems have also been reported for other tropical forest trees (Bawa 1979, Seavey and Bawa 1983).

On the basis of controlled pollinations, most dipterocarps appear to be strongly cross-pollinated. Outcrossing is the usual mode of reproduction in tropical forest trees (Ashton 1969, Bawa 1974, 1979, 1990, and references therein.) However, in dipterocarps, studies of breeding systems conducted so far are based on very small sample sizes in very few species. The data of Dayanandan *et al.* (1990) are from 2-3 trees, mostly two of each species; of Chan (1981) from 1-2 trees, and of Momose *et al.* (1994) from only one tree. Considering the variability among trees and that the distinction between self-compatibility and self-incompatibility in the family appears to be quantitative, large sample sizes will be required to precisely define the self-incompatibility systems.

Table 2. Breeding systems of Dipterocarps.

Species/Section	Percent Fruit Set		Inferred Breeding System	References
	Selfed	Crossed		
Shorea cordifolia Section Doona	0.5	21.0	Self-incompatible	1
S. disticha Section Doona	0.0	10.0	Self-incompatible	1
S. trapezifolia Section Doona	0.8	3.8	Self-incompatible	1
S. trapezifolia Section Doona	0.5	11.3	Self-incompatible	1
S. hemsleyana Section Muticae	0.0	15.2	Self-incompatible	2
S. macroptera Section Muticae	2.5	19.9	Self-incompatible	2
S. lepidota Section Muticae	1.7	24.4	Self-incompatible	2
S. acuminata Section Muticae	1.1	34.1	Self-incompatible	2
S. leprosula Section Muticae	1.6	17.0	Self-incompatible	2
S. splendida Section Pachycarpae	0.0	37.5	Self-incompatible	2
S. stenoptera Section Pachycarpae	n/a	n/a	Self-incompatible	2
S. ovalis Section Ovales	16.2	17.6	Self-compatible	2
Dipterocarpus oblongifolius	69.3	64.0	Self-compatible	2
Dryobalanops lanceolata	n/a	n/a	Self-incompatible	3
Hopea glabra Section Richetioides	n/a	n/a	Self-compatible or apomictic	2
S. maxima Section Richetioides	n/a	n/a	Self-incompatible	2
S. multiflora	n/a	n/a	Self-incompatible	2

1: Dayanandan *et al.* (1990); 2: Chan (1981); 3: Mamose *et al.* (1994).

Outcrossing Rates

More recently genetic markers in the form of allozymes have been used to quantify mating systems in species of *Dryobalanops*, *Hopea*, *Shorea*, and *Stemonoporus*. Analysis of mating systems on the basis of markers allows examination of the progeny arrays of many trees in the population. Moreover, outcrossing rate (tm) can be quantified between zero and one; zero representing complete selfing and one indicating 100% outcrossing. Mating systems of species examined so far are shown in Table 3. The outcrossing rates range from 0.617 in *Shorea trapezifolia* to 0.898 in *Stemonoporus oblongifolius*. The average rates expressed in Table 3 mask considerable variation among trees and years. The rate varied from 0.49 to 1.00 among trees in *Shorea congestiflora* (Murawski *et al.* 1994a, b). *S. megistophylla* trees in the logged forests had a lower outcrossing rate than trees in undisturbed forests (Murawski *et al.* 1994b). The difference seems to be dependent on the density of reproductive trees. Such density-dependent differences in outcrossing rates have also been shown in several other

Table 3. Outcrossing rates of Dipterocarps.

Species	Outcrossing Rate tm (± standard error)	References
Dryobalanops aromatica	0.794 (±0.059) – 0.856 (±0.063)	Kitamura *et al.* (1994)
Shorea congestiflora	0.874 (±0.021)	Murawski *et al.* (1994)
S. megistophylla	0.860 (±0.058)	Murawski *et al.* (1994)
S. trapezifolia	0.617 (±0.033)	Murawski *et al.* (1994)
Stemonoporus oblongifolius	0.898 (±0.022)	Murawski & Bawa (1993)

tropical tree species (Murawski and Hamrick 1990, 1991). Apparently, the low density of trees in logged stands reduces the inter-tree movement of pollinators and promotes self-pollination. Selfing, in part, may be aided by a weak self-incompatibility system.

Kitamura *et al.* (1994) compared outcrossing rates of *Dryobalanops aromatica* in primary and secondary forests but found no significant differences.

Self-incompatibility as well as mating system studies suggest that dipterocarps are predominantly outcrossed. Outcrossing in large populations can allow populations to harbour considerable genetic variation. In dipterocarps, mass flowering is also likely to enhance outcrossing by allowing exchange of gametes among a very large number of individuals. Not surprisingly, therefore, populations of dipterocarps show considerable genetic variation (see below).

Although the analysis of mating systems shows that the rates of outcrossing are high, it is also clear that there is a considerable potential for selfing in almost all species examined so far. Moreover, apomixis has been reported in several species (see below). While outcrossing continuously generates new genetic variation, potential for self-pollination and apomixis allows occasional new variants to spread in the population or colonise new sites, and thereby promote differentiation of taxa.

Pollen and Seed Dispersal

Pollen dispersal influences the mating system, and both pollen and seed dispersal affect population genetic structure. Limited dispersal results in inbreeding, small effective population sizes, and a high level of differentiation among populations. Extensive dispersal has the opposite effect.

Outcrossing in dipterocarps is achieved through a wide variety of pollinators that differ in their foraging ranges and therefore disperse pollen over varying distances. Appanah and Chan (1981) implicated thrips as pollen vectors for several species of Malaysian species of *Shorea*, section Muticae. The thrips breed in flower buds of the species they pollinate and, as flowering progresses, they multiply in number. The adult thrips feed on stamens and petals. As the petals of the flowers are shed from the tree the thrips fall on the ground and then move to a new cohort of subsequently opened flowers. The distances over which thrips move are not known but, because of their relatively small body size, they apparently do not fly over long distances. It is presumed that their restricted movement is not a drawback in their effectiveness as pollinators because the species they pollinate are relatively abundant.

Dayanandan *et al.* (1990) present evidence for pollination of *Shorea megistophylla* (section Doona) and *Vateria copallifera* by bees (*Apis* spp.). They also observed a wide variety of other insect floral visitors including thrips. However, the thrips acted as flower predators rather than pollinators, particularly in *V. copallifera.*

More recently, Momose *et al.* (1994) have presented evidence for pollination of *Dryobalanops lanceolata*, a large canopy tree species in Sarawak, by medium sized, stingless bees (*Trigona* spp.). They also noted the presence of many other types of flower visitors (*Coleoptera* and *Diptera*). Momose *et al.* suggest that medium sized, stingless bees constitute an important group of pollen vectors for canopy and subcanopy trees in Sarawak (see also Chan and Appanah 1980).

Clearly, the dipterocarps are pollinated by a wide variety of insects. The three detailed studies, respectively by Appanah and Chan (1981), Dayanandan *et al.* (1990), and Momose *et al.* (1994) have revealed three different classes of pollinators. Ashton (1982) in his extensive review also lists beetles and moths as flower visitors, although their role in pollination has not yet been demonstrated. Among the pollinators implicated so far, all, except thrips, are capable of moving pollen over long distances. The extent of gene flow via pollen (and seeds) is further discussed in subsequent sections.

Seed dispersal in most dipterocarps is by wind (Ashton 1982). In most species, sepals are modified into wing like structures in the fruits that allow the single seeded fruits to gyrate toward the ground. Many species growing in swamps or river banks have fruits with short sepals and may be dispersed by water (Ashton 1982). In some dipterocarps, such as species of *Stemonoporus*, fruits are without wing-like sepals. When mature, they simply fall on the ground and are apparently not removed by any disperser (Murawski and Bawa 1994) although rodents are known to hoard the seeds and, perhaps, aid in dispersal (P. Ashton, personal communication). Seeds disseminated by wind and water can potentially disperse over long distances. In *Shorea albida*, dissemination by wind up to 2 km has been documented (Ashton 1982) and although dispersal by water has not been observed in any species seeds may move over long distances in water channels.

Apomixis

Apomixis has been reported in several taxa of the family. There is embryological evidence for the existence of multiple embryos originating from a single ovule in *Shorea ovalis* ssp. *sericea* and *S. agamii* ssp. *agamii* (Kaur *et al.* 1978). Multiple seedlings from a single fruit, indicative of polyembryony, have been reported in *Anisoptera curtisii*, *Dipterocarpus baudii*, *D. cornutus*, *D. costulatus*, *Dryobalanops aromatica*, *Hopea odorata*, *H. subalata*, *Parashorea densiflora*, *Shorea argentifolia*, *S. gratissima*, *S. macrophylla*, *S. parvifolia*, *S. pauciflora*, *S. smithiana*, *Vatica pallida* and *V. pauciflora* (Kaur *et al.* 1978 and references therein) and in *Shorea trapezifolia* (S. Dayanandan, personal commnication). The percentage of multiple seedlings is low in all these species except for *S. macroptera*, *S. resinosa*, *H. odorata*, and *H. subalata* in which 30-70%, 98%, 90% and 21% seeds respectively have multiple seedlings.

Interestingly, a recent study by Wickneswari and Norwati (1994) indicates that multiple seedlings from the same seed in *Hopea odorata* have different genotypes raising the possibility that multiple seedlings may not necessarily involve apomixis. Furthermore, using genetic markers, a high outcrossing rate has been estimated for the species (Table 3). Isozyme surveys also reveal high amounts of genetic diversity within populations (Wickneswari *et al.* 1994).

Apomixis is associated with triploidy in *Shorea resinosa* and *Hopea subalata* (also possibly in *H. latifolia)* but other species displaying polyembryony are mostly diploid. The ovary in Dipterocarpaceae is usually three locular with two ovules in each loculus. Normally, only one ovule develops into a seed thus, multiple seedlings can result from occasional development of seeds from more than one ovule and the presence of such seedlings need not always imply apomixis.

Apparently, in some species apomixis is widespread while in others it occurs occasionally. Obligate apomixis for either individual trees or populations (and species) remains to be demonstrated but is a possibility in taxa with a triploid chromosome number. Certainly among tropical woody families apomixis at a scale comparable to Dipterocarpaceae has not been reported. Moreover, considering that most species in the family have a low diploid chromosome number, the common occurrence of apomixis is puzzling because apomixis is usually associated with polyploidy and hybridisation.

Apomixis could have played an important role in evolution of the family. New genetic combinations arising through mutations or hybridisation that may be partially or completely sterile can be perpetuated by apomixis. Vegetative multiplication can also maintain heterozygosity for a long time. In addition, apomixis and self-pollination may allow new genetic variants to spread at new sites. Subsequent restoration of sexual reproduction and outcrossing, combined with mutation, can introduce genetic variation in the new isolates.

Hybridisation

Hybridisation has played an important role in the evolution and diversification of angiosperms (Stebbins 1950). Hybrids in tropical trees are assumed to be rare (Ashton 1969). In dipterocarps, however, hybrids have been frequently reported. Ashton (1982) suggests that many triploid taxa in the family could be of infraspecific hybrid origin. His list includes the following: *Hopea subalata*, *H. odorata*, *Shorea ovalis* ssp. *sericea*, *Neobalanocarpus heimii*, *Shorea leprosula*, *S. curtisii*, and hybrids between *Vatica rassak* and *V. umbonata*, and *Anisoptera costata* and *A. curtisii*. Many examples of putative hybrids between species of *Dipterocarpus* have also been reported (Symington 1943). Apomixis, already noted in several taxa of the family, could certainly allow the hybrids to persist until sexual fertility is restored. Although several of the interspecific hybrids are polyploids, polyploidy in the family has so far been recorded in relatively few taxa. On the other hand, the base number x=11 observed in several genera of the family itself could be of ancient alloploid derivation.

Genetic Diversity Within and Among Populations

The existence of self-incompatibility and high outcrossing rates suggest that populations of dipterocarps should harbour high levels of genetic variation. Indeed, recent studies, based on analysis of variation at isozyme loci, have revealed considerable genetic variation in natural populations. A high level of enzymatic polymorphism in natural populations of *Shorea leprosula* was first detected by Gan *et al.* (1977). More recently, genetic diversity within and among populations of several species of *Hopea* (Wickneswari *et al.* 1994), *Shorea* (Harada *et al.* 1994), *Stemonoporus* (Murawski and Bawa 1994, Dayanandan and Bawa, unpublished data) has been quantified. Genetic diversity in many Malaysian species of *Hopea* and *Shorea* were studied using Random Amplified Polymorphic DNAs (RAPD). Considerable variation was found both within and among populations. The level of diversity in species of *Hopea* (Wickneswari *et al.* 1996) was less than in species of *Shorea* (Harada *et al.* 1994). In these studies, methods to characterise genetic diversity depended upon several assumptions about the segregation and homology of bands. Moreover, results from most RAPD surveys cannot be compared with those obtained from isozyme surveys because dominance at RAPD 'loci' makes it impossible to distinguish heterozygotes from homozygotes. Thus, genetic diversity cannot be characterised in conventional terms. Bawa and his associates have used isozymes to estimate genetic diversity in species of *Stemonoporus* and *Shorea*. In *Stemonoporus oblongifolius*, the percent of polymorphic loci range from 89% to 100%, the average number of alleles per polymorphic locus is 3.1 and mean genetic diversity for the species is 0.297. The number of loci sampled was 9 and was the same sampled for other dipterocarps and tropical trees. The estimates of genetic diversity are among the highest reported for plant species (Murawski and Bawa 1994). The values for the above parameters are lower for *Shorea trapezifolia*, but remain toward the higher end of the value reported for tropical trees. Similarly, a high level of genetic variation has been observed in *Shorea megistophylla* (Murawski *et al.* 1994b*)* and several other species of *Stemonoporus* (Murawski and Bawa, unpublished). Wickneswari *et al.* (1994) also report high levels of variation in *Hopea odorata* on the basis of isozyme studies.

Inter-population differentiation on the basis of isozyme surveys has been studied in only three species: *Stemonoporus oblongifolius* (Murawski and Bawa 1994), *Shorea trapezifolia* (Dayanandan and Bawa, in preparation) and *Hopea odorata* (Wickneswari *et al.* 1994). In all cases, there is a high level of variation among populations. In *Stemonoporus oblongifolius*, the mean Gst value, which is a measure of population differentiation, is 0.16. In other words, 16% of total genetic diversity is due to differences among populations. Interestingly, the distance among sampled populations ranged from 1.3 to 9.7 km. Thus, populations seem to differ over a relatively small spatial scale. In *Shorea trapezifolia* too the Gst value was high (0.11); in this case the most distant were separated by 43.5 km. The mean genetic distance between populations in *Hopea odorata* was 0.10 (Wickneswari *et al.* 1994).

The high level of genetic differentiation could be due to either restricted gene flow or local selection. Direct observations of gene flow in dipterocarps are lacking. Seed dispersal in *Stemonoporus oblongifolius* seems to be passive; the one seeded, heavy, resinous fruit drop under the maternal tree and the seed germinates without being removed by any disperser (Murawski and Bawa 1994). In *Shorea trapezifolia*, the seeds are dispersed by gyration, assisted by wind with most seeds falling within the vicinity of the parent. Gyration of fruits, referred to earlier, may have evolved as an adaptation to restrict dispersal to the sites in which the parents are found. Thus, gene dispersal via seeds in both species does not generally occur over large distances.

The degree of gene dispersal via pollen would depend upon the pollinators. Medium sized to large bees should be able to bring about long-distance dispersal more frequently than small bees or thrips. Both *Stemonoporus oblongifolius* and *Shorea trapezifolia* are pollinated by medium-sized bees (*Apis* spp.).

Gene dispersal has been indirectly measured in *Shorea trapezifolia* (more than one migrant per generation). Nm estimates the degree of migration between populations, and a value of Nm>1 is enough to prevent population differentiation due to drift for neutral loci (Wright 1931, Maruyama 1970, Slatkin and Maruyama 1975). In *S. trapezifolia*, the value of Nm is 1.62. This high value indicates that differentiation in *S. trapezifolia* is not due to restricted gene flow.

Ashton (1982, 1988) has shown that congeneric species in the family often occupy different edaphic zones. Moreover, within the same habitat related species may be differentiated along environmental gradients that define the regeneration 'niche'. Therefore, genetic selection within taxa of the family can readily be moulded by fine and coarse grain variation in the environment. Thus, the inter-population differentiation observed in *Stemonoporus oblongifolius* and *Shorea trapezifolia* is consistent with the hypothesis that slight variation in the habitat can allow genetic variants to differentiate along environmental gradients despite low or moderate levels of gene flow.

Summary of Diversification Processes

Most dipterocarps are outcrossed and diploid. Speciation seems to have involved allopatric differentiation of widely outcrossing populations; differentiation seems to have occurred in response to differences in soils and habitats (Ashton 1969). Aneuploidy, polyploidy, and hybridisation may have also assumed a role in the spread of some variants arising as a result of hybridisation and changes in chromosome number. At the intraspecific level, outcrossing maintains high levels of genetic variation in populations. Mass flowering combined with abundance of adults probably ensures large effective population sizes. Nevertheless, despite extensive gene flow, selection results in differentiation of populations over relatively small scales.

Research Needs

Future research needs may be best examined in the context of threats to diversity. Genetic resources are imperilled by deforestation and forest fragmentation. Moreover, selective logging often can lead to reduction in genetic variation (Kemp 1992) and alter population structure with concomitant changes in demography and genetics of subsequent generations (Bawa 1993). Global climatic change is also expected to influence plant populations, but the potential effects, deleterious or beneficial, are not well defined, particularly for the areas where dipterocarps are dominant.

Deforestation and forest fragmentation may influence diversity in several ways. Species or populations may become extinct or severely endangered. At the population level, once seemingly large, contiguous populations may be broken into relatively small, remnant patches, physically isolated from each other. Over time, gene exchange among the remnant patches may be completely eliminated and the small populations may be subject to inbreeding. Habitat fragmentation can also increase overall levels of variation if isolated populations diverge from each other. The consequences of fragmentation depend upon the degree and duration of isolation and the size of the isolated population.

Fragmentation of habitats may have deleterious effects on both the ecosystem dominants as well as rare species. The ecosystem dominants may have very large populations, and fragmentation may result in loss of genetic diversity (Holsinger 1993). Rare species may face severe reduction in population size following fragmentation. Many species of dipterocarps have adult population densities as low as 0.07 to 0.30 individuals per hectare (Ashton 1988). Some of these species occur in low population densities at more than one site and may be particularly prone to inbreeding. In addition, there may be selection for apomixis in such situations (P. Ashton, personal communication).

Selective logging can also increase the potential for inbreeding. Logging temporarily reduces adult population densities. In many tropical tree species, inbreeding has been shown to be a function of stand density (Murawski and Hamrick 1990, 1991). In *Shorea megistophylla*, as noted above, the rates of inbreeding are higher for trees from logged stands than for trees in unlogged stands. However, it should be noted that stands in properly managed forests regenerate from seedlings established prior to logging. In dipterocarps, the potential for inbreeding is also increased by the fact that self-incompatibility barriers are not strong; trees in many species are capable of setting seeds after self-pollination, but here again selfed seeds may be selected against in the presence of outcrossed seeds in the same inflorescence.

The longevity of trees may not allow many of the assumed deleterious consequences of forest fragmentation and selective logging to be manifested for a long time. Even in small patches, trees may set fruits and seeds and regenerate without apparent ill-effects. Comparative studies of reproductive output, mating patterns, and regeneration processes involving trees in large contiguous forests and small fragments may reveal the consequences of habitat alteration.

Thus, in order to fully understand the effects of deforestation, forest fragmentation, and forest management practices on forest genetic resources of dipterocarps, we need a better understanding of patterns of diversity and processes that maintain diversity. Areas of research that require immediate attention are outlined below.

Species Level Research

First, we have to identify species that are endangered or threatened with extinction. In some instances, populations of species themselves might be large, but the types of forests in which such species occur may be disappearing at a very rapid rate. Examples are the moist seasonal evergreen forests on the western slopes of western Ghats in India and throughout Indochina, the mixed dipterocarp forests in the southwest region of Sri Lanka, and the dipterocarp forests in Philippines. Fortunately, due to the work of Ashton (1982, 1988) and others, as compared to other tropical families, there is far more information available on the geographical ranges of various species and the type of habitats and soil types occupied by these species. More recently, P. Ashton has reviewed the conservation status of all Asian dipterocarps for the World Conservation Monitoring Centre at Cambridge, UK. All this information along with other data on land use patterns, fragmentation, and deforestation should be combined in a geographical information system to provide easily comprehensible graphical information on the current status of distribution of species and the conservation status of the forests in which they occur. Such a database would be particularly useful because, in many cases, information on the conservation status of family members is equivalent to information on conservation status of dipterocarp forests, the most important and dominant vegetation in very large areas of south Asia and southeast Asia.

Second, we need to identify centres of taxonomic diversity and active speciation in the family. Centres of taxonomic diversity, of course, are known on the basis of morphological criteria (Ashton 1982, 1988). Molecular techniques, however, provide means to rapidly assess species relationships and to elucidate patterns of speciation. For example, within section Doona of *Shorea*, molecular data indicates that the ‘Beraliya’ group is evolving at a higher rate than the remaining species (S. Dayanandan, personal communication).

Third, comparative studies of genetic diversity in species that occupy centres of diversity and those that occur away from zones of diversification may provide further insights into patterns of genetic diversity. As mentioned earlier, Murawski and Bawa (1994) observed an unusually high level of genetic variation in natural populations of *Stemonoporus oblongifolius*. The genus is endemic to Sri Lanka and has undergone active speciation in a small region in the southwest region of the island. The high diversity observed by Murawski and Bawa may be due to the fact that this species is found in a region which is the centre of active speciation. Similarly, comparative studies of related common and rare species, or species in different ecological zones may provide additional insights into patterns of genetic diversity among species.

Fourth, there is an urgent need to study the effects of logging on genetic diversity and other population genetic parameters such as inbreeding and gene flow. Gene Resources Areas that are being established in Malaysia (Tsai and Yuan 1995) may provide excellent opportunities for such comparative research.

Fifth, we need a better understanding of the importance of chromosomal variation, apomixis, and hybridisation in diversification at the species level and infraspecific levels. We know the species and genera in which these processes occur. However, our knowledge with respect to the incidence and ecological and evolutionary importance, particularly, of apomixis and hybridisation is very limited. Again, molecular techniques now offer new opportunities to assess the significance of these processes.

Finally, information on breeding systems and pollination mechanisms is required for many taxa to characterise genetic factors maintaining genetic variation. Such information is available for only a few species. Many large genera such as *Dipterocarpus* and *Hopea* remain unexplored.

Intraspecific Level Research

First, the most urgent need is the characterisation of the patterns of genetic variation in important species. However, in addition to ecosystem dominants and species of commercial importance, we also need to analyse the genetic structure of rare species. A better understanding of the spatial organisation of genetic variation is critical to the assessment of the effects of deforestation and forest fragmentation on genetic diversity.

Second, comparative studies of gene flow in contiguous and fragmented forests can provide information about the effective size of populations, microevolutionary forces responsible for genetic differentiation among populations, and the potential effects of deforestation and fragmentation on genetic isolation of populations that were once contiguous.

Third, comparative studies of central and peripheral populations may be useful in revealing pockets of high genetic diversity. Populations in the centre of a species range may often show more genetic variation than peripheral populations due to a higher rate of gene exchange in central populations.

Fourth, the effect of genetic diversity and inbreeding on population viability should be an area of utmost concern. Are reduced levels of genetic diversity and outcrossing associated with a decline in fitness? Decrease in fitness may be manifested as reduction in fruit and seed set, seedling vigour and overall recruitment and regeneration. It is thus critical to link genetic studies and demographic studies. Comparative studies of gene flow in fragmented and contiguous forests, described earlier, should incorporate comparative studies of the effects of genetic variation and inbreeding on reproductive output and regeneration. Mass flowering in dipterocarps also offers opportunities to gain insights into the relationship between genetic diversity and population recruitment. Sporadic flowering in off years may reduce the effective population size, increase inbreeding and mortality of seeds due to predation and lead to a disproportionately low level of recruitment. Comparative genetic and demographic studies during mass and sporadic off year flowering can provide useful information about possible effects of reduction in population size.

Fifth, many species of dipterocarps display intraspecific variation in chromosome number and apomixis. However, the frequency of chromosomal variants or apomixis within or among populations is not documented. There are now molecular tools to rapidly assay populations for the incidence of chromosomal variation, apomixis and hybridisation.

Site-specific Research

The rates of deforestation vary widely among the regions. Species diversity of dipterocarps is also not uniform throughout South and Southeast Asia. Thus, from a geographical perspective, high priority should be accorded to regions that are undergoing rapid deforestation and those that have very high species richness.

The Philippines, Sri Lanka and the Western Ghats of south India have been converted into other forms of land uses at a high rate during the last fifty years. These areas have certainly lost unique populations and perhaps species of dipterocarps. In such areas, there is an immediate need to assess the conservation status of various taxa building on P. Ashton's earlier review. Sri Lanka particularly deserves serious consideration because of the high degree of endemism: 6 out of 7 genera and 45 out of 46 species of dipterocarps are endemic to the country.

The greatest species diversity in the family is found in northwest Borneo. However, much of the cytology and genetic research cited in this paper has been conducted on species from Peninsular Malaysia and Sri Lanka. Data from genetics and population biology of the taxa that occur in northwest Borneo should provide useful insights into mechanisms regulating differentiation within and among species.

Institutional Capability and Constraints

P.S. Ashton , J. Liu, P. Hall and their associates (Harvard University), S. Appanah, H. Chan, and others (Forest Research Institute Malaysia (FRIM)) have played a key role in advancing our knowledge of the systematics, biogeography, and ecology of the family. Research in systematics and ecology is being continued at Harvard University. At FRIM the scope of research in genetic resources has been recently enlarged to include such areas as molecular evolution and population genetics.

In Sri Lanka, N. Gunatilleke and S. Gunatilleke at the University of Peradeniya have a major research programme on conservation biology of dipterocarps. This programme includes research on population biology and population genetics. N. Gunatilleke and S. Gunatilleke have collaborated with P. Ashton (Harvard University), K. Bawa and D. Murawski (University of Massachusetts, Boston).

Another major centre of research on population biology and genetics of dipterocarps is the Kyoto University. T. Inoue, K. Momose and R. Terauchi are involved in detailed studies of phenology, pollination biology and genetics of dipterocarp species in Sarawak. The work is a part of a major programme on canopy research in dipterocarp forests.

S. Dayanandan and R. Primack (Boston University) are working in collaboration with P. Ashton on a diverse range of issues in dipterocarp biology, from molecular biology to population dynamics.

Recently, the Center for International Forestry Research (CIFOR) and International Plant Genetic Resources Institute (IPGRI) have initiated a project on population genetics, specifically on the effects of forest fragmentation, logging and non-logging disturbance on genetic diversity of some dipterocarps. This programme involves a number of institutions in India, Indonesia, Malaysia and Thailand.

Apart from insufficient funding, the major factor constraining progress has been the lack of a coordinated programme with clear objectives and predetermined priorities. With the establishment of institutions such as CIFOR and IPGRI, it should be possible to undertake a cohesive research programme with well defined goals.

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Chapter 3

Seed Physiology

P.B. Tompsett

Seed is the natural vehicle for gene movement and storage. It is the usual form in which germplasm is collected. When procedures can be devised to transport and retain material in this form, many of the technical problems associated with other methods can be avoided. This advantage renders seed especially appropriate for users in tropical and subtropical countries. In general, seed is the most common form of propagation for afforestation and is the form in which breeding stock is usually retained. There are, however, considerable problems remaining in the use of seed. Some of these are discussed below for dipterocarp species in relation to the underlying seed physiology processes.

Much pioneering work on agricultural crop seed physiology was conducted over the last 20 years (see below for some references) and the principles discovered often apply to seed of woody species. These earlier results have been translated into technological principles. Thus, manuals have been published on the design of seed storage facilities (Cromarty *et al*. 1982), seed management techniques (Ellis *et al*. 1984) and a handbook on seed technology for genebanks (Ellis *et al*. 1985). Knowledge of seed physiology has thus improved practical handling and management of crop seeds.

Compared to crop species, relatively little research has been published on tropical and subtropical tree seed technology and physiology. Publications have been produced following IUFRO Seed Problems Group meetings, the most recent of which was held in Tanzania (Olsen 1996). Another source of information is a summary of some relevant seed physiology projects which has recently been published in database form (Tompsett and Kemp 1996a, b). Also, a seed compendium has been published which supplies succinct entries on many tropical trees (Hong *et al*. 1996).

A considerable amount of empirical work on the storage of forest tree seed has been carried out; a sampling is given in Chapter 4. A more physiological research approach is relatively new. Many tree species have seed that is desiccation-sensitive (‘recalcitrant’), so that moisture physiology is especially important for this group. However, in a recent review article on water in relation to seed storage, the section on desiccation-sensitive seeds comprised only 4% of the article (Roberts and Ellis 1989). More attention is, however, now being given to recalcitrant seeds (see, for example, Berjak and Pammenter 1996).

Framework of the Review

Germination is basic to all aspects of seed studies; work on germination physiology, especially in relation to temperature, is thus considered first. Another important experimental consideration is the physiological condition of the seed at the time of harvest, moisture content being the single most important factor; this is considered next in the review. Thirdly, the effect of desiccation is discussed; knowledge of this factor enables seed to be classed as orthodox (tolerant) or recalcitrant (intolerant). Finally, the effects of seed storage are considered.

The Review

Germination

In general, dipterocarp seeds germinate quickly under moist, warm conditions.

Early germination studies took the form of nursery assessments leading to ecological conclusions. A major study of this type, in which 56 dipterocarp species were assessed for germination rate and final germination, is that of Ng (1980); no conclusions can be made concerning temperature effects. Conditions were more closely controlled in experiments on *Shorea roxburghii, S. robusta* and *S. almon* by Tompsett (1985); results showed optimum germination in the range 26-31°C for these three species. Corbineau and Come (1986) found that final germination reached nearly 100% for both *Hopea odorata* and *S. roxburghii* over a broad range of temperatures, but 30-35°C was deemed optimal because germination rates were faster. More recently, a standard

Table 1. Optimum germination temperatures, germination rates and base temperature values (Tompsett and Kemp 1996a, b).

Species	Base temperature (°C)	Time to 50% final germination at the optimum temperature (d)	Optimum temperature (°C)	Radicle length defining germination (mm)
Shorea almon	n/a	n/a	26	5
Shorea siamensis	n/a	n/a	26	5
Shorea smithiana	n/a	n/a	26	3
Shorea pinanga	n/a	n/a	31	10
Hopea parviflora	n/a	11	31	5
Shorea roxburghii	n/a	11	31	5
Dipterocarpus alatus	n/a	20	26	5
Shorea robusta	n/a	4	31	5
Anisoptera marginata	n/a	6	26	3
Hopea foxworthyi	6.4	4	31	3
Hopea odorata	7.1	2	31	5
Shorea leprosula	7.5	4	31	3
Shorea parvifolia	8.3	4	26	3
Shorea contorta	8.8	7	26	3
Shorea affinis	9.4	5	26	3
Parashorea smythiesii	9.7	3	31	3
Dipterocarpus costatus	10.2	30	31	3
Dryobalanops aromatica	10.5	3	26	3
Parashorea tomentella	10.5	9	31	10
Shorea guiso	11.0	4	26	3
Anisoptera costata	11.4	5	26	3
Shorea ferruginea	12.2	6	26	3
Dipterocarpus obtusifolius	12.4	3	26	5
Cotylelobium burckii	13.0	9	26	3
Vatica mangachapoi	13.0	9	31	3
Dipterocarpus turbinatus	15.2	5	26	10
Cotylelobium melanoxylon	15.4	6	31	3
Dipterocarpus tuberculatus	15.8	13	31	5
Shorea amplexicaulis	15.8	7	26	3
Dipterocarpus zeylanicus	16.2	11	26	10
Shorea argentifolia	16.4	4	26	3

approach was adopted in a series of germination studies so that physiological parameters could be assessed (Table 1). Optimum germination for 30 species was confirmed as lying between 26°C and 31°C and the value for the time to 50% final germination, at the optimum temperature, generally ranged between 2 and 13 days. There were two *Dipterocarpus* species (*D. alatus* and *D. costatus*) that were much slower to germinate, however.

A physiological parameter relating to the theoretical value at which zero growth occurs was also assessed; this is referred to as the 'base temperature'. The base temperature is the intersect on the temperature axis for the plot of germination rate against temperature. More details of technique are given in Tompsett and Kemp (1996a, b); the parameter is further discussed below.

Chilling damage

Studies show germination is reduced or does not occur at temperatures below 16°C for several dipterocarp species (Tompsett 1985, Corbineau and Come 1986), due to chilling damage. This type of damage is also observed in the results from storage research; data show a reduced ability to survive low temperature conditions

(Sasaki 1980, Yap 1981, Tompsett 1985, Corbineau and Come 1986).

Sasaki (1980) considered seeds of (i) *Shorea* species in the 'yellow and white meranti' groups, (ii) *Hopea,* (iii) *Dipterocarpus,* (iv) *Vatica*, (v) *Dryobalanops,* (vi) *Balanocarpus* and (vii) *Parashorea* to be tolerant down to 4°C. By contrast, he believed that seeds of *Shorea* species in the 'red meranti and balau' groups were intolerant of temperatures below 15°C. He classified *Anisoptera* as a tolerant genus in a separate publication (Sasaki 1979). Yap (1981) later proposed a three-group classification: firstly, seed of species in the *Dipterocarpus, Dryobalanops, Neobalanocarpus* and *Vatica* genera were said to be intolerant of temperatures below 14°C; secondly, seed of *Shorea* species in the sections Mutica, Pachycarpae and Brachypterae were considered intolerant of temperatures below 22°-28°C; and, finally, seed of *Shorea* species in the Anthoshorea section and seed of *Hopea* and *Parashorea* could be cooled to 4°C (but were recommended to be stored at 14°C). Further details relating taxonomic classification to chilling damage are given elsewhere (Tompsett 1992). A possible explanation for the above inconsistencies is that different authors have studied the effects of chilling for different periods of time, leading to different conclusions; exposure of seed to longer periods of chilling can show up chilling damage which might otherwise have ben missed in the case of relatively chill-resistant species.

The processes behind the chilling physiology phenomenon have not been adequately studied. However, differences among species in susceptibility to chilling damage are confirmed by the base temperature data in Table 1. In particular, *Hopea* species appear the most resistant to chilling damage, since they have the lowest base temperatures. A low value for the base temperature is expected if germination ability decreases relatively slowly as germination temperature is reduced. It should be emphasised, however, that these results apply exclusively to moist seeds. Storage of dry orthodox dipterocarp seeds at low temperatures is described in the storage section below.

The differences in chilling tolerance of seeds among dipterocarp species are quantitative rather than qualitative. Seed of the 'tolerant' species *S. roxburghii* eventually suffers damage at 2°C -5°C relative to seed kept at warmer temperatures (Purohit *et al. 19*82, Tompsett 1985). Another example of chilling damage which occurred over a lengthy period of time is that to *H. hainanensis*. For this species, seed at 5°C almost all died after 6 months; by contrast, at 15°C -20 °C no loss of viability occurred (Song *et al.* 1984).

Harvest and Maturity

The condition of seed at harvest is of primary concern in the planning of all physiological experiments. Moisture contents at or near harvest are given for 25 species in Table 2, including examples from both seasonal and aseasonal dipterocarp forests. Seeds of the three species with the lowest moisture contents, which are found in seasonal forests, were collected from the ground after natural desiccation. For these seeds, drying occurs very swiftly after abscission because the open canopy exposes them to direct sunlight. Of the remaining species listed, some are derived from the dry forest and others from moist areas; they possessed a relatively high range of post-processing moisture contents between 29 and 56% (usually, seeds were just de-winged).

It has been realised for some time that there can be a considerable difference between whole-seed moisture content and moisture content of the embryo or embryo axis (Grout *et al.*,1983). Since axis or embryo moisture content is more closely related to basic physiological processes than whole seed moisture content, it is a preferable measure to use herein. Axis values have been determined for dipterocarp species (Table 2) and range from 51 to 74%, except in the case of the much lower value for the dry-zone species *Dipterocarpus tuberculatus*, which was collected after natural drying.

Seed maturation

A few developmental studies have been carried out on dipterocarp species; whole-seed moisture content has been employed in most of these as the main physiological criterion. Sasaki (1980) reported that the moisture content (wet basis) of *Shorea roxburghii* declined from 60 to 50% in the final 3 weeks of maturation on the tree. Panochit *et al.* (1986) reported a comparable decline from 40 to 30% for the same species, whilst a reduction from 59 to 49% was reported for *S. siamensis* (Panochit *et al. 19*84).

Nautiyal and Purohit (1985a) assessed changes during maturation of *S. robusta* seed; they described these changes as biphasic. Over the 60 days from anthesis to maturity, concentrations of soluble carbohydrates, starch, soluble protein and acid phosphatase were

Table 2. Percentage moisture content and oil values for processed, dewinged whole seed and excised seed parts (Tompsett and Kemp 1996a, b).

Species	Whole-seed moisture content* (percentage)	Axis moisture content* (percentage)	Embryo oil content ** (percentage)
Dipterocarpus intricatus ***	8	n/a	16
Dipterocarpus alatus ***	11	n/a	7
Dipterocarpus tuberculatus ***	11	13	19
Shorea ferruginea	29	n/a	61
Shorea argentifolia	29	51	n/a
Hopea ferrea	32	n/a	9
Shorea parvifolia	32	62	n/a
Hopea foxworthyi	34	52	n/a
Hopea odorata	36	54	20
Shorea gibbosa	37	64	n/a
Dipterocarpus costatus	38	n/a	10
Shorea macrophylla	38	66	n/a
Parashorea tomentella	40	63	n/a
Shorea amplexicaulis	40	69	57
Dipterocarpus grandiflorus	40	70	n/a
Anisoptera costata	42	n/a	33
Shorea fallax	42	70	n/a
Shorea affinis	44	63	n/a
Dipterocarpus chartaceus	47	n/a	8
Shorea leptoderma	47	61	n/a
Parashorea malaanonan	48	66	n/a
Dryobalanops keithii	50	56	n/a
Stemonoporus canaliculatus	53	64	n/a
Shorea macroptera	55	n/a	n/a
Dipterocarpus obtusifolius	56	74	n/a

*: calculated on wet weight basis;
**: calculated on dry weight basis;
***: seeds of OLDA (orthodox with limited desiccation ability) dried naturally in the field.

determined; in addition, declining moisture content, increasing germination and increasing weight of the seed were recorded. One theory proposed was that early desiccation of the seed coat may be connected with poor viability; this explanation appears unlikely since *S. roxburghii* has similar seed coat structures and is much longer-lived.

An interaction of maturity with chilling damage has been noted. Increased resistance to such damage was observed as maturity approached for *S. siamensis* (Panochit *et al. 19*84); germination declined to zero and 25% for seed collected 4 and 2 weeks respectively before maturity after storage for 28 days at 2°C, but mature seed still gave about 60% germination after 56 days of similar storage. The same effect was noted for *S. roxburghii* (Panochit *et al.* 1986).

Tang and Tamari (1973) were the first to report the post-harvest-maturation phenomenon for dipterocarp seeds. They found that *Hopea helferi* and *H. odorata* seeds blown down prematurely by a high wind increased in germination during storage. The effect was observed over a period of about one week for seeds held at 15 °C.

Desiccation Studies

Knowledge of its storage physiology category, which can be derived from desiccation studies, is the single most useful piece of physiological information about a seed. It is the key to correct seed handling procedures.

Seed storage physiology categories

Three storage category designations are recognised. Of these, the main two are:

- orthodox; and
- recalcitrant.

The orthodox type is capable of desiccation to a low moisture content (approximately 5%) and storage for several years at -20°C with little loss of viability (Roberts 1973). By contrast, the recalcitrant type is not capable of desiccation to a low moisture content without loss of germination capacity and cannot be stored for long periods of time (Roberts 1973).

A third category of seed storage physiology has been described. It was first defined in 1984 in relation to *Araucaria columnaris* seed (Tompsett 1984) and was termed 'orthodox with limited desiccation ability' (OLDA). A similar category was later defined for coffee seed and termed 'intermediate'; the name denotes its partial tolerance of desiccation (Ellis *et al.* 1990, 1991). Some recent evidence (Tompsett, unpublished), however, confirms there may be little physiological difference between this third category of seed and the orthodox type. There are, however, important practical handling difficulties associated with this third category. These problems justify its retention as a distinct storage type.

Some tropical seed is additionally subject to low-temperature damage when stored in the moist condition (chilling damage, see pages 58-59). As a result, further categories could have been included. However, it was considered preferable, for the sake of simplicity, to employ only the three desiccation-damage-based categories described above. To date, all dipterocarp species examined have been found to be subject to chilling damage when moist.

Desiccation physiology

Curves of germination percentage against moisture content percentage can be plotted for the results from controlled desiccation studies. These curves illustrate whether the seed is recalcitrant or not and give parameters for the way the seed responds when it is dried. One parameter is the lowest-safe moisture content (LSMC), defined as the value below which viability is immediately lost on drying. The value for this parameter provides a guide to the moisture content below which seed should not be held during handling procedures. LSMC values were assessed under standard drying conditions and were found to vary between 26% and 50% (Table 3). In Table 4 further LSMC data are given; although these were assessed using various desiccation methods, the results are in broad agreement with those in Table 3.

Slope and intercept parameters are presented for some species (Table 3); these define the relationship between germination and moisture content during desiccation.

Desiccation rates

It is possible that desiccation rate may influence viability; for example, seeds dried quickly might give lower germination than seeds dried more slowly and gently to the same moisture content. However, in the case of the 'recalcitrant' seed of *Araucaria hunsteinii* (Araucariaceae) no such differences were observed (Tompsett 1982). No intensive study of this sort has been carried out on dipterocarp seed. However, Amata-Archachai and Hellum (unpublished) found that immature fruits of *Dipterocarpus alatus* clearly dried quicker than mature fruits; they suggested that the difference could be because of the death on drying of the immature seeds. However, the faster loss of moisture by immature seeds could also be explained by their smaller size. Small seeds have a higher ratio of surface area to volume than large seeds, enabling quicker moisture loss. In this connection, Tamari (1976) found small seeds of *S. parvifolia* (0.3 g) gave low viability, whilst large seeds (0.5 g) gave higher viability. One explanation for the latter finding is that the smaller seeds had dried quicker and thus lost more viability than larger seeds prior to testing.

Clear-cut differences in desiccation rates among seeds of species in the same genus have been reported by Tompsett (1986, 1987); rates for *Dipterocarpus* seeds varied greatly and depended on their size and structure. At the one extreme *D. intricatus* seed required only one week to dry to 7% moisture content; at the other extreme, seed of *D. obtusifolius* under identical conditions retained c. 30% moisture content even after 5 weeks. Likewise, Yap (1986) found *S. parvifolia* seeds dried quicker than those of two larger-seeded species of *Shorea*; he believed the difference in rates to be related to pericarp thickness.

Differences in desiccation rates of the type discussed above may possibly affect both the initial post-desiccation viability and the subsequent storage life of the seed. Further studies are needed to assess these effects.

Table 3. Relationship between germination and moisture content during desiccation (Tompsett and Kemp 1996a, b)*.

Species	Lowest-safe moisture content values (percentage)**	Slope of probit line (probits per unit of moisture content percentage)	Intercept of probit line (probit percentage germination)
Shorea leprosula	26	n/a	n/a
Shorea argentifolia	28	0.1814	-3.5780
Shorea ferruginea	29	0.1912	-4.8300
Hopea ferrea	30	0.1050	-3.5660
Hopea mengerawan	30	0.1400	-3.6700
Hopea foxworthyi	31	0.0994	-2.5555
Hopea odorata	32	0.1303	-3.6450
Shorea parvifolia	32	n/a	n/a
Shorea roxburghii	32	0.1000	-2.7700
Shorea obtusa	33	0.0660	-2.4420
Shorea ovalis	33	0.1816	-5.0550
Cotylelobium melanoxylon	34	0.1303	-3.1790
Vatica mangachapoi	34	0.0919	-3.4460
Cotylelobium burckii	35	0.1400	-3.2200
Parashorea smythiesii	35	0.1743	-4.9920
Shorea macrophylla	35	0.0978	-2.6190
Shorea trapezifolia	37	n/a	n/a
Dipterocarpus costatus	38	0.0789	-1.9360
Dipterocarpus obtusifolius	38	0.0584	-2.2470
Dipterocarpus zeylanicus	38	0.1427	-3.8090
Shorea fallax	38	0.0869	-2.2470
Shorea macroptera	38	0.0867	-4.2300
Parashorea tomentella	40	0.2000	-7.1400
Shorea amplexicaulis	40	0.1307	-5.5600
Shorea congestiflora	40	0.0904	-3.6510
Shorea robusta	40	0.1300	-4.2200
Vatica odorata ssp. *odorata*	41	0.0961	-3.6290
Shorea affinis	42	0.0475	-1.6120
Shorea almon	42	0.1400	-5.4700
Shorea leptoderma	42	0.0460	-2.5280
Dipterocarpus turbinatus	43	0.1300	-5.5300
Dryobalanops lanceolata	43	0.1200	-6.0400
Dryobalanops keithii	50	0.1233	-5.0770
Parashorea malaanonan	50	0.0965	-3.9830

*: Results can be summarised by regression as a straight line if germination percentage is first transformed into probits;

**: LSMC for seeds dried at 10-15% relative humidity and 15-20°C.

The basis of desiccation damage

If the basic causes of desiccation damage could be determined, a way might be found to reduce the effect, thus enabling better survival of the seed. In this connection, Nautiyal and Purohit (1985b, c) assessed various factors for *S. robusta* seed. The quantity of nutrients leaking from the seed increased as moisture content (and germination ability) declined; it was concluded that cellular membranes in the seed had lost their semi-permeability. However, whether the apparent loss of semi-permeability was a primary result of desiccation, or whether it was one aspect of a general loss of metabolic capability could not be distinguished from the data obtained. A small decline in the absolute concentration of nutrients in the seed was observed, but the significance of this decline was not clear. Protein

Table 4. Lowest-safe moisture content values (wet weight basis) for mature seeds*.

Species	Source	LSMC (%)
*Dipterocarpus alatus***	Tompsett (unpub.)	<11***
Dipterocarpus caudatus	Tompsett (unpub.)	<47***
*Dipterocarpus intricatus***	Tompsett (1987)	<12
*Dipterocarpus tuberculatus***	Tompsett (1987)	<12
Dryobalanops aromatica	Tang and Tamari (1973)	37
Hopea hainanensis	Song *et al.* (1984)	c.30
Hopea helferi	Tang and Tamari (1973)	30
Shorea sumatrana	Yap (1986)	>40
Shorea acuminata	Chin *et al.* (1984)	<42
Shorea acuminata	Yap (1986)	>40
Shorea argentifolia	Yap (1986)	35
Shorea gibbosa	Tompsett (unpub.)	>32***
Shorea lepidota	Yap (1986)	27
Shorea pachyphylla	Tompsett (unpub.)	>56***
Shorea selanica	Tompsett (1986)	>25
Shorea siamensis	Tompsett (unpub.)	51***
Shorea singkawang	Yap (1986)	55
Shorea xanthophylla	Tompsett (unpub.)	>41***
Stemonoporus canaliculatus	Tompsett (unpub.)	43***
Vatica umbonata	Mahdi (1987)	74****

*: no slopes and intercepts available for these species;
**: seed is OLDA (orthodox with limited desiccation ability);
***: based on at least 25 seeds per germination;
****: unusually high value.

changes accompanying loss of viability of *S. robusta* have also been reported (Nautiyal *et al.* 1985).

Some authors have confused the effects of desiccation itself with the effects of ageing; in order to determine the effects of ageing, moisture contents should be kept constant. However, in studies by Song *et al.* (1983) on *Hopea hainanensis* it is clear that desiccation effects *per se* were being examined. At 36% moisture content the ultrastructure was intact, but on desiccation to 26% moisture content, which severely reduces germination percentage, various changes were observed. Vesicles appeared in the cytoplasm, vacuolar membranes ruptured and cell contents became less distinct. Cell walls and cytoplasm became separated and nuclear membranes could not be distinguished from the nucleolus. These changes illustrate a general deterioration of cellular structure rather than an effect confined to the cell membrane. In a further study (Song *et al.* 1986), desiccation to 31% was shown to disturb the ribosomes and endoplasmic reticulum, but these changes were reversed on re-hydration.

More recently, Krishan Chaitanya and Naithani (1994) measured changes in superoxide, lipid peroxidation and superoxide dismutase for seeds of *S. robusta* during desiccation. They concluded that the loss of viability observed may be caused by the cumulative effect of peroxidation products of polyunsaturated fatty acids and peroxidation of the membrane lipids.

Storage Physiology

Some aspects of seed storage are considered elsewhere: practical aspects, including the effects of gases, are discussed in Chapter 4; chilling physiology is considered above under germination effects. Topics discussed below include the following: best recorded storage periods; use of viability constants; the significance of oil contents; some aspects of tissue culture; and various associations with storage physiology.

Best storage records

An up-to-date summary of best storage records is given in Table 5. These records should not be confused with practical recommendations; if the recommended storage conditions were employed, longer storage would be expected in many cases. The best record for an OLDA species is 2829 days for *Dipterocarpus alatus* and the

Table 5. Temperatures, moisture contents and germination of mature seeds for the optimum reported storage conditions.

Species	Optimum storage achieved					Source
	Germination (%)	Days	Temp. (°C)	MC (%)	Other conditions	
Anisoptera costata	44	30	18	44	ventilated incubator, 99% rh, rib-channel PB, ventilated weekly	Tompsett (unpub.)*
Anisoptera marginata	45	84	21	48	ventilated incubator, 99% rh, PB, ventilated weekly	Tompsett (unpub.)*
Cotylelobium burckii	52	28	21	29	gas box, over water, ventilated weekly	Tompsett (unpub.)*
Cotylelobium melanoxylon	46	67	21	36	gas box, over water, ventilated weekly	Tompsett (unpub.)*
*Dipterocarpus alatus***	44	2829	-13	11	hermetic, laminated aluminium foil bag	Tompsett (unpub.)*
Dipterocarpus baudii	25	30	14	n/a	n/a	Yap (1981)
Dipterocarpus grandiflorus	87	4	n/a	40	No information.	Tompsett (unpub.)*
Dipterocarpus humeratus	30	28	15	26	PB, sealed, inflated with nitrogen	Maury-Lechon *et al.* (1981)
*Dipterocarpus intricatus***	30	2373	-20	10	hermetic, laminated aluminium foil bag	Tompsett (unpub.)*
Dipterocarpus obtusifolius	20	60	18	59	ventilated incubator 99% rh, rib-channel PB, ventilated weekly	Tompsett (unpub.)*
*Dipterocarpus tuberculatus***	77	1369	-20	12	hermetic, laminated aluminium foil bag	Tompsett (unpub.)*
Dipterocarpus turbinatus	20	177	16	42	closed box, over water, ventilated weekly	Tompsett (unpub.)*
Dipterocarpus zeylanicus	53	100	21	39	ventilated incubator 99% rh, loose	Tompsett (unpub.)*
Dryobalanops aromatica	50	16	14	38-40	n/a	Yap (1981)
Dryobalanops keithii	54	23	16	45	PB tied, sawd. (18% MC), ventilated weekly	Tompsett (unpub.)*
Dryobalanops lanceolata	92	62	21	56	PB sealed and inflated, ventilated weekly	Tompsett (unpub.)*
Hopea ferrea	40	300	16	30-50	PB then perl.	Tompsett (unpub.)*
Hopea foxworthyi	68	365	18	35	ventilated incubator at 99% rh, rib-channel PB, ventilated weekly	Tompsett (unpub.)*
Hopea hainanensis	80	365	18	35-38	n/a	Song *et al.* (1984, 1986)
Hopea helferi	85	40	15	48	n/a	Tang and Tamari (1973)
Hopea mengerawan	40	67	21	44	ventilated incubator at 99% r.h., loose	Tompsett (unpub.)*
Hopea nervosa	19	330	25	n/a	n/a	Sasaki (1980)
Hopea odorata	48	93	16	38	polythene rib-channel bag within polythene box, ventilated weekly	Tompsett (unpub.)*

Table 5. (continued) Temperatures, moisture contents and germination of mature seeds for the optimum reported storage conditions.

Species	Optimum storage achieved					Source
	Germination (%)	Days	Temp. (°C)	MC (%)	Other conditions	
Hopea parviflora	84	104	18	41	PB sealed and inflated, ventilated weekly	Tompsett (unpub.)*
Hopea subalata	40	51	4	32-43	n/a	Sasaki (1980)
Hopea wightiana	5	60	4	n/a	n/a	Sasaki (1980)
Monotes kerstingii	16	90	2	7	PB, ventilated weekly	Tompsett (unpub.)*
Neobalanocarpus heimii	80	50	14	28-47	n/a	Yap (1981)
Parashorea densiflora	90	60	25	54	n/a	Yap (1981)
Parashorea malaanonan	67	141	18	45	rib-channel PB, ventilated weekly	Tompsett (unpub.)*
Parashorea smythiesii	50	317	18	44	ventilated incubator 99% rh, PB, perl. (0% MC), ventilated weekly	Tompsett (unpub.)*
Parashorea tomentella	40	91	16	40	PB, 4% moisture content perl., ventilated weekly	Tompsett (unpub.)*
Shorea acuminata	70	30	21	38-43	n/a	Sasaki (1980)
Shorea affinis	56	253	21	35	ventilated incubator 99% rh, loose	Tompsett (unpub.)*
Shorea almon	18	32	16	45	stored on agar, some seed germinated and are included	Tompsett (1985)
Shorea amplexicaulis	30	168	21	45	PB, sealed, perl. 0-8% MC, ventilated weekly	Tompsett (unpub.)*
Shorea argentifolia	60	45	21	43	No information.	Sasaki (1980)
Shorea assamica	50	98	4	n/a	n/a	Sasaki (1980)
Shorea bracteolata	4	60	4	n/a	n/a	Sasaki (1980)
Shorea congestiflora	52	49	21	39	PB, top folded over, within gas box, ventilated weekly	Tompsett (unpub.)*
Shorea contorta	35	32	21	67	ventilated incubator 98% rh, PB, ventilated weekly	Tompsett (unpub.)*
Shorea curtisii	20	30	25	n/a	n/a	Yap (1981)
Shorea dasyphylla	24	14	21	40-46	n/a	Sasaki (1980)
Shorea fallax	50	50	21	40	PB tied, with sawd., ventilated weekly	Tompsett (unpub.)*
Shorea ferruginea	36	77	21	34	PB, sealed and inflated, ventilated weekly	Tompsett (unpub.)*
Shorea hypochra	10	60	4	n/a	n/a	Sasaki (1980)
Shorea javanica	87	30	20	13-15	moisture low	Umboh (1987)
Shorea leprosula	45	30	21	32	No information.	Sasaki (1980)
Shorea macrophylla	40	22	21	31	PB tied, with sawd., ventilated weekly	Tompsett (unpub.)*
Shorea obtusa	44	11	16	36	PB, sealed and inflated, ventilated weekly	Tompsett (unpub.)*
Shorea ovalis	87	92	21	37	No information.	Sasaki (1980)
Shorea pachyphylla	28	16	18	66	ventilated incubator 99% rh, over water	Tompsett (unpub.)*

Table 5. (continued) Temperatures, moisture contents and germination of mature seeds for the optimum reported storage conditions.

Species	Optimum storage achieved					Source
	Germination (%)	Days	Temp. (°C)	MC (%)	Other conditions	
Shorea parvifolia	40	57	18	35	ventilated incubator 99% rh, PB, with perl., ventilated weekly	Tompsett (unpub.)*
Shorea pauciflora	67	45	25	38-51	n/a	Sasaki (1980)
Shorea pinanga	50	112	21	46	ventilated incubator 99% rh, loose	Tompsett (unpub.)*
Shorea platyclados	80	58	25	n/a	n/a	Yap (1981)
Shorea robusta	54	49	15	0	partial vacuum, MC unknown	Khare *et al.* (1987)
Shorea roxburghii	52	307	16	36	PB, tied and inflated, ventilated weekly	Tompsett (1985)
Shorea siamensis	83	56	15	40-48	No information.	Panochit *et al.* (1984)
Shorea smithiana	28	46	26	44	PB sealed and inflated, ventilated weekly	Tompsett (unpub.)*
Shorea sumatrana	60	15	25	n/a	n/a	Yap (1986)
Shorea trapezifolia	100	63	21	n/a	ventilated incubator 97% rh, PB, ventilated weekly, seed was pre-germinated.	Tompsett (unpub.)*
Stemonoporus canaliculatus	20	77	18-21	47	ventilated incubator 99% rh, loose	Tompsett (unpub.)*
Vatica mangachapoi	24	85	21	40-45	PB, perl. 0% MC, ventilated weekly	Tompsett (unpub.)*
Vatica odorata ssp. odorata	48	148	18	40	ventilated incubator 99% rh, loose	Tompsett (unpub.)*
Vatica umbonata	10-50	60	10-15	n/a	n/a	Mori (1979)

*: data based on at least 25 seeds per germination;
**: seed has OLDA storage physiology (orthodox with limited desiccation ability);
MC: moisture content based on wet weight;
perl.: stored in perlite;
sawd.: stored in sawdust;
PB: stored in ventilated polythene bag.
Note: not all reports specified the seed maturity.

corresponding value for a recalcitrant species is 365 days for *Hopea hainanensis.* Five recalcitrant species were stored for over 300 days and a further eight were stored for over 100 days (Table 5). The three OLDA species all stored for over 1300 days.

Viability constants

A brief background to viability constants (meaning and derivation) is given.

The rate at which orthodox and OLDA seeds age in storage increases with temperature and with moisture contents between certain limits. Successive samples from a seedlot of high initial viability in storage will show progressively lower germination percentages, producing a curve of germination against time which is sigmoid in shape. This curve can be transformed by probit analysis to produce a straight line relationship. Results from many storage treatments (various moisture content and temperature combinations) can be analysed to give constants in a predictive equation. The equation was developed by Ellis and Roberts (1980a, b) for herbaceous species and is:

$$\mathbf{V} = K_i - P/10^{K_E - C_W \log_{10} m - C_H t - C_Q t^2} \text{ .... (Eqn 1).}$$

In this equation, V is the predicted viability, K_i is the initial viability, P is the number of days in storage, m is the moisture content (percentage fresh weight basis) and t is the temperature (°C). Viability is expressed as probit germination. The constants K_E, C_W, C_H and C_Q are

Table 6. Viability constants and standard errors for two OLDA species of dipterocarps (Tompsett and Kemp 1996a, b).

Species	K_E (se)	C_W (se)	C_H (se)	C_Q (se)
Dipterocarpus alatus	6.44 (0.72)	3.09 (0.61)	0.0329 (0.0017)	0.000478 (0.000000)
Dipterocarpus intricatus	6.34 (0.81)	2.70 (0.68)	0.0329 (0.0017)	0.000478 (0.000000)

common to all seedlots of a species. The equation has been shown to apply to tropical and temperate tree species (Tompsett 1986).

Equation 1 was derived using the following equation:

$$\log_{10} \sigma = K_E - C_W \log_{10} m - C_H t - C_Q t^2 \text{............ (Eqn 2).}$$

In this equation, σ represents the rate of loss of viability in days per probit.

The viability constants K_E, C_W, C_H and C_Q of Eqn 2 are reported for two dipterocarp species in Table 6. Ageing was observed under at least 4 temperature conditions and with several moisture content treatments at each temperature in order to obtain the parameters presented for these species. Further details of method are in Tompsett and Kemp (1996a, b).

The constants for the two *Dipterocarpus* species were similar and can be used to predict viability at the end of any storage period when moisture content and temperature are known. Thus, for *D. alatus,* a 64-year period is predicted before seed ages to 85% germination, provided the initial viability of the seed is 99.4% and storage is at -13°C with 7% moisture content. Calculations should be based on sound seed only. This approach enables decisions to be made about the cheapest conditions commensurate with attaining the objectives of storage for different purposes. The 7% moisture content value for *D. alatus* was chosen, in part, because it has proved difficult to dry the seed further.

Oil content of the seed

Details of embryo oil contents for dipterocarps are given in Table 2 and show much lower values for *Hopea* and *Dipterocarpus* than for *Shorea*.

In the predictive viability equation given above, the water status of seed was assessed using moisture content. However, a more accurate measure of seed water status in relation to physiological activity is seed water potential. Water potential is in turn related to the relative humidity which produces, at equilibrium, the moisture content under consideration. These relationships have been considered in connection with storage life by Roberts and Ellis (1989). The reason why relative humidity is of importance may be illustrated by considering the influence on longevity of the reserves in an oily seed. For a species with an oil content of 50%, ageing-associated physiological responses would be predicted at a moisture content which is about half the moisture content for the same responses in a non-oily seed, provided all other factors are identical. This is because of the hydrophobic nature of the oily reserve. The relative humidity value at equilibrium for the same physiological responses, however, would be expected to be similar for both species. Since seeds of *Dipterocarpus alatus* are not oily, it is not surprising that optimum longevity is at a relatively high moisture content near 7%. By contrast, the oily seed of *Swietenia humilis* (Meliaceae) is best stored at near 3% moisture content.

Tissue Culture

Tissue culture has been suggested as a means of storage of gene resources under slow growth conditions. Additionally, this technique can be employed for micropropagation. It is also likely that tissue culture would be needed to grow the resulting tissue after cryopreservation if the latter method proves practical. However, tissue culture of dipterocarps is not easy, high rates of cell necrosis having been observed for some species. High resin content within the tissues may be at least partly responsible for this effect for some species. However, some success has been achieved by Smits and Struycken (1983), Scott *et al.* (1988) and Linington (1991) in culturing the tissues of some *Shorea* and *Dipterocarpus* species.

Association of storage physiology with seed characters and tree habitat

Various associations have been noted for dipterocarp seeds. The LSMC, defined as the moisture content below which some germination loss occurs on desiccation, is associated with various properties of the seed and its parent tree. Seed size, seed desiccation rate, seed longevity and the habitat of the parent species have all been found to be related to storage physiology.

Storage physiology and seed size

For three *Shorea* species a relationship has been noted between seed size and desiccation tolerance; lowest-safe moisture content values increase as size increases from the small, desiccation-tolerant seed of *S. roxburghii* to the larger, desiccation-intolerant seed of *S. almon* (Tompsett 1985). A similar relationship was found in the *Dipterocarpus* genus (Tompsett 1987), but in this case it is the size of the embryo that appears more important. Thus, two relatively small-embryoed species (*D. intricatus* and *D. tuberculatus)* were shown to be OLDA in their storage physiology (and can therefore be dried with relatively little damage); on the other hand, two species with large embryos *(D. obtusifolius* and *D. turbinatus)* were shown to have high LSMC values and recalcitrant physiology. There are other species that fit this pattern (Tompsett 1986).

A further association which has been observed is that recalcitrant seeds tend to be smooth surfaced (globular), whilst OLDA seeds have tubercles or other projections from the calyx. These projections may enhance desiccation rate, leading to better storage on the forest floor (Tompsett 1987), as explained below.

Storage physiology in relation to habitat and longevity

Seeds of three recalcitrant *Shorea* species from different habitats have been found to have different desiccation tolerances. The low-rainfall area species *S. roxburghii* has seed which can be dried safely down to 35%, whereas the two monsoon or rain forest species *S. almon* and *S. robusta* cannot be safely dried below 40% moisture content (Tompsett 1985). Interestingly, the seed with the greatest desiccation tolerance (*S. roxburghii*) is also the seed with the greatest longevity.

A more extreme example is found in the genus *Dipterocarpus*. Two dry-zone, deciduous species (*D. intricatus* and *D. tuberculatus*) have OLDA-physiology seeds, whilst two other species with distributions extending into the relatively wet, evergreen areas (*D. turbinatus* and *D. obtusifolius*) have recalcitrant seeds (Tompsett 1987). The longevity of dry OLDA seeds is relatively great (Table 5), whilst recalcitrant seeds cannot be stored in the long term at present. As with other factors, these patterns have been found to extend to seeds of other species; trees from low-rainfall and sandy-soiled areas tend to have greater longevity and lower LSMC values (Tompsett 1986).

Storage physiology in relation to seed desiccation rate

The OLDA seeds of *Dipterocarpus intricatus* and *D. tuberculatus* can dry to below 10% in 2 weeks, whereas the recalcitrant seed of *D. obtusifolius* remains above 28% moisture content even after 5 weeks in the same drying conditions (Tompsett 1987). This situation may have evolved because OLDA species benefit from desiccation in terms of enhanced storage life as follows. If the wet season arrives late, so that the seeds lie on the ground for several weeks, viability is nonetheless preserved by their low moisture content under natural conditions. Conversely, the slow desiccation rate characteristic of recalcitrant seeds is protective against desiccation damage. The differences in desiccation rates observed are generally associated with seed size (small seeds dry faster) and probably also to seed anatomy.

Induction of Flowering and Seeding

Little work has been done on the artificial induction of flowering and seeding. However, Tompsett, Tangmitcharoen, Ngamkhajornwiwat and Sornsathapornkul (unpublished) have found a positive effect of the growth inhibitor paclobutrazol in promoting the flowering of *Dipterocarpus intricatus* in north-east Thailand. The best effect was found by applying the substance at 20 g/l to buds between late September and early November. The ability to control flowering would aid breeding programmes and may enhance seed production in years when it is otherwise poor.

Future Research

More work is needed to assess the seed storage physiology categories of dipterocarp species, exploring desiccation tolerance to assess whether the currently known species with OLDA seed are the only ones in existence. There are currently three such species known. A broad range of species should be included to enable a steady flow of material, despite the infrequent fruiting and the logistical problems of locating, collecting and transporting materials.

Dipterocarp seed of the OLDA type has a shorter storage life than seed of crop species if compared at the same moisture content. Thus, it has been estimated that the relevant K_E and, C_W viability constants (which indicate seed longevity) are, respectively, only 6.4 and 2.9 on the average for dipterocarp seed (Table 6), compared with 8.4 and 4.7 (Tompsett 1994) for herbaceous crops. Further research is needed to extend these findings to other OLDA dipterocarp species.

The stage of fruit development at harvest is important to ensure optimum desiccation tolerance, and consequently to ensure maximum storage potential. Further research is needed for dipterocarps in order to closely assess the relationship between harvest condition, postharvest handling, and desiccation tolerance.

Studies are needed to increase knowledge of the optimum moisture and temperature conditions for storage of recalcitrant seeds, employing controlled conditions. Especially, research is needed in relation to the chilling injury. Studies to quantify chilling damage in relation to moisture content are needed. Also, research is required to determine its relationship to underlying biochemical processes.

Although the database DABATTS (Tompsett and Kemp 1996a, b) includes a large amount of previously unpublished information on dipterocarp seed, a high proportion of its contents are the results produced by the authors. Unpublished information from other sources needs to be databased, building on DABATTS and increasing the total sum of research results readily available.

Research on the induction of flowering is necessary to improve knowledge of the causes underlying the irregular flowering of dipterocarps. Such research may provide artificial means for the induction of flowering in relation to breeding and to seed production in non-mast years.

These approaches might with benefit be extended to other tropical tree families such as the Palmae and Sapotaceae.

Relevant Institutions

As described in Chapter 4 and above (in the work of Sasaki, Mori, Tang, Tamari and Yap), Forest Research Institute Malaysia (FRIM) has played a leading role in early dipterocarp seed research, particularly in the areas of germination ecology and storage research. Current work at FRIM on cryopreservation and seedling storage is referred to elsewhere. Over the last decade, the seed physiological studies at the Royal Botanic Gardens Kew have contributed basic knowledge, creating a firm foundation for practical recommendations. The Forest Research Centre, Sandakan, Malaysia, has a seed research laboratory constructed under an FAO aid programme and has undertaken significant dipterocarp research.

In Thailand the Royal Forest Department's ASEAN Tree Seed Centre, Muak Lek, has been involved in dipterocarp studies for a number of years and has good facilities; additionally, the central laboratory in Bangkok has an active research team on the topic.

The Ecosystems Research and Development Bureau, Republic of the Philippines, is engaged in dipterocarp seed research, as are the Forest Research and Development Centre, the Biotechnology Centre and BIOTROP in Bogor, Indonesia. In India, research on biochemical aspects has been recently conducted at the High Altitude Plant Physiology Research Centre of Garhwal University, Srinagar and the Forest Research Institute, Dehra Dun has been involved in dipterocarp research in the recent past.

In China, biochemical, ultrastuctural and physiological research on dipterocarp species has been performed by staff of the Tropical Forest Research Institute, Chinese Academy of Forestry, Guangdong.

Although not involved in dipterocarp research, the Agriculture and Horticulture Department at Reading University, UK, is developing experience in the area of tropical tree seed physiology. Other institutes have contributed information in this field, but space available limits the numbers that can be included.

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Chapter 4

Seed Handling

B. Krishnapillay and P.B. Tompsett

In considering seed handling, it is important to be aware of the sources of seed quality. Many benefits flow from the use of better quality seeds, selected and handled optimally; advantages include the improved survival of seedlings and greater overall commercial returns.

However, methods to ensure high quality of seed supply are not as advanced for dipterocarps as for other forest species such as pines and eucalypts. The primary problem is seed supply and this factor is a major constraint in dipterocarp forest management. Thus, the lack of seeds in sufficient quantity and quality has discouraged the raising of seedlings in the nursery and direct sowing of seeds in the field.

The majority of dipterocarps do not flower regularly. In the aseasonal zones flowering occurs at intervals of two to five years and its accurate prediction is impossible. Consequently, it is difficult to plan major planting activities. Even in flowering years, interference by drought can cause premature fruit drop. On the other hand, flowering is generally on an annual basis in the seasonal climatic zones so that planning seed collection in these areas is easier. Although seed production can vary between years in any particular place, foresters can make more secure plans by widening the area monitored for seed supply.

A second problem in practice is the life span of dipterocarp fruits; most species have short-lived ‘recalcitrant’ seed. If seed collectors do not harvest mature seed and sow it immediately, a proportion will soon become inviable. A few species, however, have long-lived seed. Early descriptions of the short-lived nature of dipterocarp seeds include those of Troup (1921), Sen Gupta (1939) and Dent (1948). The period between collection and sowing should thus generally be as short as possible. In practice, reports of fruiting are often received at short notice; thus, in order to produce dipterocarp seedlings, a collection team has to be hastily prepared for collection, transport and sowing in the nursery. Few agencies can liaise these activities efficiently. Schaffalitzky de Muckadell and Malim (1983) considered some relevant factors.

In seasonal forests, on the other hand, the scope for forestry operations with dipterocarp species is wider, flowering being more regular and seed being longer-lived. Even in this climatic zone, however, most species are recalcitrant. Much work has been carried out on the factors controlling the longevity of dipterocarp seeds (see Chapter 3). Researchers have achieved success for species from both seasonal and aseasonal zones but have made relatively more progress with species that do not possess recalcitrant seed. Alternative means of raising planting material have been investigated as a complementary approach.

Several handbooks have been produced on the handling of tropical tree seed, a notable example being that of Willan (1985). In this chapter, wider aspects of seed handling, including biology and ontogeny, are described. In addition, seed collection, seed storage, seedling storage and cryopreservation are covered and future research priorities and prospects for successful forest seed programmes are considered.

Factors Affecting Seed Viability

When seeds (more correctly fruits) reach maturity on the mother plant, they begin to deteriorate; the rate of deterioration depends on the environmental conditions they experience. Progressively, germination rate is reduced, the number of abnormal seedlings is increased and field emergence is lowered. Cumulative damage occurs until the seed is incapable of germinating. Preferably, foresters should use seed before its viability has dropped significantly. Various factors operating before seeds arrive at the seed centre can influence initial germination percentage. These factors in relation to seed handling considerations are summarised below and more detail is given in Chapter 3.

The effect of climate and pest infestation

Climatic conditions prior to seed harvest and the physiological state of the mother tree may influence viability of the seed but experimental proof is lacking. In some years there are heavy infestations of the developing seed by pests and insects. It is possible that heavy infestations occur relatively more frequently in years when there are light crops on the tree but confirmation of this relationship is needed.

Maturity

Seed germination continues to improve up to near the time of peak maturity, emphasising the need for optimal harvest timing.

Physiological and other associated damage

During the period between collection and arrival at the seed centre, material is at risk. This applies particularly if seed is held under conditions that are either too humid or too dry, and if temperatures are too high or too low. Necrosis is liable to occur under such conditions, associated with fungal growth and viability loss.

Seed Storage Categories

Researchers have divided seeds broadly into 3 major groups on the basis of their storage behaviour. The following descriptions give the general basis for each type; more accurate definitions are presented in Chapter 3 (pages 60-61).

Orthodox seeds

This category includes seeds that can be dried to low moisture contents (about 5%) without serious deleterious effects. Under optimal conditions, the life span of this group of seeds can be extended for decades or longer.

Recalcitrant seeds

This group of seeds differs from orthodox seeds in two ways; their seeds die if they are dried below relatively high moisture contents (values are given for lowest-safe moisture contents in Chapter 3, page 62) and if they are subject to damage at low temperatures (< 16^{o} C). Even under optimal conditions survival of seeds in this group is limited. The difficulties in storing the seed led to their being described as 'recalcitrant'.

Intermediate (OLDA) seeds

A third category of seed storage physiology has been recently defined. In practice, the seeds in this group have desiccation characteristics that are intermediate between those of the orthodox and recalcitrant seeds and they have thus been termed 'intermediate'. When harvested in the usual way, seeds of this type can be dried to moisture levels of about 8-12% whilst retaining a substantial amount of (but not all) their original viability. There is also a greater susceptibility to chilling and freezing damage than is the case with orthodox seed, even when the seeds are relatively dry.

When this type of seed was first studied in detail, its physiological similarity to orthodox seeds led to the description 'orthodox with limited desiccation ability' (OLDA). However, employing the term 'intermediate' to indicate a *practical* difference from orthodox seeds is useful. This matter is further discussed in the Seed Physiology chapter.

Tropical Forest Tree Seeds

Tompsett (1994) has estimated that 72% of tree species found in the tropics may bear 'recalcitrant' seeds. Recalcitrant seeds are shed from the mother plant with very high moisture contents (about 40-60% on a wet weight basis) and germinate soon after shedding. Whilst recalcitrant dipterocarp species provide real problems, those of the OLDA type are more amenable, as described above. Tompsett (1994) found that, in the case of dipterocarp species, 94% of those examined possessed recalcitrant seed.

Seed Ontogeny

Ontogeny covers development from floral initiation through growth and differentiation to maturity of the seed. To date, very little work has been published on the ontogeny of dipterocarp species; Owens *et al.* (1991) presented a generalised, basic development diagram which may relate to certain species of the dry forest in Thailand.

Phenology

Phenology, in a broad sense, refers to the relationship between changes in seasons and climate and to the phenomena of leaf and bud formation, leaf fall, floral anthesis, fruit set and ripening. In the aseasonal dipterocarp forests from south Asia to Malesia phenological observations are an essential part of the strategy for seed procurement of dipterocarps, owing to the irregularity of their flowering and fruiting patterns.

Table 1. Likely periods for flowering and seed production of important *Dryobalanops, Dipterocarpus, Shorea,* and *Anisoptera* species (Krishnapillay, unpublished).

Species	Months												Frequency
	J	F	M	A	M	J	J	A	S	O	N	D	
Dryobalanops aromatica		x x x x					x x x x x x x						biennial
Dryobalanops oblongifolia		x x x x					x x x x x x						biennial
Shorea leprosula			x x x x x x x										3-4 years
Shorea parvifolia			x x x x x x x										3-4 years
Dipterocarpus baudii			x x x x x x x										annual
Dipterocarpus costulatus						x x x x			x x x				4-5 years
Anisoptera scaphula			x x x x										4-5 years
Anisoptera laevis						x x x x							4-5 years
Dipterocarpus kerrii			x x x x										4-5 years
Shorea macrophylla					x x x x x x			x x x x x x					annual
Shorea macroptera	x x x									x x			3-4 years
Shorea ovalis			x x x x x x x										3-4 years
Shorea platyclados					x x x x x								3-4 years
Shorea acuminata				x x x x x x x									2-3 years
Shorea bracteolata				x x x x x x x									2-3 years
Shorea curtisii		x x x x x											3-4 years

Over the last 25 years various authors have reported detailed phenological records. Studies include those of Burgess (1972), Cockburn (1975) and Ng (1981, 1984) for the Malaysian aseasonal forest, and Sukwong *et al.* (1975) for the dry forest of Thailand. In Table 1, there is a general summary for the important timber species of Peninsular Malaysia.

The infrequency and irregularity of dipterocarp flowering and fruiting in the aseasonal areas have already been referred to above. A further feature is that flowering tends to be gregarious and may be limited or may extend throughout an entire region.

Flower and seed surveys indicate:

1. whether flowering is scattered and confined to particular species or whether it is a mast flowering;
2. whether the amount of seeds available is sufficient to meet seed collection requirements;
3. whether the crop is sound or has been attacked by pests or insects; and
4. the time when the seeds will mature.

The natural trigger for mast flowering and fruiting among dipterocarps has been sought by looking for associations with several factors. Foxworthy (1932) and many others suggested an association between flowering and strong droughts but Wood (1956) disputed the conclusion. Ng (1981) suggested that a dry spell preceding leaf flush accompanied by a rising gradient of daily sunshine induces flowering. Again, Ashton *et al.* (1988) proposed that the environmental trigger is a protracted low night temperature over a period of about 3-4 days. However, experimental evidence is required to establish cause and effect. The matter is further discussed in the Seed Physiology chapter.

Seed Procurement

Current research on artificial regeneration has been reviewed by Mok (1994), whilst Barnard (1950) and Appanah and Weinland (1993) outline some procedures that have been used to procure dipterocarp seeds for planting programmes. A more detailed procurement procedure is needed. At present, most methods involve collection of seeds on an *ad hoc* basis or the collection of wildings. Seed procurement should involve planning, collection, transporting, processing, testing, temporary storage and nursery facilities. A general description of the basic activities involved in seed procurement is given below. If a large collection region is monitored, some seeding may be found every year; in practice, however, logistical and other problems make annual collection from aseasonal regions difficult.

Planning

When trees start fruiting, procurement planning has to be initiated immediately so that good-quality planting material can be obtained. The period between collection and storage or sowing should be as short as possible to reduce the chance of seed deterioration. Transport and processing should be carefully planned and, when necessary, the nursery advised so that germination space is available.

Collection

The choice of collection technique for forest tree seed is dependent on many factors, including the way the tree disperses its seeds or fruits. For recalcitrant-seeded dipterocarp species collecting seeds directly from the tree crown by climbing has several advantages. These are:

a) mature seeds can be selectively collected;
b) seed from each mother tree can be kept separate when the need arises;
c) potential losses to insect and animal interference can be minimised; and
d) damage incurred after falling onto the ground, such as that resulting from desiccation and ageing, can be limited.

Generally, collections of seeds should be made from healthy trees that have good shape and form, avoiding trees that are obviously diseased. Inclusion of immature seeds and seeds that have been lying on the ground for some time should be minimised. Various methods of collection used by the seed collection team at the Forest Research Institute Malaysia (FRIM) are described below along with their advantages and limitations. The methods can be divided into two main types. Firstly, those that do not involve climbing, the overall operation being confined to the ground (Methods 1-3). Secondly, those involving an element of tree climbing (Methods 4-5).

Factors to be considered for harvesting in the aseasonal zones are given in the summary at the end of the chapter.

1. Ground collection

Ground collection does not require employment of staff possessing both tree climbing skills and the ability to collect seed efficiently; the cost is thus reduced. Nevertheless, this method necessitates good preparation: trees must be selected and marked; and all vegetation, debris and old or premature seeds below the trees must be cleared. Proper supervision of collection is also necessary. The limitations of this method are:

a) seed collection is protracted;
b) collections have to be made daily until most of the seeds have fallen;
c) there is competition with mammals, birds and insects;
d) fungal problems, seed deterioration and premature germination are encountered; and
e) ground cover surrounding the tree is destroyed.

2. Collection using nets or canvas

With this method, nets or canvas are laid under the tree. This procedure is desirable in that undergrowth is not destroyed. The limitations of this method are:

a) it is not suitable under dense undergrowth; and
b) daily collections of fallen seeds need to be made.

3. Shaking of seed-bearing branches

This method is referred to as the ‘fishing line’ method. A local home-made catapult is used to shoot a single-filament fishing line, attached to a lead weight, over smaller branches of the tree from which seed is to be collected. A polythene rope is then pulled over the branch and back down to the ground using the fishing line; the rope is then pulled vigorously to shake down the seeds. The method is suitable for small trees and for those standing in the open. The limitations of this method are:

a) it cannot be used with very tall trees, which may be the ones possessing the best genotypes;
b) a clear view of the terminal branches is required for the lead weight to be aimed accurately;
c) it usually requires several attempts before the line is satisfactorily positioned on the right branch; and
d) the lead weight and line are not fully controllable and minor injuries may sometimes be experienced by the operator.

4. Free climbing

This method is employed by professional tree climbers. It involves the use of a neighbouring smaller tree for the initial ascent, after which the climber crosses to the main seed tree at a height where the bole is small enough to hold safely and ascend the tree. The climber cuts off and drops down small branches bearing the seeds. The limitations of this method are:

a) a suitable smaller proximal tree (or group of trees) is required;
b) it is very strenuous and time consuming which limits the number of trees that can be worked on per day; and
c) it is dangerous.

5. Methods of climbing using equipment

With the following three methods climbing gear is used to gain access to the canopy making the overall procedures much safer.

a) Tree bicycle

Trees can be climbed without causing serious damage to the tree trunk. The equipment consists of two unequally long bearing pieces with rests for the feet. Flexible steel bands are positioned around the tree trunk at the far end of the bearing pieces,. By a bicycling motion the tree climber ascends the tree moving the steel bands upwards parallel to the tree axis. During this procedure the climber wears a security belt with ropes fastened around the tree. The equipment offers a comfortable and safe basis for standing during working in the crown. This method is not suitable, however, for trees that have branches on the bole. Also, use is limited to those trees having a girth that can be easily encircled by the fastening ropes.

b) Climbing using spurs

With this method the climber uses a pair of spurs fastened under his shoes in addition to the security belt and fastening ropes which were mentioned above for the bicycle method. The climber uses the spurs by pricking its spikes into the tree bark to secure a foothold for every upward movement. The holes made by the climbing spurs are vulnerable to fungal, viral and bacterial attack, a problem which is aggravated if trees are often climbed in this way. It is thus advisable that, if this method is employed, an interval of at least a year should be allowed before a further collection is made; healing of the damaged parts on the trunk can then occur. As is the case for the tree bicycle method, the circumference must not be too large.

c) 'Roping up' method

In this method a line is shot up into the crown over two or more strong branches. The climbing rope is then drawn up over the branches and, on return to ground level, the free end is fastened at the base of the trunk. The climber then uses the rope to pull himself up using a shoemore. This method can be used whatever the girth of the trunk and does not damage the tree.

A combination of elements from different methods may be necessary; for example, it may be desirable to combine the laying-nets as in Method 2 with the shaking element of Method 3.

Seed Transportation

The length of time between collection of moist dipterocarp seed and its arrival at the seed centre is crucial in determining viability. Transport should be carefully planned to minimise delay; staff in the nursery or seed store should be advised of the schedule so that seed can be handled immediately on receipt.

Methods for transport of OLDA seeds collected in the dry condition are given in the summary at the end of the chapter. The following points are relevant in relation to the transport of moist dipterocarp seeds.

Ventilation and Moisture Content

Moist dipterocarp seeds respire intensively and so require good ventilation. If large quantities are closely packed, the seeds become anaerobic, physiological breakdown takes place, fungal growth takes hold and overheating occurs; these changes accelerate deterioration of the seed. Recalcitrant-seeded species will deteriorate rapidly if their moisture content is reduced significantly; ventilation must be provided, but without drying the seed.

If plastic bags are used to contain the seeds, their tops should either be left open and folded over or they should be tied and small holes made in their sides. Hessian or jute bags with a loose weave are also suitable for transport. Desiccation is more likely to occur if transport is in open vehicles; air movement may accelerate the process.

Temperature

Temperatures below 16^{O}C or above 32^{O}C should be strictly avoided for moist, recalcitrant seeds. Good ventilation reduces heat build-up from respiration. Seeds should be shaded from direct sunlight at all times during transport.

Long Journeys

Efforts must be made to dispatch the seeds to their destination within two days of collection. If seeds begin

Table 2. Seed (fruit) weight and size indicators at harvest (Tompsett and Kemp 1996a, b).

Species	Mean seeds per kilo	Mean length (mm)	Mean width (mm)
Shorea pinanga	30	59	32
Shorea macrophylla	33	n/a	n/a
Dipterocarpus grandiflorus	50	58	38
Shorea amplexicaulis	64	46	26
Dipterocarpus kunstleri	80	55	43
Dipterocarpus humeratus	90	35	29
Dipterocarpus obtusifolius	90	20	19
Dryobalanops keithii	100	n/a	n/a
Dipterocarpus cornutus	110	29	28
Dipterocarpus caudatus ssp. *penangianus*	120	26	23
Dipterocarpus zeylanicus	120	36	23
Dryobalanops lanceolata	120	26	23
Shorea palembanica	140	n/a	n/a
Shorea beccariana	160	36	24
Shorea fallax	160	n/a	n/a
Stemonoporus canaliculatus	160	n/a	n/a
Dipterocarpus turbinatus	170	30	20
Parashorea tomentella	180	30	20
Dipterocarpus chartaceus	200	28	22
Shorea smithiana	200	29	17
Anisoptera megistocarpa	*220*	*27*	*20*
Dipterocarpus tuberculatus	230	27	23
Shorea almon	270	n/a	n/a
Dipterocarpus alatus	360	38	30
Shorea ferruginea	440	26	13
Parashorea malaanonan	540	15	14
Shorea robusta	588	n/a	n/a
Shorea trapezifolia	670	16	9
Shorea siamensis	680	26	16
Dipterocarpus tuberculatus var. *grandifolius*	690	n/a	n/a
Dipterocarpus costatus	760	n/a	n/a
Dipterocarpus gracilis	790	15	13
Shorea ovalis	790	17	11
Shorea gibbosa	930	n/a	n/a
Parashorea smythiesii	940	17	11
Shorea argentifolia	1100	n/a	n/a
Shorea macroptera	1100	19	10
Shorea roxburghii	1195	16	8
Anisoptera costata	1200	11	11
Dipterocarpus intricatus x tuberculatus	1200	24	17
Shorea congestiflora	1300	19	8
Shorea parvifolia	1300	17	10
Shorea selanica	1300	n/a	n/a

Table 2. (continued) Seed (fruit) weight and size indicators at harvest.

Species	Mean seeds per kilo	Mean length (mm)	Mean width (mm)
Dryobalanops rappa	1400	17	9
Shorea faguetiana	1400	n/a	n/a
Shorea laevis	1600	14	9
Anisoptera marginata	1800	10	10
Shorea leprosula	1800	16	10
Shorea affinis	1900	n/a	n/a
Shorea leptoderma	1900	n/a	n/a
Shorea ovata	1900	n/a	n/a
Dipterocarpus intricatus	2800	20	17
Cotylelobium burckii	2900	10	10
Cotylelobium melanoxylon	2900	9	8
Shorea obtusa	2900	n/a	n/a
Hopea dryobalanoides	4000	10	7
Vatica odorata ssp. odorata	4000	8	7
Hopea parviflora	4100	7	6
Shorea guiso	4200	11	6
Hopea odorata	5300	8	6
Hopea foxworthyi	5500	8	5
Hopea ferrea	5800	n/a	n/a
Hopea mengerawan	6300	10	4
Hopea nigra	9000	8	5
Vatica mangachapoi	17000	5	5
*Monotes kerstingii**	45000	n/a	n/a

*: Assessment refers to seeds inside the fruit.

to germinate they can be saved by storing in rigid containers lined with moist newspaper or other absorbent materials to keep them moist during transit.

Size Considerations

There is a large range in sizes of dipterocarp seeds (Table 2) which implies that different handling procedures may be needed for moist seed of particular size ranges. For example, smaller seeds (< 2 g) would benefit from the inclusion of packing material to increase the size of air spaces between the seeds. Crumpled newspapers and polystyrene chips have been used for this purpose.

Seed Processing

The fruit of dipterocarp species, which is the unit employed for handling, is generally referred to as the 'seed'. Removal of calyx lobes ('wings') by manual abscission is carried out for all physiology types. This enables easier sowing and better contact of the seeds with the soil.

Factors which should be considered in the drying of OLDA seeds for storage are described in the summary at the end of the chapter.

Insect infestation can be a major problem in the handling of seed, especially in the genus *Dipterocarpus* (Table 3, Prasad and Jalil 1987, Eungwijarnpanya and Hedlin 1984); sometimes 100% of individual seedlots are rendered useless. Methods to reduce this problem are required and would be best supported by studies on insect behaviour. Some studies have already been carried out on recalcitrant material of the rain forest (Toy *et al.* 1992, Toy and Toy 1992); extension of such studies to include seasonal-climate species would be advantageous. Further discussion of infestation problems can be found in Chapter 7.

Methods for Storage of Dipterocarp Seeds

In the past half century, various methods of storage have been proposed for recalcitrant dipterocarp seeds and,

Table 3. Mean insect infestation statistics for species received at Kew (Tompsett and Kemp 1996a, b).

Genus	Mean percent infestation	Number of species examined	Number of species infested
Dipterocarpus	35	10	10
Shorea	16	18	12
Hopea	8	5	4
Parashorea	4	2	2
Dryobalanops	1	3	1

more recently, species with OLDA seeds have been considered. Successful long-term storage has been achieved in the case of some OLDA species.

In the case of recalcitrant seeds, some methods currently available are useful to ensure the survival of seed material during extended field collection trips, for planting and for storage in the short to medium term. However, the methods cannot ensure a continuous supply of planting materials throughout the long periods when mother trees are not fruiting.

Work on dipterocarp seed storage is reviewed in the Seed Physiology chapter but some practical storage methods are briefly discussed.

Imbibed Storage in Media such as Sawdust, Perlite and Vermiculite

Storage of recalcitrant dipterocarp seeds in sawdust, ground charcoal, perlite and vermiculite has been employed to maintain high moisture content. This is the most commonly used method for prolonging recalcitrant-seed viability. With care, seeds can be kept viable in this way for several months. Table 4 shows some of the work carried out on imbibed storage but the limitations of the method are:

a) a proportion of the seeds may germinate due to the high moisture content under these conditions; and
b) in many cases, because of the difficulties in controlling aeration and moisture content, necrosis may occur and microbial infection may set in; seed viability is then severely affected.

Storage in Airtight Containers

Dry seeds of the OLDA type have been successfully stored in airtight containers. For example, *Dipterocarpus intricatus* has been retained for 2829 days with no loss of viability observed (Tompsett and Kemp 1996a, b).

Storage under a partial vacuum has been attempted for seeds of the recalcitrant species *Shorea robusta* at 15°C (Khare *et al.* 1987); 54% viability after a period of 49 days in storage was reported, beyond which further storage resulted in the death of most of the seeds. Unfortunately, moisture content was not measured during storage so the extent to which this factor contributed to viability loss is unknown. Seed storage in airtight containers is not appropriate for recalcitrant-seeded species as it leads to an increasing depletion of oxygen in the containers, associated with progressive loss of viability.

Storage in Inflated Bags with Different Gaseous Environments

Sasaki (1980), working on recalcitrant-seeded dipterocarps of Malaysia, reported that ventilation with ambient air was essential for dipterocarp seeds to preserve viability. For example, he found that the viability of *S. roxburghii* (syn. *S. talura*) seed could be prolonged to seven months with adequate ventilation.

Table 4. Examples of optimum recorded storage in various media for imbibed seed of recalcitrant-seeded *Shorea*, *Hopea* and *Parashorea* species.

Species	Source	Optimum storage recorded				Medium
		Days	Temp. (^oC)	Germination (%)	MC (%)	
Shorea platyclados	Tang (1971)	20	16	64	27	Vermiculite
Hopea ferrea	Tompsett (1992)	300	16	40	30-50	Mainly perlite
Parashorea smythiesii	Tompsett (1992)	317	18	46	45	Perlite
Shorea fallax	Tompsett (1992)	50	21	50	40	Sawdust

MC: moisture content.

Most, but not all, studies concerning the effects on viability of gases other than ambient air have been carried out under poorly controlled conditions. In most cases inflated polythene bags were used so that the gas under test was liable to mixing over time with ambient air and, in addition, respiration of seeds inside the bag altered the gas environment.

Various gaseous environments have been assessed. Song *et al.* (1984) was able to maintain 80% viability of *Hopea hainanensis* seeds for up to 365 days by maintaining oxygen levels above 10%. On the other hand, Yap (1981) was able to store seeds of *D. oblongifolius* in bags filled with nitrogen and reported a 60% germination after a period of 60 days. However, Tompsett (1983) reported a stepwise decrease in longevity of the seed as oxygen was lowered progressively from 10% to zero per cent for the recalcitrant seed of the tropical tree species *Araucaria hunsteinii* (Araucariaceae). Carefully controlled conditions were employed; a continuous flow of the gas under test was supplied to the seed at the correct relative humidity. This study also highlighted two further points. Firstly, increased concentrations of carbon dioxide and ethylene had no beneficial effects (*Araucaria hunsteinii*; Tompsett 1983) and, secondly, oxygen levels above 21% did not enhance storage life (*D. turbinatus*; Tompsett, unpublished). There appear to be no reports that altering the gaseous environment from that of ambient air can increase longevity for recalcitrant seeds.

Storage Using Germination Inhibitors

An alternative method to prevent germination during storage is by incorporating germination inhibitors into the storage system. Substances that have been used are polyethylene glycol (PEG), sucrose, sodium chloride and abscisic acid (ABA). Goldbach (1979) reported that by treating seeds of *Meliococcus* (Sapindaceae) and *Eugenia* (Myrtaceae) with 10^{-4} molar ABA solution at 15°C it was possible to store seeds for four to six months with at least 89% final viability. This general approach for recalcitrant seed storage has subsequently not been confirmed as successful; a problem encountered with the ABA method is the speedy germination of seed during storage.

Fungicide Treatment Followed by Partial Desiccation and Storage at Controlled Temperatures

Partial desiccation was proposed as a favourable approach by King and Roberts (1979). Furthermore, several researchers have mixed fungicide with stored seeds to protect against fungal growth. However, few have conducted controlled experiments to test the effects of applying combinations of fungicide treatments with partial desiccation treatments. Nevertheless, Hor (1984) treated cacao seeds with a 0.2% benlate/thiram mixture, partially desiccated the seeds by air drying and then stored them loosely packed in polythene bags at 21-24°C. The viability of the seeds in his study was prolonged from one week to about 24 weeks with a final 50% germination. This approach needs to be further assessed with the factors separately examined.

Partial Desiccation without Fungicide

Maury-Lechon *et al.* (1981) reported partial drying of dipterocarp seeds but did not use fungicides. From their results they recommended drying seeds to half the original moisture content. This latter procedure prevents pre-germination in storage. However, as their experiments did not include undried controls, the overall benefit was not established.

Storage at Harvest Moisture Content without Fungicide Application or Partial Desiccation

The examples cited from Tompsett (1992) in Table 4 were not subjected to partial desiccation and were not combined with fungicide. Further examples are given in the Seed Physiology chapter and show a total of 13 species capable of storage for longer than 100 days.

The pre-germination problem associated with the storage of moist seed is illustrated by results for *S. roxburghii*; seeds of this species stored at 16°C with approximately 40% moisture content had about 50% pre-germination after 44 weeks of storage (Tompsett 1985). However, provided desiccation and mechanical damage to the radicle are avoided, viable seedlings can still be produced by a high proportion of the pre-germinated seeds.

Research on Seedling Storage and Cryopreservation

Despite the improvements in short to medium-term storage, it is not feasible to store recalcitrant dipterocarp seeds in the longer term. Complementary methods are being sought to ensure a continuous supply of planting material. Two approaches have been attempted at FRIM in unpublished work of Sasaki and of Krishnapillay; these comprise seedling storage and cryopreservation of seed materials.

Seedling storage under low light conditions

It is well established that dipterocarp seedlings usually have high survival and slow growth rates over periods of several months when grown under low intensity light. Many studies, including those of Brown and Whitmore (1992) and Press *et al.* (1996), report this phenomenon. The idea of using this phenomenon for the storage of recalcitrant-seeded species was first clearly proposed by Hawkes (1980).

The two methods outlined below, have been tested at FRIM: (i) storage of seedlings in a seedling chamber; and (ii) storage of seedlings on the forest floor under subdued-light conditions.

Seedling chamber storage

With this method, freshly collected seeds were surface treated with a fungicide (0.1% benlate/thiram mixture) and allowed to germinate under ambient conditions in containers kept at high humidity with moistened tissue paper. After radicle emergence, germinated seeds were packed loosely in polythene bags, trays or boxes lined with moist tissue paper and stored in a specially constructed seedling chamber in which temperature, humidity and light were controlled. The temperature was 16°C, the relative humidity was 80% and the photoperiod was 4 hours. Light was supplied from a fluorescent source, giving 80-1000 lux. Development of the germinated seeds into seedlings occurred slowly in the chamber. Seventeen dipterocarp species have been tested (Krishnapillay, unpublished); these species, with the periods they have been stored, are listed in Table 5.

Seedlings developed slowly in the chamber, barely attaining the heights of 20-25 cm over the storage periods tested. Seedlings which were transferred to the nursery and grown in polythene bags needed to be weaned in at least 70% shade for a period of 2-3 weeks before they could be placed under direct sunlight. Survival percentage was between 60 and 80%, dependent on the species.

Table 5. Storage periods for *Hopea, Dipterocarpus, Shorea and Dryobalanops* species in a subdued-light chamber (Krishnapillay, unpublished).

Species	Period of storage (months)
Hopea odorata	9-12
Hopea helferi	9
Dipterocarpus cornutus	6
Shorea macrophylla	4
Shorea leprosula	6-9
Shorea acuminata	8
Shorea longisperma	6
Shorea parvifolia	8-9
Shorea ovalis	8-9
Shorea curtisii	8-9
Shorea platyclados	8-9
Shorea bracteolata	6
Shorea macroptera	6
Shorea maxwelliana	4
Shorea pauciflora	6
Dryobalanops aromatica	5
Dryobalanops oblongifolia	4

Forest Floor

The second approach for storage of seedlings is on the forest floor under subdued light. Areas were cleared of undergrowth and freshly collected seeds were sown. Seedlings developed very slowly and so can remain within manageable heights for long periods of time.

Seedlings of *Hopea odorata* did not grow to a height greater than 10 cm under these conditions over a period of three years. Seedlings transferred to the nursery and grown in polythene bags began to increase in size rapidly. Weaning in 70% shade for 2 weeks before transfer to direct sunlight was, however, necessary. Survival was approximately 80-90%, depending on species. Eight species have been tested.

The constraints with this method are as follows. In the early stages after sowing, unprotected seeds are likely to be predated by squirrels, birds and wild boars. Fencing the area with barbed wire and covering the seed bed with a plastic sheet is thus necessary. The plastic sheet can be removed when the seedlings have emerged when damage by birds and squirrels is unlikely.

Cryopreservation of dipterocarp seed material

Cryopreservation generally refers to the preservation of material at -196°C, which is the temperature of liquid nitrogen (LN). The method is being examined at FRIM for the storage of dipterocarp seed material. At this temperature, all metabolically related sources of deterioration in the seed are greatly reduced or stopped, thus supporting preservation for very long periods. Work of this type has been carried out on some recalcitrant-seeded tree species of temperate climates

(Pence 1992). In addition, material from the recalcitrant seed of the tropical forest tree *Araucaria hunsteinii* can be cryopreserved; storage of species for four years at -20°C has been achieved, viability being measured in terms of callus production (Pritchard *et al.* 1995). Growth occurred from the radicle end of the embryo axis.

Some results achieved by Krishnapillay and colleagues (unpublished) are described. Studies were conducted on the recalcitrant-seeded dipterocarp species *Hopea odorata* and *Dryobalanops aromatica.* Embryos were first subjected to cryoprotection treatment using sucrose and dimethyl sulphoxide; following this, the embryos were partially dried to a moisture content near 14-15%. The temperature of the material was then taken to -30°C at the rate of 1°C per minute, finally being reduced to -196°C by plunging into LN. After one week the embryo axes were removed, thawed at 40°C and evaluated for survival. About 5% showed signs of swelling and/or the emergence of growth initials. These post-thawing changes were observed in the epicotylar region; no development was observed in the radicle region and none of the embryonic axes were able to grow into whole plants. Improvements to the protocol are being sought. A total of 50 excised embryo axes were used in 5 replicates for each study and for each species.

Cryopreservation has also been used for whole seeds of *Dipterocarpus alatus* and *D. intricatus* (Krishnapillay and Marzalina, unpublished). However, these species are basically orthodox in storage physiology (Tompsett 1987). Cryopreservation is not recommended for species of this storage physiology type because of the comparative practical benefits of using conventional seedbank storage at -20°C (Pritchard 1995).

The greatest proven uses of this approach have been with small pieces of tissue. Complete success in the production of entire seedlings after freezing of tissues may require the development of *in vitro* culture methods (see Chapter 3). In addition, nursery techniques for weaning the developed plantlets are required. Considerable investment of research time and resources may thus be needed to assess if the method can be useful in practice for recalcitrant-seeded material.

Summary of Seed Handling Methods

For South and Southeast Asian Dipterocarpaceae, the following current seed handling recommendations have been made (Tompsett and Kemp 1996a, b).

Collection Recommendations

Check a small sample of seeds before collecting, since insect infestation may be excessive. Collect seeds from the tree when the wings are turning from green to brown. Collection is best accomplished by shaking or plucking branches; a climber may be needed where branches are inaccessible from the ground. Plan the collection to minimise the period of time (preferably a maximum of three days) between harvest and either nursery sowing or short-term storage at the seed centre.

Transport Recommendations

Recalcitrant and OLDA seeds are considered separately.

Recalcitrant seeds should be transported moist and in ventilated containers; they should be kept as cool as possible but not below 18°C. If the wings are left intact, a reservoir of air is created which provides oxygen for respiration. This method reduces both the imbibition of moisture in the container and the accumulation of heat produced by respiration, thereby limiting the chance of germination during transport. Possible containers include open, folded-over polythene bags, closed polythene bags with small ventilation holes, and open-weave sacks. Where greater rigidity is required, the bags or sacks should be enclosed in cardboard or wooden boxes with ventilation holes. Care should be taken to avoid over-heating by exposure of the containers to direct sunlight. Additionally, seed should be retained above its lowest-safe moisture content

For species with OLDA storage physiology seeds, collections may sometimes need to be made from the ground with moisture contents at or below 12%. Dry seed of this type should be transported as follows. For use in the short-term, transport the seed at a cool temperature above 2°C; for use in the long term, transport material at as low a temperature as possible, but not below -20°C. Retain the dry seed in sealed containers during transport. For moist OLDA seed, follow the methods described for transport of recalcitrant seed.

Processing Recommendations

Remove wings for ease of handling and to reduce storage bulk for all species.

Other processing applies to OLDA species. Seeds of this type will dry well in 20°C or higher with a low relative humidity. Material should be transferred to the appropriate storage conditions as soon as the desired moisture content is reached. Retaining seeds in a monolayer in a flow of air will ensure rapid drying, thereby reducing the risk of seed ageing. Careful removal of the calyx can further reduce bulk for dry storage. However, this procedure is time consuming and may only be economic for longer-term (conservation) storage.

Storage Recommendations

Procedures are recommended separately for small and large quantities of recalcitrant seeds and for OLDA seeds.

For larger quantities of recalcitrant seeds, material should be kept at near the harvest moisture content and in media such as sawdust and perlite. Seed moisture content should be checked at the start and then periodically during storage; any wide fluctuations observed should be counteracted by increasing or decreasing the moisture content of the medium. This careful moisture content monitoring and management can reduce the rate of pre-germination. Excess moisture in the medium causes the seeds to become anoxic, whilst too little moisture lowers seed moisture content and leads to desiccation damage. Suitable containers include open-weave sacks or bags. Storage in a high-humidity room at 18°C is recommended.

The optimal condition for storage of smaller quantities of recalcitrant seed is retention within inflated polythene bags in a 99% relative humidity incubator at 18°C and at a moisture content near that of the seed at harvest. Polythene bags with rib-channel closure provide suitable packaging; alternatively, loosely-tied, thin-gauge polythene bags may be employed. Insertion of a rigid object helps to maintain an air space. Ventilation at least weekly is essential; use of air at a high relative humidity would be desirable for this purpose. Moisture content should be checked at the start and then periodically during storage; fluctuations should be counteracted by increasing or decreasing the relative humidity around the seed, if possible.

Different handling is required for OLDA species; the summarised methods for collection, processing and transport described above must be followed closely if the three storage methods below are to be effective.

a) Before sowing in the nursery, seed storage of OLDA species at about 40-50% moisture content is suitable over very short periods of about fifteen days. Moist storage avoids the risk of partial loss of viability on drying. Temperatures employed should be no lower than 18°C. The seed containers described above in relation to recalcitrant species for smaller and larger seedlots are suitable.
b) In the case of longer-term storage any initial, partial loss on drying may be outweighed by the improved final longevity achieved. Storage for conservation is possible if seed is dried to approximately 12% moisture content; material should be sealed in suitable rigid containers (e.g. Kilner jars) and retained at -20°C. Further relevant information is given in the summarised processing method above.
c) For medium-term storage periods (between 2 weeks and 24 months), OLDA seed should be retained at 2°C with other conditions as prescribed for longer-term storage.

Germination Recommendations

Remove seed wings prior to sowing in order to ensure good contact with the germination medium and germinate at approximately 26 °C -31°C. In the case of dry, de-coated OLDA seeds (de-coating is recommended for conservation storage), slow imbibition is essential. This can be achieved by retaining the material in 100% humidity for 24 hours before sowing.

Research Priorities

Changes are occurring in relation to reforestation and afforestation programmes in the regions where dipterocarps are grown. The emphasis is now on the use of indigenous species in combination with exotics. It follows that suitable planting material will be increasingly in demand. Hence, there is a necessity to increase research in the areas described below:

1. Optimising methods for the collection, processing, storage and germination of forest seeds so that seed storage life is maximised, taking into account the need for retaining the viability of seeds that germinate during storage. More detailed suggestions are given in Chapter 3.
2. When the seed storage physiology is known, other information is required. In particular, practical methods for large-scale drying are required in the case of OLDA species, and methods for the storage of bulky recalcitrant material need improvement.
3. Identification of seed-predating insects leading to assessment of their behaviour, especially in the seasonal zones, is desirable. This would complement studies undertaken already in the aseasonal areas.

4. Means to store germinated seeds as seedlings should be assessed.

Relevant Institutions with their Strengths and Potential Contributions

A national pattern of involvement in seed handling activities is given below, using the example of Peninsular Malaysia. This structure may not apply in other dipterocarp countries, but elements of it may be relevant. To carry out the tasks of procuring material for the planting programmes, there is the need for the close networking of the particular agencies involved. These can include the Forest Department of Peninsular Malaysia (FD), FRIM, and the Malaysian Timber Council (MTC). Other relevant agencies are the Agricultural University of Malaysia (UPM), the ASEAN Forest Tree Seed Centre (AFTSC) and the private sector.

Institutions with involvement in dipterocarp seed research in other countries are referred to in the Seed Physiology chapter.

Forest Department of Peninsular Malaysia

The FD consists of the Headquarters in Kuala Lumpur and 10 State Forest Departments located throughout the territory. The headquarters is responsible for planning, operational studies and development of the forestry sector as well as provision of technical advice and services and the provision of training facilities for the forest industry. The State Forest Departments are entrusted with the management of the forest in the respective states.

The role of the Forest Department in the seed and plant procurement programmes may include:

1. assessing plant demand for the each planting activity;
2. providing areas in the forest for seed collection;
3. providing manpower to be trained in carrying out phenological studies, monitoring development and collection of seeds at maturity;
4. allowing upgrade of state nurseries for large-scale plant production; and
5. providing the manpower for planting and subsequent maintenance of the planted areas.

Forest Research Institute Malaysia

FRIM is a statutory research body with the mandate to promote and improve the sustainable development of forest resources and their industrial uses through research, development and application activities.

The purpose of FRIM is to develop appropriate knowledge and technology for the conservation, management, development and utilisation of forest resources. Excellence in scientific research and development, and technology transfer to the forestry sector is also pursued.

FRIM is the research arm to the Forest Department; its role in the seed programme is:

1. providing technical expertise in tree selection, phenological monitoring, and seed collection;
2. seed handling, nursery techniques (including vegetative propagation techniques), setting up of seed orchards, seed testing, and the documentation and certification of storage details;
3. assisting in the development of a programme for seed and plant procurement; and
4. making available its international contacts for the improvement of the seed and plant procurement programme.

Malaysian Timber Council

MTC has the mission to promote the development of timber-based industry and to facilitate trade in timber within Malaysia. Among the objectives of MTC are to promote the rehabilitation of degraded forests and to encourage the reforestation of logged-out areas.

The role MTC can play to enhance the seed programme is in:

1. becoming an investment arm of the seed and plant procurement programme; and
2. assuming a role in the rehabilitation of degraded forests on a privatised basis.

Agricultural University Malaysia

The Faculty of Forestry of UPM is responsible for producing trained manpower in all aspects of the forestry sector.

The Faculty of Forestry could, as a teaching and research unit, contribute to the seed programme by:

1. providing scientists trained in the fields of seed and plant procurement;
2. disseminating research information related to seed programmes; and
3. providing training (short courses in forestry) to upgrade the skills of those involved in the seed programme.

ASEAN Forest Tree Seed Centre

This centre in Thailand serves the needs of all ASEAN countries in relation to forest seed problems common to all the ASEAN countries.

The AFTSC could assist in the seed programme by:

1. raising funds and acting as host for the training of seed research personnel;
2. providing relevant technical support through short-term consultancies; and
3. disseminating knowledge and technology gained in seed programmes.

Private Sector

The private sector is at present not significantly involved in the plantation forestry programmes in Peninsular Malaysia. However, there is interest being expressed by the large plantation holdings to go into forest plantation in support of the Malaysian government's aspirations to produce timber from sustainably managed forests.

With its long and successful experience of rubber, cocoa and oil palm plantation, the private sector could contribute to the seed programme by:

1. contributing experience in establishing large-scale plantations of forest species;
2. managing large-scale nurseries; and
3. becoming investors in forest plantations.

Institutes with Resources Relevant to Insect Research

The central laboratory in the Royal Forest Department in Thailand has a programme of research on forest tree insects. In the UK the Natural History Museum (British Museum) also has resources and relevant experience in relation to insect research.

Conclusion

In this chapter, current knowledge on handling of dipterocarp seeds has been outlined and areas indicated where further work is required. The potential exists to overcome difficulties in producing planting material, but the collaboration of several agencies is required. A suggested framework has been provided for Peninsular Malaysia. While the individual organisations may not be entirely the same in other countries, equivalent groups will need to collaborate to attain the objectives.

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Chapter 5

Seedling Ecology of Mixed-Dipterocarp Forest

M.S. Ashton

Introduction

Successful reproduction depends on the completion of a sequence of events starting with flower bud initiation and ending with the establishment of a young seedling (Smith 1986); failure of any single stage in this sequence can have catastrophic consequences for the regeneration of a new stand. Several stages of the sequence considered in this chapter are i) the dispersal of fruits; ii) germination of seed; iii) early survival; and iv) the establishment of seedlings. These stages comprise a period of reorganisation and initiation of a new forest stand after which composition and structure depends mainly upon competition and self-thinning. These stages provide an opportunity in silviculture for promoting the desired composition and stocking of the future stand. To quote from Smith (1986) 'Many of the successes or failures of silvicultural treatment are preordained during stand establishment. Physicians bury their worst mistakes but those of foresters can occupy the landscape in public view for decades'.

South and southeast Asia boast a rich history of forest research. The mixed-dipterocarp forest[1] of this region has been studied more than any other tropical forest type primarily because of its importance for producing timber. This chapter reviews the state of knowledge on the seedling ecology of regenerating mixed-dipterocarp forest and suggests future avenues of research. However, it is not an exhaustive review of the literature and in most cases cites widely available papers. There is much information on seedling dipterocarp ecology that remains unpublished or is only available at local research institutes, or university and government departments. This information in its own right deserves documentation, compilation and synthesis. Also, though this account concentrates on a review of the literature of the seedling ecology of dipterocarp species it emphasises the need to obtain information about the seedling ecology of non-dipterocarp species in mixed-dipterocarp forests. Often silvicultural management of mixed-dipterocarp forests has concentrated on the regeneration autecology of a few commercial dipterocarp species without an understanding of their interaction with other species, and their role in the successional dynamic of the whole forest. This has led to a silviculture that has focused on only the current commercial species and has tended to simplify, and in many instances degrade, the dynamic and structure of mixed-dipterocarp forests (Ashton *et al.* 1993).

Dispersal and Germination

Early studies on mixed-dipterocarp forests were done on seed phenology and dispersal mechanisms and the categorisation of tree species by dispersal agent (Ridley 1930). Subsequent work has been done in more detail on the role of seed dispersal by animals (Medway 1969, Leighton 1983, unpublished data); and on dipterocarps in particular (Fox 1972, Kochumen 1978, Dayanandan *et al.* 1990). However, these studies are few and much more long-term phenological information on seed dispersal needs to be gathered on representative guilds of species within mixed-dipterocarp forest. Future studies should also focus on the amount and distribution patterns of seed dispersed from parent trees and germination. This will lead to a better understanding of the spacing and period of time required for the retention of a residual overstorey to ensure satisfactory stocking of seedlings. This kind of information is essential for the development of natural regeneration methods.

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[1] Mixed-dipterocarp forest is defined here as that lowland and hill rain forest where the Dipterocarpaceae are predominant amongst the canopy and emergent trees of mature forest. The majority of tree species are non-dipterocarp. The soils are weathered *in situ* and would be classified as belonging to either oxisols or ultisols (USDA 1975). The climate is warm and humid with high rainfall that has little seasonality.

Work has been done on dipterocarp germination mostly during the 1970s and 80s. Many studies of dipterocarp species reported them to be recalcitrant (Jensen 1971, Tang 1971, Tang and Tamari 1973, Tamari 1976). Chapter 3 gives a more detailed review of dipterocarp germination. Other studies suggested that many non-dipterocarp species, mostly pioneers, had dormant seed buried in the soil that germinated with a marked increase in radiation at the ground surface (Liew 1973, Aminuddin and Ng 1983, Raich and Gong 1990). However, unlike the neotropics (see work by Vazquez-Yanes and Orozco Segovia 1984, Garwood 1996), no critical experiments have focused on this buried seed phenomenon. Also, relatively few studies have comprehensively evaluated patterns of germination for the whole forest in relation to successional status and taxonomy (Ng 1983). This is perhaps because past research has focused on the autecology of individual dipterocarp species. Future work should focus on clarifying the germination mechanisms of mixed-dipterocarp forest tree species in general and the role dipterocarp species play within it. Little work has focused on the competitive interactions between dipterocarps and non-dipterocarps and yet they are of direct relevance to the maintenance of dipterocarps in a managed forest.

Early Survival and Establishment of Dipterocarps

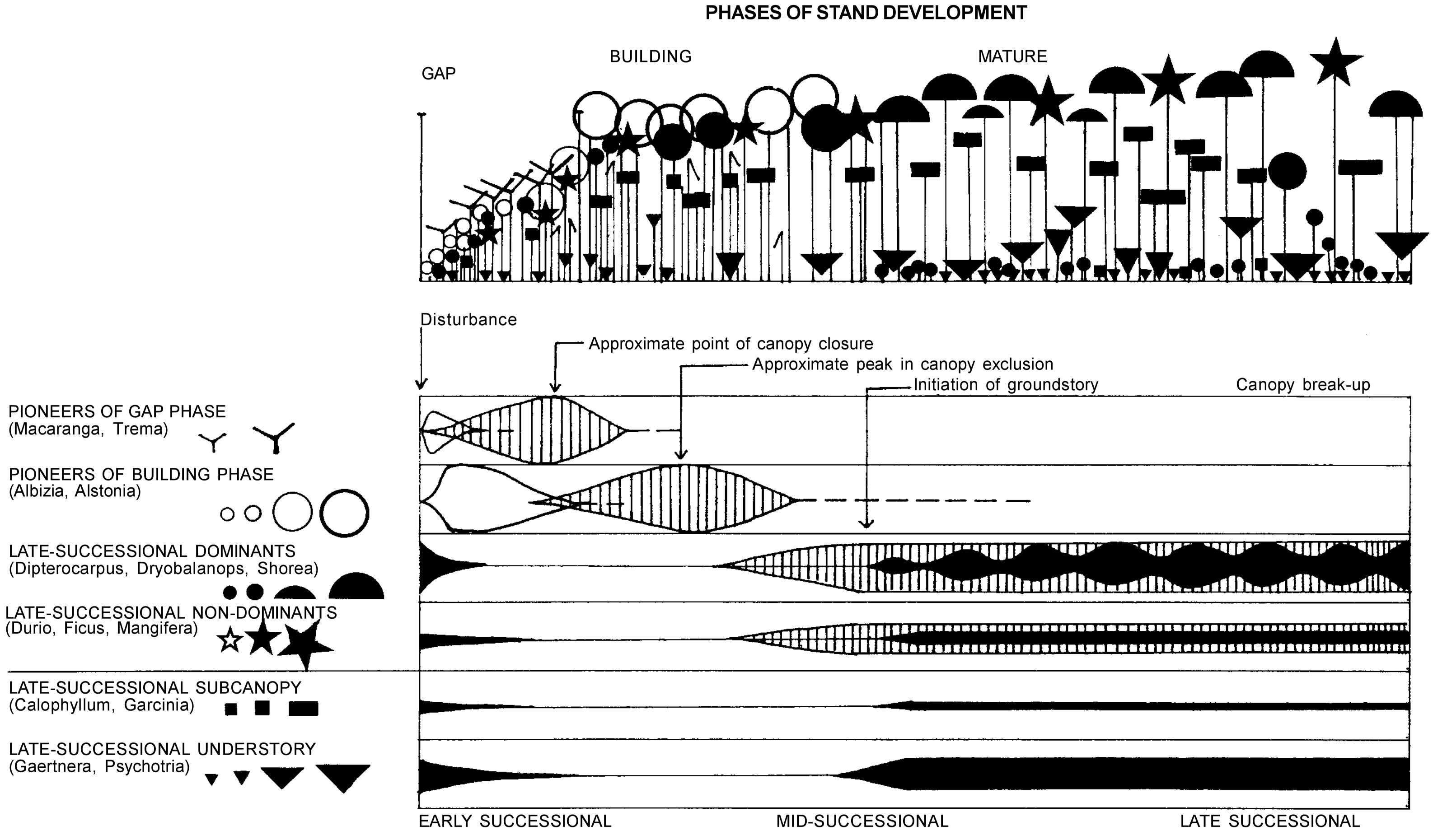
The main research objective early in this century was to develop a method for evaluation of regeneration stocking before logging (Wyatt-Smith 1963). The survey techniques that developed were usually based on line transects that assessed stocking by measures of dipterocarp seedling distribution and number. Surveys revealed that the abundance of regeneration was associated with certain dipterocarp species and sites. In many circumstances regeneration was absent particularly on the slopes of hill forests and where competing understorey palms, shrubs and herbs were present (Burgess 1975, Wong 1981, Kusneti 1992). Though measures of distribution are important to gauge adequate and even coverage of seedling establishment within a stand, measures of seedling number and density do not necessarily predict successful establishment. A measure that incorporates an estimate of seedling vigour is needed. More recent studies have used different size classes and estimates of leaf area to gauge vigour, promoting survey techniques that discard seedlings in the 'less vigourous classes' for a representation of regeneration stocking (Ashton 1990). These can be useful measures for most dipterocarp species because they have poor ability to sprout. Measures of their above-ground performance can therefore be used to predict future growth and survival.

Studies by Nicholson (1960) and others (Fox 1972, 1973, Liew and Wong 1973, Tomboc and Basada 1978, Appanah and Manaf 1994) elucidated the cyclic nature of population recruitment and survival in the groundstorey of a closed forest and demonstrated the importance of advanced regeneration in the form of a seedling bank for the successful establishment of new forest stands. Conceptual models of the regeneration dynamic have been developed that explicitly suggest the importance and reliance of mixed-dipterocarp forest on advance regeneration (see Fig. 1). This reliance is not only for dipterocarps but also for late successional canopy trees that are non masting, subcanopy trees and shrub species. Forest management should therefore focus on advanced regeneration of dipterocarp trees and similar associates. These are the trees that are the canopy dominants during the mid and late stages of forest succession. They, therefore, create the basic forest structure beneath which other strata exist, and reflect the changes in composition associated with differences in site quality.

Studies have also shown that dipterocarp species could be broadly categorised as shade-tolerant or light-demanding based on differences in frequency of recruitment and rate of seedling death. Shade-tolerant dipterocarps can have seedlings established beneath closed canopied forest for long periods of time (> 10 years). Mast years for shade-tolerant dipterocarps can therefore be fewer than relatively more light-demanding dipterocarps but still provide adequate advance regeneration establishment (Wyatt-Smith 1963, Fox 1972, Gong 1981). In general, however, all dipterocarps have cohorts of seedlings that continually replenish the seedling bank from successful mast years. Over time, seedlings die primarily from the very low light regimes of a closed forest canopy (Ashton 1995). Groundstorey levels of photosynthetically active radiation (PAR) beneath the canopy of a mixed-dipterocarp forest have often been recorded as less than 1% of that received in the open (Torquebiau 1988, Ashton 1992a).

Other studies have also suggested the importance of an increase in amounts of PAR that promotes only partial shade for dipterocarp germination and early survival

Figure 1. Regeneration recruitment frequency and stand canopy dominance of ecological species groups over different successional stages of stand development for a mixed dipterocarp forest. Examples of species are given for each ecological group along with codes denoting their structural position within the stand over time. Note the periodic recruitment of seedings for tree species belonging to the late-successional canopy dominants. (modified after Ashton 1992a).



■ Juveniles recruited under canopy light conditions and considered as advanced regeneration (seedlings, seedling sprouts, root and stem suckers). The breadth of the bar represents amount of regeneration relative to other ecological species groups.

□ Juveniles recruited under open conditions of full sun (buried seed, seed dispersed by wind or animals into opening after disturbance).

▥ Stand canopy dominance. The breadth of the bar represents the degree of dominance in relation to other ecological species groups.

(Nicholson 1960, Ng 1978). However, it was shade house investigations (Mori 1980, Sasaki and Mori 1981, Ashton and de Zoysa 1989) that clearly demonstrated that most dipterocarp seedlings require greater amounts of radiation than that received at the groundstorey of a closed canopy dipterocarp forest, but less than the amount of radiation received when exposed to full sun.

Field research on disturbance regimes of mixed-dipterocarp forest supports evidence from shade house experiments and studies of seedling population dynamics in the forest. Natural disturbances documented in mixed-dipterocarp forest are varied but most are of a kind and scale that promote the survival and release of an existing seedling groundstorey. Disturbance types include lightning strikes (Bruenig 1964), insect defoliation of canopy trees (Anderson 1964), single and multiple tree falls (Anderson 1964), and cyclones (Whitmore 1974, 1989). All allow the groundstorey vegetation to remain largely unharmed. Disturbances in mixed-dipterocarp forest that have been observed to destroy groundstorey vegetation include landslides, flooding and fire (Day 1980, Leighton and Wirawan 1986, Tagawa and Wirawan 1988). This might be one reason why dipterocarp regeneration does not establish well in parts of a forest landscape subject to lethal disturbance of the groundstorey such as steep slopes, flood plains and swidden agriculture. Current investigations focus on refining our understanding of the regeneration microenvironment of tree species in mixed-dipterocarp forest. Compared to other tree species of mixed-dipterocarp forest, dipterocarps have some general autecological characteristics that allow for their categorisation in the same regeneration guild (Table 1). Although dipterocarps have the same general autecology there are also differences among them, however, these differences are small compared to other regeneration groupings. Important questions are: what degrees of difference exist and why do they occur among species belonging to the same congeneric group. The answers are particularly relevant to understanding dipterocarp dominance in mixed-dipterocarp forests and will provide the silvical information for the fundamental treatments imposed on these forests for management purposes.

One such topic that merits attention is the site specialisation of dipterocarp regeneration. How site specific is advanced regeneration of dipterocarp species? Recent field studies demonstrate that forest gaps of different size exhibit considerable spatial (Ashton 1992a, Brown 1993) and temporal (Raich 1989, Torquebiau 1988) variation in forest groundstorey microclimate. Changes in size of small canopy openings can greatly influence the overall amount of radiation received at the groundstorey of the opening centre (Brown 1993). However, larger canopy openings provide a greater range of microclimates at the groundstorey of the opening (Ashton 1992a). Studies that monitored pre-established seedlings and new recruits (Raich and Christensen 1989, Brown and Whitmore 1992) showed that there were significant differences among dipterocarp species in survival and growth at these different microsites. Studies by Ashton *et al.* (1995) that controlled age and spacing of dipterocarp seedlings supported these findings. However, investigations by Turner (1990a, b), who monitored pre-established seedlings, suggested mixed results of dipterocarp seedling survival and growth in relation to light availability at the scale of the microsite. Studies are now investigating the competitive relationship between species for regeneration growing space through the monitoring of long-term self-thinning trials located on different sites and within different

Table 1. Silvical characteristics of canopy tree species belonging to genera assemblages (e.g. *Shorea*) that dominate the mature phase of mixed-dipterocarp forest. These characteristics should be interpreted broadly as exceptions will exist (Ashton 1992b).

Reproduction

- Pollination vectors are small insects (hymenoptera, hemiptera)
- Seed is with storage tissue
- Seed is dispersed by gravity (often aided by territorial animals such as rodents)
- Fruiting time is more or less supra-annual with distinctly different amounts of seed at each fruiting (masting)
- Seed shows no classical dormancy

Establishment and Growth

- Seed requires partial shade protection for germination and early survival
- Seedlings require an increase in light (as compared to understorey conditions) for satisfactory establishment and growth
- Seedling survival and establishment is usually site specific, according to particular biotic, microclimatic and edaphic characteristics

microenvrionments (Gunatilleke and Ashton, unpublished).

These studies have focused investigations on the spatial availability of light at the forest groundstorey and its relationship to seedling survival and growth. Findings also suggest that the seasonal variation in soil water availability, scaling up from different groundstorey microsites to across the landscape (ridge to valley), can be another factor that affects the survival and growth of dipterocarps. Ashton (1992a), Brown (1993) and Palmiotto (1993) observed seasonal periods of water stress that may play a critical role in determining seedling composition of canopy gap regeneration. Transplant experiments suggested soil water availability, related to topography (slope, ridge, valley etc.), affects the survival and growth of dipterocarps. The transplant experiments also suggested seedling survival and growth allocation was affected by interaction between soil water availability and radiation. For example, some species showed five-fold decreases in root mass between seedlings growing in the understorey of a ridgetop site as compared with those seedlings in the understorey of a valley site. Although understorey PAR was comparable between the two sites the poor root development on the ridge predisposes these species to drought. Studies by Brown and Whitmore (1992) and Ashton *et al.* (1995) suggested that seedlings of more light demanding dipterocarp species have larger leaves and that more shade tolerant species have smaller leaves and are more sensitive to heat stress. This is contrary to most other literature for example, Givnish (1988) which has mostly described the sun shade dichotomy for mature trees that are from temperate forest regions. There are only a few studies (Ashton and Berlyn 1992, Strauss-Debenedetti and Berlyn 1994) that have investigated the sun shade dichotomy for seedlings of the moist tropics.

Other studies are also providing evidence that dipterocarps are affected by soil characteristics related to the underlying parent material. Surveys by Baillie *et al.* (1987) and Ashton and Hall (1992) suggest both concentrations of total and available magnesium and phosphorus to be particularly important in determining species-site associations. However, no fertiliser studies of seedlings using field experiments have clearly demonstrated that these factors affect the establishment stage of forest development (Turner *et al.* 1993, Burslem *et al.* 1995) although some studies that are in progress are suggesting differences may occur (Gunatilleke *et al.* 1996, Palmiotto, in preparation). In these experiments different soils are being investigated to understand nutrient use efficiency of dipterocarp species whose distribution is restricted to very different levels of soil fertility. These kinds of studies are beginning to provide the basis for the development of new silvicultural regeneration methods and the refinement of currently used methods. These studies on light, soil moisture and fertility are providing knowledge for a better mechanistic understanding of regeneration dynamics of forests. In some cases they have contradicted previous understanding of forest dynamic patterns based only on observation and census methodologies. An example would be the recent findings that show discrete differences in the site-specialisation among species of *Shorea* section Doona. These species were formerly assumed to be very similar in their site requirements and therefore their silvicultural treatments were the same.

In addition, there are many biotic interactions that can moderate or accentuate patterns in the establishment of seedlings within the physical environment. For example, although no studies substantiate this, host specific ectomycorrhizae could accentuate the differential exploitation of soil nutrient resources among closely related assemblages of dipterocarp species. Studies by Becker (1983) and Smits (1983) suggest that ectomycorrhizae can play important roles in dipterocarp seedling establishment and growth. Mycorrhizal infection was found to be greater for seedlings located in small clearings than for those seedlings located beneath forest canopy. These results suggest that seedling regeneration of dipterocarps will respond more vigourously to overstorey removal if pre-release treatments create higher light environments in the understorey. In addition, Lee and Lim (1989) found that foliar phosphorus contents of *Shorea* seedlings growing on either phosphorus deficient or phosphorus rich soils were the same - indicating a difference in uptake efficiency that was attributed to ectomycorrhizae (for more detail see Chapter 6 on nutrition and root symbiosis).

Herbivory is another biotic effect that has had little investigation. Becker's (1981) studies of seedling populations found less herbivory on the leaves of a late successional, more shade-tolerant *Shorea* species as compared to more light-demanding *Shorea* species. However, no studies followed up on this work. More investigation should be done, particularly on the role of non dipterocarp tree species in mixed-dipterocrap forest.

Does the simplification of mixed-dipterocarp forest by the frequent use of various silvicultural release treatments (weeding, cleaning, liberation) favour so few commercial tree species that this may lead to greater susceptibility to disease and/or herbivory of the forest? Questions such as these need to be further tested.

Growth in Relation to Physiology and Structure of Dipterocarps

Recent seedling experiments have focused on separating the various abiotic and biotic factors that influence seedling establishment and growth under controlled conditions. Many studies have been investigating light and the different effects of light quality, quantity and duration. These experiments reinforced findings from the earlier shade house studies but demonstrated that forest understorey light quality can accentuate the poor growth and survival of seedlings in deep-shade conditions (Kamaluddin and Grace 1993, Lee *et al.,* unpublished manuscript). Experiments that simulated quality and intensity of light environments of a rain forest also demonstrated that *Shorea* species allocate dry mass proportions to roots, stems and leaves in different amounts (Turner 1989, Ashton 1995). These results show that the more shade-tolerant *Shorea* species allocate proportionately more dry mass to root development than to stem and leaves in forest understorey environments whereas the reverse is true for more light-demanding *Shorea* species.

The process of photosynthesis requires photosynthetically active radiation, water and carbon dioxide The adaptations a seedling leaf can make to its surroundings must accommodate all three. The relationship among all three factors is so closely linked that many of the leaf adaptations and adaptation responses to environmental change are the same. Heat and desiccation of leaves exposed to the full radiation of the sun can promote leaves that have similar physiological and anatomical adaptations as leaves that are drought-enduring. Leaves that have grown in the shade often resemble those of drought intolerant leaves. Alhough much work has been done elucidating differences in leaf anatomy and morphology between species of different cladistic or successional groups for other forest regions (Wylie 1951, 1954, Jackson 1967 a, b, Givnish 1988, Lee *et al.* 1990), little has been done that examines these relationships for mixed-dipterocarp forests. However, there is some evidence that suggests the same leaf anatomical and morphological trends exist for mixed-dipterocarp forest.

For species belonging to the same cladistic group or regeneration guild work has been equally negligible in mixed-dipterocarp forest. In a seedling study of *Shorea* by Ashton and Berlyn (1992) data show that differences in net photosynthesis (P_N), transpiration (E), and stomatal conductivity (g) can be associated with differences in the anatomy of *Shorea* species. General trends indicate that in experimentally controlled conditions maximum P_N rate was a good measure of the light tolerance of *Shorea.* The shade tolerant species had maximum P_N rates at relatively lower light intensity compared to that of more light demanding species. Ratios between rates of P_N and E of species at their maximum P_N light intensities can also suggest trends in water-use efficiency. This can reveal some indication of species order in relation to drought tolerance in controlled environments. Differences in physiological attributes also suggest that the greatest plasticity of response to differences in availability of light was exhibited by the most light-demanding species and the least by the most shade-tolerant. At a regional scale, Mori *et al.* (1990) showed similar patterns with dipterocarps. Those from more seasonal climates having greater rates of P_N and E, and higher levels of plasticity than dipterocarps from aseasonal everwet climates.

An array of anatomical characteristics can, in combination, partly determine the physiological light and drought tolerance of *Shorea* species in relation to their associates. Patterns suggest stomatal frequency is a factor differentiating *Shorea* species, with the most tolerant having fewer and smaller stomates than the most intolerant forms. Differences in thickness of the whole leaf blade and the leaf cuticle among species appear similarly related to both light and drought tolerance; with sun loving species having thicker dimensions of both characters than shade tolerant or demanding species. These results elucidate some of the relationships between the distribution patterns of *Shorea* species across the topography and their differences in light and drought tolerance. They also show that an important period determining site specialisation of a dipterocarp species occurs during regeneration establishment. Another area of study related to the anatomy and physiology of seedlings is tissue chemistry (foliar nutrients, secondary compounds). Although little work has examined tissue chemistry, investigations along these lines would tie in closely with studies on soil fertility, seedling herbivory and seedling physiology that have been done at larger scales or from other disciplinary perspectives.

In summary, much more work has yet to be done that clarifies relationships among similar or related species such as the dipterocarps. This work should also strive to link structure and physiology to seedling growth and mortality to gain a better mechanistic understanding of regeneration establishment. Research on seedling ecology of mixed-dipterocarp forest is substantial compared to other tropical forest regions. However, our knowledge of dipterocarp seedling ecology is fragmented and poor compared to other commercially important timber families such as Fagaceae (oak, chestnut, beech) where knowledge is fairly comprehensive for most Fagaceous forest regions. We have a long way to go!

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Chapter 6

Root Symbiosis and Nutrition

S.S. Lee

At present dipterocarps are gaining much attention, this volume being testimony to it. Since large tracts of dipterocarp forests in tropical Asia have become overlogged and/or degraded, interest in planting dipterocarps either in plantations or by underplanting in poor forests has gained momentum. With this move, research on mycorrhizas and their association with dipterocarps has gained a high profile.

Mycorrhizas are the symbiotic association between specialised root-inhabiting fungi and the roots of living plants. Harley and Smith (1983) recognise seven mycorrhizal types but only two, the ectomycorrhizas and the vesicular-arbuscular mycorrhizas (VAM) (now more popularly referred to as arbuscular mycorrhizas) occur in the Dipterocarpaceae. Dipterocarps are predominantly ectomycorrhizal but a few species have been reported to form both ectomycorrhizas and VAM (Table 1). Unlike some members of the Leguminosae, the dipterocarps are not symbiotic with nitrogen fixing bacteria.

Typical dipterocarp ectomycorrhizas are short, pyramidal or racemously branched and variously coloured (e.g. brown, black, white, yellow). A fungal sheath (mantle) characteristic of the fungal partner surrounds the host root. Underneath this sheath lie the often radially elongated epidermal cells between which are located the hyphae of the Hartig net (Alexander and Högberg 1986, Lee 1988). The surface of the sheath may be smooth but often bears hyphae or hyphal strands which radiate out into the substrate.

The role of mycorrhizas in increasing the absorptive efficiency of roots is well known. The growth of mycorrhizal hyphae into the surrounding soil effectively shortens the distance over which the slowly diffusible ions, such as phosphate, must travel before being absorbed and the association has proven particularly beneficial to the host in soils of low available phosphorus concentrations. Ectomycorrhizas are also seen to play a role in minimising nutrient losses from the nutrient cycle through leaching (Read *et al.* 1989). The production of a potent acid carboxypeptidase by some ectomycorrhizal fungi such as *Amanita* and *Boletus* (Read 1991) indicates that these fungi have the potential to mobilise the plant growth limiting nutrient, nitrogen, from protein. This implies that such ectomycorrhizal infected trees are no longer dependent upon the activities of a separate group of decomposer fungi for the release of nitrogen in the form of the ammonium ion for plant uptake. Ectomycorrhizas are also known to be able to increase the tolerance of trees to drought, high soil temperatures, organic and inorganic soil toxins, and very low soil pH. The sheath has been shown to have important storage functions, not only for phosphorus but also for other absorbed nutrients and carbon. The sheath also protects the root from pathogens, and is thought to be able to reduce water loss and allow rapid rewetting, thus lengthening root life and thereby increasing mineral uptake and retention (Janos 1985). It has also been suggested that the key role of the mycorrhizal symbiosis under natural conditions is to enable seedling persistence rather than rapid growth (Abuzinadah and Read 1989).

The presence of ectomycorrhizas in the Dipterocarpaceae has led to several hypotheses regarding the role they might play in dipterocarp biology. Ashton (1982) suggested that the clumped distribution of the dipterocarps might be reinforced by their ectomycorrhizal associations as the mycelia persist and gradually spread with the ever dispersing and coalescing clumps of the dipterocarp trees themselves. He suggested that his observation of the association of two different groups on soils of different soil phosphorus levels could

Table 1. Dipterocarp species reported to be ectomycorrhizal based on root examination. (Only the first report for the species in each location is given).

Genera Species	Location	Vegetation	Reference/Source
Anisoptera			
A. costata Korth. *(VAM also)	Thailand	Dry deciduous forest	Aniwat (1987)
A. laevis Ridl.	Pen. Malaysia	Lowland rainforest	Singh (1966)
A. marginata Korth.	Kalimantan	Lowland rainforest	Smits (1987)
A. oblonga Dyer	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
A. scaphula (Roxb.) Pierre	"	"	"
A. thurifera (Blco) Bl.	Luzon	Rainforest	Zarate et al. (1993)
Cotylelobium			
C. malayanum Sloot.	Pen. Malaysia	Dipterocarp arboretum	Hong (1979)
C. scabriusculum Brandis	Sri Lanka	Lowland rainforest	de Alwis & Abeynayake (1980)
Dipterocarpus			
D. alatus Roxb.	Thailand	Semi-evergreen forest	Aniwat (1987)
D. baudii Korth.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
D. chartaceus Sym.	Pen. Malaysia	Dipterocarp arboretum	Hong (1979)
D. confertus Sloot.	Kalimantan	Lowland rainforest	Smits (1992)
D. cornutus Dyer	"	"	Bimaatmadja in Hadi et al. (1991)
D. costatus Gaertn. f.	Thailand	Semi-evergreen forest	Aniwat (1987)
D. costulatus Sloot.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
D. elongatus Korth.	Kalimantan	Lowland rainforest	Smits (1992)
D. gracilis Bl.	"	"	"
D. grandiflorus (Blco) Blco	"	"	Smits (1983)
D. hasseltii Bl.	"	"	Smits (1992)
D. hispidus Thw.	Sri Lanka	Lowland rainforest	de Alwis & Abeynayake (1980)
D. humeratus Sloot.	Kalimantan	"	Smits (1992)
D. indicus Bedd.	India	Wet evergreen forest	Alexander & Hogberg (1986)
D. intricatus Dyer.	Thailand	Dry deciduous forest	Aniwat (1987)
D. kunstleri King	Sarawak	Kerangas	Alexander & Hogberg (1986)
D. oblongifolius Bl.	Pen. Malaysia	Lowland rainforest	Singh (1966)
D. obtusifolius Teysm. ex Miq.	Thailand	Dry deciduous forest	Aniwat (1987)
D. sublamellatus Foxw.	"	"	"
D. tempehes Sloot.	Kalimantan	Lowland rainforest	Smits (1992)
D. tuberculatus Roxb.	Thailand	Dry deciduous forest	Aniwat (1987)
D. verrucosus Foxw.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
D. zeylanicus Thw.	Sri Lanka	"	de Alwis & Abeynayake (1980)
Dryobalanops			
D. aromatica Gaertn. f.	Pen. Malaysia	Lowland rainforest	Singh (1966)
"	Kalimantan	Lowland rainforest	Smits (1992)
D. keithii Sym.	"	"	"
D. lanceolata Burck	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
"	Sabah	Lowland rainforest	Unpublished data
"	Kalimantan	Lowland rainforest	Smits (1992)
D. oblongifolia Dyer	Pen. Malaysia	Dipterocarp arboretum	Hong (1979)
D. oocarpa Sloot.	Kalimantan	Lowland rainforest	Bimaatmadja in Hadi *et al.* (1991)

Table 1. (continued) Dipterocarp species reported to be ectomycorrhizal based on root examination.

Genera Species	Location	Vegetation	Reference/Source
Hopea			
H. bancana (Boerl.) Sloot.	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
H. dryobalanoides Miq.	Kalimantan	Lowland rainforest	Smits (1992)
H. ferrea Laness.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
"	Thailand	Semi-evergreen forest	Aniwat (1987)
H. ferruginea Parijs	Pen. Malaysia	Lowland rainforest	Singh (1966)
H. iriana Sloot.	?	?	Ashton (1982)
H. jucunda Thw.	Sri Lanka	Lowland rainforest	de Alwis & Abeynayake (1980)
H. mengerawan Miq.	Kalimantan	Lowland rainforest	Smits (1992)
H. montana Sym.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
H. nervosa King	"	"	"
"	Sabah	Lowland rainforest	Unpublished data
"	Kalimantan	Lowland rainforest	Smits (1992)
H. nudiformis Thw.	Java	Dipterocarp arboretum	Setiabudi in Hadi *et al.* (1991)
H. odorata Roxb.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
"	Thailand	Semi-evergreen forest	Aniwat (1987)
"	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
H. parvifolia (Warb.) Sloot.	S. India	Wet evergreen forest	Alexander & Hogberg (1986)
H. plagata (Blco) Vidal	Luzon	Rainforest	Zarate *et al.* (1993)
H. sangal Korth.	Kalimantan	Lowland rainforest	Julich (1985)
Marquesia			
M. acuminata Gilg.	Zambia	Miombo	Hogberg & Piearce (1986)
M. macroura Gilg.	"	"	"
Monotes			
M. africanus (Welw.) A.D.C.	Zambia	Miombo	Hogberg & Piearce (1986)
M. elegans Gilg.	Tanzania	Miombo	Hogberg (1982)
Neobalanocarpus (Balanocarpus)			
N. heimii (King) Ashton	Pen. Malaysia	Lowland rainforest	Singh (1966)
Parashorea			
P. densiflora Sloot. & Sym.	Pen. Malaysia	Lowland rainforest	Mohd. Noor (1981)
P. lucida (Miq.) Kurz.	"	"	"
P. malaanonan (Blco) Merr.	Sabah	Lowland rainforest	Unbubl. data
Pentacme			
P. contorta (Vidal) Merr. & Rolfe	Philippines	?	Tupas & Sajise (1976)
P. siamensis (Miq.) Kurz.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
Shorea			
S. academia (?)	Kalimantan	Nursery	Ogawa (1992a)
S. acuminata Dyer	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. affinis (Thw.) Ashton	Sri Lanka	Lowland rainforest	de Alwis & Abeynayake (1980)
S. assamica Dyer	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. balangeran (Korth.) Burck	Kalimantan	Lowland rainforest	Smits (1987)

Table 1. (continued) Dipterocarp species reported to be ectomycorrhizal based on root examination.

Genera Species	Location	Vegetation	Reference/Source
S. bracteolata Dyer	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
"	Kalimantan	Logged over forest	Suhardi *et al.* (1992)
" *(VAM also)	Pen. Malaysia	Lowland rainforest	Norani (pers. comm.)
S. compressa Burck	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
S. curtisii Dyer ex King	Pen. Malaysia	Lowland rainforest	Singh (1966)
S. dasyphylla Foxw.	"	"	Lee (1992)
S. faguetiana Heim	Kalimantan	Lowland rainforest	Smits (1992)
S. foxworthyi Sym.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. glauca King	"	"	"
S. guiso (Blco) Bl.	"	"	"
S. henryana Pierre	Thailand	Semi-evergreen forest	Aniwat (1987)
S. hypochra Hance	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. javanica K. & V.	Indonesia	Agroforestry area	Nuhamara in Supriyanto *et al.* (1993a)
S. johorensis Foxw.	Kalimantan	Lowland rainforest	Smits (1992)
S. laevis Ridl.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
"	Kalimantan	Lowland rainforest	Julich (1985)
S. lamellata Foxw.	"	"	Smits (1992)
S. lepidota (Korth.) Bl.	Pen. Malaysia	Lowland rainforest	Berriman (1986)
S. leprosula Miq.	Pen. Malaysia	Lowland rainforest	Singh (1966)
"	Kalimantan	Lowland rainforest	Bimaatmadja in Hadi *et al.* (1991)
S. macrophylla (de Vriese) Ashton	Sarawak	?	Chong (1986)
S. macroptera Sloot.	Pen. Malaysia	Lowland rainforest	Singh (1966)
S. maxwelliana King	"	"	Becker (1983)
S. mecistopteryx Ridl.	Indonesia	?	Hadi *et al.* (1991)
S. obtusa Wall.	Thailand	Dry deciduous forest	Aniwat (1987)
S. ovalis (Korth.) Bl.	Pen. Malaysia	Lowland rainforest	Singh (1966)
"	Kalimantan	Lowland rainforest	Bimaatmadja in Hadi *et al.* (1991)
S. ovata Dyer ex Brandis	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. palembanica Miq.	Java	?	Hadi *et al.* (1991)
S. parvifolia Dyer	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
"	Kalimantan	Lowland rainforest	Bimaatmadja in Hadi *et al.* (1991)
S. pauciflora King	Pen. Malaysia	Lowland rainforest	Singh (1966)
"	Kalimantan	Lowland rainforest	Smits (1992)
S. pinanga Scheff.	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
"	Kalimantan	Lowland rainforest	Smits (1992)
S. platyclados Sloot. ex Foxw.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. polyandra Ashton	Kalimantan	Lowland rainforest	Smits (1992)
S. robusta Gaertn. f.	India	Moist deciduous forest	Bakshi (1974)
S. roxburghii G. Don	Thailand	Dry deciduous forest	Aniwat (1987)
S. scabrida Sym.	Sarawak	Kerangas	Alexander & Hogberg (1986)
S. selanica (Lamk.) Bl.	Java	Dipterocarp arboretum	Nuhamara *et al.* in Hadi *et al.* (1991)
S. seminis (de Vriese) Sloot.	"	"	Hibau in Hadi *et al.* (1991)
S. sericeiflora Fisher & Hance	Pen. Malaysia	Rainforest	Mohd. Noor (1981)

Table 1. (continued) Dipterocarp species reported to be ectomycorrhizal based on root examination.

Genera Species	Location	Vegetation	Reference/Source
S. siamensis Miq.	Thailand	Dry deciduous forest	Aniwat (1987)
S. smithiana Sym.	Kalimantan	Lowland rainforest	Bimaatmadja in Hadi *et al.* (1991)
S. stenoptera Burck	Java	Dipterocarp arboretum	Setiabudi in Hadi *et al.* (1991)
"	Kalimantan	Lowland rainforest	Smits (1992)
S. sumatrana (Sloot. ex Thor.) Sym.	Pen. Malaysia	Rainforest	Mohd. Noor (1981)
S. talura Roxb.	"	"	"
S. teysmanniana Dyer ex Brandis	"	"	"
Vatica			
Vatica sp. 1	Kalimantan	Lowland rainforest	Smits (1992)
V. chartacea Ashton	"	"	"
V. papuana Dyer ex Hemsl.	Pen. Malaysia	Lowland rainforest	Singh (1966)
V. rassak (Korth.) Bl.	Kalimantan	Lowland rainforest	Smits (1992)
V. sumatrana Sloot.	Java	Dipterocarp arboretum	Hadi & Santoso (1988)
V. umbonata (Hook. f.) Burck	Kalimantan	Lowland rainforest	Smits (1992)
Vateria			
V. indica L.	S. India	Wet evergreen forest	Alexander & Hogberg (1986)
Vateriopsis			
V. seychellarum Heim	Aberdeen greenhouse	Potted plant	Unpublished data

be consistent with the theory that dipterocarps are ectomycorrhizal. Smits (1983) suggested that the clumped distribution of dipterocarps was due to an ecological adaptation between suitable fungi and selected dipterocarp species on the different sites. He (Smits 1994) has also suggested that dipterocarp mycorrhizas contribute to speciation amongst the Dipterocarpaceae through enhanced isolation. Janzen (1974) speculated that dipterocarps which shed their litter containing large amounts of phenols and other secondary compounds required ectomycorrhizas to avoid self-toxicity. Other researchers speculate that the high mortality of outplants and lack of success in vegetative propagation of dipterocarps may be due to a lack of or death of ectomycorrhizas (Ashton 1982, Becker 1983, Smits 1983, Noor and Smits 1987). Lee *et al.* (1966) however, have shown that outplanted seedlings of *Hopea nervosa* and *Shorea leprosula* survived better and had higher levels of ectomycorrhizal infection in logged forest than in undisturbed forest.

Although dipterocarps were known to form ectomycorrhizas since the 1920s (Van Roosendael and Thorenaar, and Voogd, cited in Smits 1992), it was only in the last ten years that research into applied aspects of the dipterocarp root symbiosis, in particular its role in plant establishment and nutrition, has intensified, with the growing need for rehabilitation and reforestation. Mycorrhizas are also viewed as ‘biofertilisers’, an alternative to chemical fertilisers for infertile tropical soils where reforestation is being carried out (de la Cruz 1991). This chapter discusses the current state of knowledge of dipterocarp nutrition and root symbiosis, and identifies priorities and needs for future research.

Mycorrhizal Fungi and Dipterocarps

Mycorrhizal Associates of the Dipterocarps

Ectomycorrhizas are usually formed by members of the Basidiomycetes and Ascomycetes but in some cases may also be formed by Zygomycetes (species of *Endogone*) (Trappe 1962, Harley and Smith 1983). In the Dipterocarpaceae most observations implicate Basidiomycete genera. In Malaysia over fifty different agarics and boleti, four earthballs and a new species of *Pisolithus* have been found associated with dipterocarps (Watling and Lee 1995). The dominant fungi were species of *Amanita*, *Boletus* and *Russula* with members of the Russulaceae being most numerous. Other researchers have also reported species of *Amanita*, Russulaceae, Boletaceae and Sclerodermataceae as mycorrhizal associates of dipterocarps in Malaysia (Becker 1983, Lee 1992). Species of *Amanita*, *Russula*, *Boletus* and *Scleroderma* were reported as dominant ectomycorrhizal fungi of dipterocarps in Indonesia (Hadi and Santoso 1988, Ogawa, 1992a, Smits 1994). Similar associations have also been reported from Sri Lanka (de Alwis and Abeynayake 1980). Over a six year observation period in Kalimantan, Indonesia, 172 fungi species from 36 genera were found associated with 23 dipterocarp species with species of *Amanita*, *Boletus* and *Russula* being the dominant fungi (Yasman 1993). In the Philippines 32 species of ectomycorrhizal fungi from 11 families were found associated with dipterocarps, with species of *Russula* and *Lactarius* predominating (Zarate *et al*. 1993). In Thailand, Aniwat (1987) reported species of *Russula*, *Lactarius*, *Boletus*, *Amanita*, *Pisolithus*, *Tricholoma* and *Lepiota* as the most common genera of ectomycorrhizal fungi in dry deciduous dipterocarp forest and semi-evergreen dipterocarp forest. Such information on the identity and diversity of the mycorrhizal fungi would assist in the development of a base for understanding the relationship between mycorrhizal fungi and forest function.

It is an established fact that several different fungi can form morphologically different mycorrhizas on the root system of a single plant. Although some ectomycorrhizal fungi show some host specificity at the host genus level (Chilvers 1973), most ectomycorrhizal fungi generally have broad host ranges. In a recent experiment Yazid *et al*. (1994) showed that a strain of *Pisolithus tinctorius* isolated from under eucalypts in Brazil could form perfectly functional ectomycorrhizas with two species of Malaysian dipterocarps, *Hopea helferi* and *H. odorata*. Various studies with dipterocarps have shown that several different ectomycorrhizas may be associated with the roots of any one plant and very often the same mycorrhiza may be associated with different host species and even genera (Becker 1983, Yusuf Muda 1985, Berriman 1986, Lim 1986, Julich 1988, Hadi *et al*. 1991, Lee 1988, 1992, Smits 1994, Lee *et al*. in press).

Until the late 1980s there were only two published reports of successful isolation of indigenous ectomycorrhizal fungi associated with dipterocarps into pure culture (Bakshi 1974, de Alwis and Abeynayake 1980). However, recently successful isolations of several indigenous dipterocarp ectomycorrhizal fungi species were obtained in Indonesia, Malaysia, the Philippines and Thailand, from various dipterocarp hosts (FRIM unpublished data, Sangwanit 1993, Supriyanto *et al*. 1993a, Zarate *et al*. 1993).

Inoculation and other Studies

In most studies of the effects of mycorrhizal inoculation on dipterocarps reported thus far, seedlings have been inoculated with soil inoculum, chopped dipterocarp root inoculum or chopped fruit bodies. Such uncontrolled inoculation studies are self-limiting and non-repeatable. Controlled inoculation experiments with identified and definite fungal strains or species, in particular indigenous ones, are needed so that we can better understand dipterocarp mycorrhizal physiology and explore their potential for application in forestry. Spore inoculum in the form of capsules, tablets or powder of ectomycorrhizal fungi collected from the wild have also been used for inoculation of dipterocarps (Fakuara and Wilarso 1992, Ogawa 1992b, Sangwanit 1993, Supriyanto *et al*. 1993b), but these remain on a small scale and are dependent on fungi which fruit frequently and produce spores in abundance. Some progress has also been made in the development of controlled inoculation techniques for dipterocarps using mycelial pure cultures (Sangwanit 1993, Lee *et al*. 1995) but much fundamental research needs to be carried out before the development of appropriate delivery systems is explored.

The few reports of controlled dipterocarp mycorrhizal inoculation and synthesis have been conducted with exotic fungi, mainly *Pisolithus tinctorius* (Smits 1987, Sangwanit and Sangthien 1991, 1992, Hadi *et al*. 1991, Lapeyrie *et al*. 1993, Yazid *et al*. 1994), and *Cenococcum* (Sangwanit and Sangthien 1991, 1992). In Indonesia, successful mycorrhizal synthesis has been reported between a local isolate of *Scleroderma columnare* and seedlings of *Shorea stenoptera*, *S. palembanica*, *S. selanica*, *S. leprosula*, *Hopea mengerawan* and *H. odorata* (Santoso 1989). Successful synthesis with *Astraeus hygrometricus* on *Dipterocarpus alatus* in Thailand (Sangwanit and Sangthien 1991, 1992) and unnamed species of *Russula*, *Scleroderma* and *Boletus* on five dipterocarp species in Indonesia (Hadi and Santoso 1988) has been implied on the basis of a growth response in inoculated seedlings.

However, no data on the nature or level of mycorrhizal infection were presented. The report by Louis and Scott (1987) of mycorrhizal synthesis in root organ cultures of *Shorea roxburghii* can be discounted as their illustrations and descriptions do not show ectomycorrhizas but hyphal invasion into root cells. Moreover the fungus they used, *Rhodophyllus* sp. was from a genus not normally considered to be ectomycorrhizal.

The effects of various environmental factors on dipterocarp ectomycorrhizas and their subsequent effects on plant growth have been the subject of some recent studies. Smits (1994) suggested that the obligate nature and temperature sensitivity of the dipterocarp ectomycorrhizal relationship are the determining factors for good dipterocarp seedling performance. Yasman (1995) stated that light intensity influenced ectomycorrhizal formation in dipterocarp seedlings but that the effects varied between different host species. The physiology of how light regulated ectomycorrhizal formation was, however, not examined. According to Yasman (1995), neither light nor soil conditions represented the main factors for successful dipterocarp regeneration under a closed canopy; dipterocarp seedling survival was mainly related to the presence of mycorrhizal inoculum and the support of the seedlings by their ectomycorrhizal connections to roots from mother trees that had well illuminated emergent crowns. However, this may be an oversimplification as different species of dipterocarps have different light requirements (Mori 1980, Sasaki and Mori 1981). Lee *et al.* (in press) found high levels of ectomycorrhizal infection (60%) on seedlings of *Hopea nervosa* and *Shorea leprosula* under heavy shade in undisturbed forest supporting Yasman's (1995) hypothesis, but also found that *S. leprosula* which is a light demanding species had poor survival compared to *H. nervosa* which is a shade tolerant species.

Mineral Nutrition

It must be emphasised that very few studies have been conducted on the very important aspect of mineral nutrient requirements of dipterocarps. Fertiliser trials have been conducted for several dipterocarp species but the information presently available is far from conclusive. Although a preliminary guide for the diagnosis of nutrient deficiency of tropical forest trees has been developed (Fassbender 1988), its applicability and suitability for dipterocarps has to be tested more extensively.

Sundralingam (1983) found that NP fertilisers generally improved growth of potted *Dryobalanops aromatica* and *D. oblongifolia* seedlings. In another experiment, Sundralingam and her co-workers (1985) found that nitrogen rather than phosphorus was the most important fertiliser required for improved growth of potted *Shorea ovalis* seedlings. Madius (1983) found that potted *Shorea bracteolata* and *S. parvifolia* seedlings had improved growth and increased nutrient uptake at higher fertiliser levels, particularly when moisture supply was abundant. Turner *et al.* (1993), however, found that potted *Shorea macroptera* seedlings did not respond to fertiliser application. However, they found that the extent of mycorrhizal infection on *S. macroptera* seedlings was correlated with seedling dry mass in the unfertilised control. Similarly, Burslem *et al.* (1995) working with potted *Dipterocarpus kunstleri* seedlings, found no positive growth response to nutrient additions although addition of P increased the concentrations of K and Ca in the leaves. Burslem and his co-workers (1995) caution that results of pot bioassay experiments may be dependent on factors such as pot size, irradiance and soil moisture conditions and that conclusions drawn from such experiments need to be tested by field fertilisation experiments.

Turner *et al.* (1993) also reported that naturally regenerated seedlings of *Shorea curtisii* and *Hopea beccariana* did not show any significant response to fertiliser application in the field. They suggested that addition of nutrients to promote higher growth rates in regenerating seedlings in dipterocarp forests is unlikely to be a silvicultural practice although ensuring adequate infection could be beneficial. Aminah and Lokmal (1995) reported that outplanted rooted, stem cuttings of *H. odorata* showed a significant increase in stem diameter and height only nine to 24 months after application of granular compound fertiliser. No growth response was recorded when plants were measured earlier. Nussbaum *et al.* (1994) found that nutrient availability was the major factor limiting the establishment of *Dryobalanops lanceolata* and *S. leprosula* seedlings on degraded soils in Sabah rather than low soil moisture or high soil temperature. Preliminary results of the effects of NPK fertilisers on the growth of *D. lanceolata* and *S. leprosula* on a large-scale enrichment planting project in Sabah showed that increasing concentrations of fertiliser resulted in increased growth rates but that growth was reduced when 2000 mg of NH_4NO_3 was applied (Yap and Moura-Costa, in press). It will be interesting to see the final outcome of this large-scale field experiment.

Lee and Lim (1989) found that foliar P concentration in naturally regenerated seedlings of *Shorea curtisii* and *S. leprosula* growing in a logged over forest site with low levels of available P (5.8 to 7.1 ppm) was significantly correlated with the extent of ectomycorrhizal infection. Lee and Alexander (1994) working with *Hopea helferi* and *H. odorata* found positive growth responses to mycorrhizal infection but variable responses to nutrient treatments. They also reported the first direct experimental evidence that ectomycorrhizal infection improved P uptake and growth of a dipterocarp species, *H. odorata*. *Scleroderma dicstyosporum* and *S. columnare* were reported to increase levels of nitrogen, phosphorus and potassium in seedlings of *Shorea mecistopteryx* (Supriyanto *et al.* 1993b) but these results may have been misinterpreted. Increased plant height growth, diameter and dry weight as well as uptake of Fe, Mn, Cu, Zn and Al by seedlings of *Shorea compressa*, *S. pinanga*, *S. stenoptera*, *H. odorata* and *Vatica sumatrana* inoculated with chopped fruit bodies of *Russula* sp., *Scleroderma* sp. and *Boletus* sp. have been reported in Indonesia (Santoso 1989, Santoso *et al.* 1989). However, it is not clear whether ectomycorrhizas were formed by the test fungi or by contaminants.

In a study of site characteristics and distribution of tree species in mixed dipterocarp forests in Sarawak, Baillie and co-workers (1987) considered phosphorus the most critical nutrient while magnesium was thought to be important because of possible effects on the efficiency of the dipterocarp mycorrhizal root systems. Some species of dipterocarps, e.g. *Shorea parvifolia* were consistently associated with sites of high P status while others like *S. quadrinervis* were associated with sites of low P status. Amir and Miller (1990) found potassium to be the primary limiting nutrient in two separate forest reserves in Peninsular Malaysia. Burslem *et al.* (1994), however, are of the opinion that any of the macronutrients and micronutrients can become potentially limiting to plant growth when the primary limitation by P is overcome. From a study of soils under mixed dipterocarp forest in Brunei, Takahashi *et al.* (1994) stated that logged over forests are suitable for enrichment planting with dipterocarps since loss of soil nutrients and degradation of nutrient status would be small because of nutrient accumulation in the deeper horizons.

It is known that different tree species have differing site requirements reflecting their differing abilities to take up nutrients from intractable soil sources due to differences in root system architecture and in the particular differences in the mycorrhizal relationships between species (Miller 1991). Yasman (1995) found that light demanding *Shorea leprosula* seedlings could form many more ectomycorrhizal types than shade tolerant *Dipterocarpus confertus* seedlings. Mineral nutrition, plant light requirements and mycorrhizal infection are very intimately related but it is only recently that the importance of this relationship has begun to receive recognition. Newton and Pigott (1991a) working with oak and birch found that application of fertilisers could reduce the number of mycorrhizal types and their relative abundances. Lee and Alexander (1994) found that full nutrient application prevented ectomycorrhizal formation in *Hopea odorata* but not in *H. helferi*. This may indirectly affect the drought tolerance of the host plants and consequently have implications on forest management. Burslem *et al.* (1994) suggested that mycorrhizas play an important role in enabling *Melastoma* to grow on very nutrient poor soils despite being highly nutrient demanding. They suggested that for mycorrhizal plants, limitation by the major cations may prove more significant than limitation by P. In a more recent study, Burslem *et al.* (1995) suggest that shade tolerant seedlings of lowland tropical forest which possess mycorrhizas are not limited by P supply because the mycorrhizas effectively relieve them of P limitation and/or because such plants have a low demand for nutrients for growth at low irradiance.

It is clear that there is an urgent need for more integrated studies on dipterocarp mineral nutrient requirements and that such studies must take into consideration the role of the dipterocarp mycorrhizal association and the effect of different light regimes. While such studies are more easily conducted in the nursery with potted plants, there is also a need to test the conclusions of such experiments in the field.

Research Priorities

The need for more research into the dipterocarp mycorrhizal association is already well recognised and is actively being pursued in Southeast Asia. However, the same cannot be said of research into dipterocarp mineral nutrition requirements. With the present interest in establishing plantations of dipterocarps, fertilisers are being applied with the hope of producing enhanced or more rapid growth without a clear understanding of dipterocarp mineral nutrition requirements. This very important aspect of dipterocarp silviculture needs to be studied in much more detail. This is reflected in the current state of knowledge discussed above and in the identification of research priorities discussed below.

A word of caution before discussing future research priorities: results of many of the dipterocarp mycorrhizal studies carried out in this region, for example, the BIO-REFOR proceedings, are often difficult to interpret or not verifiable because of poor experimental design, lack of statistical analysis, or incomplete monitoring and reporting. Experiments need to be more carefully planned, controlled and monitored, to ensure that the observed effects are genuinely due to the inoculated ectomycorrhizal fungi and not from other contaminants.

In view of the multi-faceted and some yet unknown aspects of dipterocarp mycorrhizas and nutrition, and the current efforts to establish dipterocarp plantations in the region, the following research priorities have been identified. Many paraphrase the recommendations made by Malajczuk *et al.* (undated) in their Annex 1 - Recommended Research Programme on Mycorrhizal Management, as these are found to be very relevant to dipterocarp mycorrhizal research. The following should be the future research priorities for dipterocarp mycorrhizas and nutrition:

1. There is a need for more integrated studies on dipterocarp mineral nutrient requirements and mycorrhizal infection for seedling/cutting establishment in the field.

   Most fertiliser trials carried out thus far have ignored the role of mycorrhizas. They have a significant role to play in plant mineral uptake and are being considered in some quarters as possible fertiliser substitutes/supplements. Results from pot experiments have limited applicability in field conditions especially if plants in the field are interconnected by mycorrhizal links. These intact mycelial networks constitute the main source of inoculum when seedlings are grown near an established tree (Newton and Pigott 1991b, Alexander *et al.* 1992, Yasman 1995) as is likely to occur in reforestation of selectively logged dipterocarp forests.
2. The mycorrhizal dependency of dipterocarps for reforestation should be determined for each species at various ages in various habitats (different light regimes, soil nutrient levels, water retention, organic substrates).

   Mycorrhizal fungi like vascular plants may vary in their ecological and physiological requirements and under given circumstances, some fungi may benefit particular hosts more than others. The ability of a particular mycorrhizal fungus to enhance the foliar nutrient content of the host may not be indicative of the isolate's ability to improve seedling growth and subsequent outplanting performance (Mitchell *et al.* 1984). Surveys and identification of ectomycorrhizal fungi associated with dipterocarps should be continued and the results shared among workers in the region.
3. Field studies should be conducted to determine the influence of nutrition and mycorrhizal infection on dipterocarp seedling survival, and their roles in determining forest composition.

   It has been suggested that the 'nursing' phenomenon (Read 1991), i.e. regeneration of seedlings in the vicinity of parent trees whereby they become incorporated into a mycelial network, reduces tree species diversity (Alexander 1989). It is believed that because mycorrhizal fungi have a great influence on plant survival in new and reclaimed sites, tree health and site quality, they are the cornerstone to proper establishment of functional forest ecosystems (Malajczuk *et al.* undated).
4. Isolation and pure culture of indigenous ectomycorrhizal fungi should be intensified, and species associated with the desired host plant species both in unlogged and logged over forest requiring rehabilitation should be determined.

   There is evidence that some of the easily manipulated exotic mycorrhizal fungi such as *P. tinctorius* may be out competed by indigenous (co-evolved) mycorrhizal fungi in the field (see Chang *et al.* 1996). Moreover, fungi which are beneficial to the host in the natural forest may not be adapted to the degraded site where reforestation will be carried out. It has been suggested that successful establishment of indigenous ectomycorrhizal trees is limited to areas where inoculum already exists (Alexander 1989). However, Smits (personal communication) reported that dipterocarps have been successfully established on a large-scale in heavily burned secondary forest at Longnah, East Kalimantan.

5. The mycorrhizal fungi should be compared for effects on hosts in different soils under controlled conditions and for adaptability to handling in nursery inoculation processes and to nursery cultural practices.

   Brundrett *et al.* (1996) have comprehensively discussed the differential effect of various soil attributes on mycorrhizal fungal growth which have implications for tree establishment.
6. Host specificity and compatibility of selected ectomycorrhizal fungi should be determined in pot experiments with selected host species and genera.
7. Efforts on the selection of mycorrhizal fungi for inoculation of seedlings should be continued. This should be based on a set of criteria which would include satisfactory vegetative growth or abundant sporulation for production of large quantities of inoculum, adaptability to inoculation manipulation, ability to form mycorrhizas with a broad range of host species, and ability to enhance growth of the host tree (Trappe 1977, Marx *et al.* 1992).
8. Inoculation experiments should be conducted with identified or known and preferably indigenous mycorrhizal strains.

This is to ensure that results are repeatable and verifiable and for development into practical application techniques for field use. This is important for the sustained production of effective mycorrhizal inoculum.

Current Mycorrhizal Research Groups and Needs

Presently dipterocarp mycorrhizal research is most actively being pursued in Indonesia and Malaysia and to a lesser extent in Thailand. Some research has also recently begun in the Philippines.

Indonesia

Among the Southeast Asian nations, Indonesia has the most numerous researchers and research institutes engaged in dipterocarp mycorrhizal research. The main institutes are BIOTROP and Bogor Agricultural University in Bogor, Gadjah Mada University in Yogyakarta, Universitas Mulawarman and the TROPENBOS Project in East Kalimantan which includes the Association of Forest Concession Holders. A variety of topics are being investigated but most of the results are published in local Indonesian journals in Bahasa Indonesia (see Supriyanto *et al.* 1993a) and often are very brief with details of experiments missing. This situation is slowly changing with the emergence of collaborative projects funded by foreign agencies such as the European Economic Community (EEC), Overseas Development Authority of the U.K. (ODA), the Dutch TROPENBOS and the Japanese government, and as more international symposia on mycorrhizas are organised. However, there appears to be some lack of coordination and communication between the various research groups, with each group appearing to work in isolation. It has also been pointed out that many of these groups conduct research in nurseries or in small experimental dipterocarp plantations outside the area of their natural occurrence (Smits 1992). Consequently not all the results may be of equal importance for an understanding of the functioning of dipterocarp mycorrhizas under natural conditions. Comprehensive reports of the status of mycorrhizal research in Indonesia are given in Hadi *et al.* (1991) and Supriyanto *et al.* (1993a).

Malaysia

In Malaysia dipterocarp mycorrhizal research is presently only being conducted at the Forest Research Institute Malaysia (FRIM). Considerable progress has been made towards the understanding of the biology and ecology of some dipterocarp mycorrhizas, and techniques are being developed and improved for controlled inoculation of dipterocarp planting material. The research has largely benefited from collaboration with researchers from Europe under a joint FRIM-Commission of the European Communities collaborative project. The survey and identification of mycorrhizal fungi are actively being pursued under another collaborative project with the Royal Botanic Garden, Edinburgh, funded by the ODA. Results have been published in several international journals.

Thailand

There are two institutes conducting dipterocarp mycorrhizal research in Thailand, these being the Faculty of Forestry at Kasetsart University and the Royal Thai Forest Department. Most of the research has concentrated on surveys and the effectiveness of ectomycorrhizas in promoting growth of seedlings under adverse conditions. Presently dipterocarp mycorrhizal research is not very active and progress has been slow due to the limited number of researchers and funds available (Sangwanit 1993).

Philippines

Work on dipterocarp mycorrhizas in the Philippines started about five years ago at the University of Los Baños, Laguna (de la Cruz 1993) with attempts to combine dipterocarps propagated by cuttings/tissue culture and mycorrhizal inoculation. Results will be reported in a forthcoming publication (de la Cruz in press). Considerable research has been focused on the development of mycorrhizal inoculum delivery systems, mainly for use with pines and eucalypts. Some of these systems may be effective for dipterocarps but tests need to be carried out, especially under field conditions. Recently a survey of ectomycorrhizal fungi associated with pines and dipterocarps was undertaken with funding from the EEC (Zarate *et al.* 1993).

Other Groups

Some preliminary research on dipterocarp mycorrhizas has also been carried out in Sri Lanka (Abeynayake 1991). However, such work is not given much emphasis as reforestation of degraded lands with dipterocarps has not been successful and Sri Lanka is presently not using dipterocarps for reforestation on a large scale (Abeynayake 1991). In India some research was conducted on ectomycorrhizal fungi associated with *Shorea robusta* in the early 1970s (Bakshi 1974) but since then there have been no new reports of mycorrhizal research on dipterocarps.

Mycorrhiza Network Asia

Mycorrhiza Network Asia was established at the Tata Energy Research Institute, New Delhi on 1 April 1988. This network serves as a point of reference for mycorrhizal scientists in Asia and provides various services such as literature searches, a directory of Asian mycorrhizal researchers, a germplasm bank, organisation of meetings and symposia, and the publication of a quarterly newsletter, Mycorrhiza News. Mycorrhizal researchers from the various Southeast Asian countries are members or are aware of the existence of this network and meet from time to time at the Asian Conference on Mycorrhizae (ACOM); the Third ACOM was held in Indonesia in April 1994. Previous meetings were held in India (1st ACOM) and Thailand (2nd ACOM).

However, rapid progress on dipterocarp mycorrhizal research in the Southeast Asian region is constrained by several factors:

1. Insufficient numbers of suitably trained and active mycorrhizal researchers in most Southeast Asian countries. For example, there are only two scientists actively working on dipterocarp mycorrhizas in Malaysia and Thailand respectively.

   BIOTROP has conducted several training courses on mycorrhizas for participants from the ASEAN countries but it is unfortunate that most trainees do not engage in mycorrhizal research upon returning to their own countries. A slightly different problem is encountered in the Philippines where many trained researchers leave the country for better opportunities abroad. In Indonesia an encouraging situation has recently developed where practising foresters were sent by their employers, the various concession holders, to attend a two-week local training course on mycorrhizal techniques conducted by BIOTROP.
2. Insufficient budget to undertake such research.

   Most local governments do not allocate sufficient funds for basic research including mycorrhizal research. De la Cruz (1993) pointed out that much of the productive mycorrhizal research came from external grants.
3. Lack of regional collaboration.

   Much has been spoken about the need for regional research collaboration in many fields, including mycorrhizal research, but to date no concrete proposals have materialised for regional mycorrhizal research.
4. Lack of expertise in some fields of mycorrhizal research, such as identification of ectomycorrhizal fungal associates, culture and propagation of mycorrhizal inoculum.

   A local or regional flora of potential ectomycorrhizal fungi is needed as baseline information for many studies. A start has been made in several Southeast Asian countries to collect and collate such information. However, most of the research is only possible because of the collaboration of foreign experts working on short-term projects.

5. Limited access to regional research results.
   Results of many studies are reported only in local publications to which other researchers in the region have no access. Presently the most important channels of information are regional and international symposia or conferences where researchers have an opportunity to discuss their findings. Researchers should be encouraged to publish their findings in refereed journals or in publications with a wider circulation so that their results may be shared with others.
   Joint collaborative projects involving active dipterocarp mycorrhizal researchers, plant physiologists, and soil scientists from the various countries in the region and experienced scientists from the developed countries would be one approach to advancing research in this field. Training relevant personnel who would be likely to put their training into practice would also help overcome some of the problems encountered. It is envisaged that agencies such as the Center for International Forestry Research and the European Union can play pivotal roles in this respect.

Funding Requirements

Funding is required for a multi-lateral collaborative project involving scientists from related disciplines in the various Southeast Asian countries and experienced mycorrhizal researchers from the developed countries to conduct research into some, if not all, of the priority areas identified. Funding should at least be for an initial period of three years and should include components of training for local scientists and field personnel. Local scientists who will be directly involved in the research should receive relevant training in the first year of the project.

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Chapter 7

Pests and Diseases of Dipterocarpaceae

C. Elouard

Introduction

There has been relatively little research on the pests and diseases of dipterocarps. Most investigations have been directed to forest products commensurate with their economic value. Now that dipterocarps are being established by enrichment planting in forests or in extensive plantations, more attention will have to be directed to the pests and disease problems of living trees.

Pests and diseases on dipterocarps affect seeds, seedlings, saplings, trees and their products. A large proportion of earlier studies catalogued dipterocarps' pests and diseases. Little is known about their ecology, natural enemies, management and control. The only well-studied species is *Shorea robusta,* an important timber species in central and northern India and grown in plantations. Pests have been investigated on forest trees only when mortality resulted in economic loss, as for *Shorea robusta* in India. There has been considerable work on pests of Indian dipterocarps (Stebbing 1914, Beeson 1941, Bagchee 1953, 1954, Bagchee and Singh 1954, Bhasin and Roonwal 1954, Bakshi 1959, Mathur and Balwant Singh 1959, 1960a, b, 1961a, b, Mohanan and Sharma 1991). Dipterocarp diseases are mainly recorded as fungal diseases. The only record of bacterial disease is *Agrobacterium tumefaciens,* causing leaf gall formation on saplings (Ardikosoema 1954, Torquebiau 1984, Smits *et al.* 1991). An alga, *Cephaleuros virescens*, is reported causing leaf disease (Mittal and Sharma 1980, Elouard 1991).

The establishment of forest plantations and the enrichment planting of logged-over forests with local species such as dipterocarps requires collection of fruits, seed storage and raising of seedlings in nurseries. Thousands of seedlings growing in a confined place can lead to the development and proliferation of non-specific and even specific pathogens and pests. A timber trend study in India (Anon. *in* Bakshi *et al.* 1967) shows that combined loss in forest wealth due to causes like fire, decay, insects and windfall is 13 per cent. This emphasises the need for proper integrated pest and disease management to protect investments.

Pests and pathogens are present in forest ecosystems at all stages and take an active part in their ecological balance and dynamics. Though pathogen and pest damage is kept controlled at non-epidemic levels in natural forests (Augspurger 1990), logging activities change the natural balance of the forest ecosystems, and can favour proliferation of pests and pathogens. Moreover, enrichment planting and forest plantations can be a dramatic source of pest and disease propagation, particularly on monospecific plantations such as the case of the leaf blight *(Microcydus ulei)* of rubber in South America. The major epidemics recorded on dipterocarps are caused by insects on *Shorea robusta,* e.g. *Hoplocerambyx spinicornis* (Cerambycidae), an important heartwood borer in India and Pakistan, and the mealybug *Drosicha stebbingi* (Coccidae) which have caused considerable damage (Beeson 1941).

The main constraints to research on dipterocarp pests and diseases are shortage of trained staff, lack of cooperation among scientists and institutions in Asia, inadequate funding and infrastructure facilities, high cost of pest and disease identification, lack of information on the economic effects of pests in plantation forestry, and need for more contacts between researchers, foresters and staff of timber companies.

Pests

Seeds

Dipterocarp seeds are produced irregularly and sparsely in some species, and fruit production varies in quantity and quality from year to year. Mass fruiting appears to favour seed predators, but it can also be a strategy to escape complete seed destruction (Janzen 1974). Seed predation can be very high, and the crop can be completely wiped out. Curran and Leighton (1991) reported that the 1986 crop was entirely destroyed (100,000 seeds/ha) in the lowland forest of West Kalimantan. The major losses are caused by insect pests. Natawiria *et al.* (1986) observed weevils (Curculionidae) damaged 40-90% of the seeds of *Shorea pauciflora, S. ovalis, S. Iaevis, S. smithiana* and *Dipterocarpus cornutus.* Daljeet-Singh (1974) reported that weevils were responsible for more than 80% of the total seed damage in all case studies except *Shorea macrophylla,* in which the most important pests were the Colytidae. In 1991, 70% of *Dryobalanops aromatica* seeds were damaged by weevils in Malaysia (Elouard, unpublished).

While insects are the major seed pests, there is destruction by birds and mammals. Wild pigs *(Sus scrofa),* squirrels *(Callosciurus prevostii* and C. *notatus)* and monkeys *(Presbytis rubicunda)* caused damage to the crops of some species (Kobayashi 1974, Natawiria *et al.* 1986, Curran and Leighton 1991). Kobayashi (1974) observed that 80% of the mature seed crop *of Hopea nervosa* was damaged by squirrels. Parrots (*Psittacula* sp.) have been observed feeding on dipterocarp seeds (Natawiria *et al.* 1986). However, monkeys and squirrels prefer to eat other available fruit and seeds (Curran and Leighton 1991). Dipterocarp resin contains a high percentage of alkaloides and can be repellant to mammals. *Neobalanocarpus heimii* seeds are hardly eaten by mammals, but losses are due to the destruction of a part of the seed tasted by the rodents and then rejected (Elouard *et al.* 1996).

Over 80 species of seed pests have been described on various dipterocarp seeds, with both pre- and post-dispersal insect pests. The former attack the fruits on the tree before dispersal, whereas the latter attack fruits on the ground. The pre-dispersal fruit pests are weevils (Curculionidae) and Lepidoptera, and the post-dispersal ones are Lepidoptera (Toy 1988). It is rarely possible to distinguish between pre- and post-pests of Lepidoptera. The mode of attack of the weevils and Lepidoptera on dipterocarps is described by Daljeet-Singh (1974). The weevils come at the early development of the fruits, pierce the pericarp and deposit a single egg. The larvae feed on the cotyledons throughout the period of growth. The pupal chamber is made of larval frass. Usually, the fruit drops to the ground before pupation and the adult weevils remain within the fruit for a few days before emerging. They are sexually immature at emergence. The Lepidopteran predators lay their eggs on the dipterocarp fruits. On hatching, the larvae bore into the fruit, feed on the cotyledons and pupate. Prior to pupation, the larva attacks the pericarp leaving only a thin covering that the newly emerging adult can break.

Toy (1988) observed in Malaysia that species of *Nanophyes* (Curculionidae) were generic specialists and some species appeared to be even sub-generic specialists. The existence of insect pests which have a ‘familial specialisation’ raises questions on the function of mass-flowering as a pest satiation strategy (Janzen 1974). The survival of these insects between fruiting events are ascribed to three hypotheses: i) they have either alternative hosts in non-dipterocarp families; ii) dormancy; or iii) maintain more or less continuous generation of pests developing on sporadically flowering trees (Toy 1988). In a study of *Nanophyes shoreae* survival in *Shorea macroptera,* Toy observed that a maximum 1.8% of insects survived during sporadic events, thus dispersal of the insect is not probable. He suggested generalist feeding of adults is the key to their persistence between fruiting events.

Seedlings and Saplings

Few records exist on pests of seedlings and saplings in nurseries, though some reports are available for natural forests. Insects are the main source of damage as leaf feeders, borers, suckers and in gall formation. The other pests recorded are wild boars, rodents and nematodes.

There are few reports of leaf damage to seedlings and saplings (Becker 1983, Tho and Norhara 1983) and the defence properties of essential oils in mature leaves were discussed by Becker (1981). Galls causing leaf damage were reported on dipterocarp species in Singapore, Malaysia and India (Anthony 1972, 1977, Mathur and Balwant Singh 1959), mortality and setback in growth by attacking the young shoots and twigs of *Dryobalanops aromatica* saplings over 1 m tall (Anon. in Tho and Norhara 1983).

Shoot and root borers were recorded on various dipterocarp species (Beeson 1941, Chatterjee and Thapa 1970, Daljeet-Singh 1975, 1977, Sen-Sarma and Thakur 1986, Shamsuddin 1991, Smits *et al.* 1991). Shoot boring does not generally cause mortality (although it was recorded as the major factor of die-back of *Shorea teysmanniana* seedlings (Shamsuddin 1991) but rather induces the formation of multiple leaders after destroying the main shoot (Daljeet-Singh 1975, 1977, Smits *et al.* 1991). Therefore, shoot boring insects are a problem for reforestation programmes. Planting trials with *Shorea ovalis, S. leprosula, S. acuminata* and S. *parvifolia* were conducted in Malaysia, where 50% of *S. acuminata* and 7.3-16.5% of the other *Shorea* seedlings were attacked by shoot borers (Daljeet-Singh 1975).

Insect borers and nematodes can destroy roots. The lepidopteran root borer *Pammene theristhis* (Eucosmidae) has emerged as the most serious pest of the seedlings and young shoots of *Shorea robusta* (sal) in all areas where it is grown in India. It probably plays a prominent role in the regeneration-failure in sal. It has been closely associated with the dying-off of new sal regeneration in the submontane belt of Uttar Pradesh (Beeson 1941; Chatterjee and Thapa 1970). The borer has more than three generations a year: the first generation lays eggs on the seeds on which the larvae feed; the second one bores into young growing shoots of coppice or regeneration of sal up to sapling stage with the resultant die-back of leaders; and the third generation attacks and kills the young seedlings by hollowing the tap root and a part of the stem (Beeson 1941, Sen-Sarma and Thakur 1986). Nematodes were recorded feeding on rootlets of *Hopea foxworthyi* and *Shorea robusta* (Catibog 1977, Mathur and Balwant Singh 1961a).

Wild pigs *(Sus scrofa)* can completely destroy seedling regeneration (Becker 1985, Elouard unpublished). Rodents can be significant as pests of germinating seeds and the cotyledons of young seedlings (Wyatt-Smith 1958) and deer browsing was partly responsible for mortality of *Shorea robusta* seedlings and saplings in India (Davis 1948).

Trees

Tree pests were recorded in Malaysia, Thailand, Indonesia, India, Pakistan and Burma. Most of them are insects belonging to Coleoptera and Lepidoptera, causing defoliation and leaf damage, wood boring and root sucking.

The extent of the damage and the economic losses due to defoliation, essentially caused by insects, has seldom been estimated. Over 130 species of insects cause leaf damage, mostly belonging to the families Geometridae, Lymantriidae, Noctuidae, Pyralidae, Tortricidae (Stebbing 1914, Beeson 1941, Bhasin and Roonwal 1954, Ghullam Ullah 1954, Mathur and Balwant Singh 1959, 1960a, b, 1961a, b, Anderson 1961, Torquebiau 1984, Pratap-Singh and Thapa 1988, Messer *et al.* 1992).

Defoliators in India, Pakistan, Malaysia, Indonesia, Thailand and Philippines, at times cause important damage, e.g. *Shorea robusta* trees in Assam, India were entirely stripped of all green leaves over a very large area by species of caterpillars of the genus *Lymantria* (Stebbing 1914). Defoliation can lead the trees to an extremely weak state which makes them attractive and highly receptive to a lethal infestation from borers such as *Hoplocerambyx spinicornis* (Pratap-Singh and Thapa 1988). Successive defoliations can kill trees, e.g. *Lymantria mathura* on *Shorea robusta* in Assam and north India (Beeson 1941). Following defoliation, the physiology of the tree is affected by the loss of photosynthetic activity: *Shorea javanica* trees, tapped for resin in Sumatra, Indonesia, stopped their resin production (Torquebiau 1984). The attack by insects in *Shorea robusta* forests of Bangladesh appeared to be minor (Ghullam Ullah 1954). According to the author, this may be due to the presence of large colonies of the brown ant, *Oecophylla smaragdina,* known to destroy all kinds of caterpillars (except the hairy species) and to drive away beetles and bugs, thus preventing oviposition in the latter case. Ghullam Ullah noted all the *Shorea robusta* defoliating larvae are hairy caterpillars which are not destroyed by ants.

The borer-fauna of Dipterocarpaceae is very extensive, and has been mostly recorded in India. According to Beeson (1941), only one species, the heartwood borer *Hoplocerambyx spinicornis* (Cerambycidae), is capable of killing healthy trees. The other borers, or secondary borers, attack sickly trees, possibly hastening death by a year or two.

Hoplocerambyx spinicornis is widely distributed in Asia (Burma, Bhutan, India, Indo-China, Indonesia, Malaysia, Nepal, Papua New Guinea, Pakistan, Philippines, Singapore, Thailand). It is a pest of *Parashorea robusta, P. malaanonan, P. stellata, Shorea siamensis, S. assamica, S. obtusa, S. robusta, Anisoptera glabra* and *Hopea odorata.* This insect is a principal pest in the Matang Forest Reserve of Sarawak, Malaysia, and causes severe damage in central and northern India on *Shorea robusta.* Outbreaks of this insect have been recorded periodically since 1897 in Chota Nagpur, India. The grub feeds on and destroys the bast layer eventually killing the tree, and it tunnels down into the heartwood spoiling it for commercial purposes. This cerambycid has the habit of destroying the trees in patches (Stebbing 1914). It produces characteristic symptoms: i) dying-off from the crown downwards by sudden withering of the foliage in autumn or spring; and ii) profuse exudation of resin at points where the first stage larvae bore through the bark.

The biology of *H. spinicornis,* the damage caused by the insect and its control have been studied by Stebbing (1914), Beeson and Chatterjee (1925), Atkinson (1926), Beeson 1941, Bhasin and Roonwal 1954, Roonwal 1952, 1976, 1977, 1978, Mathur and Balwant Singh (1959, 1960a, b, 1961a, b), Mathur (1962), Chatterjee and Thapa (1964, 1970), Sen-Sarma *et al.* (1974), Singh *et al.* (1979), Mercer (1982), Singh and Mishra (1986), Bhandari and Pratap-Singh (1988) and Baksha (1990). The borers prefer large, mature trees, where there is more chance of completing the life cycle. But during epidemics this borer is capable of infesting every tree above 0.3 m girth and and is not confined to mature or over-mature trees. It then affects thousands of hectares of *Shorea robusta* (Sen-Sarma and Thakur 1986). The emergence of the adult beetle is closely synchronised with rainfall (June/July). The beetles lay eggs in the bark and sapwood and a heavily infested tree may contain as many as 900 living larvae. Full grown larvae tunnel into the heartwood and riddle it with galleries, making it unfit for marketing as timber (Sen-Sarma and Thakur 1986). Stebbing (1914) and Mathur (1962) described a method of trapping the insect called the 'tree-trap' system. During outbreaks, one tree per hectare is felled, and the log beaten to expose the inner bark. The adults, attracted by the inner bark, are collected by hand and destroyed. This method has been used since then and is successful in monitoring and controlling the beetle populations (Chatterjee and Thapa 1970, Roonwal 1978, Bhandari and Pratap-Singh 1988). A beetle can locate a freshly felled tree of *S. robusta* at a maximum distance of 2 km (Pratap-Singh and Misra 1981).

Many of the secondary borers attack freshly felled trees, but can occasionally attack moribund trees and hasten their death. They also attack young growth in sickly condition due to some abiotic factors (frost or drought) or biotic factors (e.g. infestation by defoliators) or kill the trees (e.g. *Massicus venustus)* by mass-attack (Beeson 1941). Most borers are not a threat for the tree itself but make it useless for construction purposes and reduce the market value of the timber.

Suckers, belonging to Cicalidae and Coccidae were reported damaging roots (Hutacharern *et al.* 1988) and leaves (Mathur and Balwant Singh 1961a). *Lacifer lacca* (Coccidae), the insect involved in the production of lac, is a sap sucker of *Shorea talura, Shorea* spp. and *Dipterocarpus tuberculatus* (Mathur and Balwant Singh 1959, 1961a, b).

Termite attacks have been reported on living dipterocarp trees (Wyatt-Smith 1958, Nuhamara 1977, Sen-Sarma and Thakur 1980, Smits *et al.* 1991). Smits *et al.* described termite attack on living *Shorea polyandra* in Kalimantan: the trees shed their leaves, while the crown became lighter and the death of the tree was manifested by the exudation of many clumps of black resin from the stem base.

Forest Products

Damage on logs and timbers are mainly caused by termites and beetles. Since it is a field of economic importance, many studies have been conducted on the identification of the pests, their biology and control methods.

Termites attacking logs and wood were studied in Malaysia, Indonesia, India, China (Mathur and Balwant Singh 1960a, b, 1961a, b, Becker 1961, Sen-Sarma 1963, Abe 1978, Sen-Sarma and Gupta 1978, Hrdy 1970, Said *et al.* 1982, Ping and Xu 1984, Dai *et al.* 1985, Quiniones and Zamora 1987, Hutacharern *et al.* 1988), but also in European and even Saudi Arabian laboratories (Alliot 1947, Badawi *et al.* 1984, 1985). Tests on the resistance of wood to termite attacks were widely conducted (Alliot 1947, Becker 1961, Sen-Sarma 1963, Schmidt 1968, Sen-Sarma and Gupta 1978, Hrdy 1970, Dai *et al,* 1985, Badawi *et al.* 1984, 1985). *Pentacme suavis, Shorea guiso, S. robusta, S. obtusa, S. stenoptera, Vatica astrotricha, Hopea hainanensis, Dipterocarpus* sp. proved to be resistant to termite attack. In other studies wood from *Dipterocarpus* spp.

was particularly susceptible to termite attack (Alliot 1947) and that of *Vateria indica* was preferred by *Microcerotermes cameroni* (Hrdy 1970). Heavy hardwoods, *Neobalanocarpus heimii* and *Vatica* sp., were the least susceptible species to termite attack. Wood of *Neobalanocarpus heimii, Shorea ovalis* and *Shorea* spp. contain repellants against *Cryptotermes cynocephalus* (Said *et al.* 1982).

Ambrosia beetles (pin-hole borers) infest logs and wood timber (Browne 1950, Bhatia 1950, Anon. 1957, Anuwongse 1972, Fougerousse 1974, Garcia 1977, Hutacharern *et al.* 1988). Browne reported the susceptibility of *Shorea leprosula* logs to attack by ambrosia beetles, more particularly *Xyleborus pseudopilifer* which usually attacks only dipterocarps, and *X. declivigranulatus* which is polyphagous. Shot and pin-hole borers attacked barked-logs of *Parashorea malaanonan* more severely than unbarked ones, as well as logs left in the shade (Anon. 1957).

Insecticide trials against termites (Mathur *et al.* 1965, Said *et al.* 1982, Schmidt 1968) found BHC, aldrex and chlordane were effective. Preservatives, such as copper-chrome-arsenic, increased wood resistance to attack of *Coptotermes curvignathus.*

Studies of treatment against insect damage on logs and wood have been mainly conducted in India. Insecticides such as BHC, fenpropathrim, fenvalerate, permethrine, telodrine, diedrex, gammexane and to a lesser extent chlordane were effective against beetles such as *Lyctus brunneus* (Lyctidae), Cerambycidae, Bostrichidae, Platypodidae and Scolytidae (Browne 1951, Menon 1954, 1958, Francia 1958, Thapa 1970, Ito and Hirose 1980, Chatterjee and Thapa 1971, Nunomura *et al.* 1980, Daljeet-Singh 1983). Thapa (1970) showed that BHC offered a satisfactory protection when sprayed on logs of *Parashorea tomentella* against cerambycids and more particularly *Dialeges pauper* and *Hoplocerambyx spinicornis.*

A minimum of 3 months immersion of *Shorea robusta* poles in water gives protection against bostrichid attack, most probably due to the leaching of sugars during soaking (Anon. 1946). Fresh water and marine borers have damaged boats and poles (Shillinglaw and Moore 1947, Anon. 1947, Edmonson 1949, Premrasmi and Sono 1964, Mata and Siriban 1976, Chong 1979, Santhakumaran and Alikunhi 1983, Chen 1985). Most records concern marine borers, though nymphs of species of mayfly (Ephemeroptera) burrow into and damage boats and submerged wooden structures in fresh water in Thailand (Premrasmi and Sono 1964).

The durability and resistance of dipterocarp timbers and poles against marine borers, mainly in the genera *Martesia, Teredo, Nausitora, Dicyathifer, Bactronophorus, Baukia, Nototeredo* and *Limnoria,* were studied by Shillinglaw and Moore (1947) and Mata and Siriban (1976). *Anisoptera polyandra* in New Guinea (Shillinglaw and Moore 1947), *Neobalanocarpus heimii* and *Shorea maxwelliana* (Chong 1979) had good natural resistance to shipworms and other marine borers. *A. polyandra is* therefore recommended for piling in new marine structures. *Shorea laevifolia* has been reported as being resistant to *Martesia* and *Teredo* species (Anon. 1947). In China, Chen (1985) demonstrated that the resistance to marine borers of hardwood is higher than that of softwood, and heartwood is superior to sapwood. Edmonson (1949) reported *Martesia* sp. destroyed rapidly apitong *(Dipterocarpus* sp.*)* and *Shorea* sp. in the Philippines. According to Santhakumaran and Alikunhi (1983), *Shorea robusta* and *Dipterocarpus indicus* had a very heavy attack whereas *D. macrocarpus* had a medium attack and *D. turbinatus* and *Hopea parviflora* had a moderate attack in 7-8 months by *Martesia* and *Teredo* species. Some treatments with creosote proved to be effective (Chong 1979, Mata and Siriban 1976).

Diseases

Seeds

Bacteria, viruses and especially fungi cause loss of seed viability. Infection takes place on the tree, during the flowering and/or development of the fruit, on the ground at the fruit fall, and during the period from harvesting to sowing in the nursery. During these stages, seed contamination can occur with organisms causing diseases in the nursery or serving as primary inocula for decay organisms specific to seedlings (Mohanan and Sharma 1991). Seeds collected from the forest floor are more liable to be infected by decay organisms. Fungal infection also occurs during seed storage, where large quantities of seeds in containers and high moisture are propitious conditions for fungal development.

Over 100 species of seed fungi have been identified in Malaysia (Hong 1976, 1981a, Lee and Manap 1983, Elouard and Philip 1994), in Thailand (Pongpanich 1988), in Indonesia (Elouard 1991), and in India (Mittal and Sharma 1982, Mohanan and Sharma 1991). Most of these fungi belong to Fungi Imperfecti (Deuteromycetes). Though a large number of species are recorded on dipterocarp seeds, their disease transmission and seed degradation is not well documented. In general, poor seed storage conditions affect seed quality and facilitate fungal infection and spread of fungi (see Chapter 4). There have been few fungicidal studies on stored dipterocarp seeds and there is a need for seed pathology research to establish suitable control methods for fungal infection both during storage and in nurseries.

Two categories of seed fungi can be identified, the storage fungi and the seedborne fungi. The first category includes saprophytic fungi growing on the seed testa, and the second refers to pathogenic fungi developing from the internal part of the seed. Both cause significant damage during storage.

Storage fungi

Storage fungi grow fast, developing from the ever-present spores in the air or on the seed testa. They rapidly invade the embryo, causing damage and decreased germination (Neergard 1977). These saprophytes do not feed on the seeds, but their excessive development leads to the rotting of the seeds. The most common species belong to the genera of *Aspergillus, Penicillium, Pestalotia, Pestalotiopsis, Gliocladium, Fusarium, Cylindrocladium* and *Lasiodiplodia.* Most of these fungi produce enormous quantities of spores spreading rapidly and infecting the whole seed stock.

Aspergillus niger was widely recorded on dipterocarp seeds (Pongpanich 1988, Singh *et al.* 1979, Mittal and Sharma 1981, 1982, Hong 1976, 1981a, Lee and Manap 1983, Hadi 1987, Elouard and Philip 1994). In India, fungicidal trials were conducted on fungi infecting *Shorea robusta* seeds, namely *Aspergillus niger, Penicillium albicans, P. canadense, Cladosporium cladosporioides, C. chlorocephalum* and *Rhizopus oryzae* (Mittal and Sharma 1981). Brassical, Bavistin and Dithane-45 proved effective. In Malaysia, Elouard and Philip (1994) tested fungicides on *Hopea odorata* seeds, and Benlate 50 and Thiram were effective without preventing germination or affecting seedling development.

Seed-borne fungi

Seed-borne fungal infection most probably takes place during the flowering period or at the early stage of fructification. The infection occurs through spores present in the environment or through inoculation of spores or mycelium by pollinating insects or predispersal insect predators while laying their eggs. Seed-borne fungi feed on living tissues, destroying the embryo and the cotyledons. The mycelium develops inside the seed and eventually covers the whole fruit. In natural stands, seed destruction is mainly caused by seed-borne fungi.

The most common seed-borne fungi belong to the genera *Fusarium, Cylindrocladium, Lasiodiplodia, Colletotrichum, Curvularia* and *Sclerotium* (Hong 1976, 1981a, Lee and Manap 1983, Charlempongse *et al.* 1984, Pongpanich 1988, Mohanan and Sharma 1991, Elouard 1991, Elouard and Philip 1994). The Basidiomyceteae *Schyzophyllum commune* has been observed on several dipterocarps (Hong 1976, Vijayan and Rehill 1990, Elouard and Philip 1994), developing on the cotyledons and embryo and ultimately covering the whole seed and producing carpophores. Infection leads to high levels of mortality: 70% of *Shorea leprosula* and *S. ovalis* seeds were rotted by a *Fusarium* species and 90% of *Shorea glauca* seeds were destroyed by *Schyzophyllum commune* (Elouard and Philip 1994).

Seedlings and Saplings

Over 40 species have been identified causing seedling diseases. The most common are in the genera *Colletotrichum, Cylindrocladium, Fusarium* and *Lasiodiplodia,* which are responsible for damping-off, wilting, root and collar rots, cankers, leaf diseases, thread blights and gall formation.

Damping-off is the rotting of seeds and young seedlings at soil level (Hawksworth *et al.* 1983) and is in most cases caused by seed-borne fungi (Hong 1981a, Lee and Manap 1983, Pongpanich 1988, Elouard l991, Elouard and Philip 1994). Collar rot, root rot and wilting (loss of turgidity and collapse of leaves (Hawksworth *et al.* 1983)) are mainly caused by *Fusarium* species (Foxworthy 1922, Thompson and Johnston 1953, Hong 1976, Lee and Manap 1983, Elouard, l991, Elouard and Philip 1994).

A canker is a plant disease in which there is sharply-limited necrosis of the cortical tissue (Hawksworth *et al.* 1983). Though most of the time stem cankers are not lethal, they still can be harmful decreasing the strength of the stem and causing it to fracture. Root and collar cankers can affect the vascular system of the plant and eventually result in plant death by wilting (Spaulding

1961, Elouard unpublished). *Schyzophyllum commune* has been reported as causing die-back of young saplings of *Shorea robusta,* cankers caused by frost or fire providing the route of entry. The fungus, once established, attacks the living sapwood killing the stem beyond the scars, and it progresses both up and down the stem (Bagchee 1954).

Various fungi cause leaf diseases, an infection of leaves characterised by spots, necrosis and leaf fall (Hawksworth *et al.* 1983), and most of them belonging to Imperfect Fungi (Deuteromycetes). In most cases, growth of seedlings and saplings is not affected, except when large spot areas (dead and necrosed cells) significantly reduce the leaf area for photosynthesis. The weakened plant becomes more susceptible to pathogen and pest attacks, or is less competitive with other seedlings and saplings in natural stands. Ultimately, the leaf becomes completely necrosed and dry and falls. On seedlings and young saplings, the defoliation can eventually lead to death (Hong 1976, Mridha *et al.* 1984, Charlempongse 1988, Harsh *et al.* 1989, Elouard l99l, Zakaria personal communication, Elouard unpublished). Some fungi, such as *Meliola* sp. develop a dense dark mat on the leaf surface, sometimes entirely covering the leaf area. Though the hyphae do not penetrate the leaf cells, chlorophyll development is hindered (Elouard l991). An alga, *Cephaleuros virescens* (Trentepholiaceae), was also recorded causing leaf disease on seedlings and saplings in India, Indonesia and Malaysia and on trees in India (Mittal and Sharma 1980, Elouard 1991).

Thread blights recorded on dipterocarps are caused by Basidiomyceteae of the genera *Marasmius* and *Corticium.* There are two kinds of thread blights, white and dark. The white thread blights are produced by the development of whitish mycelium sticking on the twigs, branches and foliar system of the seedlings and saplings. The black thread blights are horse hair-like and attached to the host by byssus. The threads do not stick to the host's organs except by the byssus, but develop an aerial network which, when too excessive, can hinder the host's development. These fungi were observed in plantation and natural forests in India, Indonesia and Malaysia (Symington 1943, Bagchee 1953, Bagchee and Singh 1954, Spaulding 1961, Smits *et al.* 1991, Elouard 1991, Elouard unpublished).

Gall formation on shoots of seedlings and saplings has been described in *Shorea javanica* plantations in Java (about 60% of the seedlings affected), man-made dipterocarp forests of Sumatra and on *Shorea* spp. and *Upuna borneensis (*100% of the plants affected in nursery) in Kalimantan (Ardikoesoema 1954, Torquebiau 1984, Smits *et al*. 1991). This gall formation is commonly attributed to a bacterium, *Agrobacterium tumefaciens.* According to Smits *et al*. (1991), the youngest leaf remains smaller than the leaves developed before infection, subsequent leaves no longer develop from the top shoot and all buds in the zone with green leaves produce side buds. This process continues until a dense clump of tiny shoots is produced at the buds' positions but without development of any normal shoots from these clumps. The plant growth is then stopped. An insect is suspected to be the vector for this bacteria (Torquebiau 1984, Smits *et al.* l991).

Trees

About 150 fungal species have been recorded on trees, mainly causing rots and decay. In addition, leaf damage, flower necrosis and cankers were also reported. Parasitic plants of the family Loranthaceae have severely damaged *Shorea robusta* in India.

Leaf disease on trees is harmful if the damaged area covers a large area of the foliar system. The fungal leaf diseases are mainly caused by species of *Asterina, Capnodium, Cercospora, Colletotrichum* (Thirumalachar and Chupp 1948, Bagchee 1953, Bagchee and Singh 1954, Chaves-Batista *et al.* 1960, Spaulding 1961, Bakshi *et al.* 1967-1972, Elouard 1991).

Cankers and rots were recorded on various dipterocarp species in Peninsular Malaysia, Thailand, Singapore, Indonesia and India (Bagchee 1954, 1961, Bagchee and Singh 1954, Bakshi 1957, 1959, Bakshi *et al.* 1967, Panichapol 1968, Hong 1976, Charlempongse 1985, Kamnerdratana *et al.* 1987, Corner 1987, l991, Elouard 1991).

Few fungal species are able to attack healthy trees. *Aurificaria [Polyporus] shoreae,* a fungus only reported on *Shorea robusta,* is capable of infecting healthy and uninjured roots, causing root rot and bark and sapwood decay. The disease results in top die back and death of trees (Bakshi and Boyce 1959). Most of fungal species are secondary parasites infecting the trees through wounds and are distinguished from the primary parasites which produce active root and stem rot. According to Bagchee (1954), at least 24 species of Hymenomycetes behave as facultative parasites of *Shorea robusta.*

Infection by heart-rot fungi on hardwood trees occurs through initial injuries caused by human activities (e.g. tapping), fire, drought, frost and other mechanical causes. These fungi establish themselves when the trees are either young or overmature. Most of these fungi live as saprophytes in jungle slash and become parasites when conditions for infection are favourable (Bagchee 1954). Trees with heart-rot can exhibit all the outward signs of healthy and vigorous growth. Heartwood is progressively decayed with age. Heart-rot in *Shorea robusta* can cause much loss of timber (e.g., 9-13%, with nearly 73% of the trees infected) (Bakshi *et al.* 1967). Bagchee (1954) reported that nearly 80% of trees with deformities have fungus-rot in their stems. Of *Shorea javanica* trees tapped for resin in Sumatra, 10% showed carpophore development on their trunks, indicating advanced infection (Elouard 1991). The fungi entering through the butt-scars and causing root damage contribute to windthrown trees (Bakshi and Boyce 1959). Infection by rot fungi is more frequent in the suppressed trees in overcrowded forests than in the trees of thinned coupes (Bagchee 1954).

Flower destruction and seed abortion may be a serious problem for seed production under forest management. However, there has been little research, and the only record is *Curvularia harveyi* on *Shorea pinanga* in Indonesia (Elouard 1991).

Parasitic plants, belonging to Loranthaceae, were observed on *Shorea robusta* in India and Bangladesh (Davidson 1945, Singh 1954, Ghosh 1968, Alam 1984) and on *S. obtusa* in Thailand (Charlempongse 1985). The parasites caused serious damage although the trees did not die (Davidson 1945, Alam 1984). The trees tended to form epicormic branching in some of the older plantations. The only method of controlling infestations of *Loranthus* appears to be eradication by lopping in the cold weather (De 1945).

Forest Products

Diseases on forest products are primarily wood decay and staining fungi (Bagchee and Singh 1954, Banerjee and Sinhar 1954, Sivanesan and Holliday 1972, Hong 1980a, b, Shaw 1984, Balasundaran and Gnanaharan 1986, Supriana and Natawiria 1987, Kamnerdratana *et al.* 1987). Most of them belong to the Basidiomyceteae and can be categorised as white rot, brown rot and soft rot. In white rot, both lignin and cellulose are attacked. In brown rot, cellulose and hemicellulose are attacked while lignin remains unaffected. In soft rot, cellulose is removed like brown rot but the mechanism of action on cell walls is different. The fungi causing soft rot belong to Ascomycetes and Fungi Imperfecti and are restricted to hardwoods (Supriana and Natawiria 1987). Decay of timber occurs mostly after felling, on wood in service and on industrial wood products. Likewise, on logs and poles an important number of wood decay fungi have been identified and control methods investigated. Most of these fungi are weak pathogens, though some can also infect living trees, e.g., *Hypoxylon mediterraneum* recorded both on trees and wood attacking *Shorea robusta* trees and hastening their death or preventing recovery (Boyce and Bakshi 1959).

Decay fungi affect boats (Premrasmee 1956, Savory and Eaves 1965) and wall framing (Singh 1986). One of the most common decay fungi is *Schyzophyllum commune* recorded in India, Indonesia, Thailand and Philippines (Bakshi 1953, Bagchee and Singh 1954, Mizumoto 1964, Supriana and Natawiria 1987, Charlempongse 1985, Quiniones and Zamora 1987).

Various dipterocarp species, *Shorea elliptica, S. hypoleuca* and *S. laevis* are highly resistant to *Chaetomium globosum* (soft rot) and *Trametes [Coriolus] versicolor* (Takakashi and Kishima 1973) and *Shorea siamensis* is extremely durable against *Coniophora cerebella, Trametes [Polystictus] versicolor* and *Daedalea quercina* (Bavendam and Anuwongse 1967). *Shorea guiso, Hopea parviflora* and *Vateria indica* proved to be resistant to several fungal species (Moses 1955, Balasundaran and Gnanaharan 1986). Veneer-faced, low-density particleboards including *Shorea* particles, tested for its resistance against *Tyromyces palustris* and *T. versicolor* proved to be resistant (Rowell *et al.* 1989).

Treatments, heating, fumigants, Wolman salt, ascu and borax, boliden K-33 and tanalith C. were tested on various wood species against decay fungi. Copper-chrome-arsenic (CCA) is the most widely used preservative in Malaysia for wood protection, but organotins are better since they have a higher fungicidal activity, provide a higher protection against the marine toredo worm, are less toxic towards mammals and more easily degradable (Hong and Khoo 1981, Hong and Daljeet-Singh 1985).

Wood staining fungi infect logs in logging areas and freshly sawn timbers in saw mills. A large amount of money is spent each year on preservatives to overcome this problem of staining (Hong 1981b). The staining does not reduce the strength of timbers but degrades their quality and value (Thapa 1971, Hong 1980a, b). Stains can be caused by moulds, resulting in superficial staining easily brushed or planed-off, and sap-staining fungi ('blue-stain'), producing deep penetration stains. The most common are *Diplodia* spp., *Ceratocystis* spp. and *Lasiodiplodia [Botriodiplodia] theobromae* (Supriana 1976, Hong 1980a, b, Charlempongse 1985). For prevention and control of stain, it is best, when possible, to process the felled timber within 1 to 2 weeks. Otherwise, chemical treatment is the only way, and the cut ends of logs should be immediately treated. The chemicals most effective against black stain and mould include the salts of chlorinated phenols (*e.g.* sodium salt of pentachlorophenol, SPP), and organic mercury compounds. These chemicals, effective against stains, have a low efficiency on green moulds (Hong 1980a, 1981b).

Physiological Disorders

Very few studies have been conducted on physiological disorders such as frost, drought, poor drainage and fire damage, except in India on *Shorea robusta* (Davis 1948, Ram-Prasad and Pandey 1987, Raynor *et al.* 1941, Griffith 1945, Anon. 1947, Bagchee 1954).

A review of the adverse factors that probably combine to cause serious dieback of *Shorea robusta* in Uttar Pradesh (India) was made by Ram-Prasad and Jamaluddin (1985) including deficient and erratic rainfall, low retention of soil moisture, nutritional imbalance of the soil, over-exploitation, unregulated grazing, fire and excess of removal of fuelwood.

Mortality of *Shorea robusta* seedlings and young saplings due to frost was mentioned (Davis 1948, Ram-Prasad and Pandey 1987, Raynor *et al.* 1941 Griffith 1945, Anon. 1947, Bagchee 1954). Frost initiates canker in advanced trees usually on the border of the forest facing the open lands and on the banks of perennial streams where the precipitation is heavy as dew or hoar frost (Bagchee 1954). Radiation frosts, creating frostholes by convection currents, kill saplings, create cankers providing the route of entry for heart-rot fungi and produce a moribund type of *Shorea robusta* which ultimately becomes the object of attack by many parasitic fungi and pests.

Drought is also an important cause of *S. robusta* mortality (Pande 1956, Seth *et al.* 1960, Gupta 1961, Ram-Prasad and Jamaluddin 1985, Khan *et al.* 1986). In Malaysia, Tang and Chong (1979) have reported a 'sudden' mortality of *Shorea curtisii* seedlings due to moisture stress. In India, Bagchee (1954) mentioned that the roots of *Shorea robusta* must be in the region of permanent water zone in order to be healthy. On the other hand, Yadav and Mathur (1962) reported excess water accumulation during the rainy season caused mortality of *S. robusta* seedlings by development of white slimy growth on the roots and Sharma *et al.* (1983) reported deaths due to poor drainage.

Fire, often of anthropogenic origin, can damage *S. robusta* (Joshi 1988, Ram-Prasad and Jamaluddin 1985, Sinha 1957, Bagchee 1954, Bakshi 1957). It results in deformity and other injuries to the immature trees such as burrs, galls, tumourous knots, cankers, and heart-rot fungi entering through wounds.

Management Aspects

There are few practical management methods directly available to foresters against pests and diseases attacks in mature dipterocarp trees. Concerning pests, the main record is the 'tree-trap' technique set up in India for reducing the population of *Heterocerambyx spinicornis.* Regular surveys of insect populations in forest plantations can help monitor the health conditions of the trees, and some insect species (Buprestidae, Bostrichidae, Cerambycidae, Scolytidae) are indicators of sickly trees (Stebbing 1914, Beeson 1941). So forest managers can identify which trees, providing shelters for insect breeding, should be removed to avoid a massive infestation of trees and logs. The infection by heart-rot fungi on trees can be reduced by removing the dying and dead trees and burning them. The danger is more important if the tree bears fungal fruiting bodies and is a source of infection (Bakshi 1956a, b). The well-known technique of digging trenches around the infected areas to isolate the infected roots and soil area can also be applied.

Bakshi (1957) suggested lowering the felling age of the trees in forests with a high incidence of heart-rot and to avoid coppicing from infested stumps. Heart-rot in the coppice standards due to *Phellinus caryophylli* and *P. fastuosus is* transmitted by grafting healthy roots with diseased ones or with decayed woody parts embedded in the ground. The disposal of slash should be a routine measure for protection of the stand against fire and as a special treatment against the decay organisms and pests which grow and breed in the slash (Bagchee 1954).

The infestation by mistletoes can be controlled by lopping before the ripening of the fruits and their dispersion by birds (De 1945).

The service life of treated wood has been estimated to be six times more than that of untreated wood. Greater utilisation of preservative treated wood would lessen the demand for timbers. An efficient conservation programme could therefore be implemented (Hong and Daljeet-Singh 1985).

Research Priorities

Pest and disease problems are going to play an important role in enrichment planting and establishment of forest plantations. As forest exploitation continues, the natural balance of pest and diseases in the forest ecosystem will be disturbed. Pathogens and pests are likely to play an important role in a wide variety of ecological and evolutionary phenomena. There is a need to formulate a good pests and diseases management programme**,** both at national and regional levels, with identification of priorities and to support the development of technology and capacity to face pests and diseases. Forestry pests and diseases on dipterocarps occur in six major categories: seed storage, nursery problems, establishment problems, chronic and sporadic problems, wood destruction and fruiting and seedling survival in natural stands.

The main constraints on dipterocarp pest and disease research are shortage of trained staff, lack of cooperation among scientists and institutions working on pests and diseases in Asia, inadequate funding and infrastructure facilities, high cost of pest and disease identification, lack of information on the economic effects of pests in plantation forestry, and the need for more contacts between researchers, foresters and staff of timber companies.

Future research should therefore include the following aspects:

1. Seed destruction and fungal infection during storage
   Although the main insect predators and pathogenic fungi have been identified, emphasis is needed on controls, their application, effectiveness and impact on seed germination and seedling development. Chemicals as well as biological controls should be tested.
2. Pest and diseases in nursery
   Except for major epidemics, attacks and infections can be managed by chemicals and cultural practices. Nevertheless, control methods need more systematic study. Biological control can also be considered as a preventive method: soil-borne fungi such as *Trichoderma* and *Gliocladium* species can be used as antagonists to soil-borne pathogens and cultured in the seedling beds.
3. Pest and diseases during establishment of seedlings and saplings in plantations and exploited forests
   Since enrichment planting and forest plantation involve investment, failure of establishment can be economically devastating. Special attention has to be given to pests and diseases of dipterocarp seedlings and saplings. Shoot destruction can become a serious problem for forest management as it induces the formation of lateral and multiple leaders. Chemical control is not practicable in large forest areas and other methods need investigation. Prevention can also be assisted by dipterocarp species mixture and diversity.
4. Defoliation and heart-rot problems
   Damage assessment systems for defoliation and heart-rot and their economic impacts are required, as well as the study of biology and ecology of the pests and pathogens. Pathogens have a major influence over forest reforestation methods and breeding programmes (Augspurger 1990). Chronic and sporadic pest and disease problems need to be more systematically studied and their economic losses fully quantified.
5. Fruit and seedling pest and diseases
   More studies on pests and diseases related to fruiting and seedling survival should be conducted to better understand fruiting and dispersal strategies, seedling survival, management and selection of the mother trees, and ability to resist pathogens and pests.
6. Insect and fungal population
   Studies on insect and fungal population ecology and dynamics are also essential for the conception of a good pest and disease management programme as well as a search for resistant individuals (mother-trees).
7. Revision of the insect taxonomy
   The long lists of identified insect pests in literature

refer to the old taxonomic classification. Still many insects have not been identified beyond genus. A thorough revision of the insect taxonomy needs to be conducted. A taxonomy training programme for Asian research staff will help to reduce costs and update laboratories' data-bases and collections.

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Chapter 8

Management of Natural Forests

S. Appanah

The view that it is not possible to manage natural forests in the tropics for their timber has its adherents. Considering the widespread failures in many countries, such a view is conceivable. A review by International Tropical Timber Organization estimated that only an insignificant amount of the world's tropical moist forests is sustainably managed (Poore 1989). Fortunately, numerous reports suggest otherwise for some dipterocarp forests of Asia. The state of tropical forest management worldwide is in such a quandary that any success, however meagre, requires close examination. Such a success may provide the flicker of hope that is so urgently needed in our efforts to save these tropical forests.

The dipterocarp forests in the perhumid zone of Asia form the cradle for a considerable proportion of life forms found on Earth. It is arguable that the only effective way to preserve a sizable portion of this biodiversity will be through effective management, including production of timber and other valuable products.

Fortunately, history is on the side of dipterocarp forests. The origins of scientific tropical forest management began in Asia, particularly in British India around the mid-19th Century. Together with teak, the dipterocarp forests were among the first tropical forests to be managed. The Indian experience formed the basis for management in the Malayan realm (Hill 1900). The conditions for management have changed considerably since then, but the experience and understanding gained form an excellent basis for developing appropriate management regimes for tropical forests.

Forest Composition, Distribution and Structure

Although the family Dipterocarpaceae is presently recognised pantropical, with three subfamilies Monotoideae (Africa, Colombia), Pakaraimoideae (Guyana) and Dipterocarpoideae (Asia), it is the last subfamily that is of significance as a timber group (Ashton 1982). The present review will be confined to the Asian subfamily. It comprises 13 genera and some 470 species, distributed from the Seychelles in the west to Papua New Guinea to the east. In Chapter 1 more details on the taxonomy, distribution and diversity of this subfamily are given (see also Champion 1936, Symington 1943, Ashton 1980, 1988).

Dipterocarps are limited to tropical climates with a mean annual rainfall exceeding 1000 mm, with only short dry spells. The Asian dipterocarp forests can be divided into two basic zones, viz. the Moist Tropical Forests and the Dry Tropical Forests (Champion and Seth, 1968, Collins *et al.* 1991). Within these two basic moist and dry tropical forests, four forest types can be distinguished (Table 1).

Our knowledge of these forests, especially the distribution of dipterocarps within them is incomplete. This is particularly the case with forests of Indochina and southern China. Under these circumstances, and for the sake of brevity, the presentation is simplified to three groups of dipterocarp forests, viz. the Dry evergreen dipterocarp forests (Dry tropical forests), Seasonal evergreen dipterocarp forests (Tropical semi-evergreen and Tropical moist deciduous forests), and the Aseasonal evergreen dipterocarp forests (Tropical wet evergreen forests). Some information on their distribution and structure is given below.

Dry Evergreen Dipterocarp Forests

These forests are found in Central and East India, Burma, Thailand and Indo-China. The forests are dry, with less than 2000 mm of annual rainfall and a dry season of 3 to 5 months. The forests are medium in stature, with an even canopy and no emergents. *Shorea robusta* (Indian sal)

Table 1. Classification of Asian dipterocarp forests (after Champion and Seth 1968, Collins *et al.* 1991).

I. Moist Tropical Forests:
1. Tropical wet evergreen-
    - 1a. Evergreen dipterocarp-
        Malaysia, Sumatra, Kalimantan, Irian Jaya, Maluku (part), Papua New Guinea, Sri Lanka (part), Peninsular Thailand, Tenasserim, Andamans and Nicobar (part), Philippines (part), Laos, Cambodia, Vietnam (part)
    - 1b. Secondary dipterocarp (seral)-
        Malabar coast
2. Tropical semi-evergreen-
    North Thailand (part), Chittagong, Laos, Cambodia, Vietnam (?) (part)
3. Tropical moist deciduous-
    Maluku (part), Palawan (part), Zambales mountains in Luzon, W. Mindanao
    Moist sal- Terai, E. slopes of W. Ghats, Chota Nagpur, Upper Burma, Assam (part)

II. Dry Tropical Forests:
4. Tropical dry deciduous (forests heavily degraded)-
    Dry sal- Western India, Burma (part)
    Indaing- Irrawaddy plains (part)

is the well known species of this zone. Sal occurs in the Himalayan foothills from northwestern Himachal Pradesh to central Assam and south to Tripura. It also spreads south along the eastern part of India up to Andhra Pradesh. Where sal occurs, it is the only dipterocarp in the forest. These forests also have five other dipterocarps, the majority of which are confined to the Indo-Burma community. The Indo-Burmese species include *S. obtusa*, *S. siamensis*, *Dipterocarpus obtusifolius*, *D. tuberculatus* and *D. intricatus*. Many of them occur as single species or codominant stands. These dipterocarps have thick bark and are fire tolerant. Today most of these forests have become more open as a result of browsing of young regeneration by cattle and felling.

Seasonal Evergreen Dipterocarp Forests

These forests are distributed north and east of the everwet Malesian region of Malaya, Borneo and Sumatra. They are found in places that experience a short but regular dry season. The forests occur in western and southern parts of Sri Lanka, western Ghats of India, the Andaman Islands, eastwards from Chittagong (Bangladesh) to southernmost Yunnan and Hainan (China), and southwards to Perlis, northwest of Peninsular Malaysia. In the eastern parts of Malesia they occur again, in parts of Sulawesi, the Moluccas, Bali, Lombok and New Guinea. Only about a 100 species of dipterocarps are found in this formation. They occur in the mature phase of the forest, with no single species dominating the canopy. About half of the canopy layer may consist of dipterocarps. They tend to be found in gregarious stands, and some like *Anisoptera thurifera* act like pioneers, colonising sites that were cultivated. Details of the species found in these forests are found in Ashton (1982), Champion and Seth (1968), Chengappa (1934), Rojo (1979), Smitinand *et al.* (1980), Vidal (1979), Johns (1976) and others.

Aseasonal Evergreen Dipterocarp Forests

These are the forests that occur in the perhumid climate of Malesia, with rainfall over 2000 mm annually, and no pronounced seasonal water stress. These forests are found all the way from southwestern Sri Lanka, Peninsular Malaysia, Sumatra, Borneo, and the Philippines. Similar but somewhat poorer forests can be found in Irian Jaya in the east. The vast majority of the dipterocarps, over 400 species, occur in this formation, with Borneo having the biggest share. A complete list of the Malesian species is given in Ashton (1982). The trees dominate the emergent layer of lowland and hill forests, but this is not the case in Irian Jaya where the dipterocarps mainly make up the canopy species. Besides the lowland and hill species, there are dipterocarp-dominated montane formations, as well as several species adapted to heaths, coastal hills, limestone cliffs, peat swamps and freshwater swamp forests. Dipterocarps may constitute between 50-60% of the emergent stratum in the rich lowland formations, but under optimum conditions, the trees may make up 80% of the emergent individuals and occur as gregarious or semi-gregarious populations.

Natural Regeneration

Dry Evergreen Forests

The best known dipterocarp forests of the dry zone are the sal forests of India. Sal fruits annually, with heavy fruiting at intervals of 3 to 5 years (Champion and Seth 1968). The flowering begins during the dry period, and the fruits mature with the rains. A mature sal can produce about 4000 viable seeds in a good year (Champion and Pant 1931), and the seeds germinate within a few days. Sal seedlings are shade tolerant and establish better under the crowns of other trees. Seedlings are able to coppice and also develop a deep taproot. They are thereby able to withstand ground fire and cattle browsing.

Other dipterocarps of this formation are believed to regenerate like sal. All flower during the dry season, and fruit with the onset of rains. A light ground fire before seed-fall assists seedling establishment. Among some species, seedling establishment seems rare in nature (Blanford 1915), and regeneration is principally by coppicing. Mature trees are known to coppice readily following injury.

Seasonal Evergreen Dipterocarp Forests

The dipterocarps of this formation belong to the mature phase of the forest. An exception is *Anisoptera thurifera* in Papua New Guinea which can establish in cultivated areas (Johns 1987). The regeneration of the dipterocarps in these forests resembles that of the sal in many ways, except for the role of fire. Dipterocarp populations flower almost annually, but flowering is only heavy at intervals of 3-4 years (Chengappa 1934). The fruits are heavily predated by insects, birds and mammals, and seedling survival is poor. In some genera like *Dipterocarpus*, many years may pass without a single seedling becoming established. They also lose their coppicing ability after the sapling stage. Overall, the low seedling survival and the early loss of coppicing ability makes it difficult to regenerate these forests after exploitation.

Aseasonal Evergreen Dipterocarp Forests

The regeneration of dipterocarps in these forests has been relatively well studied. The dipterocarps have a unique flowering characteristic - they flower at supra-annual intervals of 2 to 7 years, and the event may be widespread covering sometimes the whole region (Ridley 1901, Foxworthy 1932, Ashton 1969, reviewed by Appanah 1985). Whole forests may burst into flowering synchronously. It is not limited only to the dipterocarps though, and many other canopy and emergent species also participate in the flowering. Some localised flowerings also occur almost every year.

During heavy flowering years, each mature dipterocarp may set up to 4 million flowers, and this results in as many as 100,000 mature fruits. Much is lost to insects, birds and mammals. The ripe fruit fall somewhat synchronously, however, the winged fruits are not dispersed far from the mother trees. The dipterocarp seeds lack dormancy, and germinate soon after falling. Once established, seedling populations decline slowly only as a result of inadequate light conditions and aperiodic droughts. Growth is rapid if they are exposed to direct light (Wyatt-Smith 1963, Fox 1973). Among the dipterocarps, light demanders and shade tolerant species can be differentiated. Both grow rapidly where there is higher light intensity, but the latter species can survive longer under poorer light conditions, and in general they are the slower-growing heavy hardwoods. In contrast to dipterocarps in the other two formations, coppicing ability of the species in the everwet forests is limited, and ceases beyond the pole stage. The population structure is not the typical reverse-J shape, with the density of sapling-and pole-size dipterocarps generally low in mixed dipterocarp forests. However, this appears to be not so in some of the dipterocarp-rich forests in the Philippines.

Silvicultural Systems

A number of silvicultural systems have been developed for the long-term management of tropical forests, many with dipterocarps as the main crop. The silvicultural systems go by a bewildering number of technical names, but they can be broadly divided into Shelterwood (monocyclic) Systems and Selection (polycyclic) Systems. The situation for dipterocarps forests have been reviewed variably (e.g. Wyatt-Smith 1963, 1987, FAO 1989, Stebbing 1926, Chengappa 1944, Nair 1991, Weidelt and Banaag 1982, and others).

Simply stated, the Shelterwood System attempts to produce a uniform crop of trees from young regeneration through both heavy harvesting and broad silvicultural treatments. A new even-aged crop is established by applying preparatory and establishment cuttings to natural regeneration (i.e. seedlings and saplings) of the desired trees. At an appropriate time the remaining overstorey is removed.

The Selection System aims to keep an all-aged stand through timber cuttings at shorter intervals. Many light cuttings are made. Seedlings will become established in the small gaps. Under this system, two or more less intensive harvests are possible during one rotation, while in the Shelterwood System all marketable stems are removed at one cutting.

A variety of silvicultural systems have been tried out on dipterocarp forests, depending on markets, technological changes, landuse patterns, harvesting, regeneration, labour costs, etc. These have met with varying success. The systems in operation in India, Malaysia, Philippines and Indonesia described as forest management practices are well documented in these countries.

India

The seasonal evergreen and dry evergreen forests have been managed under the Selection System. Here it can be summarised as selective felling of exploitable trees from an area at periodic intervals, under the following circumstances: i) in mixed forests where utilisable species are few; ii) in areas that are difficult to access; and iii) in hilly terrain where heavy logging is environmentally bad.

Trees of specific girth are removed at 15 to 45 year cutting cycles, calculated from growth rates. Some safeguards are introduced such as: a 20 m minimum distance between trees earmarked for felling; climber cutting to reduce logging damage; protection buffers for riversides; and only harvesting dying and dead trees in steep areas. Treatment is carried out to assist natural regeneration, and planting is prescribed for under-stocked areas. Many of the prescriptions are not met for several reasons: plantings are inadequate and damage to residuals excessive (FAO 1984). Over time, felling cycles have been reduced, girth limits lowered, and more species exploited.

Shelterwood Systems

Shelterwood Systems were introduced when it became necessary to harvest more intensively some valuable forests, and regeneration was not assured under the selection system. The variants usually applied here are the Indian Irregular Shelterwood System, Uniform System and the Coppice System.

1. Indian Irregular Shelterwood System

Both seasonal evergreen and sal forests are managed under this system. First, all trees above exploitable diameter are removed. If advanced growth is lacking, mother trees are kept. Next, the underwood and overwood are removed periodically until regeneration becomes established. Finally, the remaining underwood and overwood is removed, except those forming future crops. All these are done over a rotation of 120 years. In addition, girdling, thinning, weeding, climber cutting and artificial planting are carried out as needed.

Lack of regeneration, especially for sal forests, appears to undermine the Irregular Shelterwood System (FAO 1989). Plantings have been tried at cost. This has not kept to schedule, and there is a temptation to reduce rotation length and exploitable girth limits.

2. Uniform System

In high value sal forests, the Uniform System has been tried. All overwood is removed at one clearfelling, and regeneration is allowed to grow up. No regeneration fellings are conducted, however, and so the system has to rely on pre-existing seedlings. The rotations are between 120 to 180 years for sal. But demand for timber is high and rotations have been shortened.

When natural regeneration is abundant, the overwood is cut completely. Groups of poles are sometimes kept as future crop trees if regeneration is poor. Where regeneration has not established, suppressed trees are retained to control weed growth. Steep slopes and eroded areas are not heavily felled. Cutting and thinning are prescribed for improving regeneration. The system should work if adequate natural regeneration can be secured. In the event it is poor, artificial regeneration has been resorted to.

3. Coppice Systems

A few variants of the Coppice Systems have been introduced for sal forests. The systems depend on shoots emerging from the cut stumps. Coppicing vigour declines with age and so short rotations are necessary. It is mainly suitable for firewood and small timber production. To produce fuelwood, a rotation of 30-40 years is used. Felling is done before the growing season, the area is protected from grazing and fire, and cleaning is done to remove excess coppice shoots and climbers. Over time, with decline in coppicing vigour, stump mortality increases. Seedling regeneration helps to compensate this loss, but seedlings are scarce because of grazing pressure. This has led to stand degradation. Variations to the system involve retention of seed trees for producing seedlings (see Tiwari 1968). Overall, the system has succeeded where biotic pressure is kept low.

4. Clearfelling System

This system is used when there is a need to change the composition of the crop to a more valuable species. The restocking is through natural or artificial regeneration, the latter used to introduce a new species or to change the forest composition. As a consequence, the more valuable teak is introduced into sal forests. The trend is to convert most of these forests into plantations, making the future of sal forests uncertain.

Peninsular Malaysia

Forest Management Systems

Forestry in the modern sense was started in 1883 with the establishment of the forestry service. Prior to introduction of forest management, logging was very selective, principally limited to the heavy hardwoods (mainly several dipterocarp secies), and only about 7m^3/ha was taken out (Barnard 1954). Silvicultural operations were limited to enrichment plantings of the heavy hardwood, chengal (*Neobalanocarpus heimii),* which failed from lack of further tendings. But the demand for timber increased, leading to over-exploitation of the select timbers. This prompted the authorities to develop a series of silvicultural systems.

1. Regeneration Fellings

In the beginning (1910-1922) Departmental Improvement Fellings were implemented. All species whose crowns interfered with the poles of any valuable timber species were removed. It was subsequently realised that such treatments had no impact on the immature trees. However, they resulted in profuse young regeneration (Hodgson 1937). The improvement fellings had in fact been regeneration fellings. After 1932, Regeneration Improvement Fellings (RIF) came in to vogue. Inferior species were gradually removed over a series of fellings. If the regeneration was verified as successful, final felling of the valuable species was carried out. This in fact resembled the classical Shelterwood Systems.

2. Malayan Uniform System

As a rule, no forests were harvested without first carrying out RIF. During the Japanese Occupation (1942-1945) many forests were clearfelled without the benefit of RIF. After the war, extensive surveys revealed that these areas contained adequate advanced regeneration without any assistance. It was realised that if the forest had adequate regeneration of the fast growing dipterocarp species, a single clearfelling release could result in a greater stocking of a more uniform crop of commercial species. This became the basis for the Malayan Uniform System (MUS), which was introduced in 1948 for managing Lowland Dipterocarp Forests (Wyatt-Smith 1963).

A detailed silvicultural system was developed (Wyatt-Smith 1963). It consists of felling the mature crop of all trees above 45 cm dbh, poison girdling all defective relics and non-commercial species down to 5 cm dbh, and releasing established seedlings. Seedling adequacy and suitable tendings underpinned the success of MUS.

3. Modified Malayan Uniform System

In the mid-1970s, most of the lowland dipterocarp forests were alienated for agricultural programmes, and forestry was confined to the hills and rough terrain unsuitable for agriculture. Under these new conditions it was considered difficult to apply the MUS. The principal problem was the lack of uniform stocking of natural regeneration. It was thought that enrichment planting could overcome this deficiency (Ismail 1966). This allowed all forests to be opened up for logging, regardless of adequate seedling stocking, a prerequisite with MUS. Planting up understocked areas was carried out in the beginning, but their performance was very variable and unsatisfactory. Now, artificial regeneration is rarely carried out, or the practice is abandoned entirely.

4. Selective Management System

In the late 1970s, the Selective Management System (SMS) was introduced. This is a simplified version of the Philippine Selective Logging System (see Appanah and Weinland 1990). The MUS was already discarded for working in the hillier terrain, and the modified-MUS proved unsatisfactory. The felling regime is formulated on the basis of a pre-felling inventory. All commercial tree species above a certain size (ideally non-dipterocarps, 45 cm dbh; dipterocarps, 50 cm dbh) are felled, provided a sufficient number of residuals are left behind to form the next cut in *ca* 30 years (Thang 1987). Therefore the SMS relies on adequacy of healthy residuals which will respond to the cutting release for the next cut some 25-30 years later. Seedling stocking is assumed to be present, or will be replenished by the maturing residuals. The SMS is regarded as more flexible for managing the highly variable forest in the hillier terrain. In situations where it is not economically equitable for the logger, the modified-MUS is prescribed which imposes an arbitrary diameter of 45 cm dbh for felling on a rotation of 50 years.

Sabah

Silviculture in Sabah followed a path similar to Peninsular Malaysia. In the early 1930s, RIF were tried on a limited scale (Fox 1968). In 1949 the Selection Improvement Fellings were introduced, to assist the pole-size trees of 10 cm dbh and above in areas logged 15 to 25 years before (Martyn and Udarbe 1976). The method involved poison-girdling non-commercial species and climber cuttings.

In 1956 a modified version of the MUS was introduced for forest regeneration (Chai 1981). The canopy was opened after felling by poison-girdling all non-commercial species as well as defective trees of commercial species down to 15 cm dbh. The next crop is expected to come from seedlings, and advance growth will be a bonus. This system became the standard regeneration technique for dipterocarp forests in Sabah.

This modified MUS underwent further changes in 1971 to become a minimum girth limit system, the so called Stratified Uniform System (Chai and Udarbe 1977). In this refinement, the advance growth for the next crop is kept. The main elements of the system include marking 25 preferred or desired trees/ha (25-59 cm dbh) for retention, and poison girdling unwanted and defective trees. Climber cutting and girdling of seed-bearers and relics is done in the 15th year.

Later, Chai and Udarbe (1977) expressed doubts on the value of the girdling practices. They argued that since logging intensity is high, much of the forest gets released anyway without further treatment. Since then, only climber cuttings are meant to be done. Furthermore, girdling of weeds or non-commercials has been stopped on account that such plants may become commercial in the future, and moreover, the operation may be harmful to the ecosystem.

Sarawak

The timber industry in Sarawak relied mainly on extensive peat swamp forests, and moved into the hill forests only in the late 1960s. Coming so late, Sarawak tended to follow the systems developed in Peninsular Malaysia (Lee 1982). At first the forests were selectively logged. The relics left behind were defective and inferior, and seedlings/saplings unlikely to reach maturity before 70-80 years.

As a result, three UNDP/FAO projects (1974-1981) were started to provide interim guidelines for managing Sarawak's dipterocarp forests (FAO 1981a, b). The study evaluated three different treatments:

1. Overstorey removal only - All overmature non-marketable trees left behind during harvesting were removed by poison-girdling.
2. Malayan Uniform System evaluated - Following logging, all other non-economical trees, which impeded growth of the seedlings were removed. Such a treatment was considered too drastic. The rough terrain and shallow soil conditions are vulnerable to heavy erosion. A modification to MUS was tried whereby the advance growth of the desirable species were saved. In this way the advance growth may be obtained even before the seedlings mature, giving in effect a polycyclic system.
3. Liberation Thinning - Desirable species were identified, and liberated from competition including removal of the overstorey to improve their growth. No specific species or species groups were eliminated, only those that restricted the growth of the selected trees. Therefore, trees of non-commercial species were left behind if they did not appear to hinder selected trees.

Mild overstorey release was insufficient to release the trees of desirable species. Both the Liberation Thinning and the modified MUS resulted in increased growth of the residuals (Hutchinson 1979), but the latter resulted in elimination of a greater number of trees which could have commercial value in the future. Despite the potential loss in the future of commercial trees, for a while liberation thinning held sway in Sarawak as the appropriate silvicultural treatment (FAO 1981b). It lost support subsequently, when Lee (1982) suggested that the boost in initial growth is not sustained, the operations are difficult, and cannot be kept up with the logging rate. Since then, Liberation Thinning is being carried out for a small portion (ca. 4%) of the forest logged annually (Chai 1984). Otherwise, the practice has reverted to selective felling based on diameter limits.

Philippines

Scientific management of dipterocarp forests began during the American Regime. From 1900 to 1942 mechanised timber extraction and processing methods were introduced. Following the Second World War, there was a surge in logging for rebuilding the country, and the only management control was a 'diameter limit' of 50 cm for cutting trees. Despite the limit, mechanisation of logging led to almost clear-cutting due to high stocking.

The above 'diameter limit' cuttings brought about the development of the Philippine Selective Logging System (PSLS), which is a modification of the Selection System used to manage old growth hardwood forest in North America. Under this system, 60% of the healthy commercial residuals in the 20-70 cm dbh classes are to be retained as growing stock for a future harvest (Reyes 1968). This has since been raised to 70% of all the commercial residuals in the 20-60 cm dbh classes.

The selective logging amounts to removing mature, overmature and defective trees with minimum injury to an adequate number of healthy residuals of commercial species to guarantee a future timber crop. Also incorporated into the system is a timber stand improvement (TSI) guideline which consists of treatments before and after the major felling to ensure the stand attains maximum timber quality and growth (Uebelhoer and Hernandez 1988). The TSI appears to be yielding results. Preliminary results indicate that liberation from crown competition results in increase in diameter: a removal of 33% basal area, resulted in up to 10% increase in basal area of crop trees in ten years.

The Philippine forests are generally very rich in dipterocarps. Therefore, the PSLS is regarded as the best silvicultural system for their forests. If logging damage is contained, and residual forests protected and post logging treatment given, another economic cut is possible after 30-45 years. While the system looks good, overcutting and bad implementation has led to degradation of vast areas of forests. Today, there is concern for the quality of the second cut.

Indonesia

From historical times, teak forests in Java have received most interest from silviculturists in Indonesia. After 1966, changes in forest policy took place and the dipterocarp forests in the other islands were opened for large scale exploitation. At first it was merely a timber felling operation. Sustained management efforts began in the 1970s when a simplified variation of the PSLS was introduced for lowland dipterocarp forests (Soedjarwo 1975). The original version, the Indonesian Selective Cutting System, locally known as the TPI (Tebangan Pilih Indonesia), relies on leaving behind an adequate number (25 stems/ha or more) of sound commercial species of 20 cm dbh and above. With this minimum guaranteed, everything above a certain diameter limit may be harvested. If the putative residuals could be met, the TPI system allowed for a short felling cycle of *ca* 30 years. If these were not present, the option was to harvest on a Uniform System rotation of *ca* 60 years. There was also a further option to clear cut and replant, although not necessarily with dipterocarps.

Compared to the PSLS, the TPI is a much simpler system. It is therefore cheaper and easier to monitor. Liberation thinning is prescribed to release residuals and nucleus trees for reseeding. Planting of seedlings to enrich the stand may be carried out if followed by subsequent tending and liberation thinning.

Pre-felling inventories in Indonesia however suggest that stands rarely have sufficient residuals of commercial species (Burgess 1989). Therefore, the second cut may have to be delayed. The TPI was subsequently modified to the TPTI (Tebang Pilih Tanam Indonesia) which resorted to the necessity of planting if the selecting fellings failed. This resulted from the conviction that it is possible to easily plant up large areas with dipterocarps (see Enrichment Planting). Unfortunately, the impression from this decision is that uncontrolled logging can be done without serious consequences, as enrichment planting can overcome the problems. Caution should be exercised here until evidence for the success of enrichment planting is clear.

Growth and Yield

One of the biggest difficulties for sustained management of dipterocarp forests is in getting reliable data on growth and yield. The data are a prerequisite for determining harvesting volumes and cutting cycles. In this respect, there is much scepticism about the growth rates being used for managing many forests in the region. A quick glance of the data from the everwet region, based on only a few sites, gives some clue to how dipterocarps are growing.

From studies in Peninsular Malaysia, Sabah, Sarawak, Philippines and Kalimantan, the following generalisations can be made. In undisturbed, virgin forests growth rates are relatively much lower compared to logged ones, and the best growth is achieved in plantation conditions (e.g. mean growth rate (diameter increment) of *Shorea* spp. in Sarawak: primary forest, 0.82 cm/yr; logged forest, 0.93 cm/yr; plantation, 1.22 cm/yr) (Primack *et al.* 1989). In any case, among the commercial species, dipterocarps grow much more vigourously than non-dipterocarps, by at least 25-35% (e.g. periodic diameter mean annual increment for Labis F. R., Peninsular Malaysia: dipterocarps, 0.85 cm/yr; non-dipterocarp commercials, 0.66 cm/yr) (Tang and Wan Razali 1981). Among the dipterocarps the light hardwoods grow faster than the heavy ones (growth rates in Peninsular Malaysia sample plantation plots: light hardwood *Shorea macrophylla*, 2.23 cm/yr; heavy hardwood *Shorea sumatrana*, 0.86 cm/yr) (Appanah and Weinland 1993). Growth rate, expressed in diameter increment, is lowest with smaller individuals, and culminates usually in the 50-60 cm diameter classes, and declines in bigger trees. This pattern of diameter increment has been seen in the Philippines (Weidelt and Banaag 1982), Sabah (Nicholson 1965), and Peninsular Malaysia (Tang and Wan Razali 1981). A sample from the Mindanao concessions in the Philippines illustrates the point:

dbh class (cm)	cm/yr
10	0.44
20	0.58
30	0.69
40	0.78
50	0.83
60	0.86
70	0.86
80	0.85
90	0.79

Following logging or liberation thinning, the residuals are known to respond to the release by increasing their growth rates. In general the increments were highest in the first years after logging, and declined slowly, and after about the fifth year the benefits of release seem to cease (Tang and Wadley 1976).

Site\ Age	Year 1	Year 2	Year 3	Year 4	Year 5
Peninsular Malaysia- Tekam F.R.	0.72	0.57	0.68	0.67	0.57
Peninsular Malaysia- Labis F.R.	0.63	0.79	0.71	0.63	n/a

Besides, the above, the trees grew faster (mean annual diameter increment) in plots where more timber was harvested (plot residual basal area) after logging (Tang and Wadley 1976):

Residual basal area (m^2/ha)	Mean annual diameter increment (cm/yr)
10-16	0.44
16-22	0.45
>22	0.55

A peculiar behaviour of all tropical trees, including that of dipterocarps, is the extremely wide range of growth rates of individual trees even within the same diameter class. The variation coefficient may reach 70-100%. This is illustrated in the mean annual diameter increment for the minimal, maximal and median growth rates (cm/yr) of *Shorea* species in primary, liberation-treated, and plantation forests in Sarawak (Primack *et al.* 1989):

Mean annual diameter increment (cm)	Primary Forest	Liberation Felling	Plantation
Minimum	0.13	0.16	0.80
Maximum	0.82	0.93	1.22
Median	0.30	0.43	0.86

Next is the variation in the growth rates within one region, and between regions. Studies of the annual diameter increment (cm/yr) of dipterocarps in the Philippine (Weidelt 1996) and Sarawak forests (Primack *et al.* 1989) illustrate these points:

Location	Mean annual diameter increment (cm)
Sarawak:	
Mersing	0.41
Bako	0.30
Philippines:	
Mindanao	0.73
Visayas	0.48
Luzon	0.52

It should be noted that dipterocarps on fertile sites in the high rainfall area of eastern Mindanao have high annual increments. The growth rates are consistently better in the Philippines than Sarawak, indicating regional differences. The forests in the Philippines should generally have better yields. Even within Sarawak, there are differences between the two forests, which can be ascribed mainly to better soil fertility at Mersing.

Despite the existence of some good information on the growth of dipterocarp trees, there is a tendency to exaggerate their growth rates. For example, in Peninsular Malaysia, the generally accepted standard for growth of trees in logged forests is above 0.8 cm/yr diameter increment, and hence a cutting cycle of about 35 years. From a quick perusal, it is obvious the realised growth is far below that assumed. Furthermore, the wide variation in growth rates between forests calls for more precise local growth data for determining cutting cycles, and national averages are inapplicable. Next, despite evidence that silvicultural treatments of girdling and liberation felling do boost the growth of the trees, this is rarely undertaken. This of course has to be taken into consideration with the costs of operations and the benefits of increased timber production.

Enrichment Planting

Enrichment planting has been a tool in dipterocarp forest management, and several dipterocarp species have been successfully planted into natural forests (Barnard 1954, Tang and Wadley 1976, reviewed in Appanah and Weinland 1993, 1996). It is indeed widely and variably practiced throughout the Asian tropics. Such planting is considered when the stocking of seedlings and saplings of desirable species is inadequate because of poor seedling survival or due to destructive logging methods. With the modified-MUS of Peninsular Malaysia, enrichment planting was supposed to be a standard practice: the deficit in natural regeneration to be artificially regenerated using dipterocarp wildings.

The success of such plantings was variable and planting efforts have invariably declined. There are several causes for this. Planting work is difficult to supervise, seedlings have to be regularly released from regrowth, and a regular supply of dipterocarp seedlings is needed. Wildings can be used, but individuals differ widely in their performance. Moreover it is costly (labour demanding). As a consequence, the efficacy of enrichment planting has been questioned (Wyatt-Smith 1963, OTA 1984).

Nonetheless, enrichment planting is receiving accelerated attention as a possible technique under the selective felling practices in Kalimantan (e.g. Smits 1993, Adjers *et al.* 1996). Extensive areas are being planted up in Kalimantan with dipterocarp wildings. Rooted cuttings have also been developed but their success in the field has not been evaluated yet. Their root structure must hold the tree during sudden wind storms.

Smits (in Panayotou and Ashton 1992) has in view a model for enrichment planting of degraded dipterocarp forests in Kalimantan. Such sites are to be first planted with an over-storey of building-phase species, and a few years later with dipterocarps raised from cuttings and inoculated with mycorrhiza. The fast growing species can be harvested in the mid-term, and this will release the dipterocarps for harvest in 50 years. One major technical problem is the difficulty in harvesting the pioneer species without causing excessive damage to the mature-phase trees (Panayotou and Ashton 1992). There is also concern for the bad form of dipterocarps raised from cuttings.

Wyatt-Smith (1963) pinpoints the conditions which merit enrichment planting, and the silvical characters necessary for species ideal for enrichment planting. The characters include regular flowering and fruiting, rapid height growth, good natural bole form, low crown diameter/girth breast height, wide ecological amplitudes, tolerance to moisture stress, and free of pests and diseases. But most of all, the species should produce timbers of high value.

All too often, enrichment planting is done without consideration for the light conditions. Supervision and follow-up maintenance are necessary, especially canopy opening treatments. With care, enrichment planting remains promising and viable. It has been successful in Karnataka and several other Indian States, and Sri Lanka, in both moist deciduous and evergreen forests.

While it is generally accepted that the best and cheapest method for regenerating dipterocarp forests is still using the natural regeneration, enrichment planting has received a new boost particularly for badly degraded forests. Under the ‘Carbon Offset’ Project, an American utility company paid for planting dipterocarps in Sabah, to offset its carbon dioxide emission in its power plants in Boston (Moura-Costa 1996). This may appear innovative, although its value will be confined to rehabilitation programmes. Planting dipterocarps may be viewed as a final resort, after natural regeneration practices have failed.

Exploitation Damage

Good harvesting systems are critical for sustainable management of natural forests. The harvesting should not irreversibly compromise the potential of the forest. The operations should never degrade it, and must also allow for rapid recovery of the stand. Studies of logging damage in dipterocarp forests begun in the late 1950s show that it has been increasing with mechanisation (Nicholson 1958, Wyatt-Smith and Foenander 1962, Fox 1968). But with properly planned and executed harvesting operations, not only is the damage contained, but so are the harvesting costs (e.g. Marn and Jonkers 1981).

Unlike the case with uniform (Shelterwood) systems, selective fellings can cause considerable damage to the future crop, the medium sized residuals. The damage intensity and extent to both trees and soils vary with the log extraction system used. Skidder-tractors are used extensively. They cause more damage to the ground surface, increasing soil erosion and retarding regeneration and growth of residuals. With precautions and improvements like pre-determined skid trails and reduced vehicle movement, damage can be considerably reduced. Logging on steep slopes (i.e. >15°), which is very damaging, should be curtailed.

Besides damage caused by extraction, felling damage too can be very intense, especially to the advanced regeneration (Nicholson 1979). Directional felling and pre-felling climber cutting reduce such damage. Although this practice has been recognised as beneficial, it is seldom carried out. Currently, several initiatives have been started in reducing logging damage to the soils and the residual vegetation under schemes called ‘Reduced Impact Logging ’ (RIL). These initiatives are mainly in Sabah (Marsh *et al.* 1996). In these RIL operations, besides cutting lianas, directional felling and pre-planned skid-trails, the operations are closely supervised so as to minimise skid trail length and blade use. A 50% reduction in all measures of damage was demonstrated compared with conventional logging for an increase of about 10-15% of direct logging costs.

High-lead yarding systems have been tried in some concessions in the Philippines and Malaysia. They are costly, difficult to maintain, and require well trained crews to maintain them. Basically, selection fellings and high-lead yarding are incompatible, as the residuals are damaged considerably. There is also heavy damage to the soil when trees are dragged uphill. However, skyline yarding systems are beginning to show considerable promise. With the simple skyline yarding where two spar trees are used, road building is reduced. The other is the Long Range Cable Crane System which uses a tight skyline with intermediate supports and a carriage with the log suspended to it vertically. The carriage travels along the skyline and dumps the suspended log at the head of the spar or tower. This has been tried in the Philippines (Heyde *et al.* 1987) and Sabah (Ong *et al.* 1996). The original carriage could only lift small logs, but the new one introduced in Sabah can lift 5 tonne logs (personal observation). The use of a skyline system reduces road building considerably, and limits damage to the soil and residual trees to a considerable extent. The skyline systems hold the answer to logging of dipterocarp forests of Southeast Asia.

Helicopter logging is now being tested in Sarawak. This system remains rather expensive and dangerous. The cost of keeping the helicopter in the air is high, and the operations have to be perfectly coordinated: trees have to be felled in advance, and the helicopter can only start its operations when a sufficient number of trees are available. The timber being harvested should have very high value. Too many accidents have happened with helicopter logging for it to be considered a viable operation. There is also the problem of illegal logging as it becomes much easier to steal timber using helicopters, and the activities are difficult to control.

Failures in Implementation of Practices

It is obvious from the above review of silvicultural practices, there is no lack of scientific methods for managing the variety of dipterocarp forests. While systematic management may be lacking (Leslie 1987, Wyatt-Smith 1987), some kind of management is being attempted for many of the forests in Asia; it is however, mainly in the form of area or volume control. It was reported that about 19% of the Asian region’s productive, closed broadleaf forest is being intensively managed (FAO 1981c). However, one can dispute if area and volume control is management.

Several factors seem to hinder true management of these dipterocarp forests. For one, it seems better to cash in the timber market now than wait for uncertain future markets. Next, there is a mismatch between declared policy and implementation. Far too few resources are allocated for management, while the rate of logging is beyond what the forestry agencies can cope with (Wyatt-Smith 1987). Some managers have adopted the ‘minimum intervention’ approach on the argument that there are still uncertainties in the value of some silvicultural treatments (Tang 1987).

Forestry agencies are unable or unwilling to implement the declared management policies, and silvicultural prescriptions are always behind schedule, or abandoned altogether. Panayotou and Ashton (1992) present several cogent reasons for this:

1. Heavy pressure from politicians to practice accelerated felling cycles, clear felling, re-entry, and leniency with regard to logging damage and illegal cuttings;
2. Uncertainty of forest tenure, due to rapid conversion of forest lands to agriculture, uneven distribution of land, and short logging tenures which discourage private investment; and
3. Grossly undervalued resources, with timber prices not including replacement or silvicultural costs and non-timber values. The stumpage and royalty fees are kept too low, and the governments do not receive the logging profits needed for silvicultural treatment.

An Evaluation

Silvicultural systems for natural forests have to ensure natural regeneration succeeds, and the quality, quantity and size of the chosen tree species are enhanced, without destroying the forest structure and function. Enrichment planting is an expensive alternative that should be minimised. Both the Shelterwood (monocyclic) and Selection (polycyclic) Systems are being purportedly used for managing dipterocarp forests in Asia. But how do the two systems stand up in real practice for managing dipterocarp forests? Shelterwood Systems depend directly on treating the desired seedlings for the next crop. This is a conceptually simple system which requires less supervision, and if done carefully, there is little damage to the next stand (Putz and Ashton, unpublished). Several workable examples of Shelterwood Systems have existed, the Malayan Uniform System being a well known one among them.

The critical factor seems to be the ease with which regeneration can be secured. It is this particular feature of dipterocarps that makes it much easier to manage them compared to other forest types. In the case of sal forests, natural forest management seems sustainable only where regeneration is easy to secure. This is the case with Coppice Systems, provided grazing and fire are controlled. The MUS has also capitalised on the profuse seedling regeneration capacity of the family.

Nevertheless there are elements within Shelterwood Systems that are discouraging:

1. Logging has to be delayed until the regeneration is ensured;
2. Rotations are long, by human terms;
3. Heavy felling might induce weed growth, and expose fragile soils to erosion; and
4. Unwanted trees which were formerly girdled can now be exploited with improved technology and diversified markets. Although such canopy openings would have allowed the highly preferred target trees to maximise their growth.

The Shelterwood Systems developed for all three dipterocarp forest types showed signs of success. But in many instances the Shelterwood Systems seem to have fallen victims of outside changes. Workable systems have thus been continuously incapacitated by the demands of society, rapid and unplanned landuse changes, illegal felling, fire and grazing, and finally our complete bewilderment with tropical ecosystems. The four examples below highlight them:

1. The Coppice Systems in India have been clearly worked out, and may be the only dipterocarp forests sustainably managed for 3 rotations or more. But the demand for timber and fuelwood in India exceeds the production. The silvicultural response has been to shorten rotations. This has not been a realistic solution because increased frequency of removal results in degradation of stumps. Leaving behind standards to assist natural regeneration to compensate for the degradation was tried. This too proved unsuccessful because these forests are close to villages and the demand for grazing lands is high. When the demand for firewood and small timber exceeded biological capacity, shorter rotations were resorted to to enhance supply. This has accelerated the decline, and the areas have to be planted up as a consequence.
2. In the Malayan case, the MUS which took form following the Japanese Occupation (1942-1945) could never really be put into practice. During the 1950s Emergency in Peninsular Malaysia guerrillas took refuge in these very forests. It was difficult to work long in a forest - it was often a case of log and leave. The 1970s saw peace and an acceleration of economic growth. Large tracts of the lowland dipterocarp forests, for which the MUS was formulated, were converted to plantations of cash crops. Thereafter, logging was confined to the hillier terrain. Here the MUS was considered unsuitable and selective fellings have been applied.
3. In some instances sheer confusion seems to have prevailed in our attempts to manage dipterocarp forests. In Malaya, Departmental Improvement Fellings of the 1930s proved ineffective on the poles

and immature trees, for they need to be repeated (Wyatt-Smith 1963). Following the initial burst, growth slows down with onset of crown competition. In the 1970s, such thinnings were introduced in Sarawak under a different name, 'Liberation Thinnings' (Hutchinson 1979). But the Department reduced such treatments on the basis that the increments are too small for the effort (Lee 1982). However, liberation thinnings to forests following a diameter limit cutting proved better (Chai 1984, Primack 1987). This resembles more a MUS except for the logging which was under diameter limits. With this kind of confusion, opportunities for better management were bypassed.

4. In other cases, the Shelterwood Systems have degenerated into selective fellings. In the Indian Irregular Shelterwood System, uncertainty of regeneration led to retention of trees below a specified girth as part of the future crop. This has led to some confusion, and silvicultural treatments benefit neither seedlings nor poles.
5. Most extreme is the case with Peninsular Malaysia. The system introduced here to manage the hill forests was called the Selective Management System (Mok 1977). One of three systems was to be applied depending on the requirements. This included the monocyclic MUS, polycyclic Selection System, and cutting and planting. But unfortunately, the Selective Management System in practice became a selective felling.

In contrast with Shelterwood Systems, the Selection System is based on maintaining the forest stand structure, by extracting proportionate number of trees from different size classes. It works well with species that can tolerate some shade, and small gaps suffice for their growth (Putz and Ashton unpublished). The system allows frequent timber extractions, but substantial management is required. Logging has to be carefully done to protect young trees.

The selection systems are not truly practised in the dipterocarp forests although the Philippines Selection Felling System in theory has the necessary silvicultural components to qualify as one. Elsewhere, Selection Systems have degenerated in practice into selective fellings based on diameter limit. This is not a silvicultural system in the classical sense. Critics claim selective fellings cannot fulfill the requirements of a polycylic system (Wyatt-Smith 1987, Appanah and Weinland 1990), and that in reality it is merely a bicyclic system. Its major difficulties are:

1. Seedling regeneration is not attended to, and this might lead to a decline in the future crops;
2. Composition of future crops cannot be controlled;
3. The intermediate class (residuals) which is poorly represented, may also be inferior, suffer much logging damage, and subsequently succumb. Overall their growth rates may also be below that forecasted;
4. The cutting cycles are over-optimistically short; and
5. The more frequent entries can damage the soil and young regeneration.

Despite the criticisms, most of the seasonal and aseasonal dipterocarp forests are selectively logged at present. Perhaps the advantages of short felling cycles, fewer tendings, and freedom from limitations of seedling regeneration have led to such a preference. Supporters nonetheless argue that the Selection System is suitable for dipterocarp forests, many of which are now in steep terrain, with spotty seedling regeneration, and are relatively inaccessible. The weakness is in the implementation. The test of course is with the second cut, which will soon take place in Malaysia and Indonesia: overall, a decline in yield is expected. The true danger lies in temporarily overcoming the problem by reducing girth limits and cutting cycles.

In the aggregate, both silvicultural systems have their pros and cons. But trying to apply a workable silvicultural system is not a simple matter. It has to ensure society's needs are met by harvesting the forest without degrading it. Despite the many mistakes and miscalculations, more has been done to develop management systems for dipterocarp forests. Nonetheless, detractors may emphasise that there is very little management in reality. That aside, it must be stated that if ever management of tropical forests is possible, the best chances are with the dipterocarp forests. Their special attributes have endowed them with several advantages in terms of easy regeneration, fast growth, and a rich commercial timber stand. So the silvicultural systems employed should attempt to enhance and exploit the special attributes of these forests.

As for the silvicultural system, no doubt we can argue in favour of selection fellings for the existing dipterocarp forests. The advantages include long regeneration period for seedling recruitment, enhanced biodiversity, guarantee of future crops from advance growth that is retained, and retaining of species and grades which may become marketable in the future. But maltreatment of the forest has become commonplace. The short cutting cycles have resulted in doubling of coupe areas, but almost as much timber as in a shelterwood cutting has been harvested. So are the problems of re-entry to logged over coupes as timber scarcity develops. Next, selection felling is regularly abused with the removal of the best stems without any attempt to redress the balance by simultaneous removal of the poorer material that can lead to genetic impoverishment of the forests. Perhaps the stage has arrived where management in the true sense can be introduced. This of course requires that besides paying proper attention to the silvicultural systems and harvesting methods, management must pay heed to other aspects like the preservation of ecological functions, conservation of biodiversity, and maintaining the integrity of the forest. In addition, the social issues that may impact on the management of a forest must be given a higher priority.

Good management is indispensable whatever the silvicultural systems. An inappropriate silvicultural system may mean that the maximum productivity of the forest has not been captured. But what really sets back tropical forests is poor harvesting practices. Usually, harvests exceed growth rates. Few of the silvicultural tendings are done, further delaying the growth of the crop. Logging using skidder-tractor systems is exceedingly damaging to the soil and the standing residuals. Soil damage, in terms of erosion and compaction is exceedingly heavy. The immediate need is to adopt harvesting practices that minimise such damage. A swing in that direction has begun in Sabah. Already, one forest reserve is being managed under tight prescriptions. Skidder-tractors are heavily controlled and limited to pre-aligned trails only, and are only operable on slopes below 15°. On steeper slopes, a long range cable crane system is used which does only limited damage to the soils and residual trees. Such developments provide us with the optimism so much needed in tropical forest management.

Additional Research Needs

1. Management systems have been applied universally over the landscape without regard to site and timber stand characteristics. This cannot be ecologically optimal. Intensive management procedures should be developed whereby silvicultural systems are applied that are more specific to the site (site categories, floristic groups, etc.).
2. Harvesting damage can be easily controlled, and the improvements realised will be immediate and several fold. Besides research to lower harvesting damage, standards for allowable harvesting damage should be drawn.
3. There is still much uncertainty about cutting cycles in selection fellings. The growth data available from few sites are broadly applied to large areas. Not only should existing growth data be reviewed rigourously so as to derive more appropriate cutting cycles, additional growth plots should be set up so all the different forest types are included.
4. In selection fellings, seedling regeneration and growth are often not given attention. Studies should be initiated to determine post-harvest fruiting and seedling regeneration characteristics, and tending procedures.
5. The response of advance growth to liberation treatments requires further investigation. Their reaction to heavy isolation, injury, soil disturbances and water stress should be studied. Will selectively logged forests require further crown liberation to optimise growth? Will promoting dense crop regrowth affect soil-moisture balance?
6. No data are widely available on regenerated stands managed under Shelterwood Systems. Such stands should be reexamined. The structure of the stand and regrowth composition would help illuminate the effect of improvement fellings and climber cutting treatments.
7. The basis for sustaining long-term forest production depends on the soil characteristics and organic matter accumulation. The impacts of harvesting on the nutrient cycles have to be further investigated. What will be the impacts of whole tree harvesting on nutrient cycles?
8. With increase in utilisation of lesser-known or lesser-used species, will selective logging be the same as in the past? How will this affect regeneration and composition of future crops?
9. With changes to the future crops likely to take place, gregarious and very common species may become even more important for management. Autecological studies of these species are needed to fine-tune the management to favour such species for future crops.

10. In most forests selective logging will soon enter into the second cut. Logged over forest will be the future source of timber in the region. Investigations are needed on the consequences of a second cut on future production, forest structure, floristic composition, and seedling regeneration.
11. Selection of species for enrichment planting programmes is still primarily *ad hoc*, usually based on what is available. Incidental observations have suggested that there is a core of species among dipterocarps (e.g. *Shorea* spp. (engkabangs), *Dryobalanops aromatica*, *Shorea trapezifolia*, and others) which share characteristics including fast growth and regular fruiting. Such species should be developed for planting, and their tolerances and growth requirements (light, water) should be investigated further.

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Chapter 9

Plantations

G. Weinland

Introduction

Research on establishment and maintenance of dipterocarp plantations has been pursued now for almost seventy years. Efforts were especially intensive in three countries: India, Indonesia and Malaysia. In India the research concentrated mainly on *Shorea robusta* because of its abundance and its significance for agroforestry systems. In Indonesia and Malaysia and some other countries of the Indo-Malayan region a wider range of dipterocarp species was investigated. The research covered the whole range of plantation problems, albeit not with the same species over the whole range. Probably with exception of *S. robusta* no other dipterocarp species has been so well studied for operational schemes. On the whole, young dipterocarp plants were considered sensitive, delicate, and unsuitable for even-aged plantations but appropriate for enrichment planting. The fear of over-exposing sensitive young dipterocarp plants to light, however, has led to frequent failures of planting operations. It was thought that the young plants needed overhead shade for survival and good growth. The wide tolerance variation among different dipterocarp species, and their changes with age, were not recognised.

In **India**, the earliest plantation efforts recorded are for *Shorea robusta* in 1860 at Barielly in Uttar Pradesh and *Hopea parviflora* in 1880 in South Kanara, Karnataka. *Hopea* was underplanted in teak plantations as a possible second storey crop in the coastal plains. Around 1890, taungya systems were started in West Bengal and Uttar Pradesh. This still continues, but on a reduced scale as there is progressively less and less clear-felling of forests. In Uttar Pradesh the main dipterocarp species was *S. robusta*, while in West Bengal, which has a more humid climate with less seasonality of rainfall, *S. robusta* was mixed with *Chukrassia tabularis* and *Michelia champaca*. The practice was to sow seeds in lines. Around 1910, *Hopea parviflora, Dipterocarpus turbinatus* and *Vateria indica* were raised in a clear-felled area in Makut (Karnataka). In South Kanara district, the home of five *Hopea* spp., techniques for raising *H. parviflora* and *H. wightiana* were already perfected by this time. The two species are raised together in private woodlots by local people, *H. parviflora* for timber and poles and *H. wightiana* for fuel wood. Currently, all these species are being planted for restoration of degraded rain forests and re-afforestation of barren land. The nursery techniques for some of these species have been standardised (Rai 1983) and experimental results on restoration of degraded rain forests have been reported (Rai 1990). In the Andaman Islands, the Andaman Canopy Lifting System was developed to secure the regeneration of dipterocarp species (Chengappa 1944). To ensure regeneration of *Dipterocarpus macrocarpus* in North East India, a system called Aided Natural Regeneration involving supplementary planting of dipterocarps, is popular. Dipterocarp plantation research or research with relevance to dipterocarps covered a very wide range. The majority of the research was devoted to *Shorea robusta.* Aspects especially investigated were seed procurement/production and germination (e.g., Verma and Sharma 1978, Rai 1983, Prasad and Parvez-Jalil 1987), soils and nutrition (e.g., Bhatnagar 1978), rehabilitation of degraded sites (e.g., Prasad 1988, Rai 1990), pests and diseases (e.g., Harsh *et al.* 1989, Sen-Sarma and Thakur 1986) and agroforestry (e.g., Jha *et al.* 1991). *In situ* gene conservation of *Vateria indica* is carried out in the Western Ghats (Negi 1994). Troup's Indian Silviculture (1980) gives a full account of silviculture in India and Burma and contains in the second volume the complete silviculture of sal (*Shorea robusta*) including plantation silviculture. Additionally, it contains the silvicultural characteristics of the following dipterocarp species: *Shorea assamica, S. talura (syn. roxburghii), S. tumbuggaia, Dipterocarpus alatus, D. bourdilloni, D. costatus, D. grandiflorus, D. indicus (syn. turbinatus), D. kerrii, D. macrocarpus, D. pilosus, D. tuberculatus, D. turbinatus, Hopea glabra, H. odorata, H. parviflora, H. utilis, H. wightiana, Vateria* *macrocarpa, V. indica, Vatica lanceaefolia and V. roxburghiana.* A comprehensive description of the dipterocarps of South Asia is contained in RAPA Monograph 4/85 (FAO 1985).

In **Nepal**, research on dipterocarps has concentrated on the management of sal (*Shorea robusta*) forests and on forest seeds and nursery procedures (e.g., Napier and Robbins 1989). In **Pakistan**, Chowdhury (1955) described the silvicultural problems of *S. robusta* and Amam (1970) trials of direct sowing. In **Bangladesh**, systematic planting of *S. robusta* started last century (1856) within the traditional taungya system. Since the late 1970s there are greater efforts to improve the management of the dipterocarp species (Das 1982). Subsequently, research has been carried out on propagation techniques (Banik 1980, Rashid and Serjuddoula 1986, Haque *et al.* 1985, Serjuddoula and Rahman 1985). Jones and Das (1979) developed a programme for the procurement of improved forest tree seeds, which is now the task of the National Tree Seed Center established in 1986 (Mok 1994). The Species Improvement Programme includes the plus tree selection of *Dipterocarpus turbinatus* and *Hopea odorata* (Nandy and Chowdury 1994). Dipterocarp species under investigation are: *Anisoptera glabra, Dipterocarpus costatus, D. pilosus, D. turbinatus, Hopea odorata* and *Shorea robusta.*

In the past, the plantation efforts in **Thailand** focussed on planting *Tectona grandis* and fast-growing exotic species. Plantations involving dipterocarps have been established since the 1980s. Consequently, research on dipterocarps has been intensified. A description of the dipterocarps of mainland South East Asia has been prepared by Smitinand and Santisuk (1981) and of the silvicultural ecology of the dipterocarps of Thailand by Smitinand *et al.* (1980). Both contain information on silvical aspects. Research has been concentrating on collection, storage and germination of seeds and on mycorrhizae (e.g., Khemnark 1980, Panochit *et al.* 1984, Panochit *et al.* 1986, Chalermpongse 1987, Boontawee and Nutivijarn 1991, Linington 1991, Kantarli 1993). Concerning dipterocarp planting stock propagation the ASEAN Forest Tree Seed Centre concentrates on vegetative propagation (Mok 1994). *Dipterocarpus alatus, Hopea odorata* and *Shorea siamensis*, amongst others, are priority species for reforestation activities and *D. alatus* and *D. turbinatus* are included in the gene conservation programme (Sa-Ardavut 1994). Species which have received attention are: *Anisoptera costata, Dipterocarpus alatus, D. costatus, D. intricatus, D. macrocarpus, D. obtusifolius, D. tuberculatus, Hopea ferrea, H. odorata, Shorea henryana, S. obtusa, S. roxburghii* and *S. siamensis.*

In **Vietnam**, some plantation work on an experimental scale is carried out in Dong Nai Province, in the Central Highlands and in Daklak Province (Doan 1985, Vu 1991, Dinh 1992). Several studies on the distribution of dipterocarps, and on the structure and dynamics of dipterocarp forests in Vietnam were carried out which contain information on silvical characters of the dipterocarps (e.g., Nguyen Nghia Thin 1985, Vu Van Dung 1985). Bieberstein *et al.* (1985) investigated the possibilities of rehabilitating areas devastated during the Vietnam War. Species investigated were: *Dipterocarpus alatus, Hopea odorata* and *Anisoptera costata*. Research on various other aspects was carried out on these species and, additionally, *Dipterocarpus dyeri, D. tuberculatus, D. obtusifolius, Shorea obtusa, S. roxburghii, S. thorelii, S. siamensis* and *Vatica odorata.*

In **Cambodia** the phenology and germination behaviour of *Hopea odorata* has been investigated by Tixier (1973).

In **Peninsular Malaysia** planting of dipterocarps started in 1900 when *Neobalanocarpus heimii* was line-planted in forest reserves but was discontinued when Commercial Regeneration Fellings were introduced in 1918. Between 1929 and 1941 experimental plantations of dipterocarps were started at the Forest Research Institute Malaysia. Main dipterocarp species planted were *Anisoptera scaphula, A. laevis, Dipterocarpus baudii, Dryobalanops aromatica, D. oblongifolia, Shorea acuminata, S. curtisii, S. leprosula, S. macroptera, S. macrophylla, S. ovalis, S. parvifolia, S. platyclados and S. sumatrana.* Dipterocarps were later used in enrichment plantings (e.g., Tang and Wadley 1976). Main species planted were those of the fast-growing hardwoods. Enrichment planting is still pursued, albeit on low scale (Chin *et al.* 1995). Barnard (1954) summarised the knowledge on artificial regeneration of dipterocarps describing the operations from planting stock procurement to post-planting tending. Wyatt-Smith (1963b) furthered the knowledge on enrichment planting and presented information on choice of species and silvicultural operations up to the tending of the established crop. The review on planting high quality timber species by Appanah and Weinland (1993) presents an overview on silvics and silviculture of many high quality timber tree species that have been planted in Malaysia. On present knowledge, the most promising dipterocarp plantation species for Peninsular Malaysia are: *Anisoptera laevis, A. scaphula, Dipterocarpus baudii, D. costulatus, D. kerrii, Dryobalanops aromatica, Hopea odorata, Shorea acuminata, S. leprosula, S. macrophylla, S. macroptera, S. ovalis, S. parvifolia, S. platyclados* (Wyatt-Smith 1963b, Zuhaidi and Weinland 1994, Darus *et al*. 1994). Darus *et al*. (1994) carried out plus tree selection for *Shorea leprosula* and *S. parvifolia,* identified a seed production area for *S. lepidota* and included several other dipterocarps in a clonal selection programme and field tests.

Sarawak embarked on plantations of dipterocarps in the 1920s by planting *Shorea macrophylla*. While such plantings were pursued on a small scale until 1975 (Kendawang 1995), the state commenced large-scale plantings of dipterocarps in 1979 after disappointing results were obtained from research on exotic fast-growing species (Mok 1994). Dipterocarp plantations are established within the Reforestation Programme for Permanent Forest Estates on areas degraded by shifting cultivation (Kendawang 1995). About 4940 ha have been planted on an operational scale with *Shorea* species of the pinanga group, especially *Shorea macrophylla* (Kendawang 1995). These plantings are based on a species-site matching procedure (e.g., Butt and Sia 1982, Ting 1986).

In **Sabah**, dipterocarp plantations have, with the exception of the enrichment plantings under the Innoprise-Face Foundation Rainforest Rehabilitation Project (Moura-Costa 1993, Moura-Costa and Lundoh 1993, 1994), only been established on an experimental scale. Until 1994 about 700 ha had been planted within the Face Foundation Project. Dipterocarp species used are: *Dipterocarpus* spp., *Dryobalanops lanceolata, Hopea nervosa, Parashorea malaanonan, Shorea argentifolia, S. johorensis, S. leprosula, S. macrophylla, S. ovalis* and *S. parvifolia.* The plantation target is 25 000 ha.

In **Indonesia**, the establishment of experimental plantations (e.g., Darmaga, Haurbentes, Pasir Hantap, Purbah Tongah and Sangau) started at the end of the 40s (Butarbutar 1986, Masano 1991, Masano *et al.* 1987, Masano and Alrasjid 1991, Omon 1986). Apart from these experimental plantations, planting of dipterocarps was mainly enrichment planting in the concession areas and regularly carried out in the state-owned concession INHUTANI II in South Kalimantan (Mok 1994). Now, the Indonesian Selective Cutting and Planting System prescribes reforesting all logged areas and since the beginning of the 90s large-scale cutting propagation is carried out. Research on dipterocarps has covered a wide field ranging from seed procurement and testing (e.g., Masano 1988a, b, Syamsuwida and Kurniaty 1989), vegetative plant propagation (e.g., Smits 1987, 1993, Umboh *et al*. 1988), plantation stock trials (e.g., Wardani *et al.* 1987 Siagian *et al*. 1989b), mycorrhizal symbiosis (e.g., Smits 1982, Santoso *et al.* 1989, Santoso 1991) to agroforestry problems (e.g., Kartawinata and Satjapradja 1983, Sardjono 1990). It appears that no specific tree improvement programme for dipterocarps has been initiated (Sunarya 1994). Dipterocarp species which received attention were: *Dipterocarpus grandiflorus, D. retusus, D. tempehes, Dryobalanops lanceolata, Hopea bancana, H. mengerawan, H. odorata, H. sangal, Shorea guiso, S. johorensis, S. leprosula, S. macrophylla, S. mecistopteryx, S. multiflora, S. ovalis, S. palembanica, S. parvifolia, S. pauciflora, S. pinanga, S. platyclados, S. selanica, S. seminis* and *S. smithiana.* Recently, a manual for the dipterocarp light hardwoods for Borneo Island has been compiled by Newman *et al.* (1996).

In the **Philippines** first research efforts on dipterocarp plantation problems commenced in the 30s (e.g., Caguioa 1938, Lantion 1938). The research work continues (e.g., Anon. 1982, 1991). Some experimental plantations were established and private companies participated in the plantation programmes (e.g., Notonton 1985). Underplanting was carried out in Benguet pine plantations (Anon. 1960) with success. Enrichment planting was rarely done with dipterocarps, but with fast-growing exotic trees species such as *Paraserianthes falcataria*. Underplanting and enrichment planting trials with dipterocarps started late (Chinte 1982, Mauricio 1987a, Abalus *et al.* 1991). Emphasis of research was on germination trials (e.g., Basada 1979, Garcia *et al*. 1983), seedling trials (e.g., Bruzon and Serna 1980, Gianan and Peregrino 1986), use of wildings as planting stock (e.g., Lantion 1938, Penonia 1972), planting trials (e.g., Tomboc and Basada 1978, Miyazaki 1989). Agpaoa *et al.* (1976) provided valuable information on planting techniques. A tree improvement programme for dipterocarps has been launched which includes seed production area and plus tree selection, establishment of clonal gardens and gene conservation (Rosario and Abarquez 1994). Promising dipterocarp plantation species are: *Dipterocarpus grandiflorus, D. warburgii, Parashorea plicata, Shorea almon, S. guiso, S. negrosensis, S. polysperma* and *S. squamata.* Newman *et al.* (1996) compiled a manual of dipterocarps for the Philippines.

Silvics

Silvics deals with the life history and general characteristics of forest trees and stands particularly refering to locality factors as a basis for the practice of silviculture.

For tree species of the high forests (a closed forest of tall trees), tolerance is their ability to grow satisfactorily in the shade of and in competition with other trees. If intolerant of shade, a species is termed a 'light demander', if tolerant, a 'shade bearer'. Discussions on how much light should be given for good growth and how much shade should be retained started early. Sanger-Davies (1931/1932) considered most of the commercial dipterocarp species as light demanders which should be given full overhead light and full space for maximum development. While larger plants need full light for good growth, young seedlings need a shelter either from existing belukar or from planted nurse crops. Indeed, planting of dipterocarps under a nurse crop (e.g., *Paraserianthes falcataria*) was successful in the experimental plantations in Indonesia (e.g., Masano *et al.* 1987**)** and Malaysia (Barnard 1954) and elsewhere in the region (e.g., Doan 1985). All shading experiments showed without doubt that optimal growth of dipterocarp seedlings is only achieved under partially shaded conditions (e.g., Nicholson 1960, Mori 1980, Sasaki and Mori 1981 and others).

There is a wide range of shade tolerance among older seedlings/saplings of dipterocarp species which follows the known pattern of higher shade tolerance for late succession species and higher light demands for earlier succession species (e.g., Strugnell 1936a). Qureshi (1963) classified about 100 tree species (including. *Shorea robusta*) as tolerant, moderately and intolerant of shade in comparison to *Acacia arabica* which is intolerant of shade at every developmental stage. In Peninsular Malaysia, field experiments on light requirements were established early in conjunction with Regeneration Improvement Systems and a discussion on canopy manipulations over young regeneration ensued (e.g., Sanger-Davies 1931/1932, Watson 1931/1932b, Walton 1936b). However, this type of experiment was abandoned when Regeneration Improvement Systems ceased in Malaya in the 1930s. JICA (1993, 1994) reported an underplanting trial where dipterocarps (*Shorea leprosula, S. parvifolia, Dryobalanops aromatica* and others) have been underplanted in *Acacia mangium* stands with different size gaps. The performance was best where two rows had been removed (9 m opening). Controlled (artificial) experiments are needed for base line information on the light requirements of species to be complemented by field trials where shade from natural vegetation is manipulated. More details on the light physiology of seedlings can be found in Chapter 3.

Mycorrhizal symbiosis with dipterocarps has received great attention in recent years. Since this field is dealt with in detail in Chapter 6, only some practical aspects are discussed here. The importance of mycorrhizal symbiosis for the survival and growth of trees is not in question. Most of the investigations deal with the identification of mycorrhizal fungi and their strains/forms (e.g., Louis 1988) and Lee and Lim (1989) have reported mycorrhizal infection of dipterocarp seedlings in logged and undisturbed forests. Host specificity of mycorrhizal fungi was reported by Smits (1982) and it is concluded that the chance of a seedling finding the right fungus is better the closer the seedling germinates and grows to the mother tree. He explains the formation of eco-unit patterns as linked to such a preference. Whether host specificity is wide spread among dipterocarps remains to be investigated. Alexander *et al.* (1992) found that the root contact of seedlings with mature trees is important for the infection with mycorrhizae which would have a bearing on the design of regeneration systems. The retention of mature trees seems to be important for this reason. Turner *et al.* (1993) investigated the effect of fertilser application on dipterocarp seedling growth and mycorrhizal infection. The application involved 10 g m^{-2} N, P_2O_5 and K_2O to *Shorea macroptera* seedlings grown in pots of forest soil (nursery condition). The results showed that mycorrhizal infection was significantly higher for fertilised seedlings. Oldeman (1990) draws attention to the fact that mycorrhizal symbiosis occurs particularly on poorer, acid soils and suspects that by changing the chemical status of the soil through fertilisation, mycorrhizal functioning might be impaired. Santoso (1987, 1989) showed that there is an increase in shoot/ ratio, dry weight of leaves, roots, stem diameter, as well as absorption potential for nutrients among several dipterocarps when inoculated with *Scleroderma columnare*. One dipterocarp species (*Shorea pinanga*) showed better results when inoculated with *Russula amatic*. Inoculation techniques for nurseries are described for example by Bakshi (1980), Khemnark (1980), Smits (1987) and Tacon *et al.* (1988). Mycorrhizal research has yielded practical incoculation techniques for nurseries.

Site requirements of dipterocarp species have only been examined systematically for *Shorea robusta* (e.g., by Yadav and Mathur 1962, Bhatnagar 1966). Butt and Sia (1982) and Ting (1986) touch on the problem in their evaluation for reforestation and rehabilitation projects in Sarawak, however, assignment of species to site was not based on species-adaptation trials. Most of the information has still to be obtained from species compilations (e.g., Foxworthy 1932, Symington 1974, Smitinand *et al.* 1980, Ashton 1982) which contain information on the natural habitat of the species, from which in many cases generalised inferences to the site requirements under plantation conditions can be made. A systematic approach to this problem through species adaptation trials is urgently needed. Such trials would include the species most likely to be used for plantation programmes. Field operations before and during planting site operation change site conditions, foremost the soil-physical structure so site management with low negative impact is important for the success of a plantation. Dabral *et al.* (1984) reported impaired rooting behaviour of *Shorea robusta* in compacted soil. Kamaruzaman (1988) showed that bulk densities in crawler tractor tracks declined to 1.52 g cm^{-3}, at which rooting is severely impaired. Gupta (1955) investigated compaction, erodibility and other soil-morphological features in *Shorea robusta* forests and taungya plantations. In the latter, cultivation and continued exposure had caused hard pans to develop which resulted in reduced seepage and increased erodibility.

When planting a species the silvicultural characters of the trees should be known. Stand density regimes depend on a clear understanding of the growth form, which is the characteristic shape, posture, and mode of growth of a tree (Ford-Robertson 1983). Troup (1980) describes silvicultural characters of 22 dipterocarp species besides *Shorea robusta*. Additional work includes that of Kadambi (1954, 1957), but, these reports cover only a small percentage of the total species of dipterocarps. Dipterocarp species differ considerably in terms of crown structure, branching habit, growth dynamics etc. Hallé and Ng (1981) worked on crown architecture, especially reiteration and aggregation. Zuhaidi and Weinland (1994) and Appanah and Weinland (1993) give information on growth form of some commercially important dipterocarp species for planting and mention the species: *Anisoptera laevis, A. scaphula, Dryobalanops aromatica, D. oblongifolia, Hopea odorata, Shorea acuminata, S. leprosula, S. macroptera, S. macrophylla, S. parvifolia, S. platyclados* and *S. ovalis*. Information on species-specific growth dynamics, which is required for the design of species mixtures, is contained, e.g., in Howard (1925), Edwards and Mead (1930), Griffith and Bakshi Sant Ram (1943), Mathauda (1953b, 1955), Ng and Tang (1974), Rai (1979, 1981a, b, 1989), Masano *et al.* (1987), Primack *et al.* (1989), Zuhaidi *et al.* (1994). Within the group of the fast-growing light hardwoods (e.g., *Shorea leprosula, S. parvifolia, S. ovalis* and *S. macrophylla*) important differences between species in growth dynamics seem to exist (e.g., Wyatt-Smith 1963b, Zuhaidi and Weinland 1994, Zuhaidi *et al.* 1994).

The following characters of a tree species to be planted should be known to the practising silviculturist: (i) control of side branch development by the leader shoot (apical dominance), (ii) phototropic sensitivity (phototropism), (iii) self-pruning capacity, (iv) type of branch formation, and (v) growth rates and growth dynamics.

In conclusion, there is a pressing need to build up information on the silvical and silvicultural properties (stress tolerance, growth form, mode of growth) of a defined set of the most promising species for plantations and on the site requirements (site adaptation) using standardised methods.

Stand Regeneration and Establishment

Regeneration of a forest is the renewal of a tree crop, whether by natural or artificial means. Renewal by self-sown seed is termed ‘natural regeneration’, by sowing or planting ‘artificial regeneration’. Formation of stands means all the operations contributing to the creation of a new crop up to the stage where it is considered established, i.e. from seed procurement, as for a nursery, to early tending. Establishment is the process of developing a crop to the stage at which the young trees may be considered established, i.e. safe from normal adverse influences e.g., drought, weeds or browsing, and no longer in need of special protection or special tending, but only routine cleaning, thinning and pruning (definition according to Ford-Robertson 1983).

Species Choice

Up to now, little systematic species elimination work has been done on plantation species with the exception of *Shorea robusta,* around which a complete silvicultural and agri-silvicultural system has developed. Anderson (1975) proposed *Shorea* spp. of the pinanga group (e.g., *Shorea macrophylla, S. pinanga* and *S. stenoptera*) as an agricultural crop. Jha *et al*. (1991) have discussed the selection and evaluation of suitable tree species and food crops for agro-forestry systems which include *Shorea robusta.*

In the Malaysian context Wyatt-Smith (1963b) presented a list of species with promise for plantation establishment. They were selected on the basis of 16 criteria, for example, fruiting frequence, seed viability, collection and nursery handling, fast, early height growth, natural bole form, self-pruning capacity, timber properties, etc. The species proposed were: *Anisoptera laevis, A. scaphula, Dipterocarpus baudii, D. costulatus, D. grandiflorus, D. kerrii, D. verrucosus, Dryobalanops aromatica, D. oblongifolia, Hopea odorata, Shorea acuminata, S. curtisii, S. leprosula, S. macrophylla, S. macroptera, S. ovalis, S. parvifolia, S. pauciflora* and *S. platyclados*.

Recently, an assessment of the dipterocarp plantation stands at the Forest Research Institute Malaysia was carried out in the field and from phenological and plantation records (Zuhaidi and Weinland 1994, Appanah and Weinland 1996). The indicators used were: overall diameter growth rate, initial height growth rate, stem shape, seedling adaptation phase, natural pruning capacity, cutting propagation capacity, site specificity, natural regeneration capacity within the rotation age, susceptibility to diseases and mode of growth. The result was that the dipterocarp species differed considerably in some aspects, especially in growth form, mode of growth, site specificity and natural regeneration capacity. In the case of undesirable mode of growth, the species was nevertheless considered suitable for planting, if the deficiency could be corrected by simple silvicultural means. As a result, 15 dipterocarp species were chosen for immediate inclusion into plantation programmes (*Anisoptera laevis, A. scaphula, Dipterocarpus baudii, D. costulatus, D. kerrii, Dryobalanops aromatica, D. oblongifolia, Hopea odorata, Shorea acuminata, S. leprosula, S. macroptera, S. macrophylla, S. parvifolia, S. platyclados* and *S. ovalis*), and 2 species (*S. bracteolata* and *S. curtisii*) were considered promising, but were not included because of lack of sufficient information and doubtful field characteristics. For the Bornean part of Malaysia species could be added, such as *Parashorea malaanonan, Shorea fallax* and *S. smithiana*, and for Indonesia *Dryobalanops lanceolata, Shorea laevis, S. macrophylla* and *S. selanica*. The most common plantation species in the Philippines are *Dipterocarpus grandiflorus*, *Shorea almon, S. contorta, S. guiso, S. polysperma* and *S. squamata* (e.g., Assidao 1950, Cacanindin 1983, Abalus *et al.* 1991). Systematic species/provenance elimination trials are urgently needed, particularly in relation to the more pronounced seasonality following the extensive removal of natural forests in many regions of the humid tropics.

Planting Stock Production

Seed

Much effort has been invested in developing methods for seed production, collection and handling. Generally, dipterocarps fruit at irregular intervals and with varying seed yield. On top of that, seed viability declines. This field is reviewed in Chapter 4. Tompsett (1991) has reviewed the storage aspects of dipterocarp seeds. Much is also known about germination (e.g., Caguioa 1938, Jensen 1971, Tixier 1973, Chai 1973, Masano 1988a, b, Ng and Mat Asri 1991, and others), the effect of harvesting time and sowing interval on germination (Haque *et al.* 1985), the effect of fruit ripeness upon germination and seedling growth of *Shorea ovalis* (Kosasih 1987), the effect of fruit collection time on the germination of *Dryobalanops aromatica* (Barnard 1954), the effect of seed size on germination of *Shorea contorta* (Basada 1979), the effect of wing colour on the germination of *Shorea pinanga* and *S. stenoptera* (Masano 1988b) and the effect of tree girth on seed viability and germination of *Shorea robusta* (Yadav *et al.*1986). Overall, the storage/germination/viability aspects are sufficiently covered.

There is definitely a lack of information on the seed yield from trees and stands (quantity of seeds during a normal seed year). Such information is only available for *Shorea robusta* (Jain 1962, Sharma 1981). In Peninsular

Malaysia, flowering and fruiting are regularly observed over a wide geographical and climatic range and reliable records are available. Darus *et al.* (1994) proposed the establishment of seed production stands in the main climatic regions of Peninsular Malaysia and a corresponding tree selection and tree improvement programme. Similar efforts on tree improvement involving dipterocarps have been made in Bangladesh (Nandy and Chowdury 1994), India (Negi 1994), Philippines (Rosario and Abarquez 1994) and in Thailand (Sa-Ardavut 1994). Much of the improvement work in the region is coordinated within the Species Improvement Network (Anon. 1994).

Seedling planting stock

'In nursery practice, a seedling is a very young tree that has not been transplanted, i.e. is growing where it germinated' (Ford-Robertson 1983). Seedling planting stock for most dipterocarp species is usually potted and leaves the nursery after about 9 months. The seedling height is about 25-50 cm.

Generative propagation is still the prevailing method of plant production in dipterocarps and is technically not a problem if seeds are planted immediately after collection. Timber companies involved in propagation of dipterocarp seedlings have the expertise to run large-scale dipterocarp nurseries professionally e.g., in Indonesia or Sabah (Moura-Costa 1993). The literature on the propagation of dipterocarp seedlings deals mainly with planting stock type (e.g., Walton 1938, Barnard 1954, Pande 1960, Joshi 1959), sowing position of seeds (Serjuddoula and Rahman 1985), response of potted seedlings to fertilisers (Kaul *et al.* 1966, Bruzon 1978, 1982, Sundralingam 1983, Sundralingam *et al.* 1985), controlled mycorrhization (Garbaye 1989, Santoso 1989, Santoso *et al.* 1989), the use of bare-root plants (Sasaki 1980b, Mori 1981).

As far as the age of the planting stock is concerned Barnard (1954) found that for most of the dipterocarp species planting stock between 3 and 8 months old is the best (e.g., *Dryobalanops aromatica, Shorea leprosula* and *S. pauciflora*). Hodgson (1937a) concluded that planting stock only a few months old is more likely to survive than older material. Seedlings of *Anisoptera* sp., *Dryobalanops aromatica* and *Neobalanocarpus heimii* were planted with cotyledons still attached. While *D. aromatica* was destroyed by rodents, the two other species survived. Kuraishy (1942) transplanted 6-week old seedlings of *Shorea robusta* successfully.

Lamprecht (1989) proposes the use of 15-20 cm tall planting stock for economic and handling reasons. Which plant size to choose, should depend on the condition of the planting sites, that is, those with intensive weed growth require larger planting stock. To reduce the amount of weeding it is preferable to plant seedlings which are large enough to overcome weed competition at an early stage although growth rates might not be better than those of smaller planting stock. Planting stock size is an important aspect but root:shoot ratio, leaf area and diameter:height ratio are as important. Sturdy plants with a low root-collar:shoot ratio tend to form roots faster and are better equipped to withstand drought stress. In a trial carried out by Moura-Costa (not dated) initial height growth rates were significantly better for sturdier plants. Species tested were: *Dipterocarpus gracilis, Dryobalanops lanceolata, Parashorea malaanonan, Shorea johorensis, S. leprosula, S. ovalis* and *S. parvifolia.*

Type of planting stock is another factor to be considered. Potted seedlings proved to be superior to bare-root planting stock (e.g., Anon. 1948a, Barnard 1949b). With the exception of a few hardy species, the survival of bare-rooted stock seems to be low (e.g., Cerna and Abarquez 1959). Rayos (1940) tested the survival of bare-rooted seedlings of *Hopea pierrei* of different sizes with their roots stored in moist sawdust before planting out. Survival was inversely proportional to storage period and seedling size. The smallest height tested was 10-20cm. Prasad (1988) found in a plantation trial on bauxite mining land that survival and growth of potted *S. robusta* plants were superior to that of plants from direct sowing.

Specific treatment of seedlings, such as shoot and root-pruning and the effect on growth and survival have been investigated. Root-pruning gave better survival and growth of planting stock. Walton (1938), Landon (1948b) and Barnard (1954) showed that survival and growth of *Dryobalanops aromatica* seedlings were superior when seedlings were wrenched (tap root severed) compared to unwrenched seedlings. The effects of shoot-pruning and stripping of the leaves on survival were inconclusive. Landon (1948b) planted *Dryobalanops aromatica* under the shade of a 20-year old *Fragraea fragrans* stand and topping, partial or total stripping of leaves had no effect on survival. Sasaki (1980a) pruned bare-rooted seedlings *Shorea talura* and *Hopea odorata* (removal of all leaves, all young parts of the stems and the tap root) and was able to store them in polythene plastic bags for several months without loss of viability. The effect of hormone application on the storage of potted seedlings has been investigated by Siagian *et al*. (1989b) for *Shorea selanica.* Dabral and Ghei (1961) applied gibbelleric acid to the shoots of *Shorea robusta* seedlings but failed to boost root development and growth.

There has been some systematic research on fertilisation of nursery planting stock. An early investigation into morphological symptoms of mineral deficiencies of nursery stock of *Shorea robusta* was carried out by Kaul *et al.* (1966). Deficiencies in N, P, K, Ca and Mg caused marked symptoms in both shoot and root development. Deficiencies in N, P and Mg affected height increment especially, while root development was affected by deficiencies in all minerals. Bruzon (1978, 1982) investigated the optimal NPK (14:14:14) fertilisation of *Shorea contorta* nursery seedlings of an average height of 15 cm grown in a mixture of potting medium and forest soil. The seedlings were fertilised (control, 2, 4, 6 and 8g) three times at an interval of approximately one month. The survival was best in the unfertilised control and with applications of 2g and 4g per seedling. Height and diameter growth were best in the 2g, 4g and 6g treatments. Survival was significantly reduced with application of 4 and 8g of fertiliser. Fertilisation with 2g NPK per plant is recommended. Bhatnagar (1978) tested the nutritional requirements of *Dipterocarpus macrocarpus* seedlings. For 1 year the potted seedlings were fertilised every two weeks with 450 and 900 mg NPK solution. Achieved height and dry weight were greatest with N and P at 900 mg application and K at 450 mg application. Sundralingam (1983) investigated the best height growth response of below 1-year old *Dryobalanops aromatica* and *D. oblongifolia* seedlings by fertilising the seedlings in a shaded nursery with 50 mg P_2O_5 (as superphosphate) and 300 mg N (applied as ammonium sulphate at 2-month intervals) per plant. The height growth was reduced to that of the control plants when the amount of phosphorus was doubled. In another experiment Sundralingam *et al.* (1985) tested the nitrogen and phosphorus requirements of *Shorea ovalis* seedlings in sand culture by fertilising seedlings with various dosages at 2-4 week intervals. After 8 months it was found that the optimal N dosage was 80 mg/plant per application and the optimal P dosage 4 mg/plant per application.

Another method to boost performance is through mycorrhizal inoculation. Garbaye (1989) reviewed the literature on natural and controlled mycorrhizal infection in tropical plantations including dipterocarp plantations. Santoso (1988, 1989, 1991) tested inocula of *Boletus, Russula* (3 species) and *Scleroderma* spp. on 45-day old seedlings of *Hopea odorata, Shorea compressa, S. pinanga, S. stenoptera* and *Vatica sumatrana* and after 6 months growth parameters such as diameter, dry weight of leaves, stems and roots were increased. Responses were best in *Hopea odorata, Shorea stenoptera* and *Vatica sumatrana* with *Scleroderma* spp., while responses of *S. pinanga* were best with *Russula* (species 2). Santoso *et al.* (1989) found that under the same experimental conditions as above all inocula increased the accumulation of micro-nutrients (Fe, Mn, Cu, Zn and Al) in leaves, stems and roots of the seedlings. Turner *et al.* (1993) investigated the effect of fertiliser application on mycorrhizal infection. NPK (combined N, P_2O_5 and K_2O) was applied at a rate of 10g m^{-2} to potted *Shorea macroptera* seedlings (potting medium: forest soil). In fertilised pots ectomycorrhizal infection was increased but the correlation between extent of infection and growth was closer in unfertilised seedlings, suggesting that seedlings may only be responsive to fertiliser addition when grown at very low nutrient availabilities. Mycorrhizal infection may be important under such conditions. Smits (1982, 1987, 1993) pointed out the importance of mycorrhizal infection in nurseries and described controlled inoculation

Wilding planting stock

'A wilding is a naturally-grown, in contrast to a nursery-raised seedling, sometimes used in forest planting when nursery stock is scarce' (Ford-Robertson 1983). Wildings were frequently used in the past and various trials have been carried out with them.

Wildings have been successfully used for planting places lacking natural regeneration. Capellan (1961) tested the possibilities of *Parashorea plicata* and *Shorea contorta* wildings as planting stock and *P. plicata* had better survival than *S. contorta.* Barnard (1954) mentions that wildings of *Shorea macrophylla, S. multiflora, Dipterocarpus baudii* and *Neobalanocarpus heimii* were successfully planted. Gill (1970), while reviewing experimental enrichment planting work in West Malaysia, found that transplanting bare-rooted wildings of *Anisoptera laevis, Shorea curtisii, S. leprosula, S.*

parvifolia and *S. platyclados* is promising. Fox (1971/72) investigated the performance of wilding stock of *Dipterocarpus caudiferus, Dryobalanops lanceolata* and *Parashorea tomentella*, of which *D. lanceolata* performed best. This was confirmed in a trial by Chai (1975). Jafarsidik and Sutomo (1988) developed a field guide for the identification of dipterocarp wildings for a production forest in West Sumatra including wildings of the genera *Anisoptera, Dipterocarpus, Hopea, Parashorea and Shorea*. Wardani and Jafarsidik (1988) put together a field guide for the identification of dipterocarp wildings of the genera *Dipterocarpus, Dryobalanops, Hopea* and *Shorea* for a forest area in West Kalimantan. Mauricio (1957) investigated factors which influence the performance of wildings of *Parashorea plicata* and *Shorea contorta* to determine: (i) the effect of the wilding size on survival, (ii) the time the wildings require to adapt to the planting site, and (iii) the most suitable size. In this experiment *P. plicata* had a higher survival, specially at heights of 20 cm and less. Lantion (1938) tested the performance and the behaviour of wildings of *Dipterocarpus grandiflorus* and *Shorea teysmanniana* and smaller plants had higher survival. The Forest Department in Malaya had a trial of *Dryobalanops oblongifolia* and *D. aromatica* in the nursery where six month-old wildings were transplanted into small claypots. *D. oblongifolia* wildings had 76% survival in the nursery and about 90% survival in the field after six months whereas *D. aromatica* wildings had a survival of 100% in the field (Anon. 1951).

Rayos (1940) tested the effect of storage time of wildings of *Hopea pierrei* on survival by covering their roots with moist sawdust. Survival was higher the shorter the storage time and it was greater for seedlings 10-20 cm high than for those in other height classes. No effect of storage time on survival rate was found by Siagian *et al.* (1989b). Moura-Costa (1993) obtained high survival rates with wildings from *Parashorea malaanonan, Shorea parvifolia* and *Dryobalanops lanceolata*. Forest-pulled seedlings were watered and kept in plastic covered chambers with high humidity until a new root system had formed. Survival in the nursery was up to 95% in a large scale operation. Barnard and Setten (1955) used wildings in an investigation on the effect of planting patch cultivation but found no difference to planting in unprepared patches. Wardani (1989) found that shoot and root-pruning increased survival of wildings. Hormone treatment of wildings for growth stimulation has been reported for *Vatica sumatrana* (Masano and Omon 1985), for *Dipterocarpus retusus* (Omon and Masano 1986), for *Shorea platyclados* (Napitupulu and Supriana 1987) and for *Shorea selanica*, (Siagian *et al.* 1989b). Increased survival rates were found for *S. platyclados* and *V. sumatrana* but not for *D. retusus* and *S. selanica*.

The Forest Department Sarawak reported the establishment of wilding nurseries as seedling reservoirs (Anon. 1948c). Before a heavy seedfall, cleanings were made beneath fruiting trees to form natural 'nurseries' which were used later to plant forests with low natural regeneration or in secondary vegetation. The seedling yield was excellent.

The use of wildings is not unequivocally supported. Wyatt-Smith (1963b) is critical about the use of wildings for the following reasons: (i) transplanting large forest seedlings is generally not successful, (ii) small forest seedlings suffer high mortality during the first two years, and (iii) the pool of young forest seedlings cannot serve as a continuous supply for large-scale plantations.

Vegetative propagation

Among the methods of vegetative propagation of grafting, air layering, tissue culture and cutting propagation, the latter is the most commonly used technique. Plant production from cuttings has been intensively investigated. Dick and Aminah (1994) have carried out a thorough review on cutting propagation of dipterocarps. Research work has been carried out on important factors influencing the rooting ability of dipterocarp cuttings, such as rooting facilities, rooting media, source of cutting material, type and treatment of cutting. According to Dick and Aminah (1994) 56 dipterocarp species have been tested, among them almost all of the species suitable for plantations. Vegetative propagation of dipterocarps is increasingly successful and has been introduced as large-scale operations in Indonesia (Sutisna, personal communication). Moura-Costa (1995) gives a detailed description of vegetative propagation techniques for *Dryobalanops lanceolata* and several *Shorea* spp. in context of plant production for large scale enrichment plantings of dipterocarps in Sabah. However, when cutting propagation is used in plantation programmes, it is necessary to precede such large-scale application by an established procedure of selection of superior stock plants. Clonal propagation of selected material from dipterocarps is in its infancy in the whole region (see e.g., Finkeldey and Havmoller 1994). Moura-Costa (1995) discusses a procedure of selecting best genotypic material at the seedling stage, the so-called

'Predictive Test for Apical Dominance'. The test has not yet been established for dipterocarps.

Some research has been carried out on tissue culture of dipterocarps. Linington (1991) grew seedlings in vitro from embryos of *Dipterocarpus alatus* and *D. intricatus*. Other *in vitro* experiments were carried out by Smits and Struycken (1983) on leaf fragments of *Shorea curtisii*, which formed callus and roots but no shoots, and on nodal explants of *Shorea obtusa* with axillary buds, which formed lateral shoots but no roots. Suspension cultures of embryonic axes of *Shorea roxburghii*, which eventually formed whole plantlets, were carried out (Scott *et al.* 1988). Umboh *et al.* (1988) described the rejuvenation of adult trees and a three step bud culture for *Shorea pinanga*. Moura-Costa (1993) describes trials in tissue culture techniques for *in vitro* propagation of *Dipterocarpus intricatus* which were successful. No commercially feasible procedure has been developed and tissue culture cannot be introduced on an operational scale at this stage.

Darus and Rasip (1990) carried out both intra and inter-species splice grafting of *Dipterocarpus baudii, Shorea parvifolia, S. leprosula* and *S. roxburghii*. It was successful and grafts grew faster than single-rooted seedlings. Chaudhari (1963) tested air-layering in *Shorea robusta* and found that it is more successful if carried out in the months of July and August (mid-monsoon) when there is a full flush of green, healthy leaves. Zabala (1986) successfully carried out air-layering of *Anisoptera thurifera* and *Shorea contorta* but was unsuccessful with *Hopea foxworthyi, H. plagata* and *Dipterocarpus grandiflorus*. Air layering was successful in *Shorea palembanica* and *Vatica pauciflora* (Hallé and Kamil 1981) and in *Shorea selanica* (Harahap 1972). Rashid and Serjuddoula (1986) rooted branches from 5 to 10-year old saplings and 50 to 80-year old trees of *Dipterocarpus turbinatus* using air-layering. Rooting was better on branches from old trees.

Planting stock production of the commercially most important dipterocarp species, whether from seeds or from cuttings, has largely been solved.

Stump plants

Stumping is used to rejuvenate over-aged planting stock and in some cases, for example, *Tectona grandis*, it is applied as a method of multiplication of the planting stock. The use of stumped plants started early. Watson (1931/1932d) found that *Dipterocarpus* spp. can be successfully stumped. Hodgson (1937a) showed that *Dipterocarpus baudii, Shorea curtisii* and *S. macroptera* can be stumped, but it was unsuccessful with *Dryobalanops aromatica, S. leprosula* and *S. pauciflora*. Barnard (1956) tested stumping of *Dipterocarpus baudii, Dryobalanops aromatica, Hopea helferi, Neobalanocarpus heimii, Shorea assamica, S. foxworthyi, S. pauciflora* and *S. sumatrana*. The stumping was carried out by pruning all side roots close to the tap root, which itself was cut to 23 cm from the collar. The shoot was cut to 14 cm from the collar. Stumping of most species was promising but *Dryobalanops aromatica* failed and the success of *Dipterocarpus baudii* was uncertain. Sasaki (1980a) found that bare-root stock of *Shorea talura* successfully transplanted after stripping off all the leaves and cutting back the leader and the tap root. In 1985, a stumping trial was carried out with *Dryobalanops lanceolata* in East Kalimantan, Indonesia, which was highly successful (Diana 1987). A trial with 2 year old bare-rooted stump plants of *Shorea robusta* carried out in West Bengal was also successful (Anon. 1959). Pande (1960) found *Shorea* spp. can be stumped and he carried out some experiments comparing stumped plants with ball transplants and basket plants. Basket plants did best. Landon (1948b) compared stumped plants of *Dryobalanops aromatica* with potted seedlings and the performance of potted seedlings was superior. Pande (1960) obtained a similar result for *Shorea robusta* when survival and growth performance of bare-rooted stump plants were inferior to ball-rooted transplants and container plants.

Hormone treatment for growth stimulation of stump plants was investigated by Masano and Omon (1985), Omon and Masano (1986), Srivastava *et al.* (1986) and Siagian *et al.* (1989a) but results were inconclusive. Mori (1981) investigated the effect of starch reserves in the stem on survival and growth of stumped bare-root transplants of 16 dipterocarp species. Some species showed high mortality after stump planting, e.g., *Shorea curtisii, S. ovalis, Hopea nervosa, H. beccariana*. Stimulation of root and shoot growth by growth regulators or fertilisers was unsuccessful in various species and some species survival and initial growth were directly related to starch reserves before planting.

Planting site

The positive role of an initial shelter for the newly planted dipterocarp trees is beyond doubt (e.g., Wyatt-Smith 1947, Chakravarti 1948, Landon 1948b, Ardikoesoema and Noerkamal 1955, Krishnaswamy 1956, Sudiono and Ardikusumah 1967). Dipterocarps, usually, are not planted on completely cleared sites. In enrichment plantings they are planted on lines cut into the forest and in plantations the plants are usually planted under the shade of a nurse crop.

Underplanting or sowing beneath a forest canopy is important in restocking forests with valuable species. Underplanting can be done in residual stands of logged natural dipterocarp forests, in secondary forests, under a planted nurse crop or in plantations where the stocking is poor. The Experimental Forests of West Java (Darmaga and Haurbentes) were established by underplanting. Ardikoesoema and Noerkamal (1955) give an account of the establishment of the *Shorea leprosula* stand in Haurbentes. Two month-old seedlings were planted under the shelter of 2 year-old *Paraserianthes falcataria* which was removed after 5-6 years. At the age of 15 years the stand had passed the pole stage. The experimental plantations in the area of the Forest Research Institute Malaysia were partially established under nurse crop, either secondary vegetation or planted nurse trees (Barnard 1954). *Paraserianthes falcataria, Peltophorum* spp. and *Adenanthera* spp. were found to be useful as nurse trees although the latter two species, which have smaller and lighter crowns, were better suited. *Dryobalanops aromatica* was established under a shelter of *Fragraea fragrans* (Landon 1948b) and on lines in secondary vegetation (Barnard 1949a). Doan (1985) reported a planting trial in Vietnam, where *Dipterocarpus alatus, Hopea odorata* and *Anisoptera costata* were planted under shade of *Indigofera teysmanii* and *Acacia auriculiformis*. Of the three species *Dipterocarpus alatus* was more light demanding. Miyazaki (1989) found that age of the nurse crop had an effect on survival of *Anisoptera thurifera.* Seedlings were planted under 8-10 year old and 2-3 year old *Acacia auriculiformis*. Mortality was higher for those seedlings planted beneath the younger nurse crop. In a sowing experiment by Tomboc and Basada (1978) seeds of *Shorea contorta* were sown: under a secondary forest canopy which allowed the sun to filter through the canopy for 1 hour daily, and in the open. Survival was significantly higher under the forest canopy, while height growth and leaf development were better in the open. Wyatt-Smith (1947) reported a successful sowing experiment with *Dryobalanops aromatica* under a 1½-2 year old secondary forest while sowing in cut lines proved a failure. The ecological role of pioneer species in the natural regeneration of logged-over dipterocarp forests is discussed. Wyatt-Smith (1947) suggested that secondary vegetation can be cheaply converted by line planting beneath its canopy in 5 to 10 years' time (depending on the amount of soil degradation that has taken place), when most of the herbs and ground flora will have been shaded out. Rosario (1982) proposes silvicultural treatments that preserve pioneer species. These proposals are similarly valid for the treatment of secondary vegetation into which dipterocarps are planted. Other researchers have tested specific forms of site preparation. Maun (1981) reported a sowing experiment in a dipterocarp forest, where germination, survival and early growth of *Shorea contorta* was tested. The treatments were five different types of cover: (1) bare soil, (2) soil with litter, (3) soil with litter and ground cover, (4) soil with litter and underbrush, and (5) soil with intact vegetation cover. Germination was best in treatment (4), survival in treatment (4) and (5) and growth performance was better in treatment (1) and (2). Ang (1991) tested survival and growth of *Shorea parvifolia* on three sites: (1) secondary forest with trees of >20 cm girdled well in advance of planting, (2) open site (large opening in forest) with 30 cm top soil removed, and (3) open site (large opening in forest) with top soil retained. Survival was similar in all three sites, but growth was best in the open site where top soil had been retained. Barnard (1949b) investigated the effect of two types of planting site preparation on survival and growth of differently prepared seedlings of *Dryobalanops aromatica*. The test site was a natural forest with invasion of *Gleichenia* spp. and *Eugeissona triste*. Part of the test site was clear-felled and burnt. A control area remained unburnt, where *Gleichenia* spp. and *Eugeissona triste* were cut only. In the unburnt site all planting stock types established, while in the burnt site only the potted seedlings succeeded. Rowntree (1940) proposed grazing as a means to control the growth of *Imperata cylindrica* to secure the establishment of *S. robusta* regeneration. Nykvist *et al.* (1994) have reported the impact of forest harvesting and replanting on the forest site. They conclude that burning should be avoided in order to reduce nutrient loss and ensure better plantation growth. A similar view was already voiced by Wyatt-Smith (1949a) for the same reason. In the trial described by Barnard (1949b) in the plots prepared by burning only potted seedlings of *Dryobalanops aromatica* succeeded. As saplings they developed strong stems and had good height growth.

Qureshi *et al.* (1968) investigated the effect of soil working and weeding on the growth and establishment of *Shorea robusta* plantations.

A common practice is to establish dipterocarp plantations by line planting into forest vegetation. Ådjers *et al*. (1995) have investigated the effect of line width, direction and maintenance on survival and performance of *Shorea johorensis, S. leprosula* and *S. parvifolia*. Line direction had little effect on survival or growth, although SE-NW line direction was best for *S. johorensis*. Line width did not affect survival, but effect on growth was significant. Line widths used were 1, 2 and 3 m. In the control, the seedlings were planted under the forest canopy without opening it above the planting line. Horizontal line maintenance was better than vertical line maintenance and growth of *S. johorensis* and *S. parvifolia* benefitted from it. Survival was not affected. Omon (1986) tested the strip width to be cut into secondary forest for optimal growth of planted *Shorea ovalis* seedlings. He found that strips 1 m wide were the best for survival and performance.

Planting patterns in the context of underplanting were discussed by Tang and Chew (1980). *Shorea parvifolia* was underplanted in two patterns: (i) line planting, and (ii) group planting in groups of 4-6 trees at final spacing. Six months later the tree crowns overshadowing the planting lines or the planting patches were removed. Differences in growth were not significant, however, survival was higher for the group planting. The authors recommend removal of overhead shade after 6 months and underplanting as group planting. Abalus *et al*. (1991) recommend groups planted at a spacing of 10 x 10 m.

In an underplanting trial at Agumbe in Karnataka, India, *Vateria indica* seedlings were planted in 1962 and observed until 1978. Those growing under lateral shade with sufficient light had grown to an average height of over 5 m in 16 years while those which had no light reaching them had survived but had grown only about 5 cm (Rai, personal communication).

Planting Techniques

Outside India, Indonesia and Malaysia no large-scale plantations of dipterocarp species exist. Although experimental forests have been established in several regions information on the establishment techniques is scarce. The most complete account of artificial regeneration in the Malaysian context is by Barnard (1956). Agpaoa *et al.* (1976) give an overview of the planting techniques in the Philippines context. Most of the information on planting techniques is contained in instructions of forest services or of companies, and thus not always readily available. Planting techniques have been worked out very well for tropical conditions and the basics are generally valid irrespective of region, species or site.

Planting methods can be classified into: (1) planting of potted seedlings or transplants, (2) planting of bare-root seedlings or transplants, and (3) planting of stumps. Normally, dipterocarps are planted as potted seedlings, when they are about 9 months old and about 25-30 cm tall. Size or age of planting stock has been investigated by various researchers. In general, potted seedlings had better survival (e.g., Barnard 1954, Cerna and Abarquez 1959). The planting holes are usually prepared to a depth of 25 cm. The seedling or transplant is removed from the container (polythene bag) with the earthball undamaged. If broken, the beneficial effect of planting seedlings or transplants with undamaged roots is lost. Different pot types were used in the past, e.g., bamboo pots, veneer pots, tin cans. However, a plastic bag of 500 cc content (e.g., 10 cm x 15 cm and 6.3 cm diameter) is the bag size commonly used. Barnard (1954) tested different sizes of bamboo pots and larger pots gave better survival. A trial on varying pot sizes using *Shorea polysperma* was carried out by Bruzon and Serna (1980) and height development in 8 cm diameter pots was best. When planting, the upper part of the earthball should be slightly below the soil surface for successful establishment, and never above it. Depth of planting was investigated, e.g., by Shrubshall (1940), and Walton (1938) who for *Dryobalanops oblongifolia* found deep planting (collar 5 cm below surface) gave the best results and shallow planting caused 75% mortality. Shrubshall (1940) also reported deep planting gave the best results. Earth is firmly placed around the plant to close the air spaces and finally, the young plants are mulched with organic material to prevent desiccation and overheating of the soil. Bare-root seedlings can be planted in two ways: hole-planted as in potted plants; and notch-planted. In notch planting a cone- or wedge-shape hole is made with a spade or a hoe. The roots of the plant are placed into the hole to the required depth and the soil firmed around the plant. Barnard and Setten (1955) reported on the comparison of planting trials of *Dryobalanops oblongifolia* in prepared planting patches and in notches. The performance of two types of seedlings were compared:

entire seedlings lifted from the soil and stripped seedlings where leaves were reduced to about one third their length. The percentage of trees surviving after one year was highest for entire seedlings planted in cultivated patches (58%). The lowest survival was found for stripped seedlings planted in notches (19.8%). Bare-root stock requires some moisture-preserving techniques to keep roots moist during transport and storage prior to planting (e.g., Strong 1939, Rayos 1940). A detailed description of the planting technique for bare-root stock is given by Agpaoa *et al.* (1976). Sometimes the planting stock is root and/or shoot-pruned or stripped partially or totally of leaves to initially reduce transpiration to facilitate establishment. Root pruning was generally beneficial (e.g., Walton 1938, Sasaki 1980a). Stripped seedlings of *Shorea talura* could be stored for several months without losing vigour and capacity for cutting propagation (Sasaki 1980a). Landon (1948b) found that stripping leaves of *Dryobalanops aromatica* was unsuccessful. Wildings are either lifted with a ball of earth or are forest-pulled. They can be either directly planted or they are kept in a temporary nursery under light shade for 3 to 6 months to recover before they are planted. Normal practice is to keep wildings for some months in a nursery until they have recovered. Very low survival rates were achieved by Lantion (1938) with forest-pulled wildings that were planted into the forest without a recovery period. Wildings of *Dipterocarpus grandiflorus* and *Shorea teysmanniana* were pulled from the forest, stored for three days (partly mud-puddled and partly not) and then planted. The average survival for mud-puddled wildings was 9.5% and for wildings not mud-puddled 2.9%. Palmiotto (1993) described a direct transplanting trial in the understorey and a gap using wildings of *Shorea hopeifolia, S. johorensis, S. leprosula, S. parvifolia, S. parvistipulata* and *S. pinanga*. Transplanting appeared to have a negative effect on survival. Survival in the understorey was between 8 and 58% and in the gap between 3 and 50%. Recovery in the nursery is important, if a high survival percentage after transplanting into the field is to be achieved (e.g., Capellan 1961, Moura-Costa 1995).

There are clear indicators of the need to fertilise initially, e.g., (1) sites where deficiency symptoms occur, (2) sites with top soil removed, (3) sites carrying vegetation indicating poor soil conditions, and (4) sites with strong weed competition. It is, at present, still too early to formulate valid fertiliser regimes. Less certain are the fertilising requirements of the newly planted seedlings. Nutrient deficiencies will occur, especially, in plantation establishment on areas that have suffered degradation to some extent (e.g., clear-felled areas and secondary forest). Moura-Costa (1993) reported fertilisation in the context of large-scale enrichment plantings with rock phosphate (100 g) applied to the planting hole. On an experimental scale, the effect of additional fertiliser application on the establishment of dipterocarps is being studied. Yap and Moura-Costa (1994) reported on the effect of nitrogen fertilisation, soil texture and other factors on biomass production of *Dryobalanops lanceolata* seedlings. Nussbaum *et al.* (1995) reported a combined experiment of soil-working and fertilisation of tree seedlings of *Dryobalanops lanceolata* and *Shorea leprosula.* The treatments were: (1) planting into compacted soil; (2) planting into compacted soil + fertilisation (100 g of rock phosphate placed in the planting hole and 40 g of granular 12:12:17 N:P:K + micronutrients placed in a ring of about 10 cm from the seedling just below the soil surface); (3) planting into compacted soil + mulching (pieces of bark which had been stripped from felled trees 1 year earlier were used to cover the plot); (4) planting of seedlings into cultivated plots (soil in the whole plot turned over and broken up to a depth of 30 cm 2 to 3 weeks before planting); (5) planting into cultivated plots + fertilisation; (6) planting into cultivated plots + mulching; and (7) planting into planting holes with soil replaced with topsoil from undisturbed forests. After 6 months of observation best diameter growth was found in treatments (2), (5) and (7). Crown diameter was also largest in these three treatments. Seedlings responded strongly to fertiliser application, while (with exception of soil replacement) response to soil working (plot cultivation or mulching) was less distinct.

Sowing

Although not a widely used technique for establishment of even aged stands, sowing has been tried in the past. It has been applied on an operational scale in India (e.g., Chakravarti 1948) and Pakistan (e.g., Amam 1970). Gill (1970) found sowing of *Shorea leprosula* promising in the context of enrichment operations. Some of the finest *Dryobalanops aromatica* stands in Malaysia were established by broadcast sowing into high forest (Watson 1935). The results of direct sowing trials are not conclusive. Shaded, cool and moist microsites seem to be essential for successful germination and survival.

Tomboc and Basada (1978) tested the performance of *Shorea contorta* sown on open areas and under secondary growth canopy. Survival was highest under the cover of the forest, while growth was better in the open. Maun (1981) suggests that it will be necessary to germinate direct-sown seeds and grow the seedlings of *S. contorta* initially in shaded conditions. Later, the vegetation should be opened for better growth of the seedlings. Similarly, Strong (1939) found in a trial of direct sowing into cultivated areas (taungya) and into high forest that the germination of *Dryobalanops oblongifolia* and *Shorea sumatrana* failed in the cultivated areas largely as a result of drought and heat. The seeds were also attacked by insects and rodents. Sowing under the shelter of *Paraserianthes falcataria* was successful with *Shorea stenoptera* (Sudiono and Ardikusumah 1967). Chakravarti (1948) found direct sowing is the only method to artificially regenerate *Shorea robusta* forests in India. The principal adverse factor to germination and survival of seeds is drought and shade is essential for successful regeneration. Suggestions on the best type of nurse crop are given. Sown seeds may be attacked by insects or rodents. Barnard and Wyatt-Smith (1949) reported high mortality in their sowing trial of *Dryobalanops aromatica* in secondary vegetation mainly caused by rodent attacks on the germinating seeds. In comparison to other methods of artificial regeneration, the sowing method is less convincing. Cerna and Abarquez (1959) compared growth and survival of *S. contorta* plants that originated from transplants and from direct-sown seeds 11 years after stand establishment. Heavy mortality of seedlings resulted from direct sowing. *S. contorta* is very sensitive to bare-root planting and planting of balled plants was the most successful method.

Stand establishment by sowing is a very wasteful practice because of the large amount of seeds needed for sowing operations,

Stand Tending

'Tending, generally, is any operation carried out for the benefit of a forest or an individual thereof, at any stage of its life. It covers operations both on the crop itself, e.g., thinnings and improvement cuttings, and on competing vegetation, e.g., weeding, cleaning, climber cutting, and girdling of unwanted growth, but not regeneration cuttings or site preparation' (Ford-Robertson 1983). Stands develop and grow through various developmental stages from seedling or coppice, through thicket, sapling, and pole, to the tree stage, i.e. to maturity, and finally to overmaturity, but sometimes ending in residual standards. Residual standards are trees that remain standing after the rest of the stand has been removed or has died.

Weeding and Cleaning

The immediate post-planting care (mainly weeding), which covers the time until the plantation can be considered established, is crucial for planting success. Weeding is an operation whereby mainly herbaceous vegetation is eliminated or suppressed during the seedling stage of the forest crop. It is, therefore, the first cleaning and aims to reduce competition within the seedling stand. Cleanings to eliminate or suppress undesirable vegetation (mainly woody including climbers) are carried out when the young plant is in the sapling stage (1.5 m height and 5 cm diameter). Cleanings are carried out during the thicket stage of a forest crop and therefore before, or at latest with, the first thinning, so that better trees are favoured. Removal of overtopping vegetation must be carried out during weeding and clearing operations in dipterocarp plantations established either under a nurse crop (natural or planted) or in existing, line-planted, taller vegetation (e.g., secondary forest). Watson (1931/32e) classified trees according to their silvicultural importance. He, especially, distinguished between undesirable weeds which needed to be eradicated under nearly all circumstances and harmless tree species which are useful for shade or cover. Barnard (1954) recommended the removal of the overhead shade as soon as the young trees have recovered from the transplanting shock. He also found that the slightly increased light due to the cutting of planting lines was beneficial. Tang and Wadley (1976) discuss the technique of line opening and shade regulation. Techniques of line opening in the context of enrichment planting are described, e.g., by Chai (1975), Tang and Wadley (1976) and Lai (1976).

A common practice is to mark planting places with small poles with the empty plastic bag pulled over the tip so that the location of the plant can be detected by the weeding crews. The weeding can be done for example, as strip or ring weeding. Normal practice is to blanket weed the planting lines and remove the weeds by slashing. However, woody vegetation grows more vigorously if cut, requiring additional weeding operations. Since the young dipterocarp plants can withstand light shade it is not necessary to remove all non-crop vegetation. It would, therefore, be more appropriate to develop more selective procedures with less competitive weeds being left.

Barnard (1954) gives the following general recommendations for weeding operations:

- plants must be kept free of climbers;
- freeing from climbers must be done before the plants have been overgrown;
- uprooting of weeds is preferable to slashing to prevent vigorous regrowth;
- grasses and young plants compete for moisture and nutrients and should be periodically removed by clean-weeding in a circle around the plant; and
- weeding should not be done with a hoe, to avoid damage to the plants.

More investigations are needed on selective weed control, including the development of risk categories for so-called weed trees and methods of suppression or elimination. Useful descriptions of weed vegetation in the Malaysian context are found in the rubber planter's manual (Haines 1940). Such a manual became necessary, when the so-called 'forestry' cultivation was introduced in rubber plantation management. The basic idea was to retain an undergrowth of non-competitive vegetation so as to prevent erosion and maintain favourable soil chemical and physical properties. Naturally, only harmless weeds could be allowed to grow in the plantations. This made it necessary to categorise the vegetation according to noxiousness and to define the treatments required. Weeds particularly noxious to young plants have been noted, e.g., Wyatt-Smith (1949b), Seth and Dabral (1961), Palit (1981). Wyatt-Smith (1963b) listed 'weed' trees that had to be poisoned irrespective of whether competing with 'economic' species or not. The control of specific types of weeds has been described, e.g., Strugnell (1934), Mitchell (1959) for *Imperata cylindrica*, Kelavkar (1968) for *Lantana camara*, and Palit (1981) and Bogidarmanti (1989) for *Mikania* spp. Liew (1973) tested methods to eradicate climbing bamboo (*Dirochloa* spp.) in Sabah and was successful with merely cutting the bamboo near the soil surface. Chemical weeding was tested by Palit (1981) in *Shorea robusta* plantations against *Mikania scandens*. Seth and Dabral (1961) tested the efficiency of 5 herbicides based on 2,4-D or 2,4,5-T in moist deciduous *Shorea robusta* forests against trees and coppice of *Mallotus philippinensis, Ehretia laevis, Ougeinia oojeinensis, Miliusa velutina, Buchanania lanzan, Aegle marmelos. M. philippinensis* proved to be resistant. Chong (1970) carried out a trial on chemical control of the stemless palm *Eugeissona triste* in *Shorea curtisii* forests. In regions with distinct seasonality, timing of the weeding operations is important. Bhatnagar (1959) related the timing of the weeding operations to the annual height increment peaks of *Shorea robusta* seedlings. He recommended carrying out weedings during or somewhat in advance of these periods, so as to help to relieve the intense competition between the *Shorea robusta* seedlings and the weeds. In *Shorea robusta* forests the so-called rain-weeding is carried out, i.e., weeding during the rainy season (e.g., Rowntree 1940, Sarkar 1941). For good growth of the young planted dipterocarps a good exposure to light is essential. In line plantings (including enrichment planting) overhead shade must be continuously absent from the planting lines. Agpaoa *et al.* (1976) give a comprehensive description of the procedure of enrichment planting and the corresponding tending operations. In underplanting under a nurse crop the overhead shade must be removed within a few years (e.g., Sanger-Davies 1931/1932, Ardikoesoema and Noerkamal 1955, Wyatt-Smith 1963b Agpaoa *et al.* 1976). Small undesirable trees (up to about 5 cm diameter) can easily be removed with a bush knife or axe. Larger trees, however, are frequently girdled or poison-girdled using arboricides. Arboricide use is described e.g., Sanger-Davies (1919), Barnard (1950, 1952), Beveridge (1957), Nicholson (1958), Roonwal *et al.* (1960), Wyatt-Smith (1960, 1961a, 1963c), Wong (1966), Liew (1971), Agpaoa *et al.* (1976), Chai (1978), Chew (1982) and Manokaran *et al.* (1989). Well known arboricides are 2,4,5-T, Garlon 4E, Tordon 22K, Velpar-L and sodium arsenite. Most of the tests were done with 2,4,5-T and sodium arsenite.

Thinnings

Thinning is 'a felling made in an immature crop or stand in order primarily to accelerate diameter increment but also, by suitable selection, to improve the average form of the trees that remain, without - at least according to classical concepts - permanently breaking the canopy' (Ford-Robertson 1983). A thinning regime is characterised by type, grade or weight and frequency. The type of thinning can be a thinning from above, where particularly the most promising, not necessarily the dominant, stems are favoured and where those trees, from any canopy class that interfere with the promising ones, are removed. Another type of thinning is the thinning from below, where particularly the dominants or selected dominants are favoured and a varying proportion of other trees is removed. Grade of thinning is a degree of thinning based on dominance, crown and stem classes, and the extent to which these classes are removed at any one thinning.

With the exception of *Shorea robusta* no thinning regimes have been developed for dipterocarp plantations. Krishnaswamy (1953) and Mathauda (1953a) studied the effect of thinning intensities on height and diameter development, stand basal area and volume increment of *Shorea robusta*. The conclusions from this thinning trial were: that the thinnings should be carried out every 5 years up to an age of 20 years and thereafter at larger intervals; and the maximum volume production is obtained under C/D-grade (heavy to very heavy low thinning as per standard definition of the terms adopted in India). In the C/D grade the dead, moribund, diseased trees, whips of co-dominant and dominant trees, defective co-dominant and dominant trees and a small proportion of sound co-dominant and dominant trees are removed. Thinning according to the C/D grade was found to be best for the production of both fuelwood and timber. Wyatt-Smith (1963a) assumed that in dipterocarp plantations a thinning cycle of 5 to 10 years would be adequate. Suri (1975a) developed a quantitive thinning model for *Shorea robusta* forests in Madya Pradesh, India. Based on the correlation between crown diameter and stem diameter a thinning model was formulated and stem density regimes for different crown disengagement levels determined. It was concluded that quantitative thinning grades can be developed for different species by studying their crown diameter/bole diameter relationship. The crown disengagement in younger stands was sometimes carried out as so-called stick thinning, i.e. starting from a selected crop tree any tree growing within a defined distance (e.g., six, nine or twelve feet) from the selected crop tree was removed for example, in a naturally regenerated, more or less even-aged stand of *Dryonbalanops aromatica* (Anon. 1948b). An important conclusion from this trial is that it is not advisable to make heavy thinnings before the overwood has been removed, since the young crop can be overtaken by climbers and secondary species benefitting from increased light. The heavily thinned treatments suffered severely from climbers and weed species, while trees damaged by the falling overwood had no neighbours to replace them.

Thinning is usually done with a bush knife (smaller trees), an axe or a saw but if the tree is not to be utilised, girdling or poison-girdling may be applied. Often girdling alone is unsuccessful and poison-girdling is recommended (e.g., Wyatt-Smith 1963b, c, Agpaoa *et al.* 1976). The trees to be removed are frill-girdled and the poison is applied into the frill. Effective chemicals have already been mentioned in the section on weeding and cleaning.

Thinning interventions require some kind of classification of the stems in the stand to be thinned. Krishnaswamy (1953) presented a detailed stem classification which is based on dominance position and within each position on vigour, soundness, crown development and other characteristics. It resembles the classification of Kraft (1884), but includes reproduction or regeneration and overmature trees (e.g., standards). Any thinning, except for schematic interventions, requires that all trees in the stand are judged according to their function. Potential final crop trees (PCT) are distinguished from non-crop trees (NCT). The PCT are those trees which owing to their straightness and evenly formed crowns are to be retained as crop trees and released from competition. NCT may have different functions. There are harmful trees that damage the crowns or stems of the PCT and should be removed. There are useful NCT which enhance growth form and branch-shedding of the PCT or have important ecological functions. There are individuals for which their future development and function is not clear and they have to be spared from thinning until the necessity for removal is beyond doubt.

In the Malaysian context Watson (1931/1932e) has classified the most common trees in Peninsular Malaysia. He classified the species into the following categories:

- quality timber trees,
- utility timber trees,
- subsidiary trees,
- insignificant trees (fillers only),
- poles,
- cover or nurse trees, which are harmless species, and
- weed trees, which are undesirable.

This classification was made for natural forests and is not really applicable for plantations.

Although there is no experience available on the tending and thinning of dipterocarp plantations outside India, some inferences can be made from tending and thinning experiments and from observations in naturally regenerated dipterocarp forests, which lead to more or less even-aged and fairly regular stands. Such stands may have resulted from, e.g., Regeneration Improvement Systems or from Uniform Shelterwood Systems, as they were, for example, applied in Malaysia. Wyatt-Smith (1963b) gives a thorough review of the thinning experience up to that time. His recommendations for thinning more or less regular crops were:

- removal of climbers of above 2.5 cm diameter, although the limit can be lower if smaller climbers prove to be damaging the crop trees,
- removal of all weed trees; also those that are going to overtop the PCT until the the next intervention,
- removal of all malformed stems of commercial species provided a stem of better form is adjacent,
- removal of all wolf trees,
- removal of co-dominants of inferior timber value,
- selective thinning of co-dominants of equivalent silvicultural and timber value that compete strongly, and
- thinning to a maximum basal area of about 1/2 to 3/4 of the expected carrying capacity of the site.

In the context of regeneration operations within the Regeneration Improvement Systems Durant (1940) was confronted with the criticism that opening the canopy would lead to luxuriant ‘secondary growth’ (what we would call today secondary forest) consisting mainly of *Randia scortechenii, Pasania* sp*., Barringtonia* sp*., Girroniera nervosa, Trema ambionensis, Macaranga* spp*., Endospermum malaccense* and various fast-growing trees of other families. It was feared that the young dipterocarps might be suppressed by these species and frequent and expensive cleanings needed. Three experimental plots were set up. Two plots were established in stands where the canopy over young regeneration had been removed by regeneration improvement fellings and one plot was laid out in an area where the canopy over young regeneration had almost completely been removed by a heavy storm. The treatments in the first plot were: (i) untouched control, (ii) cleaning (cutting back all growth other than *Shorea* spp.), and (iii) cleaning and respacing (‘thinning’ of the *Shorea* spp. to an average distance of 1.83 m leaf to leaf). The treatments in the second plot were: (i) untouched control, (ii) cleaning (cutting back everything except saplings of the desirable species), and (iii) mainly climber cutting with minimal cutting of undergrowth. In the third plot only a cleaning in favour of saplings and small poles was carried out. The objective of the first two plots was to investigate the effect of the secondary forest vegetation on survival and diameter growth of sapling-size natural regeneration of *Shorea* spp. The third plot tested whether larger regeneration (large saplings, small poles) was out of danger from its competitors. After establishment, the plots were left unattended for four years and then enumerated again.

From Durant’s experiment, inferences were made concerning the regeneration of *S. leprosula*:

- However severe the opening of the canopy, provided adequate seedling regeneration is present, *S. leprosula* can tolerate competition with other vegetation up to the sixth year.
- Cleaning and thinning after the second year will secure an even distribution of stocking and will increase the growth rates. Complete omission of tending up to the sixth year is not fatal (which is in agreement with other authors e.g., Walton 1933, 1936a, Wyatt-Smith 1949b, 1958, 1963b).
- Serious competition from secondary forest species is probably due to a comparatively few species, and, if these can only be recognised and eliminated, a considerable reduction of cleaning costs should be possible. (The species recognised as responsible for suppression were *Endospermum malaccense, Elaeocarpus stipularis, Macaranga* spp*., Paropsia varediformis* and *Quercus lucida*).
- With sufficient initial opening of the canopy, good stocking of *Shorea leprosula* can be expected to survive up to the 14th year. At this stage the crop reaches pole size, and adequate assistance can be given very cheaply by the poison-girdling of competitors around individual trees.

The conclusions are important for the tending of young naturally regenerated and more or less even aged stands originating either from natural stands or from plantation stands under the Shelterwood System. The findings of Durant (1940) can, however, not be applied without some restrictions to young plantations of dipterocarps. The initial number of stems in plantations is usually so low that omission of early tendings (weedings, cleanings) will probably entail high losses endangering stand establishment.

Strugnell (1936b) tried three treatments (only dominant trees retained; dominant and dominated trees retained; dominant, dominated and suppressed trees retained) in a young natural pole stand of *Shorea leprosula* and *S. parvifolia*. He found that the basal area of the 50 largest trees/acre was highest for the medium intervention. Sanger-Davies (1937) carried the ideas further and formulated a guide for the tending of more or less even aged stands of *S. leprosula*. In his technical recommendations, he proposed starting tending while the shelterwood is still standing.

When designing research it should be kept in mind that the beneficiary of the thinning operation is the crop tree and, therefore, indiscriminate elimination of non-crop vegetation is unnecessary. Non-crop trees have beneficial ecological functions. Mead (1937) discusses the formation of mixed stands of dipterocarps and shade-bearing non-dipterocarp understorey species with dense crowns. The species *Scorodocarpus borneensis, Mesua ferrea, Randia scortechinii, Randia anisophylla, Greenia jackii* etc. were planted in mixture with *Shorea leprosula*, which forms a rather open crown, to prevent the invasion of light demanding pioneer vegetation which impede the establishment of natural dipterocarp regeneration. Tending has, therefore, to consider also the secondary vegetation. Any inconsiderate felling should be avoided and instead it should be asked, whether such vegetation could assist in keeping the forest floor conducive to natural regeneration.

Re-establishment by Natural Regeneration

Embarking on plantations with dipterocarp species which grow relatively slowly compared with fast-growing exotics needs strong economic backing. Recent economic calculations (Kollert *et al.* 1993, 1994) have shown that it only makes sense, if at the end of the first rotation the new stands are established by natural regeneration. It is in this context that some comments are given on regenerating naturally even-aged planted dipterocarp stands, although on an operational scale this will be only a problem of decades from now. Systematic assessment of the regeneration situation and initiation of natural regeneration procedures are urgently needed for all species identified for plantation programmes and for which stands near rotation age exist. This should include research on the harvesting techniques required to reduce negative impacts on stand regeneration.

The natural regeneration of even-aged planted stands will most likely be carried out as some kind of shelterwood system. Shelterwood systems are ‘even-aged silvicultural systems, in which, in order to provide a source of seed and/or protection for regeneration, the old crop (the shelterwood) is removed in two or more successive shelterwood cuttings, the first of which is ordinarily the seed cutting (though it may be preceded by a preparatory cutting) and the last is the final cutting, any intervening cuttings being termed removal cuttings’ (Ford-Robertson 1983). Where there is adequate regeneration the old crop may be removed in a single cut (e.g., Malayan Uniform System). Preparatory felling means removing trees near the end of a rotation so as to open the canopy permanently and enlarge the crowns of seed bearers, with a view to improving conditions for seed production and natural regeneration. Here, no adequate regeneration is on the ground. Seeding felling is removing trees in a mature stand so as to effect permanent opening of its canopy (if there was no preparatory felling to do this) to provide suitable conditions for regeneration from the seed of trees that are retained. Removal felling is removing trees between the seed cutting and the final cutting, so as gradually to reduce the shelter and admit more light to aid the regeneration crop and to secure further recruitment. This type of felling is carried out over adequate regeneration.

There is almost 80 years of experience with the regeneration of natural dipterocarp forests. Experience on individual aspects of natural regeneration gained is with modification applicable to even-aged stands of dipterocarps. This does not mean regeneration systems for even-aged stands can be derived from the knowledge available now but it is possible to outline some general directions.

One important aspect of the establishment of a new generation by natural regeneration is, whether or not the stands will fruit well before the rotation has ended. A few observations have been made. Ng (1966) concluded from his work on age of first flowering of dipterocarps that many species begin to flower and bear good seed before their 30th year. Tang (1978) found three trees of *Shorea leprosula* planted in a taungya stand had fruited at the age of 7 years. Similar early ages of flowering/fruiting were reported by Lee (1980) for *Shorea pinanga* (flowering 6 years after planting) and by Suziki and Gadrinab (1988/1989) for *S. stenoptera* (fruiting 6 years after planting). Ardikoesoema and Noerkamal (1955) described a *S. leprosula* stand in Java that had fruited aged 13 years producing a moderately dense seedling crop. Appanah and Weinland (1996) evaluated the field files of the dipterocarp plantations at the Forest Research Institute Malaysia and fruiting was reported for *Shorea* *leprosula, S. macrophylla* and *Dryobalanops aromatica* stands at about 20 years age. Additionally, plantation stands of some other species (e.g., *Dryobalanops oblongifolia, Shorea macroptera*) have established regeneration. However, the exact stand age at first flowering has not been recorded.

Little information is available concerning preparatory operations. Chong (1970) reported the effect of *Eugeissona triste* (a stemless palm) control on regeneration of *Shorea curtisii*. The experiments showed that a pre-felling treatment with a light girdling and *Eugeissona triste* control undertaken after a heavy seed fall prior to felling had a beneficial effect. The operation not only increased the vigour of the established regeneration but also created conditions on the forest floor conducive to recruitment of new individuals. Raich and Gong (1990) found that seed germination demonstrates clear patterns of shade tolerance or intolerance identical to those long recognised for tree seedlings. Among the species tested were *Dipterocarpus grandiflorus, Shorea multiflora* and *Vatica nitens*. They germinated in the understorey as well as in the gaps (typically 20-30 m in diameter) but failed to germinate in larger clearings. So, if preparatory canopy openings are prepared, these openings should not exceed normal gap size.

Preparatory fellings have never played an important role. Treatment of seed trees in the natural forests to improve their crowns is unneccessary because being emergents they have already fully developed crowns. More information is available on the manipulation of the old crop over existing regeneration (regeneration fellings and final fellings). Although strictly applicable only to natural forest conditions, the basic findings should also be valid for plantations. Based on closely controlled experiments in the Wet Evergreen Forests of Sri Lanka, Holmes (1945) found that canopy conditions under seeding fellings most conducive to regeneration seem to be gaps of 20-30 m diameter evenly distributed and separated from one another by not more than one row of dominant trees. While raising the canopy gradually upwards, an ultimate canopy density of about 0.5 will be achieved. Zoysa and Ashton (1991) found that the germination of *Shorea trapezifolia* seeds planted on forest top soil with litter was little affected by partial shade or exposure to full sun. Watson (1931/1932c) discusses ‘preparatory’ fellings (strictly speaking they were regeneration fellings) for fostering natural regeneration within plantations. He states that seedlings of commercial species would establish better after opening the forest canopy, provided care is taken to prevent intrusion of weed species. He recommends removal of the lower forest canopy layers and cleaning of the undergrowth. But no fellings of this kind should be done in the absence of natural regeneration. Based on experiments of girdling understorey and upper storey trees, it was concluded that improvement systems should ensure adequate regeneration while retaining the canopy in such a condition that the lower storey is shaded preventing growth of competing vegetation (Walton 1933, 1936a, b). Only after regeneration is abundant should any drastic opening of the canopy be undertaken. The vigorous response of seedling regeneration of *Shorea* spp. to full light indicates that treatment should aim at removing the canopy as rapidly and completely as is considered safe. The extent of canopy opening, however, should depend on the light demand/shade tolerance of the species. Strugnell (1936a) investigated the effect of suppression on young regeneration of *Shorea leprosula, S. parvifolia* and *Neobalanocarpus heimii*. Removal fellings should not be delayed for too long in light-demanding species as mortality will be high and growth responses weak. Shade tolerant species may, however, react vigorously even after a long time of suppression. In some species sudden exposure on canopy opening might lead to shoot borer attack as in *Neobalanocarpus heimii* (Durant 1939). Qureshi *et al.* (1968) emphasise that, before commencing tending operations on the regeneration, the canopy density has to be reduced to ensure sufficient light for the young plants. This was tested on natural regeneration of *Shorea robusta* under a planted parent stand. In mixed stands smaller gap sizes will favour shade tolerant species and larger gap sizes light demanding species. This is an important consideration if mixed stands of shade tolerant and light demanding species are to be regenerated (e.g., Raich and Gong 1990).

The design of the regeneration system for dipterocarp plantations depends, apart from the production goal, on several other factors, e.g., the species involved, the stand condition, the regeneration behaviour and site factors. A uniform shelterwood system could, for example, be applied to *Dryobalanops aromatica* stands (Zuhaidi and Weinland 1993). They usually carry a fairly dense regeneration that is evenly distributed over the stand area. The canopy of the old crop is distinctly mono-layered. The regeneration period will be rather short and the resulting stand after final felling will be fairly regular. Species which fruit more irregularly might require more irregular canopy openings following the recruitment patches and a group shelterwood system applied. The regeneration period will be protracted and the resulting stand more irregular.

Reforestation and Afforestation of Degraded Land

Reforestation is the re-establishment of a forest crop on forest land. Afforestation is the establishment of a crop on an area from which it has always or very long been absent. Degradation in the pedological sense is 'any significant reduction in the fertility of the soil, whether in the course of its natural development or by direct or indirect human action' (Ford-Robertson 1983).

There is a growing need for rehabilitation of degraded forest sites following destructive logging, land clearing or mining. Dipterocarp species are by nature not very well suited for rehabilitation of severely degraded forest land. However, in some instances, dipterocarp species have been used with success (Ang and Muda 1989, Ang *et al.* 1992, Nussbaum *et al.* 1993, Nussbaum *et al.* 1995, Nussbaum and Ang 1996). Lately, Nussbaum and Ang (1996) have carried out a review on the rehabilitation of degraded land. Bieberstein *et al.* (1985) and Thai (1991) recommended *Dipterocarpus* spp. for the reforestation of devastated and shrub areas in Vietnam. Mitra (1967) describes the management measures carried out over large areas in West Bengal since the acquisition of all private forest lands (which were mainly *Shorea robusta* coppice forests) by the State in 1953. *Shorea robusta* was planted in eroded areas (Goswami 1957) and former bauxite mining land in India (Prasad 1988), *Hopea parviflora* on bare lateritic soil (Dhareshwar 1946) and *Dryobalanops oblongifolia* on waste land (Landon 1941). An initial burn and cultivation of planting patches were found to be beneficial. Shineng (1994) reports using dipterocarps, *Dipterocarpus turbinatus* and *Parashorea chinensis,* for establishing plantations on degraded forest land in tropical China but the growth rates of both dipterocarps were almost the lowest among 26 tree species tested. Mitchell (1963) explored the possibilities of afforesting raised sea beaches along the east coast of Peninsular Malaysia. Among the species tested was *Hopea nutans* which failed (Ang and Muda 1989). Rai (1990) describes a successful trial to restore degraded tropical rain forests of the Western Ghats (India) in which *Vateria indica, Dipterocarpus indicus, Hopea parviflora* and *H. wightiana* were used.

Agroforestry

Not many dipterocarp species have as yet been included in agroforestry systems. *Shorea robusta* is the only species which has been researched intensively in the context of the taungya system. Taungya is an 'agri-silviculture system for the raising of a forest crop (a taungya plantation) in conjunction with a temporary agricultural crop' (Ford-Robertson 1983).

Nevertheless, agroforestry systems involving dipterocarps have been practised throughout the Indian-Southeast Asian region. *Vateria indica* and *Shorea robusta* have been used in agroforestry systems in India. Sal (*Shorea robusta*) taungya is a relatively well developed system in India (Huq 1945, Osmaston 1945, Kanjilai 1945, and others). Prominent in agroforestry systems in Borneo are the dipterorcarp species that produce edible nuts (*Shorea* spp. of the pinanga group) (Seibert 1989). An agroforestry system in East Kalimantan which often involves *Shorea macrophylla* is called the 'lembo' system (Sardjono 1990). Resin tapping of *Shorea javanica* is well developed in Sumatra (Torquebiau 1984). Integration of farming into the tending and conservation of logged forests was discussed (Serrano 1987, Mauricio 1987b), as well as the propects for agroforestry to be used for the rehabilitation of degraded forest land in Indonesia (Kartiwinata and Satjapradja 1983). Watanabe *et al.* (1988) investigated a taungya reforestation method in the context of the Government Forest Village Programme in Thailand, where *Dipterocarpus alatus* is involved. An agroforestry system using dipterocarps was also tried in West Malaysia (Cheah 1971, Ramli and Ong 1972) but it has not been adopted. These are but a few examples of dipterocarp species used in agroforestry systems.

Forest Protection Aspects

The knowledge on pests and diseases of dipterocarps is scanty, but a more systematic account is given in Chapter 7. Insects attack dipterocarp fruit crops heavily (Daljeet-Singh 1974). By comparison, their seedlings are well protected (Daljeet-Singh 1975). Becker (1981) investigated potential physical and chemical defences of *Shorea* seedling leaves against insects. Diseases include fungal problems, bacterial and viral infections (Smits *et al.* 1991). Heart-rot of dipterocarps has been investigated, and is more serious in slow-growing than in fast-growing species (Hodgson 1937b, Bakshi *et al.* 1963). Stand management strategies to control heart-rot have been developed for *Shorea robusta* (Bakshi 1957).

With establishment of large-scale plantations of dipterocarps, susceptibility to diseases and pests is bound to increase. The control of pests and diseases in nurseries is well developed and advanced. Chemical control is the prevailing method to fight the attack of biotic agents. Chemical control is, however, not practicable after field planting. Prevention has to be secured by silvicultural means, e.g., species mixtures, structural diversity, avoidance of damage to trees and soil, etc. At present, there is an urgent need to survey diseases, defects and damages in existing dipterocarp plantations, particularly the incidence and possible causes of heart-rot.

Gaps in natural forests and plantations are created by natural mortality, biotic and abiotic agents. Lightning is a major cause for the occurrence of gaps not only in natural forests (Brünig 1964, 1973) but also in plantations. While in natural forests such gaps drive the regeneration dynamics, in plantations such gaps, first of all, reduce the stocking. The effect of lightning can be seen clearly in the plantation area of the Forest Research Institute Malaysia (personal observation).

Management Aspects

The available information, here, can be combined under the following categories: silvicultural systems, biological production, (especially growth), thinning schedules, stocking aspects, silvicultural diagnostics, and economics.

'A silvicultural system is a process, following accepted silvicultural principles, whereby the crops constituting forests are tended, harvested and replaced, resulting in the production of crops of distinctive form. The systems are conveniently classified according to the method of carrying out the fellings that remove the mature crop with a view to regeneration and according to the crop produced hereby' (Ford-Robertson 1983). Silvicultural systems are discussed in the context of stand regeneration of plantations after the first rotation.

In India, various silvicultural systems have been applied to encompass the wide ecological variation in the occurrence of dipterocarps. A selection system has been applied in seasonal rain forests and moist deciduous forests. Clearfelling and artificial regeneration have been carried out in moist deciduous forests where frost is absent. Various forms of shelterwood systems were applied in regions where frost was experienced. Coppice with standards was applied to *Shorea robusta* in dry areas and simple coppice systems used in wood lots in Karnataka.

While the silvicultural systems for *Shorea robusta* forests in India are clearly formulated and understood, there is little information in other parts of the region on what the silvicultural system for dipterocarp plantations should be. Most silviculturists would like to re-establish an existing dipterocarp plantation at the end of the first rotation by natural regeneration. In Malaya, Walton (1933, 1936a), Watson (1935) and others have indicated the possible species among the fast-growing light-hardwoods which can regenerate naturally in the rotation envisaged for plantations. Little is known about the capacity of plantation-grown dipterocarp species to regenerate naturally at a rotation of about 50 years. There is already some information derived from planted species, e.g., *Shorea leprosula, Dryobalanops* spp., *Shorea* spp. of the pinanga group and *S. robusta*, which can be naturally regenerated during such a rotation time. All the existing, mature, experimental, dipterocarp plantations in the region should be assessed for natural regeneration.

The growth of dipterocarps under natural forest conditions has been observed early this century (e.g., Edwards and Mead 1930, Watson 1931/1932a, Rai 1996). The observation of the growth of dipterocarps in plantations commenced only later. Analysis of 29 dipterocarp species in trial plots at the Forest Research Institute Malaysia indicates rotation ages of 40 to 50 years for the best performing species (Ng and Tang 1974). Individual volume and growth plots have also been analysed (Vincent 1961 a, b, c, d, Zuhaidi *et al.* 1994). The growth curves show a very fast early height and diameter growth with distinct differences between species in growth rates. Relatively impressive growth rates of the light red meranti group (*Shorea* spp.) have also been recorded in the Haurbentes experimental plantation stands in Indonesia (Masano *et al.* 1987, see also Ardikoesoema and Noerkamal 1955): a stand of *Shorea leprosula* achieved an average height and diameter of 44.6 m and 77 cm respectively in 35 years. *Shorea stenoptera* was similarly fast growing with an average height and diameter of 46.3 m and 75 cm respectively in 31 years. At the age of 29 years, *Shorea platyclados* stands in Pasir Hantap Experimental Forest in Indonesia have an average height of 29 m, bole length of 17 m and an average diameter of 41 cm. In Sarawak, trees of *Shorea* species of the pinanga group reached diameters between 34 cm and 75 cm between the age of 34 and 48 years (Primack *et al.* 1989). *Shorea macrophylla* showed the best growth performance, and *S. splendida* the poorest. A severe depression in growth occurred during flowering years. There is however, the danger in assuming the same growth rates in operational plantations and over the whole range of sites. Care has to be taken in economic calculations not to overestimate the performance.

Shorea robusta is the most intensively researched species concerning growth and yield. Some yield tables exist (e.g., Howard 1925, Griffith and Bakshi Sant Ram 1943). The species' growth rate under different treatments has been reported by Mathauda (1953a). The growth rates of other dipterocarp species were reported by Mathauda (1953b) and Rai (1979, 1981a, b, 1989). More recently, the long-term research sites have been reviewed and updated by Rai (1996). Under natural conditions the annual rate of diameter growth for most dipterocarp species is only 0.3 to 0.35 cm.

Among the dipterocarps, the growth and yield of *Shorea robusta* has been well investigated (Howard 1925, Griffith and Bakshi Sant Ram 1943, Krishnaswamy 1953, Mathauda 1953b, 1958, Chaturvedi 1975, Suri 1975b, Raman 1976). The maximum biomass production was 14.62 tons/ha/year during the 18th year (Raman 1976). In thinning trials, the results showed the superiority of the heavy and very heavy low thinning treatments (Krishnaswamy 1953). In India, research in thinning of plantations has been carried out, while this is not the case in other parts of the Indo-Malayan region. Dawkins (1963) introduced the crown diameter to bole diameter relation (also called growing space index) to estimate basal area density. This relation has been used for determining stand density regimes for *Shorea robusta* (Chaturvedi 1975). Suri (1975b) developed a quantitative thinning model for *Shorea robusta* which considers different types of crown disengagement regimes. Each of these crown disengagement regimes has a specific sequence of growing space index values. Rai (1979, 1981a) has reported growth rates of *Hopea parviflora* and *H. wightiana*.

Site quality has a direct influence on growth rates. However, little has been researched in this respect. The effect of elevation on height and diameter growth of *Dipterocarpus turbinatus* was investigated by Temu *et al.* (1988). The decline in height and diameter growth was relatively small compared to the increase in elevation. The cause for the decline is probably due to the rapid drop in the water table and leaching of nutrients at the higher parts of hilly terrain.

The economics of plantations of dipterocarp species have hardly been investigated. Lack of a sufficiently broad data base may have been the reason for the delay. Recently, some economic assessments were made on plantations of *Shorea leprosula*, *S. parvifolia* and *S. platyclados* in Peninsular Malaysia (Kollert *et al.* 1993, Zuhaidi *et al.* 1994, Kollert *et al.* 1994), and the following conclusions were drawn. The establishment and management of forest plantations are uneconomical if valued on financial terms alone. Forest plantations of relatively long rotations do not produce sufficient returns early enough to attract investment, especially from the private sector. Investors avoid the long gestation periods, the relatively low rate of return and the relatively high risk of investment. The venture of forest plantations will become economically attractive only by end of the first rotation, when the age class sequence is complete and future stand establishment is not by clear cut and planting but through natural regeneration.

Research Priorities

It is recommended that all research is carried out with the same set of dipterocarps (the most promising species for plantations). For species/provenance tests (species elimination, site adaptation), which usually remain untreated, it is recommended to include a standard silvicultural treatment.

- Silvics and species choice: Build up of information on silvical and silvicultural characters including site requirements, establishment of a site adaptation trial, establishment of systematic species/provenance elimination trials, evaluation of the existing dipterocarp plantations throughout the region as a basis for the above-mentioned trials.
- Seed: Seed production from trees/stands, seed orchard technology, dysgenic shifts as a basis for strategies in tree selection work.
- Planting stock production: Comparative planting stock production test, comparative cutting propagation trial, mycorrhization techniques in nurseries.

- Planting site: Site preparation techniques for line-planting/underplanting/open sites, optimal planting stock size for line planting/underplanting.
- Planting: Deficiency symptoms, fertilisation trials; if the fertilisation trials are observed over longer time (e.g., into the weeding and cleaning period), it is advisable to overlay the fertilisation trial with a tending trial that includes a standard treatment.
- Tending: Selective weeding procedures, assessment of weed vegetation concerning risks to the plantation crop, investigation into control of weed growth through shade management.
- Re-establishment by natural regeneration: Assessment of existing dipterocarp plantations near rotation age as to constitution, composition, canopy structure, regeneration status, regeneration experiments in existing older experimental dipterocarp plantations.
- Reforestation/afforestation: Investigations into site amelioration techniques, species adaptation trials, plantation site preparation procedures (nurse crops, fertilisation soil improvement procedures).
- Agroforestry: Research should continue to test the use of promising dipterocarp species as agroforestry crop trees, e.g., *Shorea macrophylla* and other members of the pinanga group, *Shorea javanica*, etc. Such research would concentrate mainly on selection as well as agri-silvicultural systems.
- Management: Stand establishment guidelines, species-site matching procedures, weeding guidelines, feasibility studies on dipterocarp plantations, development of production schemes with early financial returns, growth analysis of the existing dipterocarp plantations.

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Chapter 10

Non-Timber Forest Products from Dipterocarps

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Introduction

In the last half of the twentieth century timber has become the most important economic product from dipterocarps, but it does not have much impact on rural communities. Instead, the non-timber forest products (NTFPs) from dipterocarps such as nuts, dammar, resin and camphor, have a larger impact on the economies of the rural people and forest dwellers. In the past several decades synthetic materials have diminished the value of some dipterocarp NTFPs but at the same time others are beginning to gain value. As a result researchers have paid little attention to NTFPs and there is little detailed information on them. Their value to rural communities would have been better appreciated and critical in balancing the forces favouring logging against other socio-economic benefits. The advantages of managing NTFPs, previously known as minor forest products, are often ignored. Unlike timber, they are available at more frequent intervals and their harvesting is usually less destructive to the tree. Their value can be high, and as in some cases described here, may even pay towards the establishment of plantations for their production. In this chapter, the various NTFPs from dipterocarps are described, and wherever possible additional information on the methods of extraction, their industrial application and economic value is given.

Ancient Records of Dipterocarps

Perhaps the oldest written records of dipterocarps come from India; records of utilisation of dipterocarp timber and other products exist there since ancient times. The birth place of Buddha was Lumbini, situated on the bank of the River Rohini where there were groves of *Shorea robusta* (sal), called 'Mangala Salvana'. Sukraniti and Kautilya have regarded sal amongst the strongest timber yielding trees of the forest. Plant remains excavated from Pataliputra show that sal was used for a wooden palisade made 2000 years ago. In Southeast Asia there is a long tradition of the use of NTFPs from dipterocarps. Their trade was extensive, and from the 1st century A.D. Chinese and Indian traders regularly visited the Southeast Asian ports for these products. Marco Polo's chronicles of 1299 mention the trade of camphor (from *Dryobalanops aromatica*) by Arabs since the 6th century.

NTFPs From Dipterocarps

Much of the knowledge on the use of dipterocarp NTFPs is concentrated in two main regions, South Asia and Southeast Asia (mainly Indonesia, Malaysia, and the Philippines). In both regions, the dipterocarp products are essentially the same and four broad classes are predominant, viz., resins, dammar, camphor and butter fat. Besides these principal products, other plant parts, such as leaves and bark, are used to derive certain products. In both regions the extraction methods are common, however, the specific species yielding these products vary. Despite their importance, they have not been systematically exploited and have remained undervalued.

Resins

The dipterocarps are an important source of resins. The resin is secreted in cavities, and normally oozes out through the bark. The resins are of two kinds. The first is a liquid resin which contains resinous material and essential oils (oleoresins), remains liquid in nature and has a distinct aroma. It is often referred to as oleoresin in literature. Commercial production is often through artificial wounding. The second is the hard resin which is called dammar when obtained from dipterocarps. This is the solid or brittle resin, which results from hardening of the exudate following evaporation of the small content of essential oils. However, the classification of resins is very chaotic, and in the trade the term 'dammar' is also used occasionally to refer to an oleoresin.

Oleoresins

The genus *Dipterocarpus* is the principal source of oleoresins. The genus has large trees with erect trunks, the wood of which yields resin similar to copaiba. Other genera of lesser importance are *Shorea*, *Vatica*, *Dryobalanops* and *Parashorea*. All *Dipterocarpus* species produce a high proportion of oleoresins which come under various local names such as gurjan oil (India), kanyin oil (Burma) and minyak keruing (western Malesia). A well-known oleoresin comes from *D. turbinatus* which is the principal source of 'kanyin oil' in Burma and 'gurjan oil' in Bangladesh and India. The best yielding species are *Dipterocarpus cornutus*, *D. crinitus*, *D. hasseltii*, *D. kerrii* and *D. grandiflorus* (Malesia), *D. turbinatus* and *D. tuberculatus* (India, Bangladesh, Burma), *D. alatus* (Bangladesh, Andamans, Indochina) and *D. grandiflorus* (Philippines).

Method of Tapping

During the cold weather, a cone shaped cavity is cut into the trunk 1m from the ground and a fire lit to char the surface of the wound to induce the oleoresin flow. The oleoresin is periodically removed and when the flow stops, the wounded surface is either burnt or scraped or a fresh wound made to induce further flow. The collection season is November-May and a tree of 2 m girth can yield 9 kg of resin in one season. This resin compares favourably with balsam of copaiba (Balfour 1985).

Traditionally in Burma, oleoresin was obtained by cutting 2-3 deep pyramidal hollows, (the apex pointing towards the interior of the stem), near the base of the tree and by applying fire to the upper cut surface. The oil was collected at the bottom of the hollow which was emptied at 3 or 4 day intervals. Fire was applied every time the oil was removed and the upper surfaces of the hollow were rechipped 3 or 4 times in a season. About 180 kg of oleoresin oil was collected from 20 trees in a season. The oil was marketed locally in the form of torches and also exported. Later, tree tapping was prohibited owing to the heavy damage to the trees.

In Bangladesh, the practice was to cut a deep hollow, (transverse hole pointing downwards), in the tree and place fired charcoal in it during the night. The oil was removed in the morning and the charcoal replaced. The process was repeated until the oil ceased to flow. Three, four or more such hollows were made which often killed the tree. In Burma the charcoal practice was not adopted.

In India, in the western-Ghat division of Coorg, the oil was collected by cutting a hole into the centre of the tree. It is also reported that a large notch was cut into the trunk of the tree about 75 cm above the ground level, in which fire was maintained until the wound was charred and the liquid began to ooze out. A small gutter was cut into the wood to a vessel attached to receive the oil. The average yield from the best trees was 180 litres per season. At 3 or 4 week intervals the old charred surface was cut off and burnt afresh. Tapping occurred from November to February and sick trees were rested for 1 or 2 years.

Properties and Uses of Gurjan Oil

The exudate is milky and faintly acidic and when allowed to stand separates into 2 layers - a brown oil which floats on the surface and a viscous, whitish grey emulsion below. A pale yellow oil with a balsamic odour is obtained (yield 46%) through steam distillation of the oleoresin which leaves a dark, viscid, liquid resin.

The commercial gurjan oil is the oleoresin mixed with small quantities of oleoresin from *Dipterocarpus alatus*, *D. costatus* and *D. macrocarpus*. It is a viscid fluid, highly florescent, transparent and dark reddish brown in colour when seen against the light. It oxidises when exposed to the atmosphere. The essential oil consists of two distinct sesquiterpenes, alpha and beta gurjunene.

The resin contains a crystallisable acid, gurjunic acid ($C_{22} H_{34} O_4$), devoid of acid character as in copaiba (a resin containing a small portion of naphtha), which may be removed by warming it with ammonia and 0.08% alcohol. It is partially soluble in ether, benzol or sulphide of carbon. The portion of resin, which is insoluble even in absolute alcohol, is uncrystallisable. A remarkable physical property of this oil is that at a temperature of 130°C it becomes gelatinous, and on cooling does not recover its fluidity.

The oleoresin is applied externally to ulcers, ring worm, and other cutaneous infections. It is a stimulant to mucous surfaces and also a diuretic (Kirtikar and Basu 1935, Martindale 1958). It is an ingredient of lithographic ink and varnish and an anticorrosive coating composition for iron. It is occasionally used as a preservative for timber and bamboo. Mixed with powdered dammar from *Shorea robusta* or *S. siamensis* it forms a dark brown paste used for caulking boats and water proofing bamboo baskets used for carrying water. Gurjan oil is a good solvent for caoutchouc (unvulcanised rubber) which is applied to cloth to make it water-proof. This cloth resists insect-attacks.

Traditional Uses

a) Medicine: Ancient literature reveals that gurjan oil was used by the Mohammedans and it was first mentioned in the 'Makhzan' Materia Medica as 'Duhn-el-Garjan'. Its essential oil is effective in the treatment of genito-urinary diseases. The Pharmacopoeia of India 1868, officially describes it as a stimulant of mucous surfaces, particularly those of the genito-urinary system, and as diuretic (Watt 1899). However, users of indigenous systems of medicine in India find it less powerful than copaiba. It is useful in leucorrhoea and other vaginal discharges, psoriasis, including lepra-vulgaris and also in the treatment of leprosy (used both externally and internally). All varieties of gurjan oil are equally useful as local stimulants but red, reddish brown, pale or pale white varieties are best for internal use. The efficacy of this oil is enhanced with the addition of chaulmugra oil.

An ointment is prepared by mixing equal parts of oil and lime water. In European medicine gurjan oil was mainly used as an adulterant for copaiba.

b) Domestic and Industrial Uses of Gurjan Oil: Gurjan oil was used in Burma for torches, and later, as lamp oil. It could be used as a varnish by mixing it with some good drying oil or by evaporating the essential oil. The oil was a good substitute for linseed oil and balsam of copaiba and prized as a colourless varnish and for drying paints.

c) Trade of Gurjan in the 19th Century: In Burma and Bangladesh gurjan oil was mainly used for torches but its trade was limited due to the cheap price of kerosene. However, gurjan oil from Singapore and Malaya was a common article of trade in Thailand. The oil produced in South India and Andaman Islands was traded in Europe for use in artworks. The price of the black or dark brown varieties ('Kala gurjan Tel') was half the price of the red or reddish brown ('Lal gurjan Tel') and pale white ('Sufed gurjan Tel') varieties.

Other Sources of Oleoresin

Other South Asian species important for the production of oleoresins include *Dipterocarpus alatus* and *D. tuberculatus*. The former is found in Chittagong (Bangladesh), Andamans (India) and Burma. *D. tuberculatus* occurs in Burma, and to a restricted extent in India and Bangladesh.

Dipterocarpus alatus produces an oleoresin that contains 71.6% volatile oil. The oil known as 'kanyin oil' in Burma is an antiseptic applied to clean wounds and has been used as a substitute for copaiba in the treatment of gonorrhoea. In Burma, it is also used for treating ulcers and sores in the hoof and foot disease of cattle. The oil is used by forest dwellers to fuel torches made of rotten wood and for waterproofing the oil cloth used for Burmese umbrellas. It has been used in the preparation of lithographic inks and has been tried as a varnish and as a substitute for linseed oil in zinc paints. Its bark is a tonic given for rheumatism.

The method of tapping oleoresins from almost all other species resembles that of *D. turbinatus*. A notch is made into the trunk and the wound blazed to stimulate resin flow. Resin is collected periodically and either the wound is scraped for new flow or another wound made. The trees eventually succumb to the regular wounding, and the timber, unsuitable for construction work, is used as fuelwood. The oil and resinous thicker substance mixture is strained through a cloth whereby the clear oil separates itself from the resinous portion. *Dipterocarpus alatus* provides the wood-oil, pegu.

Dipterocarpus tuberculatus is the principal source of oleoresin known as 'In oil' in Burma and 'gurjan oil' in India. Its exudate is thicker than 'kanyin oil' from *D. turbinatus* and flows freely from the wound without the aid of fire. Throughout the year, resin oozes simultaneously from several niches on a tree. The oil was collected 4-10 times a month from August-February and 300 trees yielded about 36 kg a month. At the end of the season the dried resin was scraped off and used to make torches. Freshly collected oleoresin is a pale brown substance with specific gravity 1.029; acid value 17.8 and ester value 0. It yields a yellow brown essential oil on steam distillation. The oil is used for varnishes and for water proofing umbrellas and bamboo well-baskets. The oleoresin is used with assafoetida and coconut oil as an application for large ulcers (Watt 1889).

Shorea robusta or sal is another important producer of oleoresin in Bangladesh, India and Nepal. It yields an oleoresin known as sal dammar, 'ral' or lal dhuma'. Earlier tapping methods gave low and erratic yields. The method recently employed is to cut 3-5 narrow strips of bark 90-120 cm above the ground. When the tree is blazed the oleoresin oozes out as a whitish liquid and on exposure it hardens quickly and turns brown. The cut is freshened by scraping off the hardened resin. In about 12 days the grooves are filled with resin. The grooves are freshened and resin is collected periodically in July, October and January. A good mature tree yields about 5 kg of resin annually.

The essential oil, sal resin, on dry distillation yields an essential oil, known as 'chua oil'. The yield of the oil varies from 41 to 68% depending upon the source of the oleoresin samples. The oil is light brownish yellow in colour and has an agreeable incense-like odour, with specific gravity 0.9420, acid value 4.42, saponification value 15.72 and saponification value after acetylation 39.49. It consists of 96.0% neutral, 3% and 1% phenolic and acidic fractions, respectively. Chua oil is used as a fixative in heavy perfumes, for flavouring chewing and smoking tobacco and in medicine as an antiseptic for skin diseases and ear troubles. The non-phenolic portion of the oil has a suppressing effect on the central nervous system, the phenolic portion is less effective.

Vateria indica is also an important source of oleoresin in India. The trade names used for the oleoresin are piney resin, white dammar, Indian copal and dhupa. The trees are tapped either using semi-circular incisions or a fire is lit at the base of the tree so as to scorch the bark, which then splits and the resin exudes. The resin is in three forms: i) compact piney resin which is hard, in lumps of varying shapes, bright orange to dull yellow in colour, with a glossy fracture and resembling amber in appearance, is called Indian dammar; ii) cellular soft piney resin which occurs in shining masses, having balsamic odour, and light green to yellow or white in colour, is called a piney varnish; and iii) dark coloured piney resin from old trees. The resin is a complex mixture of several triterpene hydrocarbons, ketones, alcohols and acids along with small amounts of sesquiterprenes. On distillation, the oleoresin gives an essential oil (76%) with a balsamic odour. The oil consists of phenolic constituents and azulenes, with the latter predominating. The essential oil has a marked antibacterial property against gram negative and gram positive microorganisms (Howes 1949, Chopra *et al.* 1958). The resin readily dissolves in turpentine, camphorated alcohol and is used in the manufacture of varnishes, paints and anatomical preparations. The liquefied resin mixed with hot drying oil makes a varnish, superior to copal, for carriages and furniture. The resin is used to make incense, for setting gold ornaments, caulking boats (Trotter 1940) and in rural areas, resin mixed with coconut oil is used as torches and candles. It is a good substitute for Malayan dammar and, in solution in chloroform, for amber in photographers' varnish. The resin has medicinal value. It is credited with tonic, carminative and expectorant properties and is used for throat troubles, chronic bronchitis, piles, diarrhoea, rheumatism, tubercular glands, boils etc. Mixed with gingili (sesame) oil, it is used for gonorrhoea and mixed with pounded fruits, obtained from *Piper longum* (long-pepper), and butter or ghee it is useful for the treatment of syphilis and ulcers. An ointment of resin, wax and the fat of *Garcinia indica* is effective against carbuncles. It forms a good emollient for plasters and ointment bases (Kirtikar and Basu 1935, Chopra *et al.* 1958, WOI 1989a).

In Southeast Asia the important oleoresin trees are *Dipterocarpus cornutus*, *D. crinitus*, *D. hasseltii*, *D. kerrii* and *D. grandiflorus*. The old method of tapping is by notching a hole in the trunk and blazing to stimulate further oleoresin flow. This is repeated at about weekly intervals and the yield per tree is 150 to 280 ml per tapping (Gianno 1986). A less brutal method has been developed, known as the barkchipped method accompanied by application of chemical stimulants, which is less destructive and the yield and oleoresin quality better (Ibrahim *et al.* 1990). The oleoresin is processed to separate the essential oil from the resin. The essential oil, known commercially as gurjan balsam, is used as a fixative or a base in perfume preparations and occasionally as an adulterant of patchouli and copaiba balsam oils. Traditionally the oleoresin is used for caulking the inside of boats, coating wood as a protection against weather, in torches, and for medicinal purposes. The oil is also used to make varnishes in backyard industries (Burkill 1935). While the biggest suppliers of gurjan balsam oil are Indonesia, Malaysia and Thailand, limited quantities are produced in India and the Philippines. Sumatra is the biggest producer of all, and in 1984 it produced about 20 tonnes of the oil (Lawrence 1985). The oil is now becoming scarce with an increasing demand, resulting in increased prices. The price is currently over US $30 per four gallon tin. The oleoresin is mainly collected by natives and aborigines and has a ready market in Singapore where it is exported to Europe.

There are several other less important dipterocarps which are tapped for oleoresin:

- *Dipterocarpus bourdilloni*, a species from Kerala, India, yields opaque, straw yellow, viscid oleoresin which on standing deposits a crystalline unsaturated hydroxy ketone, $C_{24} H_{42} O_2$, M.P. 125°-126°C. When distilled with steam at 100°, 245° and 380° C it gives 37% 65% and 76% respectively, essential oil (Anon. 1989).
- *Dipterocarpus costatus* from Burma produces a resin used in the treatment of ulcers.
- *Dipterocarpus gracilis* found in Bangladesh and India, produces a good quality oleoresin used in the soap-industry and also as an antiseptic for gonorrhoea and urinary diseases.
- *Dipterocarpus grandiflorus* belonging to the Andamans, Thailand and the Malesian region, produces an oleoresin which exudes as a thick fluid which changes into a semi-plastic mass on long exposure to air. The exudate has a thick honey - like consistency and a balsamic odour, is reddish brown in colour and contains 35% volatile oil and a hard, yellow, lustrous resin soluble to the extent of 75% in alcohol. The oleoresin used in varnish is dissolved in equal parts of linseed oil and turpentine, and dries slowly to a tough hard film.
- *Dipterocarpus hispidus* of Sri Lanka produces resin that has been found to contain dipterocarpol, dammarenediol, and ocotillone.
- *Dipterocarpus indicus* is a species of west coast, tropical, evergreen forests of India. Its oleoresin is used in the preparation of spirit, oil varnishes and lithographic inks. It is also used as an adulterant of dammar and as an application for rheumatism.
- *Dipterocarpus macrocarpus* of India and Burma produces oleoresin that is used as a lubricant and in soap making.
- *Dipterocarpus obtusifolius* of Burma, Thailand, Indochina and northern Peninsular Malaysia has oleoresin that yields a clear, white or yellow resin which burns readily (Watt 1899).
- *Dryobalanops aromatica* found in W. Malesia yields an oleoresin that is aromatic, volatile and is used in medicine, in the preparation of toothpaste, powders and as a diaphoretic and antiseptic; it is also used for treating hysteria and dysmenorrhoea (Agarwal 1986).
- *Parashorea stellata*, a species found in Burma, Thailand, Indochina and Peninsular Malaysia, produces resin which is used as a fumigant.
- *Shorea siamensis*, found in Burma, yields a red resin.
- *Shorea megistophylla*, a species found in Sri Lanka, yields resin that contains ursolic acid, 2-alpha, 3-beta dihydroxyurs - 12-Cn-28-oic acid, asiatic acid and Caryophyllene (Bandaranayake *et al.* 1975).
- *Shorea obtusa* from Burma produces a white resin.
- *Shorea roxburghii*, a widespread species found in India, Burma, Thailand, Indochina and Peninsular Malaysia, yields a resin, which is used as stimulant and for fumigation (Anon. 1985a, WOI 1988).
- *Shorea tumbuggaia* is a species found in India which yields a resin which is used as an incense and as a substitute in marine yards for pitch. It is also used in indigenous medicine as an external stimulant and a substitute for Abietis; Resina and Pix Burgundica of European pharmacopoeias (Watt 1899).
- *Vatica chinensis*, a species found in India and Sri Lanka, yields abundant resin nearly transparent and yellow in colour resembling that of *V. lanceaefolia* and used in varnishes.
- *Vatica lanceaefolia* from Bangladesh, Burma and India, yields from its bark a clean, white, aromatic oleoresin which turns light amber in colour on hardening and is used as incense. When distilled, a strong smelling essential oil (9.2%) commonly known as scented balsam or 'chua' is obtained. It is used to flavour chewing tobacco with betel leaves. It also yields a strong smelling balsam 'ghunf' used in religious ceremonies. Piney tallow, dupade oil, piney yennai, or tam, obtained from the seeds is mainly used for lamps and is also suitable for soap and candle making.
- *Vatica obscura*, found in Sri Lanka, produces a gummy exudation used for caulking boats.
- *Vatica tumbuggaia*, a species found in India, yields a good quality oleoresin.

Dammars

Dammar is the hard, solid or brittle resin which hardens soon after exudation when its small content of essential oil evaporates. Although all dipterocarps produce dammar, only a few are of commercial importance. In Southeast Asia, the important genera are *Neobalanocarpus*, *Hopea* and *Shorea*. The most important Malayan varieties are 'damar mata Kuching' from *Hopea micrantha* and related species, 'damar penak' from *Neobalanocarpus heimii*, and 'damar temak' from *Shorea crassifolia* (Blair and Byron 1926). The principal dammars of India are sal dammar from *Shorea robusta* and white dammar from *Vateria indica*. *H. odorata* from Bangladesh, Burma and India, is the source of dammar, known commercially as 'rock dammar'. Dammars are also produced in the island of Borneo, Java, Sumatra, Thailand, and Vietnam. The outstanding commercial variety, the Batavian dammar, comes from *Shorea wiesneri* from Java and Sumatra (Burkill 1935).

Dammar is found as natural exudations, on living trees, in lumps on the ground beneath the trees, near dead stumps, or even found buried in the ground. These dammars are usually collected by aborigines. Natural exudation also occurs from trees which are unhealthy or damaged by the heartwood borer. Sal resin occurs in rough, stalactitic brittle pieces, 16-24 cm in size, pale creamy yellow in colour, nearly opaque with a faint resinous balsamic odour. It is produced commercially by tapping the trees.

Dammars are used traditionally for making torches, caulking boats, and handicrafts. The dipterocarpaceous resins have also been used as adulterants for the aromatic resin produced by *Styrax benzoin* (Styracaceae) which is used as an incense and medicine. Sal dammar is widely used as incense in religious ceremonies and as a disinfectant fumigant. Large quantities of dammar are an important ingredient in 'Samagri' used for cremation. It can also be used for hardening softer waxes for shoe-polish manufacture, carbon paper, typewriter-ribbon, and in inferior grades of paints and varnishes for indoor decorative work, and for mounting microscopic objects. It has been used as a plastering medium for walls and roofs and as a cementing material for plywood, asbestos sheets, etc. Tribal people in India mix the resin with bees' wax and red-ochre for fastening spear and arrow-heads.

The resin is used in indigenous medicine as an astringent and detergent and is given in diarrhoea and dysentery. It is also an ingredient of ointments for skin diseases and has curative properties against ear troubles, toothaches, sore eyes, ulcers and wounds. The resin in powder form is used as an ointment for wounds and sores (Anon. 1985a).

More recently, the dammars are being used in many technical preparations, such as in the manufacture of paints, batik dyes, sealing wax, printing inks, varnishes, linoleum and cosmetics. Triterpenes isolated from dammar have been found to exhibit *in vitro* antiviral activity against *Herpes simplex* virus type I and II (Poehland *et al.* 1987).

Dammar export is mainly from Indonesia. The following species produce high quality resins which fetch a high price: *Shorea javanica*, *S. lamellata*, *S. virescens*, *S. retinodes*, *S. assamica* ssp. *globifera*, *Hopea dryobalanoides*, *H. celebica*, *H. beccariana* and *Vatica rassak* (Jafarsidik 1987). Indonesia exports annually 2000 - 7000 tonnes worth US $1.6 million. The dammar is mainly exported to Japan, Taiwan, Singapore, Germany and Malaysia.

Dammar in Sumatra is produced mainly from dammar gardens that are part of an agroforestry system. With the decline in forest areas, farmers have resorted to developing resinous tree plantations. However, in Lampung, Sumatra, man-made dipterocarp gardens have been established since the 19th century (Rappard 1937). *Shorea javanica* a native of the region, is grown in an agroforestry system with other crop trees (Torquebiau 1984), as is *Hopea dryobalanoides*. Villagers tap the trees by cutting holes of about 10 cm wide and 15 cm deep into the trunk to stimulate resin flow. The resin is collected periodically and the holes deepened. When the hole reaches the centre of the trunk, a new hole is made. Tapping commences when the trees are about 20 years old, and continues for 30 years when production declines. A fully productive tree may produce 50 kg of resin each year. One hectare of dammar gardens can produce 4.8 tonnes per year (Torquebiau 1984).

Camphor

Trade in camphor (known as Borneo or Sumatra camphor (bhimsaini-kapur, barus kapur)) is ancient. Camphor was used mainly in China and its source was the gregarious *Dryobalanops aromatica* (kapur) forests in North and East Sumatra and Johore. Other species, such as *D. beccarii*, also yield camphor but to a lesser extent. The camphor is found in cavities or fissures in the wood in the form of solid camphor, or a light fluid called camphor oil. The tree is felled, cut into blocks and split into wedges to remove the camphor. One hundred trees rarely yield more than 8-10 kg solid camphor. In solid form it occurs in white crystalline translucent fragments, sometimes in long, 5 kg pieces. It closely resembles the camphor from *Cinnamomum camphora* but it is heavier than water, does not volatilise at room temperature, and possesses a characteristic pungent odour and burning taste. It is used in medicine, perfumery and organic syntheses. Borneo camphor is almost pure d-borneol ($C_{10}H_{17}OH$, M.P. 209°C) and is highly prized in Indian medicine. Chinese and Japanese also attribute a higher medicinal value to it than the essential oil from the wood of *Camphora officinalis*. It is converted into ordinary camphor by heating with boiling nitric acid. (Balfour 1985, WOI 1989a). *Dryobalanops aromatica* is no longer a major source of camphor now that *Cinnamomum camphora* is used in the chemical industry and camphor can be synthesised more cheaply from pinene.

Butter Fat

Another major dipterocarp NTFP in Borneo is butter fat. *Shorea* species (the Pinanga type) produce illipe nuts which are called engkabang and tengkawang in Malaysia and Indonesia, respectively. The nuts are generally collected in the wild but some experimental plantations of *S. macrophylla*, *S. stenoptera*, *S. mecistopteryx*, *S. aptera* and other related species exist in Sarawak and Kalimantan (Tantra 1979). The fruiting is somewhat aperiodic but at about four year intervals the forests fruit heavily. The natives of Borneo extract oil from the nuts for use as cooking oil (Anderson 1975). The kernels are exported to Europe, Japan and West Malaysia. The illipe fat extracted from the kernel is used in the confectionery industry, especially in the manufacture of chocolate. The illipe fat has a high melting point, and when blended with cocoa butter remains solid at room temperatures. Likewise, illipe fat is added to cosmetics such as lipstick. The illipe nuts have a high value with prices from US $2300-2700 per tonne in the 1980s (Anon. 1985b), and during peak fruiting years exports from Borneo can reach 50 000 tonnes (Wong Soon 1988).

Shorea robusta (sal) from the Indian region is another important source of butter fat. The kernels, constituting 72% of the nut weight contain 14-20% of fatty oil known as sal-butter. Sal seed oil has assumed great importance for use as a cooking medium, industrial oil, illuminant, lubricant and as a substitute for cocoa-butter. It is also suitable for soap making after blending with other softer oils. The sal fat is obtained by boiling the husk seeds in twice the volume of water and skimming off the oil which solidifies to a buttery consistency in cold weather. In India sal fruits must be collected before the onset of the monsoon when it becomes difficult to dry and decorticate them. The dried fruits can be decorticated by hand or with mechanised decorticators after manually dewinging them. The fruits are spread on a hard surface to a thickness of about 10 cm and beaten with sticks to dewing them. The oil is also obtained by solvent extraction of seeds by flaking procedure. The particle size of the kernel is reduced to 7-10 mesh by using fluted rolls and cooked at 2.25 kg cm^{-2} steam pressure with limited open steam injection so as to adjust the meal moisture content in the flaking rolls to about 15%. A steam jacketed flight screw kettle is most suitable for cooking the meal. The flakes are tempered to a thickness of 0.24 - 0.3 mm with a moisture content of 8%. They do not show any sign of disintegration on solvent impact due to the kernels' high starch content. Studies show that, even with proper conditioning of the kernels, it is not possible to obtain a good yield of fat by expeller. The fat is refined by a conventional method of alkali refining. However, the small recoverable fat content of 14% is disadvantageous because the fat contains various kinds of pigments even after refining. The glycerides of the kernel fat are a rich source of stearic and oleic acid (44.2 and 44.9%) in addition to palmatic (4.6%) and arachidic acid (6.3%).

The kernels of *Vateria indica* from India yield about 22% fat by solvent extraction. This is known as piney tallow, malabar tallow or dhupa tallow. It is extracted by boiling the powdered kernels in water, then allowing the extract to cool and skimming off the floating fat. The fat has a slight, pleasant odour and is greenish yellow at first but rapidly lightens in the air. It consists of glycerides of solid acids (53%) and liquid acids. (Puntembaker and Krishna 1932). The tallow is edible after refining, but is not in common use. It is used in confectionery and as an adulterant of ghee, in candle and soap manufacture, and for sizing cotton yarn instead of animal tallow. It is also used as a local application for rheumatism.

Tannin

The leaves and bark of several dipterocarps are a source of tannin. The bark of *Hopea parviflora* from India is a good tanning material for heavy leather, particularly when used with other tanning materials, for example myrobalan bark in a 2:1 ratio which gives a good quality, reddish brown leather resistant to mould. The bark contains 14-28% tannins and the solid extract, an astringent with slow diffusion speed, 70% tannins (Anon 1985a). The tannin content in the bark of *Dipterocarpus tuberculatus* is 24%, while young leaves have 10-12% and may be used in direct light leather tanning. Sal bark, together with the leaves and twigs, is also a promising tanning material. The tannin content is: bark 7%, young leaves 20%, twigs and leaves 22% and powder dust 12%. The aqueous extract of bark is a pale reddish colour and the tannins are of pyrogallol type. The extract is used locally for cheap tanning or in a blend with other tanning materials. The dry leaves of *H. odorata* contain 10% tannin and are used in crude tannery. The tannin extract is rich and produces strong leather (Anon. 1985a, Agarwal 1986). The fruit of *Vateria indica* contains 25% tannin.

Lac Host

A few dipterocarps are known to host the lac insect (*Lacifer lacca*), a source of lac. *Shorea roxburghii*, a species found in Burma and India, is a valuable host in South India, and yields a good crop when inoculated with 'Deverbettakusum' variety in Karnataka. *Shorea talura* is another important lac host plant of Karnataka in India (Krishnamurthy 1993). *Shorea obtusa*, a species found in Burma, is an occasional host and sal is the source of the 'Kusumi' strains of lac insect.

Other Products

In addition to the important products described above there are other dipterocarp NTFPs. The sal tree yields many of these products. Its leaves are a good source of income to the tribals in India who make them into plates and cups or use them as wrappers for home-made cigars. They are also used for thatching huts in the villages and as a medium to poor grade fodder containing 0.94% nitrogen and 2.97% ash. Sal leaves are one of the primary hosts of tassar silk-worm (*Antheraea mylitta*). Roasted sal seeds, although not very palatable, are sometimes eaten, and decorticated seeds are used as poultry feed. Dried seed meal contains: moisture 5.23%; protein 6.16%; ether extractive 16.77%, crude fibre 4.81%, N. free extractive 63.25%, calcium 0.18%, total ash 3.78% and acid insoluble ash 0.95%.

A light grey, somewhat granular cellulose gum is prepared from the bleached, bright cellulose obtained from the spent bark. This compares favourably with commercial grade technical gums. The cellulose from the spent bark is also suitable for making wrapping paper. Lignins from wood waste are used as wood-adhesive. The bark is oily, bitter, acrid and anthelmintic and can cure ulcers, wounds and itches. It is also a useful raw material for fibreboards (WOI 1988). Sal oil cake, used as cattle and poultry feed, contains 10-12% protein and about 50% starch. It can also be used as a fertiliser. Sal flowers are produced in abundance and are the source of honey. Santal tribals use the bark for preparing red and black dyes and wood ash in dyeing.

A number of minor products derived from the wood also need mention. Wood of *Shorea robusta* and *Vatica lanceaefolia* is extensively used as firewood and for making charcoal. However, fuelwood should only be harvested at the time of clear felling at fixed rotations when unsuitable wood for timber can be utilised for firewood and charcoal making. The branches and thick twigs can be converted into charcoal in a specially designed kiln for supplementing the energy requirements after converting charcoal into briquettes. Briquetted charcoal and sawdust are good fuels for domestic and industrial purposes. Briquettes made with suitable binders from inferior grade gum, gum resin or pulp and juice from Agave/Furcraea species (Verma *et al.* 1979, Gulati *et al.* 1983) without the traditional use of clay and molasses ignite easily, do not emit smoke and provide sustained heat.

The sal tree is considered to be the home of spirits and many gods, and tribals build their shrines under its shade and worship the tree as a whole. The Bagdis and Bauris tribes of Bengal are married under an arbour made of its branches. The sal tree in full bloom is worshipped in some villages by childless couples. Buddhists also worship the tree as it is believed that Buddha's mother held a branch in her hands when Buddha was born, and it was under the shade of this tree that Buddha passed the last night of his life on earth (Bennet *et al.* 1992).

Other valuable dipterocarps in the South Asian region include:

- *Hopea odorata* of which the bark is an astringent and masticatory for gums.
- *Vateria copallifera* of which the cotyledons are ground into an edible flour and the bark is used for arresting toddy fermentation (Anon. 1985a).
- *V. indica* of which the fruit is ground into flour. The seed cake, unpalatable to livestock, is used as a manure, especially in coffee plantations. However, the cake, when mixed with other concentrates such as bran or groundnut cake, can be utilised for cattle feeding. The bark is an antidote (alexipharmic) in Ayurvedic preparations. The juice of the leaves is applied to burns

and is orally administered to prevent vomiting (WOI 1989b).

Socio-economic Perspectives

In general dipterocarp NTFPs have been mainly used as subsidiary products by village people. However, some products from a few species have assumed much greater importance due to their demand. These few products have gained commercial importance in industry and trade due to their properties and chemical constituents. At present in the southern Asian countries, forest management systems have banned or restricted timber harvesting and so there is a need to generate more revenue from the NTFPs, especially during the prescribed long rotation for tree felling.

Amongst the dipterocarp genera, *Dipterocarpus*, *Dryobalanops*, *Hopea*, *Shorea*, *Vateria* and *Vatica* are the important sources for NTFPs. The oleoresin and seeds are the most important for various uses while the leaves, bark, and twigs are useful for medicinal or tanning purposes. *Shorea robusta* is the only tree considered sacred and associated with different beliefs and religions.

Critical analysis reveals that commercial extraction/ harvesting of different NTFPs aids socioeconomic development. Local harvesting of NTFPs by village and forest dwellers for traditional uses will persist. The present system of exploitation by local people is generally detrimental and therefore, improved collection methods are needed to provide sustained production and income. Value adding by local processing is desirable to increase returns.

Strategies for NTFP Development in Forest Management

Development strategies will differ for the extraction of oleoresin, seeds, bark and leaves from any species of NTFP importance. Owing to the erratic and unregulated extraction of NTFPs from different species, the economic returns do not properly accrue to the collectors. Therefore, it is essential that there are scientific measures to ensure better gains for improving the socioeconomic condition of not only the village and forest dwellers, including tribals, but also other industrial entrepreneurs associated with the utilisation, marketing and trade of the various products. Specific mention is made below of the development of NTFPs from dipterocarps:

1. Resins (Oleoresins and Dammars): These are the most important commercial products obtainable from *Dipterocarpus alatus*, *D. grandiflorus*, *D. indicus*, *D. tuberculatus* (gurjan/In oil), *D. turbinatus* (gurjan/kanyin oil), *Hopea odorata* (rock dammar), *Shorea robusta* (sal dammar), *Vateria indica* (white dammar) and *Vatica lanceaefolia*. Methods of obtaining oleoresin/dammar from these species have been discussed, but as yet there is no foolproof scientific method of tapping. Research should be done, according to the species, on: the optimum size, shape and depth of the blaze to avoid damage to a tree on a harvest rotation of several decades; the appropriate collection season and duration with adequate freshenings; and obtaining sustained, optimum oleoresin yields.
   Further, depending upon the constituents of each oleoresin, they can be put to specific industrial uses. Therefore, in order to make maximum gains from the value-added products, the raw material must be graded and processed prior to manufacturing the essential oil and various derivatives. These exercises will go a long way in improving the socio-economic conditions of all those involved in the oleoresin trade.
2. Camphor: *Dryobalanops aromatica* is the only important dipterocarp producing camphoraceous oleoresin. This is extracted when the trees are felled for wood. Marco Polo, in 1299, mentioned that its camphor was traded by Arabs in the sixth century. The camphor was obtained, from concentrated occurrences of this species in North and East Sumatra and Johore. Now, camphor from this species is not commonly used, owing to the convenient availability of alternative sources.
3. Seeds: Collection of seeds either for edible and medicinal purposes or recovery of fatty oil is made on large scale from *Shorea robusta* in South Asia and *S. macrophylla* in Malaysia, followed by *S. aptera*, *S. obtusa*, *S. stenoptera*, *Vateria indica*, *V. copallifera*, and *Vatica lanceaefolia*. To maintain the product quality and achieve maximum returns it is essential to collect the seeds in the appropriate season and stage of development and to properly grade and process them.
4. Leaves: *Shorea robusta* leaves are important for local and commercial manufacture of cups, platters and cigar wrappers. The leaves of other species, such as *Dipterocarpus tuberculatus*, *Hopea odorata* and

Vateria indica, are mostly used for tanning and medicinal purposes. To increase the collector's income, the leaves must be collected at the appropriate season and stage of growth and be properly dried and graded.

5. Bark: This is used for tanning and medicinal purposes, for example: *Dipterocarpus alatus* (medicine), *D. tuberculatus* (tannin), *Hopea odorata* (tannin), *H. parviflora* (tannin), *Shorea robusta* (tannin, medicine, gum), *Vateria copallifera* (toddy fermentation) and *V. indica* (medicine).

   Only the bark of *S. robusta* is utilised on a large scale. Collection of bark from standing trees is detrimental to tree growth, so improved methods of bark extraction are needed or bark utilised only from felled or dead trees.

There is good scope for greater utilisation of various dipterocarp NTFPs for socioeconomic development. This will be enhanced by further research and training in a range of technologies. These include: oleoresin and dammar tapping techniques; seed, leaf and bark harvesting; grading and processing standardisation; chemical evaluation of derivatives; and marketing and pricing analysis.

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