The Gramineae, Wild and Cultivated, of Monsoonal and Equatorial Asia. I. Southeast Asia

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A STUDY of the archaeology, history, and taxonomic geography of the Gramineae (Whyte 1970*a, b,* and *c*) has been undertaken to show how a number of disciplines may contribute to an understanding of the past and present distribution and dispersal of the wild and cultivated species in this family. (Archaeology is taken in the first meaning stated in the *Oxford Dictionary:* ancient history generally, systematic description or study of antiquities, in this case botanical.) The Gramineae have been selected because of their dominance or major participation in vegetation over great areas of the world, and also because they provide the major food-grain staples for human nutrition, as well as feed for domestic and wild animals.

Although botanical conclusions or speculations based upon the archaeology and history of the Gramineae must be tentative, it is believed that they may nevertheless be sufficiently well-founded to contribute to a two-way interchange with the students of human history. There are just as many tentative conclusions and theories that await confirmation by archaeologists about ancient sites and civilizations, and by students of land, vegetation, and climatic history about the evolution of land use and the early cultivation of crops.

Human archaeology and anthropology can contribute to a better appreciation by botanists of the history, evolution, and taxonomic geography of the wild and cultivated plants on which they may be working. Conversely, fieldwork by archaeologists and anthropologists will gain greatly by an ecological/historical analysis of the present vegetation undertaken by specialists in the history and evolution of vegetation and its component species. Conclusions can then be drawn regarding the geobotanical history of sites of archaeological operations and of the cultivation and domestication of food plants from the local flora or elsewhere.

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This preliminary study will show how such an interchange can contribute to integrated research. More definitive statements will follow after discussions with specialists and the clarification of examples of parallelism between human and botanical history. Harrisson (1966) has said: "Perhaps this is a moment for the rest of us to remember that it is sometimes better to publish an imperfect study sooner rather than later. It stimulates others in the same field, so that one's own inadequacies are likely to be corrected by other, better studies."

Botanical History and Geography

The geographical scope is Mainland and Island Southeast Asia, including the southern provinces of China. Plant geographers have proposed several regional groupings for equatorial and monsoonal Asia, but usually on the basis of complex vegetation types and floras.

Takhtajan (1969) would include Papua and New Guinea, but exclude the Indus basin of Pakistan from the Indo-Malesian (Indo-Malayan) subkingdom of his Palaeotropical Kingdom. Good (1966) and Dansereau (1957) recognize an Indo-Malaysian subkingdom within a palaeotropic kingdom. The Rijksherbarium in Leiden has adopted the term "Malesia" to include all those parts of western and central Malesia which are situated between southeastern continental Asia on the one side and Papua New Guinea, New Britain, and northern and northeastern Australia on the other (see also Sarawak/UNESCO 1965). The analysis adopted here on the basis of one plant family rather than total vegetation does not confirm the existence of some type of Indo-Malayan region.

There appears to be a consensus that the origin of the Asian angiosperm (flowering plant) flora, to which the Gramineae belong, is associated with continental drift in the Pacific and eastern Asia (Melville 1966). The limiting date for the time of origin of the angiosperm families in general is the period at which Africa plus South America was separated from the rest of Gondwanaland (Melville 1972, personal communication). Paleomagnetic evidence suggests that this separation took place at the beginning of the Triassic. Melville concludes that, by this time, "a number of the more important angiosperm families must already have been set on their evolutionary path; they were probably still gymnosperms at that date, but the general lines of their morphology and evolution had already been determined."

The next major event in this history of the angiosperms was their vast and rapid expansion during the Middle Cretaceous, which Takhtajan (1969) has described as "one of the most important events in the history of life upon the earth. It had a decisive influence on the future of the terrestrial animal world, especially the insects, birds and mammals. In the final reckoning, the dominance of flowering plants made possible the appearance of man. The middle of the Cretaceous was therefore the beginning of a new era in the history of life upon our planet."

Various reasons are proposed by Russian workers for this sudden expansion:

a. continental uplift, intensification of mountain-building, development of arid regions, diversification of environment marking the close of the Jurassic and leading to greater diversity of physicogeographical conditions by the late Cretaceous;

b. change of environment, creating, for example, conditions of less cloud and greater light intensity to which the ferns and gymnosperms were less adapted than the angiosperms—"children of the sun" (Golenkin 1927);
c. sharp decrease in atmospheric carbon dioxide in the Middle Cretaceous, to which the flowering plants, which lived in mountains, were already adapted (Teslenko 1967);
d. poor evolutionary plasticity and less diversity of form in Jurassic and early Cretaceous floras; and
e. great evolutionary plasticity and unusual adaptability, perfection of the vascular system, leaves, and roots of angiosperms; their co-evolution with the insects.

Some climatological reconciliation is necessary between the time of origin of the angiosperms in Gondwanaland and its segments with a cool temperate climate, the time of the breakaway of what is now called the Indian subcontinent from its southern hemisphere partners and its crossing of the equator to join southern Asia in the northern hemisphere, when there were relatively rapid climatic changes, and the period of great expansion of the angiosperms in the Cretaceous. This last event is believed by some to have occurred in or near the areas of Southeast Asia that were and still are occupied by tropical rain forest.

Takhtajan (1969) proposes that the center of origin of the modern angiosperms is in areas with a subequatorial monsoonal climate characterized by an alternation of hot and dry with moist and rainy seasons, that is, in the mountain forests of tropical Asia and the subtropical forests of the eastern Himalaya—Nepal, Assam, Upper Burma, North Vietnam, China, and Japan—the zone of contact and overlap of the tropics and subtropics of Asia. The greatest number of relict archaic "living fossils" that have persisted since the Tertiary is found in these areas; for example, in southern China (Grubov 1969).

Specialists on the Asian tropical rain forest (Corner 1971, personal communication; Anderson 1971, personal communication) would agree that the flowering plants had their origins within the tropical rain forest, but consider that there is no evidence that they were monsoon-subequatorial-adapted at first; these adaptations are secondary. The Russian workers believe that the Magnoliales are the most primitive of angiosperms; Corner (1971, personal communication) notes that all modern Magnoliales are variously advanced, and proposes his alternative "durian theory" (1949). *Durio zibethinus* (Bombacaceae) has fleshy arillate fruits with a "maist unchaste" smell which were and still are part of the nutritional ecosystem of all manner of Malayan wildlife, from elephants and tigers down to ants and beetles. This fruit, and those of other plant families, including eighteen genera of four subfamilies of the Leguminosae, is regarded as the primitive fruit of modern flowering plants. This fruit changed into the dry follicle or capsule, with small, often winged, easily detached ex-arillate seeds, or into the berry, drupe, or nut.

The rival claims of South America must also be considered:

> The actuality of a large diversified flora, originating in Jurassic-Cretaceous time in Guyana before uplift, and there perpetuated, may compromise a hypothesis of the unique origin of the angiosperms within the region of Malaysia. I would be more comfortable with the view (consistent, I believe with that of

Axelrod, 1952 and 1970, and van Steenis, 1962) of a broader geographic base for angiosperm genesis and evolution, which would provide for primal evolutionary ferment in the totality of the tropically equable, probably contiguous land mass or connected land masses of the Jurassic and early Cretaceous world. (Maguire 1971)

TAXONOMIC HISTORY AND GEOGRAPHY OF THE GRAMINEAE

These subjects call for a new approach. So far little has been done, largely because the taxonomic relations of genera and species themselves have not been finalized. There is, in the Gramineae, an extraordinary mosaic of characters which even now are changing in response to the forces of evolution and selection; there is a revolution in ideas concerning the taxonomy of this most difficult family (Whyte 1973*b*, chap. 9). C. E. Hubbard has said: "A great deal more information must be gathered before even a tentative scheme with even a moderate chance of acceptance can be produced."

Melville (1972, personal communication) would include the Gramineae in that group of angiosperm families (see above) which "must already have been set on their evolutionary path" at the beginning of the Triassic, when Africa plus South America was separated from the rest of Gondwanaland. "This means that one set of grasses would have been separated in Africa and South America, whereas the remainder would have been able to colonize or migrate into India and Australia, and by Jurassic times at least have migrated to the land masses then existing in the central Pacific." (See also Aubreville 1971 reviewing A. C. Smith 1970.)

A perhaps biased view of the significance of this family was given at a recent I.U.B.S. Symposium on the natural classification of the Gramineae (Beetle 1971). The Gramineae, comprising over 5000 valid species and over 500 genera, is sufficiently large, diverse, and old to reflect nearly the whole of angiospermous history. In the Mesozoic, the Tethys Sea divided the Old World climates, thus establishing the striking contrasts between the panicoid/chloroid and the festucoid types of grasses, the first being predominantly tropical, the second predominantly temperate. "Some species, some genera and some tribes have achieved stability and some floras their characterization much earlier than others. As the classification of the grasses becomes more natural, distribution patterns will help to reveal the historical development of these groups" (Beetle 1971).

It is generally accepted that the monocotyledons arose from the dicotyledons, and sometimes that the Bambusoideae are the ancestral group of the Gramineae. However, many species of bamboo also show specialization, and a common ancestor may be a more acceptable proposition. The criteria for primitiveness depend upon individual phylogenetic theories. The Russian interpretation (Fig. 31 of Takhtajan 1969) is that the grasses (Poales) are "the final link in a chain of anemophilous evolution, some basic stages of which may already be seen in the order Commelinales. By all accounts they arose directly from the Restionales, most likely from some extinct Flagellariaceae believed to have originated in highland areas with a low incidence of insect pollinators" (Cvelev 1969). The Bambusoideae separated first, followed by the Oryzeae, Arundinelleae (or Arundineae), Eragrostideae, Panicoideae including Paniceae and Andropogoneae, and finally Festucoideae. In the last group, further evolution is seen to have been associated with a reduction in the basic chromosome number, development of an annual habit, and simplification in structure. There is a general impression that the Andropogoneae are derived from Panicoid stock and are hence less old (Veldkamp 1971, personal communication).

Prat (1960) has given a synthesis of his ideas with those of Stebbins (1956 and 1959), Beetle (1957), Tateoka (1957*a*, 1957*b*) and Brown (1958). Prat approves of Stebbins' conclusion that no group within the Gramineae can be considered as "original." The Bambusoideae cannot be regarded as the ancestors of the family; although their flowers and fruits may have primitive characters, their anatomy and their epiderms are highly evolved. Their woody structure is certainly a secondary character, the common ancestor of the Glumiflores and the Liliflores being probably herbaceous. A hypothetical mark X has therefore been included in Prat's Figure 5 to indicate a point in the Cretaceous from which the different groups may have diverged, but unequally and not in the same manner. Thus we find differential rates of development of characters, the Festucoideae having evolved more rapidly in flower and epidermis characters, the Bambusoideae showing the converse situation.

From these taxonomic considerations the grass archaeologist and historian have to extract those data which may indicate sequence of antiquity among the recognized subfamilies, genera, and species of the Gramineae, and to relate these to geobotanical history, the ethnology and cultural anthropology of human races, and their effect on the land and vegetation. The question of centers of origin of the subfamilies of the Gramineae is relevant: the term *center of origin* or variability means something different when applied to wild species and cultivated crops respectively.

Hartley (1958, 1964) has prepared world-distribution maps of the Andropogoneae and the Paniceae. Relative species density is recorded, using the percentage of species of a particular subfamily in the total grass flora in some 300 regions. But floras are unreliable for such studies unless accompanied by an ecological and historical analysis of the total vegetation; they include both true indigenous species (which are usually few) and "recent" exotics which could not have been constituents of the vegetation before interference by man. One must also know whether the compiler was, in taxonomic argot, a "splitter" or a "lumper."

The Andropogoneae show zones of high concentration in western India and southern Indonesia. India can be accepted, but Indonesia calls for a study of the history of devegetation, fire, and shifting cultivation. Although a zone of highest concentration of the Paniceae is found in northeast South America, Hartley does not support a New World origin for the subfamily. Rather he suggests a common origin for the two subfamilies from a common panicoid stock in the warmer parts of the eastern hemisphere, probably in the East Africa/Madagascar region. This has since been confirmed by Butzin (1970*a*, 1970*b*), who finds the most "primitive" representative of the Paniceae, *Pseudolasiacus*, in Madagascar, while most of the genera considered to belong to the same tribe, Microcalamineae, are also African.

It is necessary to reexamine the proposal of Bews (1929) that the progenitor of the grasses arose in the humid tropical forests, and that migration to less uniform, more exacting and variable environments was accomplished by mutation and natural selection. Rather one may suggest, for Asia and Africa, a migration of species into the areas of formerly grassless climax forest from two directions. Mesophytic perennial species (of the Paniceae type?) would progress from their ecological niches in the tropical forest zone (coastal and river flats), from the central African lakes and marshes (Thomas 1966), or from the lakesides and marshes of Southeast Asia, Mainland and Island, into cleared forest lands, to the limits of their physiological and genetic tolerance of aridity. Conversely, from the zones of the dry *forêt claire,* for example, Africa south of the Sahara, Pakistan, western India, and the Deccan, would have come the xerophytic perennial grasses (of the Andropogoneae type?) advancing into new habitats in the cleared forest zone, to the limits of their physiological and genetical tolerance of humidity (Whyte 1973*b,* chap. 5).

Both the mesophytic and xerophytic migrants would pass through several zones of vegetational transition (Valentine 1970), physiological stress, and hence renewed speciation. Applying conclusions from ecological/historical analyses to the situation in Southeast Asia, we may recognize three periods or stages of increasing intensity of speciation:

1. the millennia before man, when the evolution of the few genera and species followed a course governed by geologic and climatic factors, in the absence of anthropogenic factors;
2. from the appearance of man in small numbers up to relatively recent times, when new exotic grasses began to be associated with early human history; and
3. the present, beginning in Malaya only some 100 or 200 years ago, in Java perhaps 500 to 1000 years ago, when large-scale clearance of forests created and is still providing extensive areas of land characterized by absence of shade and of forest humidity, and by more arid soils, an environment suitable for nonindigenous, light-requiring grasses and crops.

The second and third stages have brought together grass species from many diverse foreign environments. The opportunity for hybridization of ecotypes/genotypes which have never before met has been greatly increased. In Southeast Asia the grass taxonomist may, in due course, find many new types of specific or near-specific level in a plant family in a state of flux or taxonomic explosion.

In this discussion of evolution in the Gramineae, there is a need to consider the exact meaning in a historical context of the terms native, indigenous, and endemic. How long does a plant have to exist in an area before it qualifies for the category of indigenous? What is the significance in terms of geobotanical history of the concept of endemism? Are the forty-six species and varieties recognized as endemic for the Philippines by Merrill (1906), or the seven endemics recognized in the Flora Malesiana (Veldkamp 1971, personal communication) truly ancient relicts of a vegetation in a former age, or are they the "young beginners" of Willis (1922)?

Endemics Recognized by Flora Malesiana

Monostachya oreoboloides at 2500 to 4700 m in North Sumatra, North Borneo, southwest Sulawesi, Luzon, and New Guinea; possibly a dwarf species of *Danthonia*

Ectrosiopsis eragrostoides

Ramosia = *Centotheca*

Asthenochloa—monotypic

Polytrias—monotypic, doubtfully distinct genus

Sclerachne—monotypic; heavy, periodically inundated soil, light shade, open teak forests, padi fallows, lawns, road margins; up to 300 m in Java, Kangean Islands, Bali, Sumba, Timor

Buergersiochloa—two species, extremely rare, only few specimens collected in forests of New Guinea—habit bambusoid, one species has three lodicules—regarded by Rijksherbarium as apparently distinct, and of great phlyogenetic interest.

The geographical distribution of the Gramineae may also be studied in relation to the CO_2 compensation point in different habitats. In Java (Hofstra et al. 1972), plants with a low CO_2 compensation point (C–4 type) appear to be less common than plants with a high CO_2 compensation point (C–3 type). Plants with the C–4 pathway are found only among herbs (50 percent of herbaceous species found in the open at low altitudes, percentage decreasing with increasing altitude toward zero at 3000 m; percentage much lower in shade than in full light).

All species of Gramineae found in the open at low altitudes are of the C–4 type; species of the C–3 type are found in shade or at higher altitudes (denser cloud cover?). It is considered that the Paniceae (containing genera of both the C–4 and C–3 types) may be intermediate between the Panicoid/Chloridoid group (C–4) and the Festucoid/Arundoid group (C–3).

The taxonomic and historical origin of annual forms of the Gramineae is of fundamental importance in any study of the origin of cereals. Most botanists agree that annual forms of plant species arose from perennials. Annuality is a mechanism for escaping seasonally unfavorable environments. The change of a species population from the perennial to the annual state is a response to the physiological stress of such environments—great or increased intensity of desiccation and heat over long periods or adverse seasonal temperatures associated with higher latitudes and altitudes.

Perennials tend more toward vegetative growth, since reproduction by seed is not so essential to their continued existence. Annuals must produce large amounts of seed to allow for wastage, and the seeds are larger to help the next generation to become established. The evolution of annual forms of specific or lower status from a perennial favors dispersal of that genus into new habitats in which the perennial forms could not grow.

The annual forms of the Gramineae are characteristic particularly of arid and semiarid habitats, and are increasing in frequency with the progressive extension of man-induced desiccation. *Heteropogon contortus* is predominantly perennial in India, but an annual form is found in arid ecological niches on the Maharashtran Deccan. The occurrence of an annual form of this genus in the absence, until recently, of the perennial in Java (Monod de Froideville 1968) is to be explained in terms of adventitious introduction. The equable environments of the humid tropics are not conducive to the evolution of annuals.

Although annual species of Gramineae may occur in small percentages in arid and semiarid communities, their presence as dominants in such habitats must be regarded with suspicion. They are then probably secondary and rather low in ecological regression. The climax grass communities around deserts or in arid and semiarid zones generally are perennial; these growth forms may be progressively eliminated due to overgrazing, spasmodic cultivation, and other causes, and replaced by less demanding secondary annuals of the same, but more commonly other, genera.

Distribution and Dispersal

One might expect that the high degree of insularity within the Southeast Asian region might be appropriate for the study of the relation between insularity, plant dispersal and isolation, and speciation (Fosberg 1963; McArthur and Wilson 1967; Sauer 1969; Lowe-McConnell 1969; Stern 1971). Disjunct distribution of families and genera of flowering plants, which occurs on remote oceanic islands, for example, in the Pacific, cannot safely be attributed to separation of continents (Jardine and McKenzie 1972). However, any possible significance of the factor of genetic isolation on the Gramineae on the larger and smaller islands of the region has been largely eliminated, in prehistorical and historical times, by the movements of peoples and goods along recognized trade routes. Isolation by oceans is, however, regarded as significant in the taxonomy and cytogenetics of the species of *Oryza* (National Institute of Genetics 1969; Morishima 1968; Chu and Oka 1968).

The main thesis of this article is that up to 80 percent of the grasses now recorded for Java, Sumatra, Borneo, and Malaysia came from the west through human agency—from Africa and western monsoon Asia—and to a lesser extent from the east—Papua and New Guinea and northern Australia—very late in the geobotanical calendar. This fact is recognized for Java by Monod de Froideville (1968), but not for Malaya by Gilliland and others (1971). Merrill (1906) made such an analysis of the Gramineae of the Philippines, and concluded that they are

> strongly Malayan or Indo-Malayan, with a decided northern element in the highlands of northern Luzon, and a rather characteristic Australian one, which, strangely, is from the same northern region of the Archipelago, rather than from the southern islands, although when more extensive collections have been made in the interior of Mindanao, doubtless most of these Australian types, which at present are known in the Philippines only from northern Luzon, will be found in Mindanao.

Many of the species now to be regarded as newcomers in Southeast Asia, Mainland and Island, are found in the coral islands and atolls of the Indian Ocean (Stoddart 1966, 1970; Stoddart and Taylor 1971) and in the Andaman Islands (Bhattee and Thampi 1963); Willis and Gardiner (1931) record twelve species on Chagos Archipelago; Summerhayes (1931) records for the Seychelles one endemic species and 42 species of pantropical distribution or with African, Mascarene, or Asian affinities. These records will have to be analyzed in relation to the age of the coral islands and atolls, the availability of watering points for early mariners under sail, the movement of bird populations, and the grass floras of east Africa, the Mascarene Islands, Arabia, and western monsoon Asia (Whyte 1973*c*).

There are many high-altitude "islands" of grass species of temperate physiological relations on top of mountains of Mainland and especially Island Southeast

Asia. Their occurrence so far from their nearest temperate relatives still awaits an acceptable explanation (Whyte 1973*a*), perhaps to be related to other studies, for example, of the evolution of the Afro-alpine flora (Hedberg 1971), of the Antilles (Howard 1971), or of Mauna Loa, Hawaii (Mueller-Dombois 1967).

Three major reasons may be proposed at this time:

1. that some of these species are relicts of a temperate Gondwanaland or contemporary flora;
2. that some may have been brought there by bird vectors migrating between the temperate zones of the northern and southern hemispheres; and
3. that some may be the temperate relatives of species of the same genus which occur in the tropical and subtropical ecoclimates at lower altitudes.

Melville (1972, personal communication) has stated, with reference to the occurrence of temperate species on Kinabalu in Sabah, that he is now satisfied that at least the northern half of Borneo belonged to the Pacific continent.

> The southern half probably belonged with some other parts of Indonesia which were associated with India before the drift movements took place. This conclusion has a direct bearing on the migration of many plant species; in particular the high mountain plants of Kinabalu have their relationships in the Pacific and New Zealand; although Kinabalu is comparatively recent in origin, there is evidence that another high mountain existed in what is now Borneo at an earlier stage and has since been eroded down.

Of the seven modes of arrival of plants in the Pacific islands proposed by Carlquist (1967), those relating to dispersal by birds are relevant to a biological explanation of the grass flora of Southeast Asian mountains—seed attached to feathers, eaten and carried internally, embedded in mud on feet. A study similar to that of Moreau (1972) of the palaearctic-African bird migration systems is needed for the migrant birds of East Asia and the western Pacific. Migration of such birds as terns, godwits, and long-tailed cuckoos from the northern hemisphere to the southern and back will require investigation. Do they fly in a high arc over the equator to avoid the tropical atmosphere; do they rest on the high mountains of Taiwan, the Philippines, Malaysia, Indonesia, Papua and New Guinea; what is the content of their digestive tracts; how long is ingested food retained; how long do undigested seeds remain viable (Proctor 1968)?

Before man's arrival in Southeast Asia, the natural vegetation was a climax cover of various types of forest, highland, and swamp forest vegetation in mountains, valleys, plains, and deltas (Richards 1952). There would have been no grassland climax or climax grass covers in the region. Primitive species may have contributed in a minor way to the plant associations of the denser forests and of open sites along riverbeds and in mountains. In terms of geobotanical history and evolution, man is a very recent arrival indeed in the forest ecosystems of equatorial and subequatorial monsoon Asia; his influence in changing the environment has been significant only in recent centuries (Papua and New Guinea/UNESCO 1960; Pelzer 1968). In the present context, interest is focused on man's role in the intentional or adventitious introduction of wild and cultivated species of the Gramineae by land or sea routes.

From the earliest times, the development of a seaborne trade that is certainly older than the most ancient historical records followed a pattern imposed by the monsoons, which blew ships and men of the east to the west, and of the west to the east (Morley 1949). In the early stages, the mariners called at landfalls in Southeast Asia, such as the southern tip of Malaya or Sumatra, for water, food supplies, to barter, and to await the next favorable winds to continue their journey or return whence they came. In due course those settlements became flourishing entrepôts.

This oceangoing commerce became established along certain routes at well-defined seasons between Southeast Asia and, to the west, Sri Lanka, India, east Africa, and Arabia; to the east, the ports of China. Arabs were involved in this trade from time immemorial; Indians also participated, coming direct to the east, or first to east Africa, where they traded with tribes who came to meet them from the interior. They then sailed to Southeast Asia, where "l'abondance de perles de verroterie d'origine indienne trouvées dans les gisements néolithiques de l'Indochine et de l'Archipel prouvent que, dès la préhistoire, des relations maritimes existaient non seulement entre les diverses parties de l'Inde extérieur, mais encore entre cette dernière et l'Inde propre" (Coedès 1948).

There is some evidence that a seafaring Proto-Malay people may have reached India in outrigger boats before the arrival there of the Dravidians (Winstedt 1935); it is not known when Indonesian seafarers first reached Madagascar.

However, of these various groups, the Indians had the most profound effect on the cultural and vegetation history of Malesia, coming in increasing numbers until, about the beginning of the Christian era, Hinduized kingdoms developed along the trade routes with China. Coedès has described this progressive development:

> Il est vraisemblable, à priori, que les prêtres qui consacrèrent les premiers sanctuaires brahmaniques ou bouddhiques et les lettrés qui rédigèrent les premières inscriptions sanscrites avaient été précédés par des navigateurs, commerçants ou émigrants, fondateurs des premiers établissements hindous. Ces établissements, à leur tour, n'avaient pas toujours été créés de toutes pièces, et dans bien des cas (Oc Eo en Cochinchine, Kuala Selinsing à Perak, Sampaga à Célèbes, etc.) ils avaient été installés sur des sites néolithiques, que les navigateurs venus de l'Inde fréquentaient peut-être depuis un temps immémorial (Coedès 1948).

Wheatley (1961) considers the evidence regarding the location of the earliest centers in the Malay Peninsula mentioned by the Chinese to be inconclusive, but they were probably referring to an area near the Kra Isthmus. Since piracy had made the Straits of Malacca unsafe, from early times land routes across the northern peninsula offered a shorter, safer alternative (maps in Wheatley 1961). The most northerly, steeper routes probably required the use of elephants (although McCarthy [1902] states that bullock cart transport was the most common in Siam) and human porterage. The Indians would, according to custom, have brought in their own draft animals. Since there is no good draft animal in Bengal, the breed that they introduced was the Ongole from the Krishna Delta (now Andhra Pradesh). The coincidence of the Indian component in the Kedah breed of cattle of northern Malaysia and the predominance of Indian species of grass in the derived flora of northern Malaysia and southern Thailand are an indication of the simultaneous introduction of the cattle and the hay grasses to feed them on their sea journeys and after arrival. This led to the adventitious establishment of Indian genera and species in a new environment which approximated to their own in its monsoonal characteristics, after the forest had been reduced in extent. The spread of Islam by the Gujarati traders from the Gulf of Cambay late in the 13th century, with Malacca as a focal point, may have introduced a new element into the vegetation of that area, although the habitat was less acceptable to monsoonal species. Indian influence continued over many centuries, but became greatly intensified from the foundation of Penang as the fourth Presidency, in 1786, until 1867, when government of the Straits Settlements passed from India to London. During this time the army commissariat introduced many long-horned draft cattle and their hay supplies, which were harvested in the subcontinent. When the largest fleet ever assembled by a European power in the East left Malacca for the invasion of Java in 1811, it carried Bengali and Madrasi regiments, and horses and draft cattle with their essential feeds and fodders, which again must have come from India (Hill 1970).

These events contributed to the adventitious introduction of seeds of grasses from far distant countries. They came in packing materials, as weed seed contaminants in grain supplies, or in the sweepings of godowns or of the decks on which the animals traveled. Where the new environment was suitable, these species became established around coastal settlements and along riverine routes into the interior. The great expansion of the exotics followed the opening of the countries of Malesia for plantation agriculture, which began in the 18th century and became widespread only in the 19th century. The population of the Malay Peninsula increased, mainly by the arrival of tin miners from China and plantation laborers from India, from 300,000 in 1850 to over 9,000,000 in 1972. Stands of grasses grew up around the houses of plantation workers and in their food plots, where the combination of higher light intensity and drier soils provided conditions necessary for nonindigenous species to thrive.

Of great significance to the spread of these grasses to the foothills and more remote areas of Malesia is the movement of the shifting cultivators. They carried uncleaned crop seeds with their weed seeds wherever they moved. For much of the history of Malesia, regeneration of the forest cover was such as to eliminate these exotic herbs in the long forest cycle between burnings. They could have been renewed only by repeated contact with people from permanent settlements (silent barter as a method of accidental seed introduction into remote mountain clearings—Blagden and Skeat 1906). During the past hundred years, however, pressure on the land has increased, and the shifting cultivation cycle has become ever shorter, preventing regeneration of secondary forest and creating conditions whereby the herbaceous cover, dominated by the ubiquitous species, *Imperata cylindrica,* has become permanent.

ECOLOGICAL AND HISTORICAL ANALYSIS

The grasses of Malaya (now West Malaysia and Singapore) have been described and classified taxonomically by Gilliland and others (1971). An attempt is made here to reclassify the 220 species on the basis of their individual adaptation to environment, as indicated by site of collection or their known environmental requirements. This has been done to separate those grasses which can, on the evidence available, be regarded as truly or possibly indigenous pending the presentation of reliable data on habitat requirements and taxonomic primitiveness. It is only such grasses that are of sufficient geobotanical age to be significant in fundamental studies of the origin of the Gramineae, early speciation, the nature of primitiveness, centers of origin of subfamilies, and related matters. All other species are irrelevant to such studies; they are, as we have seen, most important in studies of dispersal in relation to anthropology and trade, and in investigations of the possibility of renewed speciation in the secondary habitats which have now been created.

The natural vegetation of the Malay Peninsula is High Rain Forest "holding the most intense rain-forest flora of the old world" (Burkill and Holttum 1923/5), which only some one or two centuries ago (Cheng 1969) dominated all but the maritime fringe, river plains, occasional forest clearings, and exposed mountain ridges. Even now this type of forest covers more than half the land area, although it is being further encroached upon by land development schemes such as the Jengka Triangle and the project in Johore.

Specialists in taxonomic geography have to learn to categorize forest covers in respect of their capacity to support growth and reproduction of the Gramineae. The ecological niches in tropical rain forest in which one might expect to find, or to have found, the few species of the Gramineae adapted to such conditions, are:

—within the forest itself

—coastal sands and muds

—river and stream banks in the interior

—high altitudes

—areas of tropical rain forest disturbed not by man but by severe windfalls in steep terrain with unstable soils (Anderson 1971, personal communication) or by slips related to long periods of heavy rain, sites that may take many decades to be colonized by anything but grass and ferns (Burgess 1972, personal communication)

—salt licks and grazed areas in the forest, especially in Borneo, visited by gaur and banteng (Burgess 1972, personal communication)

—areas affected by fire (cooking fires of hunters), or by the severe windstorms of 1883 in Kelantan, said to be related to the eruption of Krakatau and possibly responsible for the "very odd size-class distribution in the 'storm forest' of Kelantan" (Burgess 1972, personal communication)

Now, rapidly changing ecological conditions will lead to the progressive discovery of species hitherto considered exotic on sites opened to the influence of intense light and on soils which have become more arid, with the structure of gramineous or cultivated soils. The classification adopted here shows the direction in which this colonization has already occurred and its probable trend in the future.

CLASSIFICATION OF GRASS FLORA OF MALAYA

INDIGENOUS

A. some bamboos,

B. forest grasses adapted to relative shade of forest fringes (species of *Centotheca, Lophatherum,* and *Leptaspis*), some adapted to dispersal in the forest by having inflorescences or spikelets that become readily attached to the coats of passing wild animals,

C. moisture-loving and riverside species, of the genera *Oryza* and *Saccharum,* and possibly *Phragmites karka,*

D. grasses of coastal and other sands, muds, and estuaries (in part), some appearing to be indigenous *(Spinifex littoreus, Thuarea involuta, Oplismenus burmannii, Sporobolus virginicus,* and possibly *Panicum repens),*

E. grasses of limestone hills (Henderson 1939), in part, and

F. grasses of high altitudes above the forest.

POSSIBLY INDIGENOUS

grasses for which habitat data are inadequate for historical conclusions; species of *Coelorachis, Cyrtococcus, Ichnanthus, Isachne, Microstegium, Pogonatherum, Setaria, Sorghum, Themeda, Thysanolaena.*

NONINDIGENOUS

A. grasses of coastal and other sands, muds, and estuaries (in part),

B. grasses of limestone hills (in part),

C. grasses of north and northwest Malaya, extending into Thailand, grasses of western monsoon Asia, of the genera *Apluda, Arundinella, Bothriochloa, Chrysopogon, Dichanthium, Dimeria, Eragrostis, Eremochloa, Eulalia,* and *Neyraudia* (but, surprisingly, no *Sehima*), many or all of which were introduced by accident or intent, while the ancient trade routes were in operation across the Isthmus of Kra and thereabouts,

D. *ruderals* of disturbed places, paths, and roadsides, generally in good light; *weeds* of upland cultivation, shifting or settled, gardens, waste land, mostly recent arrivals during the past 100 to 200 years, as seed contaminants or in other ways; occurrence of *Phragmites karka* as a ruderal, not only on abandoned tin mines, but also along watercourses, suggests that it is not indigenous, but may have been introduced from the Indian subcontinent (also reported from streams in the Middle Andaman Islands), when the rivers of Malaya were used as inland trade routes,

E. grasses of aboriginal village-sites, their waste land, clearings in forest; much older than 200 years; a few escapes of primitive crops back to the wild, such as *Coix lacryma-jobi* and *Setaria italica,*

F. grasses of padis, ditches, canals, grasses of wetlands and swamps; probably few if any truly indigenous, and

G. introductions for economic or ornamental purposes.

Applying the same criteria to the Gramineae in the flora of Java (Monod de Froideville 1968), one finds that some 25 species may be indigenous, 66 species doubtful, and 182 nonindigenous foreigners which have arrived since the tropical rain forest was progressively cleared. The rate of colonization may have been rapid; the South American species, *Pseudechinolaena polystachya,* found for the first time near Bogor a century ago, has now spread over the whole of Java, at elevations from 200 to 1650 m.

From an analysis of the twelve species of *Panicum* recorded for Malaya, it is doubtful whether statements of their global distribution should include West Malaysia and Singapore, except as these species are constituents of a "recent" adventitious flora. Lazarides (1971, personal communication) has analyzed eleven species of *Panicum* found in the Malay Peninsula, Indonesia, Thailand, Indochina, Philippines, and Papua New Guinea, and concludes that "on a critical evaluation of available data, I must admit that I cannot present any evidence to suggest that the Malaysian species are of ancient origin. It appears that a relatively recent origin might also apply to many if not all south-east Asian members of the genus." A similar analysis is necessary for the twelve species of *Panicum* recorded by Hsu (1971) for Taiwan.

It may also be claimed that the eleven species of *Digitaria* in Malaya are not indigenous; Veldkamp (1971, personal communication) recognizes twelve species and states: "These, and many other grasses, are no doubt native and original in the region. No doubt human activity has given them a better chance for expansion, but I am sure that the abundance of contemporary individuals is of secondary importance in these studies."

Introduction, Cultivation, and Domestication of Cereals

The history of human nutrition starts with the collection of foods provided by plants and with the hunting of animals in their biological ecosystems. On the plant side, the next step is the initial cultivation of wild plants found by experience to be superior and palatable—the cutting away of wild competitors around these wild plants, and the leading to them of small canals of water to extend their season of growth and to increase their productivity. Helbaek (1969) has defined the often-misused terms "cultivation" and "domestication":

> The first word means particular and persistent interest in something. In plant husbandry, it means promotion of favourable growth conditions—changing the microbiology of the topsoil through hoeing and ploughing and, in many regions, by controlling water supply; further, by artificial dispersal of seeds and by keeping out competition from animals and plants that may infringe upon the maximum prosperity of the chosen species—in the hope that these endeavours will prove profitable also to the benefactor.

This does not necessarily mean that the cherished "cultivated" species will die if the care of the cultivator comes to an end. Domestication, on the other hand, calls for a conscious effort in the way of selection, nursing, and propagation of the crop plant, creating a reciprocal dependency or form of symbiosis between plant and man. Once fully "domesticated," a plant cannot exist in the absence of man; this, according to Helbaek's interpretation, applies equally to crop plants and to their accompanying weeds which have been exposed at the same time to spontaneous selection (Hawkes 1970*a*). On abandoned crop-land and in the absence of other biotic factors, these weeds must ultimately be eliminated by the dominant ground cover of the original vegetation, if seed sources still exist.

The terms "agriculture" and "primitive farming" are also used in an imprecise manner. In the forested regions of greater Southeast Asia (including South China) the clearing of vegetation first for shifting and then for settled agriculture could not have taken place on any significant scale until iron implements had come into general use. The earliest cultivation may thus have been in the valley bottoms, where, with great labor and given enough time, man (with stone and wood implements) might have removed a few shade trees and prepared a rough plot for stream or floodwater irrigation. He might even have been able to extend his cultivated land one or at the most two steps up the hillside, and so begin a primitive form of terracing. Scanty crops might also have been grown in the other ecological niches in the tropical rain-forest.

The Genetic Origin of Asian Cereals

The history of the evolution of those Asian members of the Gramineae which now provide most of the world's foodgrains hinges upon the taxonomic, physiological, and genetical distinction between annuals and perennials. The causes, dates, and possible geographical locations of the creation of annual forms of Gramineae out of perennial forms are highly significant to world history; the availability of such forms contributed to the origins of crop agriculture (Heiser 1969; Frankel and Bennett 1970; Hawkes 1970*a*), to the first major population explosion (Fig. 1 in Bennett 1971), and hence to the early migrations of peoples.

It is generally accepted that our understanding of the underlying causes of the movements and cultural changes of which prehistory is composed must remain imperfect until a more complete picture of ecological change has been built up. One important event in this early history of man in his ecosystem was the appearance of the grains of annual forms of the Gramineae and the consequent origins of crop cultivation. Why did these annual forms become available to man over such a relatively short time-span in geobotanical history?

It is proposed that this was because there were no annual species/ecotypes/genotypes in Asia before the end of the Pleistocene, no annuals of *Triticum* nor of the genera which have contributed to the genomic structure of wheat (*Aegilops, Secale, Haynaldia, Agropyron,* and *Elymus*) (Fig. 2 in Harlan 1971), nor annuals of *Hordeum, Avena, Setaria, Panicum,* or *Oryza.* The same interpretation may be applied to the domestication of annual cereal species of the genera *Brachiaria, Digitaria, Eleusine, Eragrostis, Pennisetum,* and *Sorghum* in the lowland and highland zones south of the Sahara described by Harlan and de Wet (1971).

During the Neothermal there occurred successive periods of fluctuating but increasing desiccation, combined with seasonally alternating low and high temperatures around the fringe of the continental anticyclonic area (figs. 1 and 5 in Jen-hu Chang 1971)—"the heartland of Asia." This would not only have been a zone of vegetational transition, say, between shrub-steppe and a grassland climax, where active hybridization and hence speciation might be expected to occur (Valentine 1970). The zone or zones of transition themselves would be moving under the influence of progressive climatic change (Whyte 1963). Thus would be provided conditions to which the ancient perennial species had not previously been exposed, conditions which promoted among the wild perennial ancestors of the food cereal annuals a slow, progressive change, probably over millennia, from perenniality to annuality, at a rate of evolution acceptable to geneticists (J. M. Smith 1968). The taxonomy of the cultivated members of the Gramineae calls for less work in the herbarium and more in the laboratory, the experimental field, or in the centers of variability themselves (Hawkes 1970*b*).

Peoples of primitive hunting and collecting communities in the desert-fringe lands of continental Asia who had been accustomed to hand-stripping the ripe heads of the perennials as one of their sources of plant food gradually began to notice a new resource being "handed to them on a platter," as it were: the large-grained annuals, which showed ever-increasing numbers and greater diversity. These new annual forms would have become established on the bare ground between the perennial species of a climax grassland that had become impoverished by desiccation and by overgrazing by the flocks and herds of the early pastoralists/hunters/collectors. They would note that the annuals had the habit of seed-shattering, and would learn to push the seeds into the ground to protect them from marauding flocks of birds, so proceeding gradually to the digging stick and to the beginnings of dryland cultivation.

Continuing and probably increasingly severe desiccation then caused the peoples themselves, with their thirsty and hungry animals, to move out of the desert fringes into regions less affected by drought, to the west and northwest, to the Anatolian Plateau, the Near East, the northwest of the Indian subcontinent, and into China. They would take with them their new-found source of food which they had learned to cultivate in a primitive manner: the annual types of the Gramineae. These types, already highly variable because of their origin, were thus introduced into entirely new environments in which their perennial ancestors had not grown before. In passing, one may note that the perennial ancestors of wheat, barley, and rye are primarily species of the Asian continental ecoclimates, and that their annual descendants (cultivated and "wild") which appeared in the Near East in particular are of a secondary, or more correctly, intrusive, ecological status in the Irano-Turanian and Mediterranean ecoclimates.

In the Near East, in particular, some of these nonindigenous annuals escaped from cultivation into the ecological niches which had formerly been occupied by local indigenous perennials, which had themselves been reduced or eliminated by overgrazing during earlier pastoral cultures, or by burning by hunters. The new annuals were already adapted to the seasonal droughts of these new environments because of their drought-escaping character of annuality. Their original variability changed in character, in cultivation and in the wild, in a secondary explosion of diversity which represents the field material of the latter-day plant collector and conserver of genetic resources (Bennett 1970*a*, 1970*b*).

It is not necessary to attribute greater ingenuity to any people, race, or culture in the introduction of these annual Gramineae into cultivation. The annual-creating conditions of desiccation and alternating high and low temperatures may have operated earlier, with greater severity and/or longer duration, in the west of the Asian continental desert fringes than in the east. If so, the *Triticum* and *Hordeum* annuals of Russia and the Near East evolved before the *Setaria* and *Panicum* of China.

Later these factors of desiccation and seasonally fluctuating temperatures extended farther, into the northern limits of distribution of the highly susceptible tropical and subtropical perennial species of *Oryza*. These species occurred in a belt from northeastern India (Bengal) to southeastern China (Kwangsi, Kwangtung, and Fukien), as already proposed by Chatterji (1951). There is no need to postulate a primary center in or around Assam and a secondary center in China, involving a direction of movement which is quite contrary to that accepted by modern anthropologists. Throughout these northern limits of the many perennial species of *Oryza* the evolution of annuals happened at the same time, producing the polyphyletic origin of cultivated rice and its many annual relatives that are incorrectly called "wild rice." Wild perennial forms of *Oryza* could not grow in nature north of the present limits of double-crop rice in the southern and southeastern provinces of China. With the appearance of annual forms within the perennial, it then became possible for the Lungshanoid cultivators to take this new crop north into less equable regions, where the winters were too cold for rice. Cultivated annual rice was also carried south with movements of peoples (and iron tools) into the densely forested lands of Southeast Asia, where until then only perennial rice had been cultivated or collected.

Asian Cereals in Early Agriculture

Agronomists and botanists find the archaeological interpretations and conclusions regarding early crop history somewhat confusing. Mesolithic hunters and gatherers inhabited limestone caves in the Malay Peninsula from about the 9th to the 3rd millennium B.C. (Tweedie 1965). Their supposed descendants, the aboriginal Semang of northern Malaya, were still hunters and collectors at the turn of the present century (Blagden and Skeat 1906), though the Sakai of the foothills and mountains were then practicing some form of primitive agriculture. Between 2500 and 1500 B.C., the neolithic ancestors of today's population, variously called Proto-Austronesian, Deutero-Malay, Indonesian, or Melanesian, began filtering in from the north. The finding in a neolithic site in South China of "reaping knives" led to the conclusion that these people knew how to cultivate rice (van Heekeren 1957). It is tempting to conclude that they brought both rice and Chinese millet *(Setaria italica)* with them into Southeast Asia and thence also into those neolithic sites in northeastern India which show evidence of Southeast Asian links (Dani 1960; Sankalia 1962). But this seems unlikely.

It is said that Lungshanoid sites in Taiwan and eastern Kwangtung dating from the end of the third millennium B.C. contain rice remains (Kwang-chih Chang 1970). The "Lungshanoid horizon of Southeast Asia is the key to the explosive spread of cereal growth in Southeast Asia" (Kwang-chih Chang 1969). Coedès (1948) believes that irrigated padi fields, plowed by buffalo and oxen, were part of the culture of Southeast Asia before the first arrival of the Indians. Complex terracing in Quang-Tri Province, Indo-China, included one or more fairly extensive wet-field terraces at the lowest level (Wheatley 1965). These were constructed by predecessors of the Vietnamese, but their exact dating remains obscure; Wheatley does not accept Wales' estimation of 2000 B.C.

In China itself, however, there is no evidence of irrigation until the 6th century B.C., and it was not used in large-scale works until the 3rd century B.C. (Ho 1969). Rice did not become the staple in South China (latitudes unspecified) until between A.D. 300 and 500 (Eberhard 1969). In Malaya, wet padi cultivation was not introduced until the 15th and 16th centuries A.D. (from Thailand into the northwest, from Sumatra into Negri Sembilan) (Cheng 1969). Dry rice cultivation was preferred until the beginning of the present century, and was practiced only by Malays.

Foresters and agronomists cannot accept the proposition that extensive irrigation works or dryland cultivation would have been possible in the forest climaxes of the humid tropics before iron implements became freely available to rural people. It is possible to conceive of rudimentary irrigation (the leading of water in channels from watercourses through partly-cleared nonwoody vegetation) to stands of swamp perennial rice by the use of stone and wooden implements. The clearing of sufficient large trees in virgin forest to give adequate light to annual grain crops is, however, out of the question until iron came into common usage. The clearing of forest that is essential for the dryland cultivation of both rice and *Setaria italica* in Southeast Asia could not have taken place until that time. It has been suggested that rice was cultivated in the Middle Yangtze only after the introduction of iron (Triestman 1968).

Neolithic peoples throughout the region were able, with their limited technology, to obtain sufficient wood for the building of boats and fuel for the firing of their pottery. The scavenging of wood on any scale must have been an extremely laborious process. Even so, it seems later to have been possible to collect sufficient fuel to provide the relatively low temperatures involved in the production of bronze in the humid tropics (Solheim 1972). Tools made of bronze are, however, of no use for the felling of tropical hardwood.

The Iron Age must have been invented in the arid zones. Where vegetation was subject to periodic droughts or long periods of desiccation, dead or dry wood from short trees and scrub could be gathered in sufficient quantity to maintain the high temperatures required, if supplementary forced draft could be provided by utilizing winds of reliable direction and velocity. As soon as the first, limited production of iron had become established, the collection of fuel was much simpler and more rapid.

Only when iron tools came into Southeast Asia from the north and northwest was it possible to fell enough wood to support a local iron industry; even then, the spasmodic wind regimes of the tropical rain forest must have posed considerable obstacles. The highly corrosive soils of humid tropical Asia are unlikely to have preserved the evidence essential for establishing the period during which iron tools came into general use. Iron from a site in Thailand has been dated at 700 B.C. (Solheim 1972). Metals were worked in Indochina from the 3rd century B.C.; iron probably came into general use here by the beginning of the Christian era. In Indonesia and Malaya, however, this did not occur until the 9th and 10th centuries A.D. (Löwenstein 1956). Wrought iron was produced in the Sarawak River delta for export to Southeast Asia from A.D. 900 to 1350 (Harrisson and O'Connor 1968).

From this it may be concluded that in the absence of the tools needed to clear the forest, the Proto-Austronesians or Deutero-Malays or Indonesians did not bring either rice or *Setaria* with them on their long migration from South China down the Malay peninsula and into Indonesia. On the alluvial floodplains of interior Malaya they probably cultivated root crops, as they did in inland Sarawak around 2000 B.C. (Harrisson 1967). Just conceivably, they may have tended perennial rice, species or ecotypes of *Oryza* in dryland, riparian, or marshy habitats.

Wet-rice agriculture in Indonesia must have developed independently; Majumdar's acceptance (1937) of the presence of irrigated rice culture in Southeast Asia before the arrival of the Indians is difficult to reconcile with the absence of iron technology. The first textual reference to the contemporary construction of a possible irrigation canal dates from around A.D. 400 (Vlekke 1959), but the text is rather too ambiguous for definite conclusions. Iron implements of Indian origin for the clearance of forest and subsequent construction of irrigation canals might have been available for public works around the coastal domains. Dutch scholars (Wertheim 1960) regard the reference to irrigation-tunnel builders in a Balinese royal edict of A.D. 896 as evidence that irrigation must have been practiced much earlier in the island.

The history of the other two ancient cereals of Southeast Asia—*Coix lacryma-jobi* and *Setaria italica*—requires further study before a clear picture can be evolved. The now pantropical *Coix lacryma-jobi* covers Southeast Asia in habitats ranging from lake water to dry hillslopes (comparable to the range of growth forms in perennial species of *Oryza*). Study is needed of *S. italica* especially in relation to the taxonomic geography of its related annual, *S. viridis,* and of their common perennial ancestors, whatever these may be.

SUMMARY

This article represents a first attempt to evolve a technique for regional studies of the archaeology, history, and taxonomic geography of a plant family of major scientific and economic significance—the Gramineae. The anthropology of Southeast Asia, Mainland and Island, and the history of land use, devegetation, economic development, and trade are considered in relation to the genera and species of Gramineae now found in this subregion of monsoonal and equatorial Asia.

It becomes possible to indicate which genera and species are older than man in the region, and are of sufficient geobotanical age to be significant in fundamental studies of the origin of the Gramineae, early speciation, the true nature of primitiveness, the centers of origin of subfamilies, and related matters.

All other species are irrelevant to such studies; they include some 80 percent of species listed in current floras. Within this group one finds not only the pantropical dross of ubiquitous distribution—*les espèces banales*—but also many species which are important in confirmatory studies of ancient communities, human migrations, wars and invasions, and trade, and in investigations of possible renewed speciation in the secondary habitat in which the species now find themselves.

In discussing the cultivated cereal members of this plant family, it is proposed that these annual types arose rather suddenly from perennial ancestors. During successive periods of intense desiccation and widely fluctuating diurnal and seasonal

temperatures early in the Neothermal, the physiological stresses operating on the existing perennials induced the genetic changes that created the drought-escaping annuals—the large-grained food grains of the future. The zones between isohyets in which this occurred in rice, and the period during which it happened, are of fundamental significance in studies of the evolution of early cropping and human nutrition and social systems throughout Asia.

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