5. Enhancement of the symbiosis

THE NEED FOR INOCULATION

Acacia rhizobia are, as we have mentioned, as widely distributed as the *Acacia* species themselves. Indeed, they sometimes occur spontaneously in anthropogenic environments, e.g. landfill in Hong Kong (Chan et al. 1998). Nonetheless, there are many soils where the population density is so low as to pose a threat to the establishment of N-fixing trees (Thrall et al. 2001a). There will be other soils where suitable strains for rhizobia-specific species will be absent. Used judiciously according to need, and performed properly, legume inoculation is a significant agency for improving plant productivity and soil fertility. 'Is it necessary to inoculate?' is a question that has been approached in different ways (Table 10).

Field experiments designed to diagnose the need for inoculation (e.g. Brockwell 1971; Date 1977; Thies et al. 1991a) are unsuitable for acacias. Bonish (1979) and Brockwell et al. (1988) used dilutions of soil samples to inoculate clover seedlings growing under aseptic conditions in test tubes to demonstrate a quick, microbiological means for characterising simultaneously the size and N-fixing capacity of soil-borne populations of rhizobia. The method could, no doubt, be refined for use as a diagnostic of the need for inoculation of acacias. A related procedure (Thies et al. 1991b) makes it possible to forecast the likely success of introducing inoculant rhizobia into the soil by considering indices of the size of the resident rhizobial population and the N status of the soil (cf. Singleton and Tavares 1986). Thies et al. (1994) put forward a unique proposal for predicting the need for inoculation on a regional basis using a geographical information system.

As our literature survey has shown, there are, among acacias, all degrees of host/rhizobial specificity in the symbiosis, varying from widely promiscuous to highly specific. Species in the latter category are those most likely to need and benefit from inoculation upon introduction into new environments where soils lack specific N-fixing rhizobia.

RESPONSES TO RHIZOBIAL INOCULATION OF ACACIAS IN FIELD AND NURSERY

Masutha et al. (1997) suggested that promiscuous species of *Acacia*, capable of nodulation and N fixation with naturalised populations of rhizobia, should be chosen for use in agroforestry programs, implying that they considered natural inoculation of acacias by resident soil rhizobia to be superior to artificial inoculation with cultures of rhizobia. We accept that proposition in situations where the numbers of acacia rhizobia in the soil are so large (say >1000 cells per gram) that introduced strains would encounter extreme competition from the resident organisms. Where, however, naturalised populations are smaller, there are excellent prospects of successfully introducing inoculant strains, provided sensible strategies are employed.

While there are only a few field reports of acacias responding to rhizobial inoculation, they document careful work and convincing results. Working with *A. mangium* in Ivory Coast, Galiana et al. (1994) reported that inoculation had a positive effect on tree growth for more than three years after outplanting. Moreover, one of the inocula persisted well and could be re-isolated from root nodules up to 42 months after transfer of the inoculated trees to the field. This particular organism (Aust13c) appears to have considerable potential as a strain for making inoculants. In Ivory Coast, 50–90% of total nitrogen in *A. mangium* trees was attributed to fixation of atmospheric N (Galiana et al. 1996). Galiana et al. (1998) reviewed these works and similarly successful experiments with *A. mangium* that had been conducted in other tropical countries. Lal and Khanna (1996) demonstrated a field response to inoculation of *A. nilotica* grown in India.

The long-term success of inoculation in the field appears to depend on the initial establishment of a vigorous crop of nodules. The nodule itself

Table 10. Indicators of the need to inoculate legume seed with effective rhizobia at time of sowing

Allen and Allen (1961) — historical indicators
1. The absence of the same or of a symbiotically related legume in the immediate past history of the land
2. Poor nodulation when the same species was grown on the land previously
3. When a legume follows a non-legume in a rotation
4. In land reclamation undertakings.
Roughley and Brockwell (1987) — microbiological queries
1. How specific is the legume in its rhizobial requirements?
2. What is the likelihood of effective rhizobia spreading from volunteer legumes?
3. Has the legume been sown previously and for how long was it grown continuously?
4. How long since the legume was last grown and, in the meantime, did conditions favour persistence of the rhizobia?
Thies et al. (1991b) — queries relating to soil indices
1. How large is the resident population of competitive rhizobia?
2. What is the level of soil nitrogen?

Source: after Brockwell et al. (1995a).

represents an environment akin to pure culture and, within it, there is great multiplication of the rhizobia. When, subsequently, nodule breakdown takes place, large numbers of viable cells are released into the soil (e.g. Reyes and Schmidt 1979; Kuykendall et al. 1982; Moawad et al. 1984; Thies et al. 1995) where they constitute a potent source of infection for new roots and may become a permanent component of the soil microflora even in the presence of competing organisms.

The total area of land worldwide under acacia plantations exceeds 5 million hectares. It is probable that most of these trees were outplanted as nursery tube stock. This practice can be exploited for inoculation. Acacias can be inoculated at the time of sowing in the nursery in a way that ensures that the seedling trees are vigorous, well-nodulated and fixing N at the time of outplanting into the field. This has been demonstrated at nurseries in Australia (Brockwell et al. 1999a). When nursery-inoculated seedlings were outplanted, their survival, growth and benefit to companion plantings of *Eucalyptus nitens* (shining gum) was better than that of uninoculated seedlings (Table 11).

Wherever restoration of native vegetation and re-establishment of tree cover over large areas

Table 11. Effect of inoculation by soil enrichment on growth of *Acacia mearnsii* in nursery and field. (N fixed calculated using natural abundance of ^{15}N with *Eucalyptus nitens* as the non-N-fixing reference plant)

	A. mearnsii		LSD (P=0.05) (n.s. — P>0.05)
	Inoculated	Uninoculated	
Nursery			
Seedlings nodulated (%) — day 126	100.0	35.0	33.0
Seedlings nodulated (%) — day 231	100.0	70.0	n.s.
Nodule score (0-5) — day 126	4.00	0.60	0.82
Nodule score (0-5) — day 231	3.00	0.95	0.73
Shoot DM (g/plant) — day 231	1.78	1.27	n.s.
Shoot DM (mg/plant) — day 231	35.7	26.4	14.6
Shoot N fixed (%) — day 126	68.3	44.4	5.9
Shoot N fixed (%) — day 231	88.3	25.3	11.8
Shoot N fixed[a] (mg/plant) — day 126	31.6	7.8	12.3
Field[a]			
Survival (%) — day 231 to day 280	96.3	90.7	4.6
Survival (%) — day 280 to day 553	98.1	91.4	3.4
Tree height (cm) — day 280	28.3	21.2	1.2
Tree height (m) — day 553	2.03	1.82	0.9

Source: after Brockwell et al. (1999a).

[a] Seedling trees outplanted into the field after 231 days in the nursery.

are major conservation issues, as in some parts of Australia, the use of tube stock becomes impracticable. Where acacias (or other leguminous trees or shrubs) are appropriate for such circumstances, it may be a more practical sowing strategy to use direct drilling or aerial seeding (Thrall et al. 2001a,b). As part of the methodology, it would be necessary to incorporate rhizobial inoculant in a seed pellet (e.g. Brockwell 1962) or to deliver the inoculant in granular form (e.g. Scudder 1975) into the seed furrow close to the seed. It is suggested that direct drilling or aerial seeding approaches using multi-strain inocula (see below) incorporated in seed pellets should be adopted as a general strategy for revegetation of degraded landscapes with shrubby legumes in Australia and, perhaps, other parts of the world where native forest has been removed. Used in conjunction with the replanting of *Eucalyptus* and/or other non-leguminous species, the benefits are likely to be enhanced. Overall, the development of practical approaches and uncomplicated techniques suitable for large-scale, low-cost establishment of native legumes is likely to lead to more efficient revegetation and soil management by landholders, and greater incentive to invest in reclamation projects due to affordable costs and higher survival rates of the sown species.

The paucity of literature relating to field inoculation of acacias indicates that most plantings rely on spontaneous nodulation from naturalised populations of rhizobia. Clearly, acacia symbioses with effective rhizobia are not properly exploited. Indeed, at the time of writing, we are unaware of any inoculant manufacturer anywhere in the world who produces (except by special request) rhizobial cultures for *Acacia* species. Until that situation is rectified, this important natural, renewable resource will remain under-exploited. Inoculant preparation involves only a few, simple, well-established steps.

INOCULANTS

The principles of inoculant production are well documented — e.g. Burton (1982); Thompson (1983); Somasegaran and Hoben (1994); other work cited by Brockwell et al. (1995a). The selection of carrier material is a critical determinant of inoculant quality. Finely ground peat (Thompson 1980) has been the inoculant carrier of popular choice for many years, though there are other promising carriers (Brockwell and Bottomley 1995). Roughley and Vincent (1967) and Date and Roughley (1977) record that inoculants prepared with sterile peat contain 100-fold more rhizobia than those made with non-sterile peat. Moreover, because mortality of rhizobia is greater in unsterilised peat, the difference increases during storage.

Strain selection

Some principles of matching acacia species and acacia rhizobia have been catalogued by Brockwell (1998). A list of characters considered desirable for rhizobial strains for legume inoculants is shown in Table 12. It is obviously not feasible to test strains for all of these characters. Naturally, the ability to form nodules and fix N on the target legume are the essential characteristics. Methods for testing for strain effectiveness for legumes in general have been described by, amongst others, Vincent

(1970), Gibson (1980) and Somasegaran and Hoben (1994). Methods adapted or specifically designed for acacias have been used by Thompson et al. (1984), Umali-Garcia et al. (1988), Galiana et al. (1990) and Burdon et al. (1999). Using such methods, Brockwell et al. (1999b) and Dippel et al. (1999) made recommendations for inoculant strains for a range of acacias to be raised in plant nurseries and destined for plantation and farm forestry. Martin-Laurent et al. (1997) demonstrated that aeroponic culture led to abundant nodulation of inoculated *A. mangium*. The method lends itself to studies of infection processes and nodule morphology and, if it can be adapted, to selection of effective rhizobial strains.

As noted earlier, there are all degrees of host/rhizobial specificity in the acacia symbiosis. However, a pragmatic approach to strain selection is essential for production of acacia inoculants because it would not be feasible to have a special inoculant for every different acacia. With respect to the N-fixing potential of any particular acacia/inoculant strain combination, we advocate the principle of seeking the best result possible rather than the best possible result. The findings of Burdon et al. (1999) and Thrall et al. (2000) give some encouragement. In studies of symbiotic associations between temperate Australian acacias and populations of native rhizobia, they found a general lack of host/rhizobia interaction effects (with notable exceptions) and concluded that, where no rhizobial strain for a particular host species is available, strains from its closest relative will have the highest probability of success in N fixation.

Table 12. Characters considered desirable for inoculant strains and inoculant carriers

Strain characters for legume inoculants	
1.	Ability to form nodules and fix N on the target legume
2.	A wide host range, i.e. the ability to fix N with a wide range of host genotypes
3.	Ability to fix N across a wide range of environmental conditions
4.	Ability to compete in nodule formation with populations of rhizobia already present in the soil
5.	Ability to form nodules and fix N in the presence of soil nitrate
6.	Ability to grow well in artificial media, in inoculant carrier and in the soil
7.	Low mortality on inoculated seed
8.	Ability to migrate from the initial site of inoculation
9.	Ability to tolerate environmental stress
10.	Ability to colonise the rhizosphere of the host plant
11.	Ability to colonise the soil in the absence of a legume host
12.	Genetic stability
13.	Compatibility with agrichemicals
Properties of good inoculant carriers	
1.	High water-holding capacity
2.	Non-toxic to rhizobia
3.	Easy to sterilise by autoclaving or gamma irradiation
4.	Readily and inexpensively available
5.	Sufficiently adhesive for effective application to seed
6.	Good pH buffering capacity
7.	Good cation- and anion-exchange capacities

Source: Thompson (1980), Keyser et al. (1992), Brockwell and Bottomley (1995), G. Bullard (pers. comm.)

There appears to be scope for selecting strains that are adapted to harsh conditions. For instance, Surange et al. (1997) identified acacia rhizobia that were tolerant of high salt concentrations and high alkalinity, and Kang et al. (1998) acid-tolerant strains.

Inoculant production

There is a profuse literature on all aspects of large- and small-scale preparation of legume inoculant. The major papers on the principles and practice include Vincent (1970), Burton (1976, 1979, 1982), Brockwell (1977), Date and Roughley (1977), Thompson (1980, 1983), Williams (1984), Somasegaran (1985, 1991), Diem et al. (1989), Keyser et al. (1992), Smith (1992) and Somasegaran and Hoben (1994).

The first step in inoculant preparation is the production of a broth with, desirably, a population density of at least one billion (1×10^9) viable rhizobial cells per mL. The broth is grown in a fermenter which can be a very simple piece of equipment (Date and Roughley 1977). The broth is then incorporated in finely ground peat which preferably has been sterilised by gamma-irradiation (Roughley and Vincent 1967) or autoclaving. Finally, the peat culture is packaged and sealed into polyethylene bags of convenient size, 'matured' at 25°C for 14 days and stored, usually at about 4°C, until it is needed. The demand for acacia inoculant is likely to be met by small fermenters. Balatti (1982), Hoben and Somasegaran (1992) and Somasegaran et al. (1992) provide specifications for small fermenters, any of which would be suitable for the production of high-titre broths of strains of acacia rhizobia.

When commercial manufacture of legume inoculants began in the 1890s, liquid (broth) culture was the preferred form. Nowadays, the vast majority of inoculants are prepared in powdered organic carriers such as finely ground peat. Nevertheless, it is feasible to manufacture and market high-quality liquid inoculant (Lie et al. 1992; Brockwell et al. 1995a). Indeed, in their experiments described earlier, Galiana et al. (1994, 1996, 1998) used liquid inoculum for nursery-grown acacia seedlings that were then outplanted. Existing inoculants of highest quality tend to be those produced by small factories under the umbrella of a quality control authority, such as those described by Roughley and Pulsford (1982), Thompson (1983) and Somasegaran (1991). The NifTAL Center and MIRCEN in Hawaii have developed a 'micro-production unit' for small-scale production of rhizobial inoculants (NifTAL Center 1993). There are two key concepts: (i) use of a sterile peat carrier (cf. Date and Roughley 1977) and (ii) dilution of the rhizobial broth culture with sterile water (Somasegaran and Halliday 1982; Somasegaran 1985) immediately before it is injected into the sealed bag of peat carrier. The unit has a number of advantages over conventional (larger-scale) methods for producing legume inoculants. First, the unit is cheap and easy to assemble. Second, the number and size of fermentors used for propagating broth cultures of the rhizobia are reduced by using the dilution technique. Third, production schedules are very flexible. Fourth, because the unit uses sterile peat as a carrier, populations of rhizobia in the inoculant may be 10 times greater than in the many commercial inoculants manufactured from non-sterile carriers (cf. Roughley and Vincent 1967; Brockwell 2004).

Fifth, the use of sterile peat increases shelf-life over that of products made with non-sterile carriers. Sixth, the unit requires little space. Last, quality-control procedures are simple and reliable. NifTAL's micro-production unit appears ideal for preparing the relatively small quantities needed to meet the likely demand for acacia inoculants.

Multi-strain inoculants

The current practice in Australia is to use a single effective strain of rhizobia in commercial legume inoculants (Roughley et al. 1984). Species-specific strains have been advocated for use in inoculants for certain *Acacia* species, e.g. *A. mearnsii* (Turk and Keyser 1992). The use of single-strain inoculants facilitates quality control (Thompson 1980), but has the major disadvantage of restricting the scope (host range) of any particular inoculant. It is common practice in most other countries to produce multi-strain inoculants. Somasegaran and Bohlool (1990) made an extensive comparison of multi- and single-strain inoculants. They found that, in almost all cases, the N-fixing effectiveness of a multi-strain inoculant exceeded or equalled the performance of the best strain in that inoculant. We therefore consider that use of multi-strain inoculants is essential to achieve successful nodulation and N fixation in acacias whenever it is proposed to use the one inoculant for more than one species.

Inoculation strategy

Although classified as free-living organisms with saprophytic properties (e.g. Chatel et al. 1968), rhizobia are very much obligated to their hosts. Virtually all rhizobial multiplication in the wild takes place in the host rhizospheres, on the root surfaces and especially within the nodules. When an inoculant culture is applied to the seed surface or introduced into a seed bed or a nursery soil tube, the rhizobia start to die. The mortality continues until the development of a seedling rhizosphere that can be colonised by the surviving rhizobia. Initial procedures should therefore aim (i) to maximise survival of the inoculant during the non-rhizosphere period, and/or (ii) to accelerate germination so that the non-rhizosphere period is reduced. Figure 3 illustrates the principles involved.

For inoculation of acacias, the principles are easily implemented. Currently, most acacia plantings in the field are made using nursery stock raised in tubes of soil. Inoculant can be incorporated into the nursery soil immediately before planting the acacia seed. This general procedure was described in each of three reports of field benefits of inoculation: Lal and Khanna (1996) used seed inoculation, Galiana et al. (1994) applied liquid inoculum to the nursery soil, and Brockwell et al. (1999a) mixed peat culture into the soil. We believe that the last procedure, termed inoculation by soil enrichment, best meets the demands of the principles illustrated in Figure 3. Higher rates of inoculation can be achieved by incorporating an inoculant into the soil than by applying it to the seed surface, and experience has shown that peat-based inocula tend to survive better in soil and in the field than do liquid inocula (e.g. Brockwell 1962).

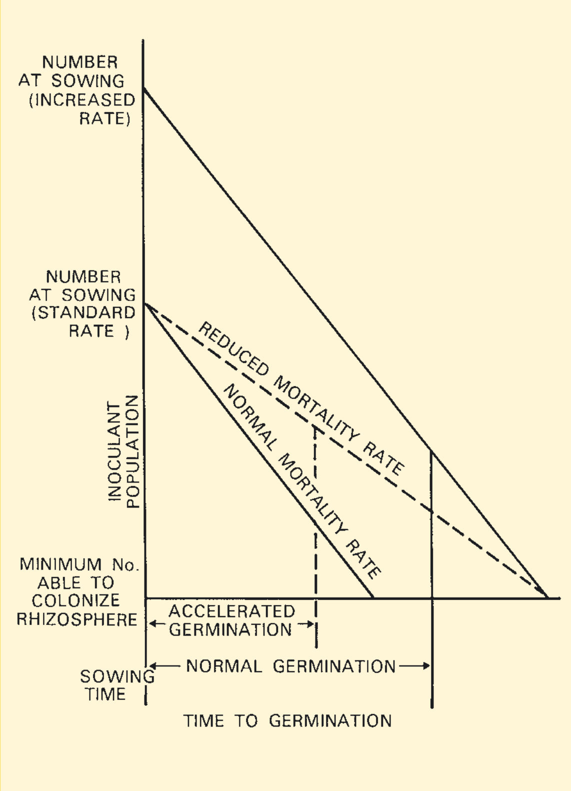


Figure 3. A schematic illustration of basic factors involved in improving the likelihood of legume nodulation following rhizobial inoculation: (i) reducing inoculant mortality, (ii) increasing rate of inoculant application, (iii) decreasing time to germination (after Brockwell 1962).

Accelerated germination of acacia seed can be effected by a pre-treatment of immersing the seeds in near-boiling water for a short time and then allowing them to imbibe the water as it cools. Indeed, some operators actually boil their acacia seed for one minute. (Strictly speaking, with most acacia seed, the pre-treatment does more than merely accelerate germination; it triggers processes that stimulate germination.) Naturally, rhizobial enrichment of the soil should be done immediately before planting the seed. To avoid death of the inoculant from desiccation and/or heat stress, the soil should, after planting, be kept moist and as cool as practicable by the use of a misting device. It is pertinent that Gassama-Dia (1997), using delayed inoculation experiments, demonstrated that the period of maximum infectibility of *A. albida* inoculated with *Bradyrhizobium* was the 13 days immediately after seed germination.

A particular advantage of soil enrichment inoculation is that it lends itself to the preparation and use of inoculant strains selected for special purposes, e.g. tolerance of salinity, acidity, alkalinity and other forms of environmental stress.

There will be situations, as in large-scale land rehabilitation (cf. Thrall et al. 2001a,b), prevention of dryland salinisation and generation of carbon, conservation and biodiversity credits, when it is desirable to establish acacias by direct seeding. Alternative means of inoculation would be required in such circumstances. In studies of rhizobial survival following aerial seeding, Hely (1965) demonstrated that inoculation and seed coating produced vigorous swards of well-nodulated, N-fixing crimson clover (*Trifolium incarnatum*). It might be possible to develop a similar procedure for acacias.

BREEDING AND SELECTION FOR ENHANCED ACACIA SYMBIOSIS

Because acacias are essentially non-domesticated plants, there must be some scope for breeding and selecting certain species for increased capacity to nodulate and fix N. We do not know, however, whether the sort of classical procedures outlined by Sprent (1994c) for an annual crop plant such as groundnut (*Arachis hypogaea*) would be applicable to perennial tree and shrub species such as acacias. On the other hand, the simple, long-standing techniques for selecting for improved symbiosis in poorly domesticated forage plants that have been described by Hutton and Coote (1972) for greenleaf desmodium (*Desmodium intortum*) and by Zorin et al. (1976) for Caucasian clover (*Trifolium ambiguum*) might have application to acacias.

Acacia genistifolia

6. Exploitation of the symbiosis

We have already pointed out that acacias are quite capable of existing in the absence of an effective symbiosis. There is no pretending that the quality of some acacia products, such as perfume oils and oyster poles, is influenced in any way by N fixation. However, sometimes it is difficult to separate cause and effect. In Australia, *A. harpophylla* is almost always associated with soils of high N status (Graham et al. 1981), but it is not possible to know with certainty whether the soil is high in N due to the presence of the acacia or if the acacia needs fertile soil to grow. Notwithstanding, there is no doubt that there are also many circumstances where the N fixed by acacias represents a valuable commodity.

NATURAL EXPLOITATION

African peoples have long recognised that the extensively distributed, widely adapted indigenous leguminous tree, *A. albida*, confers special benefits on its immediate environment and, therefore, has a significant place in agricultural practice (Felker 1978; Giller and Wilson 1991; Saka et al. 1994). *Acacia tortilis* has similar status in the dry savannas of East Africa (Giller and Wilson 1991). These trees grow in the dry season and shed their leaves in the rainy season. A traditional farming practice in many African countries is the maintenance of parklands of large *A. albida* trees, and to a lesser extent *A. tortilis*, in cultivated fields. Because the trees are deciduous in the rainy season, they do not compete for light with crop plants grown beneath them (cf. Giller and Wilson 1991). Also, *A. albida* may add substantial N to the soil as a result of the leaf fall that occurs at about the time that cash crops are sown. Indeed, in the Sahel, continuous dry-season cropping with sorghums and millets has been practised beneath *A. albida* without reductions in yields or additions of fertilisers (Porteres 1954). Yields of groundnut (*Arachis hypogea*) and cereals are often much higher under *A. albida* trees than in open fields (e.g. Charreau and Vidal 1965; Radwanski and Wickens 1967; Dancette and Poulain 1969; Charreau and Nicou 1971; Felker 1978; Poschen 1986). Moreover, the litter of *A. albida* and *A. tortilis* improves the soil environment by contributing to retention of soil moisture through an increase in soil organic matter, improving soil structure, enhancing populations of soil microfauna, and reducing extremes of evapotranspiration and soil temperature (e.g Dancette and Poulain 1969; Bernhard-Reversat 1982; Young 1989). In addition to the N added to the soil as a result of leaf and pod fall, there may well be further supplementation of soil N through underground release of N in disintegrating, decaying roots and nodules. Much of all this is a consequence of the ability of *A. albida* and *A. tortilis* to fix atmospheric N (see Table 4) although the trees might also have the capacity to access deep-soil N and N in groundwater. Additionally, both trees provide an abundance of fodder and fuelwood throughout the year and deep shade in the dry season (e.g. Bunderson et al. 1990). *Acacia albida* may be the Earth's most comprehensively utilised plant species and represents a classic example of natural exploitation of the legume symbiosis.

In both forest and savanna ecosystems, trees substantially influence the chemical and physical characteristics of the soil system through a variety of mechanisms, e.g. deposits of litter, the activity of soil macro- and microflora involved in litter decomposition, and redistribution and accumulation of soil nutrients through the scavenging and conduit properties of extensive root systems (Rhoades 1997). N-fixing trees make an additional, special contribution of N to the ecosystem and, consequently, other things being equal, represent a preferred form of vegetation in agroforestry. An apt example is the contribution made by *Acacia* species as natural understorey components of *Eucalyptus* forest ecosystems in Australia (Adams and Attiwill 1984; Hansen and Pate 1987a,b).

GENERAL EXPLOITATION

There are many examples of successful exploitation of the genus *Acacia*, and its symbiosis with root-nodule bacteria. The endemic Hawaiian legume, *A. koa*, produces substantial biomass and fixes abundant N (Pearson and Vitousek 1997). Scowcroft and Jeffrey (1999) considered that *A. koa* has potential as a nurse crop to create understorey conditions for the re-establishment of other components of Hawaiian highland forests cleared 150 years ago for pastoral use. The present rhizobial status of the soil, and therefore the need to inoculate the *A. koa*, is not known.

Acacias are used for rehabilitation of land damaged by industrial waste (e.g. Zhang et al. 1998), mining activities (e.g. Langkamp et al. 1979; Franco and de Faria 1997) and landfill (e.g. Chan et al. 1998), and for other forms of land reclamation (e.g. Kirmse and Norton 1984; Assefa and Kleiner 1998) including stabilisation of roadsides (e.g. Searle 1997). The genus has great scope for reclaiming saline land (Turnbull et al. 1998b). Coconut (*Cucos nucifera*) responded to interplanting with *A. auriculiformis* by increasing its total root biomass (Arachchi and Liyanage 1998). There is scope for using acacias to revegetate and rehabilitate degraded landscapes, such as the *Imperata* grasslands in Southeast Asia (Turnbull et al. 1998b), the Chilean secano interior (Arredondo et al. 1998), and the Atlantic lowlands of Costa Rica (Tilki and Fisher 1998). Temperate and tropical species of *Acacia* from Australia are suitable for many of these purposes.

INTERCROPPING

Intercropping of a legume with a non-legume often increases significantly the amount of symbiotic N fixed by the legume and the total amount of N uptake by the joint components of the system — e.g. rice bean (*Vigna umbellata*)/maize (*Zea mays*) (Rerkasem et al. 1988); soybean (*Glycine max*)/maize (Martin et al. 1991); French bean (*Phaseolus vulgaris*)/maize (Pineda et al. 1994). It seems likely that, at least partly, the uptake of soil N by the non-legume reduces the amount of soil N available to the legume, thereby 'forcing' it to fix more atmospheric N in order to fulfil its requirement for N. In some circumstances, however, intercropping might suppress legume yield when both plants compete for the same limited resources (e.g. Hakim et al. 1991).

Intercropping has been successfully applied to forestry. Turvey et al. (1983) reported that planted pine trees benefitted from an association with naturally regenerated *Acacia* species. The extent of the response was related to the density of the acacias. In experiments in plantations in Southeast Asia and Australia, Khanna (1997, 1998) grew mixed stands of fast-growing species of (tropical and temperate, respectively) *Acacia* and *Eucalyptus*. The *Acacia* species were actively fixing N. Their presence led to incremental growth in the *Eucalyptus* species (Table 13; Figure 4) which was attributed to enhanced N status. A similar effect has been obtained with *A. mearnsii* and *Eucalyptus nitens* (shining gum) in south-eastern New South Wales (J. Brockwell, P.A. Mitchell and S.D. Searle, unpublished data).

Khanna (1998) postulated that the improvement was brought about by underground transfer of N from the *Acacia* to the *Eucalyptus*. He ruled out the possibility of above-ground transfer in his experiments because, at the time of increased *Eucalyptus* growth, decomposition of litter on the soil surface was trivial and had contributed little or nothing to the N dynamics of the system. The literature is equivocal on the question of underground transfer of legume N to associated non-legumes. There are arguments for — e.g. work and citations by Ofiri and Stern (1987); Viera-Vargas et al. (1995) — and against — papers cited by Peoples and Craswell (1992).

Table 13. Mean tree basal area (cm^2/tree) in pure and mixed stands of *Eucalyptus globulus* and *Acacia mearnsii* grown at two densities for 45 months at Cann River, Victoria, Australia

Tree density (ratio)		**Total tree density**			
Eucalyptus	***Acacia***	**1000/ha**		**1500/ha**	
		Eucalyptus	***Acacia***	***Eucalyptus***	***Acacia***
100	0	9.1 b*	–	13.0 c	–
75	25	11.4 ab	41.4 a	15.9 ab	49.1 a
50	50	14.1 a	29.3 b	18.2 a	42.5 b
25	75	14.3 a	24.3 cd	17.3 a	36.5 c
0	100	–	19.8 d	–	25.2 d

Source: after P.K. Khanna, unpublished data.

* In any one column, values with a common letter are not significantly different from one another ($P>0.05$).

Khanna's (1997, 1998) evidence for underground transfer of *Acacia* N to *Eucalyptus* is most convincing. In further studies involving fine-root architecture, researchers in Khanna's laboratory (Bauhus et al. 2000) found 'high' concentrations of N in the fine roots of *Eucalyptus globulus* (blue gum) when it was grown in a 50:50 mixture with *A. mearnsii*. This was another indication that the improvement in the N nutrition of the eucalypts was a consequence of association with acacias.

It is interesting to speculate just how such transfers might occur. While trees are capable of using both nitrate and ammonium for growth (Devisser and Keltjens 1993; Turnbull et al. 1995), it seems unlikely that these products, released from the

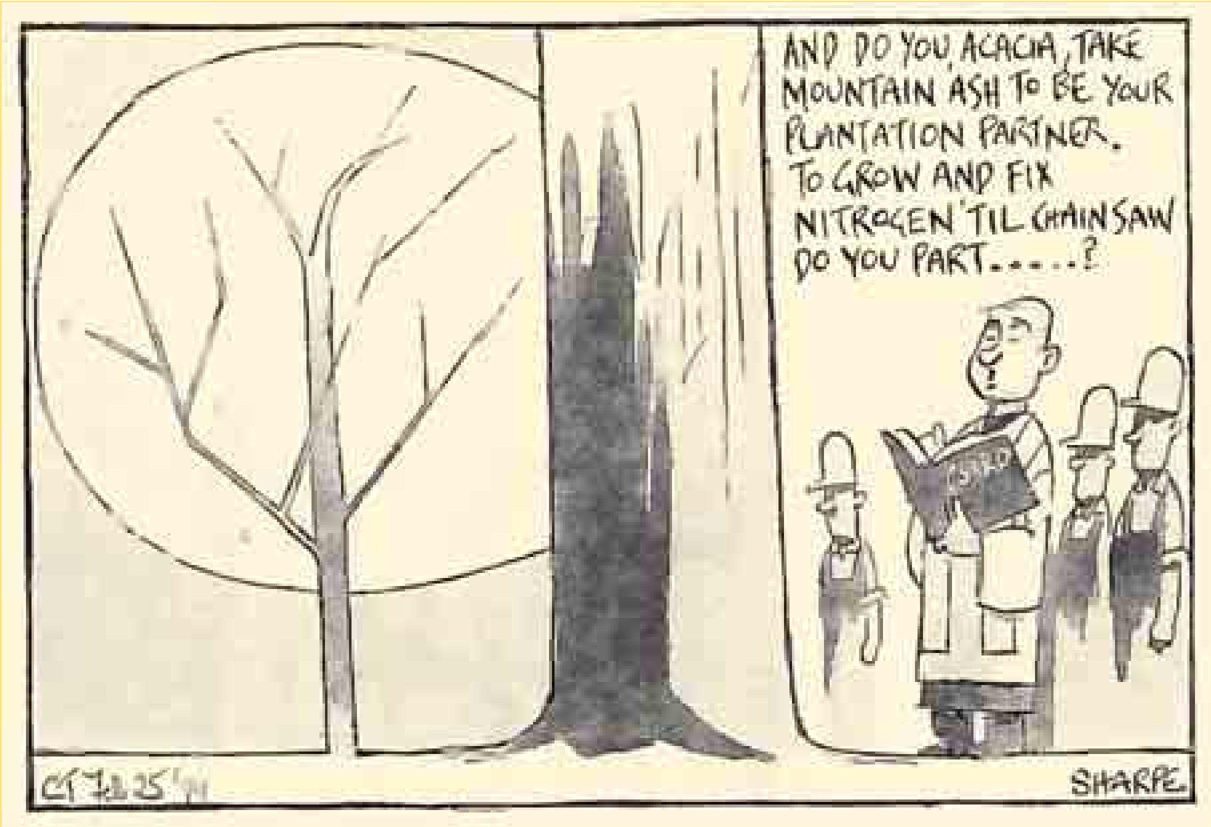


Figure 4. Cartoon about the benefits of interplanting *Eucalyptus* and *Acacia* species (with acknowledgment to *The Canberra Times*)

organic N in root and nodule debris by classical nitrification processes, would have been available for underground transfer — for the same reasons that above-ground decomposition of litter was negligible. We favour a hypothesis centred on mycorrhizal activity. Extensive, diverse populations of mycorrhiza are extremely common in forest ecosystems. Although Khanna (1997, 1998) did not say so, there is the strong likelihood that his eucalypts were mycorrhizal. Mycorrhizal plants access N as free amino acids and, as well, are able to absorb N from proteins and chitins; see several references cited by Boddey et al. (2000b). These latter sources of N also are probably absorbed in the form of amino acid which has been made available by hydrolysis by mycorrhizal proteinases, chitinases and other enzymes (cf. Leake and Read 1989, 1990).

We submit that, in forest ecosystems, underground transfer of N from N-fixing trees to non-leguminous trees is mediated by mycorrhizal pathways. This process seems more likely to be of particular significance early in the development of the ecosystem before other processes of N dynamics become fully active.

LAND RECLAMATION: PRINCIPLES AND PRACTICE — THE AUSTRALIAN EXPERIENCE

This section is based largely on recent, mainly unpublished experiences of Alison Jeavons and Meigan Waayers and colleagues in the North Central Catchment Management Authority and the Department of Primary Industries, Victoria. The observations have emerged from a series of case studies and, taken altogether, represent the conventional wisdom on the use of *Acacia* species in land reclamation in southern Australia.

General principles

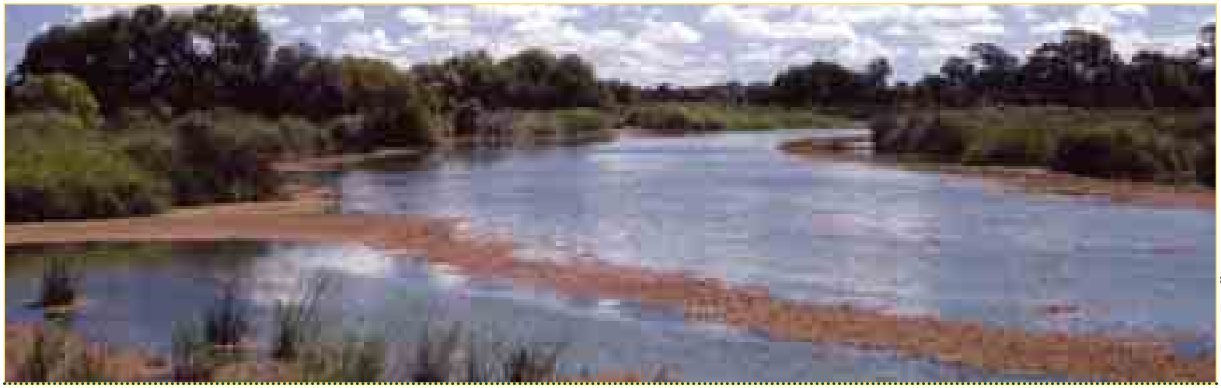
Most undisturbed or lightly disturbed Australian landscapes, from the tropics and warm and cool temperate zones to the arid regions, encompassing rainforest, woodlands and pastoral country, have acacias as a component of their understoreys or, somewhat less frequently, as dominant species. It follows, therefore, that acacias are widely considered as suitable species for revegetation of lands that have become degraded due to inappropriate land use, salinity, erosion, waterlogging and other factors leading to loss of biodiversity. It follows also that, because of the wide diversity and distribution of the genus, there is almost invariably one or more *Acacia* species appropriate for any particular revegetation situation, with the possible exception of highly saline soils.

Acacia planting has been recognised as an effective tool for erosion control since the early 1960s because, in general, acacias can be readily established on degraded land. At that time, the choice of species was most often determined merely by seed availability, readiness of germination and tolerance of adverse environmental conditions, with little concern for other principles of acclimation. An unfortunate consequence was that some of the most easily established, vigorous species, e.g. *A. baileyana* and *A. longifolia*, became serious weeds outside their natural range. Nowadays, revegetation practitioners try to establish as many species as practicable, with special emphasis on the use of local species and provenances of species, especially in undertakings directed at restoration of biodiversity. What precisely should be regarded as 'local' is hotly debated. There is a vocal body of opinion that specifies that seed should be sourced no more than 5 km from the intended point of revegetation. A much less restrictive definition is that any species is suitable for revegetation provided that it is not grown outside its natural range and that its seed is obtained from sites with the same soil type as the revegetation site and with similar rainfall. Research on these and related matters is currently in progress (A.G. Young, pers. comm.).

General practice

There are two distinct methods of establishing acacias in revegetation undertakings: outplanting tube stock and direct seeding. Each has its advantages and disadvantages, summarised in Table 14. The major difference between the methods relates to practicality. Outplanting tube stock grown in a nursery into the field is convenient and ideal for a small number of seedlings. Indeed, outplanting is the preferred option for getting greatest value from limited seed supplies. However, once the area to be sown exceeds 2–3 hectares, economies of scale favour direct seeding.[4] To give a general example, the North Central Native Vegetation Plan of the North Central Catchment Management Authority estimates that approximately 12,000 hectares of revegetation needs to be undertaken every year for the next 20 years in order to reverse the regional decline in biodiversity. Outplanting is clearly not feasible for so vast an undertaking. A more specific example relates to a revegetation project for salinity control carried out on the Big Hill range south of Bendigo, Victoria. This project saw the establishment of about one million trees and shrubs across nearly 1000 hectares of high recharge hills.

[4] Custom-built equipment for direct seeding has been described by Dalton (1990) and Scheltema (1992).



Peter Thrall

The retention of vegetation, including species of *Acacia*, *Eucalyptus* and *Allocasuarina*, preserves the integrity of streamlines.

The bulk of the work was carried out through direct seeding, for two months in each of two years, and involved three or four people. The cost of labour and materials was less than $100,000. Had the project been attempted by outplanting nursery-grown tube stock, it would have required the services of 65 people for five days each week for four months, and the total cost would have exceeded $2,000,000.

Couretsy of the Australian National Botanic Gardens

The banks of this ephemeral watercourse have been seriously eroded following removal of vegetation. Further erosion can be readily contained by revegetating with surface-sown native species including acacias.

Alsion Jeavons

Three-year-old roadside revegetation with acacias established by direct seeding

Peter Thrall

This creek side, near St Arnaud, Victoria, was at risk because understorey shrubs had disappeared. It has recently been revegetated by surface-sowing with native species, including acacias inoculated with effective strains of root-nodule bacteria.

Table 14. Comparison of the advantages and disadvantages of (i) direct seeding and (ii) outplanting of nursery-grown tube stock as means for establishment of acacias and other Australian native trees and shrubs to reclaim degraded land

	Direct seeding	Outplanting of nursery-grown tube stock
Advantages	Substantially lower costs than for other methods of planting	Time tested for reliable results
	High densities of established plants are attainable	Technology is well known and accepted
	Random plant distribution is attainable where a natural 'look' is required	Appropriate where there is a need for fixed plant density, uniform spacing or a particular species in a particular place
	Mature plants are more wind stable — because root systems have never been disturbed	Always slightly ahead in early growth compared with direct seeding; therefore useful when a quick effect is needed
	When using a wide range of species, savings on propagation and planting far outweigh costs of additional seed	Supplements direct seeding where gaps occur in the plant stand

	Direct seeding	Outplanting of nursery-grown tube stock
Disadvantages	Low rainfall, seasonal variation, erodable or heavy clay soil, insect predation and weed competition are all more critical for direct seeding than for outplanting	Considerably higher costs and much more labour intensive, especially on a broad scale, than for direct seeding
	Sometimes seedling establishment is patchy and gaps need filling	Only feasible for small-scale projects (probably never exceeding 5 ha)
	Greater quantities of seed required than for nursery-grown seedlings	
	Limited to species that germinate readily from (treated) seed	

Source: derived from Dalton (1990).

Courtesy of the Australian National Botanic Gardens

The integrity of this erosion-prone hillside on the Eyre Peninsula, South Australia, has been preserved by a stand of *Acacia pycnantha* (golden wattle).

Peter Thrall

The use of a knockdown herbicide allows surface-seeded acacias to establish without competition from weeds.

Bob Gault

Germination of acacia seed sown into the field by direct seeding is enhanced by application of smoked water into the seed furrow. This picture, showing seed and water delivered on to a concrete surface, is a simulation of the procedure.

John Brockwell

Using direct seeding to establish salt-tolerant acacias on salinity-endangered land at Bald Rock, Victoria. The seeder shown here is a modification of the one described by Dalton (1990).

General considerations

Availability of acacia seed

A significant constraint to the success of direct seeding is seed availability. As a rule, acacia seed is easily collected from the wild. However, with many species, the quantities of seed required for direct seeding of degraded land (up to 0.5 kg per hectare) often greatly outstrip the amounts available from good quality remnant stands without drastic depletion of resources necessary for sustaining populations of wildlife, especially birds. This is a particular problem in those circumstances where local provenances are considered essential for effective revegetation. As an example, the North Central Catchment Management Authority has a requirement for its revegetation program of 6000 kg acacia seed per year. Although the Authority has an exceptionally good group of seed collectors, they manage to collect only about 500 kg seed per year from within the catchment. The mining industry also has a large demand for seed for restoration of mine sites where seeding rates may be up to 35 kg per hectare. All this is reflected in the cost of commercially available acacia seed — $120–$510 per kg (Australian Seed Company 2003). Certain Australian organisations with responsibility for land reclamation are now tackling these problems through extension and training programs, one result being the establishment in recent years of a number of acacia seed orchards.

Seed germination

Acacia seed usually has high viability but is notoriously hard-seeded. Under natural conditions, except following exposure to fire, it tends to germinate slowly, intermittently and over a long period. Often only 10–40% of viable seed establishes beyond the seedling stage (Dalton 1990). Effective establishment, for both direct seeding and tube stock, requires seed treatment to enhance germinability. Immersion in boiling water (the seed imbibes while the water is cooling) and mechanical scarification are efficient means for dealing with the problem of hard seed. The use of smoked water, either as a supplementary seed treatment or delivered directly into the seedbed alongside the seed, further enhances germination. A butenolide has been identified as the compound in smoked water that stimulates seed germination (Flematti et al. 2004).

Miscellaneous constraints to acacia seedling establishment

Naturally, seedling establishment of direct-seeded acacias is best under good seasonal conditions. Nonetheless, good results have sometimes been achieved during drought.

Even with good germination following seed treatment, early growth of direct-seeded acacias is relatively slow and its continued success is dependent on effective control of first-year competition from annual weeds. It is standard practice to seed directly into a furrow placed centrally along a strip of land from which weeds have been eliminated with a knock-down herbicide. In addition to their competitive effect, some annual weeds harbour insect pests, e.g. red-legged earth mite *Halotydeus destructor* (Tuck.) (Acarina:

Eurodidae) on capeweed (*Arctotheca calendula*), which feed on acacia seedlings.

Herbivores, in particular rabbits, are partial to acacia seedlings. Wherever large rabbit populations exist in the vicinity of revegetation sites they must be controlled .

The role of the acacia symbiosis in land reclamation

Many reclamation projects involving acacias are aimed at degraded land that once carried acacias as an understorey component or sometimes as the dominant species. The soils of such land, almost certainly once contained populations of acacia rhizobia which nodulated and fixed N with their hosts. However, with the disappearance of the acacias, it appears that their rhizobia have also been lost from the soil (Thrall et al. 2001b). Restoration of healthy acacia communities therefore involves the reintroduction of effective rhizobia as well as the acacias themselves. Recent research work (Thrall et al. 2005) has shown that rhizobial inoculation (by seed coating) of direct-seeded acacias more than doubles their establishment rate and often significantly increases seedling growth rates.

An immediate consequence of these findings on seedling establishment is that it becomes possible to reduce direct seeding rates by at least half, reducing costs and the demand for seed. Moreover, increased early growth may well assist acacia seedlings to outrun first-year competition from weeds. This is an especially important consideration in revegetating riparian zones which, in Australia, are among the most endangered ecosystems. A further benefit of rapid early growth is that it is likely to make acacia seedlings more tolerant of grazing by macropods (wallabies, kangaroos) and/or feral animals (rabbits, hares).

Application of inoculant to acacia seed by seed coating is a time-consuming process, especially where several seed lots require inoculation, and may constitute a bottleneck at seeding time. A possible alternative is a free-flowing granular inoculant (cf. Scudder 1975; Brockwell et al. 1980). This product, applied directly into the seed bed through a hopper attached to the seeding equipment, has been used successfully in the United States for inoculation of soybean and peanut crops (Scudder 1975). A similar device might be useful for direct seeding of acacias.

It seems reasonable to conclude that proper exploitation of the symbiosis might reduce the cost of acacia establishment in revegetation undertakings. Although exact costs are not yet known, it is estimated that a 50% reduction in seed usage, combined with application of granular inoculant directly into the seed bed, would reduce costs by at least 20–25%.

7. General conclusions and prognosis

The body of literature relating to the symbiosis between the genus *Acacia* and its diverse rhizobia that we have reviewed is dispersed in terms of the species investigated, the aspects of the symbiotic relationship studied and the places of publication of results. There appear to be three main reasons for this: first, the genus is so large — some 1350 species; second, it is more difficult to experiment with shrubs and trees than it is with herbs; third, it has been unfashionable until recently to work with N-fixing trees. With respect to the third reason, the publication of newsletters such as *NFT News*: *Improvement and Culture of Nitrogen Fixing Trees* (published by IUFRO and CSIRO Forestry and Forest Products, Canberra) and *Farm Forestry News* (once published by the Forestry/Fuelwood Research and Development (F/FRED) Project, c/o Winrock International: Arlington, VA — publication now ceased) has created forums for exchange of experience, views and ideas and has done much to overcome any resistance that might once have existed against working with N-fixing trees. As the reference list shows, the period since 1990 has seen a proliferation of research and extension papers dealing with aspects of the symbiosis of acacias.

It became clear to us during the review of the literature that the processes of root nodulation and N fixation in the genus *Acacia,* and the procedures for studying them, are generally little different from those of other, more extensively studied legume genera. Accordingly, where there appeared to be no information about particular aspects of acacia symbiosis, we drew upon experience with other N-fixing plants.

THE PLANT

Acacia is one of the largest genera of flowering plants, widely distributed mainly in Australia, Africa and Asia and with a multitude of products extensively utilised by humans and wildlife. The genus is adapted to growth on many types of soil, including those of low fertility, and is tolerant of arid and semi-arid environments. It is a prominent component of many forest ecosystems and, as a N-fixing legume, apparently contributes substantially to natural N cycling. Although millions of hectares of land have been planted with acacias, especially for plantation and farm forestry and rehabilitation of degraded landscapes, many authorities consider that the genus is underutilised. The literature that we surveyed gave us the very strong impression that the symbiosis of acacias with root-nodule bacteria, and their capacity to fix atmospheric N as a consequence of that association, is also underutilised.

THE BACTERIA

The rhizobia that form root nodules on acacias appear to be at least as widely distributed as the plants themselves. Indeed, rhizobia capable of nodulating and fixing N with species of *Acacia* can often be found in soils in which no acacias are growing. Such organisms associate with legumes that are symbiotically related to *Acacia* species. There is a small taxonomic group of *Acacia* that is known to be non-nodulating. Otherwise, reports of failures of nodulation in natural ecosystems should be regarded cautiously. Lack of nodulation is more likely to be due to harsh environmental conditions than to absence of rhizobia from the soil.

There are diverse groups of acacia rhizobia, including fast-growing, slow-growing and very-slow-growing types. Organisms that form nodules on various acacias are certainly represented in at least four of the currently recognised genera of rhizobia. This number may be further expanded as the systematics of the Rhizobaceae becomes clearer.

It is inevitable with such diverse symbionts that host/bacterial relationships should exhibit complex interactions leading to specificity in both bacterium and plant in terms of nodule formation and N fixation. While there are very many strains of rhizobia that are able to nodulate many species of *Acacia*, the symbioses are often ineffective or poorly effective in fixing N. In other words, many but not all *Acacia* species have a requirement for specific rhizobial strains in order to express their capacity to fix atmospheric N. This characteristic has implications for the selection of strains of rhizobia for preparation of acacia inoculants. An important example of an acacia that appears highly specific is *A. mangium*. This species is native to northern Australia and Papua-New Guinea where it apparently nodulates and fixes N with resident strains of rhizobia. Where it has been introduced into the tropics of the northern hemisphere, its N fixation often appears to be impaired by the absence of specific rhizobia.

THE SYMBIOSIS

There are numerous reports of measurements of N fixation by *Acacia* species. Several mensuration procedures were used and the data that emerged are extremely variable — from virtually zero up to 200 kg per hectare per annum. There is no suggestion that the variability was an artifact of method, but some of the differences may have been a consequence of poorly effective or ineffective symbioses. Some of the reports allowed a comparison of the amounts of N fixed by acacias and by other N-fixing trees. Generally, *Acacia* fared poorly compared with genera such as *Calliandria, Gliricidia* and *Leucaena*. An examination of the circumstances revealed that the two data sets were not strictly comparable. Most measurements of acacia N fixation had been made in natural ecosystems whereas the N fixed by other tree legumes had been measured in anthropogenic ecosystems. There is a wealth of literature reporting substantial differences in the N dynamics of the two systems. In natural ecosystems, N cycling takes place at a relatively rapid rate aided by diverse macro- and microflora that decompose leaf litter above ground and root fragments and non-living components of the soil community underground.

The organic N released by these processes is transformed to nitrate by nitrifying organisms. It is well known that nitrate is an inhibitor of legume nodulation and N fixation. Where natural forest has been cleared for agriculture or silviculture, N cycling is much reduced, with lower rates of nitrification and lower levels of soil nitrate. In the circumstances of these anthropogenic ecosystems, it is only to be expected that legume N fixation would be inhibited less than in natural ecosystems. We have concluded from these considerations, and despite the superficial evidence to the contrary, that there is good reason to believe that the intrinsic N-fixing capacity of acacias is just as great as for other tree legumes.

The different elements of naturally occurring populations of acacia rhizobia were extremely variable in their N-fixing effectiveness, even in association with *Acacia* species that grew in the immediate vicinity. Some highly effective strains have been isolated that showed their superiority in glasshouse tests. There were very few reports of strain effectiveness trials in the field. The most compelling of these were the works of Galiana and colleagues (Galiana et al. 1990, 1994, 1996, 1998) in West Africa. They demonstrated impressive growth responses to inoculation of *A. mangium* with effective strains of rhizobia, as well as longevity of the inoculant in the field. The inoculation was performed by sowing seed into nursery soil augmented with rhizobial culture. The seedlings that emerged were well nodulated and continued to fix N when they were outplanted into the field. The procedure was termed inoculation by soil enrichment and has been exploited by others.

EXPLOITATION

Most of the world's acacias grow in forests or woodlands. For reasons of microbial ecological competition with populations of acacia rhizobia already resident in those soils, the chances of successfully and permanently introducing more-effective strains are nil. So there is probably little that can be done to increase the N fixation by acacias in natural ecosystems, except to improve their vigour. It is a rule of thumb (Peoples et al. 1995a, b), perhaps somewhat oversimplified, that the greater a legume's biomass the more N it fixes. Applying this principle, correction of nutrient deficiencies and control of insect pests, for instance, are legitimate means of increasing the vigour of acacias and, therefore, the amount of their atmospheric N fixation. Economic considerations would determine the practicalities of such an approach. There is one circumstance where such a course of action merits consideration. Following timber harvesting or wildfire in ecosystems where they occur, acacias are frequently the primary recolonising species and may be dominant for many months or even several years. Any strategy that might be used at this time to increase their N fixation would be of subsequent benefit to non-N-fixing components of the ecosystem. An appropriate strategy would also assist in the replenishment of the total pool of soil N which occurs when the quantity of N removed as plant (or animal) product is less than the amount of fixed atmospheric N that remains behind in legume residues.

Where acacias are used in plantation and farm forestry, there is a great untapped potential for exploiting the symbiosis. Nearly all plantation and farm trees (and shrubs) are outplanted as nursery stock. When soil enrichment inoculation is applied to nursery soil immediately before seeding, the large population of effective inoculant rhizobia in the root medium leads to prompt nodulation of the young acacia seedlings and early onset of N fixation. Seedlings that have been inoculated reach planting size more quickly than uninoculated seedlings and, therefore, require less time in the nursery. When the vigorous seedlings that result are outplanted into the field, their survival and early growth are better than those of uninoculated seedlings. These advantages may persist for some time and may lead to early closure of canopy and lower maintenance costs. In addition, the effective inoculant strains persist in the soil for several years where they would remain a continuing potent source of inoculant for the infection and nodulation of new roots.

The principles applying to successful inoculation (Figure 3) suggested that peat culture, because it appears to have a rather slower rate of mortality in storage than liquid culture, may be the preferred form of acacia inoculant for use in commercial nurseries. Indeed, peat inoculant is already used in Australian plant nurseries that produce large numbers of acacia seedlings as tube stock (Brockwell et al. 1999a). It was clear, for reasons of host/rhizobia specificity, that a single strain of rhizobia could never be expected to nodulate and fix N with the complete range of *Acacia* species in demand for plantation and farm forestry. Thus, it will be necessary to produce acacia inoculant that comprises several strains that, between them, are effective in N fixation for the range of *Acacia* species raised in nurseries.

This is not a problem in most parts of the world, where manufacture of mixed-strain legume inoculants is very often standard practice. In Australia, however, where there is a policy of single-strain inoculants, it would be necessary to have packets of inoculant containing several individual culture packs and for the user to mix the contents immediately before nursery soil inoculation by soil enrichment. Because demand for acacia inoculant is likely to be quite limited, it might be a problem to find manufacturers willing to produce small quantities of the specialised inoculant. The extent of demand can be illustrated by a simple calculation. At a conservatively sensible rate of soil enrichment inoculation, one kilogram of inoculant is enough for 10,000 acacia seedlings. This in turn is sufficient for 10 hectares of plantation. Thus, the total requirement for a large planting of 1000 hectares is just 100 kg of inoculant. The very low cost of soil enrichment inoculation of nursery-grown acacia tube stock (a fraction of a cent each, which seems a small price to pay for increased vigour, survival and growth of seedlings outplanted into the field), may be a two-edged sword. One means of dealing with the problem would be for nurseries to maintain their own stocks of acacia inoculant. Well-nodulated, N-fixing, diverse species of *Acacia* could be grown together in an 'inoculant' plot, the soil from which could later be used to enrich soil intended for the production of tube stock. Unfortunately for this proposal, some authorities legislate against the use of non-sterile soil in plant nurseries. A rather unsatisfactory solution to the problem suggested by Masutha et al. (1997) was to use only those (few) species of *Acacia* that are sufficiently promiscuous in their requirements for effective rhizobia that they are likely to nodulate vigorously and fix N abundantly with whatever populations of rhizobia occur naturally in soil.

As a result of our literature review, we are convinced that there is considerable potential worldwide and especially in Africa, Asia and Australia to enhance the vigour, N-fixing capacity and productivity of the many *Acacia* species by more fully and efficiently exploiting their symbioses with root-nodule bacteria. Simultaneously, improved symbioses would augment resources of soil N. For many species this will involve inoculation with effective rhizobia. There may also be scope, as suggested by Smith and Daft (1978), for dual inoculation with rhizobia and mycorrhizal fungi to remove other nutritional constraints. Even in circumstances where inoculation is not practicable and/or feasible, the cultivation of acacias has potential to enhance soil fertility and soil structure in plantations, on farms and in land-rehabilitation projects.

Alison Jeavons

Acacia mearnsii

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Appendix

In the text and tables, (i) acacias have been referred to by their botanical names (genus and species) whereas (ii) other plants have been referred to by their botanical names and (where known) their common names. Mostly for acacias and sometimes for other plants, the generic name has been abbreviated to an initial. Table A1 gives the botanical names of all the plants that we have mentioned, with the authorities for those names. The addition of the authority allows the plants to be identified unambiguously. It is customary to italicise botanical names but not authorities. Common names are also given. There is no 'correct' common name for a plant. Where more than one common name is given, the one listed first is merely our own preference.

Table A1. Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Acacias	
Acacia abyssinica Benth	Not known[a]
Acacia acuminata Benth.	Raspberry jam, jam wattle
Acacia alata R. Br.	Winged wattle
Acacia albida Del.[b]	Applering acacia, ana tree, winter thorn
Acacia ampliceps Maslin	Salt wattle
Acacia aneura F. Muell ex Benth.	Mulga
Acacia arabica (Lam.) Willd.[c]	Prickly acacia, babul
Acacia ataxancantha DC.	Not known
Acacia aulacocarpa A. Cunn. ex Benth.	Brush ironbark, hickory wattle
Acacia auriculiformis A. Cunn. ex Benth.	Earpod wattle
Acacia bahiensis Benth.	Not known
Acacia baileyana F. Muell.	Cootamundra wattle
Acacia berlandieri Benth.	Berlandia acacia, guajillo
Acacia brevispica Harms	Not known
Acacia cambagei R.T. Baker	Gidgee, stinking wattle
Acacia catechu (L.f.) Willd.	Catechu, black cutch
Acacia caven (Molina) Molina	Espino caven

Table A1. (cont'd) Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Acacias (cont'd)	
Acacia cincinnata F. Muell.	Scorpion wattle
Acacia confusa Merr.	Not known
Acacia crassicarpa A. Cunn. ex Benth.	Lancewood
Acacia cyanophylla Lindl.[d]	Golden wreath wattle
Acacia cyclops A. Cunn. ex G. Don	Western coastal wattle
Acacia dealbata Link	Silver wattle
Acacia decurrens Willd.	Green wattle, early black wattle
Acacia difficilis Maiden	Not known
Acacia elata A. Cunn. ex Benth.	Mountain cedar wattle, cedar wattle
Acacia erioloba E. Meyer	Not known
Acacia excelsa Benth.	Ironwood, rosewood, ironwood wattle
Acacia farnesiana (L.) Willd.	Mimosa bush, sweet wattle
Acacia fleckii Schinz.	Not known
Acacia genistifolia Link	Spreading wattle, early wattle
Acacia gerrardii Benth.	Not known
Acacia glomerosa Benth.	Not known
Acacia greggii A. Gray	Catclaw acacia, Texas mimosa
Acacia harpophylla F. Muell. ex Benth.	Brigalow
Acacia hebeclada DC.	Not known
Acacia hereroensis Engl.	Not known
Acacia hilliana Maiden	Not known
Acacia holocericea A. Cunn. ex G. Don	Candelabra wattle
Acacia homalophylla A. Cunn. ex Benth.	Yarran
Acacia imbricata F. Muell.	Imbricate wattle
Acacia implexa Benth.	Lightwood, hickory wattle
Acacia irrorata Sieber ex Spreng.	Green wattle
Acacia julifera Benth.	Not known
Acacia karroo Hayne	Karroo thorn
Acacia kempeana F. Muell.	Witchetty bush
Acacia kirkii Oliver	Not known
Acacia koa A. Gray	Koa acacia, koa
Acacia leptocarpa A. Cunn. ex Benth.	Not known
Acacia leucophloea (Roxb.) Willd.	Nimbar
Acacia leucophylla Lindl.	Not known

Table A1. (cont'd) Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Acacias (cont'd)	
Acacia littorea Maslin	Western Australian coastal dune wattle
Acacia longifolia (Andrews) Willd.	Sydney golden wattle, sallow wattle
Acacia macrostachya DC.	Not known
Acacia maidenii F. Muell.	Maiden's wattle
Acacia mangium Willd.	Brown salwood, hickory wattle
Acacia martii Benth.	Not known
Acacia mearnsii De Wild.	Black wattle, green wattle
Acacia melanoxylon R. Br.	Blackwood, Tasmanian blackwood
Acacia mellifera (M. Vahl.) Benth.	Not known
Acacia mucronata Willd. ex H.L. Wendl.	Narrow-leaved wattle, variable sally
Acacia neriifolia A. Cunn. ex Benth.	Silver wattle, oleander wattle
Acacia nigrescens Oliver	Knob thorn
Acacia nilotica (L.) Del.	Prickly acacia, babul
Acacia notabilis F. Muell.	Hickory wattle
Acacia oxycedrus Sieber ex DC.	Spike wattle
Acacia papyrocarpa Benth.	Western myall
Acacia paradoxa DC.	Kangaroo thorn
Acacia parramattensis Tindale	Parramatta wattle, green wattle
Acacia pellita O. Schwarz.	Not known
Acacia pendula A. Cunn. ex G. Don	Weeping myall, boree, myall
Acacia pennata (L.) Willd.	Not known
Acacia penninervis Sieber ex DC	Mountain hickory
Acacia pentogona (Schum.) Hook. f.	Not known
Acacia peuce F. Muell.	Waddywood
Acacia plectocarpa A. Cunn. ex Benth.	Not known
Acacia podalyriifolia A. Cunn. ex G. Don	Queensland silver wattle, Mt Morgan wattle
Acacia polyacantha Willd.	Not known
Acacia polyphylla DC.	Not known
Acacia pulchella R. Br.	Prickly Moses
Acacia pycnantha Benth.	Golden wattle, broad-leaved wattle
Acacia raddiana Savi[e]	Umbrella thorn
Acacia redolens Maslin	Ongerup wattle
Acacia reficiens Wawra	Not known
Acacia retinodes Schldl.	Wiralda, swamp wattle

Table A1. (cont'd) Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Acacias (cont'd)	
Acacia salicina Lindley	Cooba, native willow, doolan
Acacia saligna (Labill.) Wendl.[d]	Golden wreath wattle
Acacia schweinfurthii Brenan & Exell	Not known
Acacia senegal (L.) Willd.	Gum arabic, kher, senegal gum
Acacia seyal Del.	Shittimwood, talh, thirty-thorn
Acacia signata F. Meull.	Not known
Acacia silvestris Tind.	Bodalla silver wattle, red wattle
Acacia smallii Isely[f]	Huisache
Acacia stenophylla A. Cunn. ex Benth.	Eumong, river cooba
Acacia suaveolens (Smith) Willd.	Sweet wattle, sweet-scented wattle
Acacia terminalis (Salisb.) J.F. Macbr.	Sunshine wattle, New Year wattle
Acacia tetragonophylla F. Muell.	Dead finish, kurara
Acacia tortilis (Forsskal) Hayne[e]	Umbrella thorn
Acacia trachycarpa Pritz.	Sweet-scented minnie-ritchie
Acacia trachyphloia Tind.	Golden feather wattle
Acacia tumida F. Muell. ex Benth.	Pindan wattle
Acacia verniciflua Cunn.	Varnish(ed) wattle, manna wattle
Acacia victoriae Benth.	Prickly wattle, elegant wattle, gundabluie
Faidherbia albida (Del.) A. Chev.[b]	Applering acacia, ana tree, winter thorn
Other leguminous trees	
Aotus ericoides (Vent.) G. Don	Not known
Cassia siamea Lam.[g]	Djoowar, kassod-tree, Siamese senna
Cassia spectabilis DC.[g]	Not known
Chamaecytisus proliferus (L.f.) Link	Tree lucerne
Leucaena esculenta (Mocino & Sesse ex DC.) Benth.	Not known
Leucaena leucocephala (Lam.) De Wit	Leucaena, ipil-ipil, leadtree, jumbie bean
Mimosa affinis Harms ex Glaz.	Not known
Parkia biglobosa (Jacq.) R. Br. ex G. Don	African locust bean, nitta
Prosopis chilensis (Molina) Stuntz	Algarrobo, Chilean algarrobo
Senna siamea (Lam.) H. Irwin & Barneby[g]	Djoowar, kassod-tree, Siamese senna
Senna spectabilis (DC.) H. Irwin & Barneby[g]	Not known
Tamarindus indica L.	Tamarind

Table A1. (cont'd) Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Other legumes	
Abrus precatorius L.	Not known
Aeschynomene indica L.	Kat sola
Amorpha fruticosa L.	False indigo, indigo bush, bastard indigo
Amphicarpaea trisperma Baker	Not known
Arachis hypogea L.	Peanut, groundnut, goober, mani
Aspalathus carnosa P.J. Bergius	Not known
Astragalus adsurgens Pallas	Not known
Astragalus sinicus L.	Chinese milk vetch
Cajanus cajan (L.) Millsp.	Pigeonpea
Coronilla varia L.[h]	Crown vetch
Cicer arietinum L.	Chickpea, garbanzo
Daviesia ulicifolia C.R.P. Andrews	Gorse bitter pea
Desmodium intortum (Miller) Fawc. & Rendle	Greenleaf desmodium
Desmodium sinuatum Blume ex Baker	Not known
Galega officinalis L.	Goats-rue, galega
Galega orientalis Lam.	Not known
Glycine max (L.) Merr.	Soybean
Glycine soja Siebold & Zucc.	Wild soybean
Glycine wightii (Wight & Arn.) Verdc.[i]	Perennial glycine, creeping glycine
Gueldenstaedtia multiflora Bunge	Not known
Hardenbergia violacea (Schneev.) Stearn	False sarsaparilla
Kennedia prostrata R. Br.	Running postman
Lotononis bainesii Baker	Lotononis
Medicago polymorpha L.	Common burr medic, California bur clover
Medicago ruthenica (L.) Trautv.	Not known
Medicago sativa L.	Lucerne, alfalfa
Neonotonia wightii (Wight & Arn.) Lackey[i]	Perennial glycine, creeping glycine
Neptunia natans (Willd.) W. Theobald	Not known
Phaseolus vulgaris L.	French bean, kidney bean, navy bean
Pisum sativum L.	Pea, field pea
Securigera varia (L.) Lassen[h]	Crown vetch
Sesbania herbacea (Mill.) R. McVaugh	Not known
Sesbania rostrata Bremek. & Oberm.	Not known
Trifolium alexandrinum L.	Berseem clover, berseem

Table A1. (cont'd) Botanical and common names[a] referred to in this review. The first common name listed is the preferred common name.

Botanical name and authority	Common name(s)
Other legumes (cont'd)	
Trifolium ambiguum M. Bieb.	Caucasian clover, kura clover, honey clover
Trifolium dubium Sibth.	Suckling clover
Trifolium fragiferum L.	Strawberry clover
Trifolium glomeratum L.	Cluster clover, ball clover
Trifolium hybridum L.	Alsike clover
Trifolium incarnatum L.	Crimson clover
Trifolium pratense L.	Red clover, cowgrass
Trifolium repens L.	White clover
Trifolium subterraneum L.	Subterranean clover
Vigna umbellata (Thunb.) Ohwi & H.Ohashi	Ricebean
Vigna unguiculata (L.) Walp.	Cowpea
Non-legumes	
Allium cepa L.	Onion
Arctotheca calendula (L.) Levyns	Capeweed
Cucos mucifera L.	Coconut
Eucalyptus globulus Labill.	Tasmanian blue gum
Eucalyptus nitens (Deane & Maiden) Maiden	Shining gum
Lactuca sativa L.	Lettuce
Olax phillanthi R. Br.	Mistletoe
Parasponia andersonii Planch.	Not known
Sorghum bicolor (L.) Moench s. lat.	Sorghum, sweet sorghum, broom millet
Theobroma cacao L.	Cocoa
Zea mays L.	Maize, corn

[a] Authorities and common names taken from Hartley (1979), National Academy of Sciences 1979, Leigh et al. 1981, Simmons (1981, 1988), Brooker and Kleinig (1990), Wiersema et al. (1990), Tame (1992), Lazarides and Hince 1993, Searle (1996), Boxshall and Jenkyn (2001a, 2001b, 2001c, 2001d), Orchard and Wilson (2001a, 2001b), ILDIS 2002, IPNI 2002, Australian Seed Co. (2003) and Kutsche and Lay (2003). Sometimes ILDIS (2002) gives more than one authority for a particular plant species; in such cases, we give the most recent. 'Not known' refers to species for which none of the above gives a common name.

[b] *Acacia albida* is obsolete; the species is now known as *Faidherbia albida*.

[c] *Acacia arabica* is obsolete; the species is now known as *A. nilotica* subsp. *nilotica*.

[d] *Acacia cyanophylla* is obsolete; the species is now known as *A. saligna*.

[e] *Acacia raddiana* is obsolete; the species is now known as *A. tortilis* subsp. *raddiana*.

[f] *Acacaia smallii* is obselete; the species is now known as *A. farnesiana* var. *farnesiana*.

[g] *Senna siamea* and *S. spectabilis* were formerly *Cassia siamea* and *C. spectabilis*, respectively, now obselete.

[h] *Coronilla varia* is obsolete; the species is now known as *Securiga varia*.

[i] *Glycine wightii* is obsolete; the species is now known as *Neonotonia wightii*.