Tropical pasture establishment.
3. Impact of plant competition on seedling growth and survival

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Abstract

Plant competition can be a potent force influencing the success or failure of pasture establishment and hence the financial viability of pasture development. Perennial legumes, including tree legumes, are particularly vulnerable to competition because of their slow seedling growth rate. This paper reviews the effects of plant competition during pasture establishment in subtropical and tropical areas of northern Australia and advances the hypothesis that gaps in the existing pasture of adequate size are needed for reliable and effective establishment.

Root competition is generally more important than shoot competition for the growth and survival of seedlings. Variation in requirements for nutrients and the ability to form symbioses with rhizobium bacteria and, in some cases, vesicular-arbuscular mycorrhiza, enable legumes to compete successfully with, and establish in native grasslands on low fertility soils; grass establishment usually fails under such conditions. This paper discusses the need for a greater understanding of how the effects of root competition vary according to the amount and distribution of rainfall, and how the effects of fire and grazing might affect root competition in different climatic regions.

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The Problem

How should a pasture be sown and managed to ensure successful pasture establishment? Should seed be sown into a fully prepared seedbed or simply oversown into existing pasture? These questions often arise when graziers are sowing new pasture. The disturbance created, and hence the amount of existing pasture that remains after the planting operation, varies greatly according to the method of pasture sowing. Sowing method can therefore influence the amount of competition that young seedlings encounter. However, retention of the existing vegetation is not always detrimental as it (grasses as well as trees) can protect developing seedlings from exposure to extremes of high temperature and frost. A sound approach is therefore to recognise the importance and form of competition and to devise methods to minimise its effects on establishment and survival.

The ability of a plant to compete for resources may be determined by characteristics such as stature, habit, vigour, root distribution, mineral requirement, temperature and soil specificity, drought tolerance and resistance to grazing. Seedlings are disadvantaged when in competition with mature plants because of their size and limited root distribution, both at initial establishment and subsequent seedling recruitment. However, seedling survival is more critical during initial establishment because of the relatively low seeding rates (2–10 kg/ha) compared with the soil seed reserves often found (>50 kg/ha) in established pastures.

It has been common practice to recommend a cultivated seedbed, involving 2 or more tillage operations, to remove competition and enhance soil water storage (Jones and Rees 1973; Cook *et al.* 1993). However, the high cost of cultivation, and in many cases the need for timber clearing before machinery can operate, restrict its use to more intensive pastures. The relatively high nutritional value of legumes, together with their ability to establish in native pastures on low fertility soils, has led to large areas of native pasture being oversown with legumes. The oversowing of exotic grasses has not been as successful as that of legumes because they are more susceptible to competition from native grasses (Cook and Dolby 1981; McIvor and Gardener 1981; Thomson *et al.* 1983). Where legumes are oversown into existing pastures, plant competition can influence both establishment and the subsequent rate of build-up of legume in the pasture. This review summarises current knowledge on how plant competition affects pasture establishment in different situations, proposes ways of improving establishment, and highlights deficiencies in our current understanding.

The "gap" hypothesis

The role of ecological gaps in the colonisation and spread of species within plant communities has long been recognised by plant population biologists (e.g. Harper 1977; Cook 1979). On the other hand, pasture agronomists have largely ignored such processes, even though gaps are likely to have played significant roles in the outcomes of their work.

The gap concept is central to our understanding of establishment problems in pastures. It focuses on the need for gaps of appropriate size within an existing pasture to enable reliable and effective establishment of the particular species concerned. Ecological studies suggest that successful establishment is most likely to occur in gaps caused by physical disturbance (Grubb 1977; Cook and Lyons 1983; Snaydon and Howe 1986). Plant competition in gaps is reduced, allowing seedlings increased access to growth-limiting resources of water, nutrients and light. These resources are utilised, either by the surrounding vegetation or by newly established plants. Hence, the most favourable conditions for plant establishment occur when or soon after disturbance takes place, but then decline with time.

Establishment success following disturbance also declines with time (Figure 1). This principle is demonstrated for both a natural disturbance, caused by 2 forest 'blowdowns' (Figure 1a), and man-imposed disturbance aimed at enhancing legume establishment in a grassland (Figure 1b). In both cases, survival patterns of the first and later cohorts were remarkably similar, suggesting that the 2 colonising species were responding to some common principle, which we believe is reduced competition within the gaps created by disturbance. In the case of Siratro (*Macroptilium atropurpureum*), seedlings of the first cohort survived only where disturbance was created (sod-seeding and herbicide), with highest survival where the gap size was largest, i.e. where all the existing vegetation was killed with herbicide (Figure 1b). Seedlings of later cohorts, like those of *Viola fimbriatula* (Figure 1a), were relatively short lived. Such behaviour emphasises the importance of the initial establishment for species like Siratro. It may also highlight a deficiency of this legume.

A similar situation to the colonisation of the blowdowns by *Viola* was created when the trees were killed in a woodland with black speargrass (*Heteropogon contortus*) pasture. Killing the trees created gaps and resulted in better Siratro establishment than where live trees remained or where the trees had been removed some years earlier (Cook 1984; Cook and Ratcliff 1992), thus allowing the gap to close (Figure 2).

The size of gap required for successful establishment depends on the characteristics of the species and the situation in which it is being sown; species with poor seedling vigour require larger gaps than those with high seedling vigour.

We also suggest that ecological gaps may be created in situations where a lack of resources limits growth of the existing plant community, allowing the establishment of other species which have either a lower requirement for the primary resource that is limiting growth, or an alternative strategy for overcoming the resource shortfall. For example, where soil moisture is adequate, low nitrogen supply often limits the growth and competitive ability of grasses, allowing oversown legumes to establish successfully; legumes overcome N deficiency by supplying their own N through rhizobial fixation.

Competition within existing pasture and woodland

Competition from existing vegetation often limits seedling survival following oversowing (Cook *et*

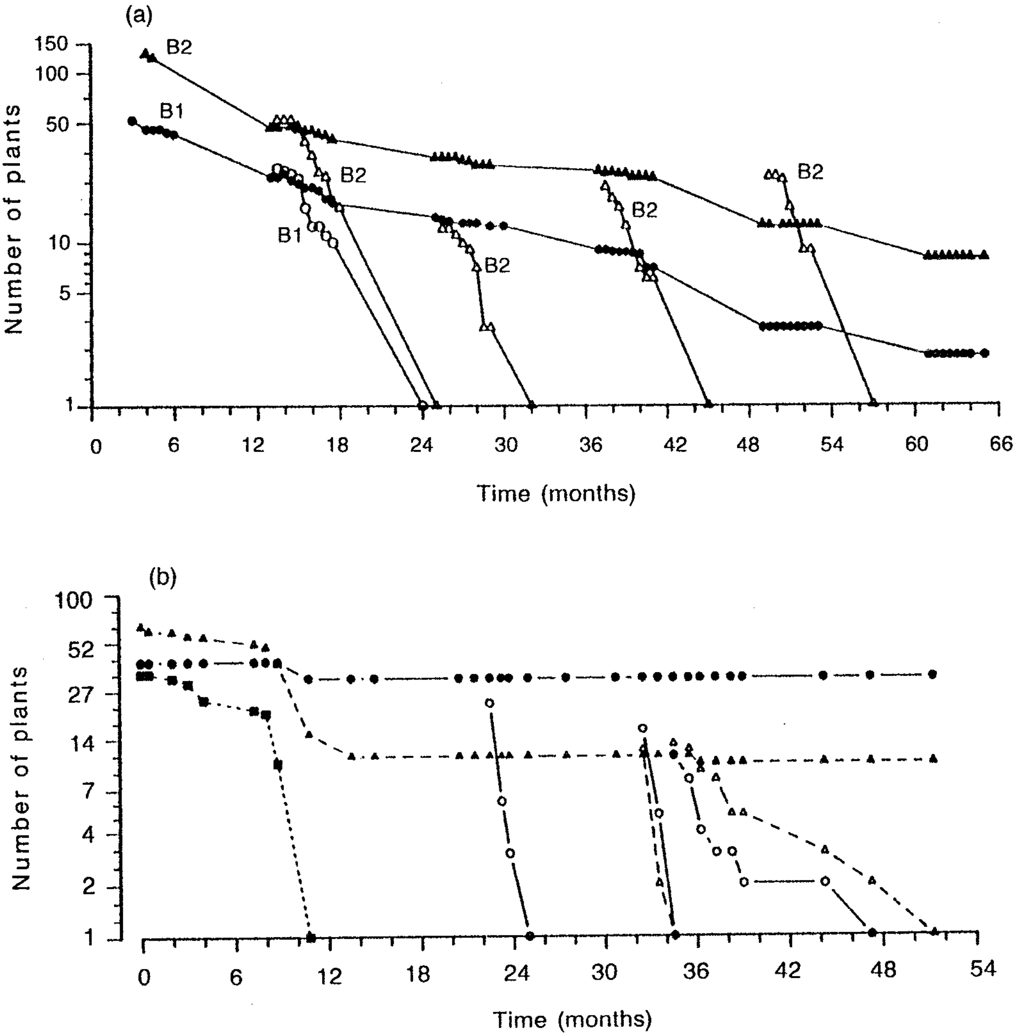

Figure 1. Establishment success (log scale) of (a) *Viola fimbriatula* and (b) Siratro relative to time of disturbance. Survival of first (solid symbols) and later (open symbols) cohorts of *Viola fimbriatula* that germinated after 2 forest 'blowdowns', B1 and B2 (from Cook and Lyons 1983). Survival of first (solid symbols) and later (open symbols) cohorts of Siratro that germinated in 3 seedbeds within a black speargrass pasture (■········■ — seed broadcast into undisturbed live native pasture; ●———● — seed broadcast into native pasture killed with herbicide; and ▲----▲ — seed sod-sown with minimal disturbance)(Cook and Ratcliff 1992).

al. 1987). It is unlikely that competition *per se* kills seedlings; rather, competition from existing vegetation may restrict growth to such an extent that the seedlings subsequently die from moisture stress, temperature stress (Cook and Dolby 1981; Thomson *et al.* 1983) or acute nutrient deficiency. Survival depends on plant size when stress is encountered. Large plants with large root systems have a clear advantage under stress conditions (Plummer 1943; Hoen 1968; Cornish 1982; Cook 1984), so seedling growth rates following emergence are critical for seedling survival (Cook and Ratcliff 1985).

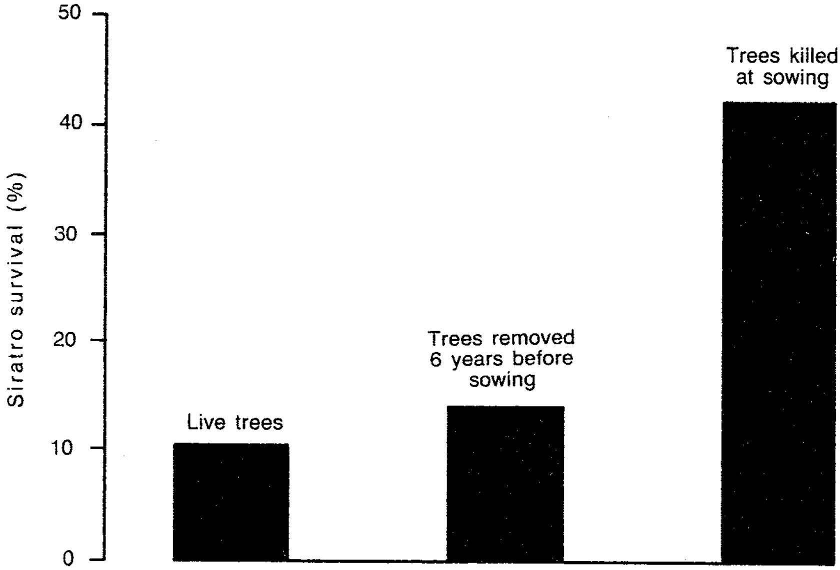

Figure 2. Effect of trees on the survival of Siratro (% of original seedlings surviving 4 years after sowing) sod-sown into a black speargrass pasture with minimal disturbance (Cook and Ratcliff 1992).

Effect of seedling size and vigour on competitive ability

Competition has a more adverse effect on the establishment of species that have slower rates of germination and/or lower seedling vigour. As a group, annual species germinate rapidly and quickly colonise gaps in the pasture. Some of the most successful instances of legume establishment following surface broadcasting into native pastures have been achieved with annual or biennial legumes, such as subterranean clover *(Trifolium subterraneum)* (Campbell 1976), Townsville stylo *(Stylosanthes humilis)* and Caribbean stylo (*S. hamata* cv. Verano) (Miller and Perry 1968; Edye and Gillard 1985). Nevertheless, even vigorous annuals, which include many weeds, have difficulty establishing and competing in strong perennial pastures (Michael 1970) where there are few gaps. Most perennial pasture legumes have relatively small seeds and lower seedling vigour than annuals and therefore have greater difficulty colonising a pasture. Slow germination and seedling growth of perennial legumes such as shrubby stylo (*Stylosanthes scabra*)(Mott *et al.* 1976; Gardener 1978) make establishment in native pastures a slow and risky procedure in stressful environments.

Most tree legumes, like some herbaceous legumes, exhibit very slow growth as seedlings and, at this stage, are vulnerable to competition from weeds (Maasdorp and Gutteridge 1986; Cooksley 1987) (Figure 3) and predation from wildlife. The poor establishment characteristics of tree legumes may be related in part to their root systems having a high component of permanent structural roots and a smaller proportion of the fine roots that are responsible for nutrient and water uptake, compared with grasses. For leucaena, slow seedling growth rates often result in an extended period of establishment and a high rate of establishment failure, except where competition from other species is eliminated. This poor establishment record is considered to be a major impediment to the planting of leucaena by graziers in Queensland (Lesleighter and Shelton 1986). Selection of tree legumes with higher seedling vigour may reduce competition problems and improve establishment. *Sesbania sesban* consistently shows superior seedling vigour compared with other tree legumes and, within the *Leucaena* genus, *L. pallida* and its hybrids show superior vigour to *L. leucocephala* cv. Cunningham (C.T. Sorensson, personal communication).

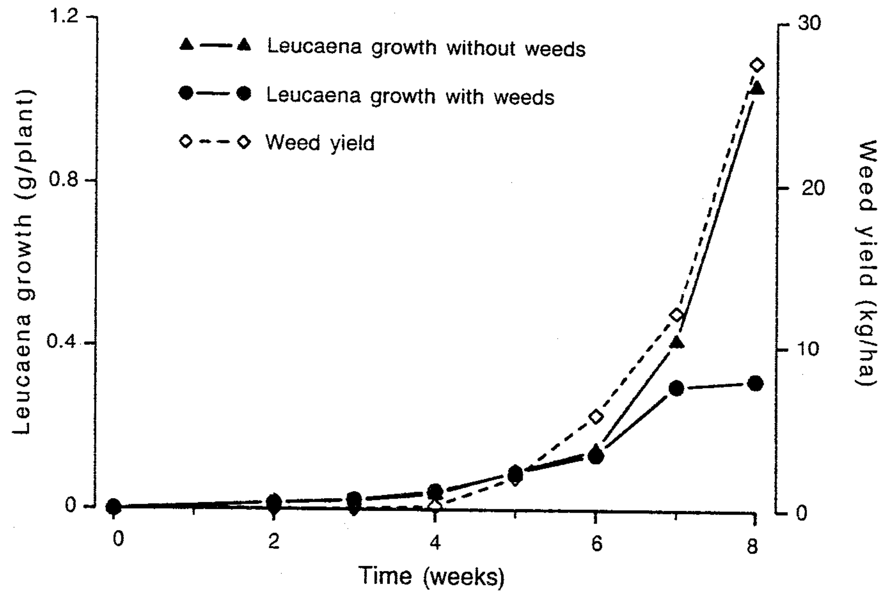

Figure 3. Effect of weeds on the growth of leucaena (from Cooksley 1987).

Root and shoot competition

Seedlings are most vulnerable to competition during the first 3 months of life, when their root systems are developing to a stage where they are more resistant to dry weather. During this time, root competition for water and nutrients has a greater influence on seedling growth than competition for light (Cook and Ratcliff 1984; 1985). Establishment success therefore depends largely on how strong the root competition is, and the extent to which it suppresses seedling growth.

To overcome root competition, the existing pasture needs to be severely suppressed or killed, to create a gap in which seedlings can establish. Measures designed to reduce competition must target the particular form of competition that is present. For example, management strategies involving defoliation and fire have greatest impact on above-ground competition for light, but often provide inadequate control of root competition (Figure 4) for seedling establishment. Neither burning nor close clipping controlled competition enough to allow grass or Siratro establishment in black speargrass pastures (Cook 1984). Single-pass sowing methods based on partial disturbance with disc or chisel ploughs also need to create gap sizes which are large enough for seedlings to establish. Lowe and Bowdler (1991) found it necessary to destroy at least 75% of the basal cover of native pastures in order to get reliable establishment of Siratro.

Moisture supply. The amount and distribution of rainfall following sowing interact strongly with root competition to influence the success of pasture establishment. Dry weather is often blamed for establishment failure in situations where better control of root competition would have led to successful establishment. This is clearly demonstrated by the establishment of 3 legumes in a black speargrass pasture during 2 summers of below-average rainfall (Figure 5). The legumes were sown into seedbeds where cultivation had destroyed either 50–60% (C1) or almost 100% (C3) of the existing pasture. With partial disturbance, legume establishment failed in 1990–91, but was successful in 1991–92 when rainfall was higher. On the other hand, legume establishment was successful in both years where complete cultivation resulted in better control of competition.

Competition for soil water is likely to be more intense under high fertility conditions. The large root systems of grasses appear to be more effective than those of legumes at extracting soil water during dry periods (Keating and Mott 1987), often to a soil water deficit below which legumes

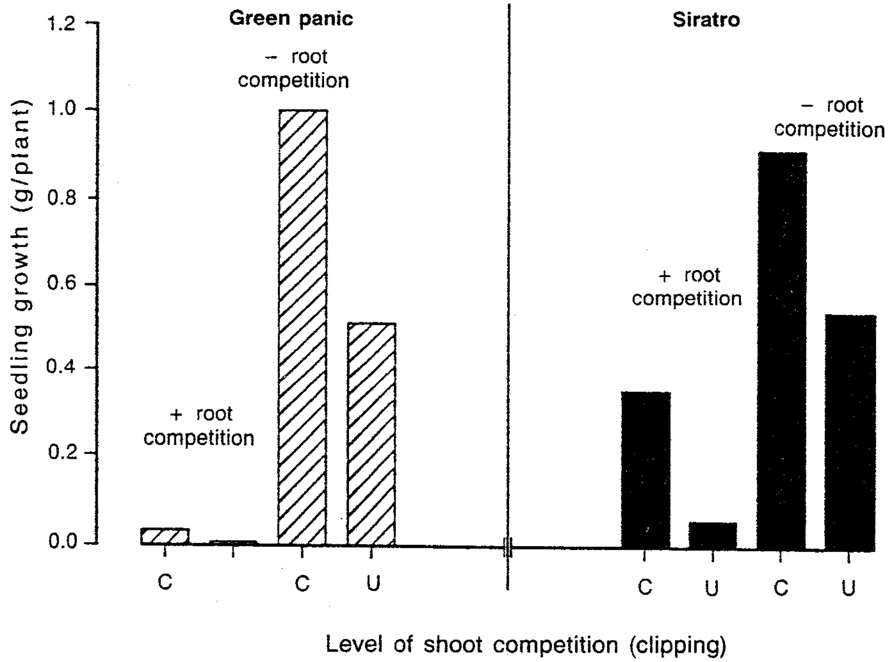

Figure 4. Effect of root competition on the growth of green panic and Siratro seedlings establishing in a black speargrass pasture that had either been clipped to a height of 3-5 cm each week (C) (yield of 520–1180 kg/ha) or left unclipped (U) (height of 40–60 cm, yield of 2500–4900 kg/ha). All plants were irrigated.

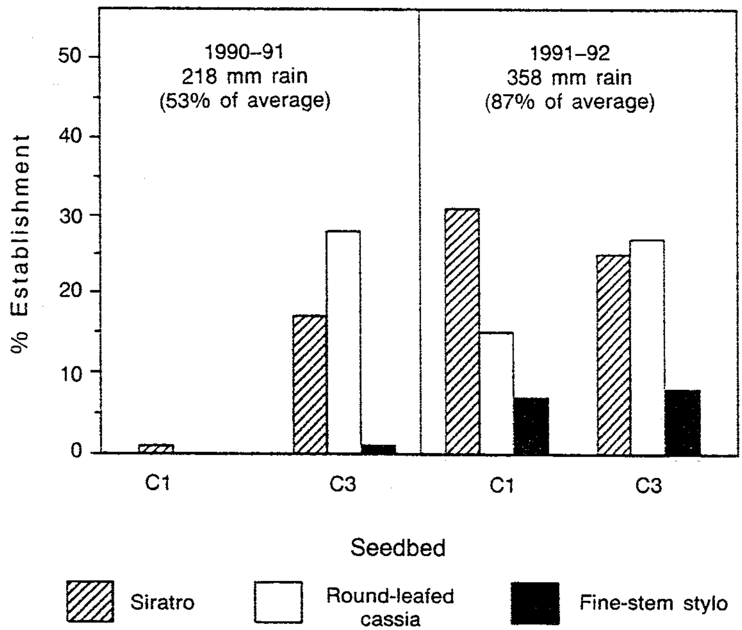

Figure 5. Effect of seedbed preparation (cultivation once (C1) or 3 times (C3) with offset discs) and rainfall (December — April) on establishment of Siratro, round-leafed cassia and fine-stem stylo, 5 months after sowing.

such as Siratro can not survive (Sheriff and Ludlow 1984). Rapid-growing nitrophilous weeds can also pose strong competition to establishing seedlings in high fertility soils (Campbell and McDonald 1979). The greatest weed problems often occur in situations where soil disturbance during seedbed preparation stimulates weed establishment.

Trees compete strongly with herbage species for soil moisture, and as McIvor and Orr (1991) point out, the effects vary geographically. The maximum pasture yield response occurs when trees are cleared at dry, infertile sites where competition for moisture and nutrients is most pronounced (Scanlan and Burrows 1990). In south-east Queensland, dry spells during the growing season are more frequent than in northern Australia and the pasture responses to tree killing are much greater (Mott *et al.* 1989; Cook and Ratcliff 1992).

The relative success of aerial seeding of legumes in north Queensland, compared with the failures commonly encountered in southern and parts of central Queensland, may be due partly to these moisture stress periods. In many cases, annual rainfall in north Queensland is less than that received in southern Queensland, but is concentrated into 4–5 summer months. The soil surface therefore remains moist for longer in the north than it does further south (McIvor and Gardener 1985), suggesting that competition for moisture may be less important in north Queensland. Analysis of the historical records of the number of wet days during the first 2 months of the wet season may facilitate decisions on the suitability of oversowing practices in different regions.

It is also possible that the long northern dry season, which may last 6–7 months depending on location, may weaken the native pastures so that they contain larger competition gaps at the beginning of the following wet season. Under such conditions, the native pastures are also likely to be more susceptible to fire and grazing, further opening up the pasture and allowing legumes to establish. The lower reliability of establishment from late wet season oversowings (R.J Jones, personal communication) supports this hypothesis. If this hypothesis is true, the probability of successfully establishing legumes in native pastures in southern Queensland should be greater immediately following periods of drought.

Nutrient supply. Soil fertility appears to have little direct effect on seedling germination (Gilbert and Shaw 1980; Coates *et al.* 1990), other than the very toxic effects of high aluminium and low pH. However, subsequent seedling growth, survival and reseeding are affected by nutrient supply. The importance of nutrient competition during seedling establishment will depend on the soil nutrient status and the specific nutrient requirements of both the competing-companion species and the species being sown. The symbiotic relationship with rhizobium provides legumes with a distinct advantage over grasses on soils of low N status. The ability of some species to form a second symbiosis with vesicular-arbuscular mycorrhiza (VAM) may also influence competitive relationships. For example, Crush (1974) and Barea *et al.* (1989) found that, when grasses and legumes were grown in mixtures in pot culture, the addition of VAM increased the growth and competitive ability of the legume.

Most tree legumes form symbiotic associations with VAM which are able to absorb various nutrients, principally phosphorus, from the soil, and transfer ions to the roots via hyphae. VAM therefore help compensate for the low root length densities of trees. Growth of leucaena without VAM infection (sterilised soil) was only 5% of that obtained in unsterilised soil (Ruaysoongnern 1990). These pot studies highlight the potential for VAM to improve the competitive ability of tree legumes during the establishment phase, but field studies are required to assess the real significance of VAM.

Tropical pasture species generally have a greater range of N and P requirements for growth than exotic temperate pasture species. For example, black speargrass plus shrubby and Caribbean stylos have a relatively low P requirement for growth; Siratro and Biloela buffel grass (*Cenchrus ciliaris* cv. Biloela) have moderate P requirements; and Nixon urochloa (*Urochloa mosambicensis* cv. Nixon) has a high P requirement (McIvor 1984a; 1984b). Shrubby and Caribbean stylos are therefore able to compete strongly with grasses under conditions of low N and low P (available P levels of 3–5 ppm) and low N and high P, whereas the higher fertility-demanding grasses can compete successfully only where both N and P levels are adequate (Coates *et al.* 1990). At very low P levels (<3 ppm available P) even stylo growth in native grass pasture is poor.

Siratro requires at least moderate P levels to compete and co-exist with grasses.

In grazed pastures, P supply had a beneficial effect on plant numbers of Caribbean stylo, but did not affect numbers of the perennial species, *S. viscosa* and shrubby stylo (Coates *et al.* 1990). Clearly, the main effect of fertiliser on the stylo population was through increased seed production (e.g. Gilbert *et al.* 1989) and regeneration, rather than on germination and first-year establishment. However, on soils of very low P status (soil P level 2–3 ppm), superphosphate also improved survival of shrubby stylo.

It has been widely demonstrated in both temperate (Cullen 1966; Campbell 1974) and tropical (Cook and Dolby 1981; Thomson *et al.* 1983; Cook 1984) regions that legumes establish more successfully than grasses when oversown into existing pastures. With low N conditions at establishment, growth and tillering of the native grasses is severely restricted. Competition for soil N between the existing native grass pastures and grass seedlings is likely to be a major factor limiting seedling growth (Cook 1980). Where soil N level is high, either because of natural soil fertility, fertiliser application, or N build up under the influence of legumes and fertiliser, introduced grasses can compete better (Gartner 1966). In low N situations, it is clearly of little value oversowing grasses into the existing pasture where competition for N and moisture will be intense. However, Indian couch (*Bothriochloa pertusa*), a tropical grass with lower fertility requirements than most other sown grasses, may be an exception in that it will establish in low fertility situations where others fail.

Soil disturbance results in a mineralisation of N, which is related in size to the organic N status of the soil. For example, in soils with large amounts of N held in soil organic matter, cultivation and fallowing can release a large amount of mineral N (up to 350 kg/ha N, Catchpoole 1992). The enhanced competitive ability of grasses relative to that of legumes under such conditions is likely to be one reason for the widespread failure of legumes and the success of sown grasses (e.g. Mears and Barkus 1970) on cultivated seedbeds in fertile clay soils. However, many soils in the tropics are of low N status and mineralisation is likely to be less than 20 kg/ha N annually.

Management to reduce plant competition

Reduced competition from the native pasture during the first 3 months after sowing favours seedling growth and enhances establishment. Methods recommended include cultivation, application of herbicides and grazing, which kill or weaken the existing pasture (Cook *et al.* 1993).

Cultivation

Complete cultivation is often necessary to eliminate competition when grasses are sown (McIvor and Gardener 1981; Cook 1984). Cultivation provides the gaps necessary for seedling establishment and also stimulates mineralisation of N to enhance grass seedling growth. In run-down pastures on fertile soils, it may be better to establish herbaceous legumes with minimal or no disturbance (with herbicide) to avoid stimulating large amounts of N mineralisation (Catchpoole 1992), which increases grass and/or weed growth. In all soils, competition for tree legume seedlings must be completely eliminated, either in a fully cultivated seedbed or in broad herbicide (> 1 m) bands, because of their extreme vulnerability to competition.

Band-seeding

The band-seeding method of establishment (Cook *et al.* 1992) was developed specifically to create gaps of a prescribed size so that a range of species could be established with a success rate of at least 80% when oversown into existing pastures in southern Queensland. Gaps are created by a band of herbicide, the width of which is adjustable by both rotating the nozzles in their holders and selecting nozzles with different spray angles. Guidelines for its use during dry seasonal conditions were developed (Cook *et al.* 1993) and, when these were adhered to, performance exceeded initial goals. A herbicide band width (gap size) of 50 cm was necessary for oversowing legumes such as round-leafed cassia (*Cassia rotundifolia*), shrubby and finestem (*S. guianensis*) stylos, Siratro and lotononis (*Lotononis bainesii*) into black speargrass pastures on low fertility soils. Narrower bands (30–40 cm) failed to provide large enough gaps to enable legume establishment under dry conditions.

Band-seeding may also be a useful method for establishing legumes in high fertility situations, such as run-down grass pastures on fertile clay soils, to avoid soil disturbance and substantial mineralisation of N. Band-seeding has the advantage of drilling the seed into the soil and controlling plant competition with minimal soil disturbance.

Broadcasting seed

The practice of broadcasting legume seed into existing pastures is most successful under low fertility situations in northern Australia, where N deficiency limits competition from the grasses for moisture and other nutrients. Attempts at broadcasting grass seed into existing pastures have often been unsuccessful without soil disturbance to release N.

Fire and increased grazing pressure have often been used to reduce competition in existing pasture oversown with legumes. However, results have been equivocal. In some situations, there was little or no effect on seedling survival (Cook 1984). Both fire and increased grazing pressure reduce competition for light, but have only a relatively small effect on root competition, except where species are susceptible to fire (e.g. Shaw 1957). Native grass species with shallow roots or above-ground growing points are more affected by wet season fires than species with deep roots or subterranean growing points (Smith 1960). Burning may also reduce the amount of 'other grasses', herbs and woody regrowth that occupy the spaces between the tussocks of black speargrass (Tothill 1983), thereby creating gaps and reducing root competition. However, fire, by removing cover, can create an arid micro-environment, markedly reducing seed germination (Mott *et al.* 1976; Cook 1984).

Positive responses in establishment following burning (Anning 1980) and clipping (Gillard 1977) have been claimed for Townsville stylo, which is sensitive to shading (Sillar 1967). Unfortunately, few of the reported experiments were carried out with an adequate control treatment to allow firm conclusions to be drawn. The only published example that we could find to support the use of fire to control plant competition was Stocker and Sturtz (1966) in which the dominant grass (*Sorghum intrans*) was extremely sensitive to wet season burning, and this situation promoted establishment of Townsville stylo. There is no critical evidence to support the use of fire in establishing legumes in perennial native pastures.

Conclusions

In most situations, root competition for nutrients and water is more important than shoot competition for seedling growth and survival. However, at present there is insufficient understanding of the relative importance of root and shoot competition in different regions, and how these effects vary with amount and distribution of rainfall. A greater understanding of these principles should allow predictions of where broadcasting seed is likely to be successful or where alternative methods of establishment are needed. Similarly, short of ploughing or spraying with herbicide, there is little knowledge of how to control root competition; the effects of fire and grazing on root competition are largely unknown.

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