

Tropical pasture establishment.

4. Population dynamics of sown species in developing pastures

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Abstract

The persistence of introduced species in pastures depends on the survival of plants from the original sowing, and the recruitment of new plants to maintain or increase population size. Recruitment can be by vegetative expansion but in many species it is by seedlings.

The population dynamics of 4 legume species (*Stylosanthes hamata*, *S. scabra*, *Macroptilium atropurpureum* and *Cassia rotundifolia*) are outlined, and the importance of seed production and soil seed banks for persistence of these species is highlighted. The effects of management (grazing, fertiliser, fire, pests and diseases) on survival, soil seed levels and recruitment are outlined, and examples are given of how these effects are reflected in changes in pasture composition. Some management guidelines based on the understanding derived from these demographic studies are presented.

Most paddocks are not uniform, and the influence of variation across landscapes on the development and dynamics of pastures is also considered. Recruitment and mortality vary across landscapes with management and seasonal conditions. Examples are presented of success and failure in different parts of a paddock, and of temporary loss of a species at the quadrat level but survival at the paddock scale.

Introduction

The persistence of introduced species in pastures depends on the survival of plants from the original sowing, and the recruitment of new plants. Management of establishing pastures aims to at least maintain and preferably increase the initial population. As Figure 1 shows, the subsequent size of the population is the net result of recruitment and mortality. For a species to colonise new areas there must be recruitment, and even when the initial numbers are satisfactory, recruitment must at least equal mortality for the species to persist.

Maintenance or increase in a population is favoured by low death rates (long-lived plants) and high seedling recruitment and/or vegetative regeneration. Different species have widely different mechanisms for persistence. For *Leucaena leucocephala* (leucaena) and *Medicago sativa* (lucerne) in grazed pastures, plant longevity is most important as regeneration is frequently low; annual species such as *Stylosanthes humilis* (Townsville stylo) with no vegetative regeneration depend entirely on high seedling numbers; *Digitaria eriantha* ssp. *pentzii* (pangola grass) depends on producing new vegetative tillers to survive and spread. Some species combine both sexual and asexual mechanisms e.g. *Trifolium repens* (white clover).

In this paper we examine the population dynamics of 4 contrasting tropical legumes highlighting differences in their persistence and regeneration pathways and the implications these have for management. We then consider the effects of management practices (grazing, fertiliser, fire) and spatial variability on the population dynamics of species within pastures. Finally, we examine future research needs relating to population dynamics of pasture species.

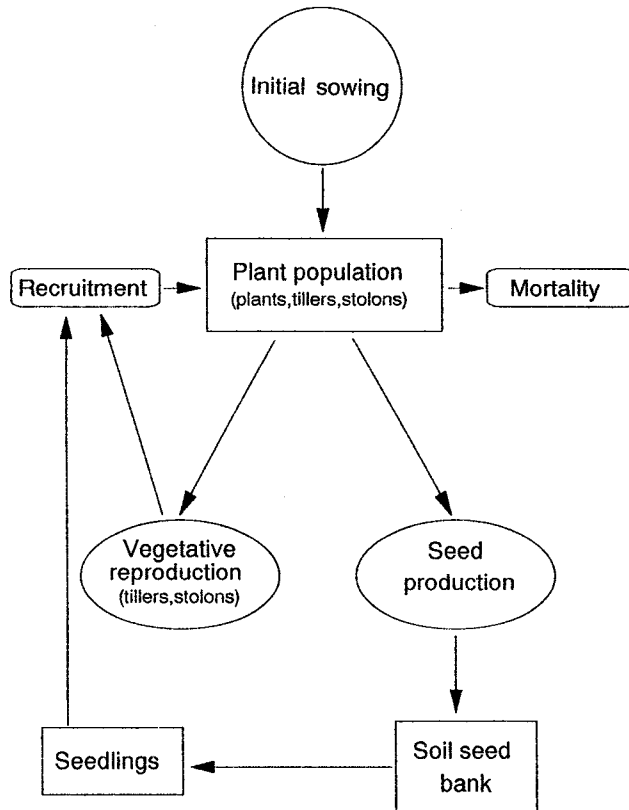


Figure 1. Components of plant population changes of pasture species.

Population dynamics of legume species in grazed pastures

Key data on the population dynamics of *Stylosanthes hamata* (Caribbean stylo), *S. scabra* (shrubby stylo), *Macroptilium atropurpureum* (Siratro) and *Cassia rotundifolia* (round-leaved cassia) are given in Table 1 for sites where the species are reasonably adapted. The data were compiled for 3 tropical sites (Lansdown, 19.7°S, 146.9°E, AAR 850 mm; Katherine, 14.5°S, 132.3°E, AAR 930 mm; and Hillgrove, 19.7°S, 145.8°E, AAR 535 mm) and 2 subtropical sites (Samford, 27.4°S, 152.9°E, AAR 1100 mm; and Narayen, 25.7°S, 150.9°E, AAR 710 mm). The table includes both published data (Gardener 1982, 1984; Jones and Bunch 1988a, 1988b; Mott *et al.* 1989; McIvor and Gardener 1993), and unpublished data of the authors.

Stylosanthes hamata cv. *Verano*

Verano acts predominantly as an annual with only a few plants surviving more than one growing season. The half-life was short (3–4 months) at all sites and as there was no vegetative regeneration, maintenance of an adequate plant population depended on seedling recruitment. Seed banks and seedling numbers were large at Lansdown and Katherine. However, in the drier, marginal environment of Hillgrove, there were few *Verano* seeds in the soil (usually fewer than 500 seeds/m²) and seedling numbers were often low, particularly in dry years when conditions for establishment were poor. Although *Verano* has persisted for 12 years at Hillgrove, it is often only a small proportion of the pasture. Success for *Verano* depends on plentiful seed production; if this fails regularly

Table 1. Population data for *Stylosanthes hamata*, *S. scabra*, *Macroptilium atropurpureum* and *Cassia rotundifolia* at 5 sites in northern Australia. Extreme values may occur outside quoted ranges. The half-lives are based on survival after the seedling phase.

Species	Parameter	Katherine	Lansdown	Hillgrove	Narayen	Samford
<i>S. hamata</i>	Half-life (mth)	3	3	4		
	Seed bank (no/m ²)	1000-6000	4000-16000	50-1000		
	Seedlings (no/m ²)	100-1000	100-1500	10-160		
<i>S. scabra</i>	Half-life (mth)	9	18	9	10-50	
	Seed bank (no/m ²)	100-1000	1000-5000	50-1000	200-4000	
	Seedlings (no/m ²)	10-300	50-500	10-150	60-500	
<i>M. atropurpureum</i>	Half-life (mth)				5-40	5-25
	Seed bank (no/m ²)				<50-400	50-500
	Seedlings (no/m ²)				5-30	5-20
<i>C. rotundifolia</i>	Half-life (mth)				4-8	4-8
	Seed bank (no/m ²)				100-5000	1000-12000
	Seedlings (no/m ²)				30-500	50-600

(e.g. due to drought or low temperatures during seed set), Verano will not persist.

Stylosanthes scabra cvv. *Seca* and *Fitzroy*

The values in Table 1 are based on *Seca* at Lansdown and Hillgrove, a mixture of *Seca* and *Fitzroy* at Katherine and both *Seca* and *Fitzroy* at Narayen. Shrubby stylo plants lived longer than Verano plants at all sites and perenniality was an important mechanism for plant persistence, particularly at Hillgrove and Narayen. Persistence of shrubby stylo has been a problem at Narayen where there was massive death of older plants from several sowings during winter in 1989 when the soil was saturated following late autumn/winter rain. The affected stands now appear to be recovering slowly but such losses could be catastrophic in pastures with small seed banks.

Seed banks and seedling numbers were lower than those measured for Verano at sites where Verano was well adapted. Despite similar recruitment and half-life values at Hillgrove and Katherine, the persistence of shrubby stylo at the two sites has been markedly different — it has persisted at Hillgrove but has disappeared from the pastures at Katherine. Success for shrubby stylo depends on both the longevity of the perennial plants and seedling recruitment with the importance of the two pathways varying between environments.

Macroptilium atropurpureum cv. *Siratro*

Siratro is unsuited to the Katherine and Hillgrove environments, and is marginally adapted to Lans-

down. No data are available on its population dynamics at these sites. At Narayen and Samford, persistence relied on both longevity of perennial plants and seedling recruitment. However, survival of *Siratro* plants at Narayen was poorer than that of *Seca* plants during summers with below-average rainfall. An important difference between *Siratro* and shrubby stylo was the lower seed set and consequently lower soil seed reserves and seedling numbers of *Siratro* (Jones *et al.* 1993).

Cassia rotundifolia cv. *Wynn*

The only data for *Wynn* are from the two subtropical sites where the survival of original plants of *Wynn* was poorer than that recorded for shrubby stylo and *Siratro*. However this was compensated for by higher seed reserves for *Wynn* (Table 1).

General features

For all species, survival of plants from the original sowing was usually greater than the survival of subsequent cohorts. This applied particularly where the original sowing was into a cultivated seedbed, but also occurred where the original sowing was into undisturbed grassland (Mott *et al.* 1989). Plants from subsequent cohorts surviving to the second growing season can have half-lives similar to (e.g. Jones and Bunch 1988b, Figure 1a), or poorer than those of the plants from the original sowing (Jones and Mannelje 1986).

It is difficult to measure the half-life of a soil seed bank because of annual seed input, as well

as loss due to decay, predation and germination. However measurements taken during periods when there has been negligible seed input have given the following half-lives — 5 months for Wynn cassia over a dry 2-year period at Narayen, 36 months for Siratro at Samford, 25–75 months for white clover at Samford, up to 145 months for *Lotononis bainesii* (*lotononis*) at a wet site in southern coastal Queensland. Soil temperature and moisture status, soil type, grazing pressure and genotype would all influence seed persistence in the soil.

The relative importance of plant persistence and recruitment

All 4 species persist as annuals or relatively short-lived perennials where long-term persistence is achieved through seedling recruitment. Except for Siratro at Samford at very light stocking rates, vegetative recruitment does not occur. Verano, the species with the lowest perennation at sites where it is adapted, has large seed banks. Siratro and shrubby stylo have greater and somewhat similar longevities in areas where they are adapted, although shrubby stylo has considerably larger seed banks. This suggests that, within reasonable ranges, there is a “trade-off” between longevity and seed set. Perhaps a key weakness of Siratro is that the seed banks are outside this reasonable range and are too low to ensure recruitment, even at moderate stocking rates.

Management effects on population dynamics

Although many aspects of the population dynamics of species are controlled by environmental factors, management is also important. At Hillgrove, timber treatment and stocking rate had major effects on the botanical composition of oversown pastures (Figure 2) and the degree of colonisation of unsown areas (Table 2). Such changes in floristic balance reflect effects of management on the population dynamics of the species, and these aspects are examined in the following section. Major changes in floristic balance are often not a slow incremental process but occur relatively suddenly with the concurrence of major weather (drought or flood), management and biological events (Torssell 1973; Taylor and Tulloch 1985).

Table 2. Effects of timber treatment and stocking rate on the proportion (%) of unsown area colonised by introduced species after 10 years.

Introduced species	Live trees		Trees killed	
	Low SR	High SR	Low SR	High SR
Verano	98	89	28	58
Seca	94	60	86	79
Urochloa	30	51	39	99
Buffel	26	72	47	55

Grazing

Grazing can affect plant survival, seed set, seedling emergence and seedling survival. While grazing pressure is the most important aspect, grazing system is also important for species such as lucerne (Leach 1978). Species differ markedly in their response to grazing. For example, Siratro is much less persistent under sustained heavy grazing due to reduced plant survival (Jones and Bunch 1988a) and seed set (Jones and Bunch 1988b; Mannetje and Jones 1990). In contrast, for Verano and Seca, increasing stocking rate either reduced (Orr and Paton 1993a), or had no effect on (Gardener 1982; Mott *et al.* 1989) seed set and seedling numbers, and no effect (Gardener 1982; Orr and Paton 1993a), or only a slight effect (Mott *et al.* 1989) on longevity. Persistence of Wynn cassia is also less affected by grazing than that of Siratro. Over a 6-year period at Samford, stocking rates of 2–4 yearlings/ha have had little effect on percentage cassia in the pasture, soil seed banks or seedling survival. At Narayen, cassia persistence has been affected less by stocking rate than by differences in rainfall pattern between years.

Grazing strategies may be used to enhance the persistence of sensitive species. Periodic resting of Siratro in autumn, for example, can improve yield, density and seed set. Fujita and Humphreys (1992) suggested that persistence of *lotononis* could be improved by light grazing during seed set in spring followed by heavy grazing during summer to avoid a buildup of grass and thus favour recruitment of *lotononis*. Even species that are less affected by grazing could benefit from seasonal spelling. During consecutive dry summers at Narayen, there was marked death of Wynn cassia plants, negligible seed set and a massive rundown in seed reserves as there were major germination events following

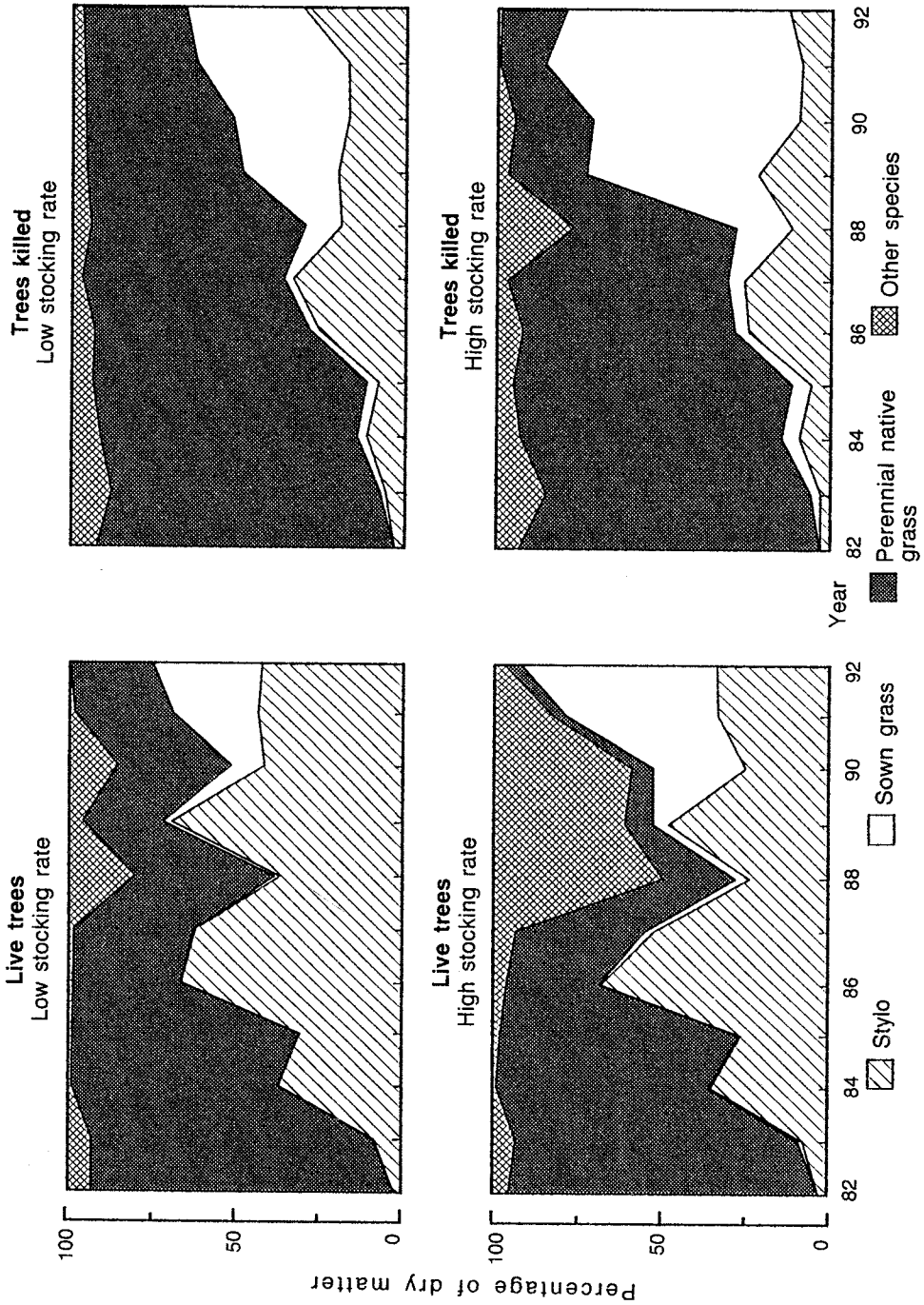


Figure 2. Effects of stocking rate and timber treatment on botanical composition of oversown pastures at Hillgrove (J.G. McIvor and C.J. Gardener, unpublished data).

isolated rainfall events. Seed reserves are critical for cassia persistence. Occasional spelling during seeding in favourable years to build up seed reserves could ensure survival of cassia through subsequent poor years.

Considerable amounts of seed are ingested by grazing animals. This can lead to loss of seeds which are digested, but those surviving passage through the digestive tract provide a means of dispersal as Gardener (1993) has shown for stylos. In general, the proportion of legume seed surviving increases with decreasing seed size and, most importantly, with increasing hardseededness (Simao Neto *et al.* 1987; Gardener *et al.* 1993). Seed numbers in faeces vary widely during the year as shown for Verano and Seca in Figure 3. During peak seeding periods, typical seed concentrations in faeces are 2–30 seeds/g OD faeces for Verano and shrubby stylo, 1–3 seeds for Wynn cassia and 0.05 seeds for Siratro. The difference between the stylos and cassia contrasts with their similar soil seed reserves (Table 1). This could be partly a result of the longer retention of stylo seed on the parent plants as contrasted with cassia, but could also reflect cassia having

lower acceptability to animals (R. Clements, personal communication). The possibility of using seed ingested by animals to establish pastures is discussed elsewhere in this volume (Cook *et al.* 1993). Very large numbers of seeds can be dispersed in faeces. Jones *et al.* (1993) calculated that during a 6-month period (January–June) each animal on a shrubby stylo pasture dispersed some 4 million viable seeds.

Dissemination of grass and weed seed in faeces may also contribute to changes in botanical composition resulting from different grazing pressures. Jones *et al.* (1991) concluded that the dominance of *Digitaria didactyla* (blue couch) and *Axonopus affinis* (carpet grass) in heavily grazed, coastal subtropical pastures could be partly due to their dissemination and subsequent colonisation from dung pats, as well as their prostrate growth habit. Concentrations of 10 viable seeds/g OD faeces were recorded from both these species during the period of peak seeding.

Non-domestic animals (both vertebrate and invertebrate) also collect and/or consume seeds. For example, ants collect considerable numbers

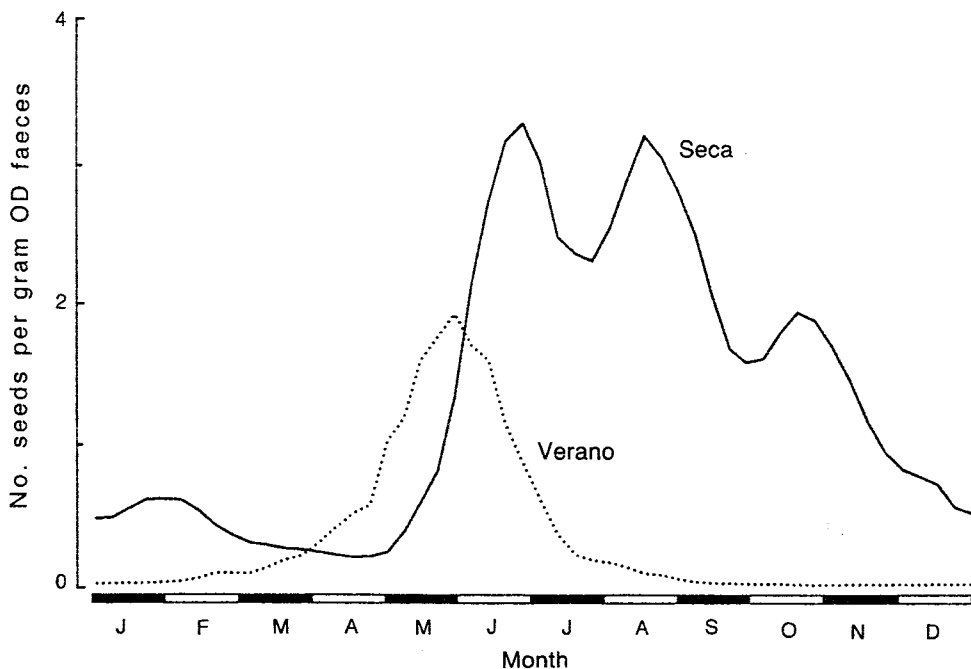


Figure 3. Seasonal pattern of seed numbers of Verano and Seca in cattle faeces at Hillgrove and Cardigan. Plotted values are 5-week running means (J.G. McIvor and C.J. Gardener, unpublished data).

of stylo seeds (Mott and McKeon 1977) and termites have been implicated in the large loss (approximately 40% of seed set) of stylo seeds during the dry season at Katherine (Mott *et al.* 1989). The impact of such losses on persistence is unknown but may be important during establishment if seed is sown on the surface a long time before germinating rain (Norman 1961; Leeuw 1974). Seed ingested by red and grey kangaroos may be protected from ants by the tough external coat of the faecal pellet of kangaroos (Barker 1987). As the faeces of kangaroos contain more seeds of more species than the faeces of sheep (Barker 1987), macropods may be a significant agent of spread. Other possible but unknown effects on species persistence and spread are the digging up of Siratro roots by kangaroo rats and bandicoots.

Fertiliser

There are many reports of the effects of fertiliser on growth and botanical composition of pastures but data on the effect on population dynamics is limited. Under conditions of extreme nutrient deficiency, plant survival is low but under less severe deficiency, plant survival is generally not affected. For example, superphosphate had little effect on survival of stylos (Gardener 1982; Mott *et al.* 1989) or Siratro (Jones *et al.* 1993). However, growth and thus seed set and subsequent seedling recruitment can be improved (Mott *et al.* 1989; Coates *et al.* 1990). For example, after a favourable season for seeding of Siratro at Narayan, seed reserves increased 5-fold in pastures fertilised with superphosphate compared with those receiving no fertiliser. This increase was reflected in subsequent Siratro densities up to 7 years later (Jones *et al.* 1993).

Fire

Fire affects both plant survival and seedling recruitment. Although the top growth is killed, some species can survive fire. Among the stylos, *Seca* is more tolerant of fire than *Verano* (Gardener 1980; Mott 1982) although *Seca* survival was poor in swards more than 3-years old (Mott 1982) and no Fitzroy plants survived a wildfire in a study by Gilbert and Shaw (1980).

Some seed is lost in fires; indeed, Gardener (1980) found most surface seed was destroyed.

The surviving seed has a higher proportion of soft seed than seed on unburnt areas (Mott 1982; Mannetje *et al.* 1983) and flushes of germination have been noted after burning (Gardener 1980; Mott 1982). Seedling densities will be higher if subsequent conditions are suitable for establishment, but, if isolated rainfall events and dry periods are experienced, seedling mortality will be high and seed reserves will decline.

Pests and diseases

Pests and diseases can have major effects on plant survival e.g. fungal diseases on lucerne (Clements *et al.* 1984); anthracnose on susceptible stylos (Irwin and Cameron 1978); amnemus weevil larvae on *Desmodium intortum* (greenleaf) and *D. uncinatum* (silverleaf) (Jones 1989); and psyllid attacks on leucaena in Indonesia (Oka 1989).

Pests and diseases can also reduce seed set by reducing plant vigour e.g. rust infection reduced seed yields of Siratro by 30% (English and Hopkinson 1983). Some insects can reduce seed set without reducing plant vigour e.g. *Heliothis* spp. on *Aeschynomene americana* (American joint-vetch). Selection or breeding of resistant varieties continues to be the only way to overcome these problems.

Spatial variation of population dynamics

The above treatment of population dynamics has not considered variation within pastures. Since pastures are not uniform, there may be wide spatial variation in survival and recruitment within a pasture. Even where the contribution of a species may be relatively stable over the whole pasture, there can be large variations at any point. Figure 4 shows such a situation for *Verano* at Lansdown — over the 8 years there was little variation in the frequency of *Verano* in the 0.25 m² quadrats (it varied between 60 and 80%) but within each quadrat there was considerable recruitment and death. *Verano* was present in 36% of quadrats every year, was never present in 12%, and in 52% it was present in some years only.

Variation can be large scale or small scale. Many paddocks contain different pasture communities and recruitment and death vary between them due to differences in soil type, soil fertility,

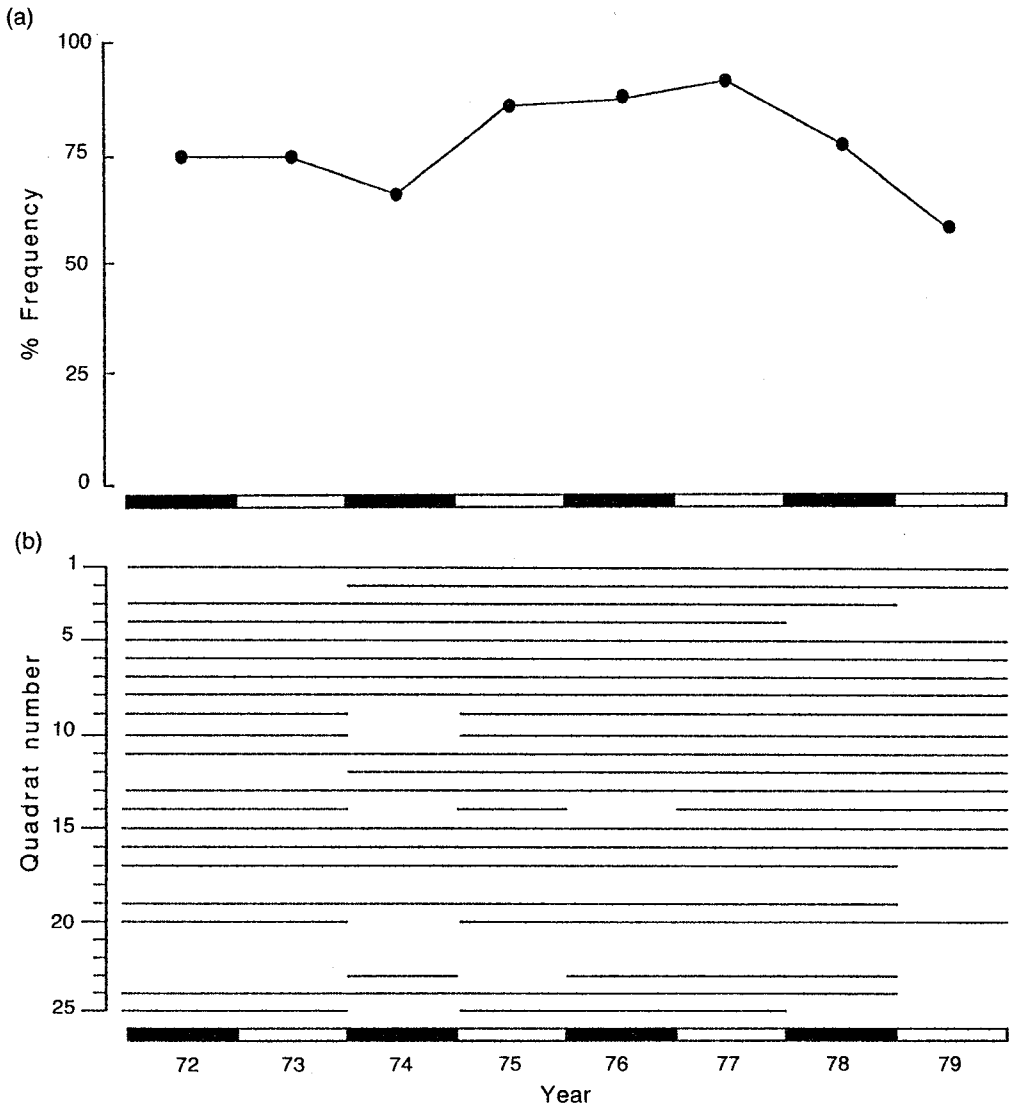


Figure 4. (a) Frequency of occurrence of Verano in a pasture at Lansdown (% of twenty-five 0.25 m² quadrats) and (b) Presence (—) or absence (---) of Verano in 25 individual quadrats in the pasture (C.J. Gardener, personal communication).

aspect, drought stress, waterlogging, and frost incidence (Taylor and Cook 1993). Management factors (stocking rate, fertiliser application, fire) and their consequent effects (grazing pressure, patch grazing, dung deposition) also induce variation. For example, the relationship between the frequency of occurrence of white clover and presentation yield during spring in 20 x 20 cm quadrats in a pasture in coastal Queensland is shown in Figure 5. There is a clear curvilinear relationship in every year with increasing presen-

tation yield being associated with decreasing presence of white clover. Since the presentation yield reflected the grazing pressure during the previous summer, decreasing grazing pressure in summer results in reduced incidence of white clover in the following spring. This confirms experimental studies showing that persistence of white clover in terms of stolon survival and seedling regeneration is enhanced by avoiding a buildup of grass the previous summer (Jones 1982).

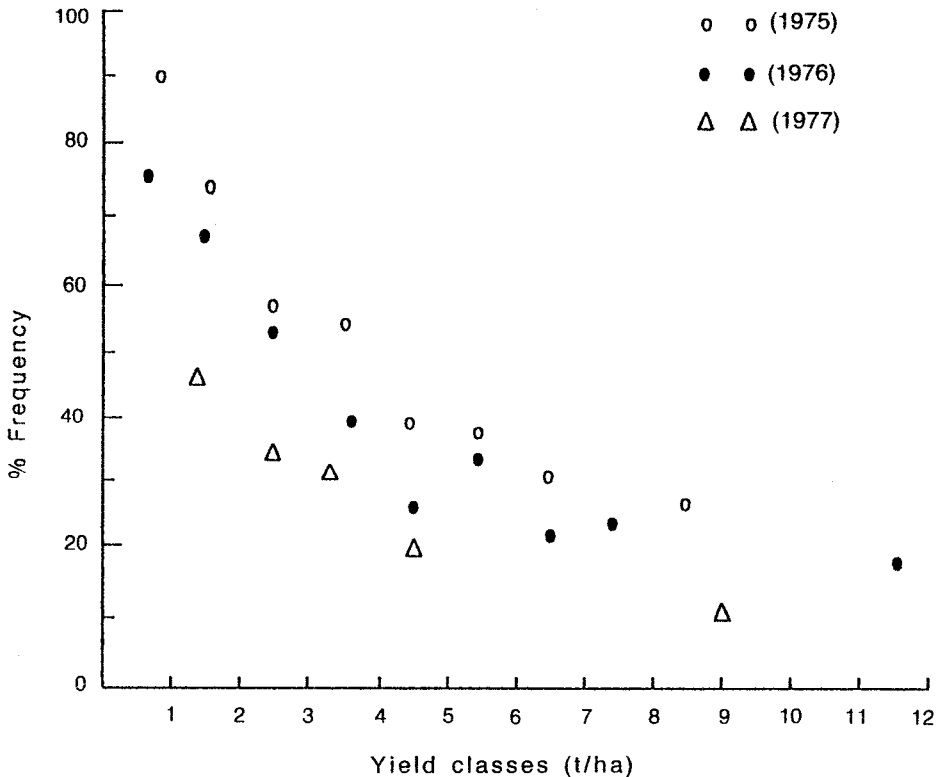


Figure 5. Frequency of occurrence of white clover in 20 x 20 cm quadrats in relation to presentation yield of the same quadrats in a pasture in coastal Queensland over 3 years (R.M. Jones, unpublished data).

Since species vary in their requirements for moisture and fertility, and in their tolerance of grazing and frost, a mixture sown evenly across a landscape soon becomes unevenly distributed. For example, within 2 years of sowing a mixture of Siratro, Wynn cassia, fine-stem stylo (*Stylosanthes guianensis* var. *intermedia*), Seca stylo, Bargoo joint-vetch (*Aeschynomene falcata*) and lotononis across an undulating landscape near Mundubbera, there was a substantially higher population of legumes on the lower parts of the landscape (Taylor and Cook 1993). The survival of individual species also varied according to position in the landscape, with Siratro and cassia the predominant legumes on the lower parts and Seca stylo the dominant legume on the ridge crest (Figure 6).

Future research on population dynamics

Understanding the population dynamics of pasture species has 3 main uses (Jones and

1980). Firstly, it can aid the development of better guidelines for grazing management to improve long-term persistence. Secondly, understanding how environmental factors affect the different pathways shown in Figure 1 can aid in better extrapolation of results to new environments. Thirdly, it may enable better definition of attributes to be sought in plant introduction and breeding programs.

At this stage we have some idea of the mechanisms of persistence of all our commercial legumes, although there are obvious differences between species and cultivars in the depth of this knowledge. The importance of seed set and hardseededness in developing seed banks and their contribution to long-term persistence is well recognised in advisory literature and often mentioned by graziers at field days. While further gains could be made in this area we need to ensure that the knowledge being sought is really required in practice. Demographic studies will be most useful when used in conjunction with other

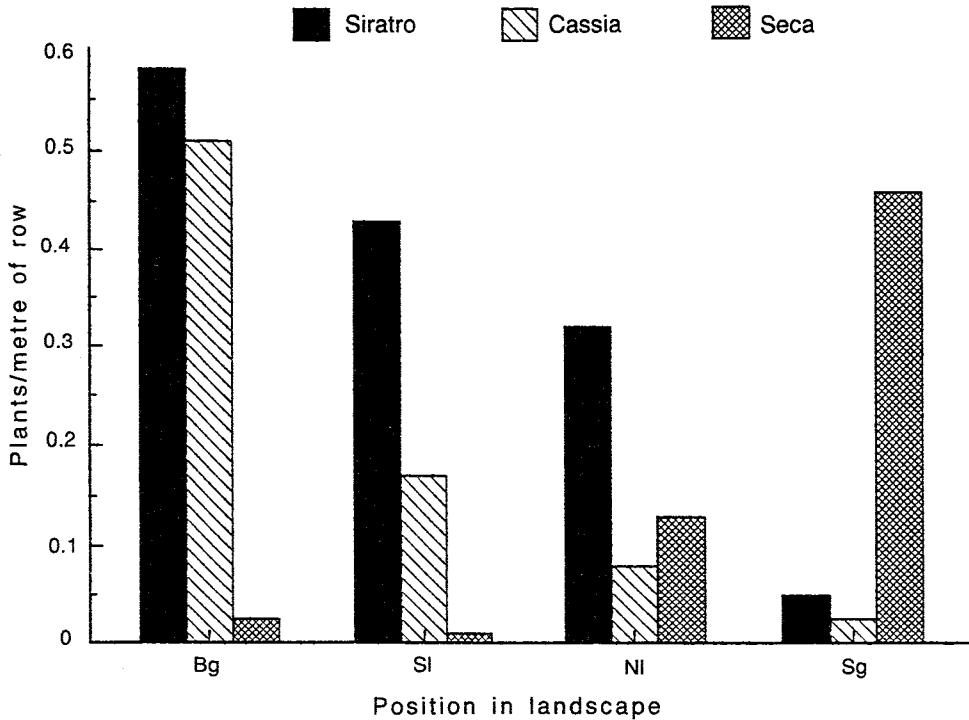


Figure 6. Effect of position in the landscape on the populations of three legumes sown in rows evenly across the landscape near Mundubbera. Bg = Blue gum (lowest part of the landscape); Sl = Silver-leaved ironbark; NI = Narrow-leaved ironbark; Sg = Spotted gum (highest part of the landscape) (Taylor and Cook 1993).

studies (e.g. competition) to find out why situations are occurring as well as to document what is occurring.

There may be greater opportunity for using knowledge of population dynamics in species improvement programs. Quantitative models of persistence may assist in selecting attributes which improve long-term persistence (Jones *et al.* 1993). For example, they may help answer such questions as — what are the relative benefits of improving plant survival by 10%, increasing seed set by 20%, and increasing hardseededness by 30%?

Although we have concentrated on legumes in this review, perhaps the greatest potential for new work on population dynamics lies with studies of colonisation and persistence of grasses and weeds. The seed of many important sown grasses appears to have only a short life in the soil. Seed banks of at least some sown grasses (e.g. *Urochloa mosambicensis* (McIvor 1987) and *Setaria sphacelata* (Jones *et al.* 1991)) are small. They may be less important for sown grasses than

for legume species although they may be critical for invasion by weedy grasses (e.g. *Sporobolus pyramidalis*). Conversely, survival of established plants may be more important for grasses than legumes. Although some studies of this type are in progress (Orr and Paton 1993b), most has been done in the rangeland areas (Hodgkinson 1992). This highlights the much poorer understanding we have of native and improved grass and weed dynamics in areas where legume introduction is feasible. Persistence of native grasses in oversown stylo pastures is already known to be a problem in some situations.

Studies of establishment and pasture development must be continued for appropriate time periods. There was very little sown grass in any of the pastures shown in Figure 2 for the first 6 years after oversowing and we could have concluded that the oversowing of the grasses was a failure. However after 10 years, these same plots were dominated by the sown grasses. Mannelje and Jones (1990) documented that Siratro was a persistent and productive legume for some 10

years at Narayen, after which persistence was poor.

Finally, we stress the need for careful thought before commencing studies of population dynamics. Experiments may need to run for several years and the measurements, particularly of survival of marked plants or seedlings, are very time consuming.

Conclusions

For the legumes considered in detail (Verano, Seca, Siratro and Wynn cassia), management of developing pastures should aim to optimise soil seed banks particularly in the first year although this is not important for some other legumes (e.g. lucerne and leucaena). Seed numbers are critical for future persistence and productivity, and the development of substantial seed banks provides the means for these species to survive conditions (either environmental or management) which are unfavourable for established plants.

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