Author's foreword:

The following review was originally written by the authors for publication by CAB International as Chapter 7 in a book of 15 Chapters edited by Philip Tow and Alec Lazenby. It can be cited as follows:

> Wolfe EC, Dear BS (2001) The population dynamics of pastures, with particular reference to southern Australia. (In) *Competition and Succession in Pastures* (Eds PG Tow, A Lazenby (CABI Publishing, Wallingford), pp. 119-148.

The book, which is held in many agricultural libraries around Australia, is now out-of-print and there are no electronic versions of its content publicly available.

The review outlines the principles of plant competition and succession in Australian pastures according to three theoretical models, namely:

- the idea of plant communities evolving along a linear pathway in response to the 'management' activities of human society through the addition of species, fertiliser and grazing animals, towards either the equilibrium (climax) or disorder (disclimax) states that are part of the theory of plant succession;
- the state and transition model, which is more flexible, accounting for the twists and turns in the pathway according to changes in management or climate; and
- the competition-stress-disturbance model, which is particularly helpful as a guide to understanding why certain species succeed in competing with other species that are present in pastures. An example is the competition that takes place between grasses, legumes and weeds – the manager works towards balancing the grass and legume components, and reducing weeds.

The chapter has been revised lightly, without including a number of recent references that could update the account to highlight additional outcomes of plant competition in southern Australia, to extend the concepts of competition and succession to specific districts (for example, dairy pastures in Tasmania) and regions (for example, tropical pastures in Queensland), to consider emerging issues (e.g., climate change) and to include the dynamics of new pasture species that have been released in Australia since 2000 (for some updated material, see the Australia Pasture Profile at https://www.csu.edu.au/research/grahamcentre/resources).

I acknowledge CAB International (Wallingford, UK), the original publisher of the book, for copyright permission, given in January 2020, to post this chapter onto the Graham Centre website as resource for scientists, pasture advisors, managers, farmers, graziers and students. I also acknowledge Dr Brian Dear and Professor Alec Lazenby for their interest and support for the idea of making this chapter generally available.

Emeritus Professor EC (Ted) Wolfe, email twolfe@csu.edu.au
Graham Centre for Agricultural Innovation (Charles Sturt University and NSW Department of Primary Industries)
January 2020

The population dynamics of pastures, with particular reference to southern Australia

E C Wolfe, Graham Centre for Agricultural Innovation (Charles Sturt University and NSW Department of Primary Industries), Wagga Wagga, New South Wales, Australia, twolfe@csu.edu.au
and
B S Dear, formerly NSW Department of Primary Industries, Wagga Wagga, New South Wales, Australia

Introduction

In Australia, as in other continents, agricultural development has resulted in substantial changes to grassland ecosystems. Australian agriculture has passed through several distinct phases since white settlement in 1788 (Table 1) (Shaw 1990, Barr and Cary 1992). In the 19th century, an initial *exploration* phase was supplanted by *exploitation* of the Australian landscape for grazing and crop production, and then followed periods of *consolidation*, *amelioration* and *restoration* during the 20th century. Not surprisingly, in response to this development, profound changes occurred in the botanical composition of Australian grasslands (Moore 1970). Of the original native species, and of those species that were either accidentally or deliberately introduced, there have been notable failures and survivors.

In this Chapter, a brief historical assessment will be given of the impact of development on grasslands in the agricultural areas of southern Australia, which are characterised by Mediterranean-type (south-western, southern) and temperate (south-eastern) climates; these grasslands have a minimum mean annual rainfall ranging from 250 to 350 mm. Examples of the botanical changes that occurred in response to grazing, plant introduction and fertilisation on the tablelands (predominantly non-arable, grazing) and slopes/plains (arable, farming) will be explored in relation to three conceptual models that have been used, worldwide, to describe and explain the interplay of climatic, edaphic and biotic factors on the dynamics of plant communities. Then, in a series of case studies, pasture species/varieties that have been notably successful in Australian agriculture will be related to these models and evaluated in terms of the processes and principles that have under-pinned the competitive success of these species. In a concluding section, experience and experimentation will be considered in relation to the future integration of conservation and agriculture in Australian rural lands.

The impact of agricultural development on the pastures of southern Australia.

Early in the 19th century, the occupation of rural Australia by British immigrants proceeded slowly but by 1860, driven in part by the discovery of gold in 1851, land settlement encompassed the south-eastern quarter of Australia from north of Adelaide to beyond Brisbane, as well as part of western Australia (Shaw 1990). In 1862, New South Wales (NSW) and Victoria were both supporting about 6 million sheep, with Queensland only a little behind. There were many difficulties during this exploration phase (Shaw 1990, Barr and Cary 1992), but the availability of suitable grasslands was not one of them (Barr and Cary 1992).

According to Shaw (1990), the period between 1850 and 1890 marked the hey-day of the pastoralists, who developed huge grazing properties using axes, dams, artesian bores and fences, along with better techniques of sheep breeding and husbandry. By 1891 there were 62 million sheep in NSW, 20 million in Queensland and 13 million in Victoria (Table 1); between 1860 and 1894, the Australian sheep population had risen from about 20 million to 100 million, and cattle from 4 million to more than 12 million (Shaw 1990).

Table 1. Agricultural development in Australia, 1820-2000*.

Phase	Year	Livestock numbers (x 10^{-6}) Sheep	Cattle	Wheat area (ha x 10^{-6})
Exploration phase	1820	0.3	<0.1	0.01
	1842	6	<0.1	0.06
	1851	17	0.2	0.1
Exploitation phase	1861	21	3.8	0.3
	1871	40	4.3	0.5
	1881	65	8.0	1.2
	1891	106	11.1	1.3
Consolidation phase	1901	72	8.5	2.1
	1911	97	11.8	3.0
	1921	86	14.4	3.9
	1931	111	12.3	6.0
	1941	125	13.6	4.9
	1950/51	116	15.2	4.2
Amelioration phase	1960/61	153	17.3	6.0
	1970/71	172	24.4	6.5
Restoration phase	1980/81	131	25.2	11.3
	1990/91	162	23.6	9.2
	1996/97	120	26.8	10.9

*The statistics for 1820-1950/51 were taken from Shaw (1990) and the more recent values from ABARE (Knopke *et al.* 1995) and the Australian Bureau of Statistics.

A combination of factors, notably overstocking, the invasion of pastoral lands by rabbits introduced in 1859, a general economic depression and bank collapses in the 1890s, and a severe drought from 1895 to 1902, arrested and then reversed the pastoral boom. Erosion, pasture degradation and a fall in livestock numbers were the consequences, outcomes predicted by P. E. de Strzelecki. In an 1840 report to Governor Gipps on his travels to the Australian Alps and Gippsland, Strzelecki expressed his concern about the exploitative practices of overgrazing and burning (Hancock 1972). Meanwhile, the farming of wheat, barley and oats had expanded steadily in area (Table 1), first in South Australia (Meinig, 1954) and Victoria (Barr and Cary 1992) and then, with the development of a railway network, in NSW. A common problem was the decline of cereal yields on land that had been farmed for several years (Donald 1967).

However, not all of the 19th century was characterised by exploitation. The rapid expansion of mechanisation and transportation from 1870, and the establishment of agricultural colleges and experimental farms during the 1890s, were notable developments in terms of their immediate benefit and future impact.

As outlined by Barr and Cary (1992), the southern Australian wheat industry was rescued from decline at the turn of the century by the new techniques of dry farming, purposeful wheat breeding and superphosphate fertiliser. However, crop yields on the poor Australian soils were still low by world standards and bare fallowing both depleted the soil of organic matter and rendered it liable to wind erosion. Green manuring with oats or lucerne was advocated, but it was not until the 1930s that a technique of ley farming[1] with annual pasture legumes was

[1]In Australia, there is a trend toward the use of "ley" to denote a one-year pasture and "phase" to denote several years of pasture, but we prefer the use of the terms "ley" and "ley farming" to embrace pastures of one to several years duration in the crop/pasture rotation.

developed and promoted (Puckridge and French 1983). Subterranean clover (*Trifolium subterraneum*), which had been discovered and promoted unsuccessfully by Amos Howard in the 1890s, was the basis of the ley farming system introduced at Rutherglen Research Station in north-eastern Victoria (Barr and Cary 1992). Ley farming with annual medics (*Medicago* spp.) was in use in the 1930's at the Roseworthy Agricultural College in South Australia (Callaghan 1935). Fertilised ley pastures, by setting in train a new succession of botanical changes in response to added fertiliser and nitrogen fixation, had the potential to alter markedly the nature of grazed pastures in the farming zones. This topic will be dealt with later in this Chapter. Because of the depression and then war, there was little change in on-farm practices or outputs between 1930 and 1950 (Donald 1967, Gruen 1990), and land degradation continued. However, investments into agricultural research during this consolidation phase produced some notable discoveries that were to underpin the rapid expansion of improved pastures from 1950 to 1970 on both arable and non-arable sites. These discoveries included successful searches (mainly within Australia - Cocks *et al.* 1980) for new varieties of subterranean clover that were intermediate between the mid-season variety Mount Barker (found in South Australia, commercialised in 1906) and the early strain Dwalganup (commercialised in Western Australia, 1929); a strain (cv. Hannaford) of annual medic (barrel medic, *M. truncatula*) that was commercialised in South Australia in 1938; the development as a sown species of a strain of *Phalaris tuberosa* (syn. *aquatica*), a perennial grass that was capable of surviving summer drought (Oram and Culvenor 1994); the realisation that deficiencies of phosphorus and sulphur were widespread in Australian soils, many of which also needed one or more of the minor (trace) elements copper, zinc, molybdenum, manganese, iron and boron (Williams and Andrew 1970); elucidation of the legume - *Rhizobium* symbiosis (Williams and Andrew 1970); and the development of a virulent strain of the myxomatosis virus for rabbit control (described by Barr and Cary 1992).

The above knowledge, allied with the 1950s boom in wool prices, financial incentives for investment in agriculture (Gruen 1990) and the advent of aerial agriculture (Campbell 1992), ushered in an amelioration phase in temperate Australian grasslands. According to the account of this phase by Crofts (1997), the area of sown pastures increased from around 5 m ha in 1950 to in excess of 25 m ha by 1970: the pasture area fertilised annually more than doubled between 1950 (7 m ha) and 1973, when a superphosphate subsidy was removed. These improved pastures consisted mainly of subterranean clover, annual medics, lucerne (*Medicago sativa*) and, in the higher rainfall areas (> 600 mm) of NSW, Victoria and Tasmania, perennial grasses such as phalaris, perennial ryegrass (*Lolium perenne*) and cocksfoot (*Dactylis glomerata*).

Finally, during the 1970s, 1980s and 1990s, a reappraisal of pasture development took place. This reappraisal occurred in response to (i) a worsening cost-price squeeze (Gruen 1990), (ii) an apparent widespread decline in the productivity of pasture legumes following the occurrence of new disease, pest and weed problems (Gramshaw *et al.* 1989), and (iii) evidence of widespread land degradation phenomena such as eucalyptus dieback, soil acidification and salinization (Goldney and Bauer 1998). The area of sown pastures in Australia has remained static at around 27 m ha since 1970, with declines from 1970 to 1985 in the area fertilised and the rate of fertiliser applied (Gramshaw *et al.* 1989). Since then, problems of oversupply in the wool industry and changing community attitudes toward conservation have given rise to initiatives that aim to integrate conservation and agricultural production, with the objective of achieving sustainable production systems. This restoration phase (Goldney and Bauer 1998) has been marked by: a reduction in the sheep population (Table 1); better documentation of the effects of and solutions to the environmental problems created by agriculture; programs and legislation to protect areas of native grasslands and woodlands; a shift in emphasis from action at the farm level to the catchment level; and improved partnerships between scientists, farmers and the community.

Pasture dynamics during the phases of agricultural development

Models of pasture dynamics

There are at least three different conceptual models that have been used as a framework for describing and explaining the interplay of climatic, edaphic and biotic factors on the dynamics of pasture communities, and for managing these communities. The first two of these models, the theory of Clementsian succession and the state and transition model, were recently discussed fully by Humphreys (1997); these models are illustrated and explained in a following section. A third theory, the competition-stress-disturbance (CSD) model, was developed and used by Grime (1977) to classify plants according to the combination of characteristics they display in response to three primary ecological factors. These factors are (i) *competition* (with the high vegetative competitive ability of some species accounting for their dominance), (ii) *stress* (with certain plant species adapted to and tolerating unproductive conditions) and (iii) *disturbance* (with some species adapted to grazing disturbance, and with ruderal species possessing an ability to invade and grow in severely disturbed but potentially productive environments). All three theories, succession, state and transition, and competition-stress-disturbance, have some usefulness in interpreting the changes in vegetation that have occurred in natural and improved pastures in southern Australia.

Species changes during the exploration and exploitation phases

Moore (1970) outlined the changes in pasture species that occurred over several decades in typical *Eucalyptus* woodland - grassland communities on the slopes and tablelands of southern NSW in response to clearing, higher grazing pressures (from sheep, cattle and rabbits) and the application of superphosphate fertiliser. The original climax vegetation, dominated by tall warm season perennial tussock grasses such as kangaroo grass (*Themeda triandra*), plains grass (*Austrostipa aristiglumis*) and poa tussock (*Poa labillarderi*), was presumably well-adjusted to the ebb and flow of the native herbivores (kangaroos, wallabies, bird life) and occasional fires. Once sheep and cattle were introduced to the tablelands and slopes in the 1830-40s, accompanied by timber-clearing operations, there began a sequential progression (Figure 1) in the botanical composition of the grasslands, toward a disclimax community (or, more correctly, a number of disclimax communities). Such communities contained an array of grazing-tolerant, cool- and warm-season native grasses, together with various naturalised annual grasses and forbs that had been introduced into Australia in agricultural seeds and feeds. This pathway of change in plant communities, from a pre-settlement, climax (stable) vegetative state through an unstable continuum of several disclimax stages, where stability was more or less maintained by ‘management’, was consistent with the original linear succession model first proposed by F. E. Clements in 1916 (Humphreys 1997). In terms of Clements’ theory, the activities of fire, grazing, clearing and fencing opposed the natural successional tendency toward pristine, climax grassland.

Loss of grazing-susceptible plant species thereby opening the sward to native and exotic invading species, nutrient redistribution, and changes in the seasonal extraction and replenishment of soil water, are the processes that presumably influenced the outcome of plant competition and the succession of plant communities in Australian grasslands, over time and space. While the main catalyst for the botanical changes that took place was grazing (a disturbance factor, in terms of Grime’s CSD model), the evidence for its specific effects is

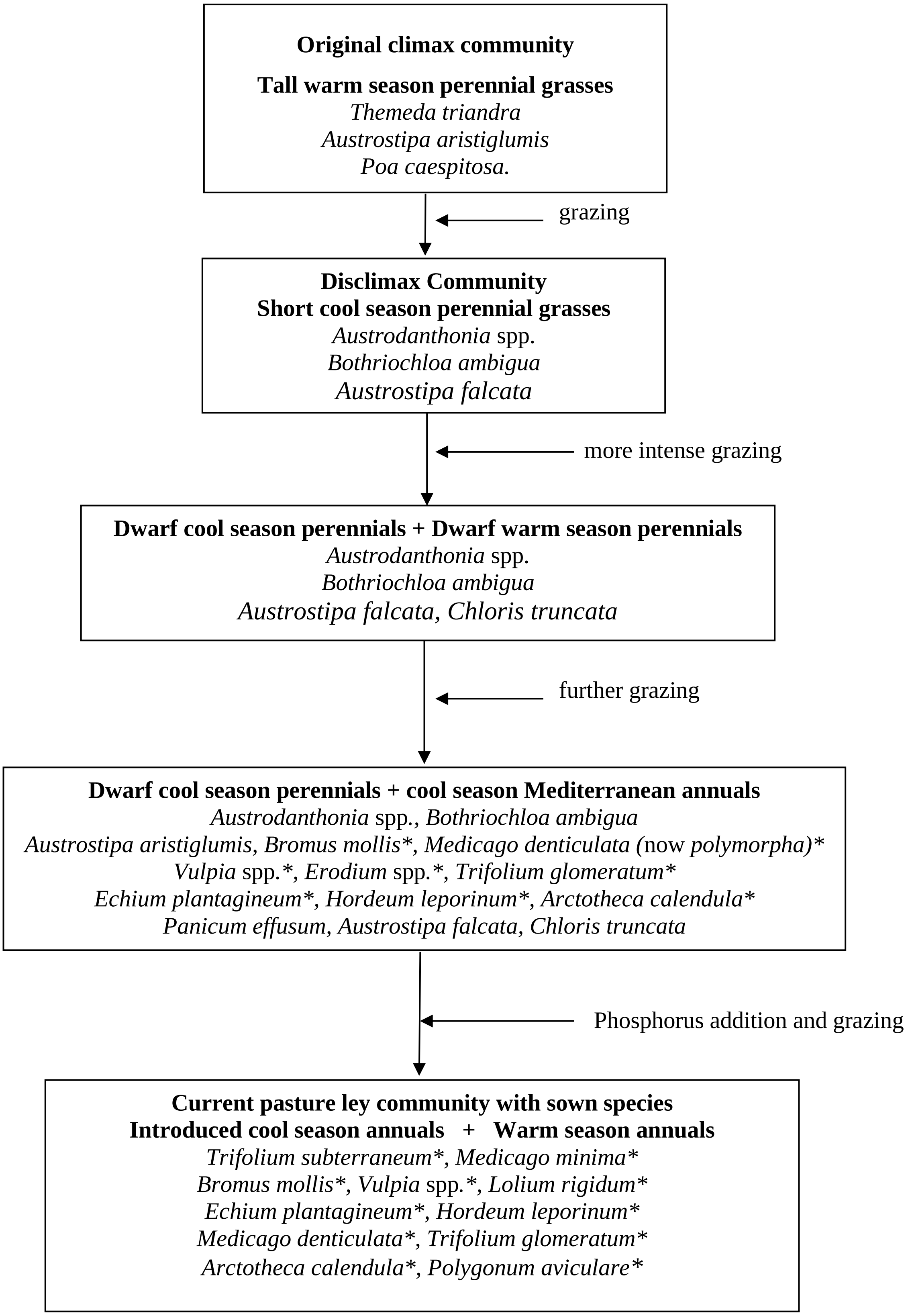

Figure 1: Botanical changes in pastures in the cropping zone of south-eastern Australia, based on Moore (1970) and modified by Dear (1998). Asterisks denote naturalised species, to distinguish them from native species.

largely anecdotal. Early reports made during the exploration and exploitation phases (Barr and Cary 1992) indicated that kangaroo grass was abundant and palatable to livestock. Kangaroo grass was sensitive either to defoliation or treading or both**;** it did not persist wherever sheep or cattle were grazed (Moore 1970). Subsequently, it was shown in South Africa (O'Connor 1996) that the persistence of *T. triandra* depended on lax defoliation, which enhanced both the recruitment and survival of seedlings.

Several other native perennial grasses were protected in part from grazing by mechanisms such as less palatable herbage (for example, *Bothriochloa ambigua*, red grass) or spiny seeds (*Austrostipa* spp., spear or corkscrew grasses). On the northern slopes of NSW, three-awned speargrass (*Aristida ramosa*), an unpalatable species, became co-dominant with red grass on extensive areas of lightly grazed grasslands (Williams, 1979). However, it has subsequently been shown that *A. ramosa* is sensitive to defoliation and the balance can be shifted back towards more palatable species, notably wallaby grass (*Austrodanthonia* spp.) and subterranean clover, by heavy grazing with mobs of sheep applied strategically in summer-autumn, coinciding with the flowering and seedling establishment of the speargrass (Lodge and Whalley, 1985).

Johnston (1996) noted that the causal relationship between grazing (defoliation, trampling) and grass species composition has not been seriously challenged. He listed several factors that may have been involved in the replacement of the original native grasses with other grasses; these include changes in plant-soil water and nutrient relations as well as timber clearing and reduced fire frequency. According to Johnston (1996), the persistence to the present day of certain productive and nutritious C_3 native grasses, notably weeping meadow grass (*Microlaena stipoides*) and the wallaby grasses, may be due, at least in part, to their preference for shade and/or the complementarity of their growth cycle and phenology with the original C_4 grasses, which are taller and better adapted to dry habitats and hot seasons.

Other important components of the degraded grasslands included many grasses, forbs and legumes that became naturalised after their entry to Australia. Sometimes this naturalisation followed their accidental introduction in agricultural produce from various destination along the sea routes from Europe and the Mediterranean region to Australia (for example, *Vulpia* spp. silver grass, *Hordeum leporinum* barley grass and *Arctotheca calendula* capeweed). In other cases, plants may have been introduced deliberately as ornamentals (for example, *Oxalis pes-caprae* soursob, *Silybum marianum* variegated thistle and *Echium plantagineum* Paterson's curse or 'Salvation Jane' - Michael (1970). Most of the strains of subterranean clover found in suburbs of Perth by J. S. Gladstones (1966) entered Australia (accidentally, not deliberately) before 1870, and some annual *Medicago* spp. were naturalised by the early 1900s (Crawford *et al.* 1989).

Michael (1970) attributed the competitive success of these alien species to their adaptability to disturbed environments and/or the absence of their native pests and competitors. Why they were so successful in competition with the native perennial grasses is open to speculation. A possible reason is that the winter-growing Mediterranean annuals depleted soil water in spring such that the summer-growing perennials were unable to survive the long, dry summers. Another factor may have been selective grazing of the perennials by sheep over summer, thereby reducing the aboveground green material of the perennials and presumably lowering energy reserves in their roots and crowns. In the case of annual legumes, one clear advantage was their capacity to fix nitrogen and thrive in the low N soils of southern Australia.

Instability of grazed pasture communities over the last half-century
During the last 50 years (the amelioration and restoration phases), the dynamics of pastures became even more complex in response to developments that accompanied or followed the pasture improvement revolution (1950-70). In addition to the grazing factor, superphosphate application and nitrogen fixation by legumes became important agents in determining the direction and pathways of botanical change. Both benefits and problems were initiated by pasture improvement, and this period of rapid change was followed by one of reassessment. Consequently, the pathways of botanical change in pasture communities became numerous and complex (Figure 2).

Humphreys (1997) postulates many reasons why the dynamics of grasslands are better described by a 'state and transition' model instead of Clements' succession model. The state and transition model is able to represent a set of multiple pathways and vegetation states occurring in response to several sets of factors. In addition, it is flexible in accommodating the notion of resilience (ability to recover) in an ecological system, whereas Clements' theory is too focussed on the concept of a single climax state, and on grazing management as the dominant factor that drives succession.

In Figure 2, adapted from Lodge and Whalley (1989) and Garden *et al.* (1996), the state and transition model is used in an attempt to summarise the nature and timing of the main changes that have occurred in grasslands on the tablelands of NSW, particularly during the last half-century. At one extreme of the time-management continuum, native and naturalised pastures were ploughed up, sown with perennial grasses and clovers, and fertilised; initially, such pastures were dominated by the sown legumes until soil nitrogen levels from rhizobial activity were sufficient to allow the grasses (and weeds) to compete effectively with the legumes. The botanical progression from initial legume-dominance towards eventual grass (or other non-legume) dominance was dependent on a minimum annual rate of superphosphate application (to stimulate and favour legume growth) and grazing (to enhance the transfer of fixed nitrogen to the associated species). For example, in grass/white clover pastures on the northern tablelands of NSW, the clover-dominant phase was intensified but the onset of grass-dominance hastened, following high annual rates of superphosphate (375 kg/ha) instead of intermediate (125-188 kg/ha/year) rates (Wolfe and Lazenby 1973). The cessation of superphosphate application to perennial ryegrass-white clover pastures in the same locality resulted in a loss of the sown species and a corresponding increase in the proportion of the native red grass (Cook *et al.* 1978).

At the other extreme of the management continuum, large areas of native pastures on the NSW tablelands were aerially sown with subterranean clover and treated with superphosphate from time to time. Introduced perennial grasses were usually not sown from the air; if they were, their establishment was frequently unsuccessful (Wolfe 1968) unless the guidelines developed by Campbell (1992) were used. These guidelines were to sow the grasses when rainfall is likely to be effective, use herbicide to minimise competition from the existing vegetation, and minimise seed theft by ants. In contrast to the difficulties associated with grass establishment, the establishment of aerially sown legumes (subterranean clover and/or white clover) was generally satisfactory. Further, so long as phosphate applications were maintained, legumes became dominant (Willoughby 1954) until the pastures were invaded by nitrogen-loving species such as annual grasses and forbs (Rossiter 1964) or thistles (Michael 1970) (Figure 2). Many such species were more aggressive for moisture, light and nutrients, and/or were better able to explore unfavourable soil conditions. Thus, many of the native perennial grasses were suppressed or eliminated by competition or by high grazing pressure.

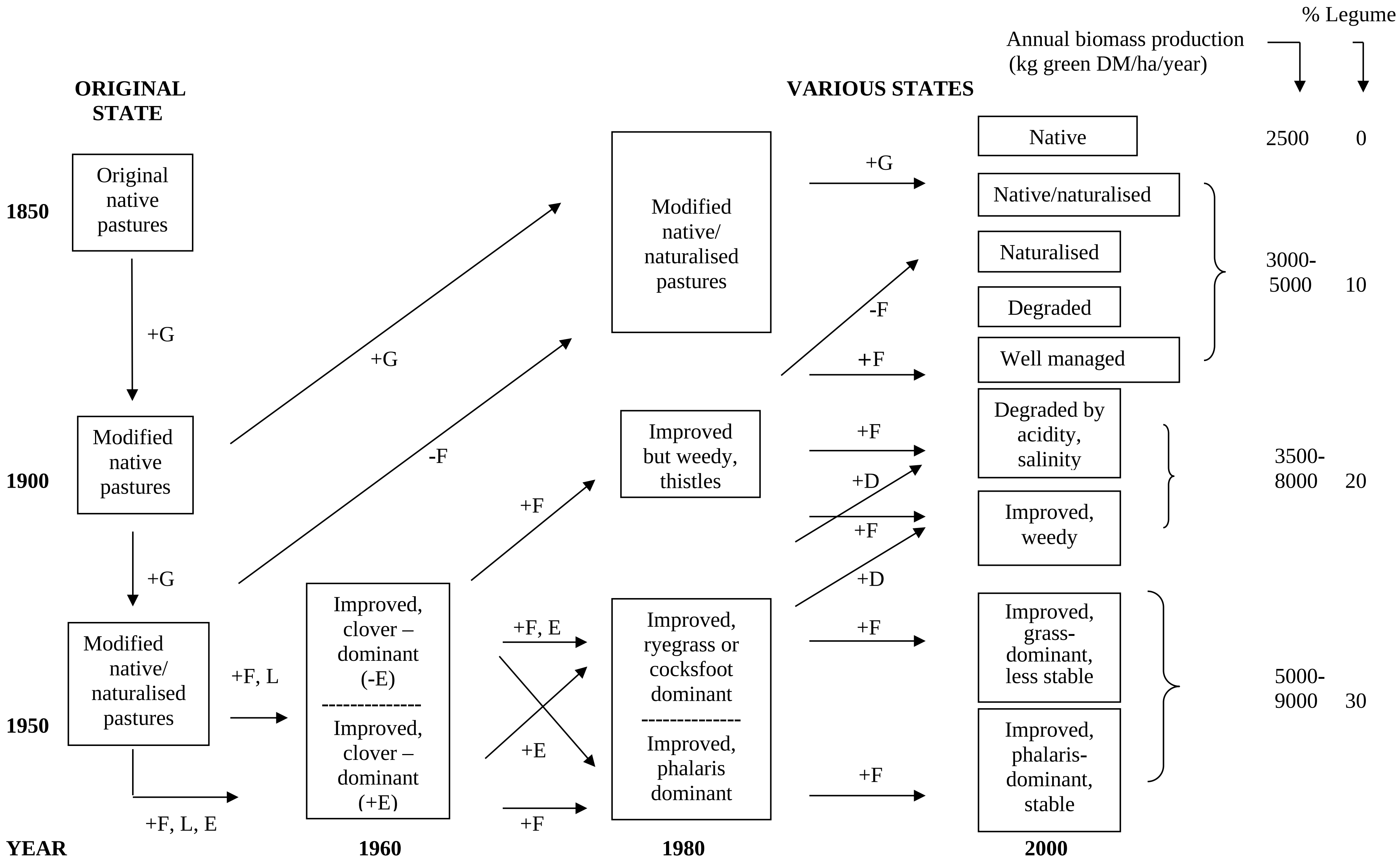

Figure 2. The application of the state and transition model to the generalised pathways of botanical change that have occurred in permanent pastures in south-eastern Australia. The main agents of change (G = grazing, F = fertiliser, L= legumes, E = exotic grasses, D = drought) are indicated.

There were several intermediate scenarios between these extremes. For example, less palatable tussocky grass species, such as Poa tussock (*Poa labillarderi*), were present in low numbers on the southern tablelands of NSW. They increased in frequency and size over time in response to the nitrogen fixed by the introduced legumes (Fisher 1972); then, heavy grazing pressure on the palatable species in the gaps between the tussocks exacerbated tussock dominance, fertiliser responses declined and the swards deteriorated into unproductive, nitrogen-deficient grasslands. Much the same sequence occurred on parts of the north-western slopes of NSW, where three-awned spear grass became dominant (Williams 1979), and on the Central Tablelands where the aggressive and indigestible serrated tussock (*Nassella trichotoma*) colonised tracts of non-arable country (Campbell 1998). This latter species, introduced from South America, became a serious weed of the grasslands of South Africa and New Zealand, as well as Australia (McLaren *et al.* 1998).

On many soil types, the prolific growth of pasture legumes that was evident in the early years of fertilised pastures in most areas of southern Australia did not continue. There were several reasons for this. From the 1970s, the general malaise of "pasture legume decline" (Carter *et al.* 1982) was evident, together with the progressively developing incidence of specific problems such as soil acidity (Cregan and Scott 1998) and the occurrence of certain pests and diseases of pastures (Panetta *et al.* 1993). Some of the possible biological, nutritional, economic and social factors involved in pasture decline are listed in Table 2.

Many of the environmental phenomena leading to change were episodic rather than progressive. Examples of episodic events include severe droughts that occurred in most decades (leading to the loss of drought susceptible, introduced perennials such as perennial ryegrass, cocksfoot and white clover); the apparently accidental introduction of three pasture aphids (the spotted alfalfa aphid (*Therioaphis trifolii*), the blue-green aphid *(Acyrthosiphon kondoi)* and the pea *aphid (Acyrthosiphon pisum*) into Australia in the late 1970s, seriously reducing the productivity and persistence of lucerne and annual medic pastures (Panetta *et al*., 1993); and the development of new races of plant pathogens, such as *Phytophthora clandestina* races that attack subterranean clover (Dear *et al*., 1993b).

In summary, both progressive and episodic occurrences produced in Australian grasslands a range of pasture states (Figure 2). The potential and actual changes, including those that occurred before the amelioration phase, are represented adequately by the state and transition model, which conforms fully with the ecological principle of succession (progressive change) but which avoids the inadequacies (linearity, inflexibility) that are embodied in the concept of a linear succession toward a monoclimax (Humphreys, 1997).

Ley pastures in the cropping belt

Ley pastures in Australian croplands (Puckridge and French, 1983) represent a different situation from that of the permanent pastures used for grazing sheep and cattle on the coast and tablelands of south-eastern Australia. In such leys, the opportunity is available to resow pasture legumes, and the time frame of the pasture phase between crop cycles is short (typically 1-5 years).

A useful conceptual representation of the population dynamics of the species in ley pastures is Grime's (1977) triangular CSD model (Figure 3) of the competition, stress and disturbance factors that influence the distribution and abundance of plant species. As noted by McIvor (1993), pasture and grassland species are located near the centre of the CSD triangle;

competition (C), stress (S) and disturbance are all important but none is overwhelming. The annual legumes used in leys are ruderal (R) species that tolerate disturbance. Ruderal species (C-R, S-R or C-S-R plants with short life cycles, high reproductive effort or other strategies for dealing with disturbed sites) take advantage of disturbance to colonise; they are favoured in productive croplands which are disturbed frequently by crop phases (cultivation, herbicide application) and by grazing during the pasture phase.

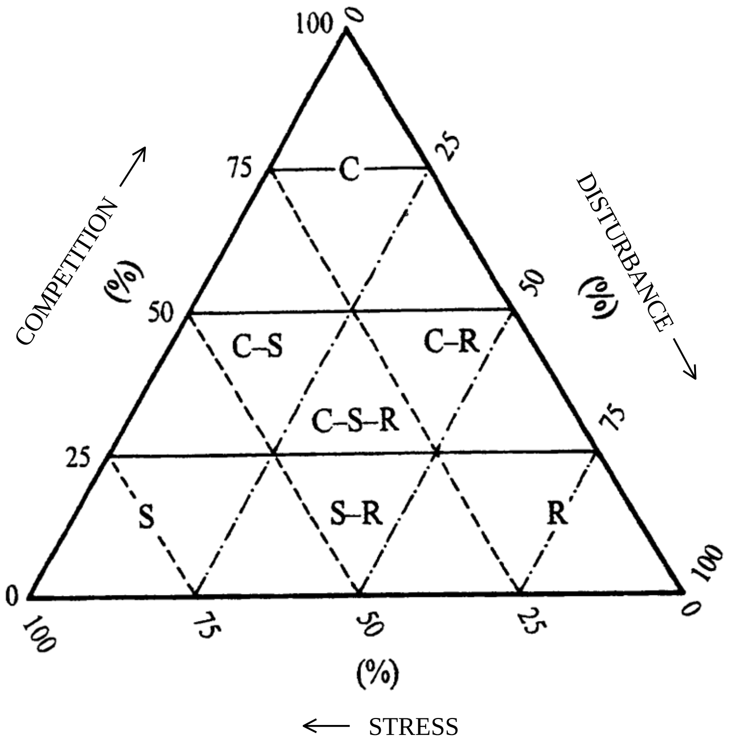

Figure 3: Adapted from Grime’s (1977) CSD model representing the factors of competition, stress and disturbance on plants, and the location of plants that possess primary strategies (C = competitors, S = stress-tolerators and R = ruderal species that are adapted to disturbance) and secondary strategies (e.g. C-S, C-S-R) of adaptation to these influences.

At the other extremes of Grime’s model, stress-tolerators (S – low growth rates and low reproductive effort) are favoured on less-disturbed, less-productive locations (e.g., acid soils). In contrast, competitors (C – high growth rate, low reproductive effort) are favoured in undisturbed, productive situations (such as abandoned cropland, or lightly grazed pastures). In permanent pastures or long leys in Australian agriculture, pasture species that exemplify success are tolerant of stress (for example, drought) and disturbance (grazing) and/or, in favourable locations, are efficient competitors for light and nutrients. Examples of such plants are phalaris, lucerne and, in locations with high annual rainfall (>750 mm), perennial ryegrass.

However, in any community, the CSD balance varies both spatially and temporally (McIvor 1993). This is particularly so in pasture leys where the annual species are examples of C-S-R plants that are adapted variously to competition (for moisture, light and nutrients), stress (acid soils, seasonal waterlogging) and disturbance (ruderal species are capable of profuse seeding and several have dormancy or other seed conservation mechanisms, and/or they are adapted in some way to grazing). A list of some common components of ley pastures and an overview of their CSD tolerance are given in Table 3. The population dynamics of subterranean clover and its companion species will be discussed in a later section.

Table 2. An updated list of the factors that are, or may be, associated with the decline of pasture legumes in southern Australia.

Medic decline, South Australia (Carter *et al.* 1982) • reduced spraying to control insect pests of pastures (earth mites and lucerne flea) • reduced application of superphosphate fertiliser to pasture • spread of sitona weevil • increased cropping intensity and consequent grazing pressure • poor grazing management and fodder conservation practices • increased use of herbicides in the cropping phase of the rotation • reduced undersowing of medic into cereal crops • rapid spread of pasture aphids (spotted alfalfa aphid, blue-green aphid and pea aphid) after introduction in 1977-78 • increased use of nitrogen fertilisers on crops (less need for medic ley) • apathy and despondency concerning value of medics
Medic decline, South Australia (Denton and Bellotti 1996) • drought • sulfonylurea herbicides (suspected) • higher populations of root lesion nematodes • zinc deficiency • *Rhizoctonia solani*
Subterranean clover decline, Southern Slopes NSW (Hochmann *et al.* 1990) • sub-optimal supply of P • root rot associated with *Phytophthora clandestina* • soil acidity
White clover decline, Northern Tablelands NSW (Hutchinson *et al.* 1995) • climatic stress, particularly the effect of January-March (late summer) rainfall on stolon survival • set-stocking at high rates, encouraging the presence of competitive annuals • soil N build-up (of secondary importance)
Annual legumes, Australia (Gramshaw *et al.* 1989) • economic trends (lower returns for beef and wool compared with cropping, removal of fertiliser subsidies, farm cost inflation during the 1970s) • insect pests and diseases (lucerne pathogens, clover scorch, root rots of *Trifolium* spp., effects of spotted alfalfa and blue-green aphids on lucerne, medics and other pasture legumes) • land degradation (soil acidity, salinisation, compaction) • changes in crop production techniques (more frequent cropping, longer cropping sequences, partial substitution of N fertilisers and pulses for pasture legumes)
High-rainfall zone and annual zone pastures, Australia (Wilson and Simpson 1993) • no regular and standardised surveys of the state of pastures, but *ad hoc* surveys have indicated sub-optimal clover content and the significant presence of unsown annual grasses, particularly in legume leys in the cropping zone • quantitative evidence is lacking on both the extent and the nature of change in botanical composition and productivity • factors that are claimed to be associated with low legume content, such as stocking rate, climatic variation, pasture age and management, are listed and reviewed. The list is similar to that of Carter *et al.* (1982) at the top of this table.

Table 3. Characteristics of some common temperate pasture species in relation to their tolerance of competition (C), stress (S) and disturbance (D).

Species		Characteristics
Subterranean clover *Trifolium subterraneum*	C S D	May be outcompeted by annual grasses for P and for light; subclover is effective in suppressing some weeds in their rosette stage (for example, St John's wort) Tolerant of Al and Mn toxicities in acid soils; *yanninicum* subspecies tolerates waterlogging; *brachycalycinum* subspecies is adapted to neutral-alkaline soils Outstanding tolerance of grazing - seedlings unattractive to livestock, plus defoliation in winter stimulates inflorescence production, burr burial and seed yield; prolific seed production, and effective seed conservation mechanisms (embryo dormancy, hardseed)
Annual medics *Medicago* spp.	S D	More effective than subclover in tolerating water stress and Zn deficiency, but sensitive to acid soils High hard seed levels guarantee persistence in semi-arid localities
Serradella *Ornithopus compressus*	S D	Very tolerant of Al toxicity in acid soils, deep rooting allows it to access Zn at depth in sandy soils Prefers sandy soils, coverage of seed by drifting sand is important in the breakdown of hard seeds
White clover *T. repens*	C S D	Competes well with grasses when soil N levels are low Adaptable to a range of soils Stoloniferous, perennial habit but drought-susceptible. However, it is a prolific seeder (low levels of hard seed) and can regenerate from seed
Balansa clover *T. michelianum*	S D	Tolerant of waterlogging Moderate levels of hard seed
Persian clover *T. resupinatum*	S D	Tolerant of waterlogging, heavy-textured soils Prolific seeder, moderate levels of hard seed
Lucerne *M. sativa*	C S D	Deep-rooted, crown habit - competes well for water Some cultivars susceptible to insects, root and crown rots Adapted to rotational grazing
Perennial ryegrass *Lolium perenne*	C D	On high-N soils, it competes well for light with white clover but shallow-rooted habit means susceptibility to Australian droughts Free-tillering, recovers well from grazing; will re-establish well from seed
Phalaris *Phalaris aquatica*	C S D	Allelopathic, most persistent of the introduced perennial grasses due to deep rooting habit Seedlings susceptible to soil acidity. Once established, strong tuber resists overgrazing
Annual ryegrass *Lolium rigidum*	C S D	Competes well for light & nutrients with clover, crops Very tolerant of Al and Mn toxicities in acid soils Prolific seeding, with dormancy mechanisms
Barley grass *Hordeum leporinum*	C D	Effective scavenger for soil P Prolific seeder, seeds unattractive to livestock
Silver grass *Vulpia* spp.	C D	Allelopathic Herbage unattractive to livestock; prolific seeder
Capeweed *Arctotheca calendula*	D	Mature plants unattractive to livestock; prolific seeding and complex seed dormancy mechanisms
Paterson's curse *Echium plantagineum*	C D	Tall when mature, shading out competitors Not eaten by cattle and horses at any stage, nor by sheep when mature
Saffron thistle *Carthamus lanatus*	D	Prolific seeding; herbage not attractive to livestock
Skeleton weed *Chondrilla juncea*	S D	Deep rooting and therefore drought tolerant; susceptible to biocontrol agents Prolific seeding

As in the high rainfall zone, problems have been reported in the ley pasture system in Australia (see Table 2, p. 12). The problems were due in part to the attitudes of landowners, who focussed their attention more on the higher economic returns from crops when livestock prices were low during the 1980s and 1990s (Reeves and Ewing 1993), and to the factors underpinning the apparent decline in the legume content of ley pastures (Carter *et al.* 1982, Hochmann *et al.* 1990, Gramshaw *et al.*, 1989), factors that are reported and listed in Table 2. Solutions have been found in liming (Cregan and Scott 1998), improved agronomy (Hochmann *et al.* 1990), and the selection and release of tolerant cultivars of annual legumes (Collins and Stern 1987). A promising technique, winter cleaning with herbicides (a combination of glyphosate and paraquat), has been developed to reduce weed content and boost the legume content of ley pastures (Thorn 1992). Further improvements in the effectiveness of legumes in ley pastures are likely through the increased use of lucerne as a component of leys (Peoples *et al.* 1998), and the adoption of pasture monitoring protocols to assist farm managers identify key indicators of pasture legume production and guide management accordingly (Crosby *et al.* 1993, Wolfe *et al.* 2006).

However, there are additional threats, such as the evolution or introduction of new weed ecotypes or new disease races, and the development of herbicide resistance in weeds, that are likely to cause problems in legume leys. The failure of Group A and Group B selective herbicides to control annual ryegrass (*Lolium rigidum*), a common component of wheat-belt pastures before the advent of these selective herbicides, is one issue that is now causing particular concern (Powles *et al.* 1997). Another concern with herbicides is the deleterious effect of some residual herbicides on pasture legumes, particularly on alkaline soils where the degradation of these herbicides is slow (Gillett and Holloway 1996).

Summary

During the last two centuries, there have been profound shifts in the botanical composition of temperate pastures in Australia, and the pace of change has increased in recent decades. Because of the complexity of the interactions between pasture species and environmental phenomena, no one model is available to explain the dynamics of pastures. However, the state and transition model is a useful and flexible way of representing and understanding pasture dynamics. The focus of the competition-stress-disturbance model is on the short-term response of individual plant species to these three factors and thus it complements the plant community focus of the state and transition model. The use of these two models is recommended as a way of understanding both the ecology and agronomy of grasslands/pastures. They are used in the next section in case studies that illustrate the success of some pasture species in the Australian environment.

Successful Australian pasture species

Pasture components - exotic or native?

A recent estimate (Hill 1996) of the potential areas of adaptation in Australia for the main sown pasture species - all of which were originally introduced into Australia - is given in Table 4. This vast potential may be compared with another recent estimate, that of the relative importance of pasture types in NSW (total area of sown pastures 5-6 m ha, Australia 25-30 m ha) (Table 5), derived from an Australian temperate pastures database (Pearson *et al.* 1997). The current distribution of introduced pasture species is broadly depicted in Figure 3 [after Moore (1970) and Hill (1996)]. The main features of this map are the inland aridity barriers to the occurrence of all species, together with other boundaries (climatic, soil pH) that are applicable to the distribution of annual legumes (Donald 1970). However, despite the emphasis in Australian agronomy on exotic pasture species, native pastures still cover a much

Table 4. Estimated potential areas of adaptation for nine temperate annual and perennial pasture species in Australia (Hill 1996).

Pasture species	Area (million ha)	% of freehold + leasehold land
	South-eastern Australia	
Subterranean clover	60.8	67.8
Balansa clover	23.7	26.5
Persian clover	30.7	34.3
Barrel medic	27.0	30.1
Serradella	37.4	41.7
White clover	20.7	23.0
Lucerne	86.4	96.4
Perennial ryegrass	19.4	21.6
Phalaris	33.9	37.8
Total, south-eastern	89.6	100.0
	South-western Australia	
Subterranean clover	20.8	94.0
Balansa clover	4.9	22.3
Persian clover	5.8	26.0
Serradella	7.2	35.6
Barrel medic	17.1	77.3
White clover	0.2	1.0
Lucerne	9.3	42.1
Perennial ryegrass	<0.2	<1.0
Phalaris	2.7	12.0
Total, south-western	22.1	100.0

Table 5. The relative importance (on an area basis) of pasture species, genera and types in NSW, 1995 (from Pearson *et al.* 1997).

Description	Percentage by area
Unimproved native pasture	62.5
Improved (fertilised) native pasture	16.8
Subterranean clover	14.8
White clover	6.0
Lucerne	4.5
Phalaris	3.4
Cocksfoot	2.2
Annual medics	2.1
Perennial ryegrass	1.5
Tall fescue	1.1
Annual ryegrasses	0.4
Serradella	0.2

larger area than that of introduced plants (Table 5). While pasture legumes must be based the locally adapted variants of exotic germplasm, there is a strong case for the use of management options that utilise adapted native grasses, and for the inclusion of a wider range of perennial grasses, particularly C_4 species, for pastoral use (Johnston *et al.* 1999). Johnston *et al.* (1999) questioned the amount of research and development effort that has gone into replacing indigenous grasses with exotic introductions, many of which fail to persist over the frequent droughts that characterise the Australian climate. They reviewed the evidence for the persistence, productivity and nutritive value of several species of native grasses in grazed pastures, and argued for strategies that utilise adapted, palatable grasses such as wallaby grass in low-input situations, or even C_4 native grasses in areas that are prone to hydrologic imbalance. Importantly, Johnston *et al.* (1999) acknowledged the folly of a “one-or-the-other” philosophy, compared with an approach that achieves complementarity between a low-input, conservative approach to pasture management and the high-input, exotic approach to pasture improvement that has produced notable gains in the productivity of Australian agriculture.

In the winter-dominant rainfall areas of southern NSW and northern Victoria, the presence of a persistent perennial grass in permanent, grazed pastures appears essential for several reasons. Annual pastures in such areas have a potential mid-winter imbalance in the supply (relatively high) and demand (low) for water and nitrate in the soil profile (Johnston *et al.* 1999). A persistent perennial component increases the pre-winter soil water deficit (for example, 135 mm for annuals, 210 mm for perennials - Whitfield 1998) and thereby helps overcome this potential imbalance. Minimising the flows of water beyond the plant roots counters dryland salinity (Passioura and Ridley 1998) and reduces the rate of soil acidification (Ridley *et al.* 1999). Such differences are meaningful to the achievement of hydrologic balance, particularly between the 600 and 800 mm average annual rainfall isohyets in northern Victoria and southern NSW. Soil degradation is common in these areas due to a combination of factors (recharge, salt loads in the soil profile, poorly-buffered soils) (Passioura and Ridley 1998).

The better water use of palatable perennial grasses enhances livestock production compared with pastures based on annuals or poorly persistent perennials (Axelsen and Morley 1968). Furthermore, a persistent perennial grass component in pasture prevents or reduces the incidence of undesirable weeds such as thistles (Michael 1970) and the ingress of unpalatable native and introduced tussock grasses, as discussed earlier.

Case studies.

Some case studies of successfully introduced pasture plants are reviewed below. Successful pasture species in Australia are those which are stable (resistant to change), resilient (able to recover) and productive. Case studies of a number of introduced pasture plants that have been successful in the Australian environment are relevant to the future ideal of sustainable production. They demonstrate some principles that apply to the success or failure of desirable pasture species, and highlight lessons that should have been learnt. The dynamics of phalaris swards and subterranean clover pastures are treated in most detail, reflecting their success and greater importance in Australian agriculture than is the case elsewhere.

Phalaris - a persistent grass in Australia.

The ‘Australian’ commercial cultivar of phalaris is, according to experiments (e.g. Hill 1985) and experience (Watson 1993), the most persistent of the temperate perennial grasses that have been introduced and sown in Australia. In southern NSW and Victoria, varieties of phalaris are capable of reliable persistence down to a median annual rainfall of 500 mm, whereas perennial ryegrass will persist only where the rainfall is at least 700mm. Between these isohyets, where phalaris and to a lesser extent cocksfoot are the only reliable perennial grasses, there is a considerable area of land (Figure 4) at risk due to land degradation. Even in wetter tableland localities where more than 700-800 mm rainfall is received annually, phalaris has survived occasional droughts that have killed cocksfoot, tall fescue (*Festuca arundinacea)* and perennial ryegrass (Fitzgerald *et al.* 1995).

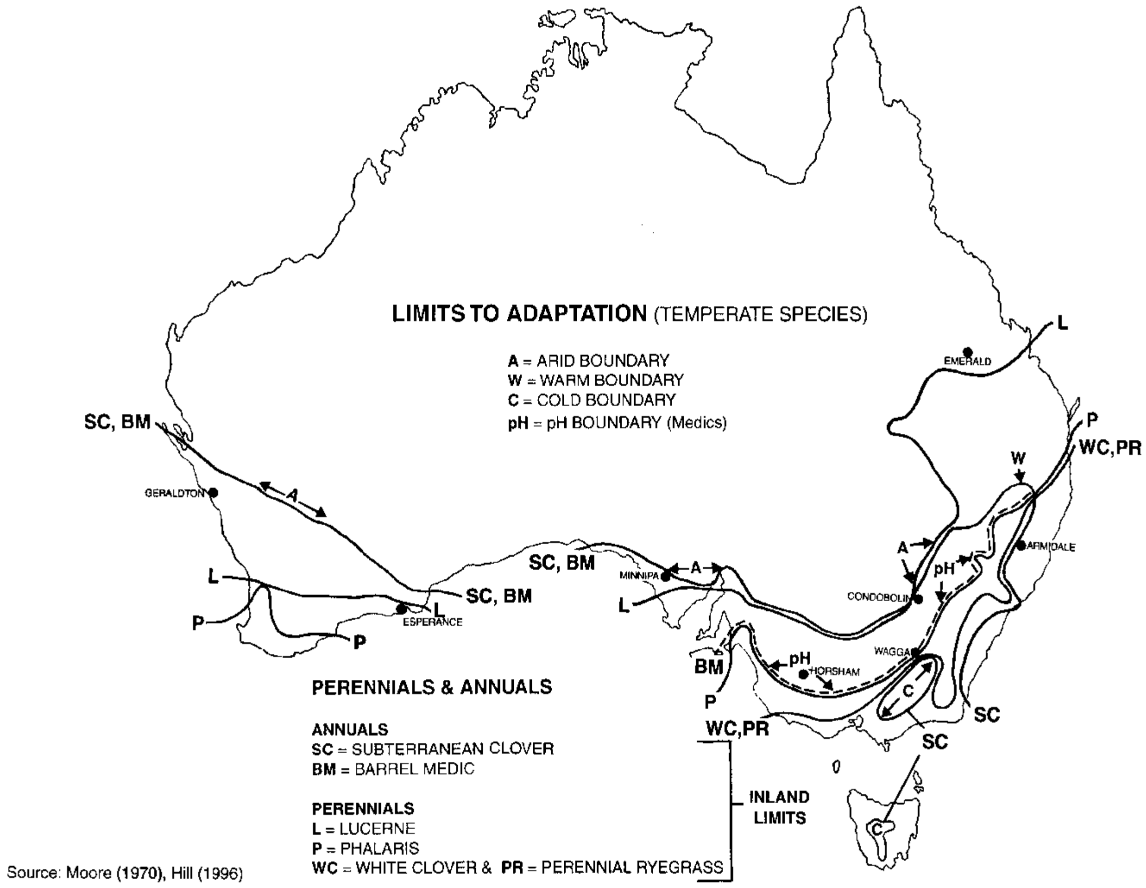

Figure 4: The limits to the growth and survival of pasture species, after Moore (1970) and Hill (1996).

A deep-rooted and prostrate habit, dense tillering, partial summer dormancy and the presence of a large underground rhizome are features associated with the outstanding persistence of the original 'Australian' strain of phalaris (Oram and Culvenor 1994). The strong persistence of 'Australian' phalaris and the importance of stocking rate was illustrated by Hutchinson (1992), who compared over 28 years the presence of phalaris with annual grasses in pastures grazed by sheep on the Northern Tablelands of NSW (Figure 5). The stability and resilience of phalaris following grazing and drought, at least at low (10 sheep/ha) and medium (20 sheep/ha in earlier original 'Australian' strain of phalaris (Oram and Culvenor 1994). The persistence of 'Australian' phalaris and the importance of stocking rate was illustrated by Hutchinson (1992),years, then 15 sheep/ha) stocking rates (Figure 5), contrasts with the death of white clover (Hutchinson *et al.* 1995, Hutchinson and King 1999), perennial ryegrass, tall fescue and cocksfoot in improved pastures on the Northern Tablelands in droughts such as those that occurred in 1965, 1980-82 and 1994 (Fitzgerald *et al.*, 1995). Similar observations on the susceptibility of perennial grasses to high stocking rates and drought have been made in long-term grazing experiments and on farm paddocks on the central tablelands (Kemp and Dowling 1991) and the southern tablelands (Axelsen and Morley 1968) of NSW. The ecological importance of a relatively stable perennial grass component, and the high cost of re-establishing this component if it is lost, makes it important that persistence, rather than "productivity", be the first priority in selecting grass cultivars.

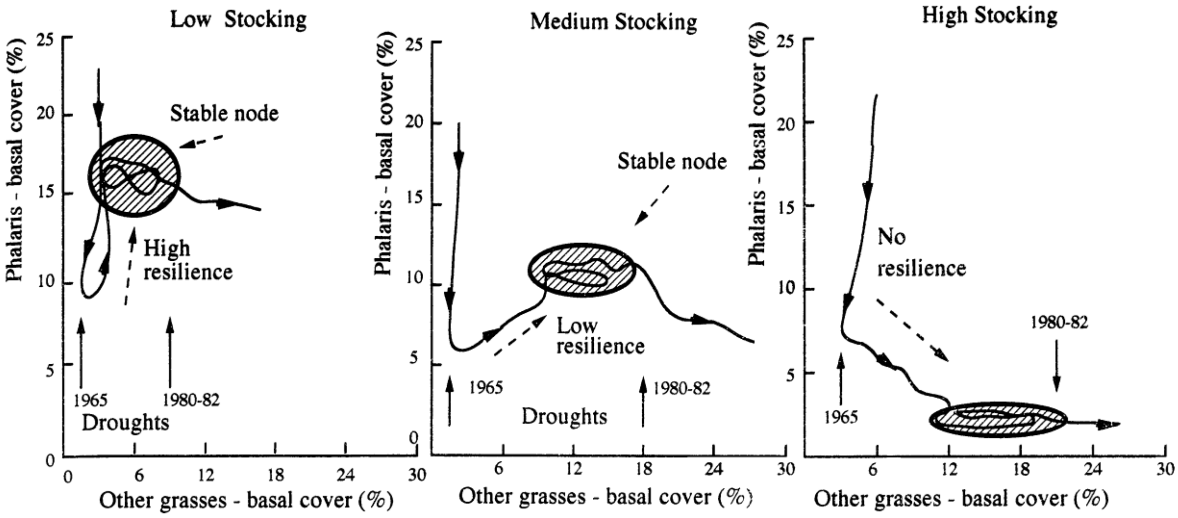

Figure 5: The stability and resilience of phalaris from 1964 to 1991 (inclusive) on the Northern Tablelands of NSW, after Hutchinson (1992).

Many farmers are reluctant to grow phalaris (Barr and Cary 1992) because of perceivable but avoidable management problems (palatability, dominance, animal disorders) and other beliefs (establishment difficulty) associated with growing the plant. There are also some qualifications that need to be made to the use of phalaris to create relatively stable improved pastures. First, the newer, winter active cultivars of phalaris released during the 1960s and subsequently (cvs Sirocco, Sirolan, Sirosa) have been found to be up to 50% less persistent, measured as basal cover, than the ‘Australian’ phalaris cultivar (Culvenor and Oram 1992). According to Oram and Culvenor (1994), ‘Australian’ phalaris has a more prostrate, densely tillered habit than the newer, winter-active cultivars (Sirosa, Sirolan), and it has more capacity for rhizomatous spread; for these reasons it is suited to heavy grazing. Selection in grazed swards for basal cover, which has a higher heritability than the spreading ability of spaced plants (Oram and Culvenor 1994), is a potential way of improving the persistence of future cultivars of phalaris. Second, as reported in Oram and Culvenor (1994), phalaris was found to be intolerant of high soil aluminium (Al) levels that, together with a high availability of soil manganese, may adversely affect plants in highly acid soils (pH_{Ca}<5.2) (Cregan and Scott 1998). While a buildup in soil Al levels may be constrained by the ability of well-established, deep-rooted phalaris to capture leached nitrate, attempts to establish phalaris on soils that are already acid may be thwarted by the sensitivity to Al of the root growth of the establishing phalaris seedlings, particularly if phalaris is competing with a companion weed species that is tolerant of high acidity. The effect of differential tolerance to Al on competitive relationships in perennial grass/annual ryegrass binary mixtures 24-36 weeks after sowing was shown in a pot experiment (Rubzen 1996) (Table 6). The grasses used were phalaris (cv. Sirosa, sensitive to Al) and cocksfoot (cv. Porto, highly tolerant), and the ryegrass ecotypes were either collected from an acid soil site where Al was present at potentially toxic levels (A-ryegrass) or from an alkaline soil site that contained no free aluminium (B-ryegrass). In the alkaline soil pots, both ryegrasses suppressed phalaris or cocksfoot, but in acid soil the competitive outcomes were determined by the level of tolerance of each of the grasses to aluminium: the A-ryegrass ecotype suppressed the sensitive phalaris but A-ryegrass was suppressed by the highly Al-tolerant cocksfoot cultivar. These results indicate that the difficulty of establishing a sensitive plant type on acid soils may be exacerbated by the presence of an adapted competitor. Sources of aluminium tolerance for phalaris are currently being used in a breeding program to produce a tolerant cultivar (Oram and Culvenor 1994).

Table 6. Relative changes in the yield[a] of the components[b] of 50:50 binary mixtures (replacement series design) compared with the yield of each component in monoculture (Rubzen, 1996).

Soil treatment in pot	Binary mixtures	
Acid soil (pH 3.7, 2.3 ug/mL Al)	A-ryegrass/phalaris +87% > -82% A-ryegrass/cocksfoot -37% < +40%	B-ryegrass/phalaris -50% < +39% B-ryegrass/cocksfoot -85% < +86%
Alkaline soil (pH 8.2, 0.01 ug/mL Al)	A-ryegrass/phalaris +73% > -70% A-ryegrass/cocksfoot +68% > -77%	B-ryegrass/phalaris +69% > -65% B-ryegrass/cocksfoot +72% > -67%

[a] Regrowth was measured from the second to the third harvest, i.e. from 24 to 36 weeks after sowing.

[b] Companion grasses were: cocksfoot (cv. Porto): ED Al_{50} value[c] = 272 µM, v. highly tolerant
phalaris (cv. Sirosa): ED Al_{50} value = 28 µM, sensitive

Ryegrasses were: A-ryegrass: ED Al_{50} value = 188 µM, highly tolerant
B-ryegrass: ED Al_{50} value = 21 µM, highly susceptible

Note: The ED Al_{50} value is the equivalent dose (concentration) of aluminium in solution that would produce a 50% toxic response (in this case, a 50% reduction in root extension) compared with the nil-effect control.

In summary, phalaris is the most persistent of the temperate perennial species introduced into Australian agriculture. However, due to the constant disturbance of grazing, successional change in perennial pastures is consistently directed towards annualisation (Hutchinson and King 1999). According to Hutchinson and King (1999), the loss of sown and palatable perennial grasses can be explained “as a balance between their strong competitive ability under conservative stocking *versus* their vulnerability to increased levels of disturbance from the combination of high stocking rates and grazing preference”. Stresses, such as drought and poor fertiliser management (Cook *et al.* 1978, Hutchinson and King 1999), exacerbate this vulnerability.

Lucerne, and competition between the components of lucerne mixtures

In southern Australia, lucerne (*Medicago sativa*) has an area of potential adaptation that is greater than that for any other pasture species (Hill 1996, Figure 4). In practice, the wider adoption of lucerne has been constrained by its susceptibility to acid soils, the need for a rotational grazing regime to ensure its survival (Leach 1978, Lodge 1991), the incidence of insect pests and disease (Lodge 1991), and by the attitudes of farmers and graziers who perceive lucerne to be a special-purpose pasture rather than an all-rounder. Hence, lucerne is usually sown in “hay paddocks” as the only component of a pasture. However, there is advocacy of lucerne as a component of permanent or semi-permanent grass-clover pastures, and with subterranean clover or medic in ley pastures, as a means of enhancing livestock production (Wolfe *et al.* 1980), N fixation (Peoples *et al.* 1998), and/or water extraction from the soil profile (Crawford and Macfarlane 1995; Dear 1998). This potential warrants a short consideration of the dynamics of lucerne mixtures.

In permanent pastures, lucerne is not a particularly compatible component when associated with a perennial grass. The grass either competes strongly for moisture with lucerne during summer and autumn (Wolfe and Southwood 1980), or the rotational grazing management that is essential for the plant's survival (Leach 1978, McKinney 1974) does not suit the growth/survival of the companion grass.

In ley pastures, too, there is incompatibility between the components of the recommended lucerne/annual legume mixtures. Annual legumes such as subterranean clover usually are grown with lucerne to provide winter feed when lucerne growth is poor. These lucerne mixtures are frequently unstable (Leach 1978) and, in lower rainfall environments (<500 mm annual rainfall), gaps develop between the lucerne plants. The gaps are either bare or, when soil N levels increase, occupied by opportunistic annual grasses such as *Vulpia* spp. Surface soil erosion is encouraged along with high levels of dust contamination in the wool. Wolfe and Southwood (1980) found that lucerne grew best with Geraldton, the least productive of three subterranean clovers used, and that seed yield of subterranean clover could be increased by increasing the lucerne row spacing. More recently, it has shown that lucerne can reduce subterranean clover persistence in two ways, reducing the seed set of the subclover and the establishment of clover seedlings in autumn. Lucerne dries out the soil surface rapidly during clover seedling germination and establishment, particularly when there is an early autumn break and temperatures and evaporation rates are high (Dear and Cocks 1997). This results in a smaller proportion of the seed pool successfully establishing (Dear 1998).

Hence, while lucerne is a valuable pasture species, its use has been somewhat constrained, due in part to its need for rotational grazing and to its incompatibility with other pasture components. The improvement of relationships between lucerne and companion species is a worthwhile topic for future research.

The success of subterranean clover in pastures

Characteristics of subterranean clover

In Mediterranean-type climates, subterranean clover is a species that is well adapted to continuous grazing with livestock (Collins 1978). During summer, the pool of hard seed (seed with an impermeable seedcoat) is partially protected from grazing by burr (pod) burial but losses of up to 50% of the seed bank over summer have been recorded (Dear and Jenkins 1992). During winter, when grazing pressure is high (supply of green herbage < demand for green feed), the continued close grazing of the prostrate herbage stimulates seed production in spring (Collins 1978). During spring, low grazing pressure on green herbage (supply > demand) and burr burial protects the developing inflorescences. The only time when subterranean clover is vulnerable to grazing is at the seedling stage; fortunately, livestock avoid grazing the young seedlings.

In spite of the adaptation of subterranean clover to grazing, pastures commonly contain a number of other vigorous sown and invading species, with the sown clover component comprising 30% or less of the pasture biomass. The nature of competition between subterranean clover and other species, and between strains of subterranean clover, is important from several perspectives. These include the selection of cultivars that are more vigorous and successful in environments where clover decline is occurring, and the need to replace oestrogenic strains (high-formononetin strains that cause ewe infertility) with low-formononetin cultivars. An account of the key population characteristics that determine the success of the species provides an ideal introduction to a consideration of the relationships of subterranean clover with its competitors.

Rossiter (1966) reviewed the characteristics that seem to be associated with the long-term success of strains of subterranean clover, namely their survival/productivity over a number of seasons or crop/pasture cycles. He listed the seed producing capacity of a strain as an important determinant of success or failure. However, it is our experience with testing hundreds of subterranean clover strains and crossbreds over several years in NSW that, rather than inherent differences between strains in their potential seed production, local success depends on the degree of fit between their inflorescence development (triggered by the temperature and light regime - Archer *et al.* 1987) and the soil moisture profile in spring. For maximum seed production of subclover (similar to annual medic, about 200 g/m^2 - Wolfe 1985), moisture conditions must be non-limiting during the flowering and seed development phases (Collins 1981; Blumenthal and Ison, 1993), a total of about 70 days. This ideal is rarely achieved in the Australian environment, and a target seed production of 60 g/m^2 is sufficient for a high quality subclover pasture (Dear *et al.* 1993a). A practical guideline, to optimise the balance between spring herbage production (later-maturing cultivars produce more spring herbage) and the amount of seed, is to choose a cultivar that flowers and sets seed just before soil moisture usually runs out in spring.

The strong relationship between increasing rainfall and time to maturity of subterranean clover observed in environments of southern Australia does not always hold in the plant's countries of origin. Piano *et al*. (1993) found that although mean populations of *T. subterraneum* subspecies *subterraneum* collected in Sicily increased with increasing rainfall, in *T. subterraneum* subspecies *brachycalycinum* the effect of altitude was greater and rainfall less marked. There is also evidence that seed production characteristics of subterranean clover strains of similar maturity can vary. Piano and Pecetti (1997) found that despite Geraldton and Seaton Park commencing flowering at a similar date, Geraldton had a shorter flowering period and generally a higher seed yield. Small-seeded strains of subterranean clover have also been shown to reach a mature seed weight faster than larger-seeded lines (Pecetti and Piano, 1994). This trait may contribute at least in part to the success and dominant position of small-seeded strains of subterranean clover, such as cvs Goulburn, Denmark and Leura, in recent releases from the Australian breeding program where high seed production is considered a high priority.

Rossiter (1966) also identified conservation of seed, particularly through hardseededness, as a crucial trait for success. The importance of hardseededness has been borne out consistently in wheat-belt environments in Western Australia (Smith *et al.* 1996) and NSW (Wolfe 1985, Dear *et al.* 1993a). In Western Australia, where the incidence of false breaks (early rains separated from the main onset of rainfall, resulting in germination of the seed and subsequent death of seedlings) is low, hardseededness is important to enable subterranean clover seed reserves to carry through a 1-2 year cropping phase. In NSW, the cropping phase is 4-6 years long and most pastures are resown rather than regenerating from hard seed. However, in NSW, the seasonal “break” is much less well defined than in the more typical Mediterranean climate of south-western Australia (Cornish 1985); false breaks may reduce the number of seedlings that survive to well below the target of about 1500 $plants/m^2$ that is needed to optimise the early dry matter production of sub clover. Hence, in most environments, moderate to high levels of residual hardseededness (20%-60%) are sought in sub clover cultivars, even in mid-season strains (Dear *et al.* 1993a).

Increased levels of hardseededness can also be used to guard against a failure to set adequate levels of seed due to herbicide damage, insect attack or drought (Dear and Sandral 1997) (see Figure 6). Indeed, near the arid boundary for annual legumes, such as at Condobolin in central NSW (Cornish 1985), annual medics are preferred to subterranean clover: not only are they more tolerant of water stress during seed development (Wolfe 1985), but also because cultivars with very high levels of residual hardseededness are available (Cocks *et al.* 1980). On the other hand, in cool, moist environments such as northern NSW (Lodge *et al.* 1990) and Tasmania (Evans and Hall 1995), a low level of residual hardseededness (<20%) is needed for persistence of subterranean clover: the cool climate and summer growth modify the soil temperature profile, slow the rate of hardseed breakdown during summer and enhance the survival of seedlings in autumn.

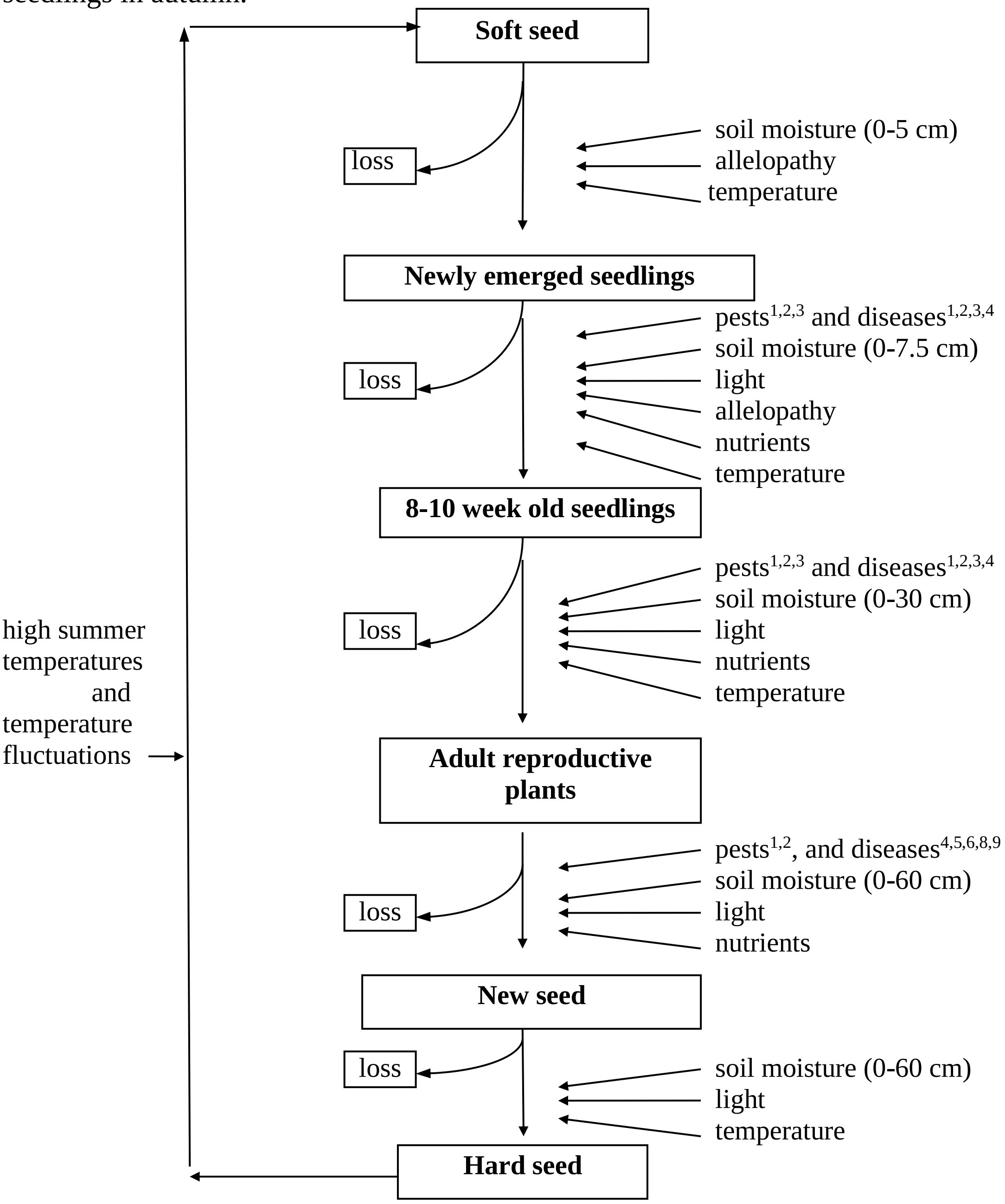

Figure 6: Stages in the life cycle of subterranean clover and pathways by which the presence of perennial pasture plants or their residues may influence the outcome.

Pests include: (1) Red legged earth mites and Blue Oat Mites, (2) Lucerne flea, (3) Aphids.

Diseases include: (1) *Phytophthora clandestinum*, (2) *Pythium* spp., (3) *Rhizoctonia*, (4) Viral diseases, (5) *Kabatiella caulivora*, (6) *Cercospora sp.*, (7) *Fusarium*, (8) *Oidium* spp., (9) *Pseudopeziza trifolii*

Smith *et al.* (1996) showed that, amongst legume species that have a similar hard seed level, the pattern of breakdown from hard to soft (permeable) seed differed, with some breaking down more rapidly in summer and early autumn, while others had a delayed pattern. The latter pattern resists false breaks but it may decrease competitive ability with rapidly germinating weed species. Thus, in a summer-dominant rainfall environment, Lodge (1996) showed that the seedling recruitment of subterranean clover and barrel medic was highest when they germinated in mid-summer, whereas with other legumes it was highest with an autumn germination.

Other notable characteristics of subterranean clover are those that confer resistance or tolerance to various limiting factors, including diseases such as clover scorch (Collins and Stern 1987) and root rots (Dear *et al*. 1993b), insect pests (Gramshaw *et al.* 1989), soil nutrient deficiencies/toxicities and waterlogging (Reed *et al.* 1985). These characteristics are important in ensuring the adaptability and competitive ability of particular cultivars and strains of subclover in stressful (Grime 1977) situations.

As noted by Rossiter (1966, 1977) there are attributes of subterranean clover, other than those mentioned above, that are not well understood in terms of their effects on competition between strains within a season. Little attention has been given to the vegetative stage properties listed by Rossiter (1977); properties such as seedling establishment capability, leaf size and petiole length may bear on the success or failure of one strain growing with another, or with other species. For example, when the defoliation of a mixture of subterranean clover strains was infrequent, a later maturing, longer petiole strain (Clare) was able to overtop early maturing, shorter strains (Seaton Park, Daliak) (Hill and Gleeson 1991). This result agreed with an earlier study by Rossiter and Pack (1972), who found that increased stocking rates during vegetative growth improved the competitive performance of cv. Geraldton, a short-stature strain, by restricting the over-topping effect of the taller Woogenellup cultivar.

Cocks *et al.* (1982) found that the high formononetin content of some subterranean clover strains was an important characteristic associated with their long-term success in mixed populations, since sheep prefer to eat cultivars with a low content of formononetin (Rossiter, 1974). More recently, Cocks (1992) found that levels of genistein, another of the three phyto-oestrogens in subterranean clover, tended to increase with time in divergent genotypes of subterranean clover in the field. Genistein is thought to be one of the phytoalexins, substances produced by plants to activate enzyme defences in response to infection by fungi and bacteria (Bell 1981, reported in Cocks 1992a).

In summary, the ability of subterranean clover to survive and compete in plant communities is determined by a number of known factors, of which time to reach maturity and hardseededness are paramount. However, the influence of some other characteristics of the species on competitiveness is not precisely known.

Competition between subterranean clover and other annual species

There have been a number of long-term studies undertaken on the dynamics of annual pastures in the Mediterranean climate of southern Australia (Rossiter 1966, Cocks 1994a). These studies are relevant, at least in an ecological sense if not strictly an agronomic one, to species frequency and productivity in *short-term* subterranean clover leys that regenerate, or are sown, after a cropping phase. The conditions at the end of the cropping phase, such as depleted levels of soil N and low levels of disease organisms, favour the early growth of clover. Thereafter, the success of subterranean clover during the pasture phase is determined by factors such as the size of the populations of other annual grasses and herbs, seasonal conditions, phosphate supply and defoliation/grazing (Rossiter 1966).

In southern Australia, the main competitors with subterranean clover in annual ley pastures are barley grass, annual ryegrass, silvergrass, brome grasses (*Bromus* spp.), capeweed, and erodium/storksbill (*Erodium* spp.) (Rossiter 1966). Low annual legume contents in mixed pastures can be traced to differences between non-legumes and legumes in a number of characters associated with establishment. For example, McWilliam *et al*. (1970) found differences between legumes and grasses in the water absorption of seeds, rates of germination, and early root elongation; in their experience, annual ryegrass was superior to annual legumes in its ability to germinate under moisture stress. The evidence for subterranean clover, reviewed by Rossiter (1966), indicated that, once germinated, subterranean clover seedlings were more susceptible to moisture stress than common associate species, such as barley grass, capeweed, erodium, and Paterson's Curse. According to Rossiter (1966), non-legumes were robust in years in which "false breaks" occurred in mid-autumn, while the contribution of subterranean clover declined as a result of insufficient numbers of surviving plants. However, if the early break was followed by moist conditions, subterranean clover was favoured; late rains favoured a range of species including subclover (Rossiter 1966).

In addition to population density, phosphate supply and defoliation regimes also affect the botanical composition of annual pastures in southern Australia (Rossiter 1966). In southern NSW, a series of investigations on ley pastures grazed by sheep (Ayres *et al*. 1977) revealed that subterranean clover dominated heavily-grazed leys at moderate levels of phosphate supply and low levels of soil N, but barley grass quickly became dominant if superphosphate was topdressed at moderate to high rates (>150 kg/ha annually), particularly if stocking rates were low. This and other work on defoliation (Collins 1978) and management (FitzGerald 1976) of subterranean clover led on to recommendations for clover leys in southern NSW (Southwood and Wolfe 1978). These recommendations, which are still current[2] (Dear and Sandral 1997) were: choose a persistent cultivar of subterranean clover; establish at 3-10 kg/ha under a light seeding rate (<20 kg/ha) of a cover crop (barley); fertilise the cover crop with additional superphosphate for the pasture phase (a total of 180 kg/ha, drilled); avoid or minimise topdressed phosphate during the pasture phase by monitoring the trend in soil phosphate levels; graze leys continuously with at least moderate stocking rates of sheep during the vegetative phase of growth; and, avoid excessive defoliation (grazing, hay cuts) during spring.

In the 1990s, subterranean clover was more successful than annual grasses due to the availability and use of clover cultivars that were more persistent than the ones they replaced (Dear and Sandral 1997), and to the application of herbicides to reduce the presence of pasture species that are weeds during the cropping phase (Powles *et al.* 1997). One species that declined was annual ryegrass which, from the 1970s, was the target of a range of selective herbicides, but it has now developed resistance to most of these chemicals (Powles *et al.* 1997). Another species that declined was barley grass, which was a common associate of subterranean clover in well-fertilised pastures (Ayres *et al.* 1977); lower rates of superphosphate applied to leys, higher stocking rates and herbicides were the probable factors that led to a lower frequency of this grass.

Conversely, silvergrass (*Vulpia* spp.) has apparently increased in frequency in ley pastures, presumably due to less competition with ryegrass and higher stocking rates. According to Leys *et al.* (1991) and Dowling *et al.* (1997), the incidence of vulpia has increased substantially in the last decade, primarily through its tolerance of selective herbicides that have removed one of its competitors, annual ryegrass, and the adoption of reduced tillage practices that leave the seed bank intact near the soil surface. Other factors that have favoured an increasing incidence

[2]During and after the millennium drought, dry conditions in early spring appear to be more frequent, and cover crops are now regarded as an impediment to the successful establishment of under-sown pastures.

of vulpia, and attributes that contribute to its competitiveness are listed in Table 7.

Table 7. Factors favouring dominance of *Vulpia* spp. in pasture swards, southern NSW (based on Leys *et al.* 1993; Dowling *et al.* 1997).

Management and edaphic factors
• Reduced use of disc plough
• Widespread use of selective herbicides to control annual ryegrass
• Reduced vigour of annual legumes due to pathogens, lower fertiliser use
• Heavy grazing
• Allelopathic effects of plant residues on annual legumes
• Transfer of seed in hay
• Lower soil pH
• Occurrence of droughts
Characteristics of Vulpia contributing to competitiveness
• High seed production capacity
• Low palatability
• Delayed early growth
• Multiple germinations, seed dormancy

The herbicide simazine is one of the widely used options to control vulpia but there is concern that the current use of simazine on triazine-tolerant canola varieties and on lupin crops, and its possible use to winter-clean pastures, will hasten the development of simazine-tolerant vulpia biotypes. The development of non-chemical methods for controlling vulpia is now a priority, but progress may be slow. The findings of Leys *et al.* (1993) and Dowling *et al.* (1997) indicated that competition from other species was by itself insufficient to suppress vulpia (Table 8). Although increasing the density of clover reduced seed set by vulpia in the first year, there was no difference between the density treatments by the third year; the inclusion of a competitive grass (annual ryegrass, itself a weed) was the most effective strategy in the experiments of Leys *et al.* (1993). Dowling *et al.* (1997) concluded that the key components of an integrated control strategy for vulpia were a persistent clover strain, the inclusion of a competitive grass, forage conservation and other seed capture techniques, and grazing management.

Table 8. Effect of subterranean clover density on *Vulpia* invasion in pastures at Wagga Wagga, southern NSW (Leys *et al.* 1993).

Pasture density/composition	Vulpia density and seed production/m^2				
	1990		1991		1992
	Plants	Seeds	Plants	Seeds	Plants
Low subclover density	720	1,071,300	22,610	432,000	9,200
Medium subclover density	860	536,200	13,370	399,700	7,700
High subclover density	550	239,300	8,890	386,100	9,720
Medium subclover density + annual rye grass	640	179,400	4,290	173,300	2,530

Subterranean clover in mixtures with perennial species

Most studies of the ecology of subterranean clover have involved monocultures and few have studied its ability to coexist with perennial species. There are two main environments where subterranean clover is grown with perennials. The first is in predominantly permanent pastures in the higher rainfall (> 500 mm annual rainfall), elevated tableland environments of NSW, Victoria and Tasmania, where subterranean clover occurs with phalaris or cocksfoot. The second is in parts of the cropping zone, where subterranean clover has been sown in combination with lucerne as part of 4-6-year ley phase between cropping phases.

The ability of subterranean clover to form stable mixtures in swards with perennial grasses has been poor (Dear 1998). Typically, the annual legume content declines over time leading to grass-dominant, N deficient, less productive swards. There are several possible reasons for the inability of subterranean clover to respond to the decreasing grass vigour as N availability declines. The hard seed breakdown of the subterranean clover seed bank (Figure 6) may be depressed by the smaller diurnal temperature fluctuations at the soil surface, due in part to the increased cover of residual herbage. Another view is that allelopathic chemicals released by the grass residues inhibit germination and survival of subterranean clover seedlings (Leigh *et al.* 1995). More recently, it has been shown that the seedling survival and early growth of subterranean clover can be greatly reduced by competition for moisture with perennials; perennials such as lucerne or phalaris decrease the favourable period of soil moisture following a rainfall event in late summer or early autumn (Dear and Cocks 1997). This deficiency leads to a more rapid desiccation and smaller size of clover seedlings and increased seedling mortality. Furthermore, a combination of shading by the perennial and lower available nitrate levels in the presence of perennial grass decreased clover seedling growth rates (Dear *et al*. 1998).

In spring, also, competition between subterranean clover and perennials (phalaris, lucerne) was found to be important - the quantity of seed set by subterranean clover was inversely related to the amount of light intercepted by the canopy of perennial plants (Dear 1998). Seed production by subterranean clover is known to be sensitive to shading (Collins *et al*. 1978). In Dear's (1998) experiments, the presence of perennials did not apparently increase the level of moisture stress experienced by the companion annual legumes in spring.

An extreme case of the shading effect may account for the strong competitive advantage of white clover over subterranean clover. The combination of these two species is most likely to occur in environments such as the Northern Tablelands of NSW, where at least 60% of the total annual rainfall (>700 mm) occurs in summer, outside the growing period of the annual. The studies of Smith and Crespo (1979) and Hill and Gleeson (1990) pointed to the ability of white clover to elongate its petioles in spring and shade the companion subterranean clover, resulting in large reductions in seed set of the annual. Another important factor could be the large losses in subterranean clover seed reserves that can occur when the environment remains moist after seed set (Archer 1990).

Summary
In subterranean clover pastures, recent work has filled in many gaps in our understanding of competition between and within species. Higher stocking rates, lower rates of superphosphate applied to ley pastures, shorter leys, the release of improved pasture cultivars and winter cleaning are factors that, if anything, are making it easier for farmers to grow legume-dominant subterranean clover pastures. However, the advent of herbicide resistant weeds and the increasing use of perennial species are issues that could intensify competition between subterranean clover and non-legumes.

Species dynamics in annual* Medicago *pastures
The available reviews of medic pastures (Cocks *et al.* 1980, Crawford *et al.* 1989) place less emphasis on the competitive ability of medics than the ability of individual species to grow, produce seed and persist. This emphasis is understandable, since in Australia medics are

traditionally grown in short-term pasture/crop leys, where the survival and regeneration of the medic after the cropping phase is of paramount importance (Puckridge and French 1983). Another possible constraint to long-term studies of species relationships in medic pastures is the medic decline syndrome (Table 2), which was first reported in the 1980s (Carter *et al.* 1982) after a devastating occurrence of the spotted alfalfa aphid and the blue-green aphid in the late 1970s. This decline has continued in pastures in South Australia, where low soil phosphorus and zinc levels and *Pratylenchus* nematodes have also been implicated (Denton and Bellotti 1996). The extensive use of residual sulfonylurea herbicides is another factor considered to be affecting the persistence of annual *Medicago* spp. grown in rotation with crops. In recent years, medic breeding and evaluation in Australia has been dominated by the need to develop aphid-tolerant varieties; the program has resulted in the release of new barrel medics (*M. truncatula),* cvs Parraggio, Sephi, Caliph and Mogul, and strand medics (*M. littoralis*, cvs Harbinger AR and Herald).

The vulnerability of medic pods to ingestion by sheep and goats is a critical factor determining the amount of the germinable seed pool present in autumn winter, thereby influencing the ability of medic to maintain high plant populations in longer term pastures. Dear and Jenkins (1992) found sheep could remove 200 to 600 kg/ha medic seed in 7 days when grazed at a high stocking rate. The greater proportion (up to 95%) of the seed is digested with the recovery of seed in sheep pellets being inversely proportional to the size of seed (Russi *et al*. 1992).

Shallow seed burial has been shown to enhance the rate of softening in the first year (Cocks 1993) as well as prevent ingestion of pod by stock. Hence most successful farming systems involving medics require frequent cropping and shallow seed incorporation. Deep ploughing, as commonly practised in west Asia and north Africa, results in poor regeneration (Cocks 1994b). Another benefit of shallow burial of seed is the improvement in seed-soil contact which assists uptake of water when rainfall is light (Cocks 1993). Seeds in surface pods often fail to germinate with light falls of rain, and although this can be an advantage to prevent premature germination and depletion of the seed bank, it can shorten the growing season and reduce dry matter yield in good seasons (Cocks 1993).

The benefit of sowing mixtures of annual medics in Australian farming systems has not been widely reported. Latta and Carter (1996) concluded that there were benefits in combining an early maturing small seeded cultivar, such as Harbinger AR, with a mid season larger soft seeded cultivar (Paraggio), to maximise seed production and regeneration. The relationships between annual medics and competing species should be included in any future monitoring program to evaluate the long-term contribution of these newer varieties to agriculture.

Increasing the diversity and stability of annual pasture swards.

The legume improvement programs in Australia are changing their emphasis after 50 years of mainly concentrating on developing new cultivars of subterranean clover and annual medics. They are being refocussed towards new previously uncultivated annual legume species. This development in part reflects the significant progress that has been made in subterranean clover towards the objectives of lowering oestrogens, increasing hardseededness and improving resistance to leaf and root diseases by breeding programs (Nichols *et al.* 1994). But it also reflects a need to find species adapted to niches not suited to subterranean clover and introduce new adaptive mechanisms not contained within subterranean clover or annual *Medicago* spp. These include greater adaptation to waterlogging, different patterns of hard seed breakdown, small seeds which can pass through the rumen undigested, aerial seeding for ease of harvesting and greater insect tolerance. A good example of how other species may fill gaps in pastures is the colonisation by *T. clusii* of poorly drained niches within subterranean clover pastures (Cocks 1994a). Cocks (1994a) also suggested that the lack of species diversity in Australian pastures may be slowly resolving itself through a combination of hybridisation, mutation and the spread of species by grazing animals. This process can be accelerated by carefully targeting selection and introduction programs.

Equally importantly, the change in emphasis is also an attempt to increase the diversity of species in pasture swards. In response to temporal and spatial variation, diversity may produce small but important improvements in ecosystem stability and resilience, at least in terms of biomass if not in botanical composition (Tilman 1996). Diversity is also a step away from the annual legume monocultures, which have dominated Australian pastoral systems, monocultures that have been vulnerable to diseases, such as clover scorch (*Kabatiella caulivora*) or root rots in subterranean clover, or pests like the spotted alfalfa aphid.

The use of more diverse mixtures of legume species[3] opens up a whole new area of plant competition that has received very limited study. While many of the factors identified earlier in competition between genotypes of the same species may be important, other factors will be involved. For example, a study by Dear and Coombes (1992) found when *Trifolium subterraneum*, *Medicago murex* and *T. michelianum* were grown in binary mixtures, seed production by *T. michelianum* was, relative to the monoculture yields, more sensitive to competition than either of the other species, setting only 59-81 kg/ha in mixtures compared to 287-514 kg/ha by the other two species. Whether this was due to the crash grazing system employed or shading of one species by another could not be determined. Another finding was the need for heavy grazing over summer for *T. michelianum* to regenerate satisfactorily the following autumn (Dear and Coombes 1992). In contrast, the seed reserves of larger seeded species such as *M. murex,* contained in a large pod on the soil surface, can be severely depleted by stock over summer resulting in poor recruitment the following year.

These findings reinforce the challenge of choosing a grazing strategy that maintains diversity, profitability and sustainability of pasture mixtures. In extensive areas where grazing management is less well controlled, it may be more important to select species combinations that can survive under a particular grazing regime rather than attempt to force species together with divergent grazing needs despite the desirability of other agronomic characteristics. These combinations have important implications for breeding and selection programs and how new species are evaluated. Evaluating species in monocultures in small plots may be inappropriate, and it may be preferable to evaluate combinations of species under realistic grazing regimes to discover their dynamics, productivity, stability and resilience. Such an approach is in line with proposals by Cocks (1992) who concluded that, due to the complexity of the possible interactions, the evaluation of species mixtures should be conducted in farmers paddocks under practical management conditions.

[3] A national effort (Nichols et al. 2007) was directed towards producing annual legumes to deal with particular problems and opportunities, such as legume adaptation on difficult soils (acid, waterlogged or saline), weed and insect threats, longer pasture and cropping phases, deeper-rooted plants to reduce groundwater accessions, and the need for easily harvested and sown seed. As a result, an expanded range of species and cultivars are now available for the wheat belt in WA and other States. Cultivars of pink or French serradella (*Ornithopus sativus*), gland clover (*Trifolium glanduliferum*), bladder clover (*Trifolium spumosum*) and biserrula (*Biserrula pelicinus*) are the most successful recent outputs from this well-executed program (Loi et al. 2005, Nichols et al. 2007).

Conclusions

This review has highlighted the main developments that have occurred, and how they have shaped the dynamics of species relationships, in southern Australian pastures. The main phases were a century and a half (1800-1950) of exploitation of Australian native grasslands (a phase that is continuing, albeit at a slower rate), a short and intensive period (1950-1970) of pasture improvement with fertilisers and exotic species, and a period of re-evaluation during the last thirty years of the twentieth century. This last period has provided an opportunity to consolidate the knowledge of scientists, and add the experience of farmers and graziers, to reflect on successful and unsuccessful aspects of pasture management in relation to future of permanent and ley pastures in Australian agriculture.

In this review, a number of gaps in knowledge were indicated. First, there was a lack of knowledge on the effects of "management" (subdivision, grazing and fertilisation) on plant communities, covering a representative range of native, naturalised, and exotic species. Fortunately, work is underway to enhance the understanding of agriculturists, ecologists and pastoralists on the separate effects of defoliation, trampling, and nutrient addition/depletion on plant-soil-water relations in native and improved grasslands. A feature of this work is a greater emphasis on the impact of species on soil erosion and on the hydrology of catchments (Johnston *et al.* 1999).

Second, there is a need for a more theoretical approach to grassland dynamics, in which the observed changes in productivity and botanical composition are related to useful frameworks that might help integrate knowledge and explain phenomena. In this respect, the application of the state and transition model (Humphreys 1997) to plant succession in permanent pastures, and the competition-stress-disturbance model (Grime 1977) to ley pastures, are recommended. Both models eschew the dogma that is associated with the traditional Clementsian (linear) model of succession, and they are flexible enough to encompass not only breadth of knowledge but also the targeting of a particular problem or issue.

Third, the review has pointed to a lack of quantitative evidence available for the decline in legume and total pasture productivity that has reportedly (Carter *et al.* 1982) occurred in pastures in southern Australia. A survey undertaken by ABARE in 1999 revealed that farmers in the cropping zone of Australia were predominantly satisfied with both the productivity and quality of their pastures. The separate views of researchers and farmer/graziers need further exploration and, as suggested by Wilson and Simpson (1993), there is scope for regular and standardised surveys of the state of pastures. Strategic long-term studies of pasture relationships, similar to those undertaken by Hutchinson and colleagues (Hutchinson 1992, Hutchinson *et al.* 1995; Hutchinson and King 1999) on permanent pastures on the Northern Tablelands of NSW, are warranted. The lack of such studies for some pasture types, such as those based on annual medics, must be overcome.

In Australian croplands, developments such as the changing spectrum of crop weeds and the escalating importance of herbicide resistance are likely to force agronomists and managers to place a greater value on monitoring, understanding and manipulating the population dynamics of pasture/weed species, during both the cropping and pasture phases of rotations. In grazing lands, too, the scene is changing due to enhanced community perceptions of the sustainability of catchments and the aesthetic value of landscapes. Developments such as new pests and diseases, or the loss of key herbicides due to community or corporate imperatives, will ensure the need for theoretical and applied studies of plant competition and pasture dynamics.

References

ABARE (1999) Australian Bureau of Agricultural and Resource Economics, personal communication.

Archer KA (1990) The effects of moisture supply and defoliation during flowering on seed production and hardseededness of *Trifolium subterraneum* L. *Australian Journal of Experimental Agriculture* **30**, 515-522.

Archer KA, Wolfe EC, Cullis BR (1987) Flowering time of cultivars of subterranean clover in New South Wales. *Australian Journal of Experimental Agriculture* **27**, 791-797.

Axelsen A, Morley F (1968) Evaluation of eight pastures by animal production. *Proceedings of the Australian Society of Animal Production* **7**, 92-98.

Ayres JF, McFarlane JD, Gilmour AR, McManus WR (1977) Superphosphate requirements of clover-ley farming. 1. The effects of topdressing on productivity in the ley phase. *Australian Journal of Agricultural Research* **28**, 269-285.

Barr NF, Cary JW (1992) *Greening a brown land: an Australian search for sustainable land use.* MacMillan, Melbourne, pp. 343.

Blumenthal MJ, Ison RL (1993) Water use and productivity in sub. clover and murex medic swards. II. Seed production. *Australian Journal of Agricultural Research* **44**, 109-119.

Callaghan AR (1935) Activities at Roseworthy Agricultural College 1934-35. *Journal of the Department of Agriculture of South Australia* **39**, 310-318.

Campbell MH (1992) Extending the frontiers of aerially sown pastures in temperate Australia: a review. *Australian Journal of Experimental Agriculture* **32**, 137-148.

Campbell MH (1998) Biological and ecological impact of serrated tussock (*Nassella trichotoma* (Nees) Arech.) on pastures in Australia. *Plant Protection Quarterly* **13**, 80-86.

Carter ED, Wolfe EC, Francis CM (1982) Problems of maintaining pastures in the cereal-livestock areas of southern Australia. (In) *Proceedings of the 2nd Australian Agronomy Conference, Wagga Wagga* (Ed. MJT Norman) pp. 68-82 (Australian Society of Agronomy, Parkville, Victoria).

Cocks PS (1992) Evolution in sown populations of subterranean clover (*Trifolium subterraneum* L.) in South Australia. *Australian Journal of Agricultural Research* **43**, 1583-1595.

Cocks PS (1993). Seed and seedling dynamics over four consecutive years from a single seed set of six annual medics (*Medicago* spp) in north Syria. *Experimental Agriculture* **29**, 461-472.

Cocks PS (1994a) Colonisation of a South Australian grassland by invading Mediterranean annuals and perennial pasture species. *Australian Journal of Agricultural Research* **45**, 1063-1076.

Cocks PS (1994b) Effect of tillage system on the spontaneous regeneration of two annual medics (*Medicago* spp.) after wheat in north Syria. *Experimental Agriculture* **30**, 237-248.

Cocks PS, Craig AD, Kenyon RV (1982) Evolution of subterranean clover in South Australia. 2. Change in genetic composition of a mixed population after 19 years' grazing on a commercial farm. *Australian Journal of Agricultural Research* **33**, 679-695.

Cocks PS, Mathison MJ, Crawford EJ (1980) From wild plants to pasture cultivars: annual medics and subterranean clover in Australia. (In) *Advances in legume science.* (Eds RJ Summerfield, AH Bunting) Royal Botanic Gardens, Kew, pp. 569-596.

Collins WJ (1978) The effect of defoliation on inflorescence production, seed yield and hardseededness in swards of subterranean clover. *Australian Journal of Agricultural Research* **29**, 789-801.

Collins WJ. (1981) The effects of length of growing season with and without defoliation on seed yield and hardseededness in swards of subterranean clover. *Australian Journal of Agricultural Research* **32**, 783-792.

Collins WJ, Rossiter RC, Monreal RA (1978) The influence of shading on the seed yield of subterranean clover. *Australian Journal of Agricultural Research* **29**, 1167-1175.

Collins WJ, Stern WR (1987) The national subterranean clover improvement program - progress and directions. (In) *Temperate pastures, their production, use and management.* (Eds. JL Wheeler, CJ Pearson, GE Robards) Australian Wool Corporation/CSIRO, Melbourne, pp. 276-278.

Cook SJ, Lazenby A, Blair GJ (1978) Pasture degeneration. 2. The importance of superphosphate, nitrogen and grazing management. *Australian Journal of Agricultural Research* **29**, 19-29.

Cornish PS (1985) Adaptation of annual *Medicago* to a non-Mediterranean climate. *Technical Bulletin 32. The ecology and agronomy of annual medics* (Ed. Z Hochmann) pp. 13-16. (Department of Agriculture, Sydney, New South Wales).

Crawford EJ, Lake AWH, Boyce KG (1989) Breeding annual *Medicago* species for semiarid conditions in southern Australia. *Advances in Agronomy* **42**, 399-437.

Crawford MC, Macfarlane MR (1995) Lucerne reduces soil moisture and increases livestock production in an area of high groundwater recharge potential. *Australian Journal of Experimental Agriculture* **35**, 171-180.

Cregan P, Scott B (1998) Soil acidification - an agricultural and environmental problem. (In) *Agriculture and the environmental imperative.* (Eds J Pratley, A Robertson) CSIRO, Melbourne, pp. 98-128.

Crofts FC (1997) Australian pasture production: the last 50 years. (In) *Pasture production and management.* (Eds JV Lovett, JM Scott) Inkata Press, Melbourne, pp. 1-16.

Crosby JR, Bellotti WD, Kerby JS, Harrison R (1993) Farmer attitudes towards pastures in the cereal-livestock zone of South Australia. (In) *Proceedings of the 7th Australian Agronomy Conference, Adelaide* (Eds GK McDonald, WD Bellotti) pp. 321-324 (Australian Society of Agronomy, Parkville, Victoria).

Culvenor RA, Oram RN (1992) The persistence of phalaris under grazing. (In) *Proceedings of the 6th Australian Agronomy Conference, Armidale* (Eds KJ Hutchinson, PJ Vickery) p. 551 (Australian Society of Agronomy, Parkville, Victoria).

Dear BS (1998) Ecology of subterranean clover growing in association with perennial pasture species. PhD thesis, University of Western Australia, Perth, Australia.

Dear BS, Cocks PS (1997) Effect of perennial pasture species on surface soil moisture and early growth and survival of subterranean clover (*Trifolium subterraneum* L.) seedlings. *Australian Journal of Agricultural Research* **48**, 683-693.

Dear BS, Cocks PS, Wolfe EC, Collins DP (1998) Established perennial grasses reduce the growth of emerging subterranean clover seedlings through competition for water, light and nutrients. *Australian Journal of Agricultural Research* **49**, 41-51.

Dear BS, Coombes N (1992) Population dynamics of *Trifolium subterraneum*, *Medicago murex* and *Trifolium balansae* grown in monocultures and mixtures. (In) *Proceedings of the 6th Australian Agronomy Conference, Armidale* (Eds KJ Hutchinson, PJ Vickery) pp. 284-287. (Australian Society of Agronomy, Parkville, Victoria).

Dear BS, Cregan PD, Murray GM (1993a) Comparison of the performance of subterranean clover cultivars in southern New South Wales. 1. Persistence, productivity, and seed yields. *Australian Journal of Experimental Agriculture*, **33**, 581-590.

Dear BS, Jenkins L (1992) Persistence, productivity, and seed yield of *Medicago murex, M. truncatula, M. aculeata,* and *T. subterraneum* on an acid red earth soil in the wheat belt of eastern Australia. *Australian Journal of Experimental Agriculture* **32**, 319-329.

Dear BS, Murray GM, Cregan PD, Taylor PA (1993b) Comparison of the performance of subterranean clover cultivars in southern New South Wales. 2. Effects of *Phytophthora* *clandestina* and bromoxynil on seedling survival, growth, and seed set. *Australian Journal of Experimental Agriculture* **33**, 591-596.

Dear BS, Sandral GA (1997) Subterranean clover in NSW- identification and use. Agfact P2.5.16, second edition. (NSW Agriculture, Sydney, New South Wales).

Denton MD, Bellotti WD (1996) Factors involved in the annual medic decline syndrome in the Murray Mallee, South Australia. (In) *Proceedings of the 8th Australian Agronomy Conference, Toowoomba* (Ed. A Asghar) pp. 192-95 (Australian Society of Agronomy, Parkville, Victoria).

Donald CM (1967) Innovation in agriculture. In *Agriculture and the Australian economy.* First edition (Ed. DB Williams) Sydney University Press, Sydney, pp. 57-86.

Donald CM (1970) Temperate pasture species. (In) *Australian grasslands.* (Ed. RM Moore) ANU Press, Canberra, pp. 303-320.

Dowling PM, Leys AR, Plater C (1997) Effect of herbicide and application of superphosphate and subterranean clover seed on regeneration of vulpia in pastures. *Australian Journal of Experimental Agriculture* **37**, 431-438.

Evans PM, Hall EJ (1995) Seed softening patterns from single seed crops of subterranean clover (*Trifolium subterraneum* L.) in a cool temperate environment. *Australian Journal of Experimental Agriculture* **35**, 1117-1121.

Fisher HJ (1972) Effect of nitrogen fertiliser on a kangaroo grass (*Themeda australis*) grassland. *Australian Journal of Experimental Agriculture and Animal Husbandry* **14**, 526-532.

FitzGerald RD (1976) Effect of stocking rate, lambing time and pasture management on wool and lamb production on annual subterranean clover pastures. *Australian Journal of Agricultural Research* **27**, 261-275.

FitzGerald RD, Harris CA, Ayres JF (1995) Impact of drought on survival of pasture species. *Proceedings of the 10th Annual Conference, Grassland Society of NSW, Armidale* (Eds J Ayres, D Michalk, H Lloyd Davies) p. 76. (Grassland Society of New South Wales, Orange, NSW).

Garden D, Jones C, Friend D, Mitchell M, Fairbrother P (1996) Regional research on native grasses and native grass-based pastures. *New Zealand Journal of Agricultural Research* **39**, 471-485.

Gillett DC, Holloway RE (1996) The effects of a sulphonyl urea herbicide on annual medic in alkaline soil. (In) *Proceedings of the 8th Australian Agronomy Conference, Toowoomba* (Ed. A Asghar) pp. 653 (Australian Society of Agronomy, Parkville, Victoria).

Gladstones JS (1966) Naturalised subterranean clover (*Trifolium subterraneum* L.) in Western Australia: the strains, their distributions, characteristics and possible origins. *Australian Journal of Botany* **14**, 329-354.

Goldney DC, Bauer JJ (1998) Integrating conservation and agricultural production: fantasy or imperative? (In) *Agriculture and the environmental imperative* (Eds J Pratley, A Robertson) CSIRO, Melbourne, pp. 15-34.

Gramshaw D, Read JW, Collins WJ, Carter ED (1989) Sown pastures and persistence: an Australian overview. (In) *Persistence of forage legumes.* (Eds GC Marten, AG Matches, RF Barnes, RW Brougham, RJ Clements, GW Sheath) American Society of Agronomy/Crop Science Society of America/Soil Science Society of America, Madison, pp. 1-21.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* **111**, 1169-1194.

Gruen FH (1990) Economic development and agriculture since 1945. (In) *Agriculture and the Australian economy*. Third edition (Ed. DB Williams) Sydney University Press, Sydney, pp. 19-26.

Hancock WK (1972) *Discovering Monaro - a study of man's impact on his environment.* Cambridge University Press, London. pp. 209.

Hill BD (1985) Persistence of temperate perennial grasses in cutting trials on the central slopes of New South Wales. *Australian Journal of Experimental Agriculture* **25**, 832-839.

Hill MJ (1996) Potential adaptation zones for temperate pasture species as constrained by climate: a knowledge-based logical modelling approach. *Australian Journal of Agricultural Research* **47**, 1095-1117.

Hill MJ, Gleeson AC (1990) Competition between white clover *(Trifolium repens* L.) and subterranean clover (*Trifolium subterraneum* L.) in binary mixtures in the field. *Grass and Forage Science* **45**, 373-382.

Hill MJ, Gleeson AC (1991) Competition between Clare and Seaton Park, and Clare and Daliak subterranean clovers in replacement series mixtures in the field. *Australian Journal of Agricultural Research* **42**, 161-173.

Hochmann Z, Osborne GJ, Taylor PA, Cullis B. (1990) Factors contributing to reduced productivity of subterranean clover (*Trifolium subterraneum* L.) pastures on acidic soils. *Australian Journal of Agricultural Research* **41**, 669-682.

Humphreys LR (1997) *The evolving science of grassland improvement*. Cambridge University Press, Cambridge, pp. 261.

Hutchinson KJ (1992) The grazing resource. (In) *Proceedings of the 6th Australian Agronomy Conference, Armidale* (Eds KJ Hutchinson, PJ Vickery), pp. 54-60 (Australian Society of Agronomy, Parkville, Victoria).

Hutchinson KJ, King KL, Wilkinson DR (1995) Effects of rainfall, moisture stress, and stocking rate on the persistence of white clover over 30 years. *Australian Journal of Experimental Agriculture* **35**, 1039-1047.

Hutchinson KJ, King KL (1999) Sown temperate pasture decline - fact or fiction? *Proceedings of the 14th Annual Conference, Grassland Society of NSW, Queanbeyan*, pp. 78-86. (Grassland Society of New South Wales, Orange, NSW).

Johnston WH (1996) The place of C_4 grasses in temperate pastures in Australia. *New Zealand Journal of Agricultural Research* **39**, 527-40.

Johnston WH, Clifton CA, Cole IA, Koen TB, Mitchell ML, Waterhouse DB (1999) Low input grasses useful in limiting environments (LIGULE). *Australian Journal of Agricultural Research* **50**, 29-53.

Kemp DR, Dowling PM (1991) Species distribution within improved pastures over central NSW in relation to rainfall and altitude. *Australian Journal of Agricultural Research* **42**, 647-659.

Knopke P, Furmage B, Walters P, Krieg A (1995) Agriculture in the Australian economy. (In) *Australian agriculture*, Fifth edition (Ed. F. Douglas). Morescope Publishing, Melbourne. pp. 17-34.

Latta RA, Carter ED (1996) Annual medic cultivar mixes in semi-arid farming systems. (In) *Proceedings 8th Australian Agronomy Conference, Toowoomba* (Ed. A Asghar), pp. 361-64 (Australian Society of Agronomy, Parkville, Victoria).

Leach GJ (1978) The ecology of lucerne pastures. (In) *Plant relations in pastures*. (Ed. John R Wilson) CSIRO, Melbourne, pp. 290-308.

Leigh JH, Halsall DM, Holgate MD (1995) The role of allelopathy in legume decline in pastures. 1. Effects of pasture and crop residues on germination and survival of subterranean clover in the field and nursery. *Australian Journal of Agricultural Research* **46**, 179-188.

Leys AR, Cullis BR, Plater B (1991) Effect of spraytopping applications of paraquat and glyphosate on the nutritive value and regeneration of vulpia *(Vulpia bromoides* (L.) S. F. Gray). *Australian Journal of Agricultural Research* **42**, 1405-1415.

Leys AR, Dowling PM, Plater B (1993) The effect of pasture density and composition on vulpia. *Proceedings of the 10th Australian Weeds Conference, Brisbane,* pp. 193-197.
Lodge GM (1991) Management practices and other factors contributing to the decline in persistence of grazed lucerne in temperate Australia: a review. *Australian Journal of Experimental Agriculture* **31**, 713-724.
Lodge GM (1996) Seedling emergence and survival of annual pasture legumes in northern New South Wales. *Australian Journal of Agricultural Research* **47**, 559-574.
Lodge GM, Whalley RDB (1985) The manipulation of species composition of natural pastures by grazing management on the northern slopes of New South Wales. *The Australian Rangeland Journal* **7**, 6-16.
Lodge GM, Whalley RDB (1989) Native and naturalised pastures on the Northern Slopes and Tablelands of New South Wales. *Technical Bulletin 35* (New South Wales Agriculture and Fisheries, Sydney, NSW).
Lodge GM, Murison RD, Heap EW (1990) The effect of temperature on the hardseed content of some annual legumes grown on the northern slopes of New South Wales. *Australian Journal of Agricultural Research* **41**, 941-955.
McIvor JG (1993) Distribution and abundance of plant species in pastures and rangelands. (In) *Grasslands for our world.* (Ed. MJ Baker). SIR Publishing, Wellington, pp. 100-104.
McKinney GT (1974) Management of lucerne for sheep grazing on the southern tablelands of New South Wales. *Australian Journal of Experimental Agriculture and Animal Husbandry* **14**, 726-734.
McLaren DA, Stajsic V, Gardener MR (1998) The distribution and impact of South/North American stipoid grasses (Poaceae: Stipeae) in Australia. *Plant Protection Quarterly* **13**, 62-70.
McWilliam JR, Clements RJ, Dowling PM (1970) Some factors influencing the germination and early seedling development of pasture plants. *Australian Journal of Agricultural Research* **21**, 19-32.
Meinig DW (1954) *On the margins of the good earth.* South Australian Government Printer, Adelaide, pp. 231.
Michael PW (1970) Weeds of grasslands. (In) *Australian grasslands.* Ed RM Moore. ANU Press, Canberra, pp. 349-360.
Moore RM (1970) Southeastern temperate woodlands and grasslands. (In) *Australian grasslands.* Ed. RM Moore. ANU Press, Canberra, pp. 170-190.
Nichols P, Collins W, Gillespie D, Barbetti M (1994) Developing improved varieties of subterranean clover. *Journal of Agriculture, Western Australia* **35,** 60-65.
O'Connor TG (1996) Hierarchical control over seedling recruitment of the bunch-grass *Themeda triandra* in a semi-arid savanna. *Journal of Applied Ecology* **33**, 1094-1106.
Oram RN, Culvenor RA (1994) Phalaris improvement in Australia. *New Zealand Journal of Agricultural Research* **37**, 329-339.
Panetta FD, Risdell-Smith TJ, Barbetti MJ, Jones RAC (1993) The ecology of weeds, invertebrate pests and diseases of Australian sheep pastures. (In) *Pests of pastures: weed, invertebrate and disease pests of Australian sheep pastures.* (Ed. ES Delfosse) CSIRO, Melbourne, pp. 87-114.
Passioura JB, Ridley AM (1998) Managing soil water and nitrogen to minimise land degradation. (In) *Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga* (Eds DL Michalk and JE Pratley) pp. 99-106. (Australian Society of Agronomy, Wagga Wagga).
Paul JA (1999) Critical parameters for monitoring ley pastures. Unpublished PhD thesis. Charles Sturt University, Wagga Wagga, Australia.

Pearson CJ, Brown R, Collins WJ, Archer KA, Wood MS, Petersen C, Bootle B (1997) An Australian temperate pastures database. *Australian Journal of Agricultural Research* **48**, 453-465.

Pecetti L, Piano E (1994) Observations on the rapidity of seed and burr growth in subterranean clover. *Journal of Genetics and Breeding,* **43** 225-228.

Peoples MB, Gault RR, Scammell GJ, Dear BS, Virgona JM, Sandral GA, Paul J, Wolfe EC, Angus JF (1998) The effect of pasture management on the contributions of fixed N to the N economy of ley-farming. *Australian Journal of Agricultural Research* **49**, 459-474.

Piano E, Spanu F, Pecetti L (1993) Structure and variation of subterranean clover populations from Sicily, Italy. *Euphytica* **68**, 43-51.

Piano E, Pecetti L (1997) Effect of water stress during flowering on seed yield in subterranean clover (*Trifolium subterraneum* L.) cultivars. Current situation and future prospects for forage cultivation in grasslands and pastures, Lodi, Italy. *Revista-di-Agronomia* **31**, 229-232.

Powles SB, Preston C, Bryan IB, Jutsum AB (1997) Herbicide resistance: impact and management. *Advances in Agronomy* **58**, 57-93.

Puckridge DW, French RJ (1983) The annual legume pasture in cereal-ley farming systems in southern Australia: a review. *Agriculture, Ecosystems and Environment* **9**, 229-267.

Reed KFM, Schroder PM, Eales JW, McDonald RM, Chin JF (1985) Comparative productivity of *Trifolium subterraneum* and *T. yanninicum* in south-western Victoria. *Australian Journal of Experimental Agriculture* **25**, 351-361.

Reeves TG, Ewing MA (1993) Is ley farming in Mediterranean zones just a passing phase? (In) *Grasslands for our world.* (Ed. MJ Baker) SIR Publishing, Wellington, pp. 810-818.

Ridley AM, Simpson RJ, White RE (1999) Nitrate leaching under phalaris, cocksfoot and annual ryegrass pastures and implications for soil acidification. *Australian Journal of Agricultural Research* **50**, 55-63.

Rossiter RC (1964) The effect of phosphate supply on the growth and botanical composition of annual type pasture. *Australian Journal of Agricultural Research* **15**, 61-76.

Rossiter RC (1966) Ecology of the Mediterranean annual-type pasture. *Advances in Agronomy* **18**, 1-56.

Rossiter RC (1974) The relative success of strains of *T. subterraneum* L. in binary mixtures under field conditions. *Australian Journal of Agricultural Research* **25,** 757-766.

Rossiter RC (1977) What determines the success of subterranean clover strains in south-western Australia. (In) *Exotic species in Australia - their establishment and success.* (Ed DJ Anderson). Ecological Society of Australia, Sydney, pp. 76-88.

Rossiter RC, Pack RJ (1972) Effect of stocking rate and defoliation on relative seed production in a mixture of two subterranean clover strains. *Journal of the Australian Institute of Agricultural Science* **38**, 209-211.

Rubzen BB (1996) The adaptation of plant and weed species to acid soil environments. PhD thesis. Charles Sturt University, Wagga Wagga, Australia.

Russi L, Cocks PS, Roberts EH (1992) The fate of legume seeds eaten by sheep from a Mediterranean grassland. *Journal of Applied Ecology* **29**, 772-728.

Shaw AGL (1990) Colonial settlement 1788-1945. (In) *Agriculture and the Australian economy*. Third edition (Ed. DB Williams) Sydney University Press, Sydney, pp. 1-18.

Smith RCG, Crespo MC. (1979). Effect of competition by white clover on seed production characteristics of subterranean clover. *Australian Journal of Agricultural Research* **30**, 597-607.

Smith FP, Cocks PS, Ewing MA (1996) Short-term patterns of seed softening in *Trifolium subterraneum*, *T. glomeratum*, and *Medicago polymorpha. Australian Journal of Agricultural Research* **47**, 775-785.

Southwood OR, Wolfe EC (1978) Identifying and using subterranean clovers. New South Wales, Division of Plant Industry, Bulletin P473 (Second edition). NSW Government Printer, Sydney.

Thorn CW (1992) Management of annual legume pastures for crop and animal production. (In) *Transfer of biologically fixed nitrogen to wheat.* (Ed. JF Angus) GRDC, Canberra, pp. 93-108.

Tilman D (1996) Biodiversity: population versus ecosystem stability. *Ecology* **77**, 350-363.

Watson RW (1993) Phalaris. Agfact P 2.5.1, NSW Agriculture, Orange, pp. 40.

Whitfield DM (1998) Hydrologic utility of phase farming based on winter rainfall in south eastern Australia. (In) *Proceedings of the 9th Australian Agronomy Conference, Wagga Wagga* (Eds DL Michalk, JE Pratley), pp. 823-26 (Australian Society of Agronomy, Wagga Wagga).

Williams AR (1979) A survey of natural pastures in the north-west slopes of New South Wales. Department of Agriculture, New South Wales, Technical Bulletin 22, pp.36.

Williams CH, Andrew CS (1970). Mineral nutrition of pastures. (In) *Australian grasslands.* (Ed. RM Moore) ANU Press, Canberra, pp. 321-338.

Willoughby WM (1954) Some factors affecting grass-clover relationships. *Australian Journal of Agricultural Research* **5**, 157-180.

Wilson AD, Simpson RJ (1993) The pasture resource base: status and issues. (In) *Pasture management technology for the 21st century.* (Eds. DR Kemp, DL Michalk) CSIRO, Melbourne. pp. 1-25.

Wolfe EC (1968) Cattle bloat in southern New England, NSW, 1961-66. *Proceedings of the Australian Society of Animal Production* **7**, 123-128.

Wolfe EC (1985) Subterranean clover and annual medics - boundaries and common ground. *Technical Bulletin 32*, pp. 23-28 (Department of Agriculture, Sydney, New South Wales).

Wolfe EC, Lazenby A (1973) Grass - white clover relationships during pasture development. 2. Effect of nitrogen fertiliser with superphosphate. *Australian Journal of Experimental Agriculture and Animal Husbandry* **13**, 575-580.

Wolfe EC, Southwood OR (1980) Plant productivity and persistence in a mixed pasture containing lucerne at a range of densities with subterranean clover or phalaris. *Australian Journal of Experimental Agriculture and Animal Husbandry* **20**, 189-196.

Wolfe EC, Fitzgerald RD, Hall DG, Southwood OR (1980). Beef production from lucerne and subterranean clover pastures. *Australian Journal of Experimental Agriculture and Animal Husbandry*, **20** 678-687.

Wolfe EC, Paul JA, Cregan PD (2006) Monitoring ley pastures and their response to winter cleaning. *Australian Journal of Experimental Agriculture*, **46**, 1023-1033.