Chapter 7
Plant mortality and plant traits important for persistence

Introduction

The persistence of pasture species and even cultivars varies with the environment and management applied. Species which are adapted to an environment survive longer than those that are not. This has been shown by a number of workers including McWilliam (1968), Arcioni *et al.* (1985) and Volaire (1994, 1995). Phalaris is commonly recorded in the literature as a persistent species (eg. Robinson and Simpson 1966; Hutchinson 1970; Hill 1985), while perennial ryegrass and cocksfoot are generally considered less persistent (eg. Hein and Vinall 1933; Robinson and Simpson 1966; Hutchinson 1970). However, what are the traits which make one species persistent and another less so?

Many people, through experimentation and anecdotal evidence, have suggested different plant traits that assist the persistence of grasses during periods of stress; either management and/or environmental stress. Drought survival has been suggested to increase with high carbohydrate reserves (Arcioni *et al.* 1985; Volaire 1994), deep rootedness (McWilliam and Kramer 1968), increased plant size (Hoen 1968b) and dormant buds (Hoen 1968a; McWilliam 1968; Oram 1983; Oram and Freebairn 1984). Plant regrowth and survival following repeated defoliation has been suggested to be associated with carbohydrate (Davies 1965; Alberda 1966) and nitrogen reserves (Volenec *et al.* 1996), synchronous tillering (Mott *et al.* 1992; Culvenor 1993a) and plant morphology (Culvenor 1993b).

Understanding plant responses to drought is important in evaluating mechanisms of drought tolerance (West *et al.* 1990). The same can be said for tolerance to defoliation stresses. Correlation matrices and multiple regression are common methods for studying linkages between traits, causes and responses (eg. Ortega *et al.* 1992), with some work also having been conducted on the persistence of single plant species (eg. Carrow 1996; Volaire 1994, 1995; Culvenor and Oram 1996; Volaire and Lelièvre 1997). Persistence appears to be a complex trait (Wilkins 1991), so it is through methods such as multiple regression and principle components analysis that plant traits can be linked to persistence.

There are two aims of this chapter: firstly, to quantify the plant losses resulting from the combined defoliation and moisture stresses, and secondly, to investigate the contribution of various plant traits (described earlier in this thesis) in predicting mortality/persistence of perennial pasture grasses defoliated at different intensities during drought.

Materials and methods

Trial design and treatments

Details of the trial site preparation, establishment, design, rain–out shelter and treatments are described in detail in Chapter 3. The methods with specific application to this chapter are described below.

Plant mortality

During the recovery period, following the application of 50 mm rain at the end of each experimental season, any plant which had previously received a vitality score of 1 (no green foliage and presumed either dead or dormant, Chapter 4) at the end of the experimental season which did not recover was scored as 0, or dead.

The total number of dead plants were analysed within an experimental season as a split–split plot using the statistical package Genstat 5 (Genstat 5 Committee 1987).

Traits important to plant persistence

Correlation matrices and multiple regression were used to determine which of the measured plant traits described in previous chapters were most highly correlated with plant mortality. Only those species which had half or more of the observations with plant death recorded were used in the analysis. Therefore, in SS, only cocksfoot and perennial ryegrass were analysed, while in SA, all species except tall fescue and weeping grass were assessed.

As the six grasses showed different responses to the treatments imposed throughout the experiment, the species were analysed separately for each experimental season. As some of the traits measured consisted of only one replicate of data, the data were analysed twice. In the first analysis, the data consisting of two replicates were averaged, giving all variables a total of six observations (three moistures and two defoliations per species). This analysis contained all variables. Only correlations were determined on these data due to the small number of observations (I. Davies, pers. comm.). In the second analysis, those traits with only one replicate of data (eg. root weights) were removed, and both replicates of the remaining variables used to increase the number of observations to 12 per trait. This analysis contained fewer variables but had a greater number of observations. Correlation matrices and multiple regression were conducted on these data.

There were 50 independent variables used in the initial SS season analysis (including root characteristics), while there were 68 independent variables in the initial SA season analysis (Table 7.1). Minitab was used to produce correlation matrices. Stepwise regression was conducted with Minitab to produce suggested models. Inter–correlation between variables was checked and variables removed when necessary.

Table 7.1: Independent variables used to determine associations with mortality in the Spring–Summer and Summer–Autumn experimental season analyses. The number of assessments are indicated in brackets.

Spring–Summer	Summer–Autumn
Basal area (2)	Basal area (3)
Change in basal area (1)	Change in basal area (3)
DW Yields (spring, summer and total) (3)	DW Yields (summer, autumn and total) (3)
WSC concentration (2)	WSC concentration (4)
Change in WSC concentration (1)	Change in WSC concentration (4)
Fructan concentration (2)	Fructan concentration (4)
Change in fructan concentration (1)	Change in fructan concentration (4)
Fructan/WSC ratio (2)	Fructan/WSC ratio (4)
Change in Fructan/WSC ratio (1)	Change in Fructan/WSC ratio (4)
DMD (3)	DMD (3)
Change in DMD (3)	Change in DMD (3)
Nitrogen (3)	Nitrogen (3)
Change in N (3)	Change in N (3)
Effective rooting depth (1)	Effective rooting depth (1)
Total root weight (2)	Total root weight (2)
Change in total root weight (1)	Change in total root weight (1)
Root weights-individual depths (8 x 2)	Root weights-individual depths (8 x 2)
Proportion of roots in the upper 20 cm (2)	Proportion of roots in the upper 20 cm (2)
Seasonal rainfall (1)	Seasonal rainfall (1)

Results

Plant mortality

There were significantly greater plant losses of perennial ryegrass and cocksfoot than the other species following the SS treatments (main effect, P<0.001). Plant losses were greater in the 40% drought treatment plots (P<0.05) for both species (Figure 7.1). There was no effect of moisture regime on plant death in the other species. Defoliation severity did not affect plant death. During the SA season, plant death ranged from 14% in wallaby grass and cocksfoot to no plant death in tall fescue (averaged over the other treatments), however the differences were not significant (data not shown). Plant death during the SA season was not significantly affected by any of the treatments applied.

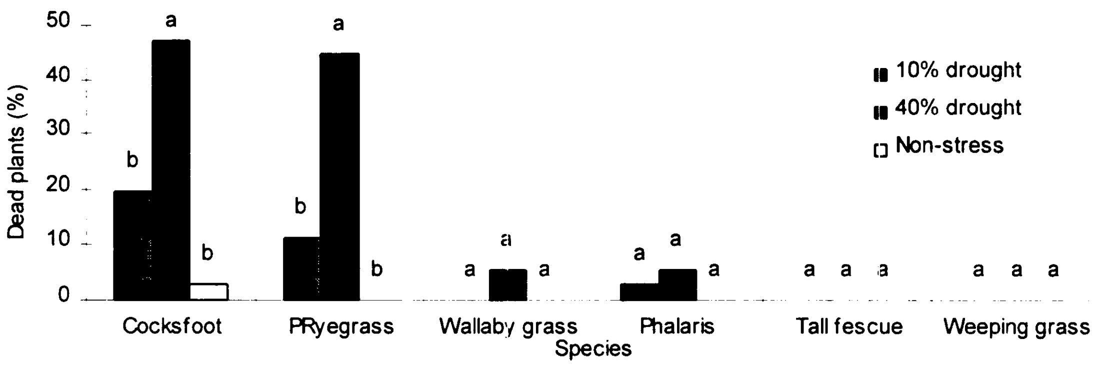

Figure 7.1: Percentage of plants, of six perennial grass species, which died during the Spring–Summer season at three moisture treatments; 10% drought, 40% drought and non-stress moisture. The data are averaged over the two defoliation intensities. Like letters above each bar indicate no significant difference within a species (P<0.05).

Traits important to persistence

The traits that were most highly correlated with mortality varied with species and season (Table 7.2), with many of the traits inter–correlated. In general, plant mortality was negatively correlated with individual plant traits and positively correlated with changes in the individual traits. Some of the traits found to be correlated (P<0.05) with mortality with six observations per trait were not highly correlated when the number of observations was increased to 12, with different traits being isolated in some species.

While the type and timing of the measurement for each trait varied, the following can be deduced: a decline in carbohydrate reserves and basal area were associated with plant mortality of most species studied in this thesis (n=6 and 12). A deep rooting system appears to be associated with the survival of phalaris (n=6). The decline in nutritive quality and autumn DM yield were associated with losses of wallaby grass.

Table 7.2: Plant traits most highly correlated with plant mortality in the Spring–Summer and Summer–Autumn experimental seasons (P<0.05). Traits for both 6 (n=6) and 12 (n=12) observations per trait are presented. The four species tested were cocksfoot (CO), perennial ryegrass (PR), phalaris (PH) and wallaby grass (WG). Where n=6, r≥0.82 (P<0.05) and n=12, r≥0.58 (P<0.05).

	n=6						n=12					
	Spring–Summer		Summer–Autumn				Spring–Summer		Summer–Autumn			
Plant traits	CO	PR	CO	PR	PH	WG	CO	PR	CO	PR	PH	WG
Basal area (Dec)								-0.61				-0.69
Basal area (Mar)					-0.87		-0.66	-0.71	-0.73		-0.89	
Basal area (Jun)					-0.87				-0.70		-0.84	
ΔBasal area (Dec–Mar)					0.86					0.64	0.78	
ΔBasal area (Dec–Jun)					0.82						0.68	
WSC (Apr)									0.59			
WSC (Jun)			-0.94									
Fructan (Feb/Mar or Jun)		-0.90						-0.67	-0.63			
F–WSC ratio (D/J, F/M or Apr)		-0.85	0.85				-0.65	-0.63	0.60			
ΔWSC (Dec/Jan–Jun)			0.90									
ΔWSC (Apr-Jun)									0.70			
ΔFructan (Dec/Jan–Jun)			0.83									
ΔF–WSC ratio (D/J–F/M)			0.94				-0.65		0.65			
ΔF–WSC ratio (D/J–Jun)			0.83	0.88								
Rooting depth					-0.93							
Root wt-section (Dec)				0.84								
Root wt-section (Mar or Jun)	-0.79+	-0.84										
N (Dec)						-0.89						
N (Jun)											-0.61	
Yield (Autumn)												-0.70
Yield (SA)												-0.63

+ Not significant

Multiple regression indicated that basal area (the timing of assessment varied) was important in predicting plant death in the species assessed in both experimental seasons. The models are presented in Table 7.3. Fructan (total or proportion of WSC) was also related to the survival of cocksfoot and perennial ryegrass during SS. The degree of decline in DM yield (either summer or the SA season) was important for the survival of cocksfoot and wallaby grass during SA.

Table 7.3: Linear models indicating plant traits which are important for predicting plant mortality during the Spring–Summer and Summer–Autumn experimental seasons (n=12).

Species	Model	Coefficients	Adj R^2	P
	Spring–Summer			
Perennial ryegrass	Fructan (Feb/Mar)	-16.7	58.9	<0.01
	Basal area (Dec)	-5.4		
	Constant	121.21		
Cocksfoot	Basal area (Mar)	-6.1	53.6	<0.05
	ΔF–WSC ratio (Dec/Jan–Feb/Mar)	-28		
	Constant	108.8		
	Summer–Autumn			
Perennial ryegrass	ΔBasal area (Dec–Mar)	3.3	34.6	<0.05
	Constant	21.35		
Cocksfoot	Basal area (Mar)	-5.7	72	<0.01
	DW yield (Summer)	-0.089		
	Constant	112.3		
Phalaris	Basal area (Mar)	-1.58	76.3	<0.001
	Constant	74.05		
Wallaby grass	Basal area (Dec)	-5.7	70.1	<0.01
	DW yield (Total SA season)	-0.225		
	Constant	111.75		

Discussion

Plant mortality

It is not surprising that there were greater losses of perennial ryegrass and cocksfoot than phalaris or tall fescue, as both are commonly reported to be more sensitive to drought (Kemp 1981; Brouwer *et al.* 1994) and defoliation during drought (Hein and Vinall 1933; Robinson and Simpson 1966; Hutchinson 1970). However the extent of the cocksfoot losses was somewhat surprising. The high losses could have been due to two factors. Firstly, the plants had been growing in the field for only 9–12 months when the treatments were imposed. While Porto cocksfoot is reported as having good seedling vigour (Brouwer *et al.* 1994), observations in a field environment suggest that it needs to be managed leniently during its establishment year to ensure persistence (G. Blair, pers. comm.). Secondly, as discussed in Chapter 4, the lawn mower defoliates plants differently to animals. In the field, animals graze individual cocksfoot plants into small round–topped tussocks. In contrast, the lawn mower decapitated many of the tussocks, killing the center of many. Pook and Costin (1970) reported a decline in perennial ryegrass and an increase in phalaris in a perennial ryegrass–phalaris sward that was grazed continuously during drought.

The significant differences between plant losses of individual species in the SS season and the lack of differences following the SA season suggests that perennial ryegrass and cocksfoot were more susceptible to management practices during the SS period, while all species had similar sensitivities during the SA period. As the plants in this study were still in their establishment year, the extra three months of lenient management received by the SA season plants may have enabled them to become better established (e.g. larger basal area and more roots at depth), thereby making them more resistant to the treatments imposed.

The most interesting result in this chapter was the greater plant losses of cocksfoot and perennial ryegrass in the 40% SS drought compared to a 10% drought. This suggests that perennial ryegrass and cocksfoot are most susceptible to management stresses, such as defoliation, during the relatively frequent but moderate dry periods experienced on the Northern Tablelands. Extensive plant losses are likely if a pasture is mis–managed during these times. No previous reports of greater plant death at moderate droughts compared to severe droughts have been found, however, there have been few studies conducted which concurrently assess a range of controlled but 'realistic' droughts in the field. Studies reported in the literature which have assessed a range of moisture regimes (eg. Volaire and Thomas 1995) generally define drought as equivalent to no rainfall over times ranging from 7 to 80 days (eg. Molyneux and Davies 1983; Thomas 1986b; Volaire and Thomas 1995). Drought in the temperate regions of Australia and indeed in most environments throughout the world, in which intensive pasture and livestock production is practised, is not an extended period with no rain.

There are reports of differences in persistence of grass species under different defoliation regimes that vary from the non significant effect on mortality as found in this study (eg Albertson *et al.* 1953; Hutchinson 1970). As suggested in Chapter 6, it is possible that the effect of defoliation severity was overridden by the frequency at which defoliations were applied in this study. An etiolated regrowth study, conducted on this experiment following the SS season (King *et al.* 1996), showed that, although there were no differences in plant losses due to defoliation regime, the severe defoliation regime significantly reduced the regrowth potential of a number of the species, especially tall fescue.

The persistence of individual species varies depending on the environment and management regime (Arcioni *et al.* 1985; McWilliam 1968). In a study on the persistence of grass species (grown with subterranean clover) on the central slopes of New South Wales (over 6–8 years), phalaris and cocksfoot were the most persistent species and perennial ryegrass and Demeter tall fescue the least persistent (Hill 1985). A southern Western Australia study of the persistence of pure swards of perennial grass species (after 2 years) ranked the species (in order of average persistence): perennial ryegrass>phalaris>cocksfoot>tall fescue (Saunders 1993). The results presented in this chapter are different from these and suggest that after nine months of establishment and six months of SS drought and defoliation treatments, tall fescue and weeping grass were the most persistent together with phalaris and wallaby grass, while cocksfoot and perennial ryegrass were least persistent.

Traits important to plant persistence

It is acknowledged that the range in plant deaths in this experiment was not extensive in all species and the number of observations per trait measured was small. However, there are few data sets that contain the number of variables for the range of species covered in this study. Correlation matrices and multiple regression, as used in this study, can indicate the type of characteristics that may be important to persistence of perennial grasses under different intensities of drought and defoliation. Persistence is believed to be a complex trait (Wilkins 1991; Cunningham *et al.* 1994), hence plants may be lost from a pasture due to a deficiency, change or depletion in more than one plant trait/characteristic.

Both analyses (n=6 and n=12) were used in this study for two reasons: the number of observations per trait and the number of traits. The first analysis had the advantage of including all traits measured, but the disadvantage of only six observations per trait. The second analysis had the advantage of an increased number of observations, but included fewer traits. Many of the traits found to be highly correlated with mortality with six observations, were not highly correlated with 12 observations. The decline in correlation is to be expected when there are a number of different independent variable observations for the same dependant variable values (for example, there may be three different basal area readings for one mortality reading). To overcome this, more observations per trait are necessary. It is also important to remember that correlations indicate associations and not necessarily causal relationships.

Plant mortality was highly correlated with a decline in basal area and a decline in carbohydrate reserves in the introduced species assessed in both seasons. Deep rootedness was also highly correlated with phalaris survival during the SA season. Wallaby grass responded differently to the other species with plant mortality during the SA season being highly correlated with declines in nutritive quality and DM yield. The plant traits associated with plant persistence of the introduced species in this study are consistent with the literature. The literature on the introduced species is more extensive than for the two native species used in this experiment.

The decline in basal area was indicated as having a high association with plant mortality in the introduced species assessed in both SS and SA. When ground cover is maintained, the amount of soil moisture available for growth is increased (Brougham 1959). Culvenor and Oram (1996) used basal area and plant density measures to determine persistence of phalaris swards. A large basal area may be important in reducing competition from other species and indicates a better opportunity to utilise the resources available, including soil water, nutrients and sunlight. Plants with large basal areas also have more tillers and possibly a larger root system than those with small basal areas (Hoen 1968b).

Carbon reserves were found to be important in this study and have also been considered important for plant persistence by other authors also (eg. McKell *et al.* 1966; Arcioni *et al.* 1985; Volaire 1994, 1995). It has been reported that WSC levels need to be maintained at or above 16–20% to ensure good regrowth potential following defoliation (Davies 1965), hence it is unlikely that plants die because they have depleted all of their reserves, but die once levels are below a viable threshold (Parsons 1993). The change in the fructan–WSC ratio, an indicator of hydrolysis of fructans, was positively correlated with plant mortality in several of the introduced species. That is, as plant death increased, the proportion of fructans to WSC decreased compared to the earlier measurement. Volaire (1994) also reported conversion of fructans and sucrose into simple sugars (during a four month drought), however she concluded that hydrolysis resulted in better cocksfoot plant survival. In this study, greater summer hydrolysis was associated with greater plant death. This could suggest that there is a time (between 4–6 months) and carbohydrate threshold for which hydrolysis is a strength, before becoming a weakness. However, whether hydrolysis of fructans contributes to plant mortality or is a response to stress in weakened plants cannot be distinguished.

Persistence of perennial grasses during prolonged periods of drought depends to a large extent on plant root development in relation to the available soil moisture (Pook and Costin 1971; Jupp and Newman 1987). Many workers have considered deep rootedness important for survival (eg. McWilliam and Kramer 1968; Pook and Costin 1971). The results presented in this chapter also support this hypothesis. Garwood and Sinclair (1979) found that the drought tolerance of grass species appeared to be primarily determined by the volume of soil being exploited by the roots for water. A deep root system allows a plant to utilise deep water sources when the upper layers have been exhausted. If a plant cannot utilise this water, it has to either go dormant or die. Survival of phalaris has been reported to depend on the plant's ability to maintain an adequate water supply at the base of its dormant culms (McWilliam and Kramer 1968).

While not measured in this study, summer dormancy has been suggested as one of the important components of persistence in perennial grasses grown in arid conditions (Laude 1953; Oram and Freebairn 1984). Similarly, endophyte infection, reviewed by Joost (1995), has been reported to improve the drought tolerance of some species. For example, tall fescue infected with *Acremonium coenophialum* was found to have enhanced tiller density and survival during severe water deficit (West *et al.* 1993). A study was conducted on the endophyte status of the seed and plants in the trial used in this experiment. Endophytes were detected in the seed of the perennial ryegrass but only at a low level. There was no living endophyte found in any of the vegetative samples of the six species in this trial (Li 1995).

It seems somewhat odd that persistence could be correlated with quality or yield, however Culvenor and Oram (1996) have also found relationships between persistence of phalaris and plot productivity. The regressions varied with phalaris cultivar and were also related to soil fertility factors (mainly P, K and Mn). Culvenor and Oram (1996) reported some plant losses of phalaris with significant plant mortality recorded only following a long summer drought and on sites that tended to have shallower soil profiles. They suggested that poor persistence may be associated with stresses larger than those in their experiment, for example, severe overgrazing during drought. Work by Robinson and Archer (1988) indicated that the year–round relative growth rate of wallaby grass was similar to phalaris and tall fescue, however its growth rates were lower during the cooler months and higher during the warmer months. As plants grow during the warmer months of the year and accumulate reserves to survive during periods of reduced growth, it is understandable that yield may be an important indicator of plant persistence in wallaby grass.

Conclusions

1. Perennial ryegrass and cocksfoot were sensitive to moderate SS drought resulting in greater plant losses than the other species. During the SA season all species had similar sensitivity to the treatments imposed with some plant losses across all treatments.

2. Plant mortality was highly correlated with basal area and carbohydrate reserves. Deep rootedness was associated with the survival of phalaris, while nutritive quality and autumn DM

yield were associated with wallaby grass survival.

3. Multiple regression indicated that basal area was one of the single most important plant traits for predicting plant death. Carbohydrate reserves were also important in predicting plant death in SS while DM yield was important in plant mortality during SA.

Chapter 8
General discussion

Perennial grasses form the most stable component of improved pastures on the tablelands and slopes of temperate Australia (Kemp 1991). Variable rainfall means that overstocking during droughts is a major cause of biological thresholds of pasture plants being exceeded. This occurs on the Australian rangelands (Mott *et al* 1993), and much of Australia, including the temperate high rainfall areas such as the Northern Tablelands of New South Wales.

Findings from this research

Results from the research reported in this thesis highlighted that the species studied responded differently to the treatments imposed Some of these differences included, the lack of flowering of cocksfoot during drought (especially during the SS season), the continual increase in basal area of several species during summer irrespective of drought (SS season), the different responses in nutritive value of weeping grass, and the greater water use of phalaris and weeping grass during the SS season. The range in responses to the treatments imposed indicates that each species requires specific management strategies. Cook *et al.* (1958) said 'unfortunately, responses of a plant to grazing at various seasons of the year, at various frequencies and intensities, and under various environmental conditions are so complex that a set of exact grazing principles cannot be developed, even for a single species'. The results from this study support this statement. However, it is impractical to test every species in every environmental–management combination. If vegetation types could be identified based on species mechanisms and responses, as suggested by Parsons (1993), then the behaviour of proportions of the flora may possibly be summarised and used to predict changes in vegetation. While this sounds ideal, the results from this study suggest that the process is not simple.

Species that are commonly used and recommended in the grazing industry require three attributes: good persistence, high DM production and high nutritive value. The species used in this study have been ranked for these three traits (measured during this experiment). Each trait was allocated an arbitrary and subjective 'trait importance factor' in relation to its individual importance to the grazing industry. The rankings have been multiplied by the importance factor, then summed to indicate their relative performance in this experiment. The rankings, trait importance factors and relative performance of each species are presented in Table 8.1. Using this system, tall fescue was the best performing species. The remaining species had similar relative performances with cocksfoot and wallaby grass being the poorest performers.

Table 8.1: The relative performance of perennial grass species during the drought experiment conducted at Chiswick, Armidale. The species were ranked for persistence, dry matter yield and nutritive value (measured during the experiment and averaged over the treatments and the seasons imposed). The species are ranked as 1–6 (highest to lowest) for each trait. The trait importance factor is a subjective factor between 0–1 indicating the importance of each trait in the overall performance of the species. The performance score is the sum of the product of each trait ranking by the trait importance factor. The best performing species have the lowest performance scores.

	Persistence	Yield	Nutritive value	Performance score
Importance factor:	1	0.8	0.6	
Tall fescue	1	1	1	3.4
Weeping grass	1	6	3	9.4
Phalaris	4	5	2	10.6
Perennial ryegrass	5	3	3	11.0
Wallaby grass	3	4	6	12.8
Cocksfoot	5	2	5	13.2

In recent years there has been an increasing interest in native grasses and their role in animal production. Early reports that they were unproductive, of low quality and unresponsive to fertiliser (Donald 1975) led many producers to sow introduced species. Subsequent research has found that some native species do have potential as forage grasses; weeping grass and wallaby grass are two of these grasses (Lodge 1983; Archer and Robinson 1988; Robinson and Archer 1988; Jones 1995). The results presented in this thesis support reports that the native species are persistent, especially weeping grass, and indicate that their responses to stresses are different from the introduced species.

Weeping grass has the ability to maintain green foliage of good nutritive value for an extended period once drought stress has began, however after a certain period of drought stress, the plants cease to grow and enter a stage of dormancy or rest. The trigger or threshold that causes this cessation of plant growth and decline in quality is not known. Wallaby grass also had a different response to the treatments imposed. It showed the ability to continuously produce flowering stems from spring through to autumn (the entire assessment period in this experiment). Work on wallaby grass at Wagga Wagga found that seedling recruitment was an important component of the maintenance of basal cover under certain drought conditions (J. Virgona, pers. comm.).

The treatment that had the most substantial effect on plant traits, that is environmental (moisture treatment) or management treatment (defoliation intensity), varied with season, but tended to be somewhat consistent across traits. For example, during the SS season, drought tended to slow phenological development, resulting in the plants remaining vegetative, while during the SA season, severe defoliation tended to inhibit development. Similarly drought had a greater effect on carbohydrate reserve levels during the SS season, while defoliation intensity had a greater effect on reserve levels during the SA season. As summer is the common season and the seasonal responses are so different, this treatment consistency suggests that the environment during spring is an important factor, determining the potential response and effect of defoliation or continued drought during the following months.

Closer investigation of the effect of the treatments on carbohydrate reserves further supports this hypothesis. The rainfall received during the spring period appears to affect the carbohydrate reserves differently in the subsequent months. When preceded by a spring drought, the concentration of carbohydrate reserves declined, however when preceded by a spring with good rainfall, carbohydrate reserve levels increased.

Whilst the environmental conditions overrode the management effects during the SS season, grazing a pasture to leave approximately 1500 kg DM/ha residual will assist maintaining reserves during the drought and following months. It will also ensure that there is adequate green leaf for photosynthesis.

There were greater plant losses in SS than SA, especially in cocksfoot and perennial ryegrass. This reinforces the need for pastures to be moderately grazed during the spring period to ensure summer survival. Persistence during drought can be improved by maintaining high plant basal area. It is also important to adopt management strategies that maintain high levels of plant reserves during spring and summer, and good yields during summer and autumn. These practices include lenient grazing, even spelling, during spring so that the plants can progress to flowering.

Reducing both grazing intensity and frequency during drought to maintain the pasture at approximately 1500 kg DM/ha biomass will enhance plant survival. Maintaining good herbage cover throughout a drought will ensure a high leaf area for photosynthesis in an attempt to reduce substantial carbohydrate reserve losses via high plant respiration during drought and assist in recovery once the drought is relieved

One of the advantages of perennial grasses is their lower cost of production, as they do not need to be sown as frequently (Wilkins 1991). Scott (1996) calculated that the longer a pasture persists, the lower the cost to the producer (Figure 8.1). If a pasture lasts 3–5 years, the cost of the herbage produced is about $25/t, while if the pasture lasts 10 years, the cost drops to about $10/t.

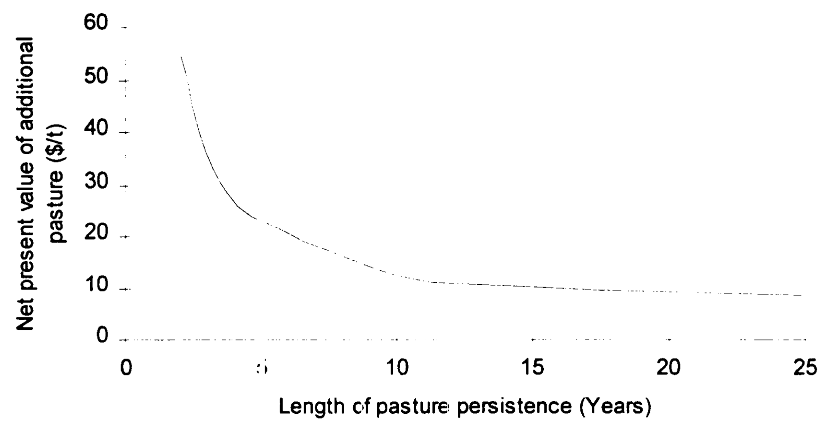

Figure 8.1: The net present value (cost) of pasture produced for each year a pasture persists. Calculations are based on a sown pasture with annual fertiliser applications which persists 2–25 years, using real inflation rates (Source: Scott 1996).

Degraded pastures, as a result of mismanagement, lead to a fall in animal production as both the dry matter production and its nutritive value are reduced. The loss of perennial pastures can be expensive. Replanting a pasture can cost between $150–250/ha (J. Scott, pers. comm.). Perennial pastures tend to be deeper rooted and have a longer growing season than annual species. Deep drainage below the root zone has increased with the replacement of deep rooted native vegetation with shallow rooted species. This increased deep drainage contributes to soil acidification and salinisation (Ridley *et al.* 1990, 1997). Hence, deep rooted perennial species offer a practical means of reducing land degradation (Ridley *et al.* 1997).

Breeding for plant persistence is compatible for nutritive value, however it is often inversely related to high herbage yield (Wilkins 1991). Therefore it is necessary to breed for productivity and persistency simultaneously. The physiological thresholds need to be defined for plant death, as it is unlikely that plants die when they have depleted all of their resources (eg. carbon, nitrogen and meristems). It is more likely that they die when they fall below thresholds of viability (Parsons 1993).

This experiment had a number of strengths, including the provision of controlled levels of drought and defoliation intensities, being able to monitor individual species without the responses being confounded by competition from other species and the unselective grazing of the lawn mower. Due to compromises that were necessary to acquire these controlled conditions, there were also a number of weaknesses. These include relatively low plant densities for some species, some plant scalping by the lawn mower and the monthly fertiliser application.

Plant populations of 25 plants/m^2 were used to represent plant densities which could be expected in mature established pastures. While this may be a suitable density for large crowned species, such as phalaris, it was too low for small crowned species such as cocksfoot and wallaby grass.

Selective grazing by sheep on trial plots of 1m^2 made mowing the logical alternative. However, the two problems with using a lawn mower on plants with raised crowns were decapitation and the complete removal of all plant material, leaving the ground bare.

Fertiliser was applied monthly to the trial area, in an attempt to reduce any effect of diminished nutrient cycling by the continual removal of surface debris. If regular fertiliser application encourages root development near the soil surface, as suggested by Fulkerson *et al.* (1993), this may have contributed to lack of rooting at depth (Chapter 6).

In an experiment such as this, it is impossible to test every combination of drought, defoliation and species. However, through the use of pasture models and decision support software (DSS), results can be extended beyond the trial site at Chiswick. Computer models and DSS are becoming increasingly sophisticated and more readily available. Models such as GrazFeed and GrassGro are increasing in popularity, and provide a unique means of drawing together findings from many decades and facets of research. The combined use of models and Geographic Information Systems (eg. Hill *et al.* 1996) provide an approach which will become more widely used in the future. Much of the data collected in this study will be valuable to those developing models and DSS, such as GrassGro. By providing data over a range of seasonal and management conditions, better species parameter sets will be developed, ultimately leading to better agreement between models and experimental data.

Future research

The work reported in this thesis has highlighted a number of areas that would benefit from further study. These include:

1. Wider testing of the finding that plant losses can be greater during moderate than severe drought, and any interaction with seasonal timing.

2. Further examination of the carbohydrate and nitrogen reserves of different species and any interaction with environment, management and season.

3. Determine the thresholds for growth and production of weeping grass.

4. Examine the flowering behaviour of cultivar Taranna versus other wallaby grass cultivars.

5. Quantify the critical nutrient thresholds for sustaining perennial grass pastures during drought. Plant persistence has been reported to be higher in pastures that are well fertilised (Fulkerson *et al.* 1993; Watson 1993), however thresholds are not known. This is an important management issue given that in times of financial difficulty the application of fertiliser is often postponed hence depleting these important and valuable reserves.

6. Extend the responses of species to drought and defoliation stresses to studies with mixed swards. Work is necessary to quantify the competition between plants of the same and different species.

Conclusions

1. Results from this research highlighted that the species assessed had different responses to the drought and defoliation treatments imposed, thus suggesting that different management strategies may be needed for individual species. Tall fescue was the overall best performing species, while the other species had similar performances.

2. Environmental factors (moisture regime) tended to have a greater effect on plant responses during SS, while management practice (defoliation intensity) had a greater effect during the SA season.

3. The rainfall during spring affected plant carbohydrate reserves during the spring months and the response during the subsequent summer months. Drought during spring resulted in a decline in carbohydrate reserves during the summer period, while a spring with good rainfall resulted in an increase in carbohydrate reserves.

4. Perennial grasses are more likely to die during moderate SS drought. Therefore, pastures need to be moderately grazed during dry spring periods to ensure summer survival.

5. Persistence during drought is related to maintaining high plant basal area, hence practices which encourage crown development will increase plant persistence. Adopting management strategies that maintain high levels of plant reserves during spring and summer and good

yields during summer and autumn are also important.

6. During dry periods or droughts, reducing both grazing intensity and frequency to maintain a pasture with approximately 1500 kg DM/ha biomass will enhance plant survival. Maintaining good herbage cover throughout a drought will ensure that carbohydrate reserves are maintained, also a high leaf area for photosynthesis, which will assist plant recovery once the drought is relieved.

Chapter 9
References

Ackerson, R. C. and Hebert, R. R. 1981. Osmoregulation in cotton in response to water stress. *Plant Physiology* 67: 484–488.

Ackerson, R. C., Krieg, D. R. and Sung, F. J. M. 1980. Leaf conductance and osmoregulation of field–grown sorghum genotypes. *Crop Science* 20: 10–14.

Akin, D. E. 1989. Histological and physical factors affecting digestibility of forages. *Agronomy Journal* 81: 17–25.

Alberda, T. H. 1957. The effects of cutting, light intensity and night temperature on growth and soluble carbohydrate content of *Lolium perenne* L. *Plant and Soil* 8: 199–230.

Alberda, T. H. 1966. The influence of reserve substances on dry–matter production after defoliation. *Proceedings of the X International Grassland Congress*. pp. 140–147.

Albertson, F. W., Riegel, A. and Launchbaugh, J. L. Jr. 1953. Effects of different intensities of clipping on short grasses in west–central Kansas. *Ecology* 34: 1–20.

Alexander, R. H. and McGowan, M. 1961. A filtration procedure for the *in vitro* determination of digestibility of herbage. *Journal of the British Grassland Society* 16: 275–276.

Amin, M. R. and Thomas, H. 1996. Growth and water relations of diverse populations of *Lolium perenne* exposed to drought in field, glasshouse and controlled environment. *Journal of Agricultural Science, Cambridge* 126: 15–23.

Anon. 1993. *Effects of drought on New South Wales*. Department of Water Resources, New South Wales.

Anon. 1995. Microlaena. *Microlaena stipoides*. *Plant Varieties Journal, Australia* 8: 27–28.

Archer, K. A. and Robinson, G. G 1988. Agronomic potential of native grass species on the Northern Tablelands of New South Wales. II. Nutritive value. *Australian Journal of Agricultural Research* 39: 425–436.

Arcioni, S., Falcinelli, M. and Mariotti, D. 1985. Ecological adaptation in *Lolium perenne* L.: Physiological relationships among persistence, carbohydrate reserves and water availability. *Canadian Journal of Plant Science* 65: 615–624.

Aspinall, D., Nicholls, P. B. and May L. H. 1964. The effects of soil moisture stress on the growth of barley. I. Vegetative development and grain yield. *Australian Journal of Agricultural Research* 15: 729–745.

Auda, H., Blaser, R. E. and Brown, R. H. 1966. Tillering and carbohydrate contents of orchardgrass as influenced by environmental factors. *Crop Science* 6: 139–143.

Baker, B. S. and Jung, G. A. 1968. Effect of environmental conditions on the growth of four perennial grasses. II. Responses to fertility, water and temperature. *Agronomy Journal* 60: 158–162.

Barker, D. J., Chu, A. C. P. and Korte, C. J. 1989. Ryegrass herbage yield components and their response to water deficit stress. *Proceedings of the XVI International Grassland Congress*. pp. 503–504.

Begg, J. E. and Turner, N. C. 1976. Crop water deficits. *Advances in Agronomy* 28: 161–217.

Belesky, D. P. and Fedders, J. M. 1994. Defoliation effects on seasonal production and growth rate of cool–season grasses. *Agronomy Journal* 86: 38–45.

Biddiscombe, E. F. 1953. A survey of the natural pastures of the Trangie district, New South Wales, with particular reference to the grazing factor. *Australian Journal of Agricultural Research* 4: 1–28.

Biddiscombe, E. F., Hutchings, R. J., Edgar, G. and Cuthbertson, E. G. 1956. Grazing management of natural pastures at Trangie, New South Wales. *Australian Journal of Agricultural Research* 7: 233–247.

Bildusas, I. J., Dixon, R. K., Pfleger, F. L. and Stewart, E. L. 1986. Growth, nutrition and gas exchange of *Bromus inermis* inoculated with *Glomus fasciculatum*. *New Phytologist* 102: 303–311.

Biswell, H. H. and Weaver, J. E. 1933. Effect of frequent clipping on the development of roots and tops of grasses in prairie sod. *Ecology* 14: 368–390.

Bittman, S., Simpson, G. M. and Mir, Z. 1988. Leaf senescence and seasonal decline in nutritional quality of three temperate forage grasses as influenced by drought. *Crop Science* 28: 546–552.

Black, J. L. 1987. Nutritional criteria for forage nutritive value. In *Improving the nutritive value of forage* (Convenor K. J. Hutchinson). SCA Technical Report Series No. 20, Canberra. pp. 29–43.

Blaikie, S. J. and Martin, F. M. 1987. Limits to the productivity of irrigated pastures in south–east Australia. In *Temperate Pastures: Their production, use and management* (Eds. J. L. Wheeler, C. J. Pearson and G. E. Robards). Australian Wool Corporation and CSIRO, Melbourne, Australia. pp. 119–125.

Blaser, R. E., Brown, R. H. and Bryant, H. T. 1966. The relationship between carbohydrate accumulation and growth of grasses under different microclimates. *Proceedings of the X International Grassland Congress*. pp. 147–150.

Boyer, J. S. 1971. Resistances to water transport in soybean, bean, and sunflower. *Crop Science* 11: 403–407.

Branson, F. A. 1953. Two new factors affecting resistance of grasses to grazing. *Journal of Range Management* 6: 165–171.

Breakwell, E. 1923. *The Grasses and Fodder Plants of New South Wales*. Department of Agriculture NSW, Sydney.

Briske, D. D. 1996. Strategies of plant survival in grazed systems: A functional interpretation. In *The Ecology and Management of Grazing Systems* (Eds. J. Hodgson and A. W. Illius). CAB International, Oxon, UK. pp. 37–67.

Brizuela, M. A., Detling, J. K. and Cid, M. S. 1986. Silicon concentration of grasses growing in sites with different grazing histories. *Ecology* 67: 1098–1101.

Brougham, R. W. 1956. Effect of intensity of defoliation on regrowth of pasture. *Australian Journal of Agricultural Research* 7: 377–387.

Brougham, R. W. 1957. Some factors that influence the rate of growth of pasture. *New Zealand Grassland Association* 19: 109–116.

Brougham, R. W. 1959. The effects of frequency and intensity of grazing on the productivity of a pasture of short–rotation ryegrass and red and white clover. *New Zealand Journal of*

Agricultural Research 2: 1232–1248.

Brougham, R. W. 1960. The effects of frequent hard grazings at different times of the year on the productivity and species yields of a grass–clover pasture. *New Zealand Journal of Agricultural Research* 3: 125–136.

Brouwer, D. W., Ison, R. L. and O'Reilly, M. V. 1994. *A guide to better pastures in temperate climates*. 5th Edition. NSW Agriculture, Newcastle.

Brown, R. H. and Blaser, R. E. 1965. Relationships between reserve carbohydrate accumulation and growth rate in orchardgrass and tall fescue. *Crop Science* 5: 577–582.

Brown, R. H. and Blaser, R. E. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (*Dactylis glomerata*). *Crop Science* 10: 213–216.

Bukey, F. S. and Weaver, J. E. 1939. Effects of frequent clipping on the underground food reserves of certain prairie grasses. *Ecology* 20: 246–252.

Burton, G. W., DeVane, E. H. and Carter, R. L. 1954. Root penetration, distribution and activity in southern grasses measured by yields, drought symptoms and P^{32} uptake. *Agronomy Journal* 46: 229–233.

Burton, G. W., Jackson, J. E. and Hart, R. H. 1963. Effect of cutting frequency and nitrogen on yield, *in vitro* digestibility, and protein, fiber, and carotene content of coastal bermudagrass. *Agronomy Journal* 55: 500–502.

Busso, C. A., Richards, J. H. and Chatterton, N. J. 1990. Nonstructural carbohydrates and spring regrowth of two cool–season grasses: Interaction of drought and clipping. *Journal of Range Management* 43: 336–43.

Campbell, D. 1968. *Drought: Causes, Effects, Solutions.* F. W. Cheshire, Sydney.

Carrow, R. N. 1996. Drought avoidance characteristics of diverse tall fescue cultivars. *Crop Science* 36: 371–377.

Chapman, D. F. and Lemaire, G. 1993. Morphogenetic and structural determinants of plant regrowth after defoliation. *Proceedings of the XVII International Grassland Congress*. pp. 95–104.

Cheplick, G. P. and Clay, K. 1988. Acquired chemical defences in grasses: the role of fungal endophytes. *Oikos* 52: 309–318.

Clement, C. R., Hopper, M. J., Jones, L. H. P. and Leafe, E. L. 1978. The uptake of nitrate by *Lolium perenne* from flowing nutrient solution. II. Effect of light, defoliation, and relationship to CO_2 flux. *Journal of Experimental Botany* 29: 1173–1183.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53: 209–233.

Collins, M. 1991. Nitrogen effects on yield and forage quality of perennial ryegrass and tall fescue. *Agronomy Journal* 83: 588–595.

Colwell, J. D. 1965. An automated procedure for the determination of phosphorus in sodium hydrogen carbonate extracts of soils. *Chemistry and Industry* 14: 873–875.

Cook, C. W., Stoddart, L. A. and Kinsinger, F. E. 1958. Responses of crested wheatgrass to various clipping treatments. *Ecological Monographs* 28: 237–272.

Crooke, W. M. and Simpson, W. E. 1971. Determination of ammonium in kjeldahl digests of crops by an automated procedure. *Journal of the Science of Food and Agriculture* 22: 9–10.

Culvenor, R. A. 1993a. Effect of cutting during reproductive development on the regrowth and regenerative capacity of the perennial grass, *Phalaris aquatica* L., in a controlled environment. *Annals of Botany* 72: 559–568.

Culvenor, R. A. 1993b. Persistence of *Phalaris aquatica* L. in response to grazing. *Proceedings of the XVII International Grassland Congress*. pp. 145–146.

Culvenor, R. A. 1994. The persistence of five cultivars of phalaris after cutting during reproductive development in spring. *Australian Journal of Agricultural Research* 45: 945–962.

Culvenor, R. A. and Oram, R. N. 1996. Comparison of winter–active phalaris with the Australian cultivar under rotational grazing. 1. Basal area and plant density. *Australian Journal of Experimental Agriculture* 36: 277–286.

Cunningham, P. J., Blumenthal, M. J., Anderson, M. W., Prakash, K. S. and Leonforte, A. 1994. Perennial ryegrass improvement in Australia. *New Zealand Journal of Agricultural Research* 37: 295–310.

Cutler, J. M., Rains, D. W. and Loomis, R. S. 1977. The importance of cell size in the water relations of plants. *Physiologia Plantarum* 40: 255–260.

Davidson, J. L. and Milthorpe, F. L. 1966a. Leaf growth in *Dactylis glomerata* following defoliation. *Annals of Botany* 30: 173–184.

Davidson, J. L. and Milthorpe, F. L. 1966b. The effect of defoliation on the carbon balance in *Dactylis glomerata*. *Annals of Botany* 30: 185–198.

Davidson, R. L. 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. Annals of Botany 33: 571–577.

Davidson, R. L. 1978. Root systems - the forgotten component of pastures. In *Plant Relations in Pastures* (Ed. J. R. Wilson). CSIRO, Melbourne. pp. 86–94.

Davies, A. 1965. Carbohydrate levels and regrowth in perennial rye–grass. *Journal of Agricultural Science* 65: 213–221.

Davies, W. J. and Zhang, J. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annual Review of Plant Physiology and Plant Molecular Biology* 42: 55–76.

Davis, C. H. 1941. Absorption of soil moisture by maize roots. *Botanical Gazette* 101: 791–805.

Davis, L. A. and Laude, H. M. 1964. The development of tillers in *Bromus mollis* L. *Crop Science* 4: 477–480.

Davis, W. E. P. 1960. Effects of clipping at various heights on characteristics of regrowth in reed canarygrass (*Phalaris arundinacea* L.). *Canadian Journal of Plant Science* 40: 452–456.

Denison, R. F. and Perry, H. D. 1990. Seasonal growth rate patterns for orchardgrass and tall fescue on the Appalachian Plateau. *Agronomy Journal* 82: 869–873.

Dina, S. J. and Klikoff, L. G. 1973. Effect of plant moisture stress on carbohydrate and nitrogen content of big sagebrush. *Journal of Range Management* 26: 207–209.

Donald, C. M. 1975. Temperate pasture species. In *Australian Grasslands* (Ed. R. M. Moore). Australian National University Press, Canberra. pp. 303–320.

Ernest, K. A. 1994. Resistance of creosotebush to mammalian herbivory: temporal consistency and browsing–induced changes. *Ecology* 75: 1684–1692.

Evans, P. S. 1971. Root growth of *Lolium perenne* L. II. Effects of defoliation and shading. *New Zealand Journal of Agricultural Research* 14: 552–562.

Fairey, N. A. 1985. Productivity, quality and persistence of perennial ryegrass as influenced by cutting/fertility management and ploidy. *Canadian Journal of Plant Science* 65: 565–571.

Falcinelli, M., Veronesi, F., Russi, L. and Pollidori, P. 1993. Persistence and productivity of some forage varieties and land races of different origin grown in central Italy. *Proceedings of the XVII International Grassland Congress.* pp. 266–268.

Fitzgerald, R. D. and Lodge, G. M. 1997. *Grazing management of temperate pastures: literature reviews and grazing guidelines for major species.* Technical Bulletin No. 47. NSW Agriculture.

Foley, J. C. 1957. *Droughts in Australia: Review of records from earliest years of settlement to 1955.* Bulletin No. 43. Commonwealth Bureau of Meteorology, Melbourne.

Foss, J. G. 1983. Persistence, yield and quality of reed canarygrass (*Phalaris arundinacea* L.) varieties at different sites in Norway. *Meldinger fra Norges Landbrukshøgskole* 62: 1–31.

Frank, A. B. and Bauer, A. 1991. Rooting activity and water use during vegetative development of crested and western wheatgrass. *Agronomy Journal* 83: 906–910.

Frank, A. B., Bittman, S. and Johnson, D. A. 1996. Water relations of cool–season grasses. In *Cool–Season Forage Grasses* (Eds. L. E. Moser, D. R. Buxton and M. D. Casler). Agronomy Monograph No. 34. pp. 127–164.

Frasier, G. W. and Cox, J. R. 1994. Water balance in pure stand of Lehmann lovegrass. *Journal of Range Management* 47: 373–378.

Fry, J. D. and Butler, J. D. 1989. Responses of tall and hard fescue to deficit irrigation. *Crop Science* 29: 1536–1541.

Fulkerson, W. J. 1994. Effect of redefoliation on the regrowth and water soluble carbohydrate content of *Lolium perenne*. *Australian Journal of Agricultural Research* 45: 1809–1815.

Fulkerson, W. J. and Michell, P. J. 1987. The effect of height and frequency of mowing on the yield and composition of perennial ryegrass—white clover swards in the autumn to spring period. *Grass and Forage Science* 42: 169–174.

Fulkerson, W. J. and Slack, K. 1995. Leaf number as a criterion for determining defoliation time for *Lolium perenne*: 2. Effect of defoliation frequency and height. *Grass and Forage Science* 50: 16–20.

Fulkerson, W. J., Slack , K. and Lowe, K. F. 1994. Variation in the response of *Lolium* genotypes to defoliation. *Australian Journal of Agricultural Research* 45: 1309–1317.

Fulkerson, W. J., Slack, K., Moore, K. and Rolfe, C. 1993. Management of *Lolium perenne/Trifolium repens* pastures in the subtropics. I. Effect of defoliation interval, seeding rate and application of N and lime. *Australian Journal of Agricultural Research* 44: 1947–1958.

Gaff, D. F. 1980. Protoplasmic tolerance of extreme water stress. In *Adaptation of Plants to Water and Higher Temperature Stress* (Eds. N. C. Turner and P. J. Kramer). John Wiley and Sons, New York. pp. 207–230

Garber, L. F. 1931. Food reserves in relation to other factors limiting the growth of grasses. *Plant Physiology* 6: 43–71.

Garwood, E. A. 1967. Seasonal variation in appearance and growth of grass roots. *Journal of the British Grassland Society* 22: 121–130.

Garwood, E. A and Sinclair, J. 1979. Use of water by six grass species. 2. Root distribution and use of soil water. *Journal of Agricultural Science, Cambridge* 93: 25–35.

Garwood, E. A., Tyson, K. C. and Sinclair, J. 1979. Use of water by six grass species. 1. Dry–matter yields and response to irrigation. *Journal of Agricultural Science, Cambridge* 93: 13–24.

Gavande, S. A. and Taylor, S. A. 1967. Influence of soil water potential and atmospheric evaporative demand on transpiration and energy status of water in plants. *Agronomy Journal* 59: 4–7.

Genstat 5 Committee. 1987. *Genstat 5 Reference Manual*. Clarendon Press, Oxford.

Gentilli, J. 1971. The main climatological elements. In *Climates of Australia and New Zealand. World Survey of Climatology. Volume 13* (Ed. J. Gentilli). Elsevier Publishing Company, The Netherlands. pp. 119–188.

George, J. M., Hutchinson, K. J. and Mottershead, B. E. 1970. Spear thistle (*Cirsium vulgare*) invasion of perennial pastures *Proceedings of the XI International Grassland Congress*. pp. 685–688.

Georgiadis, N. J and McNaughton, S. J. 1988. Interactions between grazers and a cyanogenic grass, *Cynodon plectostachyus*. *Oikos* 51: 343–350.

Georgiadis, N. J. and McNaughton, S J. 1990. Elemental and fibre contents of savanna grasses: variation with grazing, soil type, season and species. *Journal of Applied Ecology* 27: 623–634.

Gerwitz, A. and Page, E. R. 1974. An empirical mathematical model to describe plant root systems. *Journal of Applied Ecology* 11: 773–781.

Gifford, R. O. and Jensen, E. H. 1967. Some effects of soil moisture regime and bulk density on forage quality. *Agronomy Journal* 59: 75–77.

Gonzalez, B., Boucaud, J., Salette, J., Langlois, J. and Duyme, M. 1989. Changes in stubble carbohydrate content during regrowth of defoliated perennial ryegrass (*Lolium perenne* L.) on two nitrogen levels. *Grass and Forage Science* 44: 411–415.

Greacen, E. L., Correll, R. L., Cunningham, R. B., Johns, G. G. and Nicolls, K. D. 1981. Calibration. In *Soil Water Assessment by the Neutron Method* (Ed. E. L. Greacen). CSIRO, Australia. pp. 50–81.

Greenhouse, S. W. and Geisser, S. 1959. On methods in the analysis of profile data. *Psychometrika* 24: 95–112.

Greenwood, K. L. 1996a. Colour images enhance interpretation of soil water content data. *Proceedings of the Australian and New Zealand National Soils Conference, Melbourne*. pp. 89–90.

Greenwood, K. L. 1996b. Soil physical properties under pasture after long–term grazing by sheep. PhD Thesis, University of New England, Armidale.

Hamblin, A. P. 1985. The influence of soil structure on water movement, crop root growth, and water uptake. *Advances in Agronomy* 38: 95–158.

Harris, W. 1978. Defoliation as a determinant of the growth, persistence and composition of pasture. In *Plant Relations in Pastures* (Ed. J. R. Wilson). CSIRO, Melbourne. pp. 67–85.

Harris, W. and Lazenby, A. 1974. Competitive interaction of grasses with contrasting temperature responses and water stress tolerances. *Australian Journal of Agricultural Research* 25: 227–246.

Heady, H. F. 1964. Palatability of herbage and animal preference. *Journal of Range Management* 17: 76–82.

Heathcote, R. L. 1973. Drought perception. In *The Environmental, Economic and Social Significance of Drought* (Ed. J V. Lovett). Angus and Robertson, Sydney. pp. 7–14.

Hein, M. A. and Vinall, H. N. 1933. Persistence of grass and legume species under grazing conditions. *Journal of the American Society of Agronomy* 25: 595–602.

Hellkvist, J., Richards, G. P. and Jarvis, P. G. 1974. Vertical gradients of water potential and tissue water relations in Sitka spruce trees measured with the pressure chamber. *Journal of Applied Ecology* 11: 637–667.

Hilder, E. J. 1963a. Demeter fescue. *Field Station Record. Division of Plant Industry, CSIRO* 2: 34–44.

Hilder, E. J. 1963b. Growth curves of three grass species at Armidale, NSW. *Field Station Record. Division of Plant Industry, CSIRO* 2: 25–28.

Hilder, E. J. 1963c. The performance of several grasses in swards. *Field Station Record. Division of Plant Industry, CSIRO* 2: 9-24.

Hill, B. D. 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, M. J. 1989. The effect of differences in intensity and frequency of defoliation on the growth of *Phalaris aquatica* L. and *Dactylis glomerata* L. *Australian Journal of Agricultural Research* 40: 333–343.

Hill, M. J and Watson, R. W. 1989. The effect of differences in intensity and frequency of defoliation on the growth of Sirolan phalaris in the field. *Australian Journal of Agricultural Research* 40: 345-352.

Hill, M. J., Donald, G. E., Vickery, P J. and Furnival, E. P. 1996. Integration of satellite remote sensing, simple bioclimatic models and GIS for assessment of pastoral development for a commercial grazing enterprise. *Australian Journal of Experimental Agriculture* 36: 309–

321.

Hoen, K. 1966. The effect of temperature and soil moisture on summer survival of two varieties of *Phalaris tuberosa*. *Australian Journal of Experimental Agriculture and Animal Husbandry* 6: 280–282.

Hoen, K. 1968a. Summer dormancy in *Phalaris tuberosa* L. *Australian Journal of Agricultural Research* 19: 227–239.

Hoen, K. 1968b. The effect of plant size and developmental stage on summer survival of some perennial grasses. *Australian Journal of Experimental Agriculture and Animal Husbandry* 8: 190–196.

Horst, G. L. and Nelson, C. J. 1979. Compensatory growth of tall fescue following drought. *Agronomy Journal* 71: 559–563.

Hsiao, T. C. 1973. Plant responses to water stress. *Annual Review of Plant Physiology* 24: 519–570.

Hsiao, T. C., O'Toole, J. C., Yambao, E. B. and Turner, N. C. 1984. Influence of osmotic adjustment on leaf rolling and tissue death in rice (*Oryza sativa* L.). *Plant Physiology* 75: 338–341.

Hutchinson, K. J. 1970. The persistence of perennial species under intensive grazing in a cool temperate environment. *Proceedings of the XI International Grassland Congress*. pp. 611–614.

Hutchinson, K. J. 1991. The stability and resilience of grazing systems – managing for their sustainable development. *Proceedings of the International Conference on Sustainable Land Management*. pp. 297–303.

Hutchinson, K. J. 1992. The grazing resource. *Proceedings of the 6th Australian Society of Agronomy Conference*. pp. 54–60.

Hyder, D. N. 1972. Defoliation in relation to vegetative growth. In *The Biology and Utilization of Grasses* (Eds. V. B. Youngner and C. M. McKell). Academic Press, New York. pp. 304–317.

Jacques, W. A. 1956. Root development in some common New Zealand pasture plants. IX. The root replacement pattern in perennial ryegrass (*Lolium perenne*). *New Zealand Journal of*

Science and Technology 38A: 60–165.

Jacques, W. A. and Edmond, D. B. 1952. Root development in some common New Zealand pasture plants. V. The effect of defoliation and root pruning on cocksfoot (*Dactylis glomerata*) and perennial ryegrass (*Lolium perenne*). *New Zealand Journal of Science and Technology* 34: 231–248.

Jameson, D. A. and Huss, D. L. 1959. The effect of clipping leaves and stems on number of tillers, herbage weights, root weights, and food reserves of little bluestem. *Journal of Range Management* 12: 122–126.

Jones, C. E. 1995. Value, management and permanence of native grasses. *Proceedings of the 5th Annual Conference Tasmanian Branch of the Grassland Society, Victoria*. pp. 42–48.

Jones, M. B., Leafe, E. L. and Stiles, W. 1980. Water stress in field–grown perennial ryegrass. II. Its effect on leaf water status, stomatal resistance and leaf morphology. *Annals of Applied Biology* 96: 103–110.

Jones, M. M. and Rawson, H. M. 1979. Influence of rate of development of leaf water deficits upon photosynthesis, leaf conductance, water use efficiency, and osmotic potential in sorghum. *Physiologia Plantarum* 45: 103–111.

Joost, R. E. 1995. *Acremonium* in fescue and ryegrass: Boon or bane? A review. *Journal of Animal Science* 73: 881–888.

Julander, O. 1945. Drought resistance in range and pasture grasses. *Plant Physiology* 20: 573–599.

Jupp, A. P. and Newman, E. I. 1987. Morphological and anatomical effects of severe drought on the roots of *Lolium perenne* L. *New Phytologist* 105: 393–402.

Jury, W. A., Gardner, W. R. and Gardner, W. H. 1991. *Soil Physics*. 5th Edition. John Wiley and Sons, New York.

Kearsley, M. J. C. and Whitham, T. G. 1989. Developmental changes in resistance to herbivory: implications for individuals and populations. *Ecology* 70: 422–434.

Kellner, K. and Bosch, O. J. H. 1992. Influence of patch formation in determining the stocking rate for southern African grasslands. *Journal of Arid Environments* 22: 99–105.

Kemp, D. 1991. Defining the boundaries and manipulating the system. *Proceedings of the 6th*

Annual Conference of the Grassland Society, NSW. pp. 24–30.

Kemp, D. R. and Culvenor, R. A. 1994. Improving the grazing and drought tolerance of temperate perennial grasses. *New Zealand Journal of Agricultural Research* 37: 365–378.

Kemp, H. 1981. *Ryegrasses in New South Wales*. 2nd Edition. Department of Agriculture, New South Wales. Agfact P2.5.2.

Ketellapper, H. J. 1960. The effect of soil temperature on the growth of *Phalaris tuberosa* L. *Physiologia Plantarum* 13: 64 –647.

King J. R., Boschma, S. P., Scott, J. M. and Hill, M. J. 1996. Etiolated regrowth as a measure of potential forage grass recovery following drought stress in New South Wales, Australia. *Canadian Journal of Plant Science* 76: 811.

King, K. L. and Hutchinson, K. J. 1976. The effects of sheep stocking intensity on the abundance and distribution of mesofauna in pastures. *Journal of Applied Ecology* 13: 41–55.

Kramer, P. J. 1980. Drought, stress, and the origin of adaptations. In *Adaptation of Plants to Water and High Temperature Stress* (Eds. N. C. Turner and P. J. Kramer). John Wiley and Sons, New York. pp. 7–20.

Langer, R. H. M. 1977. Grass species and strains. In *Pastures and Pasture Plants* (Ed. R. H. M. Langer). A. H. and A. W. Reed, Sydney. pp. 65–83.

Langlands, J. P. and Bennett, I. L. 1973. Stocking intensity and pastoral production. I. Changes in the soil and vegetation of a sown pasture grazed by sheep at different stocking rates. *Journal of Agricultural Science, Cambridge* 81: 193–204.

LaRue, M. E., Nielsen, D. R. and Hagan, R. M. 1968. Soil water flux below a ryegrass root zone. *Agronomy Journal* 60: 625–629.

Laude, H. M. 1953. The nature of summer dormancy in perennial grasses. *Botanical Gazette* 114: 284–292.

Lawlor, D. W. 1972. Growth and water use of *Lolium perenne*. II. Plant growth. *Journal of Applied Ecology* 9: 99–105.

Lees, J. and Reeve, I. 1994. *TPSKP 1994 Producer Survey (M.414) – Report to the Meat Research Corporation*. The Rural Development Centre, University of New England, Armidale.

Lees, J. and Reeve, I. 1995. Summary of the 1994 producer survey. *Temperate Pastures Newsletter (MRC). No. 95/1.* pp. 4–5.

Levitt, J. 1980. *Responses of Plants to Environmental Stresses. Volume 2. Water, Radiation, Salt, and Other Stresses.* 2nd Edition. Academic Press, New York.

Li, X. S. 1995. *Incidence and significance of fungal endophytes in selected grass species on the Northern Tablelands of NSW.* Diploma of Science in Agriculture Thesis, University of New England.

Lodge, G. M. 1983. Grazing management of native and natural pastures on the northern slopes of New South Wales. PhD Thesis, University of New England, Armidale.

Lodge, G. M. 1993. *Danthonia richardsonii* Cashmore (wallaby grass) cv. Taranna. Register of Australian Herbage Plant Cultivars. *Australian Journal of Experimental Agriculture* 33: 393–394.

Lodge, G. M. and Whalley, R. D. B. 1989. *Native and natural pastures on the Northern Slopes and Tablelands of New South Wales: A review and annotated bibliography.* Technical Bulletin No 35. NSW Agriculture & Fisheries.

Lorenz, R. J. and Rogler, G. A. 1967 Grazing and fertilization affect root development of range grasses. *Journal of Range Management* 20: 129–132.

Ludlow, M. M. 1980. Stress physiology of tropical pasture plants. *Tropical Grasslands* 14: 136–145.

Ludlow, M. M., Fisher, M. J. and Wilson, J. R. 1985. Stomatal adjustment to water deficits in three tropical grasses and a tropical legume grown in controlled conditions and in the field. *Australian Journal of Plant Physiology* 12: 131–149.

Magcale–Macandog, D. B. and Whalley, R. D. B. 1993. Factors affecting the distribution of *Microlaena stipoides* on the Northern Tablelands of New South Wales. *Proceedings of the XVII International Grassland Congress.* pp. 311–313.

Matsuda, K. and Riazi, A. 1981. Stress–induced osmotic adjustment in growing regions of barley leaves. *Plant Physiology* 68: 571–576.

Matthew, C., Xia, J. X., Chu, A. C P., MacKay, A. D. and Hodgson, J. 1991. Relationship between root production and tiller appearance rates in perennial ryegrass (*Lolium perenne*

L.). In *Plant Root Growth: An Ecological Perspective*. Special Publication No. 10 of the British Ecological Society (Ed. D. Atkinson). Blackwell Scientific Publications, Oxford.

May, L. H. and Milthorpe, F. L. 1962. Drought resistance of crop plants. *Field Crop Abstracts* 15: 171–179.

McClymont, G. L. 1969. Nutritional value of plant matter and factors affecting its intake by animals. In *Intensive Utilization of Pastures* (Ed. B. J. F. James). Halstead Press, Sydney. pp. 38–41.

McDonald, R. C., Isbell, R. F., Speight, J. G., Walker, J. and Hopkins, M. S. 1990. *Australian Soil and Land Survey–Field handbook*. 2nd Edition. Inkata Press, Sydney.

McKell, C. M., Whalley, R. D. and Brown, V. 1966. Yield, survival, and carbohydrate reserve of hardinggrass in relation to herbage removal. *Journal of Range Management* 19: 86–89.

McNaughton, S. J. 1978. Serengeti ungulates: Feeding selectivity influences the effectiveness of plant defense guilds. *Science* 199: 806--807.

McNaughton, S. J. 1983. Compensatory plant growth as a response to herbivory. *Oikos* 40: 329–336.

McNaughton, S. J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. *The American Naturalist* 124: 863--886.

McNaughton, S. J. and Tarrants, J. L. 1983. Grass leaf silicification: Natural selection for an inducible defense against herbivores. *Proceedings of the National Academy of Sciences, USA* 80: 790–791.

McWilliam, J. R. 1968. The nature of the perennial response in Mediterranean grasses. II. Senescence, summer dormancy, and survival in *Phalaris*. *Australian Journal of Agricultural Research* 19: 397–409.

McWilliam, J. R. 1986. The national and international importance of drought and salinity effects on agricultural productivity. In *Plant Growth, Drought and Salinity* (Eds. N. C. Turner and J. B. Passioura). CSIRO, Australia. pp. 1–13.

McWilliam, J. R. and Kramer, P. J. 1968. The nature of the perennial response in Mediterranean grasses. I. Water relations and summer survival in *Phalaris*. *Australian Journal of Agricultural Research* 19: 381–395.

Meyer, S. J., Hubbard, K. G. and Wilhite, D. A. 1993. A crop–specific drought index for corn: II. Application of drought monitoring and assessment. *Agronomy Journal* 85: 396–399.

Meyers, G. 1996. Predictability and the role of the oceans in the climate system. *"Of droughts and flooding rains". Occasional paper CV03/95. Managing with Climate Variability Conference*. pp. 10–15.

Michelena, V. A. and Boyer, J. S. 1982. Complete turgor maintenance at low water potentials in the elongating region of maize leaves. *Plant Physiology* 69: 1145–1149.

Milchunas, D. G. and Lauenroth, W. K. 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs* 63: 327–366.

Milewski, A. V., Young, T. P. and Madden, D. 1991. Thorns as induced defenses: experimental evidence. *Oecologia* 86: 70–75.

Millar, G. 1991. Phalaris absorbs more soil moisture at depth than perennial ryegrass. In *Proceedings of the 6th Annual Conference of the Grassland Society, NSW*. pp. 95–96.

Minson, D. J., Harris, C. E., Raymond W. F. and Milford, R. 1964. The digestibility and voluntary intake of S22 and H.1 ryegrass, S170 tall fescue, S48 timothy, S215 meadow fescue and germinal cocksfoot. *Journal of the British Grassland Society* 19: 298–305.

Minson, D. J., Raymond, W. F. and Harris, C. E. 1960. Studies in the digestibility of herbage. VIII. The digestibility of S 37 cocksfoot, S 23 ryegrass and S 24 ryegrass. *Journal of the British Grassland Society* 15: 174–180.

Misra, G. and Singh, K. P. 1982. Effect of soil moisture and clipping stresses on the nutrient (N, P and K) concentration, uptake and use efficiency in one temperate and two tropical grasses. *Plant and Soil* 69: 413–421.

Mitchell, K. J. and Coles, S. T. J. 1955. Effects of defoliation and shading on short–rotation ryegrass. *New Zealand Journal of Science and Technology* 36A: 586–604.

Molyneux, D. E. and Davies, W. J. 1983. Rooting pattern and water relations of three pasture grasses growing in drying soil. *Oecologia* 58: 220–224.

Morgan, J. M. 1983. Osmoregulation as a selection criterion for drought tolerance in wheat. *Australian Journal of Agricultural Research* 34: 607–614.

Morgan, J. M. 1984. Osmoregulation and water stress in higher plants. *Annual Review of Plant Physiology* 35: 299–319.

Mott, J. J. McKeon, G. K. and Day, K. A. 1993. Prediction of plant mortality under grazing – a conceptual approach. *Proceedings of the XVII International Grassland Congress*. pp. 167–168.

Mott, J. J., Ludlow, M. M., Richards, J. H. and Parsons, A. D. 1992. Effects of moisture supply in the dry season and subsequent defoliation on persistence of the savanna grasses *Themeda triandra, Heteropogon contortus* and *Panicum maximum*. *Australian Journal of Agricultural Research* 43: 241–260.

Munnich, D. J., Simpson, P. C. and Nicol, H. I. 1991. A survey of native grasses in the Goulburn District and factors influencing their abundance. *The Rangeland Journal* 13: 118–129.

Nagarajah, S. and Schulze, E.–D. 1983. Responses of *Vigna unguiculata* (L.) Walp. to atmospheric and soil drought. *Australian Journal of Plant Physiology* 10: 385–394.

Neiland, B. M. and Curtis, J. T. 1956. Differential responses to clipping of six prairie grasses in Wisconsin. *Ecology* 37: 355–365.

Norris, I. B. 1982. Soil moisture and growth of contrasting varieties of *Lolium, Dactylis* and *Festuca* species. *Grass and Forage Science* 37: 273–283.

Norris, I. B. and Thomas, H. 1982a. Recovery of ryegrass species from drought. *Journal of Agricultural Science, Cambridge* 98: 623–628.

Norris, I. B. and Thomas, H. 1982b. The effect of droughting on varieties and ecotypes of *Lolium, Dactylis* and *Festuca. Journal of Applied Ecology* 19: 881–889.

Oram, R. N. 1983. Ecotypic differentiation for dormancy levels in oversummering buds of *Phalaris aquatica* L. *Botanical Gazette* 144: 544–551.

Oram, R. N. (Ed.) 1990. *Register of Australian Herbage Plant Cultivars*. 3rd Edition. CSIRO, Australia.

Oram, R. N. and Culvenor, R. A. 1994. Phalaris improvement in Australia. *New Zealand Journal of Agricultural Research* 37: 329–339.

Oram, R. N. and Freebairn, R. D. 1984. Genetic improvement of drought survival ability in

Phalaris aquatica L. *Australian Journal of Experimental Agriculture and Animal Husbandry* 24: 403–409.

O'Reilly, M. V. 1981. *A guide to better pastures in temperate climates*. 4th Edition. Wright Stephenson & Co, Australia.

Orodho, A. B. and Trlica, M. J. 1990. Clipping and long–term grazing effects on biomass and carbohydrate reserves of Indian ricegrass. *Journal of Range Management* 43: 52–57.

Ortega, S. J. A., Sollenberger, L. E., Quesenberry, K. H., Cornell, J. A. and Jones Jr., C. S. 1992. Productivity and persistence of rhizoma peanut pastures under different grazing managements. *Agronomy Journal* 84: 799–804.

Ourry, A., Bigot, J. and Boucaud, J. 1989. Protein mobilization from stubble and roots and proteolytic activities during post–clipping regrowth of defoliated perennial ryegrass. *Journal of Plant Physiology* 134: 298–303.

Ourry, A., Bigot, J., Kim, T., Boucaud, J. and Salette, J. 1993. Reserve mobilisation during regrowth after cutting of forage species: quantification and physiological mechanisms in ryegrass and lucerne. *Proceedings of the XVII International Grassland Congress*. pp. 121–122.

Ourry, A., Boucaud, J. and Salette, J. 1990. Partitioning and remobilization of nitrogen during regrowth in nitrogen–deficient ryegrass. *Crop Science* 30: 1251–1254.

Ourry, A., Gonzalez, B., Bigot, J., Boucaud, J. and Salette, J. 1989. Nitrogen and carbohydrate mobilizations during regrowth of defoliated *Lolium perenne* L. *XVI International Grassland Congress*. pp. 513–514.

Parsons, A. J. 1993. Plant growth Chairman's summary paper. *Proceedings of the XVII International Grassland Congress*. pp. 176–178.

Passioura, J. B. and Munns, R. 1984. Hydraulic resistance of plants. II. Effects of rooting medium, and time of day, in barley and lupin. *Australian Journal of Plant Physiology* 11: 341–350.

Perrier, E. R., McKell, C. M. and Davidson, J. M. 1961. Plant–soil–water relations of two subspecies of orchard grass. *Soil Science* 92: 413–420.

Peterson, R. A. 1962. Factors affecting resistance to heavy grazing in needle–and–thread grass. *Journal of Range Management* 15: 183–189.

Pollock, C. J. 1986. Fructans and the metabolism of sucrose in vascular plants. *New Phytologist* 104: 1–24.

Pollock, C. J. and Jones, T. 1979. Seasonal patterns of fructan metabolism in forage grasses. *New Phytologist* 83: 9–15.

Pook, E. W. and Costin, A. B. 1970. Changes in pattern and density of perennial grasses in an intensively grazed sown pasture influenced by drought in southern New South Wales. *Australian Journal of Experimental Agriculture and Animal Husbandry* 10: 286–292.

Pook, E. W. and Costin, A. B. 1971. Root distribution and soil moisture studies in some perennial ryegrass and phalaris pastures on the Southern Tablelands, south–eastern Australia. *Field Station Record. Division of Plant Industry. CSIRO* 10: 59–72.

Prebble, R. E., Forrest, J. A., Honeysett, J. L., Hughes, M. W., McIntyre, D. S. and Schrale, G. 1981. Field installation and maintenance. In *Soil Water Assessment by the Neutron Method* (Ed. E. L. Greacen). CSIRO, Australia. pp. 82–98.

Renard, C. and François, J. 1985. Effects of increasing water stress on simulated swards of *Festuca arundinacea* Schreb under wind tunnel conditions. *Annals of Botany* 55: 869–879.

Rhoades, D. F. 1985. Offensive–defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. *The American Naturalist* 125: 205–238.

Richards, A. J. 1986. *Plant Breeding Systems*. Allen and Urwin, London.

Richards, J. H. 1993. Physiology of plants recovering from defoliation. *Proceedings of the XVII International Grassland Congress*. pp. 85–94.

Richards, J. H. and Caldwell, M. M. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: A field study with *Agropyron* species. *Journal of Applied Ecology* 22: 907–920.

Ridley, A. M. and Simpson, R. J. 1994. Seasonal development of roots under perennial and annual grass pastures. *Australian Journal of Agricultural Research* 45: 1077–1087.

Ridley, A. M., Slattery, W. J., Helyar, K. R. and Cowling, A. 1990. Acidification under grazed annual and perennial grass based pasture. *Australian Journal of Experimental Agriculture* 30: 539–544.

Ridley, A. M., White, R. E., Simpson R. J. and Callinan, L. 1997. Water use and drainage under phalaris, cocksfoot and annual ryegrass pastures. *Australian Journal of Agricultural Research* 48: 1011–1023.

Robertson, J. H. 1933. Effect of frequent clipping on the development of certain grass seedlings. *Plant Physiology* 8: 425–447.

Robinson, G. G. 1976. Productivity and response to nitrogen fertilizer of the native grass *Danthonia racemosa* (Wallaby grass). *Australian Rangeland Journal* 1: 49–52.

Robinson, G. G. and Archer, K. A. 1988. Agronomic potential of native grass species on the Northern Tablelands of New South Wales. I. Growth and herbage production. *Australian Journal of Agricultural Research* 39: 415–423.

Robinson, G. G. and Simpson, I. H. 1966. Performance of three perennial grass species during the winter drought, 1965 at Shannon Vale Nutrition Station. *Agricultural Gazette of New South Wales* 77: 743–747.

Ruby, E. S. and Young, V. A. 1953. The influence of intensity and frequency of clipping on the root system of brownseed paspalum. *Journal of Range Management* 6: 94–99.

Ryle, G. J. A. and Powell, C. E. 1975. Defoliation and regrowth in the graminaceous plant: the role of current assimilate. *Annals of Botany* 39: 297–310.

Saunders, C. M. 1993. Persistence and production of perennial grasses in southern Western Australia. *Proceedings of the XVII International Grassland Congress*. pp. 462–464.

Schnyder, H. and Nelson, C. J. 1987. Growth rates and carbohydrate fluxes within the elongation zone of tall fescue leaf blades. *Plant Physiology* 85: 548–553.

Schuster, J. L. 1964. Root development of native plants under three grazing intensities. *Ecology* 45: 63–70.

Scott, J. D. 1957. The study of primordial buds and the reaction of roots to defoliation as the basis of grassland management. *Proceedings of the VII International Grassland Congress*. pp. 479–487.

Scott, J. M. 1996. Pasture management and stocking rate policies. In *A Users Guide to Drought Feeding Alternatives* (Eds. I. Rowe and N. Cousins). University of New England, Armidale. pp. 75–84.

Shewmaker, G. E., Mayland, H. F., Rosenau, R. C. and Asay, K. H. 1989. Silicon in C-3 grasses: Effects on forage quality and sheep preference. *Journal of Range Management* 42: 122–127.

Silsbury, J. H. 1961. A study of dormancy, survival, and other characteristics in *Lolium perenne* L. at Adelaide, SA. *Australian Journal of Agricultural Research* 12: 1–9.

Simpson, P. 1992. Herbage quality of two yearlong green native grasses. *Proceedings of the 7th Annual Conference of the Grassland Society, NSW.* pp. 86–87.

Simpson, R. J. and Bonnett, G. D. 1993. Fructan exohydrolase from grasses. *New Phytologist* 123: 453–469.

Simpson, R. J. and Culvenor, R. A. 1987. Photosynthesis, carbon partitioning and herbage yield. In *Temperate Pastures: Their production, use and management* (Eds. J. L. Wheeler, C. J. Pearson and G. E. Robards). Australian Wool Corporation and CSIRO, Melbourne, Australia. pp. 103–118.

Smetham, M. L. 1973. Grazing management. In *Pastures and Pasture Plants* (Ed. R. H. M. Langer). A. H. and A. W. Reed, Sydney. pp. 179–228.

Smith, D. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissue. *Wisconsin Agricultural Experimental Station, Research Report* 41: 1–11.

Smith, R. C. G. and Johns, G. G. 1975. Seasonal trends and variability of soil moisture under temperate pasture on the Northern Tablelands of New South Wales. *Australian Journal of Experimental Agriculture and Animal Husbandry* 15: 250–255.

Smouter, H. and Simpson, R. J. 1989. Occurrence of fructans in the Gramineae (Poaceae). *New Phytologist* 111: 359–368.

Spollen, W. G. and Nelson, C. J. 1994. Response of fructan to water deficit in growing leaves of tall fescue. *Plant Physiology* 106: 329–336.

Sprague, V. G. and Sullivan, J. T 1950. Reserve carbohydrates in orchard grass clipped periodically. *Plant Physiology* 25: 92–102.

Steen, E. and Larsson, K. 1986. Carbohydrates in roots and rhizomes of perennial grasses. *New Phytologist* 104: 339–346.

Stone, L. R., Horton, M. L. and Olson T. C. 1973. Water loss from an irrigated sorghum field: I. water flux within and below the root zone. *Agronomy Journal* 65: 492–495.

Sullivan, J. T. and Sprague, V. G. 1943. Composition of the roots and stubble of perennial ryegrass following partial defoliation. *Plant Physiology* 18: 656–670.

Sullivan, J. T. and Sprague, V. G. 1949. The effect of temperature on the growth and composition of the stubble and roots of perennial ryegrass. *Plant Physiology* 24: 706–719.

Sullivan, J. T. and Sprague, V. G. 1953. Reserve carbohydrates in orchard grass cut for hay. *Plant Physiology* 28: 304–313.

Taylor, J. A. 1980. Merino sheep and intrapaddock patterning of herbaceous species on the northern Tablelands of New South Wales, Australia. PhD Thesis, University of New England, Armidale.

Thomas, H. 1986a. Effect of rate of dehydration on leaf water status and osmotic adjustment in *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. *Annals of Botany* 57: 225–235.

Thomas, H. 1986b. Water use characteristics of *Dactylis glomerata* L., *Lolium perenne* L. and *L. multiflorum* Lam. plants. *Annals of Botany* 57: 211–223.

Thomas, H. and Evans, C. 1990. Influence of drought and flowering on growth and water relations of perennial ryegrass populations. *Annals of Applied Biology* 116: 371–382.

Thornley, J. H. M. and Johnson, I. R. 1990. *Plant and Crop Modelling. A Mathematical Approach to Plant and Crop Physiology*. Oxford University Press, New York.

Tilley, J. M. A., Deriaz, R. E. and Terry, R. A. 1960. The *in vitro* measurement of herbage digestibility and assessment of nutritive value. *Proceedings of the VIII International Grassland Congress*. pp. 533–537.

Toft, N. L., McNaughton, S. J. and Georgiadis, N. J. 1987. Effects of water stress and simulated grazing on leaf elongation and water relations of an East African grass, *Eustachys paspaloides*. *Australian Journal of Plant Physiology* 14: 211–226.

Tomanek, G. W. and Albertson, F. W. 1957. Variations in cover, composition, production and roots of vegetation on two prairies in western Kansas. *Ecological Monographs* 27: 267–281.

Torbert, H. A., Edwards, J. H. and Pedersen, J. F. 1990. Fescues with large roots are drought tolerant. *Applied Agricultural Research* 5: 181–187.

Trlica, M. J. Jr. and Cook, C. W. 1971. Defoliation effects on carbohydrate reserves of desert species. *Journal of Range Management* 24: 418–425.

Troughton, A. 1957. *The Underground Organs of Herbage Grasses*. Commonwealth Agricultural Bureaux, England.

Troughton, A. 1981. Length of life of grass roots. *Grass and Forage Science* 36: 117–120.

Tuomi, J. and Augner, M. 1993. Synergistic selection of unpalatability in plants. *Evolution* 47: 668–672.

Turner, N. C. 1979. Drought resistance and adaptation to water deficits in crop plants. In *Stress Physiology in Crop Plants* (Eds. H. Mussell and R. C. Staples). John Wiley and Sons, New York. pp. 343–372.

Turner, N. C. 1986a. Adaptation to water deficits: a changing perspective. *Australian Journal of Plant Physiology* 13: 175–190.

Turner, N. C. 1986b. Crop water deficits: a decade of progress. *Advances in Agronomy* 39: 1–51.

Turner, N. C. and Begg, J. E. 1978. Responses of pasture plants to water deficits. In *Plant Relations in Pastures* (Ed. J. R. Wilson). CSIRO, Melbourne. pp. 50–66.

Turner, N. C. and Begg, J. E. 1981. Plant–water relations and adaptation to stress. *Plant and Soil* 58: 97–131.

Turner, N. C. and Jones, M. M. 1980. Turgor maintenance by osmotic adjustment: a review and evaluation. In *Adaptation of Plants to Water and High Temperature Stress* (Eds. N. C. Turner and P. J. Kramer). John Wiley and Sons, New York. pp. 87–103.

Turner, N. C. and Kramer, P. J. 1980. *Adaptation of Plants to Water and Higher Temperature Stress*. John Wiley and Sons, New York.

Turner, N. C., Begg, J. E. and Tonnet, M. L. 1978. Osmotic adjustment of sorghum and sunflower crops in response to water deficits and its influence on the water potential at which stomata close. *Australian Journal of Plant Physiology* 5: 597–608.

Turner, N. C., O'Toole, J. C., Cruz, R. T., Yambao, E. B., Ahmad, S., Namuco, O. S. and

Dingkuhn, M. 1986. Responses of seven diverse rice cultivars to water deficits. II. Osmotic adjustment, leaf elasticity, leaf extension, leaf death, stomatal conductance and photosynthesis. *Field Crops Research* 13: 273–286.

Ungar, E. D. 1996. Ingestive behaviour. In *The Ecology and Management of Grazing Systems* (Eds. J. Hodgson and A. W. Illius). CAB International, Oxon, UK. pp. 185–218.

Van Dyne, G. M., Brockington, N. R., Szocs, Z., Duek, J. and Ribic, C. A. 1980. Large herbivore subsystem. In *Grasslands, Systems Analysis and Management*. pp. 269–537.

Vegis, A. 1964. Dormancy in higher plants. *Annual Review of Plant Physiology* 15: 185–224.

Vieira, A. 1980. Grazing value of *Microlaena stipoides* (Labill.) R.Br. on sheep camps on the Northern Tablelands of New South Wales and its response to fertiliser when growing in a glasshouse. Diploma of Science in Agriculture Thesis, University of New England, Armidale.

Virgona, J. M. and Barlow, E. W. R. 1991. Drought stress induces changes in the non–structural carbohydrate composition of wheat stems. *Australian Journal of Plant Physiology* 18: 239–247.

Volaire, F. 1994. Effects of summer drought and spring defoliation on carbohydrate reserves, persistence and recovery of two populations of cocksfoot (*Dactylis glomerata*) in a Mediterranean environment. *Journal of Agricultural Science, Cambridge* 122: 207–215.

Volaire, F. 1995. Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. *Journal of Applied Ecology* 32: 56–66.

Volaire, F. 1995. Growth, carbohydrate reserves and drought survival strategies of contrasting *Dactylis glomerata* populations in a Mediterranean environment. *Journal of Applied Ecology* 32: 56–66.

Volaire, F. and Lelièvre, F. 1997. Production, persistence, and water–soluble carbohydrate accumulation in 21 contrasting populations of *Dactylis glomerata* L. subjected to severe drought in the south of France *Australian Journal of Agricultural Research* 48: 933–944.

Volaire, F. and Thomas, H. 1995. Effects of drought on water relations, mineral uptake, water–soluble carbohydrate accumulation and survival of two contrasting populations of cocksfoot (*Dactylis glomerata* L.). *Annals of Botany* 75: 513–524.

Volenec, J. J. 1986. Nonstructural carbohydrates in stem base components of tall fescue during regrowth. *Crop Science* 26: 122–127.

Volenec, J. J., Ourry, A. and Joern, B. C. 1996. A role for nitrogen reserves in forage regrowth and stress tolerance. *Physiologia Plantarum* 97: 158–193.

Watanabe, K., Nonaka, J. and Saiga, S. 1996. Seasonal changes in productivity and quality of temperate grasses and the fluctuations with years. 2. Changes of estimated dry matter digestibility. *Grassland Science* 42: 123–129.

Watson, R. W. 1993. *Phalaris*. 1st Edition. NSW Agriculture. Agfact P2.5.1.

Weaver, J. E. 1947. Rate of decomposition of roots and rhizomes of certain range grasses in undisturbed prairie soil. *Ecology* 28: 221–240.

Weaver, J. E. 1950. Effects of different intensities of grazing on depth and quantity of roots of grasses. *Journal of Range Management* 3: 100–113.

Weaver, J. E. and Zink, E. 1946. Length of life of roots of ten species of perennial range and pasture grasses. *Plant Physiology* 21: 201–217.

Weeda, W. C. and Goold, G. J. 1990. Effect of grazing management on the performance of newer pasture cultivars. *Proceedings of the New Zealand Grassland Association* 52: 145–149.

Welbank, P. J., Gibb, M. J., Taylor, P. J., and Williams, E. D. 1974. Root growth of cereal crops. In *Rothamsted Experimental Station Report for 1973 (Part 2)*. pp. 22–66.

West, C. P., Izekor, E., Turner, K. E. and Elmi, A. A. 1993. Endophyte effects in growth and persistence of tall fescue along a water–supply gradient. *Agronomy Journal* 85: 264–270.

West, C. P., Oosterhuis, D. M. and Wullschleger, S. D. 1990. Osmotic adjustment in tissues of tall fescue in response to water deficit. *Environmental and Experimental Botany* 30: 149–156.

Whalley, R. D. B. 1973. Drought and vegetation. In *The Environmental, Economic and Social Significance of Drought* (Ed. J. V. Lovett). Angus and Robertson, Australia. pp. 81–98.

Whalley, R. D. B. and Davidson, A. A. 1969. Drought dormancy in *Astrebla lappacea, Chloris acicularis,* and *Stipa aristiglumis*. *Australian Journal of Agricultural Research* 20: 1035–

1042.

Whalley, R. D. B. and Huxtable, C. H. A. 1993. Domestication of the Australian perennial grass, *Microlaena stipoides*. *Proceedings of the XVII International Grassland Congress*. pp. 214–215.

Whalley, R. D. B. and Rose, H. I. 1988. Variation in *Microlaena stipoides* (Labill.) R.Br. and its potential for improvement as a rangeland grass. *Proceedings 3rd International Rangelands Congress*. pp. 283–286.

Wheeler, D. J. B., Jacobs, S. W. L and Norton, B. E. 1990. *Grasses of New South Wales*. University of New England Publishing Unit, Armidale.

Wheeler, J. L. and Corbett, J. L. 1989. Criteria for breeding forages of improved feeding value: results of a Delphi survey. *Grass and Forage Science* 44: 77–83.

White, L. M. 1973. Carbohydrate reserves of grasses: a review. *Journal of Range Management* 26: 13–18.

White, R. H., Engelke, M. C., Morton, S. J. and Ruemmele, B. A. 1992. Competitive turgor maintenance in tall fescue. *Crop Science* 32: 251–256.

Whittet, J. N. 1936. *Pasture improvement in Northern Tableland districts*. Department of Agriculture NSW Bulletin.

Whittet, J. N. 1964. *Pastures*. Department of Agriculture, New South Wales.

Wilkins, P. W. 1991. Breeding perennial ryegrass for agriculture. *Euphytica* 52: 201–214.

Wilkinson, D. R. and Burke, G. 1995 Low–cost manual equipment for sampling the soil profile. *Proceedings of the 10th Annual Conference of the Grassland Society, NSW*. pp. 111.

Wilson, J. R., Brown, R. H. and Windham, W. R. 1983. Influence of leaf anatomy on the dry matter digestibility of C_3, C_4 and C_3/C_4 intermediate types of *Panicum* species. *Crop Science* 23: 141–146.

Woodman, H. E. and Norman, D. B. 1932. Nutritive value of pasture. IX. The influence of the intensity of grazing on the yield, composition and nutritive value of pasture herbage (Part IV). *Journal of Agricultural Science, Cambridge* 22: 852–873.

Woodman, H. E., Norman, D. B. and French, M. H. 1931. Nutritive value of pasture. VII. The influence of the intensity of grazing on the yield, composition and nutritive value of pasture herbage (Part III). *Journal of Agricultural Science, Cambridge* 21: 267–323.

Wright, G. C., Smith, R. C. G. and McWilliam, J. R. 1983a. Differences between two grain sorghum genotypes in adaptation to drought stress. I. Crop Growth and yield responses. *Australian Journal of Agricultural Research* 34: 615–626.

Wright, G. C., Smith, R. C. G. and Morgan, J. M. 1983b. Differences between two grain sorghum genotypes in adaptation to drought stress. III. Physiological responses. *Australian Journal of Agricultural Research* 34: 627–636.

Young, T. P. 1987. Increased thorn length in *Acacia depranolobium* – an induced response to browsing. *Oecologia* 71: 436–438.

Youngner, V. B. 1972. Physiology of defoliation and regrowth. In *The Biology and Utilization of Grasses* (Eds. V. B. Youngner and C. M. McKell). Academic Press, New York. pp. 292–303.