Chapter 1
Introduction

Droughts are an inevitable and recurring feature of world agriculture (McWilliam 1986). Despite attempts to predict droughts and reduce their impact, they are still the single most important factor which affect world food supplies. Droughts also affect the condition and stability of the land resource from which our food supplies are produced (McWilliam 1986; Hsiao 1973).

'Drought' is a relative term and has been defined differently for a number of countries throughout the world. An 'absolute drought' in Britain is a period of at least 15 consecutive days with less than 0.25 mm rain (Foley 1957; Campbell 1968; Heathcote 1973). In the United States of America, a drought is a period of 21 days when the rainfall is 30% less than the average (Campbell 1968).

Foley (1957) broadly defined drought in Australia as 'a period of rain deficiency, extending over months or years, of such a nature that crops and pasturage for stock are severely affected, if not completely burnt up and destroyed, water supplies are seriously depleted or dried up, and sheep and cattle perish'. The definition of drought and how it is perceived often determines the response of decision makers to a drought event (Anon 1993). Carr (1966, cited in Heathcote 1973) divided drought into three classes. An agricultural drought is one which occurs 'when soil moisture and rainfall are inadequate during the growing season to support healthy top growth to maturity and to prevent extreme crop stress and wilt'.

Drought is different from other natural hazards as it is a 'creeping phenomenon' (Gillette 1950, cited in Meyer *et al.* 1993). It accumulates gradually, sometimes persisting over long periods of time, thereby making it a difficult task to determine when a drought begins and when it ends. Secondly, droughts differ from one another in three factors; intensity, duration and spatial coverage (Gentilli 1971). Furthermore, the perception of drought severity depends on the demands made by human activities and by the vegetation on a region's water supplies (Meyer *et al.* 1993).

Droughts in agriculture are caused by the unreliability and variability of rainfall, not the total lack of it (Campbell 1968). An analysis of the characteristics and frequency of drought in Australia (Reynolds *et al.* 1983, cited in McWilliam 1986) highlighted that although the patterns of drought were unique to

Australia, they had much in common with other drought prone continents of the world. In the last 100 years or so, Australia has endured nine major widespread droughts and a large number of severe regional droughts (McWilliam 1986). At least five of these droughts have occurred in the last 60 years: 1940–41, 1944–45, 1965–67, 1977–82 (excluding 1978 and 1981) and 1993–94. The area of Australia affected by a number of these droughts is shown in Figure 1.1.
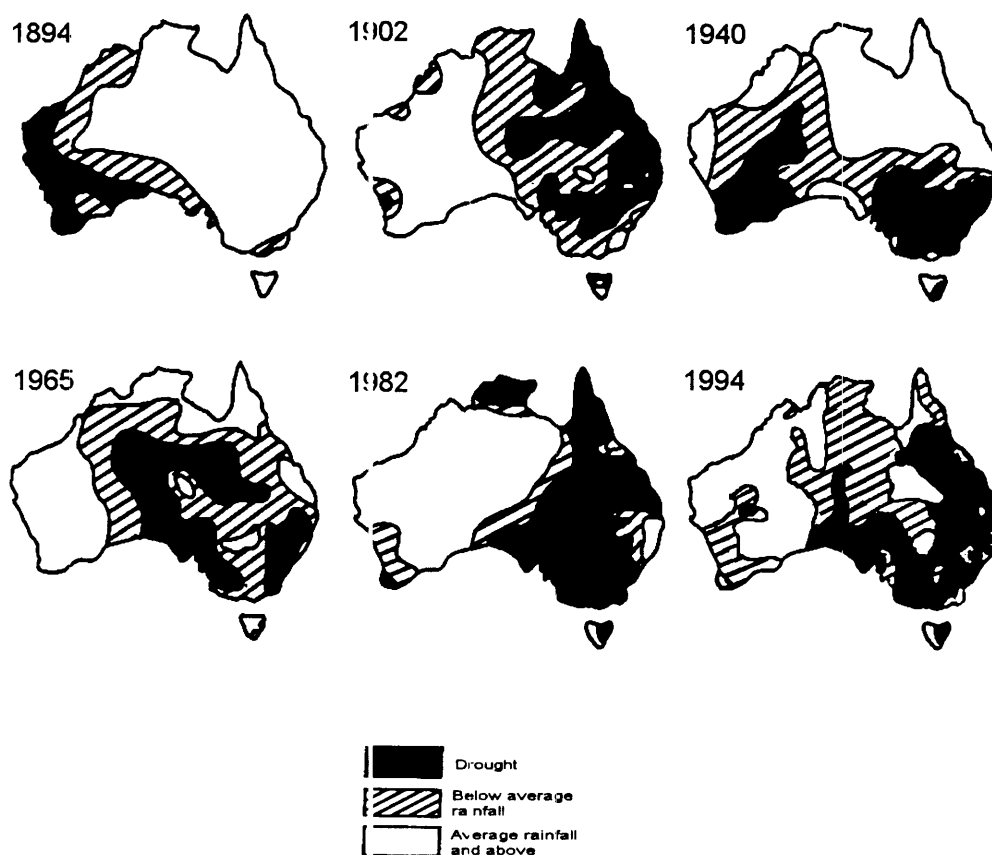

Figure 1.1: Areas of Australia affected by six major droughts in the last 110 years, (Modified from McWilliam 1986. Source: Bureau of Meteorology).

Although the timing of droughts in Australia is largely unpredictable, it is predictable that droughts will occur. It is unlikely that the continent will be free from major drought more than 20 years in every 100. Of the remaining 80 years, 60 will be identified as having droughts which cover less than 20% of the continent. In 15 of the 100 years, droughts can be expected to cover 20–50% of the continent,

while in 2 of every 100 years, major widespread droughts will cover over 50% of the continent (Reynolds et al. 1983, cited in McWilliam 1986). Although the meteorological conditions necessary for rain are known, the equivalent physical conditions necessary to predict drought are not (McWilliam 1986). However, work is being conducted in Australia to develop climatic seasonal and inter–annual predictions using coupled numerical models based on measurements from the ocean and atmosphere (Meyers 1996).

The 1965–66 drought on the Northern Tablelands, New South Wales revealed how serious an effect drought can have on sown pastures and pasture persistence. Prior to 1965, the most widely sown species on the Northern Tablelands were cool–season temperate northern hemisphere perennials, with smaller areas of species originating from Mediterranean regions (Whalley 1973). As a result of the 1965–66 drought there were extensive losses of white clover, cocksfoot and ryegrasses from pastures, particularly where they were heavily stocked. Although white clover did re–establish in areas which were top dressed with fertiliser, there was little reappearance of either the ryegrasses or cocksfoot (Whalley 1973). Phalaris, tall fescue and lucerne suffered fewer losses during the drought (Robinson and Simpson 1966; Hutchinson 1970; Whalley 1973). High stocking rates reduced the survival of pasture species during the drought and resulted in the invasion of weedy species (George et al. 1970; Hutchinson 1970; Whalley 1973).

The 1994 drought reinforced the knowledge that drought is a common occurrence on the Northern Tablelands, with severe drought occurring about one year in 12 (K. Hutchinson, pers. comm.). The drought also reminded both graziers and researchers that the mechanisms which control pasture survival under the joint effects of moisture stress and grazing are not well understood. The perception on the Northern Tablelands is that perennial pastures are not persisting (Lees and Reeve 1994, 1995) and are being replaced by annuals and/or undesirable, less palatable species.

During dry periods when the available pasture becomes limited, pastures tend to be grazed more frequently and to a shorter height (Smetham 1973). This is not a sustainable management system as it will not maintain the productivity of the pasture. Plant mortality would be reduced if stock received supplementary feed hence reducing grazing intensity and lengthening the rotation interval (Smetham 1973).

'The very large range of persistence of sown perennial grasses under year–long grazing and with prolonged periods o˙ moisture stress emphasises the need to study the physiology of survival and production of grazed plants.' (Hutchinson 1970)

While this was stated over two decades ago there is still little known about the persistence of native and introduced pasture species, especially under the combined stresses of drought and defoliation. Understanding the effects, and improving the defoliation and drought tolerance of temperate perennial grass species is important (Kemp and Culvenor 1994) so that pasture persistence can be increased.

The aims of this thesis are to:

1. Investigate the separate and interactive effects of defoliation, drought intensity and season on the production, nutritive value and persistence of six perennial grass species commonly grown on the Northern Tablelands of New South Wales.

2. Investigate the role of carbohydrate reserves as a strategy for regrowth and survival of temperate perennial grasses during drought and defoliation stresses.

3. Investigate the use of soil water and distribution of roots of perennial grasses subjected to varying intensities of drought and defoliation.

4. Investigate plant traits that may be important in the persistence of perennial grasses under drought and defoliation stresses.

With a better understanding of persistence and how pasture grass species respond to defoliation intensity during drought, better management strategies can be developed to enhance their persistence.

Following this introduction, a review of the literature draws together the published literature on the mechanisms and responses of cool–season perennial grasses to drought and defoliation stresses. After the literature review is a chapter describing the construction of the rainout shelter, a description of the trial, treatments and general materials and methods.

Four experimental chapters investigate various aspects of production, nutritive value, carbohydrate reserves, roots and soil water. The final experimental chapter describes the plant losses which occurred during the experiment as a result of the drought and defoliation treatments imposed. Plant traits important in determining plant mortality or persistence were investigated.

The thesis concludes with a general discussion. The section summarises the results of the experimental chapters and discusses their application to grazing system management and their potential extension beyond the region of this study. Areas for future research are also proposed.

Chapter 2
The mechanisms and responses of grasses to drought and defoliation stresses

Mechanisms of drought surv val

Water stress affects nearly every aspect of plant metabolism and growth, including morphology, physiology and biochemistry (Hsiao 1973; Whalley 1973). Adaptation is a strategy by which plants survive unfavourable conditions and can involve either morphological or physiological changes. Drought resistance can integrate responses from a range of biological processes to a number of environmental stresses. That is, there is no simple relationship between performance in different environments and any one physiological characteristic (Amin and Thomas 1996).

It is important to remember that the mechanisms of drought survival are not mutually exclusive and plants can have more than one mechanism of adaptation (Kramer 1980). These mechanisms of drought survival have been categorised in a number of different ways. Begg and Turner (1976) divided the mechanisms into morphological and physiological adaptations. Turner (1979) divided the mechanisms of drought resistance using the resistance classes of May and Milthorpe (1962): drought escape, drought endurance with high internal water content (drought avoidance) and drought endurance with low internal water content (drought tolerance). Kramer (1980) suggested use of the terms dehydration postponement and dehydration tolerance instead of 'drought', which is a meteorological and not a plant phenomenon. In this chapter the resistance categories proposed by Turner (1979) are used with Kramer's (1980) terminology, that is, drought escape, dehydration postponement and dehydration tolerance.

Drought escape

Annual and ephemeral species

Drought escape involves the plant completing its life cycle in the short period of time that moisture is available (Whalley 1973; Turner 1979, 1986a). There are two main mechanisms involved in drought escape: rapid phenological development and developmental plasticity (Turner 1979, 1986b). As this type of drought escape is not applicable to perennial grasses, it will not be discussed further.

Dormancy

Although dormancy and dormant buds have not been included as a mechanism of drought survival by Turner (1979; 1986a, 1986b) and Kramer (1980), and only briefly mentioned by Frank et al. (1996), they have been described as a mechanism of 'drought escape' (eg. Silsbury 1961, McWilliam and Kramer 1968; Ludlow 1980; Kemp and Culvenor 1994) and 'drought recovery' (Ludlow 1980;

Kemp and Culvenor 1994). It seems likely that dormancy has been excluded as a mechanism of drought resistance for two reasons. F rstly, dormancy is not triggered by a single factor, but by a combination of factors, such as soil moisture and temperature (Ketellapper 1960; Vegis 1964; Hoen 1966) and secondly, many of the reviews of drought mechanisms are for annual crop species, of which dormancy is not relevant.

There are two dormancy states: true dormancy and relative or conditional dormancy (Vegis 1964). True dormancy is the condition where a plant cannot be induced to return immediately to normal growth. Conditional dormancy is an imposed dormancy due to the lack of a necessary environmental factor. While conditionally dormant species are not as drought hardy as those with true dormancy, their buds are generally able to survive hot, dry conditions for several months (Oram 1983). Dormancy can be divided into either summer dormancy or winter dormancy. In the Australian temperate pasture zone where winter temperatures are relatively mild, summer dormancy is the most important.

Summer dormancy is generally considered to be closely associated with the availability of soil water (Laude 1953). However, in phalaris it involves a strong interaction between soil moisture and temperature (Ketellapper 1960), especially in the latter part of summer (Hoen 1968a). The range in dormancy also varies (Laude 1953) For example phalaris cultivars can be divided into three dormancy categories: (1) semi–winter dormant––moderate summer dormancy, (2) winter active––low to moderate summer dormancy and (3) winter active––highly summer dormant (Watson 1993). While phalaris is well recognised as a summer dormant species, other perennial grass species that have some degree of summer dormancy include tall fescue, perennial ryegrass and cocksfoot (Laude 1953; Silsbury 1961; Volaire 1995). Drought induced dormancy has been reported for species such as *Astrebla lappacea*, *Enteropogon acicu aris* and *Stipa aristiglumis* (Whalley and Davidson 1969).

Dehydration postponement

Dehydration postponement or drought avoidance is the ability of a plant to maintain a high level of plant tissue water status during dry periods (Whalley 1973). The mechanisms include osmotic adjustment, maintenance of cell volume, maintenance of water uptake and reduction of water loss (Turner 1986b).

Turgor maintenance

The main mechanism of turgor maintenance is osmotic adjustment. Osmotic adjustment allows turgor to be maintained as the leaf potential and water content decrease (Begg and Turner 1976; Frank *et al.* 1996), and the solute concentration increases (Turner and Jones 1980). This turgor may then maintain cell elongation and leaf expansion for a longer period, possibly at a reduced rate, as water deficits develop (Hsiao 1973). Osmotic adjustment has been reported in many agriculturally important cool-season grasses (eg. Gavande and Taylor 1967; Thomas 1986b; West *et al.* 1990).

The contribution of osmotic adjustment to drought resistance in plants was reviewed by Morgan (1984). The degree of osmotic adjustment in species can vary with the speed with which the dehydration occurs (Thomas 1986b). Osmotic adjustment has been associated with a range of physiological processes including maintaining stomatal opening and photosynthesis (Turner *et al.* 1978; Jones and Rawson 1979; Ackerson *et al.* 1980; Ackerson and Hebert 1981; Wright *et al.* 1983b; Ludlow *et al.* 1985), delaying leaf rolling and senescence (Wright *et al.* 1983a 1983b; Hsiao *et al.* 1984), maintaining root growth (Morgan 1984), and maintaining or even increasing yields during water–limited conditions (Morgan 198 }; Wright *et al.* 1983a; Morgan 1984). Tissue age has also been reported to affect osmotic adjustment with the younger, expanding leaf tissue having a greater capacity to adjust than mature leaf tissue (Matsuda and Riazi 1981; Michelena and Boyer 1982; West *et al.* 1990).

During periodic moderate drought, acclimatised grasses are able to maintain leaf expansion for a longer period of time as subsequent stress develops, and recover following rewatering with rapid leaf growth (Toft *et al.* 1987). During severe prolonged droughts, osmotic adjustment in meristematic and elongating leaf tissue allows tiller survival via turgor maintenance (Toft *et al.* 1987). The protection and survival of meristematic and elongating tissues through droughts is essential if the persistence of the plant community is to be assured (West *et al.* 1990).

Other mechanisms of turgor maintenance are the increase in cell elasticity and the decrease in cell size. The elasticity of cells affects the relationship between relative water content and the components of tissue water potential. Elasticity is affected by cell size, cell wall thickness and Young's modulus of elasticity which is affected by cell wall lignification (Turner 1979, 1986b).

Leaves which develop during drought generally have small cells, indicating that cell expansion is affected by moisture stress more than cell division (eg. Lawlor 1972; Jones *et al.* 1980). The small

cells also tend to have thick cell walls (Cutler *et al.* 1977; Levitt 1980; White *et al.* 1992) which assists keeping them rigid, thereby reta ning more water as the leaf water potential falls compared to thin–walled cells (Turner 1979; Frank *e al.* 1996).

Maintaining water uptake

The maintenance of water uptake requires the growth of roots into soil which has plant available water, enabling continued extraction of water during periods of low rainfall (Turner 1986b). The rate of plant dehydration is influenced by di ferences in the rate of water lost from the plant and the rate of water uptake by the roots. Water uptake is dependent on root distribution, root hydraulic properties and soil properties. Plants which requir rapid water uptake require large dense root systems (Frank *et al.* 1996).

Shoot–root ratios often decrease durin soil water deficits (Turner and Begg 1978), sometimes by enhancing root growth, but usually by a reduction in shoot growth (Frank *et al.* 1996). Factors such as endophyte status (West *et al.* 1993), ne natode presence (West *et al.* 1987, cited in Frank *et al.* 1996) and mycorrhizal infection (Bildusas *it al.* 1986) have also been reported to affect the drought resistance of plants.

Hydraulic resistance to water flow in a plant affects water uptake by plants with variation occurring between species (Boyer 1971; Hellkvi t *et al.* 1974; Passioura and Munns 1984). A high hydraulic resistance between the soil and shoot may result in relatively lower water potentials in the leaves than roots compared with a low hydraulic re istance. Plants with high hydraulic resistances are likely to be more sensitive to aerial stresses and le s sensitive to soil water stress than plants with low hydraulic resistances (Turner 1986a).

Reducing water loss

Mechanisms and plant characteristics which reduce water loss include: reduced leaf expansion, leaf shedding, accelerated senescence, lea movement and orientation, leaf flagging and leaf rolling, glaucous covering, pubescence, stomatal distribution, surface ridging and epicuticular waxes (Begg and Turner 1976; Turner and Begg 1981, Renard and François 1985; Turner 1986a, 1986b). These attributes assist in reducing the area or effectiveness of the plant to intercept radiation, that is, radiation shedding (Turner 1986a, 1986b). However, the interaction between these attributes is inconclusive and varies with species.

Leaf area can be reduced by either a reduction in leaf area development and/or leaf senescence. Leaf growth is often, but not always, more sensitive to water deficits than the rate of photosynthesis (Turner and Begg 1978; Nagarajah and Schulze 1983; Turner et al. 1986). Both leaf expansion and senescence are reported as being sensitive to water deficit (Turner and Begg 1981), however, leaf growth does appear to be more sensitive than senescence (Turner et al. 1986).

The response of stomata to leaf water potential and leaf turgor is well documented. It was initially thought that stomata do not close until a critical threshold level of leaf water potential is reached (Begg and Turner 1976). Subsequent research, however, showed that stomatal conductance can decrease approximately linearly with leaf water potential or leaf turgor pressure (Jones and Rawson 1979) and that the speed with which stomata close can vary. There is more recent evidence that suggests that grass stomata respond directly to soil water content, rather than plant water status (reviewed by Davies and Zhang 1991).

Dehydration tolerance

Dehydration tolerance or drought tolerance with low plant tissue water potential, is the ability of a plant to continue growing during moderate drought conditions (Whalley 1973; Turner 1979; Barker et al. 1989). Plant growth regulators have been suggested to be involved in dehydration tolerance (Levitt 1980; Davies and Zhang 1991). Osmotic adjustment (Hsiao et al. 1984), sugar accumulation and high cellular elasticity (reviewed by Turner 1986b) have also been reported to improve dehydration tolerance.

Desiccation is a result of severe dehydration. Desiccation tolerance has been suggested to depend on the ability of cells to withstand physical, physicochemical and metabolic injury, such as mechanical injury, membrane degradation, protein denaturation, gene mutation and impaired respiration (Gaff 1980). Resurrection plants are examples of plants that demonstrate extreme desiccation tolerance, with the ability to be able to withstand extreme water stress and revive again when water is available (Turner and Kramer 1980).

Plant responses to drought

The responses of plants to drought are interactive, whereby a change in one characteristic may lead to compensation by other characteristics (Frank et al. 1996). Plant responses to drought are discussed in four categories: above ground growth and development; root growth and development; plant reserves

and nutritional value.

Above ground growth and development

During drought, sward growth can be l mited by a number of interrelated factors, including soil water deficit, high radiation and evaporation. nutrient shortage (Morrison *et al.* 1974, cited in Norris 1982) and supra–optimal temperatures (Norris 1982). The interaction between species or variety, developmental growth stage, and management regime can also affect sward growth (Hughes *et al.* 1977, cited in Norris 1982) and botanic al composition (Pook and Costin 1970).

The most noticeable effect of drought is a reduction in plant growth rate and dry matter yield (Perrier *et al.* 1961; Baker and Jung 1968; Norr s 1982). However, these effects are modified by the timing and severity of the water deficit, and plant phenology. Tiller numbers, rates of leaf extension and leaf appearance are reduced by soil water deficit, although the extent of each varies (Aspinall *et al.* 1964; Brown and Blaser 1970; Norris 1982; Volaire 1994). Short–term water deficits generally result in a reduction in yield and nutritive valu:, while long–term water deficits can result in plant death, especially in species with only marginal drought tolerance.

When drought is intermittent, seasona productivity is influenced by the rate and extent of recovery from water deficit (Frank *et al.* 199€). Recovery following drought varies with drought intensity (Volaire 1994). In cocksfoot, autumr recovery following a summer drought in a Mediterranean environment was correlated with tiller lensity, water soluble carbohydrate content and fructan content (Volaire 1995).

Root growth and development

The abundance of roots present near the soil surface extract available water from the top of the profile. However as the profile dries, deeper roots extract water from greater depths until the soil becomes too dry to support growth (Davis 1941; Hamblin 1985). While roots need to be present to utilise water available at depth (Troughton 1957), there is also some movement of water up the soil profile in response to an active root system (LaR ie *et al.* 1968; Stone *et al.* 1973).

The development of an extensive rcot system is essential for the establishment and continued productivity and survival of grasses (F ank *et al.* 1996). Root growth has been reported to increase in some pasture grasses during drought (Molyneux and Davies 1983; Volaire and Thomas 1995), with the additional growth being mostly fiom lateral root initiation and elongation (Jupp and Newman

1987).

A greater proportion of deep roots give deep–rooted species an advantage over shallow–rooted species during drought (Garwood and Sinclair 1979). Although the rooting depths of six species in southeastern USA were found to be similar, the root distribution with depth varied (Burton et al. 1954). In the drought susceptible species 94% of the root mass was confined to the upper 0.6 m of soil, compared to 65–69% of roots in the drought tolerant species.

Plant reserves

The effects of drought on plant reserves varies with species, the degree of moisture stress and the stage of plant development (Brown and Blaser 1965, 1970; Trlica and Cook 1971). Carbohydrate reserves tend to accumulate during periods in which the temperature is favourable for photosynthesis but suboptimal for foliage growth (Blaser et al. 1966; Youngner 1972).

In cool–season grasses, soluble proteins and amino acids are the main nitrogen reserves (Ourry et al. 1989) and fructans are the main carbon reserves (Gonzalez et al. 1989). Carbon reserves have traditionally been studied as the primary source of plant reserves, responsible for regrowth and persistence. However, Volenec et al. (1996) pointed out that nitrogen also plays a significant role as a plant reserve and should be viewed as one physiological mechanism enabling forages to regrow and hence persist.

The effects of drought on plant carbohydrate reserves are varied. There have been reports of little change during drought, unless growth is stimulated by defoliation or rain, both resulting in carbohydrates being depleted (Troughton 1957). Other work has reported carbohydrate accumulation during water stress and related it to continued photosynthesis after other growth processes have slowed (Julander 1945; Blaser et al. 1966; Dina and Klikoff 1973; Hsiao 1973; Busso et al. 1990). Bukey and Weaver (1939) however, found that carbohydrate levels were reduced during a summer drought. These discrepancies suggest either that species have different adaptations to drought or that they respond differently to droughts of different intensity (Troughton 1957).

There have been reports that plant carbohydrates are hydrolysed during drought (Virgona and Barlow 1991; Spollen and Nelson 1994; Volaire 1994) Water stress during grain filling of wheat affected the composition of the non–structural carbohydrate pool, but not the rate of decline (Virgona and Barlow 1991).

Nutritive value

Plant nutritive value during a season varies with species, leaf–stem ratios, phenological changes, leaf senescence and lignification (Bittman *et al.* 1988). Woodman *et al.* (1931) found that the main effects of severe drought on plant herbage nutritive value were: a reduction in crude protein, an increase in crude fibre, a reduction in the moisture content of the forage and a decline in forage nutritive value. There are contradictory results on the effect of drought on plant digestibility (eg. Garwood *et al.* 1979), including no effect (Harris and Lazenby 1974). Bittman *et al.* (1988) reported that drought reduced the rate of seasonal decline in digestibility by slowing the rate of increase in acid detergent fibre and lignin.

The varied effects of drought on the nutritive value of species are due to the involvement of more than one process and the differences in drought severity. Drought usually increases leaf senescence in plants, however the sensitivity of grasses varies widely (Bittman *et al.* 1988). Factors that reduce leaf area to conserve water also reduce forage yield and nutritive value (Frank *et al.* 1996).

The effect of drought on nitrogen content is also somewhat contradictory (Woodman *et al.* 1931; Gifford and Jensen 1967; Garwood *et al.* 1979; Misra and Singh 1982; Bittman *et al.* 1988). In extreme situations, growth may be slowed by drought induced nutrient deficiency. Water deficit has been reported to increase the rate of seasonal decline in nitrogen and phosphorus concentration, probably by increasing the rate of leaf senescence (Bittman *et al.* 1988).

Grazing and defoliation survival mechanisms

Grazed pasture systems are complex and the response of a pasture to stress varies depending on whether the pasture is based on a single species or a number of species. While single species swards are used in the work presented in this thesis, and the swards were defoliated mechanically, not with animals, mixed swards are included in this section for completeness.

Grazing, 'a more or less destructive process', involves the periodical removal of plant photosynthetic area resulting in a sudden decrease in the photosynthetic activity and a corresponding decrease in root growth (Biswell and Weaver 1933). Selective grazing by herbivores increases the stress upon that species. Defoliation is generally considered in terms of three parameters: frequency, intensity and growth stage (Harris 1978). Factors affecting grazing, including preference and palatability have been reviewed by Van Dyne *et al.* (1980).

Grazing resistance, within the context of grassland and pasture management, describes the relative ability of plants to survive and grow in grazed systems (Briske 1991, cited in Briske 1996). Resistance to grazing increases with a decrease in: erectness of plant growth, growth rate, shoot apex elevation, leaf elevation, time of floral differentiation, proportion of reproductive shoots and palatability (Branson 1953; Neiland and Curtis 1956; Scott 1957; Peterson 1962). Resistance also increases with improved leaf replacement potential, which varies with growth stage and species (Hyder 1972). Grazing resistance is inversely related to herbage production (Hyder 1972).

The management regime can also affect the expression of mechanisms of grazing tolerance (Briske 1996). Stocking rate influences plant utilisation and therefore the relative expression of a species' grazing resistance. The expression and importance of grazing avoidance and tolerance mechanisms varies with season (Briske 1996), therefore the impact of grazing varies throughout the year. Plant species preference and grazing intensity are also affected by the species of grazing animal (Heady 1964). Animal species graze pastures differently, for example in their grazing pattern and their bite type (Ungar 1996). The ingestive behaviour, including species bite differences, is reviewed by Ungar (1996).

The contribution of individual plant traits to grazing resistance has been extensively reviewed, one of the more recent by Briske (1996). The reviews generally include both invertebrate and vertebrate animals. In this section, grazing resistance to vertebrates is divided into avoidance and tolerance strategies.

Avoidance strategies

Grazing avoidance involves mechanisms which reduce the severity and probability of grazing (Briske 1996). Plant avoidance strategies consist of constitutive, spatial and temporal mechanisms.

Constitutive mechanisms

Constitutive mechanisms consist of mechanical traits, biochemical compounds and defensive symbiosis. They remain relatively constant in time and space (Rhoades 1983, cited in Briske 1996) and form the 'background–level' of plant resistance to grazing (Ernest 1994).

Mechanical characteristics of plants are often assumed to act as deterrents to grazing animals, however their effect is not well reported (Briske 1996). Deterrent attributes such as awns, sharpened calluses are not reported as deterrents, while waxes, trichomes and the presence of vascular bundles have only

limited effect on the grazing preference of mammals (Theron and Booysen 1966, cited in Briske 1996; Wilson *et al.* 1983; Akin 1989). Leaf roughness is considered one of the most important mechanical characteristics influencing grazing preference, followed by fiber content and nutritive value (Coley 1983).

Grasses are known to possess a wide range of compounds, some of which are deterrents to animals, however most deter insects only (Briske 1996). Grasses have been reported to contain toxins (Oram and Culvenor 1994; Joost 1995) which can cause severe disorders in grazing animals, such as staggers and sudden death. Cyanide and cyanogenic glycosides (Georgiadis and McNaughton 1988) have also been reported, however, their relative importance is not known.

Symbioses between fungi and plants have been reported. For example, ergot alkaloids produced by fungi in infected grasses may protect plants against grazing (Cheplick and Clay 1988), hence protecting the fungus' reproductive structures also.

Spatial mechanisms

Spatial avoidance mechanisms affect the vertical and horizontal distribution of plant canopies thereby limiting grazing access (Briske 1995). This is achieved via plant growth form and species associations.

Taller grasses tend to be grazed in preference to shorter, more prostrate grasses (Hein and Vinall 1933; Weaver 1950; Tomanek and Albertson 1957; Lodge and Whalley 1989). Short grasses are more difficult for animals to graze, therefore leaving a greater green leaf and stem residual for regrowth (Smetham 1973). Low plant growth points also have less chance of being grazed (Branson 1953; Hyder 1972). Plant habit affects the pattern in which tissue is removed and the type of tissue removed (Richards 1993). Plant growth habits can be modified under grazing, however the capacity to change varies with species (Kydd 1966, cited in Hutchinson 1970) and defoliation intensity (Hyder 1972).

The palatability of different species to livestock varies and can therefore affect the frequency and intensity of grazing in mixed swards (McNaughton 1978; Tuomi and Augner 1993). Palatable species are grazed in preference to the less palatable species. The unpalatability of some species, such as weeds is a survival mechanism. Grazing preference can also be greater at one growth stage than another within the same species (McClymont 1969; Briske 1996).

Temporal mechanisms

The extent to which grazing avoidance is expressed varies with growing season and the period following defoliation. Inducible defences are avoidance mechanisms which increase with increased grazing intensity (Rhoades 1985). Examples include the presence of silica within cells (McNaughton and Tarrants 1983; Brizuela *et al.* 1986), cyanide (Georgiadis and McNaughton 1988) and increasing the number of mechanical deterrents with defoliation, such as thorns (Young 1987; Milewski *et al.* 1991). Note, however that the effect of silica on grazing preference has not been well established (Shewmaker *et al.* 1989) and thorns are not applicable to grasses.

Asynchronous tiller development is the phased development of dormant buds at different rates so that the risk of losing the majority of meristematic tips in any one defoliation is reduced (Chapman and Lemaire 1993; Culvenor 1993a). Sirolan phalaris can suffer a high level of stem decapitation in summer due to synchronous apical elevation (Culvenor 1993a). Decapitation can result in reduced regrowth, smaller tiller bases, fewer dormant buds and lower carbohydrate reserves (Culvenor 1993a). In some species (eg. *Themeda triandra*), synchronised bud development can result in the growth of virtually all tiller buds, leaving few for replacement if apical meristems are lost due to defoliation (Chapman and Lemaire 1993).

Changes in plant characters as it ages can affect the behaviour, growth and survival of animals that consume them. These changes are termed developmental resistance (Kearsley and Whitham 1989). The decline in nutritional value and palatability of plant tissue with increasing maturity is well recognised (McClymont 1969; Georgadis and McNaughton 1990). Developmental resistance may also be an important mechanism in the development of patch grazing (Kellner and Bosch 1992) and 'grazing lawns' (McNaughton 1984). Selective grazing resulting in uneven utilisation with patches of predominantly palatable species and patches of unpalatable species is called patch grazing (Kellner and Bosch 1992). Grazing lawns are the result of frequent, intensive grazing which selects for prostrate, small leaved, dwarfed species and ecotypes (McNaughton 1984).

Tolerance strategies

Grazing tolerance consists of mechanisms which promote plant growth following defoliation (Briske 1996). Tolerance to grazing consists of both morphological and physiological mechanisms.

Morphological mechanisms

The growth of grasses is dependant upon the availability and activity of apical meristems, intercalary meristems and axillary buds (Briske and Richards 1995, cited in Briske 1996).

The rate at which foliage is removed affects a plant's response, the two extremes being continual loss of a small proportion of a plant's leaf area and the loss of a large proportion of photosynthetic area in one event (Richards 1993). The recovery of a plant following defoliation depends on the regrowth capacity of the plant and the type of defoliation, and also upon the plant's abiotic (eg. light, water and nutrients) and biotic (eg. competition and presence of grazing animals) environment (Richards 1993).

The potential to lose the majority of the active stem meristems in one defoliation period is greater in species with synchronous tiller development (Chapman and Lemaire 1993), but varies with plant phenological development and season (Branson 1953; Culvenor 1993a). Although synchronous tillering generally increases the susceptibility of grasses to grazing, seasonal variation in defoliation tolerance is less pronounced in species with asynchronous tiller development (Briske 1996). Grazing resistance can vary within a species. For example, in phalaris, the lack of persistence of some of the newer cultivars is believed to be due to morphological differences, such as plant erectness, tiller size, tiller density and plant spreading ability (Culvenor 1993b). Australian phalaris with a low crown is morphologically well adapted to grazing, whilst Sirosa phalaris is more erect, has a higher crown and lower basal area, thus making it more accessible to grazing animals, and resulting in a smaller residual leaf area following grazing (Culvenor 1993b).

Seed production and the development of a seed bank is an important mechanism in some species, and can be considered as either a grazing tolerance or avoidance strategy (Briske 1996).

Physiological mechanisms

Physiological mechanisms include compensatory processes and compensatory growth (Briske 1996). Processes include compensatory photosynthesis, resource allocation, nutrient absorption and shoot growth (Richards 1993; Briske and Richards 1994, 1995, cited in Briske 1996). The occurrence, frequency, extent and significance of compensatory processes on plant growth and productivity is not well understood (Briske and Richards 1995, cited in Briske 1996), however are believed to involve both intrinsic and extrinsic mechanisms (McNaughton 1982, cited in McNaughton 1983).

The capacity of a plant to produce new leaf quickly is a characteristic of defoliation tolerant plants and genotypes (Richards and Caldwell 1985). One of the most important factors contributing to the production of new leaves following defoliation is the presence of active shoot meristems (Richards 1993). A plant is generally less affected by the loss of old leaves than the loss of the same amount of young leaves (reviewed by Richards 1993).

Photosynthetic rates of foliage on defoliated plants are often higher than those of foliage of the same age on undefoliated plants (Richards 1993). Compensatory photosynthesis of leaves of defoliated plants has been reported in a range of species and can occur in mature and expanding leaves present prior to defoliation, as well as new regrowth leaves (Richards 1993).

Plant responses to defoliation

The responses of forage plants to defoliation can be categorised into physiological and morphological responses (Chapman and Lemaire 1993), and may be modified by environmental and management factors (eg. Alberda 1957). Physiological responses are generally defined as those occurring over short time periods, whereas morphological responses are considered to occur over longer time periods (Chapman and Lemaire 1993). The extent to which these physiological and morphological responses affect plant characteristics varies with the defoliation regime and the balance obtained between the supply and demand of resources required by the plant for growth (Chapman and Lemaire 1993). Under infrequent, lax grazing systems, plants may be able to maintain balanced root and shoot growth through short term physiological responses only. However, under severe defoliation practices, morphological adjustments may be necessary to ensure continued whole–plant growth. Species and genotypes vary in their response to defoliation (Fulkerson et al. 1994) and their ability to adapt (Chapman and Lemaire 1993).

There are two principles needed when trying to understand the way plants respond to defoliation (Chapman and Lemaire 1993). The first, is that defoliation removes photosynthetic tissue, thereby disturbing the supply of carbohydrates for plant growth. The second, is that plant processes generally work to maintain a 'dynamic equilibrium' with their environment to ensure optimal use of resources for growth and reproduction. In this section, plant responses to defoliation are discussed in four categories: above ground growth and development; root growth and development; plant reserves and nutritive value.

Above ground growth and development

The response to defoliation varies with the sward composition. A mixed sward is more complicated than a single species sward, however both are included in this section. Dry matter production is affected by both frequency and height of cutting (eg. Biswell and Weaver 1933; Burton *et al.* 1963; Fulkerson and Michell 1987; Hill 1989, Hill and Watson 1989; Belesky and Fedders 1994). The effect of cutting height and interval on yield can also change with season. For example, on a perennial ryegrass—white clover sward, mowing height had a greater effect on herbage yields during autumn–winter, while in spring, the harvest interval was most important (Fulkerson and Michell 1987).

Defoliation intensity affects the regrowth rate (Brougham 1956; Fulkerson and Slack 1995), time to reach maximum growth rate and the leaf area index. The more intense the defoliation, the lower the initial rate of regrowth (Brougham 19;6; Fulkerson 1994; Fulkerson and Slack 1995) and the longer the time necessary to reach maximum growth rate (Brougham 1956). However, the maximum growth rate attained is similar irrespective of defoliation intensity (Brougham 1956). The optimum leaf area index varies between species and gene type due to different growth forms. The time taken to achieve this critical leaf area index also varies with the time of year and the height at which the pasture is defoliated (Brougham 1957; Smetham 1973).

When residual heights of 10–12 cm are retained, higher growth rates and increased tillering per plant result, leading to more harvests and higher dry matter yields (Davis 1960). At low residual stubble heights (approximately 2.5 cm), the stubble either deteriorates and dies or continues to grow weakly (Albertson *et al.* 1953; Davis 1960; Fulkerson 1994). Albertson *et al.* (1953) found that severe defoliation stimulated growth, but as the plants weakened, growth decreased. Pasture persistence is therefore reduced by severe defoliation (Fulkerson *et al.* 1993).

There are conflicting results in early work on the effect of defoliation intensity on tillering (Troughton 1957), possibly due to the different experimental methods used (Youngner 1972). Other research has found that defoliation stimulates tillering (eg. Jameson and Huss 1959; Fulkerson and Michell 1987), however, continuous or frequent severe defoliation can weaken tillers (Fulkerson 1994; Fulkerson and Slack 1995) affecting both tiller number and size (Hill 1989; Hill and Watson 1989). Cutting phalaris at the early boot growth stage stimulated tiller development, overcoming dormancy. However, persistence of the stand was reduced if these tillers did not survive to form viable buds (Hill 1989; Culvenor 1994). Cutting which removes growing points, can result in the death of many tillers (Maeda and Ehara 1962, cited in Youngner 19 '2). Differences in tillering response to cutting height may be

related to photosynthetic supply and a >ical dominance. Defoliation which removes leaves retards tiller growth by reducing photosynthetica ly active tissue, and thereby carbon assimilation (Youngner 1972). Tillering is also reduced by lo v light intensity (Davis and Laude 1964; Auda *et al.* 1966) and shading (Mitchell and Coles 1955).

In general, grasses are less abundant ɛnd have a reduced ground cover when heavily grazed (Schuster 1964). The timing, severity and frequency of defoliation also affects the stability and resilience of a species (Hutchinson 1992) and the composition of a pasture (Fulkerson and Mitchell 1987; Kemp 1991). Overgrazing, or intense grazing, results in changes in species composition; from tall grasses to short grasses (Weaver 1950; Tomane < and Albertson 1957), from desirable species to less desirable species (Kemp 1991) and often from perennial species to annual species (Biddiscombe 1953; Hutchinson 1970).

Root growth and development

Much of the research into root growth and development was conducted prior to the 1970s. These, and subsequent studies, indicated that with severe or continual defoliation, root number and branching are reduced (Robertson 1933; Albertson *et al.* 1953), as are root diameter (Biswell and Weaver 1933), root weight (Biswell and Weaver 19:3; Robertson 1933; Weaver 1950; Cook *et al.* 1958; King and Hutchinson 1976) and the depth of root penetration (Robertson 1933; Weaver 1950; Ruby and Young 1953).

Troughton (1957) reviewed early studies which found that the lower the cutting height and/or the shorter the cutting interval, the greater the reduction in root weight. The degree of reduction in a plant root system is related to the severity and frequency of defoliation (Garber 1931; Albertson *et al.* 1953). The more severely a plant is cut the longer the period before root growth resumes (Jacques and Edmond 1952). Defoliation severity is generally more detrimental to root growth than defoliation frequency (Schuster 1964), however, reduced severity of one will offset an increased severity of the other (Youngner 1972). Matthew *et a.* (1991) found that seasonal differences in root production were greater than differences due to grazing intensity. These contradictory results may be largely due to methodology, for example, the sampling technique, root washing method, sieve size and live versus total roots.

Increased stocking rate has been reported to reduce root mass near the surface (Langlands and Bennett 1973; King and Hutchinson 1976), however another study of root length density (suggested as a

good surrogate for root mass) found ro effect of stocking rate (Greenwood 1996b). Milchunas and Lauenroth (1993) found that although the common perception is that grazing has a negative affect on root systems, many of the studies were conducted in pot experiments rather than field studies. They concluded that the number of negative impacts of grazing on aboveground production reported in the literature were accompanied by a similar number of positive responses as negative responses below ground.

The consequences of overgrazing are carried over from season to season (Schuster 1964; Davidson 1978). Extensive defoliation leading to a reduction in root development may result in any of five outcomes: a shallow root system which is inadequate in dry periods, a reduced competitive advantage against weeds, a slow recovery after defoliation, a lack of vigour in the spring flush of growth or severe damage from pests whose effects would normally be innocuous (Davidson 1978).

Plant reserves

The level of plant reserves fluctuate both seasonally (Troughton 1957) and during regrowth following defoliation (Sullivan and Sprague 1943). After defoliation, both carbon (Sullivan and Sprague 1943, 1949, 1953; Sprague and Sullivan 1953; Alberda 1966; Ryle and Powell 1975; Volenec 1986; Fulkerson 1994; Fulkerson and Slack 1995) and nitrogen reserves (Davidson and Milthorpe 1966b; Volenec et al. 1996) are utilised from the roots, remaining leaf sheath, leaf base and stem (Smetham 1973) until the plant has produced sufficient photosynthetic area to sustain itself (Troughton 1957; Clement et al. 1978; Richards 1993). The remobilisation of carbon reserves during regrowth follows the same pattern as nitrogen reserves, which suggests that the regulatory mechanisms may be the same (Ourry et al. 1993).

The effect of defoliation practices upon plant carbohydrate levels accumulated vary depending on the severity, frequency and timing of the defoliations (Julander 1945; Sullivan and Sprague 1950; Davidson and Milthorpe 1966a, 1966b; Volaire 1994). The more stubble remaining following defoliation, the greater the photosynthetic area, therefore the faster the recovery. Defoliation should be managed to ensure the full expression of regrowth potential and thus, the replenishment of carbohydrate reserves (Fulkerson 1994; Fulkerson and Slack 1995). Plants which are frequently defoliated have little opportunity to rebuild reserves, so therefore have a slower regrowth capacity and yield less (Smetham 1973; Fulkerson 1994; Fulkerson and Slack 1995). Tiller death on plants with low carbohydrates has been reported (Alberda 1966). The losses are thought to have been due to the sacrifice of tillers as a result of insufficient reserves for regrowth. Severe depletion of reserves has

been suggested as the main cause of thinning of poorly adapted species (Arcioni *et al.* 1985; Volaire 1994).

Nutritive value

Forage nutritive value under different management regimes has been of interest to scientists for many decades (eg. Woodman *et al.* 1931). There are a number of factors which affect the nutritive value of pastures: growth stage, ratio of leaf and stem, soil and plant fertility, the amount of available soil water during growth, the nutritive value of any dead residues, season and the plant species (Minson *et al.* 1960; Minson *et al.* 1964; McClymont 1969). Greater differences in nutritional value exist within a species at different stages of growth than between different grasses at the same stage of growth (McClymont 1969).

Close or frequent cutting can increase the nutritive value of pastures (Albertson *et al.* 1953; Burton *et al.* 1963). Closely clipped grasses remain green, succulent and high in protein in comparison to lightly clipped or unclipped grasses (Albertson *et al.* 1953). The more lenient the cutting regime, the greater the decline in nutritive value experienced (Woodman *et al.* 1931). Woodman *et al.* (1931) suggested a cutting regime of one month to ensure good forage nutritive value while maintaining the persistence of the pasture.

Persistence and the interaction between drought and defoliation

Most of the factors which affect dry matter production can be considered as acting independently, however the same cannot be said for those affecting survival. Persistence is a complex trait with little known about its genetic basis (Cunningham *et al.* 1994). Persistence has different definitions depending upon the type of work being conducted, for example, Cunningham *et al.* (1994) defined persistence as the rate at which tiller density declined. In this experiment, plant persistence is the survival of an individual plant, that is, the opposite to plant death or mortality.

Few studies have reported extensive plant death due to drought in adapted cool–season grasses. While this may suggest that drought is not a common cause of mature plant losses in the field, drought combined with other factors such as defoliation, may reduce plant persistence. Establishing plants or swards may be more susceptible to drought and defoliation due to a smaller root system, poorer vascular system development, thin cell walls, weak membranes and low carbohydrate reserves (Frank *et al.* 1996).

The interaction of defoliation and drought can also lead to changes in botanical composition. Plant losses due to drought are more likely in mixed swards than pure swards where a drought resistant species may be more competitive and crowd out a less resistant species (Frank *et al.* 1996). For example, the combined effect of drought and intensive grazing resulted in a decline in perennial ryegrass and an increase in phalaris (Pook and Costin 1970). For grass species to persist in grazed ecosystems they need to possess mechanisms for enduring grazing and periods of environmental stress (West *et al.* 1990).

A close relationship between plant mortality due to grazing and major climatic patterns has been observed in the Australian savannas (Mott *et al.* 1992). Overstocking of Australian rangelands during drought, as a result of the variable rainfall, is one of the major causes of vegetation thresholds being exceeded (Mott *et al.* 1993) leading to a shift in the stability of the system. In a long–term stocking rate experiment (28 years) at Armidale, New South Wales, one of the major features of the experiment was the interaction between grazing intensity and climate (Hutchinson 1991, 1992). There were changes in species composition of the phalaris––white clover pasture at each stocking rate during the experiment, however, the pasture was more stable at the low grazing intensity than the high grazing intensity. At the high grazing intensity (30 sheep/ha then reduced to 20 sheep/ha), the proportion of phalaris fell, with the change in botanical composition accelerated by drought. At the low grazing intensity (10 sheep/ha), there was a reduction in phalaris due to drought, however it recovered during the favourable years which followed. These effects are shown in stability diagrams (Figure 2.1).

Conclusion

The effect of defoliation has been extensively studied world wide over many decades. The effect of moisture stress or drought has also been studied, but not to the same extent. There has been little work published on the interaction of the two and the effect of seasonal timing on persistence of perennial grass species.

Perennial grasses form the most stable component of perennial pastures (Kemp 1991) in the temperate regions of Australia. Although Australia is a dry continent and suffers droughts, there is still relatively little understanding on the persistence and stress thresholds of perennial grass species.
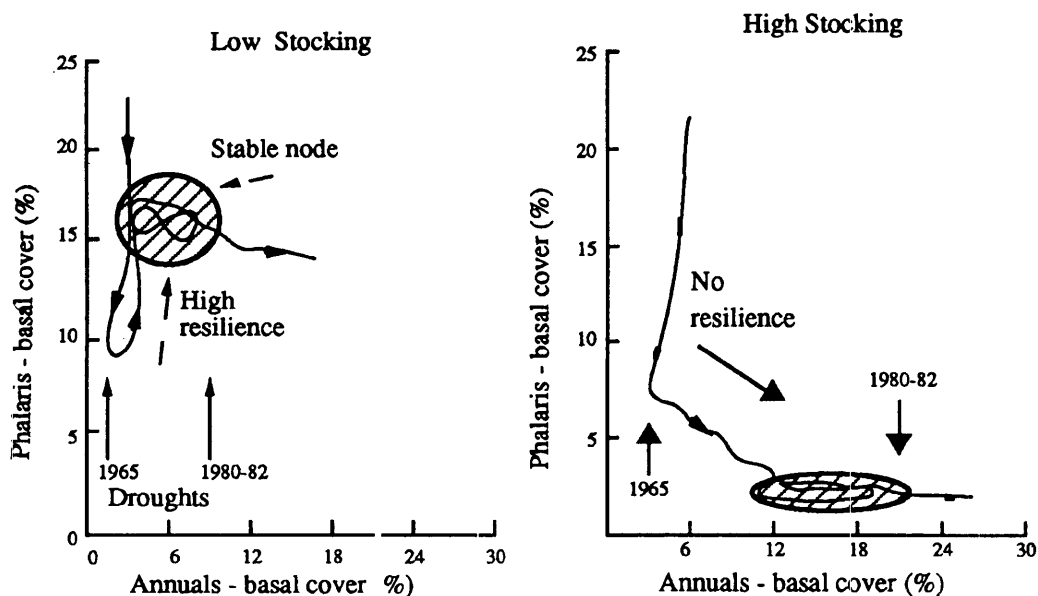
Figure 2.1: Stability and recov ry over 28 years of sown phalaris versus the ingress of annual species (as indicated by basal cover). The experiment was set stocked, at low and high stocking rates and experienced two major droughts, 1965 and 1980–82 (Source: Hutchinson 1991).

This review has highlighted a number of deficiencies in the research:

1. Although there are general trends in the way some plants respond to defoliation and moisture stresses, there are contradictions amongst the literature. These contradictions suggest that the mechanisms and responses involved are complex and vary with species.

2. There have been few studies that have investigated a range of drought intensities in the field using realistic rainfall sequences. This review has also indicated that there are few studies that have investigated the persistence of pasture grasses, particularly under the combined stresses of drought and defoliation.

3. Much of the work reviewed in this chapter has focussed on the physiology of the plant and plant responses. Plant physiology however is not the focus of this thesis. Work is needed to define the stress thresholds of perennial grasses under the combined stress of drought and defoliation. From this type of study, it is also possible to investigate the association of individual traits and/or a combination of traits with plant persistence, and to develop management practices to enhance persistence during periods of drought.

Chapter 3
Rain–out shelter construction, trial design and treatments

Location of trial and site description

The experimental trial was established at Chiswick, CSIRO's Pastoral Research Laboratory 16 km south of Armidale on the Northern Tablelands of New South Wales. Armidale is situated approximately 30° S, 151° E at an altitude of approximately 1070 m. The average annual rainfall at Armidale is 790 mm. The rainfall is slightly summer dominant, 60% falling between October and March (Smith and Johns 1975). The site is situated on a slight (1%) North West slope. The site was chosen for its uniform, well drained soil type and proximity to laboratories and facilities. The soil description is shown in Table 3.1.

Preparation of the trial site

An area of 50 m x 150 m was selected for the trial. The trial area was sprayed with Roundup® (glyphosate) on 1 November 1993 to kill the previous pasture of annuals, *Danthonia* spp. and *Phalaris aquatica*.

In November 1993, a trench digger was used to excavate to a depth of 1 m around 1 m² experimental plots (Plate 3.1). The trencher sat on thick sheets of plyboard to prevent the soil surface from being disturbed and to minimise soil compaction. Soil from the trenches was moved outside the plot area with the top soil stored separately. Construction grade plastic sheeting (Fortacon) was used to wrap each soil 'island' vertically to 1 m to prevent water and root movement between plots (Plate 3.2). The trenches were back filled with the saved soil. The top soil was steam treated (16 hrs at 80°C) to kill weed seeds and then placed back in the trenches. A 1 m deep trench was also dug around the experimental area and lined with plastic sheeting to prevent water moving into the area laterally.

Table 3.1: Soil profile description (using McDonald *et al.* 1990) for the drought trial site at Chiswick, CSIRO Pastoral Research Laboratory, Armidale.

Horizon	Soil Property	
A1	Colour	1(YR 3/4 dry
(0–12 cm)	Texture	Silty clay loam
	Structure (large peds)	Weak 5–10 mm subangular blocky peds
	(small peds)	Weak <2 mm subangular blocky peds
	Fabric	Rough ped
	Consistence	Very weak
	Segregations	Few fine manganiferous nodules
	Field pH	6.)
A2	Colour	7.5 YR 3/3
(12–26 cm)	Texture	Clay loam
	Structure (large peds)	Moderate 20–50 mm subangular blocky peds
	(small peds)	Weak 10–20 mm subangular blocky peds
	Fabric	Rough ped
	Consistence	Firm
	Segregrations	Many medium ferromanganiferous nodules
	Field pH	6.5
B1	Colour	5 YR 4/6
(26–64 cm)	Texture	Light clay
	Structure (large peds)	Moderate 20–50 mm subangular blocky peds
	(small peds)	Moderate 5–10 mm subangular blocky peds
	Fabric	Rough ped
	Consistence	Firm
	Segregrations	Very many coarse ferromanganiferous nodules
	Voids	N1 pores
	Field pH	6.5
B2	Colour	7.5 YR 5/6
(64–108 cm)	Texture	Light clay
	Structure (large peds)	Moderate 20–50 mm subangular blocky peds
	(small peds)	Moderate 5–10 mm subangular blocky peds
	Fabric	Rough ped
	Consistence	Very firm
	Segregrations	Few medium ferromanganiferous nodules
	Voids	N1 pores
	Field pH	9.5
B3	Colour	10 YR 5/8 with many very coarse (>30 mm) prominent red mottles
(108–150+ cm)	Texture	Light clay
	Structure (large peds)	Moderate 50–100 mm angular blocky peds
	(small peds)	Moderate 5–10 mm subangular blocky peds
	Fabric	Rough ped
	Consistence	Weak
	Segregrations	N1
	Voids	N1 pores
	Field pH	9.5

Plate 3.1: A trench digger was used to excavate to 100 cm, around 1 m² plots. The digger sat on thick plyboard to help prevent soil compaction.

Plate 3.2: The soil 'islands' were individually wrapped in construction grade plastic before the trenches were back–filled with soil. The plastic sheeting was used to prevent water and root movement between plots.

Construction of the rain—out shelter

An automatic rain—out shelter was designed and constructed by the CSIRO workshop team at Chiswick. The construction followed consultation with designers of existing rain—out shelters from northern New South Wales (J. Morgan, NSW Agriculture) and southern Queensland (M. Foale, CSIRO Division of Tropical Crops and Pastures). The aim of the shelter was to exclude all natural rainfall from the trial area.

The rain—out shelter consisted of two roofs, each 16 x 16 m (Figure 3.1). Each roof was a modular truss design, manufactured from rectangular hollow section steel weighing 2.86 tonnes. The 15° pitch roofs were clad with translucent Alsynite sheeting. Each roof sat on two 80 m horizontal rails, elevated 1.8 m at the lowest point, with approximately 2 m clearance under the shelter at the lowest point.

The roofs were attached to a continuous steel rope, looped around the winch drum at one end and a spring—loaded rope tensioner at the other (Figure 3.1). The roofs travelled in opposite directions, with one roof attached to the upper rope, the other to the lower rope. The roofs sat at opposite ends of the rail during dry periods. The winch drum was driven by a 3—phase geared motor.

When it rained, closure of the roofs was activated by an electrical pulse from either one of two tipping—rain gauges (Plate 3.3). The rain gauges were activated by 0.25 mm of rain. The second rain gauge was a backup in case of a malfunction or blockage. The electronic pulse from the rain gauge was sent to the winch motor triggering it to automatically start, closing the roofs in 45 sec to cover the plots. The open and close positions were controlled by electronic limit switches mounted on the elevated rails with stoppers at the extreme points to prevent the roofs over running. When stopped, the roofs were held in position by an electromagnetic brake. The roofs automatically opened 1 hr after the last rain gauge tipped, moving off the plots. Prior to the roofs moving in either direction, a warning siren sounded for 10 sec to alert all people near the shelters.

The shelter's automatic micro—controller and electronic monitoring device were designed and constructed by the Electronic Services Unit, University of New England, Armidale. The position of the roofs was reported and saved to floppy disk every 4 min. The time of each tip of the rain gauges and each opening and closing of the roofs were also recorded. In the event of a malfunction, a modem with a recorded message contacted first the workshop then pre—designated home phone numbers alerting personnel of a problem.
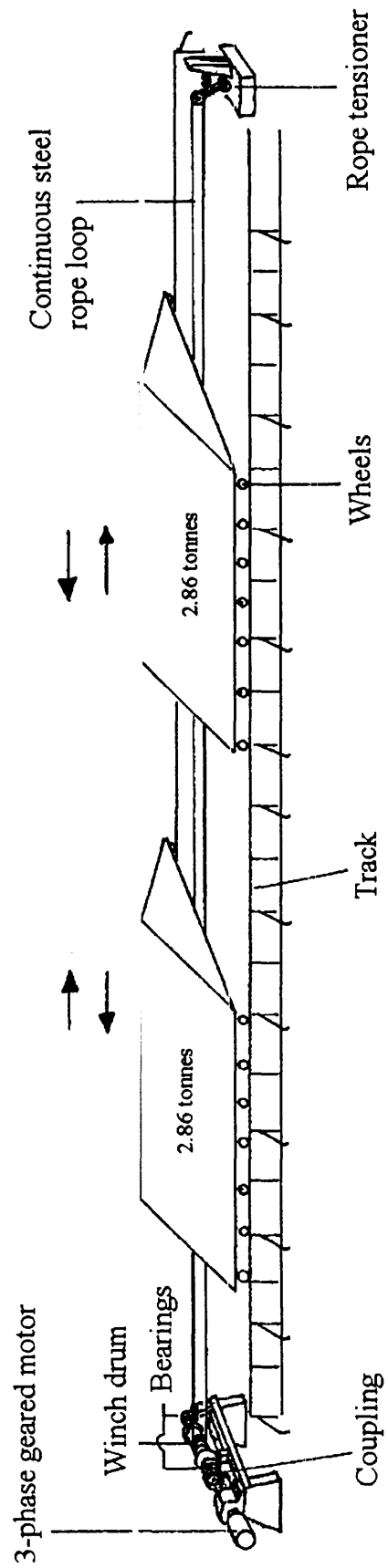
Figure 3.1: The rain–out shelter consisted of two roofs, each 16 m x 16 m. The roofs were attached to a continuous steel rope, looped around the winch drum and the spring–loaded rope tensioner. One roof was attached to the upper rope, the other to the lower rope (Drawn by G. Burke).

While the roofs were closed, covering the plots, the water from the roofs was collected and stored in a 125 000 L plastic–lined underground tank adjacent to the trial area. The treatment plots were watered using the water collected from the roofs. The water was pumped from the tank and applied with a fine spray nozzle according to the designated water treatments.

A 2 m high rabbit proof fence built around the trial area was used for security and animal control.

Plate 3.3: Two tipping rain gauges measured the rainfall. When 0.25 mm was received in either rain gauge the tipping mechanism caused an electronic pulse to be sent to the controller. The second rain gauge was installed as a backup in case of malfunction or blockage.

Trial establishment

Seeds of the six perennial grass species used in the experiment (named below) were planted into individual celled Speedling Trays® in a glasshouse in August 1993. They were watered frequently and fertilised fortnightly with Aquasol® (N:P:K 23:4:18). After 6 weeks the seedlings were thinned to one plant per cell and cut to encourage tillering (Plate 3.4a). The seedlings continued to be watered, fertilised and cut until they were transplanted into the field.

Yates weed mat® was laid over the trial area in December 1993 to help control weeds and reduce soil

water evaporation. On 20–23 December 1993, the 4 month old seedlings were transplanted into the trial area, one species per plot. A grid was placed on each 1 m² plot to mark the position of the 25 space–planted plants in a 5 x 5 plant configuration. Using a 50 mm diameter shallow soil corer, holes were made at each position and a seedling planted. The transplanted plants were well watered to ensure good growth and survival following transplanting into the field (Plate 3.4b). The trial was fertilised fortnightly with Aquasol®.

Plate 3.4: (a) Seeds were planted into individual celled Speedling Trays® in the glasshouse. After 6 weeks the seedlings were thinned to one plant per cell and cut to encourage tillering. (b) Four month old seedlings were transplanted into the trial, one species per plot. Each plot contained 25 plants, planted in a 5 x 5 plant configuration. Weed mat was used to reduce weed invasion and soil water evaporation. The photo was taken approximately 6 weeks after transplanting.

In April 1994, the weed mat was removed from the trial area to allow for thickening of the plant crowns and to encourage the plants to cover the ground surface. Tall fescue seedlings were planted into the trenches between plots.

The trial and treatments

The trial consisted of two blocks, each approximately 10 m x 12 m. Each block was a split–split plot design; split on moisture, defoliatior and species with two replicates (Figure 3.2). Each block consisted of 72 experimental plots, each 1 m² with spare 'lane–way' plots separating each moisture treatment.

Perennial grass species

The trial consisted of six perennial grasses including both introduced and Australian native species. The species chosen are commonly grown on the Northern Tablelands. The four introduced species were: *Festuca arundinacea* Schreb. (tall fescue) cv. Demeter, *Dactylis glomerata* L. (cocksfoot) cv. Porto, *Lolium perenne* L. (perennial ryegrass) cv. Victorian and *Phalaris aquatica* L. (phalaris) cv. Sirosa. The two native species were: *Microlaena stipoides* (Labill) R. Br. (weeping grass) cv. Shannon and *Danthonia richardsonii* Cashmore (wallaby grass) cv. Taranna. The characteristics of each species are presented below.

Tall fescue

Festuca arundinacea Schreb. is native to Europe and Asia (Whittet 1964; Brouwer *et al.* 1994). It is a deep rooted perennial, best adapted to relatively cool climates with an annual rainfall of 600–750 mm and a reliable summer rainfall (Brouwer *et al.* 1994). Fescues were some of the first species used in pasture trials in the high rainfall temperate areas of Australia (Whittet 1964; Brouwer *et al.* 1994). Tall fescue is adapted to a range of environments, is persistent under a wide range of management regimes, produces good yields, has a long growing season and good seed production (Torbert *et al.* 1990).

A robust perennial grass with rounded tillers, tall fescue also has large dark–green leaves with distinct ribs on the upper surface (Langer 1977) and is able to avoid drought stress by extracting subsoil moisture via a deep root system (Garwood and Sinclair 1979; Fry and Butler 1989).

Tall fescue is slow to establish, hence it is vulnerable to competition from other species during this time. In general, spring growth is high and autumn growth is good (Langer 1977). It is persistent under lower stocking rates and is favoured by a conservative management regime (Hutchinson 1970). Most tall fescue cultivars remain relatively green during a dry summer (Langer 1977) and are resistant to cold weather and frosts (Langer 1977; Brouwer *et al.* 1994). Whilst tall fescue prefers fertile soils, it is

SS

	R1		R2			
	D1		**D2**		**D1**		**D2**
M3	Ms	Lp	Fa	Dr	Fa	Dr	Lp	Dr	**M2**
	Dg	Pa	Pa	Ms	Ms	Lp	Fa	Pa	
	Fa	Dr	Lp	Dg	Pa	Dg	Dg	Ms	
M2	Dg	Lp	Dr	Dg	Dr	Lp	Fa	Dr	**M1**
	Dr	Pa	Ms	Pa	Pa	Dg	Lp	Ms	
	Ms	Fa	Fa	Lp	Fa	Ms	Dg	Pa	
M1	Lp	Fa	Pa	Dr	Fa	Dg	Dr	Lp	**M3**
	Dr	Ms	Dg	Lp	Lp	Pa	Ms	Pa	
	Dg	Pa	Ms	Fa	Dr	Ms	Dg	Fa	

SA

	D1		D2		D1		D2		
M3	Dg	Ms	Ms	Fa	Ms	Dg	Fa	Dr	**M2**
	Pa	Lp	Lp	Pa	Dr	Pa	Lp	Dg	
	Dr	Fa	Dr	Dg	Fa	Lp	Ms	Pa	
M2	Dr	Pa	Lp	Pa	Dr	Dg	Dg	Dr	**M1**
	Fa	Lp	Fa	Dr	Lp	Pa	Lp	Ms	
	Ms	Dg	Dg	Ms	Fa	Ms	Fa	Pa	
M1	Ms	Dg	Pa	Dc	Dg	Pa	Ms	Pa	**M3**
	Fa	Pa	Lp	Ms	Dr	Fa	Fa	Lp	
	Lp	Dr	Dr	Fa	Lp	Ms	Dg	Dr	

Figure 3.2: Drought experimen: trial plan. The trial consisted of two blocks. Each block was a split–split plot with two rep icates. The species were: tall fescue (Fa), cocksfoot (Dg), perennial ryegrass (Lp), phala is (Pa), weeping grass (Ms) and wallaby grass (Dr). The moisture treatments were: 10% drought (M1), 40% drought (M2) and non–stress (M3). The defoliation treatments were severe defoliation (D1) and moderate defoliation (D2). The blocks were: Spring–Summer SS) and Summer–Autumn (SA), and the replicates R1 and R2.

a widely adapted species, being toleran: of acid and alkaline soils and able to withstand poor drainage (Langer 1977; Brouwer *et al.* 1994).

In the work presented in this thesis tall 'escue cv. Demeter was used. Cultivar Demeter was introduced by CSIR in 1931 (O'Reilly 1981; Oram 1990). Although Demeter has a slow seedling growth rate it is well adapted to areas with good summer and autumn rainfall (Brouwer *et al.* 1994) and has a longer effective growing season than phalaris and ryegrass (Hilder 1963a–c). Cultivar Demeter produces good growth all year round, especially in areas with good summer and autumn rainfall. In the Armidale, New South Wales district Demeter will produce good growth through mid–summer provided soil moisture is adequate, and greater growth than Australian phalaris in autumn and winter (Hilder 1963b–c).

Cocksfoot

Dactylis glomerata L. is a native of northern Europe, northern Africa and temperate Asia (Brouwer *et al.* 1994). It has become naturalised in many of the higher rainfall areas with an annual rainfall of 750 mm and above.

There are two groups of cocksfoot. The first group is of northern European origin while the second group is of Mediterranean origin. Although the periods of maximum production vary, the growth form of both groups of cocksfoot is similar. Cocksfoot is a tufted perennial grass with flattened tillers (Langer 1977) and a relatively dense root system to 50 cm depth (Ridley and Simpson 1994). The leaves are smooth, varying in colour from light green to blue green (Brouwer *et al.* 1994).

Cocksfoot cv. Porto was used in the research presented in this thesis. Cultivar Porto was introduced by CSIRO in 1955 (Oram 1990). Selection and field testing were conducted by the Tasmanian Department of Agriculture and a new cultivar released in 1972. Cultivar Porto is a late maturing cultivar and grows actively during both summer and winter. It has good seedling vigour and early growth, and is one of the more productive cultivars in areas with 450–1100 mm annual rainfall (Brouwer *et al.* 1994).

Perennial ryegrass

Lolium perenne L., a native grass of E irope and Asia (Whittet 1964; Brouwer *et al.* 1994), is adapted to the cool coastal and upland areas of New South Wales, Victoria, Tasmania and South Australia (Brouwer *et al.* 1994). Perennial rye;rass has undergone selection and improvement in Australia, resulting in cultivars ranging in summer dormancy, maturity and resistance to moisture stress.

Perennial ryegrass is an erect species with little lateral spread. Perennial ryegrass is resistant to cold and frost (Kemp 1981; Brouwer *et al.* 994), with summer growth dependant on the degree of summer dormancy (Brouwer *et al.* 1994) and water supply (Blaikie and Martin 1987).

Perennial ryegrass cultivars vary in their ability to grow and recover after drought (reviewed by Thomas and Evans 1990), however they are generally considered to be sensitive to drought (Kemp 1981). Persistence of perennial ryegrass varies with physiological growth stage (Thomas and Evans 1990), moisture stress (Brougham 1960) and defoliation intensity (Brougham 1960; Hutchinson 1970).

Perennial ryegrass cv. Victorian, used in the research presented in this thesis, was selected from ecotypes in old established pastures in the Central and Western Districts of Victoria by the Victorian Department of Agriculture in 1936 (Kemp 1981). It is an early maturing cultivar which grows from early autumn, through winter and spring, with peak production in spring and autumn. Cultivar Victorian is better adapted to areas of western Victoria, with their hot, dry summers and an annual rainfall of 500–700 mm, than other cultivars (Kemp 1981; Oram 1990; Brouwer *et al.* 1994).

Phalaris

Phalaris aquatica L. is a native of southern Europe and the Mediterranean region (Brouwer *et al.* 1994). Phalaris is common on the tablelands, slopes and some coastal districts of New South Wales.

Phalaris is a deep rooting perennial grass adapted to climates with mild, moist winters and hot, dry summers with an annual rainfall of 4)0–750 mm. It can withstand dry conditions and is persistent under heavy grazing. Phalaris has been shown to be highly drought resistant in many countries with Mediterranean–type climates. The persistence of phalaris is assisted by a deep rooting habit and summer dormancy (McWilliam and Kramer 1968), however the actual persistence varies with physiological growth stage (Hoen 1968a, 1968b), grazing intensity and rainfall (Hutchinson 1970). Whilst phalaris grows best in fertile heavier soils and is not tolerant of acid soils, it is adapted to a

wide range of soils (Brouwer *et al.* 199-1; Watson 1993).

A productive species, phalaris produces good quality grazing for 8–12 months depending on the environment and management (Watson 1993). Phalaris grows best during autumn and spring, but also produces well during winter (Brouwer *et al.* 1994). Spelling during spring is recommended to encourage bud production (Hill and Watson 1989). Phalaris typically becomes dormant during summer following seeding (Brouwer *et al.* 1994).

Phalaris cv. Sirosa was used in the work presented in this thesis. Sirosa is an upright cultivar with larger seeds than other cultivars which germinate fast and grow vigorously, giving a reliable establishment and greater yields in its early years (Oram 1990; Brouwer *et al.* 1994). Sirosa phalaris has a similar morphology to Australian phalaris (Oram 1990), but is a more erect cultivar with a smaller crown (Culvenor 1993b; Watson 1993), has longer leaf sheaths, broader laminae, thicker and taller culms, greater seedling vigour and greater adult winter robustness (Oram 1990). Sirosa has been selected for low levels of dimethyltryp amine alkaloids and is adapted to areas with an annual rainfall exceeding 450 mm (Oram 1990; Brouwer *et al.* 1994).

Weeping grass

Microlaena stipoides was previously known as *Ehrharta stipoides*. The genus *Microlaena* contains about 10 species native to Australia, New Zealand, New Guinea, and some Pacific Islands. Commonly called weeping grass, it is spread throughout the high rainfall zone (Wheeler *et al.* 1990; Brouwer *et al.* 1994), from the Cape York Peninsua in Queensland, south to Victoria and Tasmania, also in some coastal districts of South Australia and the south west region of Western Australia (Whalley and Rose 1988; Brouwer *et al.* 1994). *Microlaena* spp. are soft succulent grasses with slender tufted year–long green foliage (Breakwell 1923), a rhizomatous habit and grow to a height of 15–70 cm tall (Whalley and Rose 1988).

A year–long green perennial (Taylor 980), *M. stipoides* provides feed during the winter and early spring months on the Northern Tablelands of New South Wales (Robinson and Archer 1988). It has been reported as being as productive and having similar nutritive values as highly selected introduced grasses (Vieira 1980; Archer and Robinson 1988; Robinson and Archer 1988). *M. stipoides* is able to grow in a wide range of soil types, and is tolerant of acid soils (Munnich *et al.* 1991; Brouwer *et al.* 1994).

Weeping grass is sensitive to cultivation (Magcale–Macandog and Whalley 1993), however it will re-establish in grazed pastures. *M. stipoides* is persistent under heavy grazing and tends to increase in abundance after droughts (Lodge and Whalley 1989). *M. stipoides* shows a wide range of phenotypic and genetic variation (Richards 1986) and is well adapted to Australia's generally low fertility soils, and areas prone to erratic rainfall and drought (Lodge and Whalley 1989).

Weeping grass cv. Shannon, released following selection at the University of New England Armidale, was used in the work presented in this thesis. Cultivar Shannon is short, commonly less than 30 cm tall, and has a 'partially erect' habit with soft drooping leaves (Anon. 1995). It is adapted to acid soils and was selected for use along roadsides, on golf courses and low maintenance public lands in the high rainfall areas of temperate Australia (R.D.B. Whalley, pers. comm.).

Wallaby grass

Danthonia spp. are native to Australia. They are prevalent throughout New South Wales, on the Tablelands and Slopes, along the Central and North Coast and the North and South Western Plains (Vickery 1956, cited in Lodge 1993). *Danthonia* spp. can also be found in Queensland, Victoria and South Australia (Brouwer *et al.* 1994).

Danthonia spp. are considered year–long green perennials (Taylor 1980; Lodge and Whalley 1989) and are known for their drought persistence, palatability and production, particularly in winter (Breakwell 1923; Brouwer *et al.* 1994). Being frost tolerant, *Danthonia* spp. grow in both the winter and summer. They usually have two flowering periods, one in late–spring to early–summer, the other in autumn (Lodge 1983). *Danthonia* spp. can withstand heavy grazing (Breakwell 1923) and have been found to increase in frequency with grazing (Whittet 1936).

Danthonia richardsonii Cashmore, commonly called wallaby grass, is a widespread grass throughout the Southern Tableland and South Western Slopes, in areas which have not been over–stocked (Whittet 1964). It has a tussocky habit with soft narrow leaves. *D. richardsonii* can be distinguished from other *Danthonia* spp. by its glaucous–green overall appearance and the whiteness of the mature spikelets (Whittet 1964).

Selection for improved *Danthonia* spp. genotypes has been conducted at NSW Agriculture's Centre for Crop Improvement, Tamworth. Two cultivars have been released: *D. richardsonii* cv. Taranna and *D. linkii* Kunth cv. Bunderra. Wallaby grass cultivar Taranna was used in this study. It is an erect plant able to grow up to 70 cm tall, although it generally grows to 50–60 cm. Taranna was selected for

greater herbage production and seed retention (Lodge 1993). While Taranna has most active production during spring and early summer, it is also frost hardy and produces green leaf during the winter (Lodge 1993).

Defoliation treatments

Two defoliation intensities were imposed. They represented 'severe' and 'moderate' defoliation. The 'Pasture Management Envelope' described by Kemp (1991) was used to set the benchmark biomass levels within which the pasture was maintained (Figure 3.3). The severe defoliation treatment maintained the pasture between 600–900 kg DM/ha. This range was considered to represent heavy grazing which would be below the threshold for persistence. The moderate defoliation treatment, maintaining the pasture between 1500–2000 kg DM/ha, was considered as more favourable for persistence and presented a reasonable compromise between harvestable yield and maintaining the plant's energy reserves.
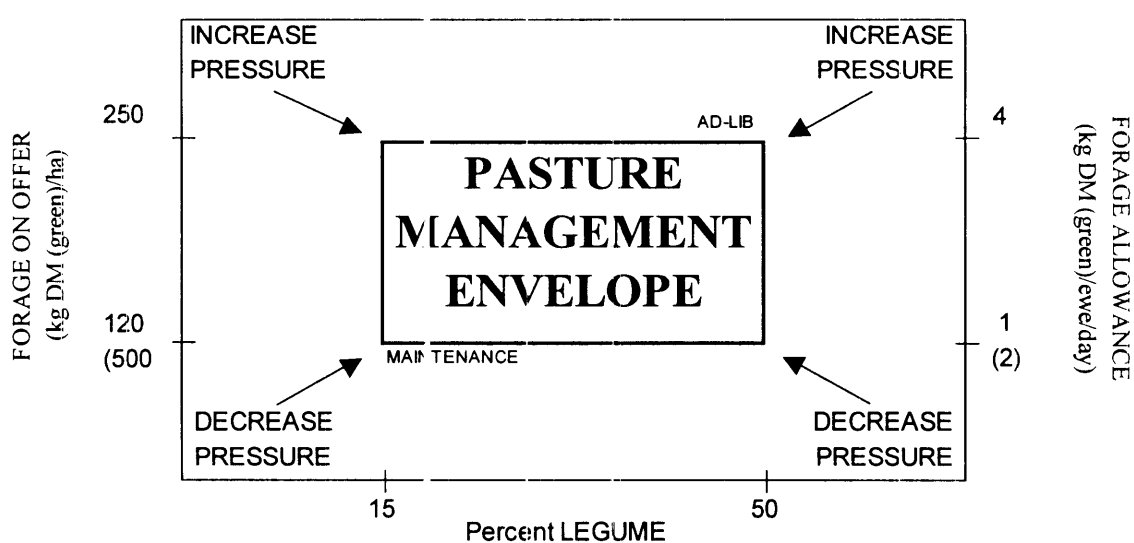

Figure 3.3: The pasture management envelope indicating the boundary dry matter forage on offer biomasses recommended to maintain a productive and persistent pasture (Source: Kemp 1991).

The defoliation treatments were imposed using a lawn mower with a catcher. The lawn mower was set at the same height for all species. Residuals were calculated in August 1994 then recalculated and adjusted in November 1994 (Table 3.2). The individual species swards were noticeably different by

the November adjustment.

Table 3.2: Cutting height and residual biomass for the severe and moderate defoliation treatments at the start of the experiment and following adjustment in November 1994.

	Initial		Adjusted	
	Ht (mm)	Residual (kg/ha)	Ht (mm)	Residual (kg/ha)
Severe	30	1026	27	838 (653 [+])
Moderate	40	1488	40	1140 (1408 [++])

+ Residual biomass excluding tall fescue and phalaris.

++ Residual biomass excluding weeping grass and wallaby grass.

Moisture treatments and experimental seasons

Three moisture treatments were defined for the experiment. Two represent droughts which are typical of the Armidale region and the third was a 'non–stress' or control moisture treatment. The drought treatments were chosen from 130 years of historical rainfall records to represent a 'severe' and 'moderate' drought. The severe drought was defined as 10–percentile rainfall (seasonal rainfall which occurs 1 year in 10) and the moderate drought as 40–percentile rainfall (seasonal rainfall which occurs 4 years in 10). The two drought treatments are herein named 10% drought and 40% drought.

The timing of a drought during the growth cycle of a perennial grass may affect the way a species responds. For this reason, two six–month seasons were chosen for the treatment application: Spring–Summer and Summer–Autumn. The Spring–Summer experimental season (SS) began 1 September 1994 and finished 28 February 1995. The Summer–Autumn experimental season (SA) began 1 December 1994 and finished 31 May 1995.

The rainfall occurring in the two 'typical' seasonal drought treatments and example years are shown in Table 3.3. To determine the characteristic rainfall sequences and volumes for each percentile, the number of rain–events (any period during which rain was recorded) and dry–events (any period during which rain was not recorded) were calculated for the years isolated for further study using a computer program (C. Simpson, unpublished). The total rainfall volume per rain–event was also determined. The procedure used to calculate rainfall sequences for the two drought treatments is outlined in Appendix 1. The data collected from the historical rainfall records were used to create unique rainfall

sequences to simulate each drought treatment. The timings and volumes of water applied are shown in Figure 3.4 and outlined in detail in Appendix 1. The water application for the non–stress moisture treatment was calculated as 80% of the daily pan evaporation and applied 2–3 times a week. The pan evaporation for the nine months of the experiment are shown in Table 3.4.

Table 3.3: Seasonal rainfall for the 10% and 40% drought treatments with some example years in which these seasonal rainfall volumes were received.

Season	Percentile	Seasonal Rainfall	Example Years
Spring–Summer	10%	323 ± 8 mm	1951 1982 1988
	40%	427 ± 8 mm	1979 1984 1987
Summer–Autumn	10%	284 ± 13 mm	1922 1929 1939
	40%	413 ± 6 mm	1943 1948 1986

Water was applied to the plots in the designated water treatments using a hand–held hose with a fine spray rose. Care was taken to ensure that each plot received an accurate amount of 'rainfall' (timed water applications of a known volume) on the designated day with no run–off.
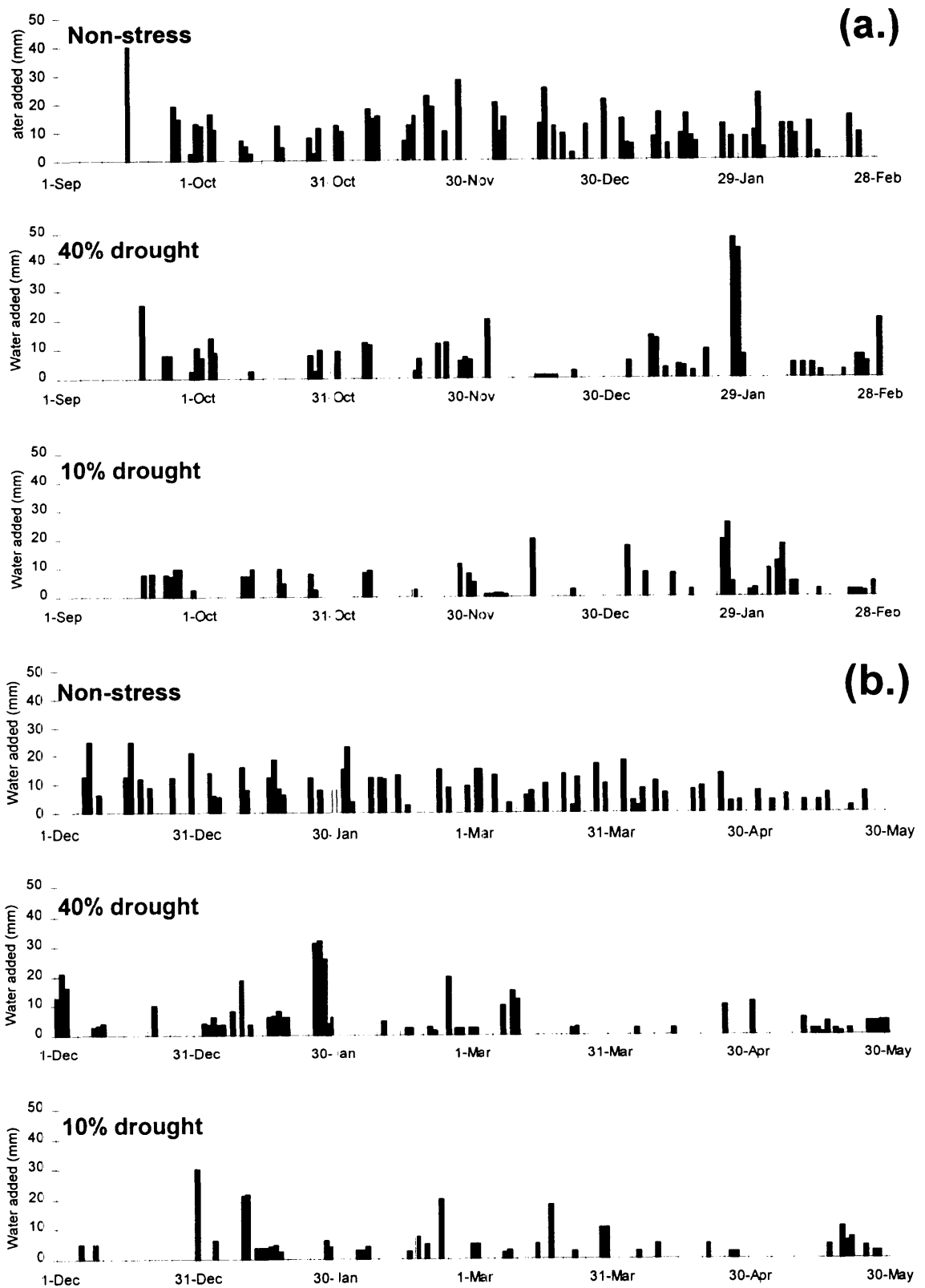
Figure 3.4: Water added as 'rainfall' for the Non–stress, 40% drought and 10% drought during the 1994–95 (a) Spring–Summer and (b) Summer–Autumn experimental seasons.

Table 3.4: Monthly pan evaporation (mm) at Chiswick, CSIRO Pastoral Research Laboratory, Armidale, New South Wales. Data are for the period September 1994 to May 1995, the long–term averages (1959–1993) and includes the six–month experimental season totals.

	Month									Season totals	
	Sep 1994	Oct	Nov	De:	Jan 1995	Feb	Mar	Apr	May	Spring–Summer	Summer–Autumn
1994–95	122.0	153.9	167.8	189 7	167.9	126.1	155.1	107.9	63.3	927.3	810.0
Long–term	85.3	116.6	141.6	169 7	175.7	147.6	133.1	93	59.7	836.5	778.8

Fertiliser regimes

In September 1994, the fertiliser regime was altered from Aquasol® to reduce the levels of nitrogen, phosphorus and potassium and to increase those of sulphur and magnesium. The fertiliser regime is detailed in Table 3.5. Available phosphorus levels were assessed (Colwell 1965) in March 1994 and March 1995, rising from 27.36 ppm to 32.2 ppm during the 12 months.

Table 3.5: Nutrients applied to the trial area as fertiliser. Aquasol was applied prior to September 1994. From September a modified mix (G. Blair, pers. comm.) was used. The fertilisers used in the modified mix are also listed. Annual rates of fertiliser nutrient application are provided for comparison.

Nutrient	Aquasol (kg/ha/yr)	Modified mix (kg/ha/yr)	Fertilisers used in modified mix (kg/ha)
N	239	120	Urea 221
P	42	20	DAP 87
K	187	20	$MgSO_4$ 92
S	<1	20	K_2SO_4 45
Mg	0	8.5	

At the start and completion of the experiment

At the start of each experimental period each defoliation treatment was cut to its stated defoliation height. Soil moisture was recorded for all moisture treatments using the neutron probe. More details on the specific methods used are described in the relevant experimental chapter.

The second experimental year (1995–96)

The data reported in this thesis are for the 1994–95 experimental seasons only. The trial did continue into the second year (1995–96) with the SS season commencing on 1 September 1995. During the 1994–95 season the Northern Tablelands, and indeed much of New South Wales and the eastern districts of Australia were experiencing a major drought. In September 1995 it started to rain with substantial rain falling in November 1995 and again throughout January 1996 (Figure 3.5). The 1 in 50 year drought of 1994–95 had turned into a 1 in 50 quarter year 'wet'. In the five months from September 1995 to February 1996, the district received 700mm. The average annual rainfall in Armidale is approximately 790mm. During this period there was no natural rainfall on the plots as the rain–out shelters functioned correctly, however on 24 January 1996 one of the neutron probe tubes was found to be full of water, indicating the presence of ground water. Temporary piezometers were dug at different locations around the trial and ground water was found within 15 cm of the surface indicating a perched water table.
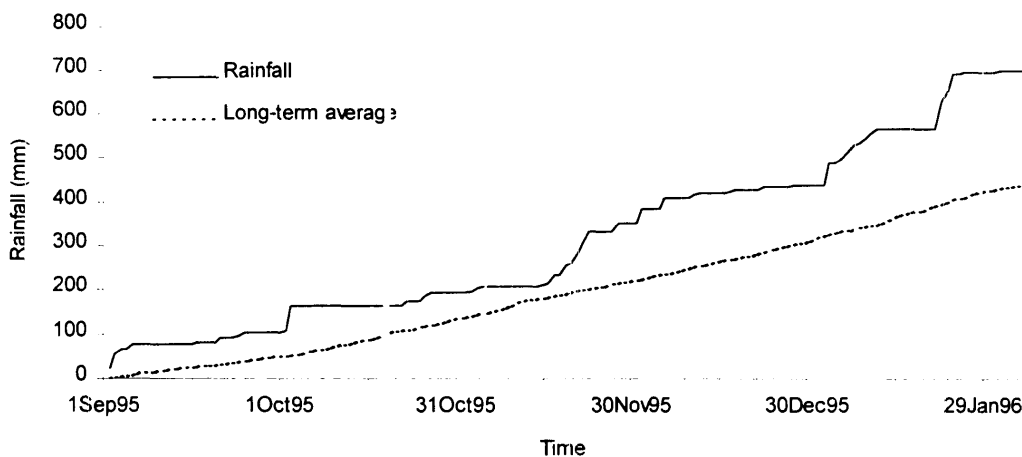

Figure 3.5: Cumulative rainfall for the period 1 September 1995 to 5 February 1996 and the long term average (1950–1994)

At the time that perched water table was discovered, the SS season was only five weeks from completion, so the seasonal treatments were continued with no adjustments. However, in the SA experimental season block (which had commenced 1 December 1995), all watering was suspended, with the measurements continuing. The soil water content was monitored weekly in the hope that the trial would drain and dry quickly so that the treatments could continue. While the profile did dry, it did not dry to the extent that the drought treatments could continue. The SA season finished on 31

May 1996. Colour contour graphs, created using Spyglass®, indicated that the water content started to increase from October 1995 (Figure 3.1). As the data collected during the 1995–96 season could not be used to quantify stress thresholds of grasses during drought, the data are not reported in this thesis.
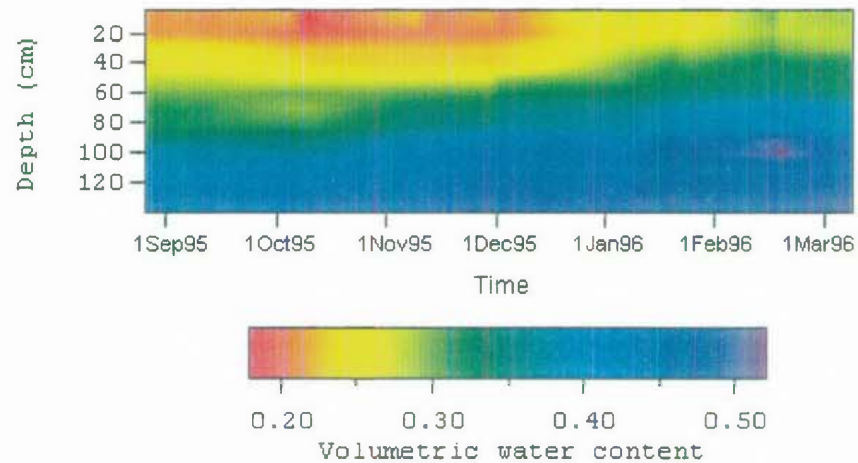

Figure 3.1: The volumetric water content (m^3/m^3) down the soil profile and through time, in a phalaris (severe defoliation—non–stress moisture treatment) plot during the 1995–96 Spring–Summer season. The figure shows the rise in water content due to the perched water table.

Acknowledgements