

Investigating the physiology and management of
cocksfoot (*Dactylis glomerata* L.) and
prairie grass (*Bromus willdenowii* Kunth.)
as alternative perennial grass species for the
dairy industry in southern Australia

by

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Declaration

Except where reference is made in the text of the thesis, this thesis contains no material published elsewhere or extracted in whole or in part from a thesis by which I have qualified for or been awarded another degree or diploma. No other person's work has been used without due acknowledgement in the main text of the thesis. This thesis has not been submitted for the award of a degree or diploma in any other tertiary institution.

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November 2006

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List of common abbreviations

ADF – acid detergent fibre
C – carbon
°C – degrees Celsius
Ca – calcium
Cl – chlorine
cm – centimetre
CP – crude protein
d – day
DDM – digestible dry matter
DM – dry matter
g – gram
ha – hectare
IVDMD – *in vitro* dry matter digestibility
K – potassium
kg – kilogram
l – litres
LSD – least significant difference
m – meter
ME – metabolisable energy
mg – milligram
Mg – magnesium
MJ – mega-joule
mm – millimetre
N – nitrogen
Na – sodium
NDF – neutral detergent fibre
P – phosphorus
s.e. – standard error
t – tonne
TNC – total non-structural carbohydrate
WSC – water-soluble carbohydrate

Abstract

This thesis examined the productivity and pasture herbage quality of cocksfoot (*Dactylis glomerata* L.) cv. 'Kara' and prairie grass (*Bromus willdenowii* Kunth.) cv. 'Matua', under leaf stage based defoliation management. Leaf stage (number of live leaves per tiller) is a generic measure of plant development and was used to investigate the physiology underlying the regrowth response of these species following defoliation, and to determine optimal defoliation management of cocksfoot and prairie grass plants.

A survey was undertaken of Tasmanian dairy farmers, to establish the current and potential use of perennial ryegrass (*Lolium perenne* L.), cocksfoot and prairie grass, and to evaluate quantitatively farmer perception of the feed quality, palatability and dry matter (DM) production of these species under dryland conditions. The survey responses confirmed that perennial ryegrass is currently the dominant perennial grass species utilised in Tasmanian dairy pastures and that the herbage quality, palatability and annual DM production of perennial ryegrass under dryland conditions is generally considered to be substantially higher than for cocksfoot and prairie grass.

An initial field study investigated the effect of defoliation management based on leaf regrowth stage on the productivity and herbage quality of perennial ryegrass, prairie grass and cocksfoot under dryland conditions. The DM yield and quality of cocksfoot and prairie grass were found to be comparable with perennial ryegrass under appropriate defoliation management. While the 2-leaf to 3-leaf regrowth stage was previously well-recognised as the most favourable defoliation interval for perennial ryegrass pastures, this study showed that a defoliation interval coinciding with regrowth of four leaves provided an optimal balance between pasture productivity and herbage quality for cocksfoot and prairie grass.

The physiology underlying the regrowth response of cocksfoot and prairie grass following defoliation was further investigated in a series of four glasshouse studies. Changes in the physiology and herbage quality of prairie grass during regrowth were examined, and results provided further evidence that the optimal defoliation interval

for prairie grass is the 4-leaf stage of regrowth, as this is when increased water-soluble carbohydrate (WSC) levels in the stubble coincide with a resumption of tillering and root growth, but is prior to the reduction of herbage quality due to increased senescent and stem material.

The role of nitrogenous (N) and WSC reserves during regrowth of these species was further investigated, concluding that as with perennial ryegrass, the stubble (tiller base below 50 mm height) is the primary storage site for energy reserves and the priority sequence for allocation of WSC reserves follows the expected order of leaf growth, root growth and tillering for both species. Nitrogenous energy reserves were found to play a minor role in the regrowth of cocksfoot plants following defoliation. For prairie grass, although WSC reserves were identified as the primary contributor to plant regrowth following defoliation, there was a strong relationship between stubble N concentration and regrowth parameters. The distribution of WSC reserves within the stubble of cocksfoot and prairie grass was also determined. The pattern of WSC accumulation in the stubble of these species suggests that the previously adopted defoliation stubble height of 45-50 mm (optimal management for perennial ryegrass) is also suitable for the persistence of cocksfoot and prairie grass. However, while decreasing defoliation height to 30 mm may be acceptable for cocksfoot, prairie grass is more sensitive to defoliation severity, with defoliation below 45 mm not recommended.

Differences between four cocksfoot and four brome cultivars (including Kara and Matua) under leaf stage based defoliation management in the glasshouse were examined. Variation between cultivars indicated that there are some improvements resulting from selection and breeding within the cocksfoot and brome genera since the commercial release of Kara and Matua. However, whether the overall value of the newer cultivars to dairy pasture systems exceeds the value of the original cultivars is yet to be determined.

The remaining potential limitations to the use of Matua and Kara in the dairy industry, as highlighted in this thesis, include slow establishment of Kara in the field, high rates of seeding for Matua, and relatively high fibre levels for both cultivars compared with perennial ryegrass. However, the overall results show that under

defoliation management based on leaf stage, an optimal balance between pasture yield, persistence and herbage quality can be achieved, supporting the future use of cocksfoot and prairie grass in dryland dairy pastures of southern Australia.

Chapter 1

Introduction

In the cool temperate region of the dairy industry in Australia - comprised of Gippsland, southwest Victoria, Tasmania and the south coast of New South Wales - the dominant pasture grass species is perennial ryegrass (*Lolium perenne* L.), commonly sown in a mixed sward with white clover (*Trifolium repens* L.; Mason 1993).

In this region, perennial ryegrass is widely accepted as the highest quality and most palatable and productive of the temperate grasses. Since its introduction into Australia from Europe over 100 years ago, breeding efforts have focused on improving forage yields and herbage quality. The resultant cultivars are easily established and are also successfully managed, due to years of agronomic research that have accompanied breeding efforts. Yet despite the improvements of these cultivars, limitations associated with using perennial ryegrass in southern Australia are considerable. They include poor production and persistence of pastures under dry and/or hot conditions (Waller and Sale 2001), a requirement for relatively high levels of irrigation application (and a tendency to become dormant if irrigation becomes sub-optimal), susceptibility to a range of pasture pests and pathogens (Lancashire and Latch 1966; McQuillan and Ireson 1987; Clarke and Eagling 1994; Waller and Sale 2001), a requirement for relatively high levels of soil fertility (Lambert *et al.* 1986; Frame and Tiley 1988) and the presence of the endophyte fungus *Neotyphodium lolii*, the causative agent of ryegrass staggers (Reed *et al.* 2000).

In the literature, cocksfoot (*Dactylis glomerata* L.) and prairie grass (*Bromus willdenowii* Kunth.) have compared well against perennial ryegrass as dryland pasture species, in terms of higher summer/autumn dry matter (DM) production (Vartha 1977; Belton 1992; Milne *et al.* 1993; Moloney 1993; Fraser 1994; Graham *et al.* 2000). These species also have lower requirements for water and soil fertility (Barker *et al.* 1993; Norton *et al.* 1999), higher tolerance of pests and pathogens (Guy *et al.* 1986; Belton 1992; Lolicato and Rumball 1994; Slay 2002) and the absence of endophyte fungi. While the literature clearly indicates that cocksfoot and

prairie grass have great potential as dryland dairy pasture species in cool temperate Australia, the reputation of these species among the dairy farming community is poor. This attitude was explored in the current thesis by means of a mail questionnaire, which aimed to establish the current and potential use of perennial ryegrass, cocksfoot and prairie grass within the Tasmanian dairy industry, and to evaluate quantitatively farmer perception of the herbage quality, palatability and dryland DM production of these species.

In the past, species comparisons of pasture productivity, herbage quality and persistence have often been based on a management regime developed for ryegrass pastures (to the detriment of the alternative species) or from studies that have involved defoliation of different species at exactly the same time (Greenhalgh and Reid 1969; Jung *et al.* 1976; Balasko *et al.* 1995; Johnson and Thomson 1996; Hainsworth and Thomson 1997). Species-specific management of these alternative grasses is required to provide an objective assessment of their individual value as dairy pasture species.

Leaf regrowth stage (number of fully expanded leaves per tiller) is a generic measure of plant regrowth, as leaf appearance rate is primarily influenced by temperature and to a lesser extent moisture availability, and is independent of cultivar type and soil fertility (Mitchell 1953; Barker *et al.* 1985; Van Loo 1992). Leaf stage is an indicator that is readily distinguished in the field and glasshouse and has been used to identify the optimum time for defoliation of pasture plants, based on the physiological state of the plant and its suitability to be grazed (Fulkerson and Donaghy 2001). Previous studies have identified the 4-leaf regrowth stage (four leaves per tiller) as the optimal time for defoliation of both cocksfoot (Rawnsley *et al.* 2002) and prairie grass (Fulkerson *et al.* 2000; Slack *et al.* 2000).

The objectives of this thesis were to examine the productivity and pasture herbage quality of cocksfoot cv. 'Kara' and prairie grass cv. 'Matua', under leaf stage based defoliation management; to investigate the physiology underlying the regrowth response of these species following defoliation; and to verify optimal defoliation management of cocksfoot and prairie grass plants, through a series of field and glasshouse studies.

Chapter 2

Literature Review

2.1 Background

2.1.1 The dairy industry in southern Australia

The Australian dairy industry has been classified into four feedbase regions (Mason 1993), based on climatic variability (Table 2.1).

Table 2.1 Feedbase regions defined for the Australian Dairy Industry (source: Mason 1993).

Region	Climatic Region	Feedbase
Tasmania Southern Victoria South coast of NSW	Cool Temperate	Ryegrass/white clover
Western Australia S.E. of South Australia N.E. of Victoria S.W. of Victoria	Mediterranean	Dryland - Annual ryegrass/ subterranean clover Irrigation – Perennial ryegrass/ white clover/paspalum/kikuyu
Goulburn and Murray Valleys and Maffra area in Victoria Riverina of NSW	Inland Irrigation	Ryegrass/white clover/paspalum
North coast of NSW Queensland	Subtropical	Tropical grass in summer Annual ryegrass, oats in winter or perennial ryegrass, prairie grass

The Cool Temperate Region, which comprises Tasmania, Southern Victoria and the South Coast of New South Wales, receives over 800 mm of rainfall annually. This relatively high rainfall supports a perennial ryegrass and white clover feedbase and a long, reliable pasture season (Fulkerson and Doyle 2001). Within Tasmania, annual rainfall is variable – from less than 900 mm in the northeast of the state to over 1,200 mm on the West Coast. Approximately 65% of Tasmanian dairy farms use irrigation to some extent (Dairy Research and Development Corporation 2002). The majority of dairy farmers in the northeast depend on irrigation to supplement particularly low summer rainfall.

The Tasmanian dairy industry provides 6% of Australia's total milk production, and contributes approximately 24% of the \$857 million gross value of Tasmania's agricultural production (DairyTas 2006). Milk production in Tasmania has increased by almost 43% since 1990, from 340 to 600 million litres per year, mainly as a result of increased herd size (63%) and milk production per cow (18%). In recent years, there has been a trend of smaller farms to exit the industry and the remaining farms to increase in size (DairyTas 2006). As on-farm pasture generally remains the most cost-effective source of feed, maximisation of pasture growth and utilisation is an important means to increase milk production (Fulkerson and Doyle 2001). Utilised pasture may be directly grazed by stock or cut and conserved for later feeding.

2.1.2 The importance of temperate pastures in the dairy industry

Pasture based dairy systems are more profitable than confinement systems of similar size (Hanson *et al.* 1998), and are capable of higher milk output per hectare at low cost (Penno *et al.* 1996). In contrast, confinement production systems have higher costs but are able to support higher milk output per cow than pasture based systems (Dillon *et al.* 2005).

In the United States, dairy farmers have traditionally used high-energy supplements to increase milk production, as concentrate feed prices are relatively low. In Australia, concentrate feeds are more expensive and the price received for milk is lower, so in the Cool Temperate Region, pasture is the major source of nutrients for dairy cows. In such pasture-based systems, utilisation of home-grown herbage is a key contributor to profitability, and so increasing pasture growth and utilisation is an important objective for the Australian dairy industry. To achieve this, extension programs in most regions of Australia have encouraged the adoption of pasture management practices, with the aim of improving pasture growth and utilisation.

Under irrigation, annual utilisation of pasture in Tasmania can reach 18 t DM/ha (D Donaghy pers. comm.). However, mean pasture consumption on farms in Tasmania was estimated to be 10.6 t DM/ha for the 2004/2005 season (Anon. 2006). In Gippsland pasture consumption was recently estimated to range between 3.0 and 9.0 t DM/ha. Fulkerson and Doyle (2001) suggested that these figures are representative of the Cool Temperate Region, and that the variation may be due to differences in

pasture production, stocking rate and grazing management/feeding practices. Seasonality of pasture production within and between years has been identified as an important limitation to animal production in temperate regions (Christian 1987). The extreme effect of climate on pastures used to feed dairy cows must be minimised to stabilise farm income.

In Tasmania, extended periods of low and/or variable rainfall cause a feed gap to occur on dryland dairy farms during the summer months. In fact, lack of summer pasture DM production has been ranked as the highest priority focus for Tasmanian pasture research and extension efforts (Andrews and Mason 1998). It has long been recognised that overgrazing during the summer (through decreased grazing interval and increased intensity of defoliation), accelerates the widespread death of desirable pasture plants (Brougham 1960). Adoption of the grazing management approach developed by Fulkerson and Donaghy (2001) may be the key to preventing overgrazing (and undergrazing), therefore aiding the persistence of perennial ryegrass-based pastures. This approach places the emphasis on the readiness of plants to be grazed and therefore maximises pasture growth and persistence, as well as plant nutrient status.

The perennial pastures of temperate regions are a renewable resource. They require infrequent planting and grow in predictable annual cycles. Knowledge of how grasses and legumes grow and regrow after defoliation, combined with an understanding of their interaction with grazing animals, may enable the dairy farmer to enhance pasture production and therefore farm profitability (Rohweder and Albrecht 1995). However, the complexity of the dairy system must not be underestimated. After over a decade of intensive research effort, better understanding of the interactions between the environment, feed-related variables and animal production continues to be a long-term goal of Australian dairy research and extension (Fulkerson and Doyle 2001).

2.2 Structure of the grass plant

This section describes the structure of a typical grass plant, as illustrated in the Figure 2.1.

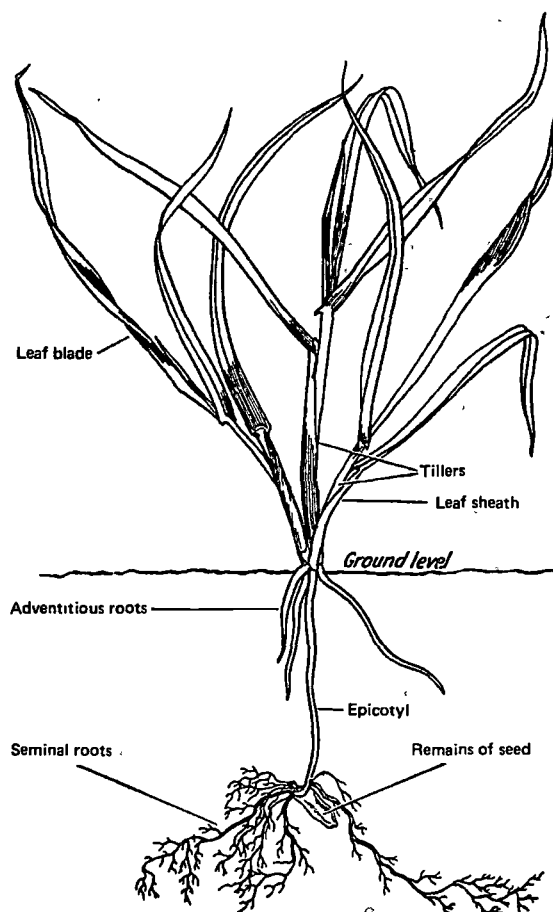


Figure 2.1 Young grass plant, with labelled leaf blade and sheath, tillers, seminal and adventitious roots (source: Langer 1973).

2.2.1 Leaf

The leaf is the principal photosynthetic organ of the grass plant. Substances manufactured in the leaves are transported in the phloem to sites of utilisation, including developing plant parts and storage tissues. Water and minerals are simultaneously transported in the xylem from plant roots to the leaves (Raven *et al.* 1999).

Each leaf is composed of the sheath and leaf blade (or lamina). The sheath surrounds the stem above the node where it is attached (Nelson and Moser 1995). A new leaf

starts as a small swelling, which grows upwards and sideways to eventually form a sheath and lamina.

New leaves appear in regular sequence from the growing point (or apical meristem), located at the centre of the shoot. As long as environmental conditions remain constant and no competition arises, leaves appear at regular intervals on any one shoot during the early stages of vegetative growth (Cooper 1964). Leaf emergence is largely determined by two factors: the rate of leaf extension (elongation) and the length of the sheath tube through which the emerging leaf grows (Grant *et al.* 1981). The stem apex supports a number of young leaves at different stages of development at any one time (Langer 1973). The number of leaves per tiller is relatively constant, maintained by the rates of leaf appearance and leaf senescence (Duru and Ducrocq 2000a).

Leaf length generally increases, while lamina digestibility decreases from one leaf insertion level to the next (i.e. with each successive emerged leaf) (Wilson 1976; Ducrocq and Duru 1997; Duru *et al.* 1999; Duru and Ducrocq 2000a), with a lower decrease in digestibility when defoliation is more frequent (Duru *et al.* 1999). These changes are related with an increase in sheath length with leaf insertion level (Duru and Ducrocq 2000a) and a decrease in the digestibility of a lamina from tip to base (Duru *et al.* 1999).

Leaf size is determined by leaf length and width, which can vary independently (Cooper 1964). Mitchell and Soper (1958) investigated the effects of contrasting light and temperature regimes on the pattern of cell size and cell number in the leaf epidermis, and found that differences in leaf width of perennial ryegrass and paspalum (*Paspalum dilatatum*) were largely due to differences in the number of cell rows across the leaf. In contrast, differences in leaf length were based primarily on changes in cell length. The effects of temperature and light on leaf development are further discussed in Section 2.7.1.

A vegetative perennial ryegrass tiller maintains up to three live leaves, with the oldest leaf (the first to appear) undergoing senescence as the fourth leaf emerges (Fulkerson and Donaghy 2001). For this reason, perennial ryegrass is often referred

to as a '3-leaf plant'. Similarly, prairie grass and cocksfoot maintain four to five live leaves per tiller, and are referred to as 4 to 5-leaf plants. An increase in the rate of leaf appearance will trigger an increase in the rate of leaf senescence.

2.2.2 Tillers.

A tiller is a side-shoot that arises from a bud in the leaf axil of the parent shoot. Each tiller is a replica of the parent shoot, possessing its own apical meristem, leaves, nodes, internodes and adventitious roots. In turn, buds can form in the axils of tiller leaves, giving rise to new tillers. The original shoot gives rise to primary tillers and the primary tillers can then produce secondary tillers. The secondary tillers give rise to tertiary tillers and the pattern continues to form a plant composed of a number of tillers at different stages of growth.

Within a plant, tillers are mutually dependent on one another. Troughton (1960) reported on previous studies, in which one tiller's root in a perennial ryegrass plant was allowed to absorb radioactive phosphorus (P) from a nutrient solution. Within six hours, the P was present in every tiller. Troughton (1960) argues that tillers within a plant should not be regarded as independent units, but the plant must be considered as a whole.

As tillers differ in their time of origin and size, they will not respond in the same way to environmental conditions, even when conditions are uniform for the whole plant. For example, very young tillers are particularly vulnerable to stresses (e.g. drought and nutrient deficit) because they have only just begun to produce adventitious roots and are thus still dependent on their parent tiller. As emerging daughter tillers are in competition with other sinks for energy reserves, they are often sacrificed to allow continued leaf growth if resources are limited (Langer 1973).

Perennial grasses are capable of tillering at any time of the year, although seasonal growth patterns do exist. Autumn growth is dependent on the number of vegetative tillers produced at the end of the summer by plants that have survived the winter/spring, as the new season's growth is initiated by these tillers (Knight 1965). There is almost continual death and replenishment of tillers on the same plant, and therefore within a pasture (Langer 1973). The life span of a tiller is generally less

than a year (Langer 1979). However, it is possible for a tiller to behave as an annual, a biennial, or to remain vegetative (Langer 1990). The response of individual tillers is of great importance, as it determines the extent of growth, production and survival of a perennial grass plant.

2.2.3 Reserves

Plant reserve substances have been defined by Weinmann (1948), May (1960) and White (1973) as carbohydrate and nitrogenous compounds, which after being formulated by the plant, are stored to provide energy for future maintenance and growth. Other studies have shown that while nitrogenous compounds are used in respiration, they are not stored and utilised as are carbohydrate reserves, and are not as important as carbohydrates in supporting growth (Alberda 1966; Smith and Silva 1969; Wilson and Robson 1970). The findings of Davidson and Milthorpe (1965, 1966a) confirm that substances other than carbohydrates are used in respiration and new growth, and that these substances, presumed to include nitrogenous compounds, are mobilized rather than stored as reserves. Non-structural carbohydrates are generally recognised as the primary reserves (Troughton 1957), and include the monosaccharides glucose and fructose, the disaccharides sucrose and maltose, and the polysaccharides fructosan and starch (Smith 1973).

Polysaccharides are present in higher concentrations than the monosaccharides and disaccharides, and fructosan is the predominant reserve carbohydrate accumulated by temperate pasture plants. For example, ryegrasses contain mainly fructosan, as well as small quantities of sucrose, glucose and fructose (Weinmann 1948). These reserve carbohydrates are collectively referred to as water soluble carbohydrates (WSC).

According to De Cugnac (1931; cited in Weinmann 1948), two groups of grasses exist – identified by the type of reserve carbohydrates accumulated. Plants in the first group [including perennial ryegrass, cocksfoot, tall fescue (*Festuca arundinacea* Schreb.) and timothy (*Phleum pratense* L.)] accumulate fructosans, usually with sucrose, but no starch in their vegetative organs, while the second group [including heath falsebrome (*Brachypodium pinnatum* L.), bermuda grass (*Panicum dactylon* L.) and reed grass (*Spartina polystachya* Michx.) store sucrose with or without starch, but no fructosan. De Cugnac (1931) tentatively suggested the grasses accumulating

fructosan are generally native to cool, temperate climates, and the grasses storing sucrose and starch are generally adapted to warm regions.

In the past, many scientists assumed underground organs to be the major storage region for carbohydrate reserves (Weinmann 1948; Troughton 1957). However, further studies have clearly shown that the main storage region for WSC reserves in grasses is in tiller bases, herein termed 'stubble' (Sullivan and Sprague 1943; Baker and Garwood 1961; Marshall and Sagar 1965; Davidson and Milthorpe 1966a; Vartha and Bailey 1980).

Vartha and Bailey (1980) investigated the tissue location of soluble carbohydrates in Westerwolds ryegrass (*Lolium multiflorum* L.) in winter. The separation of aboveground tissues into leaf and stubble (2.5 cm above ground level) confirmed that the location of soluble carbohydrates was in the stubble and that the percentage in roots was relatively low. Fluctuations of reserves in the stubble were much greater than in leaf or root tissues. Marshall and Sagar (1965) determined that non-structural carbohydrates in the roots of Italian ryegrass were not mobilised to the shoots to support regrowth following defoliation. They concluded that "the classical view of a transference of compounds from root to shoot following defoliation (Troughton 1957) therefore seems unlikely to be correct in perennial grasses without special storage organs" (p369). Davidson and Milthorpe (1966a) found that the decrease of carbohydrate reserves in cocksfoot roots following severe defoliation could account for less than one tenth of the carbohydrate requirements for root respiration.

Stored reserves are essential for plant development, particularly when there are interruptions to photosynthetic activity (as occurs with defoliation) and the current energy supply is unable to meet plant growth and maintenance requirements. The role of WSC reserves in regrowth following defoliation is discussed in Section 2.4.1. The involvement of WSC reserves in improving plant stress tolerance has also been shown, during periods of heat, frost and drought. The role of reserves during times of stress is possibly to promote rapid recovery after the stress, rather than actually protecting the plant against direct stress effects (Donaghy 1998).

The extent of WSC accumulation by plants depends on the balance between photosynthesis on the one hand and respiration, plant growth rate, stage of development and on environmental conditions on the other (White 1973). When plants are actively growing, WSC reserves are lower than when plant growth is slow, as WSC reserve requirements for growth are greater than WSC supplied by photosynthesis.

In the leaf, WSC concentration fluctuates diurnally, largely due to changes in sucrose content (Waite and Boyd 1953; Kingsbury 1965). In the United Kingdom (Waite and Boyd 1953), New Zealand (Kingsbury 1965) and Australia (Fulkerson and Slack 1994a), WSC reserves in perennial ryegrass plants were found to peak in mid-afternoon and decrease during the night. Fulkerson and Slack (1994a) reported an increase in leaf WSC levels of around 0.5% per hour throughout a sunny day. Similarly, diurnal WSC reserve fluctuations have been recorded in the United States for lucerne (*Medicago sativa* L.), tall fescue, brome grass (*Bromus inermis* L.) and Kentucky bluegrass (*Poa pratensis* L.) (Curtis 1944; Holt and Hilst 1969).

Seasonal conditions that promote photosynthesis and reduce respiration result in the greatest accumulation of WSC reserves. In New Zealand, Kingsbury (1965) noted that the seasonal concentration of WSC in perennial ryegrass was greatest after a sunny afternoon in early winter. Vartha and Bailey (1980) recorded a depression in the WSC concentration in biennial ryegrass during an overcast period. During winter, when there is sunshine but low temperatures (minimising respiration), WSC concentration is usually highest (Donaghy 1998).

Generally, high temperatures result in low levels of WSC reserves, as loss of carbohydrates through respiration exceeds production of carbohydrates through photosynthesis (Alberda 1965). In a controlled environment, Baker and Jung (1968) grew timothy, brome grass, cocksfoot and Kentucky bluegrass and found that WSC reserves declined to a greater extent under high night temperatures (up to 18°C) than under high day temperatures (up to 35°C). This can be explained by the increase in photosynthesis that is associated with high day temperature. Increasing day temperature causes an increase in photosynthesis as well as respiration, while

increasing night temperature (or increasing day temperature above the optimum for grass growth) only increases respiration (White 1973).

Levels of WSC reserves are generally lower in younger tissue (tiller and leaf tips) than in mature plant tissue (tiller and leaf sheath). As the proportion of stem material increases with maturity, WSC concentration increases (Smith 1973). In the United Kingdom, a field study by Waite and Boyd (1953) showed that in the stubble of perennial ryegrass plants, WSC reserves accumulated during stem elongation and then declined as the seed head formed – the sucrose converting to starch for storage in the seed. The same pattern was reported by Griffith (1992) in biennial ryegrass and by Sprague and Sullivan (1950) in cocksfoot. Additionally, in perennial ryegrass, Fulkerson and Slack (1994a) recorded an increase in WSC reserves within a regrowth cycle from approximately 4% at the 1-leaf stage, to 15% at the 3-leaf stage.

2.2.4 Roots

The root system of a grass plant is comprised of both seminal and adventitious roots. Seminal roots are the first to develop and are essential for the establishment of a young plant. However, they account for only 5% of the overall root mass of both annual and perennial grasses during the first year of growth (Langer 1979). Seminal roots are very efficient absorbers on a unit weight basis, but they are not abundant enough to satisfy a plant's water and nutrient needs. More specifically, Cornish (1982) found that the xylem cross-sectional area of the subcoleoptile internode of seminal roots is generally not adequate to supply sufficient water to developing seedlings.

Successful establishment of grass seedlings requires the development of adventitious roots, which arise from nodes and become the principle absorbing system (Langer 1973). These roots have larger xylem vessels than seminal roots and are essential for good seedling water relations (Cornish 1982). Heavy branching, particularly in the upper soil horizons, makes the adventitious root system suitable for efficient uptake of top-dressed fertiliser (Nelson and Moser 1995). With each tiller capable of producing its own adventitious roots, the grass plant forms its typical fibrous root system (Langer 1973).

Aguirre and Johnson (1991) drew attention to the need for further research to characterise seedling root morphology of pasture grass species and to relate these characteristics to shoot development. The authors utilised the methods of Klepper *et al.* (1981, 1984) (developed for wheat) to identify the individual axes of seminal and adventitious roots of four popular range grasses of the Western United States, and related their findings to shoot development. The pattern of root and shoot development was similar in the four species, with early initiation of root elongation and branching (both seminal and adventitious) relating to enhanced above-ground growth. One of the significant barriers to use of cocksfoot in temperate pastures of southern Australia is slow establishment compared with perennial ryegrass. It would be valuable to assess the possibility that delayed seedling development of this species in the field may be related to root growth patterns.

Species differ in the depth and distribution of roots, in both seedling and mature phases of growth (Nelson and Moser 1995). Sanderson *et al.* (2002) compared the seedling growth and development of prairie grass, grazing brome grass (*B. stamineus* Desv.) and cocksfoot in controlled environment cutting studies. Matua prairie grass developed a greater root mass and length earlier than cocksfoot, while cocksfoot had a greater number of roots than Matua or grazing brome grass at the conclusion of the study (75 days following sowing). Shaffer *et al.* (1994) studied root growth of prairie grass, tall fescue and smooth brome grass during establishment using a mini-rhizotron technique. Prairie grass showed an ability to rapidly establish nodal roots at greater depth, resulting in more uniform root distribution than the other two cool-season forage grasses.

Evans (1977) compared the root morphology of established cocksfoot and perennial ryegrass plants under controlled conditions and found that cocksfoot roots extended deeper into the soil, while the diameter of perennial ryegrass roots was greater. In this study, the overall surface area (determined from both length and diameter measurements) of perennial ryegrass roots was lower than for cocksfoot (Table 2.2). Ridley and Simpson (1994) also measured relatively dense cocksfoot roots at a depth of 100-500 mm. In contrast, McKenzie (1996) assessed the effect of grazing frequency and intensity on root production of perennial ryegrass under subtropical conditions in South Africa and measured approximately 75% of its root mass in the

surface 50 mm of soil. In subtropical Australia, approximately 95% of total root DM for perennial ryegrass was present in the surface 50 mm of soil in summer and autumn, regardless of whether a 1-leaf or 3-leaf defoliation treatment was employed (Donaghy and Fulkerson 2002). In agreement with this pattern, Steynberg *et al.* (1994) observed shallow rooting in Italian ryegrass.

Table 2.2 Root length and surface area per unit weight and root diameter for perennial ryegrass and cocksfoot (adapted from Evans 1970).

Species	Length per unit weight (cm/mg)	Mean diameter (mm)	Surface area per unit weight (mm ² /mg)
Perennial ryegrass	30.6	0.19	181
Cocksfoot	44.4	0.16	220

In cocksfoot and brome grass, Oswalt *et al.* (1959) found that N fertilisation (168 kg/ha) generally increased the weight of shoots and decreased the weight of roots. As the rate of N was increased (168-673 kg/ha), root diameter was increased, but the number of roots and rate of elongation decreased. Oswalt *et al.* (1959) suggested that the inhibition of root elongation under N fertilisation caused the plants to feed near the soil surface for a longer period of time.

Brouwer (1966) identified carbohydrate supply as the limiting factor in root development in rapidly growing plants. Extension growth is particularly responsive to changes in the supply of carbohydrates. For example, on defoliation (a sudden decrease in the surface area of photosynthetic tissue), root growth is reduced immediately and even when stubble reserves are high, root growth quickly slows down (Brouwer 1966). The effect of defoliation on root growth is described in more detail in Section 2.4.3. Similarly, when the rate of photosynthesis slows down due to low light intensity, the interrupted carbohydrate supply disrupts root growth. With increasing light intensity, both shoot and root growth accelerates, but according to Brouwer (1966), root growth accelerates to a greater extent than shoot growth.

There is no consensus in the literature regarding the seasonal pattern of root replacement in perennial grasses. One popular view is that the root system of these grasses is replaced annually (Stuckey 1941; Jacques 1956; Jacques and Schwass

1956; Caradus and Evans 1977), while a contrasting view supports continuous root turnover (Garwood 1967; Troughton 1981; Matthew 1992). In autumn and winter a greater proportion of photosynthates are partitioned to root growth (Davidson 1978). This is evident in the increased formation of new adventitious roots from autumn to spring, as observed by supporters of both views (Stuckey 1941; Jacques 1956; Jacques and Schwass 1956; Caradus and Evans 1977; Matthew 1992).

Donaghy and Fulkerson (1998) established the priority for WSC reserve allocation following defoliation of perennial ryegrass, and this ranking explains increased growth rates of roots under low temperature conditions. The priority for energy reserves in the grass plant follows the order of respiration, leaf growth, recommencement of WSC reserve accumulation, root growth, tiller initiation and lastly, full replenishment of stored WSC reserves. Under cool conditions, respiration rates are low and therefore more energy is available for the remaining plant growth functions. Energy is directed into leaf growth, root growth and replenishment of WSC reserves, as tiller initiation does not generally take place during winter due to its dependence on light and higher temperatures.

According to the annual replacement theory, most 'old' perennial ryegrass roots disintegrate just after the new ones develop in late autumn. This species was therefore said to possess an 'annual root system', while slower and longer surviving cocksfoot roots were labeled 'perennial' (Stuckey 1941; Caradus and Evans 1977). Jacques' description of annual pattern of root formation and replacement for perennial ryegrass is represented diagrammatically in Figure 2.2.

A significant criticism of Jacques' (1956) description of root replacement in perennial ryegrass is that it "presents only a conceptualized diagram without data" (Matthew 1992, p15). Data derived from direct measurement of individual roots support the view that roots are continually replaced throughout the year (Garwood 1967; Troughton 1981; Matthew 1992). While earlier work showed that root formation did not occur during summer under New Zealand conditions, Matthew (1992) observed continual root production during late spring and a growth peak in early summer. Such results support the hypothesis that perennial grass roots may be replaced at a more frequent rate than previously recorded (Garwood 1967; Troughton

1981; Ridley and Simpson 1994). With roots arising from individual tillers, one would expect the lifespan of these roots to coincide with part or all of the lifespan of the associated tillers, and not for longer than the tiller lifespan, explaining the rapid root turnover described by Matthew (1992).

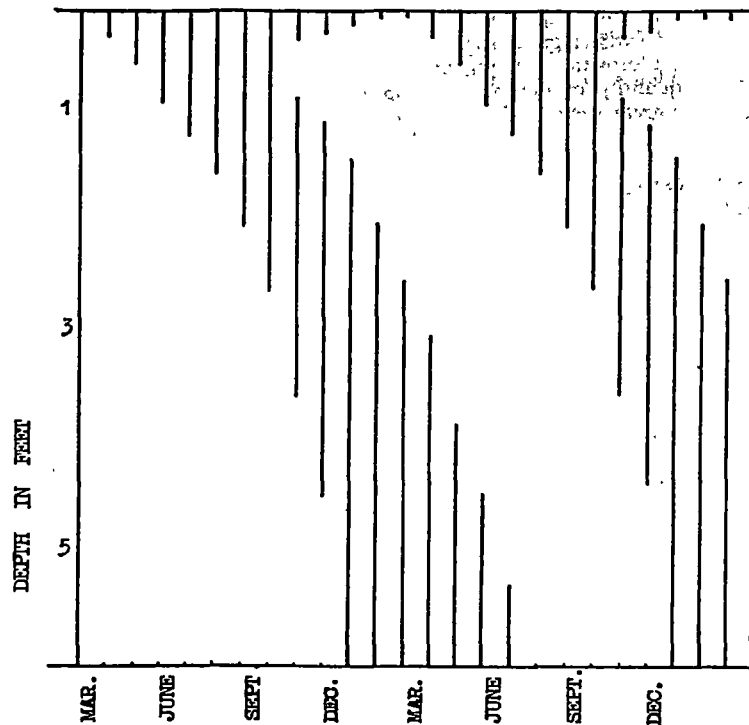


Figure 2.2 Idealised diagram indicating regions of absorption of perennial ryegrass roots. The lines show the region where absorption is taking place, the blanks represent where cortex deterioration or where death through rising water table or redundancy have taken place (source: Jacques 1956).

Garwood (1967) recorded growth of perennial ryegrass roots for no longer than eight months before cortex deterioration commenced. The considerable period of time required for root disintegration to reach completion was suggested as a possible explanation for claims of greater root longevity based on dry weight measurements. In this study, care was taken to simulate conditions under grazing, through the use of 6-year old pasture swards and defoliation at 4-week intervals (immediately following sampling). Garwood (1967) warns that patterns of observed root growth for newly established plants, singly spaced plants (rather than swards) and undefoliated plants

may not be an accurate representation of seasonal variation in the root growth of pastures under grazing.

2.3 Herbage quality

The quantity of forage DM consumed each day is the most important factor limiting animal production (Minson 1987). Provided that no mineral deficiencies exist and excess forage is available, the quantity of DM consumed depends on the quantity of indigestible fibre in the forage and the physical form of the fibre (Minson 1987). Voluntary intake is therefore correlated with the digestibility of herbage on offer (Blaxter 1960; Freer 1981). However, Minson (1987) stated that this relationship is a broad generalisation that breaks down in some situations. For example, an important point of contention about this general relationship has been the range of herbage quality over which it applies. Freer (1981) pointed out that senescent herbage, with a digestibility of less than 40%, often possesses low N and mineral levels, which act to limit microbial activity in the rumen. At the opposite end of the range, when forage is of high digestibility, voluntary intake may be controlled by physical factors, such as metabolic size of the animal, rather than the energy requirements of the grazing animal (Conrad *et al.* 1964). While the primary requirement for maintenance of dairy cattle is for energy-yielding nutrients, there are specific requirements for amino acids, glucose, fatty acids, minerals and vitamins, which depend on the stage of development, size, type and level of production of the animal (Beever *et al.* 2000).

2.3.1 Minerals and vitamins

Optimal animal production requires feed with a balance of nutrients including minerals and vitamins. Beever *et al.* (2000) explained that fresh herbage generally contains adequate levels of fat-soluble vitamins (A, E and K) to meet the requirements of ruminants. Additionally, rumen bacteria are able to synthesise sufficient quantities of the B vitamins, and vitamins C and D can be synthesised by the animal (provided the animal has sufficient exposure to sunlight in the case of vitamin D).

Herbivores require 21 mineral elements and of these, potassium (K), chlorine (Cl), iron (Fe), molybdenum (Mo), cadmium (Cd), lithium (Li) and nickel (Ni) are usually present in forages in quantities sufficient to largely satisfy the needs of a ruminant

(Buxton and Mertens 1995). Minson (1990) describes the quantities of minerals contained in herbage and their utilisation by ruminants in detail.

The minerals of highest importance in the diet of a dairy cow are calcium (Ca), P, magnesium (Mg), sodium (Na), K, sulphur (S) and Cl. When a deficiency of one of these essential elements occurs, a specific deficiency symptom or metabolic disorder may develop, and a lowered growth rate or reduced milk production will almost certainly result. The mineral requirements of a lactating cow are shown in Table 2.3.

Table 2.3 Estimates of the mineral requirements (g/kg DM) for a lactating cow (Adapted from Holmes and Wilson 1984).

Milk yield (l/d)	Live weight change (kg/d)	Intake (kg DM/d)	Ca	P	Mg	K	Na	Cl
25	-0.5	14.8	3.9	3.9	2	54	1.2	2.4
15	0	11.9	3.3	3.2	1.3	54	1.0	1.9
10	0.5	11.4	3.5	3.1	1.1	40	0.9	1.5

2.3.2 Protein

The N contained in herbage can be divided into true protein and non-protein N (NPN). True protein generally comprises 60-80% of herbage N. The NPN is largely composed of nucleic acids, free fatty acids, amides and nitrate (Buxton and Mertens 1995). The simplest expression of the protein content of forage is crude protein (CP) (Minson 1987), which is the sum of true protein and NPN, expressed as CP equivalents ($N \times 6.25$). Highly producing, lactating dairy cows require a CP concentration of 190 g/kg DM (Buxton and Mertens 1995).

Crude protein in leaf blades is generally twice that of stems and is present in higher concentrations in immature tissues than mature herbage. In fact, Minson (1990) studied CP concentrations in a range of grass species and reported a decrease with advancing forage maturity at a mean rate of 0.22%/d. The level of available N in the soil influences the CP concentration of grass herbage. Nitrogen fertilisation therefore significantly alters CP concentrations, and under moderate to high rates of N during spring growth in temperate areas, Buxton and Mertens (1995) suggest the protein concentration of immature grasses may well be higher than the means reported by

Minson (1990). Interestingly, an increase in CP is usually accompanied by a decrease in WSC concentration (Buxton and Mertens 1995). This can be explained by the stimulatory effect of N on growth and the subsequent use of WSC reserves in the development of structural material and in respiration. However, the larger leaves that result from applied N have increased photosynthetic capacity, eventually restoring WSC reserves.

2.3.3 Energy

The net energy value of feed is the proportion of forage that can be utilised by the ruminant for maintenance and production (Minson 1987). For a lactating cow, the principal need for energy is to meet body maintenance requirements. As energy increases above a maintenance level, it is either stored in body tissue or used in the production of milk. Carbohydrates, proteins and lipids are the nutrients in plants which provide most of the energy that sustains animal production. Carbohydrates provide up to 80% of the energy used by grazing ruminants (Buxton and Mertens 1995).

Available energy is inversely related to the cell wall content in herbage. While plant cell contents are almost entirely available to ruminant livestock, the availability of plant cell walls varies considerably with wall composition and structure (Van Soest 1982). As stems have a higher concentration of cell walls than leaves in most forages, stems have lower digestibility than leaves (Buxton and Mertens 1995). The digestibility of forage is more important in determining energy availability to animals than its gross energy. Variation in digestibility between temperate grasses is often a determining factor for farmers in the selection of grass species for animal production systems.

Terry and Tilley (1964) determined the *in vitro* DM digestibility (IVDMD) of the leaf blade, leaf sheath and stem fractions of perennial ryegrass, cocksfoot, timothy and tall fescue, and found that each fraction had a high digestibility during early stages of growth. With increasing maturity, stem digestibility declines at a far more rapid rate than leaf digestibility, while leaf sheath digestibility decreases at an intermediate rate. Decreased digestibility is associated with a reduced content of

water-soluble and protein constituents in the plant, as well as a reduction in the digestibility of fibre (Terry and Tilley 1964).

Before ear emergence, the digestibility of cocksfoot and ryegrass fell gradually (0.2% per day), compared to after ear emergence (0.5%). Terry and Tilley (1964) suggested that these patterns may be explained by changes in the proportions of leaf blade, leaf sheath and stem with increasing maturity, combined with the different rates of decline in digestibility of these fractions. Prior to ear emergence, leaf blade is the most predominant fraction, which declines in digestibility the most slowly (0.2% per day). The stem is the main fraction following ear emergence, and declines in digestibility the most rapidly (0.8%).

Duru *et al.* (1999) examined the digestibility of cocksfoot whole blade and blade segments under three defoliation treatments. The digestibility of the youngest fully expanded lamina decreased with each successive leaf, with the greatest decrease associated with the least frequent defoliation. A consistent decline in lamina digestibility from tip to base was also reported. The decreasing digestibility of successive leaves (Wilson 1976; Ducrocq and Duru 1997; Duru *et al.* 1999) is explained by the increasing proportion of sclerenchyma and vascular tissue with increasing insertion level of a leaf on the tiller (Ducrocq and Duru 1997). This in turn may be related to an increase in the maximum length of the leaf blade with each successive leaf (Wilson 1976).

In a number of studies, herbage quality has been found to increase with grazing severity in rotational (Kristensen 1988) and continuous (Binnie and Chestnut 1994) grazing systems. Duru *et al.* (1999) argue that these differences could have resulted from differences in the digestibility of green laminae, rather than a lower proportion of stem and less mature leaf material. Although this trend may hold true, it would be unwise for a producer to adopt severe grazing patterns solely in the hope of increasing herbage quality. As discussed in Section 2.4.1, severe defoliation (frequent and/or close defoliation) can exhaust plant carbohydrate reserves and lead to an inability to recover from grazing, lack of sward persistence, and in extreme circumstances, to plant death.

Ducrocq and Duru (1997) investigated the changes in green lamina digestibility during regrowth in relation to water deficit. The decrease in digestibility with increased leaf insertion level was smaller for water stressed plants, and was associated with a greater reduction in leaf appearance rate and a smaller increase in the length of successive leaves. Water stress reduced growth and delayed plant development, which seemed to be responsible for differences in herbage digestibility.

Chemical changes in spring-grown compared with autumn-grown grass reflect differences in morphology. Plants without flower stalks in autumn generally possess lower crude fibre and lignin contents and are more digestible than plants with a high proportion of stem in spring (Brown *et al.* 1963). Brown *et al.* (1963) investigated changes in the digestibility of leafy tall fescue regrowth in autumn and measured a significant increase in WSC. Mean temperatures decreased in autumn and consequently the growth rate of fescue decreased. The rate of respiration and new tissue synthesis may have decreased more rapidly than the rate of photosynthesis as a result of reduced temperatures and light conditions, leading to an accumulation of WSC reserves in stem bases.

Wilson and Ford (1973) examined a wide range of tropical and temperate grass species to compare the effects of temperature on IVDMD and the concentration of soluble carbohydrates. The content of total soluble carbohydrates (TSC) was found to be higher for temperate than tropical grasses under all temperatures. The biochemistry of C₄ plants may influence conditions for carbohydrate accumulation in tropical grasses and partly explain this difference. Wilson and Ford (1973) suggest that the effects of temperature on digestibility are worth considering in relation to the changes in TSC concentration. In 10 of the 11 temperate species examined, the fall in TSC concentration with temperature was equal to or greater than the decrease in digestibility concentration. With soluble carbohydrates being completely digestible, a relationship between the two parameters is likely.

In Australia, metabolisable energy (ME) is the recommended method of expressing the energy value in feed, because it eliminates the variation caused by form of production (Minson 1987). The main factors affecting ME concentrations are those that influence digestibility of feed. The fibre content of herbage has the greatest

effect on digestibility and can be separated into two fractions through a process involving the boiling of a small sample for an hour, before filtering (Van Soest 1982). After filtering, the insoluble material is known as neutral detergent fibre (NDF) – the cell wall fraction which includes hemicellulose, cellulose, lignin and some ash. The acid detergent fibre (ADF) fraction consists of cellulose, lignin and silica. The difference between the NDF and ADF percentages is accepted as an estimate of hemicellulose. As mentioned previously, cell wall content (or NDF) and available energy are inversely related. The concentration of NDF in diets of highly producing dairy cows should be in the range of 270-290 g/kg DM, to allow for adequate energy and also to maintain adequate fibre in the diet (Buxton and Mertens 1995).

2.4 Regrowth following defoliation

As in White (1973), the effects of defoliation on plant regrowth have been classified into three simplified categories. In this section the impact of defoliation on WSC reserves, leaf area/tillering and root growth are discussed, as well as their roles in consequent regrowth.

2.4.1 WSC reserves

Upon defoliation, the plant's source of carbohydrates is suddenly removed and a temporary carbohydrate shortage occurs, inducing utilisation of stored soluble carbohydrates for growth and respiration (Davidson and Milthorpe 1966a). It is generally agreed among investigators that carbohydrate reserves located in the stubble are utilised as an energy source to initiate new growth of perennial grasses until photosynthesis is sufficient to sustain plant respiration (White 1973). Following severe defoliation, carbohydrate reserves in both stubble and roots generally decline for an initial period, then increase when new photosynthetic tissue is able to produce carbohydrates in excess of those required by current growth (Sullivan and Sprague 1943; Alberda 1960).

Sullivan and Sprague (1943) studied carbohydrate changes in stubble and roots of perennial ryegrass under glasshouse conditions, for 36 days following partial defoliation. Water-soluble carbohydrates, including glucose, fructose, sucrose and fructosan, decreased rapidly in stubble and roots for several weeks before rising

again. During the same period, considerable growth of foliage and roots took place, and these changes were interpreted as being due to utilisation and then re-storage of WSC reserves.

In 1960, May reassessed the role of carbohydrates in pastures, arguing that a reduction in carbohydrate percentage following plant defoliation does not necessarily imply a causal role for these reserves in initiating or promoting regrowth. May (1960) advised that results in many circumstances only warrant the more general conclusion that a decrease in non-structural carbohydrates can be largely accounted for by their use in respiratory substrate, and that the remainder would be available for translocation and synthesis at new growing points.

In 1965, Davies countered May's (1960) argument that carbohydrate reserves are merely accumulates (not necessarily related to regrowth following defoliation), with a study in which short-term treatments were used to establish a range of carbohydrate levels in stubble, without affecting plant size. Results showed that plants subjected to treatments did show differences in recovery following defoliation and that leaf growth and the onset of tillering after defoliation were associated with the level of carbohydrates present in the stubble at the time of cutting. Similarly, Alberda (1966) found that the weight of perennial ryegrass with low carbohydrate reserves did not increase for seven days following defoliation, while the weight of plants with high carbohydrate reserves took only four days to increase.

Davidson and Milthorpe (1965, 1966a, 1966b) measured the respiratory and photosynthetic rates for cocksfoot plants in growth chambers, and concluded that regrowth following defoliation relied on reserves for only two to four days. After this period, regrowth depended on other factors, such as rate of photosynthesis and nutrient uptake. During the first four days following severe defoliation of cocksfoot (all leaf blades removed and sheaths cut to 25 mm), photosynthesis almost exactly equalled respiration so that no net contribution to new growth was made. The dry weight of regrowth equalled the weight lost from roots and stubble. Wilson and Robson (1970) showed similar results with ryegrass plants.

Booyesen and Nelson (1975) measured a reduction in the quantity of stubble WSC reserves in tall fescue during the first three to four days of regrowth. At around eight days, replenishment of these reserves commenced. Using the same pasture species, Volenec (1986) observed decreases in all non-structural carbohydrate fractions to approximately half their original concentrations at four days following defoliation to a height of 75 mm (Table 2.4). Reducing and non-reducing sugars significantly increased by the 14th day of regrowth, while concentrations of starch and fructan remained relatively low until the 21st and 24th day of regrowth, respectively.

Table 2.4 Changes in concentration of non-structural carbohydrates of intact stem bases of tall fescue during regrowth (source: Volenec 1986).

Days of regrowth	Reducing sugars (g/kg structural)	Non-reducing sugars (dry weight)	Starch	Fructan	Total non-structural carbohydrates (TNC)
0	13.3	41	65	715	834
2	6.1	27	54	632	719
4	5.2	20	38	454	517
7	9.7	18	40	362	430
10	9.2	25	43	491	568
14	13.0	35	47	461	556
17	13.5	28	42	330	414
21	12.9	31	51	460	556
24	15.3	35	61	661	772
Mean	10.9	29	49	507	596
BLSD†	5.1	7	11	235	244

† Bayes least significant difference between means at the 5% level of probability (k-ratio = 100)

Gonzalez *et al.* (1989) measured changes of non-structural carbohydrates in stubble of defoliated ryegrass plants over a 28-day period, and observed a clear two-phase response. During the first six days following defoliation, there was a rapid decrease in sugar content in stubble (4.4% reduction), with 74, 87, 78, 91 and 61% of fructose, glucose, sucrose, oligo-fructans and poly-fructans mobilized. From 6 to 28 days, a rise in tissue content of carbohydrate fractions coincided with the development of foliage and tillers, and initial reserve levels were almost resumed.

Danckwerts and Gordon (1987) exposed the youngest leaves of single tillers of vegetative perennial ryegrass plants to ^{14}C and quantitatively analysed the partitioning, storage and re-mobilisation of the ^{14}C -labelled assimilate for 22 days after defoliation. The advantage of this technique is the ability to differentiate between current photosynthate, short-term storage products and long-term carbohydrate reserves. The following findings prove beyond doubt, that carbohydrate reserves in stubble are associated with regrowth following defoliation:

1. Depletion of reserve ^{14}C from stem bases was greater from defoliated plants compared with undefoliated plants.
2. A portion of depleted ^{14}C was incorporated into new growth after defoliation.
3. Incorporation continued for some days after defoliation, despite the fact the plant had produced a substantial amount of new photosynthetically active tissue.

The fact that depletion of labile ^{14}C from roots and stem bases of defoliated plants was greater than the total ^{14}C recovered in new growth confirms previous conjectures that some of the reserves depleted after defoliation are used in respiration. The authors concluded that defoliation results in greater depletion of reserves than occurs under undisturbed conditions, through re-mobilisation and utilisation of carbohydrates in regrowth.

Utilisation of reserves following defoliation largely depends on mobilisation and translocation processes. May (1960) suggested that a 'mobilising' hormone may trigger the initiation of carbohydrate movement and notes the lack of evidence in support of carbohydrate concentration initiating mobilisation. However, concentration gradients appear to influence translocation (rate and direction) of sugars through phloem tissue following defoliation.

While the rate of regrowth has been shown to be influenced by leaf area (Davies 1974; Section 2.4.2) and WSC reserves in the stubble (Alberda 1966), WSC reserves are affected by the interval between defoliations (Fulkerson *et al.* 1994) and defoliation severity (Troughton 1957).

Grant *et al.* (1981) conducted a grazing study in which ryegrass swards were grazed for 12-day periods with stock numbers set to result in heavy, medium and light grazing (removal of 64, 32 and 16 kg organic matter/sheep). Grazing of one area occurred in summer and another in autumn. In summer, WSC reserves in plants of heavily grazed pasture showed signs of recovery by the 8th day of the regrowth period. In autumn however, particularly under warm, low-light conditions when WSC reserves were generally declining, defoliation had a longer lasting effect.

Fulkerson and Slack (1995) confirmed the findings of Davies (1965) – that frequently cut ryegrass plants have a lower WSC concentration in leaf and stubble than plants cut less frequently. When perennial ryegrass was defoliated three times at the 1-leaf regrowth stage, compared with once at the 3-leaf stage, stubble WSC reserves were reduced from 17.5 to 2.5% (Fulkerson and Slack 1995). When perennial ryegrass plants were subsequently cut at the 3-leaf stage compared to the 1-leaf stage of the regrowth cycle, WSC reserves were quickly restored close to initial levels and DM production was maximised (Fulkerson and Slack 1995).

Davidson and Milthorpe (1966a) measured CO₂ exchange of roots and shoots and changes in soluble carbohydrates during eight days following defoliation of cocksfoot plants. Results emphasised the impact of defoliation severity on WSC reserves and the possibility that other substances may also be mobilised for growth and respiration following removal of photosynthetic tissues. When only leaf blades were removed, changes in WSC reserves could account for net respiratory losses and the extent of regrowth that took place. However, with defoliation to 25 mm, even high concentrations of WSC reserves were inadequate for respiration and new growth, and the authors suggest other substances (i.e. proteins) must have been re-mobilised for this purpose.

The results of a study carried out by Wilson and Robson (1970) showed that the DM regrowth of S24 ryegrass plants cut to a stubble height of 60 mm was equal to the weight increase of uncut plants. While the weight of the 0-20 mm stubble segment of plants cut once to 20 and 40 mm stubble height decreased during the four days immediately following defoliation, the weight of stubble of plants cut to 60 mm was maintained or increased. The WSC concentration of the 0-20 mm stubble segment

was inversely related to the severity of the cutting treatments, with 26% WSC reserves in uncut plants, compared with 16% in plants cut once to 100 mm, and 4% in plants cut once to 20 mm.

Response to defoliation management differs between species. The recommended defoliation interval for perennial ryegrass is the 2- to 3-leaf regrowth stage and cutting to a stubble height below 50 or 60 mm adversely affects subsequent regrowth. For prairie grass, frequency of defoliation is also of great importance in relation to regrowth, with four to five leaves per tiller recognized as the optimal defoliation interval. Defoliation interval is generally of primary importance, followed by stubble height - of secondary importance (Bell and Ritchie 1989; Fulkerson and Donaghy 2001). Hume (1991a) found that when prairie grass was cut at four-week intervals (which coincided with the production of four to five leaves), there was no significant difference in regrowth between plants cut to 30 mm and plants cut to 60 mm stubble height.

Donaghy and Fulkerson (1998) conducted a study to determine the priority of the ryegrass plant for leaf growth, root growth and tiller initiation following defoliation. Variable levels of stubble WSC reserves were obtained through different defoliation intervals (1-leaf versus 3-leaf stage), exposure to different ambient night temperatures for one week prior to defoliation (8°C versus 20°C) and different defoliation heights (20 versus 50 mm). Regrowth responses were interpreted in relation to both quantitative and timescale effects. In a time sequence, the priorities for WSC reserve allocation were in the descending order: leaf > root > daughter tiller, as evidenced by the order in which growth of these organs commenced. These findings agree with those of Jacques (1937), who recognised that following defoliation, the strongest demand for food reserves is the replenishment of photosynthetic tissue. Donaghy and Fulkerson (1998) found that sensitivity to low levels of WSC reserves in terms of the absolute effect on growth was greatest for root elongation and survival, followed by tiller initiation and leaf growth. Root elongation was 59 times higher in plants with high WSC concentrations compared with low concentrations (1.18 versus 0.02 mm/d).

As well as inhibiting current herbage growth, the depletion of reserves by severe defoliation may have long term effects, with diminished productivity during the years following cutting or grazing (Weinmann 1948). Depletion of reserves below a critical level may lead to plant death, and on a large scale (e.g. a paddock), lead to invasion by undesirable grass and weed species (Biswell and Weaver 1933). Davies (1965) determined that concentrations of WSC reserves in stubble below 16-20% resulted in slowed regrowth.

Studies have generally shown that low to moderate rates of N application increase WSC reserves, and that moderate to high rates decrease reserves (White 1973). Gonzalez *et al.* (1989) observed recovery of stubble WSC reserves following defoliation and found that the final balance of carbohydrate fractions in N deficient plants differed to that of defoliated control plants (lower glucose and fructose).

Graber and Ream (1931) discovered that Kentucky bluegrass only utilised an abundance of N to produce more vegetative growth when height or frequency of defoliation maintained a productive level of WSC reserves. In the greenhouse, addition of N was found to aggravate the deleterious effects of frequent defoliation on the root system (Harrison 1934). Plants died when defoliated 14 times at weekly intervals when supplied with N, while plants under the same defoliation treatment but without N application survived. Roots and rhizomes decreased in size and weight under an abundant N supply (particularly when combined with optimal temperatures), presumably due to excessive mobilisation and exhaustion of WSC reserves to support rapid foliage growth.

Volenec (1986) examined changes in the concentration of WSC reserves in individual stubble tissues during regrowth. The discovery of short-chain fructans in the bases of elongating leaves compared to the long-chain fructans stored in leaf sheaths, prompted the suggestion that different purposes may exist for these compounds. In conclusion, Volenec (1986) stressed the importance of separating the tissues known for the storage role (outer sheaths) from the meristematic region (inner leaves) during studies focused on stored energy use.

Voltaire and Gandoin (1996) made similar recommendations following analysis of the consistency of the relationship between summer survival and WSC accumulation over time. While neither total WSC nor fructan contents of whole tiller bases could not be directly related to drought survival over two years of growth, the WSC content in live enclosed leaves during drought seemed to be associated with regrowth after drought (irrespective of sward age). Therefore, a focus mainly on the youngest enclosed leaves rather than on whole tiller bases may benefit further study of the relationship between reserve accumulation and drought survival.

Interestingly, the effect of grazing on regrowth is not identical to that of defoliation – it may be more or less detrimental, depending on the circumstances (White 1973). Grazing may be more detrimental than defoliation, if it removes all herbage from some plants and not from others in close proximity, as ungrazed plants draw available water and nutrients away from grazed plants. However, grazing may be less detrimental than defoliation if it leaves ungrazed tillers on a plant while removing others – allowing re-mobilisation of WSC reserves from ungrazed to grazed tillers (Marshall and Sagar 1965).

The most appropriate basis for evaluating WSC reserves is by weight in storage tissue. Concentration of WSC (measured as a percentage or g/kg on a DM basis) is not as reliable a measure, as small tillers with a high WSC concentration contain a smaller total amount of WSC than larger tillers with a lower WSC concentration. Additionally, WSC reserves generally reach an equilibrium concentration, regardless of the weight of storage tissue. Total amount of WSC (or content) is therefore a superior criterion than concentration of WSC for determining the importance of reserves for regrowth (Smith 1974; Booysen and Nelson 1975; Fulkerson and Slack 1995; Donaghy and Fulkerson 1998). Additionally, the regenerative capacity of perennial grasses is also related to tiller size, which is larger for cocksfoot than perennial ryegrass. Therefore, for any given WSC concentration, there is likely to be a significantly higher WSC content in cocksfoot than in ryegrass (Rawnsley *et al.* 2002).

May (1960) emphasises that care should be taken in the interpretation of results from defoliation studies. For example, the influence of climate may limit one's ability to

attribute variable WSC reserves in response to defoliation to species differences. Sullivan and Sprague (1949) discovered that carbohydrate losses following defoliation to 37 mm occurred rapidly under high temperatures, while losses were substantially lower at lower temperatures. Additionally, efforts should be made to eliminate error due to diurnal fluctuations in carbohydrate content by conducting sampling at a standard time (May 1960), for example, within three hours following sunrise (Fulkerson and Slack 1994a).

2.4.2 Leaf area and tillering

Following defoliation, the photosynthetic capacity of remaining tissue depends on the height of cutting, plant growth habit and the age of remaining leaves (White 1973). Davidson and Milthorpe (1966a) showed that the rate of photosynthesis of young cocksfoot leaf blades was about 2/3 higher than sheaths. Leaves appear to be most photosynthetically active on emergence from the sheath, the rate then decreasing with age (Jewiss and Woledge 1967; Treharne *et al.* 1968).

As alluded to in Section 2.4.1, various investigators have shown that the rate of regrowth of defoliated grass plants is interrelated with residual leaf area, as well as carbohydrate reserves (Ward and Blaser 1961; Smith 1974; Booysen and Nelson 1975). Ward and Blaser (1961) subjected individual cocksfoot tillers with high and low levels of carbohydrate reserves to different defoliation treatments (cutting to ground level versus 55 mm). The regrowth response of tillers was measured at intervals during a 35-day recovery period. Carbohydrate reserves were involved in stimulating regrowth up to 25 days after defoliation, evident by a decrease in reserves for several days, followed by an increase. After this period, regrowth rates were dependent on leaf area.

In a similar study, Booysen and Nelson (1975) evaluated the four combinations of high and low WSC reserves (HC and LC, respectively), and high and low residual leaf area (HL and LL) in terms of regrowth of tall fescue in a controlled environment at 20°C. Results indicated that leaf area was of greater importance in determining relative growth rates (increase of plant weight per unit of weight present per unit of time) following defoliation. During the first 10 days of regrowth, plants with high leaf area (HC/HL and LC/HL) continued growth at an appreciable rate, irrespective

of the level of WSC reserves (Figure 2.3). After 10 days, relative growth rate values for the four treatments were similar. However, the authors acknowledge that patterns of DM accumulation and relative growth rate of the total plant do not necessarily reflect the rate of production of harvestable herbage.

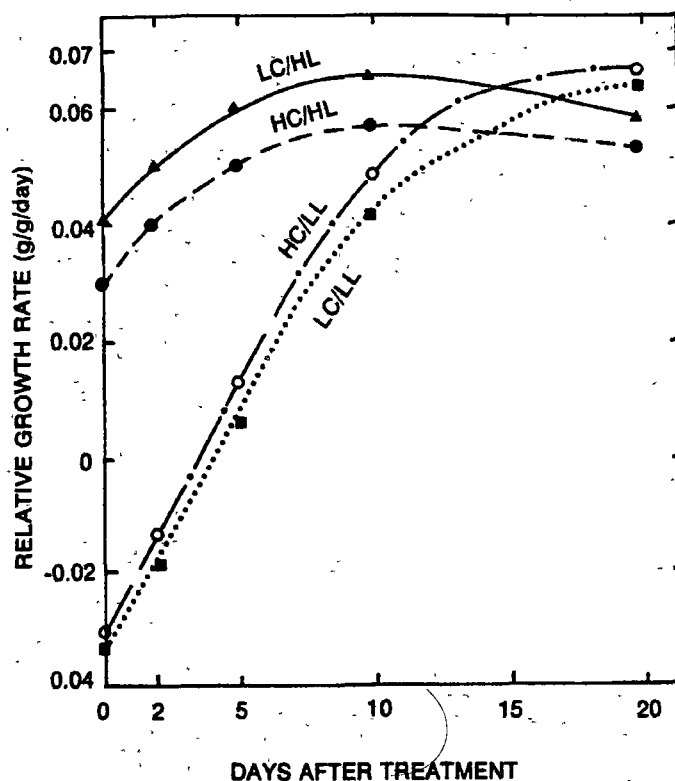


Figure 2.3 Relative growth of tall fescue plants during a 20 day regrowth period following treatments to obtain high and low WSC reserves (HC and LC) and high and low residual leaf area (HL and LL) (source: Booysen and Nelson 1975).

The pattern of leaf area development during regrowth was also monitored and interpreted as a reflection of the rate of regeneration of the plant's photosynthetic area (Booysen and Nelson 1975). As shown in Figure 2.4, the rate of leaf expansion was only reduced when both leaf area and WSC reserves were limiting (LL, LC), suggesting that the high leaf area (HL) and high carbohydrate (HC) treatments in this study were comparable energy sources for plant regrowth following defoliation.

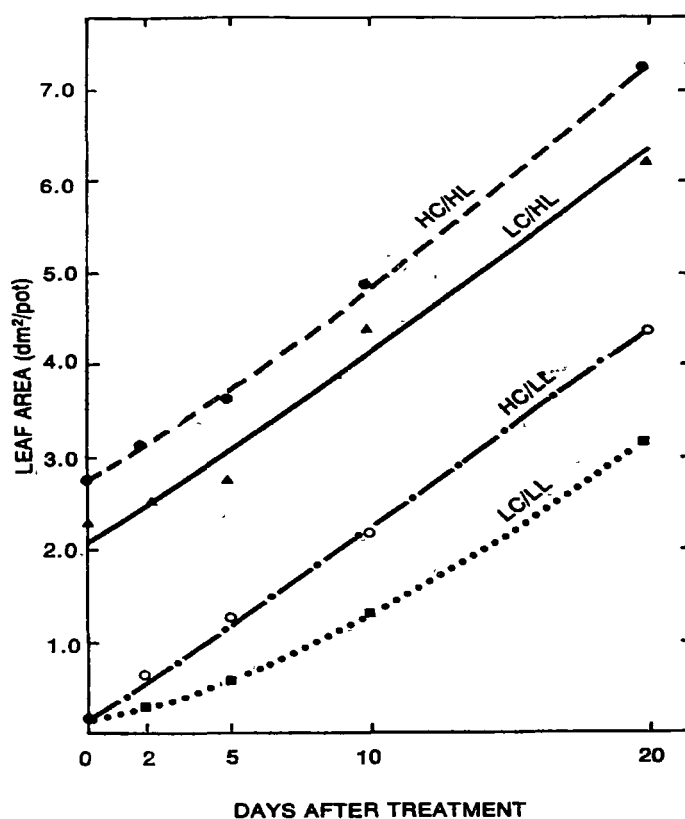


Figure 2.4 Leaf area increase of tall fescue plants during a 20 day regrowth period following treatments to obtain high and low WSC levels (HC and LC) and high and low residual leaf area (HL and LL) (source: Booysen and Nelson 1975).

The growth of new tillers is also significantly influenced by both leaf area and carbohydrate reserves. Ward and Blaser (1961) observed an association between tiller regrowth and reserves for 25 days following defoliation of cocksfoot plants, with a higher rate of DM accumulation for plants with high reserves compared to plants with low reserves (0.46 versus 0.07 g/tiller, respectively). After the 25-day period, when carbohydrate reserves in tillers were higher and similar for all plants, DM accumulation was much higher in plants with a greater original leaf area.

Ward and Blaser (1961) found that in plants with high carbohydrate reserves (HC), the rate of developing new basal tillers was much higher than for plants with low levels of carbohydrate reserves (LC). At 15 days after cutting, HC plants had developed 3.5 new tillers/original tiller, while LC plants had developed a mean of 1.4 tillers. At 35 days, there were 10.0 compared with 7.8 tillers on HC and LC plants,

respectively. Leaf area did not influence tillering, but had a significant effect on the regrowth of new tillers.

The findings of Donaghy and Fulkerson (1998) and Fulkerson and Slack (1995) confirm that depletion of WSC reserves in perennial ryegrass (through frequent and close defoliation) limits the survival of a plant by inhibiting the tiller initiation process and increasing death of young tillers. Rate of tillering quickens with a greater number of leaves per tiller - 3.5 for perennial ryegrass (Fulkerson *et al.* 1993). Fulkerson and Slack (1995) explained that the higher level of WSC reserves at this stage of growth appears to trigger initiation of new daughter tillers. This hypothesis is in agreement with observations of a positive relationship between WSC reserves in the stubble of tall fescue and tillering (Booyesen and Nelson 1975) and tiller weight (Davies 1965; Fulkerson and Slack 1994a).

2.4.3 Roots

In rapidly growing plants, the carbohydrate supply has been shown to limit root growth (Brouwer 1966). Defoliation immediately reduces the photosynthetic ability of a plant, resulting in decreased carbohydrate supply to the stubble. The rate of root growth and new root initiation therefore decreases immediately (Brouwer 1966), almost ceasing in some instances (Davidson and Milthorpe 1966a; Danckwerts and Gordon 1987; Donaghy and Fulkerson 1998). Leaf regrowth is naturally the plant's first regrowth priority (to restore greater photosynthetic capacity), and without accompanying root growth, the root to shoot ratio soon resumes its pre-defoliation status (Brouwer 1966).

As carbohydrates are mobilised to the leaf from the stubble to replenish photosynthetic tissue, the root is "temporarily starved" (Jacques 1937). In agreement with this finding, Evans (1972) found that adding sugar to the root medium largely countered the suppression of root elongation that occurs in response to defoliation. These results confirmed that cessation of root growth in such circumstances occurs as a result of a low supply of WSC reserves to the roots.

The reduction in root growth following defoliation may result in a decrease in the capacity of existing roots to absorb nutrients and water (Davidson and Milthorpe 1965). Root extension and mineral absorption recommence when leaf area has expanded to supply sufficient photosynthate to adequately meet all current requirements. The time taken for roots to resume growth following defoliation also generally increases with closer and more frequent defoliation (Donaghy and Fulkerson 1998).

Evans (1973) confirmed that root elongation of perennial ryegrass, cocksfoot and timothy following repeated defoliation treatments to 100 mm, 50 mm and 25 mm, was related to the percentage of leaf lamina remaining after the initial defoliation. The proportion of marked roots that ceased to elongate was greatest in plants subjected to the most severe defoliation treatment. Repeated defoliation to 25 mm caused almost complete cessation of root elongation in these grasses. Similarly, Crider (1955) found that the percentage of roots that stopped growth varied with the percentage of removed foliage, for eight pasture species.

Biswell and Weaver (1933) worked with prairie grasses of North America and found that the root weight of plants defoliated four to seven times at fortnightly intervals averaged only 10% compared with undefoliated controls. They also reported that “investigators are in agreement that the more frequent and drastic the defoliation treatment the less is the yield of tops, rhizomes and roots” (p370). Many studies since have resulted in the same conclusion (Jacques and Edmond 1952; Crider 1955; Evans 1971; 1973; Hodgkinson and Baas Becking 1977).

After studying the effect of defoliation frequency on 11 grass species, Klapp (1942; cited in Weinmann 1948) came to the conclusion that frequent cutting reduced plant persistence and generally affected roots and rhizomes to a greater extent than herbage yields. The more recent findings of Donaghy and Fulkerson (1998) confirm this conclusion, showing that the greatest absolute effect of reduced WSC reserves (as occurs with frequent and close defoliation), was on root elongation and survival of perennial ryegrass. Root elongation rate was 59 times higher in plants with high carbohydrate reserves (as a result of grazing to 50 mm at the 3-leaf stage) than in the

low carbohydrate plants (grazed to 20 mm at the 1-leaf stage), while tiller number per plant was six times higher and leaf DM four times higher in high carbohydrate plants.

In 1943, Klapp (cited in Weinmann 1948) reported results of a study in which mixed pasture plots were subjected to different grazing frequencies for four years. Roots and rhizomes were sampled to a depth of 500 mm at the end of this period, and results showed a relative increase between underground development and the frequency of grazing. In pastures grazed 19 times per year, root bulk was less than half of that in plots grazed or cut three times annually. As a result of frequent defoliation, it is clear that root size is reduced. Donaghy and Fulkerson (1998) drew attention to the possibility that plants with less developed root systems are at greater risk of 'sod-pulling' (uprooting by grazing animals) – an event observed by Thom *et al.* (1986) in New Zealand and Donaghy and Fulkerson (2002) in subtropical Australia.

Crider (1955) also observed the effect of repeated defoliations on root growth. Removal of 90% of foliage in a single defoliation resulted in complete cessation of root growth for 17 days. When 90% of foliage was repetitively removed at three weekly intervals, root growth failed to commence for the remainder of the four month experimental period. The reduction in root size, weight and number that occurs due to frequent defoliation then acts to inhibit shoot development. In particular, tiller number and vigour have been shown to suffer as a result of frequent defoliation (Jacques 1937).

Response to defoliation treatments appears to differ for individual grass species. Harrison and Hodgson (1939) subjected five grass species to three heights of defoliation at weekly intervals. Yields of foliage and underground organs decreased with increasing severity of defoliation in all grasses, but the extent of injury caused by continuous, close cutting varied between species. The three rhizomatous species [Quack grass (*Agropyron repens*), brome grass and Kentucky bluegrass] suffered smaller reductions in their root weights by close cutting than the two species without

rhizomes (cocksfoot and timothy). These findings are in agreement with Klapp's (1942; cited in Weinmann 1948) conclusion that species with well-developed root systems and particularly rhizomatous grasses are relatively resistant to defoliation. Hodgkinson and Baas Becking (1977) also found that species differed in their root response to defoliation.

2.4.4 Implications for management

Stubble WSC reserves decline following defoliation, as the stored reserves provide energy for continued respiration and the growth of new shoots. Although photosynthesis begins as soon as the new leaves emerge, replenishment of WSC reserves does not begin until three-quarters to one new leaf of a perennial ryegrass plant has regrown, as all WSC reserves accumulated from photosynthesis are being used for new growth (Fulkerson and Donaghy 2001). Increasing the severity of defoliation (closeness and frequency) increases the plant's reliance on stored reserves for regrowth.

The effects of variables such as temperature (Sullivan and Sprague 1949) and season (Waite and Boyd 1953) on both WSC reserves and growth rate, make it sensible to base defoliation management on a physiological plant factor that indicates WSC reserve status and stage of plant regrowth. The number of fully expanded leaves is the obvious choice (Fulkerson and Slack 1994a) and is an indicator easily distinguished in the field. Leaf number per tiller signals the onset of senescence and is related to the degree of restoration of reserves. In contrast, the results of a study conducted by Brougham (1960) showed the detrimental effects of alternative management practices on the persistence of ryegrass, cocksfoot and white clover plants. When a frequent and hard grazing regime was applied year-round, growth and yields were maximized during winter, but widespread death of all species occurred in summer. Using leaf number as an indicator of plant "readiness" takes into account seasonal changes in ambient temperature (which is the primary determinant of leaf appearance interval).

Regrazing of perennial ryegrass is advised after two leaves per tiller have grown, allowing sufficient time for WSC reserve replenishment. Earlier regrazing will deplete WSC reserves, reduce the extent and speed of regrowth and have a negative impact on plant survival and herbage quality (Fulkerson and Donaghy 2001). Compared with more frequent and closer defoliation, grazing ryegrass at the 3-leaf stage of regrowth to a stubble height of around 50 mm (Fulkerson and Slack 1995) allows more rapid replenishment of WSC reserves, and a greater proportion of WSC reserves to be allocated to maintain a more active root system and initiate new tillers. This management regime has been shown to maximize growth and persistence of perennial ryegrass, as well as optimize levels of most nutrients in pasture required by dairy cattle (i.e. protein, WSC, Ca, K and Mg) (Fulkerson *et al.* 2000).

More severe grazing (to a stubble height lower than 50 mm) limits the storage capacity of WSC reserves and thereby decreases regrowth and persistence. Root development also suffers as a result of severe defoliation (both intensity and height) in perennial ryegrass and cocksfoot (Jacques and Edmond 1952), which acts to inhibit the health and growth of the entire plant. Arcioni *et al.* (1985) and Fulkerson *et al.* (1993) have noted lack of persistence in perennial ryegrass coinciding with poor root development. Less severe defoliation results in unacceptable levels of leaf senescence and reduced rates of tillering, which lead to under-utilisation of available DM (Fulkerson and Slack 1995). Grazing of ryegrass should not be delayed long after plants reach the 3-leaf stage, as pasture senescence reduces the potential utilisation by the grazing animal (Fulkerson and Donaghy 2001).

In cocksfoot, it is at the 4-leaf stage of regrowth that WSC reserves increase significantly in both stubble and roots, indicating that this is the point where WSC supply from photosynthesis is in excess of growth and respiration requirements (Rawnsley *et al.* 2002). Prairie grass maintains five to six live leaves per tiller (Belton 1992) and the optimal time for defoliation is between the 3.5-leaf and 5-leaf stages (Hume 1991a). Fulkerson *et al.* (2000) compared the effect of grazing intervals based on the 1.5-leaf stage and 3.5 to 4-leaf stage, on the productivity and persistence of prairie grass over a three year period. While grazing at the 1.5-leaf stage did not allow sufficient time for replenishment of carbohydrate reserves

(resulting in reduced growth and survival), grazing at the 3.5 to 4-leaf stage favoured growth throughout the year.

2.5 Perennial ryegrass and alternative pasture species

2.5.1 The role of perennial ryegrass in temperate pastures

Perennial ryegrass is a prolific tillering, compact grass (Kemp *et al.* 1999). Its highly branched, shallow root system produces adventitious roots from the basal nodes of tillers. Perennial ryegrass is native to Europe, temperate Asia and northern Africa and because of its value as a pasture plant, it is now extensively sown in the United Kingdom, Europe, North and South America, South Africa, New Zealand and Australia (Lamp *et al.* 1990). Generally, perennial ryegrass cultivars do not tolerate extreme temperatures or drought, and this species is therefore most abundant in pastures of wet, mild-temperate climates. With optimal growth occurring at 18°C, high summer temperatures result in a lower than optimal growth rate (Kemp *et al.* 1999). Perennial ryegrass is adapted to medium to high fertility soils that are well drained.

In southern Australia, perennial ryegrass is the most widely used dairy pasture grass species - commonly sown in a mixed sward with white clover. The popularity of perennial ryegrass is largely due to its reputation as a high herbage quality dairy pasture species. Claims that perennial ryegrass possesses higher IVDMD and TNC than a variety of other cool-season perennial grasses are also common (Greenhalgh and Reid 1969; Jung *et al.* 1976; Balasko *et al.* 1995). However, such reports often result from experiments in which herbage quality parameters of a range of species are compared with those of perennial ryegrass, under a management regime developed for ryegrass pastures, to the detriment of the alternative species (Section 2.6).

Under appropriate environmental and management conditions, perennial ryegrass has the potential to supply ME concentrations of 12 MJ/kg DM (Table 2.5) and produce an impressive amount of high herbage quality feed for most of the year. However, under suboptimal environmental conditions, perennial ryegrass exhibits poor persistence and lower herbage quality, which may result in feed shortages.

Table 2.5 Metabolisable energy concentration (MJ/kg DM) of perennial ryegrass at different plant growth stages (Adapted from Waite *et al.* 1964).

Growth stage	Metabolisable energy (MJ/kgDM)
Young-leafy	12.0
Late-leafy	10.8
Seed head emergence	10.9
Seed setting	8.9

2.5.2 Limitations of perennial ryegrass

Perennial ryegrass is perceived and readily adopted as the highest herbage quality, most palatable and productive of the temperate grasses. Since its introduction into Australia from Europe over 100 years ago, breeding efforts have focused on improving forage yields and herbage quality. The resultant cultivars are easily established and are also successfully managed, due to years of agronomic research that have accompanied breeding efforts. Yet despite the improvements of these cultivars, there remain a number of major limitations of perennial ryegrass in southern Australia. They include:

- poor production and persistence under dry and/or hot conditions
- a requirement for relatively high levels of irrigation application, and a tendency to become dormant if irrigation becomes sub-optimal
- susceptibility to pests, requiring chemical usage for eradication
- a requirement for relatively high levels of soil fertility
- presence of the endophyte fungus can cause animal health problems

Hot, dry summers are commonly blamed for the decline of perennial ryegrass in southern Australia (Waller and Sale 2001). A study conducted by Waller *et al.* (1999) in Hamilton, Victoria, showed that perennial ryegrass pastures failed to persist under particularly dry summer conditions (1996-1997). Ryegrass growth ceased early during the summer and the regeneration of tillers was significantly lower by the following winter, with tiller density decreasing from approximately 7000 tillers/m² in winter 1996 to 4000 tillers/m² in winter 1997. Even optimal pasture management (a tactical stocking system developed to maximise survival) did not benefit perennial ryegrass persistence during the particularly dry summer conditions.

Fulkerson and Slack (1994b) investigated the effect of irrigation on the production and survival of perennial ryegrass over a relatively dry summer on the north coast of New South Wales. When irrigation was supplied at a rate that was sufficient only to keep plants growing, productivity of a ryegrass/clover mix was maintained between 2826-5515 and 3210-5396 kg DM/ha in summer and the following autumn/winter, respectively. Survival of irrigated plants was 34% greater than dryland pasture plants, emphasising the importance of moisture for the persistence of this species.

Poor persistence and growth of perennial ryegrass during the summer (i.e. as a result of low rainfall) results in an immediate feed shortage when it is present as the dominant pasture species. The reduced plant density allows gaps to form in the pasture sward and colonisation of these gaps by weeds then leads to decreased herbage quality. Kemp and Dowling (1991) explained that the invasion by weeds is largely a reflection of climatic conditions, particularly rainfall during summer and autumn. This process has been observed in non-irrigated Tasmanian pastures, as a result of extended periods of low and/or variable summer rainfall. Lack of DM production also occurs during the summer months if irrigation is suboptimal.

In southern Australia, perennial ryegrass is susceptible to attack by a variety of pasture pests, including corbies (*Oncopera* spp.), cockchafers (*Aphodius*, *Adoryphorus*, *Scitala*, *Sericesthis* and *Saulostomus* spp.), lucerne flea (*Sminthurus viridis*) and armyworms (*Persectania* and *Mythimna* spp.). Among the most damaging of the invertebrate pests that consume perennial ryegrass in south-eastern Australia are the black-headed pasture cockchafer (*Aphodius tasmaniae*), black field cricket [*Teleogryllus commodus* (Walk.)] and pasture webworm (*Hednota* spp.) (Waller and Sale 2001). Ryegrass plants have limited ability to recover from attack (McQuillan and Ireson 1987) and pest invasions often lead to the complete death of patches of ryegrass pasture. As chemical control methods become increasingly undesirable and less readily available, pasture pests become more difficult to control.

Clarke and Eagling (1994) list two viruses of perennial ryegrass in Australia – barley yellow dwarf virus and ryegrass mosaic virus - and suggest there is potential for the introduction of other viruses. A wide range of fungal infections occur in perennial ryegrass, with crown rust (*Puccinia coronata*) considered the most significant. It is

capable of reducing herbage yield and palatability as well as root weight, tiller number and leaf area (Lancashire and Latch 1966), and leaf WSC levels (Donaghy and Fulkerson 2002). Other fungal pathogens that infect perennial ryegrass in Australia are net blotch (*Drechslera dictyoides*), spot blotch (*Helminthosporium* spp.), stem rust (*Puccinia graminis*) and blind seed disease (*Gloeotinia granigena*). These pathogens reduce the yield of perennial ryegrass and the latter two infect the inflorescence and reduce seed yield (Cunningham *et al.* 1994).

Perennial ryegrass displays a significant response to increased nutrient supply, particularly to increased N and P. Lambert *et al.* (1986) carried out a six year study at Ballantrae, New Zealand, and found that reducing application rates from 57 to 11 kg P/ha per year (as superphosphate) reduced annual production by 37%. Similarly, Frame and Tiley (1988) observed a greater growth response of perennial ryegrass to high levels of N compared with some common pasture grasses and weeds. Although perennial ryegrass has a competitive advantage in high soil N conditions, under conditions of low soil fertility, alternative species (considered as low fertility plants) can be as productive as perennial ryegrass.

A fungal endophyte is often present in perennial ryegrass and has a significant effect on both the performance of ryegrass pastures and on the health of grazing animals. The advantages of ryegrass infected with the endophyte include improved seedling establishment (Reed *et al.* 1985), increased herbage yield (Popay *et al.* 1999), increased persistence and the deterrence of chewing insect pests and the aphids that transmit barley yellow dwarf virus (Cunningham *et al.* 1993). However, the endophyte produces neuro-muscular toxins such as lolitrems and ergovaline, which are toxic to stock and cause 'ryegrass staggers' – a condition characterised by muscle twitching, unsteadiness and rapid breathing. High endophyte pastures can also reduce milk production (Valentine *et al.* 1993). Most ryegrass cultivars sown in Australia have high endophyte levels (Reed *et al.* 2000).

The limitations of perennial ryegrass may be overcome by alternative pasture species that are more productive during summer months, are tolerant of, or resistant to attack by pasture pests and that do not contain an endophyte. An investigation of alternative

grasses is therefore necessary to assess these species as potential replacements for perennial ryegrass in the dairy pastures of southern Australia.

2.5.3 Alternative grasses to perennial ryegrass

Commercially available temperate (C₃) grasses that are able to overcome some of the limitations of perennial ryegrass include tall fescue, phalaris (*Phalaris aquatica* L.), cocksfoot and prairie grass.

2.5.3.1 Tall fescue

Tall fescue is an upright-growing, cool-season bunchgrass. This perennial has the ability to spread and form a dense sod through the production of short rhizomes (Miller 1984). According to De Battista and Boulton (1990), promotion of rhizome production in tall fescue is a desirable goal for breeders because the rhizomes enhance persistence under stressful conditions.

Tall fescue is adapted to a wide range of climates and soils. It is able to survive and grow in low, wet, poorly drained areas and under shaded conditions. Most cultivars have a growing season from spring to autumn, with little or no growth during the winter. However, those of Mediterranean origin have a growing season extending from autumn to late spring, becoming dormant during the summer (Lamp *et al.* 1990). The Continental cultivars are more productive than ryegrass during dry summers, recovering quickly following summer drought conditions to out-produce perennial ryegrass during autumn (Kemp *et al.* 1999).

The growth of tall fescue is less leafy than cocksfoot at similar stages of maturation (Table 2.6). As with all grasses, grazing management has a significant effect on the herbage quality of tall fescue. Minimising the presence of senescent material and seedhead helps to maintain good herbage quality (Kemp *et al.* 1999).

Hemken *et al.* (1979) stated that tall fescue was not a popular pasture choice for dairy farmers in the United States due to the presence of an endophyte and its adverse effect on milk production. However, later studies showed that milk production of dairy cows fed on endophyte-free tall fescue was equivalent to that from consumption of other cool-season grasses (Strahan *et al.* 1987).

Table 2.6 Leaf blade to stem plus sheath ratios of tall fescue and cocksfoot at various stages of maturity (source: Miller 1984).

Maturity stage	Tall fescue	Cocksfoot
Boot	1.97	2.16
Headed	0.43	1.04
Early bloom	0.30	0.68
Late bloom	0.29	0.56
Seed	0.26	0.47

It appears that the inferior herbage quality of tall fescue compared with perennial ryegrass (Lowe *et al.* 1999a;b) – which often relates to less efficient milk production (Johnson and Thomson 1996; Hainsworth and Thomson 1997) – is one of the main reasons why tall fescue is not more widely adopted as a dairy pasture species today. Lowe and Bowdler (1995) found fescue cultivars to be more productive in the subtropics than a range of perennial temperate grasses (including perennial ryegrass), with higher yields and greater persistence. However, they concluded that better animal performance would improve farmer acceptance of this species.

2.5.3.2 Phalaris

Phalaris is a large-tillered, deep-rooted, rhizome-producing perennial. Phalaris originated in the Mediterranean (Langer 1973) and is therefore well-adapted to soils that are wet during winter and dry during summer. It can be grown successfully on a wide range of soil types and will tolerate acidic, alkaline or waterlogged conditions for long periods (Lamp *et al.* 1990). However, it does require moderate to high soil fertility (Kemp *et al.* 1999).

Like perennial ryegrass, chemicals associated with fungal infection of phalaris plants (tryptamine alkaloids) cause ‘phalaris staggers’ in grazing stock (Langer 1973). The risk of stock death as a result of this condition can be minimised by avoiding grazing phalaris-dominant pastures following periods of stress. Presence of the alkaloid also decreases the palatability of phalaris (Kemp *et al.* 1999). Phalaris is not seriously affected by insect pests and is resistant to grass grub (Hainsworth and Thomson 1997).

Clarke and Eagling (1994) reported that phalaris is resistant to a wide range of diseases, including various races of crown rust, stem rust, leaf rust (*Puccinia recondite*), stripe rust (*Puccinia striiformis*), a range of *Helminthosporium* species and *Cochloibolus* species, a range of mildew (*Erysiphe graminis*) isolates from other grasses and cereals, ergot (*Claviceps* spp.) and a range of viruses.

Production of phalaris is good in winter and early spring, while summer production is largely dependent on rainfall. Phalaris does not remain productive through periods of drought, but is able to persist due to its deep roots, rhizomes and ability to become vegetatively dormant (Lamp *et al.* 1990). Reed (1996) explained how phalaris escapes summer drought – by surviving as underground axillary buds, which maintain turgidity by drawing subsoil water from 1-2 m depths.

Frame and Morrison (1991) measured the annual herbage production of a number of perennial pasture species under defoliation (every six to seven weeks to a residual height of 30-40 mm) in the United Kingdom. Phalaris produced less DM than perennial ryegrass and prairie grass during the first year (6.8 versus 12.7 and 13.4 t DM/ha respectively), and did not persist to be measured during the second and third years of the trial. In contrast, Lowe and Bowdler (1995) investigated the growth and persistence of a variety of perennial temperate grasses under irrigation in the Queensland subtropics, and described the phalaris cv. 'Maru' as the most persistent grass. While Frame and Morrison (1991) concluded that the phalaris cultivar evaluated had unsatisfactory agronomic potential, Lowe and Bowdler (1995) encouraged further evaluation of the species under grazing.

While phalaris may offer advantages over perennial ryegrass in terms of production and persistence in subtropical climates, and under irrigation (Mitchell 1997), summer dormancy and the risk of phalaris staggers limit the potential of this species as an alternate species in temperate southern Australia, under dryland conditions.

2.5.3.3 Cocksfoot

Cocksfoot is a cool-season bunch grass, with morphological types ranging from plants with many small, prostrate tillers to plants with a few large, erect tillers (Kemp *et al.* 1999). The original cocksfoot cultivars of northern Europe are suited to cooler,

high-rainfall environments (Lolicato and Rumball 1994). More recently, cultivars have been derived from Portuguese and Algerian material and are therefore adapted to winter-growing, dry-summer conditions (Knight 1968). These cultivars provide additional summer and autumn yield, insect pest tolerance and a reduction in animal intake of fungal toxins (Moloney 1993).

Cocksfoot cultivars can therefore be classified into two main groups. ‘Mediterranean types’ exhibit high summer dormancy, while ‘Intermediate types’ exhibit moderate summer dormancy. Kara is an Intermediate type cocksfoot and is described as a winter active, drought tolerant cultivar, bred to thrive during winter and sustain relatively stable yields during summer months. In National Forage Variety Trials, carried out in Canterbury, New Zealand, DM yield data from eight replicated trials (1991-2000) showed that Kara out produced two other popular intermediate types ‘Wana’ and ‘Tekapo’ by at least 4 t DM/ha on a yearly basis (New Zealand Plant Breeding and Research Association 2001).

Cocksfoot is distributed worldwide in areas of moderate to high rainfall, with mild winters and warm summers, and is regarded as one of the most important perennial grass species sown in temperate Australia (Avery *et al.* 2000). Although cocksfoot persists under low to medium soil fertility conditions, it responds favourably to higher soil fertility. Cocksfoot is shade tolerant – its second common name ‘orchardgrass’ owing to the ability of the grass to persist under orchard conditions (Miller 1984).

Cocksfoot is relatively slow to establish compared with perennial ryegrass (Moot *et al.* 2000) but once established, it is able to compete effectively with weeds and other pasture plants for resources and to maintain its population in a mixed sward (Borman *et al.* 1990). Along with native perennial grasses and several other introduced species [i.e. black mountain rye (*Bromus macranthos*), slender wildrye (*Elymus trachycaulus*) and red fescue (*Festuca ovina*)], cocksfoot has been labelled a “low input grass”, referring to its ability to persist under the range of environmental constraints common in Australia (Norton *et al.* 1999). An established cocksfoot pasture will persist for many years, when managed appropriately.

According to Langer (1973), cocksfoot is capable of tolerating drought conditions during the germination and seedling phases. Under appropriate management, mature cocksfoot plants not only survive, but also remain highly productive during summer months (Christie and McElroy 1995). In a Tasmanian study, cocksfoot displayed superior growth in late spring and early summer compared with perennial ryegrass (Anon. 1987). Kemp *et al.* (1999) attribute the persistence of cocksfoot under dry conditions to its deep rooting system.

The herbage quality of cocksfoot is also heavily dependent on management. Regrowth of cocksfoot is rapid and when it is allowed to senesce, cocksfoot becomes coarse and unpalatable. However, defoliation before the 5-leaf stage maintains high herbage quality, with an ME range of 10.3 to 11.5 MJ/kg DM (Mitchell 1997; Rawnsley 2000). Cocksfoot pasture management is ideally based on the emergence of four live leaves per tiller, as this is the recommended physiologically-determined cue for defoliation (Mitchell 1997; Rawnsley 2000).

Although many diseases and insect pests attack cocksfoot, there are few reports regarding economic losses of any significance. In summary, cocksfoot is tolerant of low soil fertility, insect attack and drought conditions, and is therefore worthy of greater consideration as a valuable alternative to perennial ryegrass in southern Australia.

2.5.3.4 Prairie grass

Prairie grass is a tall, perennial plant with long, broad leaves. Native to South America, prairie grass was originally introduced to Australian pastures because of its high palatability and ability to grow in cool conditions (Lamp *et al.* 1990). While the persistence of prairie grass in temperate Australian pastures was initially poor (largely due to mismanagement), it did persist and become widespread as a volunteer species. During the last decade, prairie grass has regained attention from researchers and farmers, with management focused on the physiological status of the prairie grass plant. Matua prairie grass from New Zealand is the most popular prairie grass cultivar worldwide.

In the humid conditions of the Pampas region in Argentina, with sufficient water supply, prairie grass grows throughout the year and maximum herbage accumulation occurs in spring (Scheneiter and Rimieri 2001). In temperate environments, prairie grass has a more rapid growth rate than perennial ryegrass in summer and autumn (Hume 1991b), and therefore has the potential to fill the typical feed gap in southern Australia during these months.

Prairie grass has a large seed (10.5–12.2 mg compared to 0.65–0.78 mg for cocksfoot and 1.71–2.19 mg for perennial ryegrass), but is relatively slow to germinate. However, growth is then rapid – particularly the establishment of dense, uniform roots at depth (Shaffer *et al.* 1994; Andrews *et al.* 1997). Further studies are required to determine whether the rooting characteristics of prairie grass are responsible for the drought tolerance of this species (Shaffer *et al.* 1994).

Due to its upright habit and a low tillering capacity, prairie grass does not tolerate continuous and close grazing. Persistence of this pasture species is therefore dependent on careful grazing management, which combined with reasonable soil fertility, should ensure palatability and good production throughout the year. Low tiller number is compensated for by greater tiller weight. Prairie grass maintains five to six live leaves per tiller compared with three for perennial ryegrass, a greater area per leaf and a higher leaf area per plant (Hume 1991b). The ability of prairie grass to carry spring growth through into summer while maintaining high herbage quality has been partly attributed to the longer life span of its leaves (Belton 1992).

Prairie grass is susceptible to smut fungus, but is thought to be largely resistant to insect attack (Langer 1973). Summer growth, drought tolerance, insect tolerance and high palatability make prairie grass worthy of consideration as an alternative to perennial ryegrass in southern Australia.

2.6 Cocksfoot and prairie grass as alternatives to perennial ryegrass in southern Australia

Although perennial ryegrass may continue to be the dominant pasture grass of Tasmanian dairy pastures and of the wider Cool Temperate Region, the dryland areas of southern Australia may benefit from the introduction of alternative species. In

New Zealand, recent studies have shown that alternative species outperformed perennial ryegrass in terms of milk production, largely as a result of greater summer pasture production (Thom *et al.* 1998; Thom *et al.* 2001).

Under dryland conditions, both cocksfoot and prairie grass remain active, responding well to limited summer rainfall and maintaining a longer growing season than ryegrass (Belton 1992). The reversion of many New Zealand and Tasmanian dryland pastures to cocksfoot dominance over several years emphasises the adaptive nature of this species to dry summer conditions (Milne *et al.* 1993; Moloney 1993; Fraser 1994; Graham *et al.* 2000). Cocksfoot is even able to sustain growth on the dry hill country of New Zealand. The production and persistence of five oversown grass species were measured over an eight year trial period at six sites, and cocksfoot was described as the most persistent of the species, particularly at the driest sites (Barker *et al.* 1993).

The ability of these plants to remain active during summer months may be due to greater water-use efficiency, which may in turn be due to morphological (i.e. rooting or tillering) or physiological (i.e. greater regulation of transpiration losses) behaviour, or a combination of these attributes.

Maintaining plants in a vegetative state through species-specific management regimes is essential for retaining the high herbage quality and productivity of alternative grasses. In New Zealand, the results of cocksfoot trials were discouraging, showing that cocksfoot exhibited no benefits over ryegrass in terms of milk production (Johnson and Thomson 1996; Hainsworth and Thomson 1997). However, these studies were based on the use of a common management strategy – developed for ryegrass-based pastures and therefore favouring ryegrass performance. Similarly, early studies of prairie grass in Tasmania were unsuccessful due to the difficulties encountered in regard to grazing management (Belton 1992).

A study conducted in South Australia by Mitchell (1997) illustrated the importance of managing species according to their particular requirements for growth and production. Cocksfoot pastures were managed under two grazing systems – one based on pasture mass (one of the more accurate systems of rotation management for

perennial ryegrass) and the other based on emergence of four live leaves per tiller (recommended as the ideal physiologically-determined cue for defoliation of cocksfoot). The rotation based on cocksfoot leaf regrowth stage resulted in the highest pasture utilisation in spring, when over 60% of total pasture growth occurred.

Species-specific management of these grasses is required to obtain an objective assessment of their individual value as dairy pasture species. Furthermore, an investigation of related physiological parameters will increase our understanding of the reasons behind the impressive summer production of these alternative grasses.

2.6.1 Potential production, herbage quality and persistence of cocksfoot compared with perennial ryegrass

Cocksfoot pastures are capable of production at least equivalent to ryegrass pastures – as illustrated by the two studies described below. In Tasmania, a grazing study compared the growth of ryegrass (cv. ‘Ellett’) and cocksfoot (cv. ‘Porto’) pastures over two years (Anon. 1987). During the first year (1985), utilisation of ryegrass was greater than cocksfoot (15.6 versus 11.6 t DM), largely due to the more rapid establishment of ryegrass. However, during the second year, utilisation levels were very similar (12 versus 11 t DM for ryegrass and cocksfoot, respectively). Figure 2.5 shows the growth rates of ryegrass and cocksfoot from this study, and highlights the superior growth of cocksfoot in late spring and early summer. A second series of studies conducted in South Australia (Mitchell 1997) provided a similar growth comparison between cocksfoot and ryegrass based pastures. Mean utilisation of pastures over three years (1994-1996) was 5.5 and 5.0 t DM for ryegrass and cocksfoot pastures, respectively.

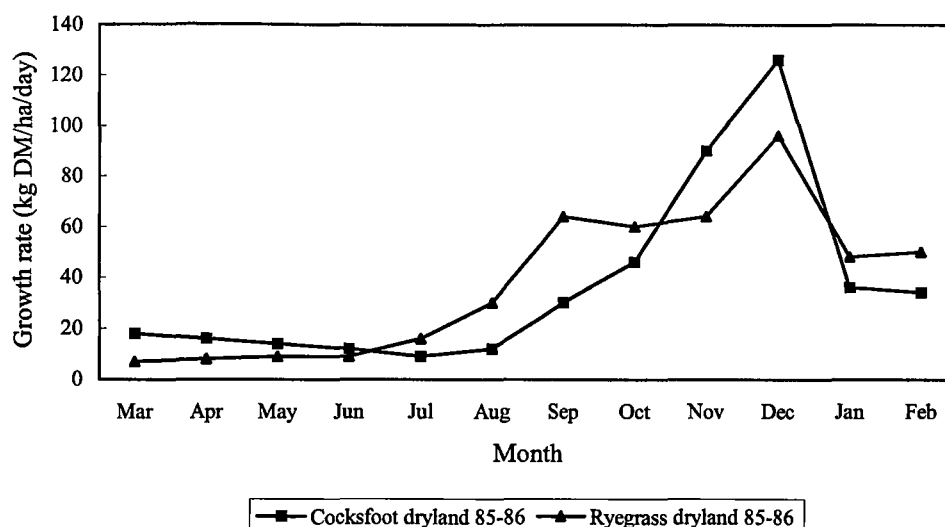


Figure 2.5 Growth rates of ryegrass (cv. Ellett) and cocksfoot (cv. Porto) dryland pasture from establishment in autumn 1985 to summer 1986 (source: Anon. 1987).

These studies prove that the production capability of cocksfoot is comparable with that of perennial ryegrass. Nevertheless, the true potential of cocksfoot was underestimated by the use of grazing management practices developed for perennial ryegrass pastures. Cocksfoot was therefore overgrazed in winter and early spring (when cocksfoot establishment and leaf appearance is slower than ryegrass), and undergrazed in late spring and early summer (when cocksfoot leaf appearance is faster than ryegrass). Overgrazing results in slow recovery from defoliation while undergrazing leads to leaf senescence and decreased herbage quality. The full productive potential and growth pattern of a well-managed cocksfoot based pasture is therefore yet to be reported (D Donaghy pers. comm.).

Theoretically, the productive potential of cocksfoot can be estimated using the following reasoning (Donaghy unpublished data). Perennial ryegrass and cocksfoot produce a similar number of leaves per tiller annually (25-32 versus 25-35 leaves per tiller, respectively). As previously mentioned, cocksfoot leaf emergence is slower than ryegrass during winter, but faster from late spring to early autumn under dryland conditions (Rawnsley 2000). Ryegrass pastures are denser than cocksfoot pastures (approximately 5000 versus 2500-3000 tillers/m²) (Donaghy unpublished data; Rawnsley 2000), but cocksfoot produces a larger leaf and pseudostem than ryegrass (Brock *et al.* 1996; Rawnsley 2000) and therefore up to four times more DM. Using

these figures, cocksfoot pastures (which have 50% less tillers but produce 200% more DM/tiller compared to ryegrass) have at least 50% more productive capacity than ryegrass pastures – a potential yield of 16 t DM/ha compared with the 10-11 t DM/ha productive capacity of perennial ryegrass (Bowman 1999; Blair 2002).

Cocksfoot has a widespread reputation as a poorer herbage quality pasture species than perennial ryegrass. This reputation has been created and supported by reports from projects in which management has been based on the opposing species or simultaneous harvesting of all species. Collins and Casler (1990) suggest that significant differences in herbage quality parameters associated with the spring grown herbage of cocksfoot, brome grass, timothy, tall fescue and canary grass (*Phalaris arundinacea* L.) sampled at the same date, were related to differences in reproductive maturity.

The herbage quality of cocksfoot decreases more rapidly than the quality of ryegrass, due to a large increase in the stem fraction as a percentage of total plant DM, and a larger decrease in stem digestibility compared to leaf blade or leaf sheath (Terry and Tilley 1964; Berg and Hill 1989). Kunelius *et al.* (1974) found that IVDMD can decrease as much as 0.82% and CP as much as 0.35% per day as cocksfoot plants mature in the spring. When compared with other temperate grasses at the same date, cocksfoot is therefore likely to be of lower herbage quality due to its advanced maturation.

When cocksfoot is cut after the early bloom stage of development, it provides little more than a maintenance level of energy for livestock (Miller 1984). In contrast, with defoliation before the 5-leaf stage, high herbage quality can be maintained with an ME range of 10.3-11.5 MJ/kg DM (Mitchell 1997; Rawnsley 2000). Table 2.7 shows the herbage quality (above 50 mm regrowth height) of cocksfoot and ryegrass plants in a field study, over a 37-day regrowth period following grazing (Rawnsley 2000).

Table 2.7 Herbage quality and mineral content [mean \pm standard error (s.e.)] of cocksfoot and ryegrass plants sampled six times over a 37-day regrowth period from grazing in late March 2000 (source: Rawnsley 2000).

Herbage quality	Cocksfoot	Ryegrass
Metabolisable energy (MJ/kg DM)	10.2 \pm 0.2	10.8 \pm 0.1
Crude protein (% DM)	21.3 \pm 1.7	19.3 \pm 0.9
Calcium (% DM)	0.32 \pm 0.01	0.29 \pm 0.01
Potassium (% DM)	2.24 \pm 0.13	2.26 \pm 0.13
Magnesium (% DM)	0.28 \pm 0.01	0.27 \pm 0.01
Sodium (% DM)	0.60 \pm 0.03	0.60 \pm 0.03
Phosphorus (% DM)	0.45 \pm 0.03	0.42 \pm 0.03

Bland and Dent (1964) conducted a cocksfoot variety trial in Yorkshire and found that digestibility and animal preference also varied between varieties. A significant positive correlation between herbage removed and total sugar content was discovered, as well as a negative correlation between herbage removed and fibre content. The varieties more acceptable to grazing animals, with higher WSC reserves and less fibre, were generally the earliest maturing varieties. The high WSC content was associated with a thick, succulent stem, which was highly acceptable to livestock. For this reason, maximum pasture utilisation and animal productivity are dependent on grazing herbage before it becomes fibrous and lignified.

2.6.2 Potential production, herbage quality and persistence of prairie grass compared with perennial ryegrass

Research in New Zealand has shown Matua prairie grass to be highly productive (particularly during winter), highly palatable to cattle and sheep at all stages of development (including reproductive), highly nutritious (more nutritious than ryegrass during reproductive phases) and resistant to many New Zealand pasture pests (DeLacy 1987). Vartha (1977) conducted a study on the South Island of New Zealand, cutting dryland pastures of prairie grass and ryegrass at monthly intervals over three years. Dry matter utilisation was reported to be greater for prairie grass than ryegrass pastures (13.2 versus 8.6 t DM/ha), largely due to the greater summer productivity of prairie grass. In fact, of the four pasture grasses tested in this study (prairie grass, cocksfoot, timothy and perennial ryegrass), perennial ryegrass was reported to be the lowest yielding grass in the second and third years from sowing.

Another study compared the productivity of prairie grass and perennial ryegrass in New Zealand and showed superior yields of prairie grass, with at least 30% greater DM production and more uniform growth throughout the year. From March to September, prairie grass produced 6.3 t DM/ha, while perennial ryegrass yielded 4.2 t. On a daily basis during the winter trial period, the growth rate of Matua was 25-30 kg DM/ha compared with 5-10 kg DM/ha for perennial ryegrass (DeLacy 1987).

In a mowing trial conducted on heavy soil in Canterbury, New Zealand, Matua produced more DM than ‘Grasslands Nui’ perennial ryegrass (Fraser 1982). Under an infrequent but severe (to 30 mm) cutting regime, Matua was superior to both perennial and annual ryegrasses in all seasons.

The performance of prairie grass in the subtropics has also been investigated (Fulkerson *et al.* 2000) and was found to be superior to perennial ryegrass in terms of production and persistence in this environment (Table 2.8). Fulkerson *et al.* (2000) showed that prairie grass out yielded perennial ryegrass by at least 9 t DM/ha during the first and second years from sowing at two sites in northern New South Wales. In the third year at the Wollongbar site, ryegrass production ceased altogether, while prairie grass produced 11.3 t DM/ha. Both prairie grass and ryegrass pastures were managed according to phenological development, once again highlighting the importance of species-specific management.

Table 2.8 Annual utilisation (kg DM/ha) of the grass only component of ryegrass and prairie grass irrigated pastures at two sites in northern NSW (source: Fulkerson *et al.* 2000).

	Casino		Wollongbar	
	Ryegrass	Prairie grass	Ryegrass	Prairie grass
1997	6532	9030	6466	10144
1998	3184	10051	1698	13277
1999	4815	7784	0*	11300

*Ryegrass pastures at the Wollongbar site failed to persist beyond two years.

In a Tasmanian study, prairie grass was shown to be unproductive with poor persistence, when a grazing regime based on best management practice for ryegrass-

based pastures was applied to both pasture types (Anon. 1987). In a later study, prairie grass was managed to leave longer post-grazing residuals and was allowed to set seed in spring. Utilisation from the prairie grass rose to 2, then 4 t greater than utilisation of ryegrass in successive years (Department of Primary Industries 1987). The growth rates of prairie grass and ryegrass from the later study are shown in Figure 2.6. Prairie grass exhibited faster growth than ryegrass in autumn and early spring (51% greater yield March to September) and out-yielded ryegrass by 30% annually.

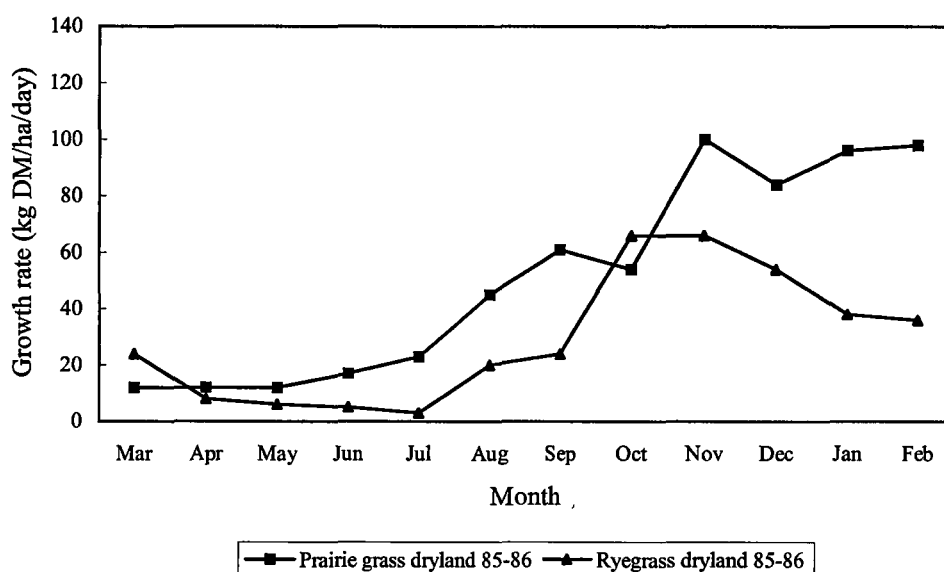


Figure 2.6 Growth rates of ryegrass (cv. Ellett) and prairie grass (cv. Matua) dryland pastures from establishment in autumn 1985 to autumn 1986 (source: Anon. 1987).

Persistence of prairie grass has the potential to decline significantly during the years following sowing, due to decreased tiller density (Belton 1992). Lowe *et al.* (1999a) found that the survival of mature prairie grass plants from one year to the next was very low in the Australian subtropics. Fulkerson *et al.* (2000) recommend allowing prairie grass to set seed every two to three years as a means to encourage seedling emergence and enhance persistence in this climate. Delaying grazing until new daughter tillers have appeared has also been suggested as a means to increase persistence (Black and Chu 1989). According to Thom *et al.* (1989), the observed decline in persistence of prairie grass pastures in New Zealand may be accelerated by

attack from a range of insect pests. However, none of these pests are endemic to Australia (Belton 1992).

Although these studies have clearly shown prairie grass is capable of greater production than perennial ryegrass, the grazing management approach commonly utilised in pasture research has limited further investigation of its productive capacity. When grazed in the same manner as ryegrass-based pastures (as is common practice), prairie grass is disadvantaged, particularly from late spring to early autumn when the leaf appearance rate of prairie grass is more rapid than for ryegrass (Donaghy unpublished data). Grazing management based on the physiological status of the prairie grass plant is more efficient than grazing management based on herbage accumulation (Thom *et al.* 1990; Fulkerson and Donaghy 2001). Investigation of prairie grass pastures under favourable management is needed to ascertain the growth pattern, herbage quality and true productive potential of prairie grass in temperate environments.

As with cocksfoot, the productive potential of prairie grass compared to perennial ryegrass can be estimated theoretically (D Donaghy pers. comm.). Under dryland conditions, prairie grass produces more leaves per tiller annually than perennial ryegrass (30-42 versus 25-32 leaves per tiller, respectively), as prairie grass leaf appearance is similar to perennial ryegrass during winter, but faster from late spring through to early autumn (Hume 1991b; Donaghy unpublished data). Although prairie grass pastures are much less dense than ryegrass pastures (600-900 prairie grass tillers/m² versus up to 5000 ryegrass tillers/m²) (Thom *et al.* 1989; Thom *et al.* 1990; Fulkerson *et al.* 2000), prairie grass produces a larger leaf and pseudostem, and therefore more DM from March to October (Belton 1992).

According to these calculations, prairie grass pastures have 85% less tillers but produce 450% more DM/tiller, compared to perennial ryegrass. A conservative estimate of prairie grass pasture production therefore exceeds ryegrass pasture production by at least 200%. While potential utilisation from dryland prairie grass pasture is then calculated at 31 t DM/ha, a realistic estimate (taking into account climatic limitations) is 18-21 t DM/ha in high rainfall temperate areas (Donaghy unpublished data).

Under appropriate management, prairie grass can be of a similar high herbage quality to perennial ryegrass (Fulkerson *et al.* 2000). No difference between IVDMD of perennial ryegrass and prairie grass was found in studies in either subtropical Australia (Lowe *et al.* 1999a) or temperate New Zealand (Crush *et al.* 1989). Lowe *et al.* (1999a) reported similar ME concentrations for these grasses in summer and autumn (Table 2.9). In winter, ME concentrations of both perennial ryegrass and prairie grass were higher than in the other seasons.

Table 2.9 *In vitro* dry matter digestibility (IVDMD%) and metabolisable energy (ME; MJ/kg DM) concentration of feed on offer in prairie grass and perennial ryegrass pastures at the middle of each season from summer 1992-93 to winter 1994 (source: Lowe *et al.* 1999a).

	IVDMD (%)		ME (MJ/kg DM)	
	P. ryegrass	Prairie grass	P. ryegrass	Prairie grass
Summer 1992-93	56.4	56.7	7.4	7.5
Autumn 1993	59.8	59.1	7.9	8.0
Winter 1993	78.7	78.7	10.4	10.3
Spring 1993	73.2	62.1	9.6	9.1
Summer 1993-94	63.0	59.7	8.4	8.0
Winter 1994	75.5	75.2	9.8	9.8

One of the nutritional limitations of prairie grass is its low Mg content (Thom *et al.* 1990; Fulkerson *et al.* 2000). However, the effect of low Mg content in prairie grass pastures on milk production has been shown to be insignificant. Wilson and Grace (1978) found no response in milk production when cows grazing prairie grass were given 10 g of Mg supplement per day. Crush *et al.* (1989) compared the chemical composition of Matua prairie grass to perennial ryegrass and identified P and Na as further minerals Matua possessed in lower concentrations than perennial ryegrass. However, animal uptake of the minerals did not vary significantly between the two pasture types, indicating minimal effect on grazing livestock.

The high yields of prairie grass must be converted into increased milk production if this temperate perennial pasture grass is to be successfully integrated into southern Australian dairy forage systems. Compared with perennial ryegrass, prairie grass is able to provide similar milk production and milk quality. Reporting on the results of

a study that compared milk production of cows grazing perennial ryegrass, Italian ryegrass, tall fescue and prairie grass, Lowe *et al.* (1999b) describe Matua prairie grass as “the most consistent performer, achieving high milk and pasture production levels and excellent gross margin figures” (p682). Consistently producing the most forage on offer translated to good pasture utilisation and superior spring milk yields (Table 2.10).

Table 2.10 Milk production and milk quality for cows grazing prairie grass and perennial ryegrass in subtropical south-east Queensland (source: Lowe *et al.* 1999b).

	Mean milk yield (kg/cow/d)	300-day milk yield (kg/cow)	Milk fat (%)	Protein (%)	Lactose (%)
<i>1992-93</i>					
P. ryegrass	16.7	3817	3.86	3.14	4.83
Prairie grass	16.2	3669	3.88	3.15	4.91
<i>1993-94</i>					
P. ryegrass	23.7	6879	3.76	3.33	4.73
Prairie grass	21.6	6240	3.87	3.22	4.78
<i>1994-95</i>					
P. ryegrass	22.4	5001	3.77	2.87	4.63
Prairie grass	22.6	5332	4.14	2.93	4.80

Thus, as an alternative to perennial ryegrass, prairie grass compares well in terms of production, persistence and herbage quality, when managed according to phenological development.

2.7 Factors affecting plant growth and persistence in pastures

2.7.1 Temperature and light

The response of grazed temperate grasses to temperature varies between species in terms of their growth habit, leaf appearance rate, leaf area expansion, tiller production and carbohydrate levels in roots or stems (Hill and Pearson 1985).

Temperature and light are both primary determinants of leaf growth. It is generally agreed that 20-25°C is the optimal temperature range for most aspects of leaf growth for grasses (Duru and Ducrocq 2000a). However, the various components of leaf expansion have different optimal temperatures. At about 25°C, leaves appear most

rapidly and are longest, but they are widest at 15°C. As a result, leaf area is greatest at about 20°C (Cooper 1964).

Mitchell and Soper (1958) compared leaf growth of perennial ryegrass plants subjected to a higher temperature (24°C) and shading (ranging from full shade to 20% daylight), with plants subjected to 14°C and full light conditions. Under shaded conditions at 24°C, leaf blades were approximately twice the length and half the width of those grown in full daylight at 14°C. Interestingly, when plants were later transferred from one treatment to the other, leaves in mid-growth developed similar dimensions of those fully matured under the contrasting conditions. The authors concluded that the size of the stem apex and primordium did not limit the leaf dimensions at maturity, i.e. leaf dimensions were adaptable to prevailing conditions.

Like temperature, light is thought to have different effects on leaf length and width. While the effect of light on leaf appearance rate and leaf width is inconclusive, Cooper (1964) found that low light intensity acted to substantially increase leaf length. Cooper (1964) concluded that temperature and light have “different morphogenetic effects on the various components of expansion of the leaf surface, and that these effects can be traced back to differences in the pattern of cell division and extension in the young leaf” (p57). As explained in Section 2.2.1, differences in leaf width are primarily based on the number of cell rows across the leaf, while differences in leaf length are largely due to changes in cell length (Mitchell and Soper 1958). For example, under low temperatures, cells and therefore leaf length are shorter.

The significant development effects of light on leaf size are due to the essential role of light in photosynthetic reactions (Raven *et al.* 1999). Treharne *et al.* (1968) suggest that light intensity is the principal environmental variable affecting photosynthesis, while other factors such as temperature, water, nutrients and carbon dioxide may act to limit the maximal photosynthetic response.

Treharne and Cooper (1969) measured different temperature optima for growth between two temperate species [oats (*Avena sativa*) and perennial ryegrass] and two tropical species [maize (*Zea mays*) and buffelgrass (*Cenchrus ciliaris*)]. The

difference in growth response was attributed to differences in temperature optima of the main CO₂-fixing enzymes (Treharne and Cooper 1969). The activity of ribulose-1,5-biphosphate carboxylase is higher in temperate-origin grasses and is maximised between 20 to 25°C, while the activity of phosphoenolpyruvate carboxylase peaks between 30 to 35°C in tropical-origin grasses. The authors suggest that the temperature sensitivity of these enzymes may be an important factor influencing leaf photosynthesis.

Wilson and Ford (1973) examined a wide range of tropical and temperate grass species to compare the effects of temperature on IVDMD and the concentration of WSC reserves. To avoid stage of plant development influencing the assessment of temperature effects, plants were harvested at the same stage of early vegetative development – two days after the fifth leaf on the main stem had reached maximum length. Increasing temperature (from 21/13°C to 32/24°C day/night combinations) had no effect on the digestibility of most tropical grasses at the 5-leaf stage, while the digestibility of the temperate grasses declined as temperature increased. The digestibility of the temperate grasses was generally higher than that of the tropical grasses at 21/13°C, but virtually no difference between the two groups was recorded at 32/24°C.

It is generally recognised that the optimal temperature for root growth is lower than that for shoot growth. At low temperatures, root weights peak – in early spring, with high WSC reserves in the plant, root growth exceeds shoot growth (Brouwer 1966). As temperatures increase, the typical flush of spring growth occurs and shoot growth exceeds root growth. Davidson (1969) further investigated the differing response of root and foliage weights to temperature. Results showed that root to shoot ratios were lowest at the optimal soil temperature for 12 pasture species and as soil temperature departed further from the optimum (either lower or higher), root growth relative to shoot growth increased.

Harrison (1934) grew Kentucky bluegrass in a greenhouse and found that the root and rhizome weights of plants grown at 15.5°C exceeded those of plants grown at 26.7°C or 37.8°C. Darrow (1939) observed a similar growth response to temperature and also noted a difference in root morphology. At lower temperatures roots were

larger in diameter, white, succulent, and coarsely branched. High temperature plants possessed small, light brown and very finely branched roots. Root elongation was greatest at lower temperatures. Stuckey (1941) drew attention to the fact that while root growth often ceases during summer, cell division in the root tips of grasses took place very near freezing point.

Forbes *et al.* (1997) conducted a study in which the impact of temperature change on the longevity of perennial ryegrass roots was investigated. A clear trend of decreasing longevity with increasing temperature was determined. While almost 70% of roots at 15°C survived for over 35 days, only around 16% remained alive at 27°C. The authors recognised that their observations may have been influenced by the effects of temperature on other soil processes (i.e. N mineralisation) and concluded: “although the data truly represent what occurred as a consequence of different temperatures it does not permit identification of the mechanism responsible” (p89). Soil moisture (which was closely regulated) and mycorrhiza fungi (less than 1% at all temperatures) were eliminated as possible interactions.

2.7.1.1 Cocksfoot

As previously discussed, under non-irrigated conditions, cocksfoot displays greater summer and autumn growth than perennial ryegrass. Jung and Kocher (1974) claim that cocksfoot is also better able to survive adverse winter conditions than ryegrass. Moot *et al.* (2000) were the first to use the thermal time approach to determine the thermal time (Tt) and thermal base (Tb) requirements for the germination and emergence of common New Zealand pasture species. Thermal time is calculated as the mean temperature between two developmental stages minus the base temperature, below which no development occurs (Moot *et al.* 2000). Cocksfoot had a relatively high Tt requirement (Table 2.11) – providing a partial explanation for the slow establishment of this pasture species, particularly when sown during autumn.

Table 2.11 Estimates of the base temperature (Tb) in degrees Celsius (°C) and the thermal time (Tt) requirements in degree days (°Cd) for germination of herbage grass species (adapted from Moot *et al.* 2000).

Species	Cultivar	Tb (°C)	Tt (°Cd)
Perennial ryegrass	Nui	2.4	70
	Ruanui	1.4	78
	Embassy	1.9	93
Cocksfoot	Apanui	0	240
	Wana	0	319
Prairie grass	Matua	1.2	162
Phalaris	Maru	2.3	110
Tall fescue	Roa	2.1	120
Timothy	Kahu	3.5	70

Baker and Jung (1968) found that the optimal day/night temperature combination for cocksfoot was 21.6/11.7°C. As day temperature was increased from 21.6°C to 34.8°C, cocksfoot yield decreased by 64%. Similarly, Eagles (1967) observed an increase in the relative growth rate of the whole cocksfoot plant as temperature increased up to 20°C, and a decrease in relative growth rate above this temperature. However, the effect of temperature on the pattern of vegetative growth was also influenced by the climatic origin of the population.

Taylor *et al.* (1968) showed that cocksfoot cultivars originating from different climates may respond differently to the same temperatures and that growth at any given temperature may also be influenced by light intensity. Treharne *et al.* (1968) related differences in cultivar/temperature interactions to variation in rate of apparent photosynthesis. Results showed that a Portuguese cocksfoot ecotype (Mediterranean origin) possessed a significantly higher photosynthetic rate at 21°C and 29°C than the cultivars S.143 (semi-warm continental climatic origin) and 'Boone' (cool-marine climatic origin).

Treharne *et al.* (1968) found that the optimal leaf age for photosynthesis (the young newly expanded leaf stage) coincided with the optimal exposure of these leaves to light, from a position in the upper canopy of the cocksfoot sward. Older, shaded leaves in the lower canopy exhibited a small net loss of WSC reserves because

respiration exceeded photosynthesis. There is an obvious need then, to adopt a grazing management approach that minimises shading and senescence of grass leaves. The grazing of pasture with senescent material leads to both wastage of feed through rejection by grazing stock and reduced herbage quality (Fulkerson and Donaghy 2001).

When equal radiant energy was supplied to two cocksfoot populations, photoperiod had a significant effect on the pattern of leaf growth (Templeton *et al.* 1969). Plants exposed to a shorter 10-hour photoperiod exhibited more rapid leaf emergence than plants exposed to a longer 20-hour photoperiod. Short photoperiod plants also had a greater total length of exposed leaf blades during early weeks of growth and a lower shoot to root ratio. However, the rate of cocksfoot leaf emergence in mid-summer (new leaf every 7-10 days) is approximately five times faster than the winter rate (Rawnsley 2000), despite the fact the photoperiod in mid-summer is particularly long. Such results are a reminder to consider the importance of interactions between environmental variables and their overall effect on plant growth.

2.7.1.2 Prairie grass

Hill and Pearson (1985) noted inhibition of reproductive development in prairie grass with increasing temperature, with non-reproductive development occurring as temperatures increased above a day/night combination of 24/19°C. At 15/10°C, prairie grass headed within 200 days of sowing, while at 18/13°C, heading took place within 238 days. The early flowering observed at 15/10°C appeared to suppress leaf production, markedly reducing leaf dry weight.

Hill *et al.* (1985) based experiments on the hypothesis that there are differences in seedling growth between species and between cultivars of temperate grasses that are attributable to differences in plant growth and responses to temperature. The results showed that for optimal establishment of Matua prairie grass, day temperatures should be between 18 and 21°C. Outside this narrow range, both DM yield per tiller and tiller number per plant decline. At low (15/10°C) and high (24/19°C) temperatures Matua is disadvantaged, with delayed and slow tillering. At low temperatures, germination is also inhibited and rate of dormancy increased (Hill *et al.*

1985). When Matua was sown in soil at 7.9°C in a New Zealand-based trial, it took over 50 days from sowing for 70-80% emergence (Hume 1991d).

Although prairie grass is noted for its high winter yields, extremely cold winter conditions inhibit productivity considerably. Frame and Morrison (1991) observed the effect of low winter temperatures and air frost on prairie grass growth in the United Kingdom. Winter damage and winter kill of tillers and leaves prior to spring led to a sparse sward with poor productivity. Frequent air frost and low soil and air temperatures caused stunting and discolouration of prairie grass growth, which did not improve until the following summer.

2.7.2 Soil properties

Grasses have high demands for mineral N and as a result, the soil concentration of mineral N under pasture is often below the required levels to sustain optimal growth. Grasses require mineral N to produce protein and chlorophyll, and at levels sufficient for tillering, leaf elongation, regrowth after grazing and reproduction. Grass roots can absorb, effectively utilise and produce similar yields from ammonium, nitrate or urea forms of N (Simpson 1987).

As dairy pastures in Tasmania generally incorporate white clover with a grass species (currently perennial ryegrass), consideration of the effect of fertiliser regimes on the clover pasture component is necessary. Application of N to a grass and clover mixture increases the growth rate of the grass component, leading to grass dominance and in some cases, eventual elimination of the clover component through shading (Miller 1984). Additionally, application of N reduces clover nodulation and N fixation – the response varying with clover cultivar, *Rhizobium* strain, form and amount of N, age and size of the host plant, and environmental conditions (Young 1958; cited in Frame and Newbould 1986). The value of overall increased herbage production must be weighed against the detrimental effects of N fertiliser on clover performance. Strategic N application and appropriate management to minimise the resultant shading should then encourage the production and persistence of both grass and clover pasture components of a mixed sward.

Phosphorus is required for good root development early in the plant life cycle (Miller 1984). Without an adequate supply of P, the plant will not reach its maximum growth, yield or reproductive potential. The functions of P range from the primary mechanism of energy transfer to the coding of genes, which cannot be performed by any other nutrient (Miller and Reetz 1995). In a controlled glasshouse study Templeton *et al.* (1969) found that increasing the P supply hastened cocksfoot leaf elongation, increased the length of individual leaves and increased the total length of exposed leaf blades.

Potassium is taken up in large amounts by plants and unless the soil is replenished with K, deficiencies will ensue. Potassium aids plants in resisting attack from disease and insects, cold weather, and drought, and its functions include stomatal opening and closure, and sugar transport (Miller and Reetz 1995). A high N rate will increase uptake of both N and K from the soil, which in turn may reduce Mg uptake (MacLeod 1965; Auda *et al.* 1966; Singh *et al.* 1967).

2.7.2.1 Cocksfoot

While cocksfoot is well known for its ability to survive under moderate soil fertility and drought conditions, sufficient nutrition, moisture and drainage are required for uniform DM production throughout the year.

When soil fertility is low, the greatest proportion of total seasonal yield for cocksfoot occurs in spring (Miller 1984). With N and K fertilisation, grass yield increases due to the increased number of tillers, and increased leaf DM/tiller. The results of a study carried out by Totev *et al.* (1994) suggested an annual N rate of 160 kg/ha was particularly cost-effective. Although the response of perennial ryegrass to N fertiliser was greater than the response of cocksfoot to N (133% increase in ryegrass yield versus 90% increase in cocksfoot yield), the cocksfoot pasture had a greater overall DM yield than ryegrass under the recommended rate of N (11 versus 5.4 t DM/ha).

The effect of N on growth (a decrease in the proportion of highly digestible stem material) results in decreased IVDMD of cocksfoot herbage, when N is supplied close to or later than the heading stage (Duru *et al.* 2000). Duru and Ducroqc (2000b) observed a greater increase in mature lamina length between successive leaves and

therefore a greater length of senescent leaves under N supply of 120 kg/ha, as well as a more rapid rate of leaf senescence, and suggested these changes further explain the fall in herbage digestibility that follows N fertilisation.

Volaire and Thomas (1995) investigated the response of two cocksfoot populations to prolonged soil moisture deficit and found that leaf extension ceased, plant moisture content declined and WSC reserves decreased in both cultivars as drought progressed. The most pronounced difference between the two populations was the survival of all tillers of the drought resistant population and the death of 34% of the susceptible population's tillers. An important adaptive trait of the drought resistant plants was the ability to accumulate greater concentrations of WSC in tiller bases. The role of WSC reserves in response to drought conditions is discussed in Section 2.4.1.

2.7.2.2 Prairie grass

High soil fertility is required for high production levels of herbage and persistence of prairie grass. Scheneiter and Rimieri (2001) explained that this is why, without other limiting factors, N fertiliser is needed to keep high tiller population density in swards. The significant response of prairie grass to N was shown through the linear response of annual DM accumulation to increasing levels of N fertiliser, indicating that N was still limiting growth at the highest N levels of 375 kg/ha per year. However, a previous study showed no difference in annual DM accumulation over fertiliser rates of 168 kg/ha per year (Belesky and Stout 1994).

Clark (1985) recommended application of N soon after seedling emergence (e.g. 50 kg/ha urea) to accelerate establishment and ensure satisfactory yields. High soil fertility should then be maintained by applying at least 250 kg/ha of superphosphate equivalent fertiliser with strategic applications (i.e. in autumn or spring) as required.

As well as high soil fertility, prairie grass requires free drainage, a $\text{pH}_{(\text{water})}$ between 6.0 and 6.5, and very low aluminium (Al) levels. Tillering is reduced under low fertility or acidic conditions (Stewart 1996). According to Thom *et al.* (1990), successful establishment of prairie grass in a cultivated seedbed may require higher than usual inputs of elemental fertiliser and lime. Clark (1985) claims that best

establishment of Matua follows a green-feed crop like turnips or rape. This helps improve initial soil fertility and minimise the threat of weeds.

2.7.3 Pests and pathogens

Invertebrate pests can cause substantial losses to pasture production and can result in deterioration of the sown species in the sward. Unfortunately, the timing and distribution of outbreaks are unpredictable and there have been few quantitative studies to rank the effects of invertebrate pests on pasture productivity. This makes it difficult to quantify the damage and economic importance of invertebrate pests in southern regions of Australia (Allen 1987).

Similarly, research of pasture grass diseases in southern Australia is lacking. Prior to 1970, diseases of Australian pastures were not considered a serious problem and were therefore not investigated or controlled. This perception prevails today, despite the fact the development of improved pastures using introduced legumes and grass species has increased the likelihood of pastures suffering economic loss from plant diseases (Clarke and Eagling 1994). Overseas studies indicate the importance of the impact viral and fungal diseases have on pasture productivity and herbage quality and the need for investigation of the distribution, incidence and effect of these diseases in Australia (Johnstone and Barbetti 1987).

2.7.3.1 Cocksfoot

There have been few reports of serious pests and pathogens of cocksfoot in Australia and New Zealand (Lolicato and Rumball 1994). Additionally, cocksfoot appears to be resistant to many insects and diseases. Fraser (1994) monitored changes in dryland pasture composition over five years in Canterbury, New Zealand, and reported the apparent resistance of cocksfoot to grass grub (*Costelytra zealandica*). While grass grub densities increased to high levels (220/m²) in perennial ryegrass pastures and severely reduced the ryegrass plant population, a lower grass grub density occupied the cocksfoot population with no apparent loss of plants.

Similarly, Slay (2002) reported the results of a study in which the tolerance of cocksfoot to Tasmanian grass grub (*Oxychanus fuscomaculatus*) in Hawke's Bay, New Zealand, was proven. Three years after sowing new pastures, cocksfoot based

pastures had lower levels of Tasmanian grass grub larvae than the perennial ryegrass based pasture. Between mid-2001 and 2002, perennial ryegrass pasture showed a 115% increase in larvae/m², and a 75% increase in the distribution of larvae in the paddock, while cocksfoot pasture showed a reduction in both larval population and distribution. The apparent tolerance of cocksfoot may be explained by higher plant density during summer (which translates to a less attractive site for egg laying), as well as a strong root system (inhibiting burrowing and subsequent egg laying of the beetles).

Newly sown pastures are particularly susceptible to the larvae of Argentine stem weevil (*Listronotus bonariensis*), a pest of New Zealand pastures. This is of particular importance for cocksfoot plants, which can take over two years to reach their full growth potential. However, mature cocksfoot plants are considered to be tolerant of this pest (Hume and Chapman 1993).

Few pathogens are known to have a significant detrimental effect on cocksfoot pasture in the temperate climate of southern Australia. In Tasmania, barley yellow dwarf virus has been identified as a potential threat to pastures, but was found to be less problematic for cocksfoot than perennial ryegrass and tall fescue (Guy *et al.* 1986). Stem rust is an important disease of cocksfoot, but many cultivars display resistance. A number of viruses of cocksfoot have not yet been detected in Australia, including cocksfoot mottle, cocksfoot mild mosaic and cocksfoot streak viruses (Clarke and Eagling 1994).

2.7.3.2 Prairie grass

In New Zealand, damage caused by Argentine stem weevil, Hessian fly and black beetle have been recognised as an important factors involved in pasture decline – evident in reduced plant and tiller density and a general decline in growth (Thom *et al.* 1989).

Argentine stem weevil is an important insect pest of prairie grass. Mature plants are less susceptible than seedlings because they have a higher proportion of thick, fleshy tillers, which act to protect growing points from damage (Thom *et al.* 1989). Recent reports from New Zealand suggest that prairie grass is also highly susceptible to

Hessian fly (*Mayetiola destructor*). Thom *et al.* (1989) reported a tiller death range of 20-82% due to damage by Hessian fly between November 1987 and May 1988. Black beetles (*Heteronychus arator*) are a localised pasture pest in the northern North Island of New Zealand, and are responsible for sporadic tiller death of up to 4% in prairie grass swards (Thom *et al.* 1989).

Leaf spot and leaf tip dieback were the symptoms of a foliar disease outbreak in New Zealand, caused by the anthracnose fungus *Colletotrichum graminicola*. Visual estimates suggested the rotting herbage resulted in up to 50% DM loss (Thom *et al.* 1989). Head smut (caused by *Ustilago bullata*) is another pathogen noted for its detrimental effect on prairie grass productivity. This fungus can reduce seedling establishment, and reduce productivity and seed yields of infected swards. Seed treatment ensures good seedling establishment by reducing effects of both *U. bullata* and soil-borne fungal pathogens (Falloon 1985). Susceptibility to powdery mildew in northeast United States has also been reported (Leath *et al.* 1990), where many prairie grass leaves were killed as a result of the fungal pathogen covering a large proportion of leaf surface.

None of the pests and pathogens described have been observed in Tasmanian prairie grass pastures (Belton 1992). However, control of lucerne flea has been identified as a requirement for the successful establishment of prairie grass pastures in Tasmania. Lucerne flea appeared to favour prairie grass over perennial ryegrass, attacking only white clover in a ryegrass/clover mixture, and both prairie grass and white clover in a prairie grass/clover mixture. Marked visual effects were observed on prairie grass plants, particularly on younger leaves and seedlings (Belton 1992).

2.7.4 Influence of grazing management

The results of early studies of cocksfoot and prairie grass were often misleading due to the difficulties encountered in regard to grazing management. Species-specific management of dairy pastures is required for the maintenance of high herbage quality and productivity, as well as maximisation of pasture utilisation. Grazing management is most effective when based on the physiological status of the grass plant (Fulkerson and Donaghy 2001).

However, even when grazing is managed in relation to a plant's growth cycle, either earlier defoliation or cutting for conservation may be necessary at times, to ensure utilisation of growth peaks (Fulkerson *et al.* 1993).

2.7.4.1 Cocksfoot

When the effect of grazing management, fertiliser, land aspect and slope on cocksfoot productivity and persistence were measured, results showed that cocksfoot was most dramatically affected by grazing management (Barker *et al.* 1991). As is the case with many grasses, cocksfoot is better suited to rotational grazing than continuous grazing (Chapman and Campbell 1986). Under continuous grazing, the persistence of cocksfoot is generally very poor (Avery *et al.* 2000; Warn 1998). Continuous grazing (Lambert *et al.* 1983) and close grazing reduce the performance of cocksfoot, largely as a result of damage to elevated growing points and reduced tillering caused by treading (Brougham 1960). Out of 10 pasture species, Edmond (1964) found that perennial ryegrass ranked first and cocksfoot eighth in terms of tolerance to heavy treading.

Brock *et al.* (1996) reported the significant effect of grazing management on the DM and length of leaves, tillers and stems, which occurs to a greater extent for cocksfoot than ryegrass. While perennial ryegrass suffered a 60% DM reduction under set stocking compared with rotational grazing, the production of Grasslands Wana cocksfoot decreased by 75%. The cocksfoot cultivars Grasslands Kara and Grasslands Apanui failed to survive at all under a prolonged period of set stocking. Perennial ryegrass and Wana were able to survive (although they were inhibited by) the frequent defoliation of continuous grazing by adopting a more prostrate growth habit than the more erect Kara and Apanui. Similar investigations confirmed that even the productivity of Wana - a cultivar developed to withstand moderate to severe grazing pressure (Moloney 1993) - is considerably inhibited by continuous grazing, with less than half the DM produced compared with plants subject to rotational grazing (Barker *et al.* 1991).

Under rotational grazing, defoliation interval has a significant effect on plant persistence and productivity. Fulkerson *et al.* (1993) explained how increased defoliation frequency reduces the persistence and production of pasture grasses.

Surviving, but weakened plants have reduced root weight and energy reserves, and are therefore more vulnerable to stresses the following season (i.e. moisture and pathogens). Extending the defoliation interval up to the onset of leaf senescence should increase pasture persistence and production, provided the herbage can be effectively utilised.

Rawnsley *et al.* (2002) reported on the results of a glasshouse study in which the physiological and morphological changes in cocksfoot during regrowth following defoliation were investigated. A significant linear relationship existed between leaf and root DM produced at each leaf regrowth stage and stubble WSC content (mg/tiller). There was significantly higher total WSC content in stubble and roots at the 5-leaf and 6-leaf stages, than at any previous regrowth stage. These results led to the conclusion that the optimal grazing interval for cocksfoot swards lies between the four and five leaves per tiller stage of regrowth. Delaying defoliation until after this stage results in loss of herbage DM and herbage quality, due to the onset of leaf senescence and an increase in fibre content. The importance of WSC reserves in regrowth following defoliation is further discussed in Section 2.4.1.

2.7.4.2 Prairie grass

Matua prairie grass is sensitive to overgrazing and therefore grazing recommendations generally promote infrequent defoliation. It is widely accepted that the interval between grazing or cutting must be long enough to allow sufficient regrowth between grazing events (Alexander 1985; Clark 1985; Stewart 1996). Management based on the physiological state of the sward has been shown to increase the persistence and production of prairie grass considerably (Black and Chu 1989; Thom *et al.* 1990; Fulkerson and Slack 1995). Reports on the effects of grazing on prairie grass productivity and persistence state that both frequent and close grazing are detrimental (Hume 1991a;c). Certainly, rotational grazing has benefits over continuous grazing – but how long should the grazing interval be, and how closely should pastures be grazed during each defoliation event?

Alexander (1985) measured the persistence and productivity of irrigated Matua prairie grass pastures under four grazing regimes using sheep – frequent or infrequent (grazed every three or six weeks), with lax or severe defoliation (grazed to

7.5 or 2.5 cm). Matua performance was consistent and impressive under infrequent severe grazing, whereas production under infrequent laxly grazed pastures declined. In the pasture grazed frequently and severely, clover and weeds began to replace Matua plants. This was partially reversed by implementation of infrequent and severe grazing.

Black and Chu (1989) based grazing interval on the time it took for new tillers to appear. Tiller appearance was regarded as an indication of increasing carbohydrate levels and therefore an energy reserve status adequate to support regrowth following defoliation. When new tillers appeared, close grazing was implemented. Positive results included higher pasture intake and utilisation, more DM harvested and an increased plant population density.

Fulkerson *et al.* (2000) found that a grazing rotation based on the 3.5 to 4-leaf regrowth stage favoured prairie grass growth throughout the year. In contrast, setting the grazing interval at the 1.5-leaf stage was shown to significantly reduce plant survival and productivity over a period of three years, as the short grazing interval did not allow sufficient time for the plant to replenish its energy reserves. When grazed at the 4-leaf stage, more than twice as many plants survived the summer and twice as many seedlings were recruited the following autumn, compared with grazing at the 1.5-leaf stage. As leaf appearance interval largely depends on ambient temperature, the grazing interval can be set at an appropriate regrowth stage (i.e. four leaves per tiller), irrespective of season or location (Fulkerson and Donaghy 2001).

For prairie grass, the low number of tillers per plant is thought to heavily contribute to the sensitivity of this species to frequent grazing (Hill and Pearson 1985). Rapid attainment of a leaf area sufficient to maintain a positive carbon balance is dependent on individual leaf growth from relatively few tillers. The duration of each regrowth under frequent grazing may not be adequate for leaf area expansion to provide sufficient carbohydrate storage to support further tiller production (Hill and Pearson 1985).

Management during autumn is of particular interest to researchers and farmers because prairie grass is capable of maintaining herbage of high herbage quality throughout autumn. Hall *et al.* (1996) implemented a variety of management practices during autumn to investigate the effect on herbage quality. Results showed the management practices that allowed prairie grass to mature in autumn reduced CP concentrations but had a limited effect on IVDMD content. Delaying harvest in spring caused a decrease in both CP and IVDMD, but not to the extent reported for other cool-season grasses. With respect to herbage quality, grazing management can therefore be relatively flexible during autumn. However, autumn management practices have a significant effect on other parameters, including plant survival and DM yield.

Jung *et al.* (1994) discovered that winter survival of prairie grass was greatly improved by harvesting in early autumn (rather than late autumn) and/or multiple harvests, leaving relatively high stubble (12.5 versus 7.5 cm). These autumn management treatments also improved spring yield and vigour. Rest periods longer than 50 days during autumn had detrimental effects of seedling survival, winter hardiness, spring forage production and plant vigour. A rest period during summer was also recommended to allow natural reseeding to proceed.

Chapter 3

The effect of leaf stage based defoliation management on perennial ryegrass, prairie grass and cocksfoot under dryland conditions: Regrowth, tillering and water-soluble carbohydrate content

3.1 Introduction

The dryland dairy regions of southern Australia may benefit from the introduction of cocksfoot and prairie grass, alternative species that have been shown to possess good persistence and productivity attributes comparable to perennial ryegrass under appropriate management (Crush *et al.* 1989; Mitchell 1997; Lowe *et al.* 1999a; Fulkerson *et al.* 2000).

The reversion of many New Zealand, southern Victorian and Tasmanian dryland pastures to cocksfoot dominance over several years emphasises the adaptive nature of this species to dry summer conditions (Moloney 1993; Fraser 1994). Under appropriate management, mature cocksfoot plants not only survive, but also remain productive during summer months (Christie and McElroy 1995). With a well-reported tolerance of low soil fertility (Norton *et al.* 1999) and of attack by insects and pathogens (Guy *et al.* 1986; Fraser 1994; Lolicato and Rumball 1994; Slay 2002), cocksfoot is worthy of consideration as an alternative to perennial ryegrass in southern Australia.

Prairie grass is another potential alternative for the dairy pastures of southern Australia, as it is characterised by good summer growth, drought tolerance, insect tolerance and high palatability (Fraser 1982; DeLacy 1987). Vartha (1977) reported that DM utilisation of prairie grass was 53% greater than that of ryegrass (13.2 versus 8.6 t DM/ha) in a dryland study on the South Island of New Zealand, largely due to the greater productivity of prairie grass over the summer months.

Species-specific management of these grasses is required to obtain an objective assessment of their individual value as dairy pasture species. Leaf stage is a useful plant-related indicator of the optimal time to defoliate, based on the physiological

state of the plant and its readiness to be grazed (Fulkerson and Donaghy 2001). It is a generic measure of regrowth, as leaf appearance rate is primarily influenced by temperature and to a lesser extent moisture availability and is independent of cultivar type and soil fertility (Mitchell 1953; Barker *et al.* 1985; Van Loo 1992).

Water-soluble carbohydrate levels are affected by defoliation severity, as indicated by residual height of the stubble (Troughton 1957; Davidson and Milthorpe 1966a; Wilson and Robson 1970), as well as the interval between defoliations (Davies 1965; Bell and Ritchie 1989; Hume 1991a; Fulkerson and Slack 1994a; Fulkerson and Slack 1995; Fulkerson and Donaghy 2001). Defoliation interval is generally of primary importance, followed by stubble height (Bell and Ritchie 1989; Fulkerson and Donaghy 2001).

For perennial ryegrass, the optimal time of defoliation has been defined as the 2-leaf to 3-leaf stage of regrowth. This interval allows sufficient time for the replenishment of WSC energy reserves in the stubble, which in turn maximises leaf growth, root growth and tillering (Fulkerson and Donaghy 2001). Cocksfoot maintains around five live leaves per tiller, with defoliation recommended between the 4-leaf and 5-leaf stages (Rawnsley *et al.* 2002). Prairie grass maintains between five and six live leaves per tiller (Belton 1992) with defoliation recommended between the 3.5-leaf and 5-leaf stages (Hume 1991a; Fulkerson *et al.* 2000).

A field study was undertaken to investigate the effect of leaf stage based defoliation management on the herbage productivity and survival of perennial ryegrass, prairie grass and cocksfoot.

3.2 Materials and methods

3.2.1 Site

This study was conducted between April 2003 and May 2004, on a black vertosol, haplic soil (Isbell 1996) at the University of Tasmania Farm, Cambridge, Tasmania, Australia (elevation 10 m, longitude 147°E, latitude 43°S, annual rainfall 602.3 mm). The mean daily maximum and minimum temperatures and monthly rainfall for this study period are shown in Figure 3.1. Intermittent irrigation of the plots from April to June 2003 aided the establishment of seedlings, but was discontinued for the

remainder of the study. The soil had a high nutrient status (Olsen P = 64.8 mg/kg, Ammonium acetate K = 224 mg/kg), with a neutral topsoil [pH (H₂O) = 6.7].

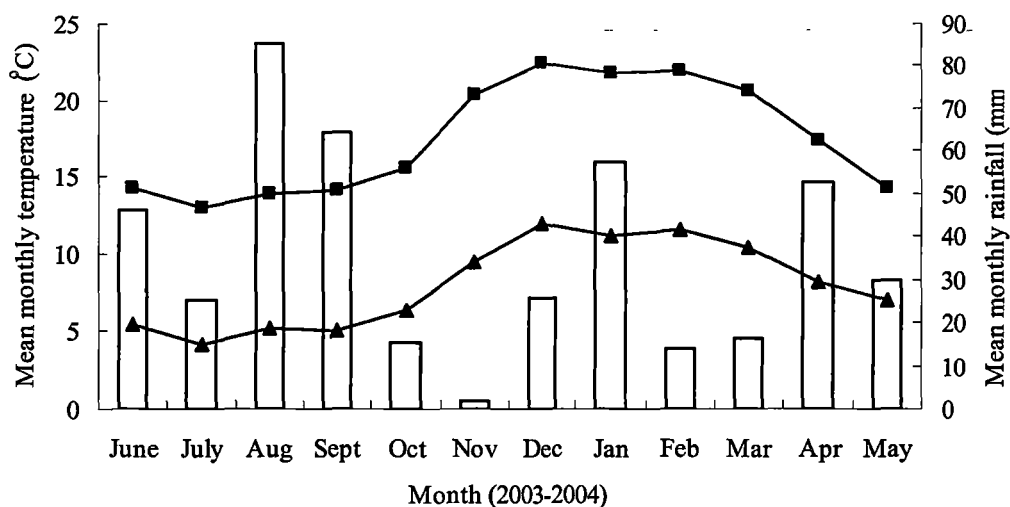


Figure 3.1 Mean monthly maximum (■) and minimum (▲) temperature and monthly rainfall (□) for Cambridge, Tasmania, from June 2003 to May 2004.

3.2.2 Pasture establishment

The site was sprayed with the non-selective herbicide Roundup® (a.i. 36% glyphosate), ploughed and then harrowed prior to sowing. Plots were hand sown on April 29 2003, with 25 kg/ha of Impact perennial ryegrass, 18 kg/ha of Kara cocksfoot and 55 kg/ha of Matua prairie grass. Mixed fertiliser (3% N, 15% P, 13% K) was applied prior to harrowing at a rate of 133 kg/ha. Urea (46% N) was applied at a rate of 100 kg/ha at approximately two months from sowing, and then at monthly intervals until November, when declining soil moisture levels reduced the effectiveness of the applied N. On June 17 2003, the selective herbicides Bromicide 200® (a.i. 20% bromoxynil) and MCPA 500® (a.i. 50% MCPA) were applied at 1.5 L/ha to eradicate wild radish (*Raphanus raphanistrum* L.) and smaller populations of other broad-leaved weeds. A second herbicide application of MCPA 500® was applied (2.2 L/ha) on July 23 2003, to control stagger weed (*Stachys arvenis* L.) which had germinated following the first herbicide application. On August 20 2003, when plants were three months old (coinciding with the 3-leaf stage of perennial ryegrass and the 4-leaf stage of both cocksfoot and prairie grass), the plots were defoliated to a height of 45 mm with a rotary mower.

3.2.3 *Experimental design*

Thirty-six 2 by 3 m plots were arranged in a split plot design, with species as the main treatment plots and defoliation interval arranged as subtreatment plots. Each treatment was replicated four times.

Treatment details were as follows:

Species: Perennial ryegrass, cocksfoot or prairie grass.

Defoliation interval: Defoliation interval treatments were implemented from October 2003 to June 2004, with defoliation management based on the time taken for either two, three or four leaves per tiller to fully expand for each species. The expansion of each new leaf was termed a 'leaf stage'.

3.2.4 *Measurements*

Defoliation treatments and associated measurements commenced in September 2003, and were completed in June 2004, when the accumulative leaf regrowth stage for each treatment coincided (i.e. with 2-leaf, 3-leaf and 4-leaf stage treatments implemented six, four and three times, respectively).

A herbage sample from each plot was collected at each defoliation event and a target grass sub-sample taken for subsequent analysis of ME, digestible dry matter (DDM), ADF, NDF and total N concentrations. The results from these measurements are reported in Chapter 4.

Herbage DM yield

Herbage yield for each species in response to defoliation treatments was determined by harvesting each plot to a height of 45 mm. The resultant total plot wet grass sample was weighed immediately and a subsample (approximately 100 g fresh weight) taken and dried at 60°C for 48 hours for determination of yield on a DM basis. Pasture DM yield (converted to kg DM/ha) was obtained for each species at each defoliation event.



Plate 1 Measuring wet weight from field plots of perennial ryegrass, cocksfoot and prairie grass.

Botanical composition

A herbage sample above 45 mm height was collected from three locations within each plot (approximately 100 g fresh weight) immediately prior to each defoliation event, from approximately the same location at each defoliation treatment. Each sample was mixed thoroughly and sorted into the following categories: target grass species (i.e. ryegrass, cocksfoot or prairie grass), other grass species and broadleaved weed species. These samples were dried separately at 60°C for 48 hours, and the dry weight recorded.

WSC reserves

In September and November 2003, and January, March and May 2004, plants from each plot were destructively harvested for WSC analysis. Three individual grass plants were randomly selected from each plot and harvested to ground level no later than three hours after sunrise, to negate the confounding effect of diurnal fluctuations in WSC content (Fulkerson and Slack 1994a). Care was taken to collect plants at a similar stage of phenological development (i.e. vegetative or reproductive), as the

pattern of WSC accumulation and storage changes as tillers become reproductive (Sprague and Sullivan 1950). After harvesting, leaves of each plant were removed so that 45 mm of stubble remained. Each stubble sample was stored on ice to minimise loss of WSC reserves through respiration, and samples were then frozen at -18°C for 24 hours prior to freeze-drying. Following freeze-drying, individual tiller DM yield and number of tillers per plant were recorded. Samples were ground through a 1 mm screen and analysed for WSC reserves at New South Wales Department of Primary Industries Laboratories by Technicon Industrial Method number 302-73A, derived from the method outlined by Smith (1969; Appendix A.1).

Plant density

In September and November 2003, and January, March and May 2004, the number of individual target grass, other grass and broadleaved weed plants inside two 30 x 30 cm quadrats for each plot were recorded. The quadrats were placed in the same locations at each monitoring event.

Tiller dynamics

On October 8 2003, eight individual tillers were marked with a wire loop along a diagonal transect across the full length of each plot. At 400 mm intervals along the transect a mature vegetative tiller without visible daughter tillers was selected and clearly identified with an anchored loop. Every three weeks from this date, the marked tillers were monitored and their status (live or dead, with or without a daughter tiller) recorded.

3.2.5 *Statistical analysis*

All statistical analyses were performed using the program SPSS (Version 11.5, SPSS Corporation, Wacker Drive, Illinois, USA). Least significant difference (LSD), as defined by Steel and Torrie (1960) was used for mean separation. Species and defoliation interval means for accumulated herbage DM yield were compared with an ANOVA split plot design. Means for plant density, tiller DM yield and number, WSC content and rates of daughter tiller initiation and tiller death, were compared using an ANOVA three-way factorial design with replication (time of assessment by species by defoliation interval).

3.3 Results

3.3.1 *Herbage DM yield and growth rates*

Irrespective of species, plants defoliated at the 2-leaf stage yielded significantly less DM than plants defoliated at the 3-leaf ($P < 0.05$) and 4-leaf stages ($P < 0.01$; Table 3.1). There was no significant ($P > 0.05$) difference in DM yield between plants defoliated at the 3-leaf and 4-leaf stages.

Table 3.1 Total accumulated production (t DM/ha) of prairie grass, cocksfoot and perennial ryegrass between October 2003 and June 2004, defoliated at the 2-leaf (2L), 3-leaf (3L) and 4-leaf stages (4L) of regrowth.

Leaf regrowth stage	Production (t DM/ha)				LSD ($P = 0.05$)
	Prairie grass	Cocksfoot	Ryegrass	Mean	
2L	5.15	3.73	3.98	4.28	0.35
3L	5.88	4.16	4.30	4.78	
4L	6.07	4.47	4.52	5.02	
Mean	5.70	4.12	4.27		
LSD ($P = 0.05$)	0.82				

Perennial ryegrass exhibited the slowest leaf appearance rate (mean 23 days per leaf compared with 22 days per leaf for cocksfoot and 16.5 days per leaf for prairie grass), and at the final defoliation of ryegrass plots, cocksfoot had produced an additional 1.25 leaves per tiller, which was equivalent to an additional 0.29 t DM/ha. Prairie grass produced an additional 3.5 leaves per tiller, equivalent to an additional 1.15 t DM/ha. When this additional growth was included and total DM yield of each species compared over the 242 days of treatments (October 7 2003 to June 6 2004), prairie grass yielded significantly more ($P < 0.001$) DM (5.70 t DM/ha) than both cocksfoot (4.12 t DM/ha) and perennial ryegrass (4.27 t DM/ha), while the difference in production between cocksfoot and perennial ryegrass was not significant ($P > 0.05$; Table 3.1).

The growth rate of prairie grass was generally greater than the growth rates of perennial ryegrass and cocksfoot, regardless of defoliation interval (Figure 3.2). Defoliation of prairie grass and cocksfoot at the 4-leaf stage resulted in greater growth rates compared with defoliation at the 2-leaf or 3-leaf stages of regrowth. In contrast, perennial ryegrass exhibited the greatest growth rate during spring when

defoliated at the 2-leaf stage of regrowth, and then exhibited greater growth rates under an extended defoliation interval during summer and autumn.

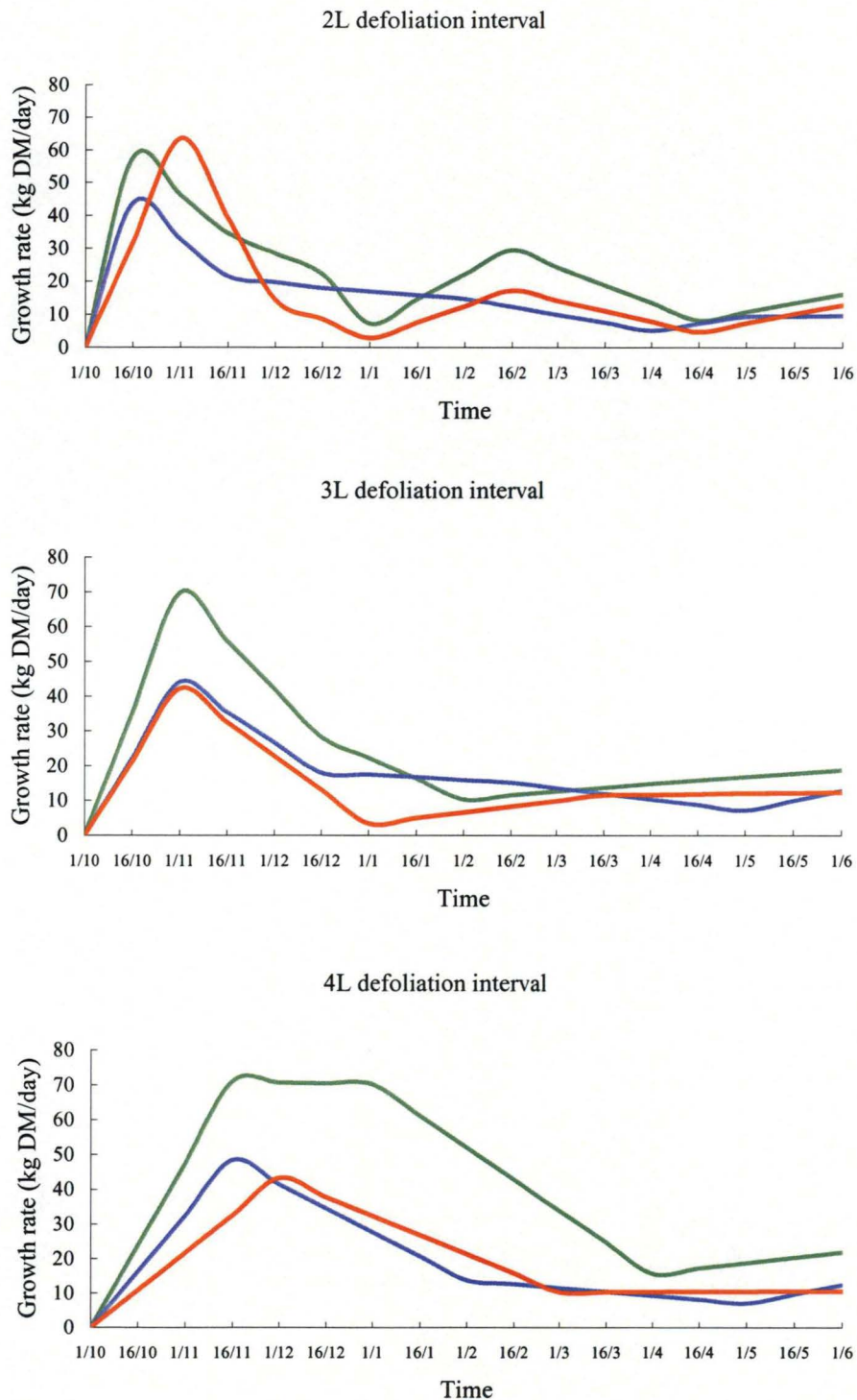


Figure 3.2 Mean growth rates (kg DM/day) for prairie grass (—), cocksfoot (—) and perennial ryegrass (—), at the 2-leaf (2L), 3-leaf (3L) and 4-leaf (4L) stages of regrowth, from October 2003 to June 2004.

3.3.2 WSC content

Defoliation interval had a significant ($P < 0.01$) effect on WSC content of all three species. Plants defoliated at the 4-leaf stage (13.7 mg/tiller) contained a significantly greater mean WSC content than plants defoliated at the 3-leaf ($P < 0.05$; 12.2 mg/tiller) and the 2-leaf stage ($P < 0.001$; 11.2 mg/tiller). There was no significant ($P > 0.05$) difference in WSC content between plants defoliated at the 2-leaf and 3-leaf stages of regrowth.

There was a significant ($P < 0.001$) interaction between species and time of assessment for WSC content (Table 3.2). Cocksfoot had a significantly higher ($P < 0.05$) WSC content than perennial ryegrass and prairie grass during late spring and summer. The species effect changed over time, with a significantly higher ($P < 0.05$) WSC content for prairie grass compared with perennial ryegrass and cocksfoot in early spring and autumn (Table 3.2).

Table 3.2 Mean WSC content (mg/tiller) of prairie grass, cocksfoot and perennial ryegrass defoliated at bi-monthly intervals.

	WSC content (mg/tiller)		
	Prairie grass	Cocksfoot	Ryegrass
Sept	33.0	13.9	7.0
Nov	10.3	21.0	9.0
Jan	8.2	15.3	8.2
Mar	16.5	7.9	8.3
May	12.9	5.8	8.4
LSD ($P = 0.05$)	3.3		

3.3.3 Plant density

There was a significant ($P < 0.01$) interaction between species and time of assessment for plant density (Table 3.3). Perennial ryegrass had a significantly higher ($P < 0.01$) plant density than cocksfoot, which in turn was significantly higher ($P < 0.01$) than prairie grass. The mean plant density of all species was significantly higher ($P < 0.01$) in January than for other assessment dates, with the exception of prairie grass in September. Prairie grass plant density was significantly lower ($P < 0.05$) in March and May compared with January. Defoliation interval had no significant ($P > 0.05$) effect on plant density throughout the experiment.

Table 3.3 Mean plant density (no. plants/m²) of prairie grass, cocksfoot and perennial ryegrass at bi-monthly intervals.

	Plant density (no/m ²)		
	Prairie grass	Cocksfoot	Ryegrass
Sept	183	259	284
Nov	149	217	312
Jan	184	306	385
Mar	128	218	319
May	119	153	263
LSD ($P = 0.05$)	29		

3.3.4 *Tiller DM yield and tiller number*

There was a significant ($P < 0.01$) interaction between species and time of assessment for both tiller DM yield and tiller number (Table 3.4). Mean individual tiller DM yield was consistently lower ($P < 0.01$) for perennial ryegrass than for both prairie grass and cocksfoot. Defoliation interval had a significant ($P < 0.05$) effect on individual tiller DM yield (data not presented), with defoliation at the 2-leaf stage (49 mg/tiller) resulting in significantly smaller tillers ($P < 0.05$) than defoliation at the 4-leaf stage (54 mg/tiller). There was no significant ($P > 0.05$) difference in tiller DM yield between the 2-leaf and 3-leaf stage treatments or the 3-leaf and 4-leaf stage treatments. Defoliation interval did not have a significant ($P > 0.05$) effect on tiller number per plant. There was a significantly greater ($P < 0.001$) mean tiller number per plant for perennial ryegrass compared with both prairie grass and cocksfoot, with the exceptions of the November and May assessments (Table 3.4). In November there was no significant ($P > 0.05$) difference between species, and in May there was a significantly greater ($P < 0.05$) mean tiller number per plant for prairie grass compared with cocksfoot. For all species there was a trend of increasing tiller number per plant with time of assessment.

Table 3.4 Mean tiller DM yield (mg/tiller) and tiller number per plant for prairie grass, cocksfoot and perennial ryegrass at bi-monthly intervals.

	Tiller mass (mg/tiller)			Tiller number/plant		
	Prairie grass	Cocksfoot	Ryegrass	Prairie grass	Cocksfoot	Ryegrass
Sept	78	52	23	12.8	10.0	17.6
Nov	51	60	28	13.8	12.2	16.1
Jan	61	69	35	17.4	15.8	27.7
Mar	76	61	40	23.0	21.3	27.7
May	52	48	37	25.5	20.3	22.4
LSD ($P = 0.05$)	8			4.0		

3.3.5 Tiller dynamics

There was evidence of a trend for a lower rate of daughter tiller initiation and an increased rate of tiller death for prairie grass compared with ryegrass and cocksfoot (Figure 3.3). However, there was no consistent significant ($P > 0.05$) difference in the proportion of daughter and dead tillers between species. Leaf stage defoliation treatments did not have an effect on tiller dynamics.

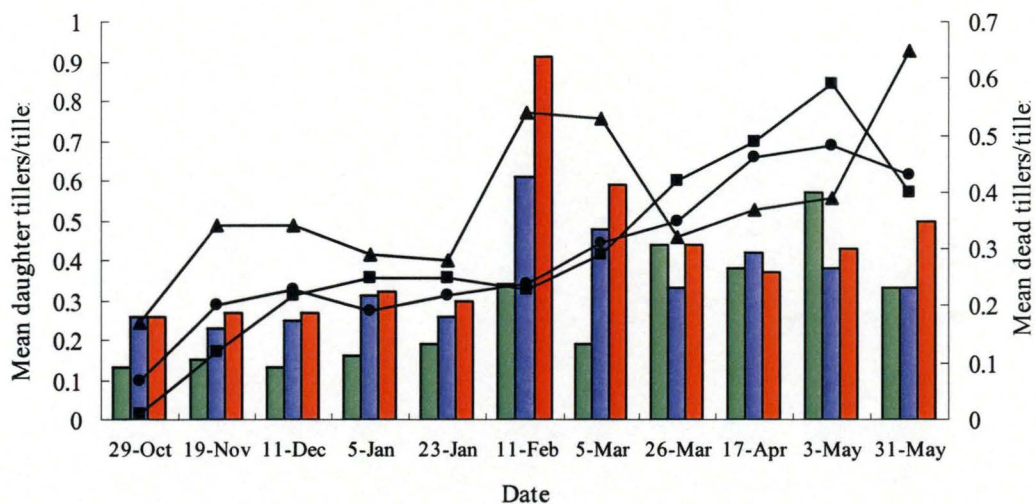


Figure 3.3 Mean proportions of daughter tillers per original marked tiller for prairie grass (■), cocksfoot (■) and perennial ryegrass (■), and dead tillers per original marked tiller for prairie grass (▲), cocksfoot (■) and perennial ryegrass (●) during the measurement period.

3.3.6 Botanical composition

The proportion of target species in cocksfoot plots was lower than for ryegrass and prairie grass plots at the beginning of the measurement phase, independent of defoliation interval (Figure 3.4). Cocksfoot plots were heavily invaded by other grass species during establishment, and to a smaller extent, broad-leaved weeds. By late December 2003, there was considerably less difference in the percentage composition of the target species.

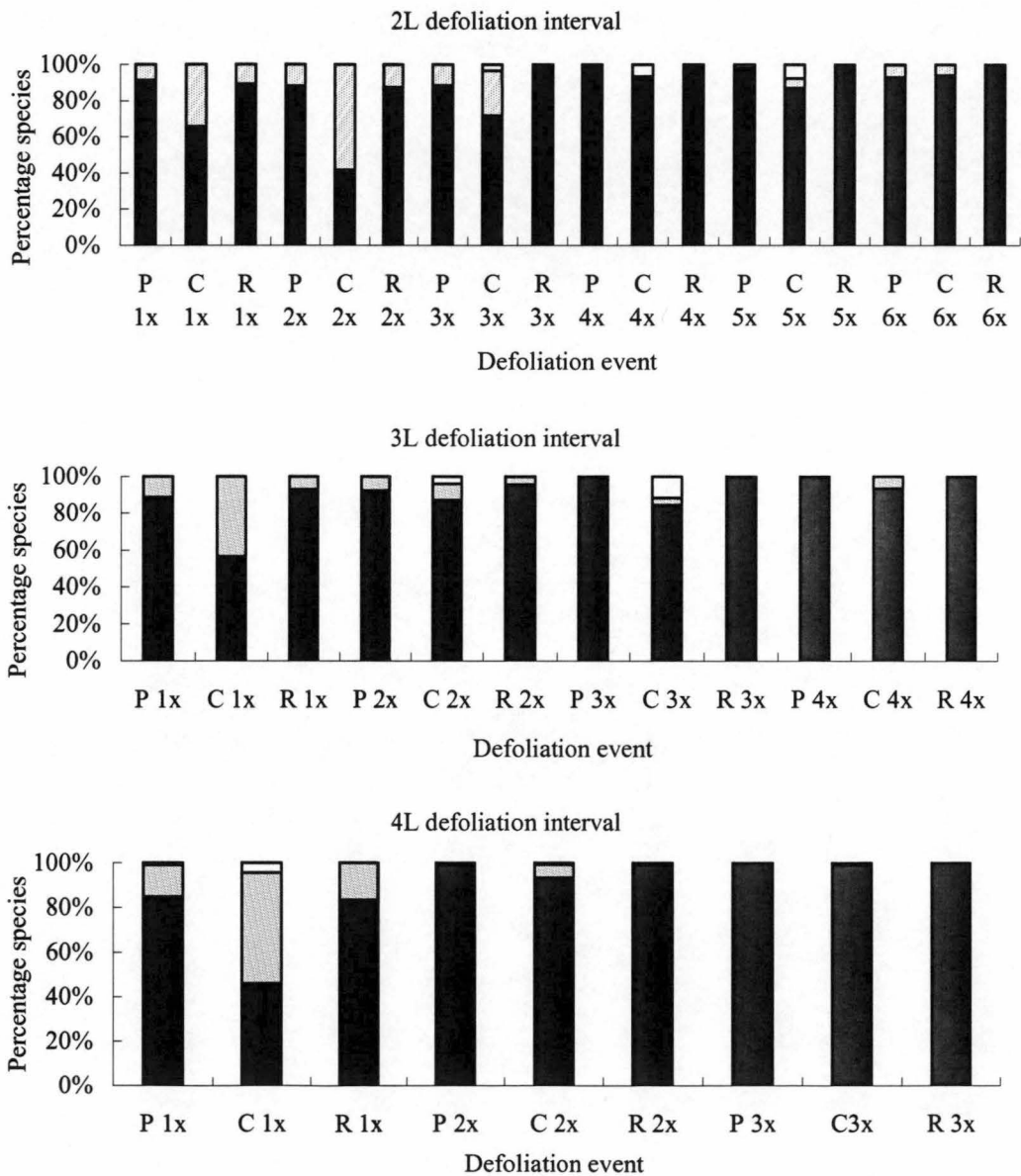


Figure 3.4 Percentage of target grass species (■), other grasses (▨) and broad-leaved weeds (□) in prairie grass (P), cocksfoot (C) and ryegrass (R) plots, under 2-leaf

(2L), 3-leaf (3L) and 4-leaf (4L) stage treatments, with defoliation event denoted by 1-6x.

3.4 Discussion

While perennial ryegrass is widely regarded as one of the most productive perennial pasture species, its productivity under the low rainfall conditions of the current study (433.7 mm annual rainfall compared with the mean annual rainfall of 602.3 mm) was inferior to prairie grass and equal to cocksfoot. There were considerable differences between species in terms of WSC content, patterns of tiller initiation and death, plant density and herbage DM yields. These differences altered over time in response to seasonal climatic changes. Defoliation interval had a marked effect on both WSC content and herbage DM yield of perennial ryegrass, cocksfoot and prairie grass.

Defoliation at the 4-leaf stage of regrowth led to greater WSC accumulation than defoliation at the 3-leaf and 2-leaf stages, while defoliation at the 2-leaf stage resulted in reduced DM production of all species compared with less frequent defoliation. The effect of less frequent defoliation on accumulation of WSC was particularly evident for prairie grass, with greatly increased DM yield during the summer months. Defoliation interval had no effect on plant density or tiller number per plant (the delayed effects of frequent defoliation would be expected the following year, after imposition of treatments), but there was a significant reduction in the tiller DM yield of plants defoliated at the 2-leaf stage of regrowth compared with plants defoliated less frequently. These results demonstrated that less frequent defoliation of pasture plants leads to greater WSC assimilation and therefore leaf and tiller DM accumulation during the subsequent recovery period (Hume 1991a;c; Stewart 1996; Fulkerson *et al.* 2000; Rawnsley *et al.* 2002).

The defoliation interval range in this study did not have an effect on tiller initiation and death of perennial ryegrass, as the defoliation treatments used were within the recommended defoliation interval for this species (i.e. between the 2-leaf and 3-leaf stages of regrowth; Fulkerson and Slack 1995; Fulkerson and Donaghy 2001). However, one would expect defoliation at the 2-leaf stage to disadvantage initiation and increase death of prairie grass and cocksfoot tillers compared with less frequent defoliation (Hume 1991a;c; Fulkerson *et al.* 2000; Rawnsley *et al.* 2002).

Basing defoliation intervals on leaf regrowth stages enabled a comparison of the leaf developmental rates of the three species, with prairie grass exhibiting the most rapid leaf regrowth rate, followed by cocksfoot and then perennial ryegrass. The differences in developmental rate resulted in different defoliation dates for each species. Perennial ryegrass was the last species to reach its final leaf stage defoliation treatments, by which time prairie grass and cocksfoot had produced a significant amount of additional herbage (0.29 and 1.15 t DM/ha, respectively), which was taken into account in the final DM results.

Despite low plant density and tiller number per plant, prairie grass out-yielded ryegrass and cocksfoot by at least 25%, reflecting its faster leaf appearance rate and larger leaves (Belton 1992; Hume 1991b). The current study recommends defoliation at the 4-leaf stage for prairie grass in preference to defoliation at the 2-leaf or 3-leaf stages, due to increased DM yield, and this is in general agreement with Fulkerson *et al.* (2000).

Although a higher level of herbage DM yield and WSC content resulted from defoliation of ryegrass at the 4-leaf stage compared with defoliation at the 2-leaf stage, death of the first leaf upon appearance of the fourth leaf increased the proportion of dead material and therefore decreased herbage quality and palatability (Fulkerson and Slack 1995; Fulkerson and Donaghy 2001). The recommended defoliation interval for perennial ryegrass remains between the 2-leaf (during periods of rapid growth e.g. spring) and 3-leaf (remainder of the year) stages to maximise growth rates, in agreement with Fulkerson and Donaghy (2001).

Despite its slow establishment, DM production of cocksfoot over the entire study period was equal to that of ryegrass. The results from this study are in agreement with Rawnsley *et al.* (2002), supporting the 4-leaf stage of regrowth as the optimal defoliation interval to maximise DM productivity and WSC accumulation.

The level of WSC reserves in cocksfoot was higher than in perennial ryegrass and prairie grass during late spring and summer. This occurrence was possibly a physiological response to dry, warm conditions, and as such, would contribute to the drought resistance of this species. For example, cocksfoot yields after recovery from

drought have been closely correlated with reserves of WSC stored in tiller bases during summer (Volaire and Thomas 1995).

In early spring and again in autumn prairie grass contained the highest level of WSC reserves. Fulkerson *et al.* (1998) reported results of a study in which prairie grass displayed the ability to accumulate more WSC reserves in spring than perennial ryegrass, concluding that this may reflect differences between species in respiratory loss of carbohydrates when under heat stress.

As the growth rates of prairie grass and cocksfoot were relatively high during these periods, the WSC reserve build up was therefore not due to slower growth but more likely due to a mechanism within the plants that increased photosynthesis or decreased respiration. Over time, these patterns of WSC accumulation may contribute to the enhanced persistence of prairie grass and cocksfoot compared with perennial ryegrass, thus requiring further study.

The WSC content of perennial ryegrass remained relatively constant throughout the measurement period, but was generally lower compared with WSC reserves in cocksfoot (September to January) and prairie grass (September, March to May). The growth rate of perennial ryegrass gradually increased from January 2004 (two months earlier than for cocksfoot), in response to summer rainfall. It is likely that the increased growth rate and tillering of perennial ryegrass from January 2004 reflected the utilisation of an increased pool of energy reserves accumulated between the November and January measurement periods, when growth rates were relatively low.

Tiller initiation of cocksfoot and ryegrass was greatest in February and March, following a period of increased rainfall in late December and January. Cocksfoot is well known for its rapid recovery following dry conditions (Norris 1982); in this case increased WSC reserves most likely contributed to increased tiller initiation. A return to dry conditions in February and early March (coinciding with a reduced WSC content for cocksfoot following tiller initiation) reversed this trend, resulting in the abortion of newly initiated daughter tillers by perennial ryegrass and cocksfoot plants during autumn. Prairie grass displayed contrasting patterns of daughter tiller initiation and tiller death compared with perennial ryegrass and cocksfoot. The summer rainfall did not have an effect on tiller initiation of prairie grass; instead the

tiller death rate of prairie grass increased during this time. Summer temperatures (maximum daily temperatures over 21°C) during the first year of establishment of the current study were possibly above the optimal temperature range for prairie grass (Hill *et al.* 1985), coinciding with a reduced WSC content and therefore the abortion of daughter tillers by stressed parent tillers (Langer 1973). The low WSC reserves and increased death rate of tillers contributed to the decreased growth rate of prairie grass between January and March (although still higher than for perennial ryegrass and cocksfoot), and reduced plant density from March 2004.

Between March and early May 2004, there was a period of significant rainfall and a reduction in temperature (maximum daily temperatures between 14 and 20°C). These conditions were favourable for tillering in prairie grass. The tiller death rate of prairie grass decreased, while WSC content and tiller initiation increased, resulting in an increased growth rate from April 2004 under the 4-leaf stage defoliation treatment.

Frequent defoliation was detrimental to the productivity of all species. Defoliation interval did not drastically affect plant survival during the first year of establishment and over the dry summer period, with no effect on plant density or tiller number, irrespective of species. However, over time, more frequent defoliation would be expected to adversely affect persistence through decreasing WSC reserves (Fulkerson and Donaghy 2001).

Prairie grass was the most productive species in this dryland study, maintaining the highest growth rates throughout the measurement period. Unlike perennial ryegrass and cocksfoot, it did not respond to summer rainfall, but utilised accumulated energy reserves to support increased growth rates and tillering following the autumn break. Perennial ryegrass and cocksfoot yielded approximately 4.2 t DM/ha, while prairie grass yielded 5.7 t DM/ha. These are relatively low yields, but given that the study was undertaken under dryland conditions, within a 242-day measurement period, and during the first year of pasture establishment, they are satisfactory. This study confirmed that defoliation of prairie grass and cocksfoot at the 4-leaf stage, and perennial ryegrass between the 2-leaf and 3-leaf stages of regrowth, maximises productivity and survival from spring to autumn under dryland conditions. The effect

of defoliation management on the herbage quality of these species must also be considered and is reported in the following chapter.

Chapter 4

The effect of leaf stage based defoliation management on perennial ryegrass, prairie grass and cocksfoot under dryland conditions:

Herbage quality

4.1 Introduction

The perception that alternative pasture grasses are of poorer herbage quality than perennial ryegrass is largely the result of studies in which management was based on perennial ryegrass (to the detriment of the alternative species) or involved defoliation of different species at exactly the same time (Greenhalgh and Reid 1969; Jung *et al.* 1976; Balasko *et al.* 1995; Johnson and Thomson 1996; Hainsworth and Thomson 1997). Defoliation management based on leaf regrowth stage provides an objective assessment of the individual value of alternative grasses as dairy pasture species.

Defoliation of cocksfoot prior to the 5-leaf stage maintains ME in a range of 10.3 to 11.5 MJ/kg DM (Mitchell 1997; Rawnsley 2000). With a well-recognised tolerance of low soil fertility (Norton *et al.* 1999) and of attack by insects and pathogens (Guy *et al.* 1986; Fraser 1994; Lolicato and Rumball 1994; Slay 2002), cocksfoot is worthy of consideration as an alternative to perennial ryegrass in southern Australia.

The summer growth, drought tolerance, insect tolerance and high palatability of Matua prairie grass make this cultivar a potential alternative for the dairy pastures of southern Australia. Under appropriate management, prairie grass can be of a similar high herbage quality to perennial ryegrass (Crush *et al.* 1989; Lowe *et al.* 1999a; Fulkerson *et al.* 2000). Prairie grass maintains five to six live leaves per tiller (Belton 1992) and the optimal time for defoliation is thought to be when between the 3.5-leaf and 5-leaf stages (Hume 1991a; Fulkerson *et al.* 2000).

The current field study was conducted to provide an objective comparison of perennial ryegrass, prairie grass and cocksfoot under a management regime based on the physiological status of the grass plant. The aim was to quantify and compare changes in herbage quality under leaf stage based defoliation intervals.

4.2 Materials and methods

See Chapter 3 for site, pasture establishment and experimental design details.

4.2.1 Measurements

Defoliation treatments and associated measurements commenced in September 2003 and were completed in June 2004, when the accumulative leaf stage for each treatment coincided (i.e. with 2-leaf, 3-leaf and 4-leaf treatments implemented six, four and three times, respectively).

Leaf DM yield and botanical composition were measured at each defoliation event, plant density and WSC reserves were determined at bi-monthly intervals, and tiller dynamics were monitored every three weeks. The results from these measurements are reported in Chapter 3.

Pasture herbage quality

A herbage sample (above the height of 45 mm) was collected from three locations within each plot immediately prior to each defoliation event, from approximately the same location at each defoliation treatment. A target grass sub-sample (approximately 100 g wet weight) was separated from the sample and dried at 60°C for 48 h, ground through a 1 mm screen and analysed for ADF, NDF, total N and DDM concentrations using Near Infra Red (NIR) Spectrometry at Hamilton FeedTEST Laboratories (Victoria Department of Primary Industries, Hamilton, Australia; Appendix A.1).

Metabolisable energy values were calculated from predicted DDM values using the formula:

$$\text{ME} = 0.164 (\text{DDM}\% + \text{EE}), \text{ where EE} = \text{ether extract (\% of DM)}, \\ \text{assumed to be 2\% (Australian Fodder Industry Association 2002).}$$

Crude protein (%) was calculated using the following formula:

$$\text{CP} = \text{N concentration} \times 6.25$$

Energy per hectare (MJ/ha) was calculated using DM measurements from the same measurement period (Chapter 3), using the following formula:

$$\text{MJ/ha} = \text{ME} \times \text{kgDM/ha}$$

Reproductive tillers

On October 8 2003, eight individual tillers were marked with a wire loop along a diagonal transect across the full length of each plot. At 400 mm intervals along the transect a mature vegetative tiller without visible daughter tillers was selected and clearly identified with an anchored loop. Every three weeks from this date, the marked tillers were monitored and their status (reproductive or vegetative) recorded.

4.2.2 Statistical analysis

All statistical analyses were performed using the program SPSS (Version 11.5, SPSS Corporation, Wacker Drive, Illinois, USA). Least significant difference, as defined by Steel and Torrie (1960) was used for mean separation. Treatment means for each quality component were compared using an ANOVA split plot design. Reproductive tiller means were compared for each time of assessment using an ANOVA two-way factorial design with replication (species by defoliation interval).

4.3 Results

4.3.1 Metabolisable energy

There was a significant ($P < 0.05$) interaction between species and defoliation interval for ME (Table 4.1). The ME concentration of perennial ryegrass was significantly higher ($P < 0.001$) than the ME concentration of cocksfoot, which was significantly higher ($P < 0.001$) than the ME concentration of prairie grass for each defoliation treatment. The ME concentration of cocksfoot and prairie grass plants defoliated at the 2-leaf stage was significantly higher ($P < 0.05$) than that of plants defoliated at the 4-leaf stage of regrowth.

Table 4.1 Mean metabolisable energy (ME) concentration (MJ/kgDM) of prairie grass, cocksfoot and perennial ryegrass, defoliated at the 2-leaf (2L), 3-leaf (3L) and 4-leaf stages (4L) of regrowth.

Leaf regrowth stage	ME (MJ/kgDM)		
	Prairie grass	Cocksfoot	Ryegrass
2L	10.44	10.87	11.45
3L	10.18	10.86	11.60
4L	10.22	10.70	11.38
LSD ($P = 0.05$)			0.16

4.3.2 Fibre

There was a significant ($P < 0.05$) interaction between species and defoliation interval for ADF and NDF concentrations (Table 4.2). The ADF and NDF concentrations for prairie grass were significantly higher ($P < 0.001$) than for cocksfoot and perennial ryegrass. The ADF concentration for cocksfoot was significantly lower ($P < 0.001$) than for perennial ryegrass, while the NDF concentration for perennial ryegrass was significantly lower ($P < 0.001$) than for cocksfoot, regardless of defoliation interval. For prairie grass, there was a positive relationship between leaf regrowth stage and fibre content, with a significantly greater ($P < 0.05$) ADF concentration when plants were defoliated at the 4-leaf stage compared with the 2-leaf stage of regrowth.

Table 4.2 Mean acid detergent fibre (ADF) and neutral detergent fibre (NDF) concentrations (% of DM) of prairie grass, cocksfoot and perennial ryegrass, defoliated at the 2-leaf (2L), 3-leaf (3L) and 4-leaf stages (4L) of regrowth.

Leaf regrowth stage	ADF (%)			NDF (%)		
	Prairie	Cocksfoot	Ryegrass	Prairie	Cocksfoot	Ryegrass
2L	26.86	22.61	25.80	59.82	57.69	55.11
3L	29.22	22.84	25.12	61.96	58.94	53.02
4L	29.39	23.00	26.24	61.57	58.91	53.09
LSD ($P = 0.05$)			1.22			1.74

4.3.3 Crude protein

For all species, plants defoliated at the 4-leaf stage had a significantly lower ($P < 0.001$) CP concentration than plants defoliated at the 2-leaf stage of regrowth (Table

4.3). For prairie grass, there was a significant ($P < 0.001$) difference in CP concentration between each defoliation treatment, CP concentration decreasing with increasing defoliation interval. For perennial ryegrass there was no significant ($P > 0.05$) difference in CP concentration between plants defoliated at the 2-leaf and 3-leaf stages of regrowth, and for cocksfoot there was no significant ($P > 0.05$) difference in CP concentration between plants defoliated at the 3-leaf and 4-leaf stages of regrowth.

Table 4.3 Mean crude protein (CP) concentration (% of DM) of prairie grass, cocksfoot and perennial ryegrass, defoliated at the 2-leaf (2L), 3-leaf (3L) and 4-leaf stages (4L) of regrowth.

Leaf regrowth stage	CP (%)			Mean	LSD ($P = 0.05$)
	Prairie grass	Cocksfoot	Ryegrass		
2L	16.15	22.41	14.24	17.60	1.14
3L	13.96	21.08	13.29	16.11	
4L	12.39	20.38	11.16	14.65	
Mean	14.17	21.29	12.90		
LSD ($P = 0.05$)	1.19				

There was a significant ($P < 0.001$) species effect on CP concentration (Table 4.3). The CP concentration of cocksfoot was significantly higher ($P < 0.001$) than the CP concentration of prairie grass, which was significantly higher ($P < 0.05$) than the CP concentration of perennial ryegrass.

4.3.4 Energy per hectare

On an energy per hectare basis, there were significant differences between species ($P < 0.001$) and defoliation interval ($P < 0.01$) (Table 4.4). Prairie grass yielded significantly greater ($P < 0.001$) energy per hectare (5.85×10^4 MJ/ha) than cocksfoot (4.44×10^4 MJ/ha) and perennial ryegrass (4.90×10^4 MJ/ha). There was no significant ($P > 0.05$) difference in energy per hectare between cocksfoot and ryegrass. There was a significantly lower ($P < 0.01$) energy per hectare for plants defoliated at the 2-leaf stage of regrowth compared with plants defoliated less frequently. There was no significant ($P > 0.05$) difference in energy per hectare between plants defoliated at the 3-leaf and 4-leaf stages of regrowth.

Table 4.4 Mean energy per hectare (MJ/ha) for prairie grass, cocksfoot and perennial ryegrass, defoliated at the 2-leaf (2L), 3-leaf (3L) and 4-leaf stages (4L) of regrowth.

Leaf regrowth stage	ME (MJ/ha x 10 ⁴)			Mean	LSD (<i>P</i> = 0.05)
	Prairie	Cocksfoot	Ryegrass		
2L	5.38	4.05	4.55	4.66	0.34
3L	5.98	4.52	4.99	5.16	
4L	6.20	4.77	5.15	5.37	
Mean	5.85	4.44	4.90		
LSD (<i>P</i> = 0.05)	0.81				

4.3.5 Reproductive tillers

There was a significantly lower ($P < 0.05$) proportion of reproductive tillers for cocksfoot compared with prairie grass and perennial ryegrass until early March. From late March there was no consistent difference between species (Figure 4.1). Defoliation interval did not have a significant ($P > 0.05$) effect on proportions of reproductive tillers.

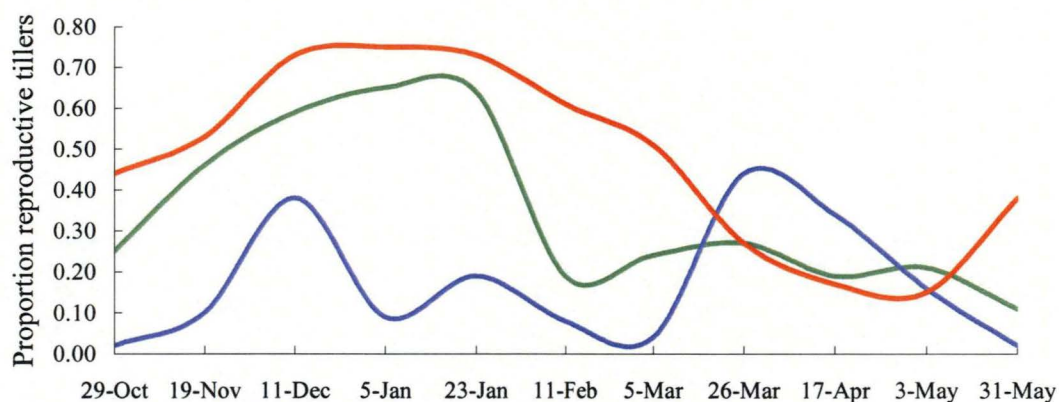


Figure 4.1 Mean proportion of reproductive tillers per original marked tiller for prairie grass (—), cocksfoot (—) and perennial ryegrass (—), between October 2003 and May 2004.

4.4 Discussion

In this study, differences in herbage quality resulted from species (perennial ryegrass, prairie grass and cocksfoot) and defoliation interval (2-leaf, 3-leaf and 4-leaf stages of regrowth) treatments.

As defoliation interval increased, there was evidence of a trend for decreasing ME concentration for the three species, largely as a result of decreasing digestibility. The decreasing digestibility of successive leaves on a grass plant can be explained by the increasing proportion of sclerenchyma and vascular tissue with increasing leaf number on a tiller (Ducrocq and Duru 1997). This in turn may be related to an increase in the maximum length of the leaf blade with each successive leaf (Wilson 1976).

The lower ME concentrations for plants defoliated at the 4-leaf stage of regrowth also corresponded with lower CP concentrations. Decreasing CP concentrations with increasing maturity is not unusual; Minson (1990) investigated the CP concentrations of a range of grass species and reported a mean rate of decline of 0.22% per day. The low CP and ME concentrations in general may reflect the stressful effect of low soil moisture on plants.

In this study, each grass was defoliated at species-specific leaf stage based defoliation intervals, providing an objective comparison that revealed a statistically significant but not unacceptable difference in ME concentrations between cocksfoot and perennial ryegrass.

These results challenge the common perception that cocksfoot should not be used in dairy pasture systems due to its unacceptable herbage quality. This perception is largely the result of studies in which management was based on perennial ryegrass (to the detriment of cocksfoot) or involved defoliation of the two grasses at exactly the same time (Greenhalgh and Reid 1969; Balasko *et al.* 1995; Johnson and Thomson 1996; Hainsworth and Thomson 1997). The rate of leaf regrowth for cocksfoot is shorter than for perennial ryegrass from late spring to early autumn under dryland conditions (Chapter 3). When compared to other temperate grasses at the same date, cocksfoot may therefore have a lower ME due to its advanced stage of

maturity. The higher NDF concentration of cocksfoot compared with perennial ryegrass in the current study suggests that intake of cocksfoot pasture by grazing animals may be limited by the bulky nature of the herbage. As outlined in Section 10.3.3 however, recent studies in Tasmania have shown that possible differences in intake have not translated into differences in milk production between the species.

The ME concentration of prairie grass was consistently lower than the ME concentration of both cocksfoot and perennial ryegrass, reflecting a lower DDM (75.74-77.29% compared with 84.28-85.59% for ryegrass). Relatively high fibre and low CP concentrations (as a result of a high proportion of reproductive tillers and therefore stem material) limited the digestibility of prairie grass. Crude protein in stems is generally half of that in leaf blades (Minson 1990), and stem digestibility declines with increasing maturity at a far more rapid rate than leaf digestibility (Terry and Tilley 1964). It is possible that the cool temperate conditions induced greater reproductive development in prairie grass (Hill and Pearson 1985), resulting in a consistently higher proportion of stem than for perennial ryegrass and cocksfoot.

The energy per hectare of prairie grass exceeded the energy levels of cocksfoot and perennial ryegrass by at least 9500 MJ/ha. The superior productive capacity of prairie grass compared with cocksfoot and perennial ryegrass was largely due to a faster leaf appearance rate and larger leaves (Hume 1991c; Belton 1992; Chapter 3).

There was evidence of a greater proportion of reproductive tillers for perennial ryegrass than the other species for the majority of the experiment, translating into increased ADF concentrations compared with cocksfoot. Cocksfoot maintained a higher CP concentration (mean 21.3%) than both perennial ryegrass (mean 12.9%) and prairie grass (mean 14.2%). While the mean CP concentration for cool-season grasses is 12.9% (Minson 1990), this relatively low level of protein limits the productivity of lactating dairy cows. Assuming herbage has an ME concentration of 11 MJ/kgDM, CP concentrations between 12.0 and 13.2% reduce milk production by at least 5 L/day compared with a CP concentration of 17.7% (Holmes and Wilson 1984). The uncharacteristically low CP concentration for perennial ryegrass in relation to cocksfoot in this study may have resulted from the greater proportion of reproductive ryegrass tillers in the analysed samples compared with cocksfoot (plant material above the height of 45 mm). The low CP concentrations for perennial

ryegrass and prairie grass, and high ADF and NDF concentrations for the three species can be partially explained by the collection of data between September and May (omitting the winter period when protein levels are generally higher and fibre levels lower), under dryland conditions.

The recommended defoliation interval range to maximise productivity and persistence of prairie grass is between the 3.5-leaf and 5-leaf stages of regrowth (Hume 1991a; Fulkerson *et al.* 2000; Chapter 3). Although more frequent defoliation of prairie grass would result in herbage with a higher herbage quality (lower fibre and higher CP concentrations), it would threaten plant persistence due to the exhaustion of WSC energy reserves (Fulkerson *et al.* 2000; Slack *et al.* 2000; Chapter 6).

Although ME concentrations were higher for cocksfoot plants defoliated at the 2-leaf and 3-leaf stages compared with defoliation at the 4-leaf stage of regrowth, increased DM production with increased defoliation interval resulted in greater energy per hectare from plants defoliated at the 4-leaf stage of regrowth. In agreement with Rawnsley *et al.* (2002), the 4-leaf stage of regrowth is therefore recommended to maximise both plant productivity and energy availability in cocksfoot.

Metabolisable energy levels were lower for ryegrass plants defoliated at the 4-leaf stage of regrowth compared with plants less frequently defoliated. This was most likely due to increased dead material resulting from death of the first leaf upon appearance of the fourth leaf. The productivity of perennial ryegrass (Chapter 3) and energy per hectare were higher at the 3-leaf stage compared with the 2-leaf stage of regrowth; therefore defoliation at the 3-leaf stage maximised the energy availability of this species. In line with the recommendation of Fulkerson and Donaghy (2001), defoliation of perennial ryegrass between the 2-leaf and 3-leaf stages of regrowth - adjusting defoliation interval seasonally - maximises the productivity and quality of ryegrass herbage.

In conclusion, results from this study challenge the common perception that the herbage quality of cocksfoot is unsatisfactory to meet the needs of lactating dairy cows. Defoliation of cocksfoot at or before the 4-leaf stage of regrowth maintained

ME concentrations between 10.70 and 10.87 MJ/kg DM and minimised reproductive development. The herbage quality of prairie grass was considerably lower than for cocksfoot and perennial ryegrass, but a higher productive capacity resulted in prairie grass providing the greatest energy on a per hectare basis.

Changes in the herbage quality and physiology of cocksfoot during regrowth have been investigated in more detail by Rawnsley *et al.* (2002), but further research is required for prairie grass. Chapter 5 describes the physiological and herbage quality changes in prairie grass throughout one full regrowth cycle (i.e. 6-leaf stage) following defoliation.

Chapter 5

Changes in the physiology and herbage quality of prairie grass during regrowth

5.1 Introduction

Although several studies have clearly shown prairie grass is capable of greater herbage production than perennial ryegrass (Vartha 1977; Fraser 1982; DeLacy 1987; Fulkerson *et al.* 2000), when grazed in the same manner as ryegrass-based pastures (as is common practice), prairie grass is disadvantaged, particularly from late spring to early autumn when the leaf appearance rate of prairie grass is more rapid than for ryegrass (Chapter 3).

For example, in a Tasmanian study, prairie grass was initially shown to be unproductive with poor persistence (Anon. 1987) because existing best management practice for ryegrass-based pastures was applied to both pasture types. In a subsequent study, prairie grass was grazed to leave longer post-grazing residuals and allowed to set seed in spring. Utilisation from the prairie grass pasture rose to 2, then 4 t DM/ha greater than utilisation of ryegrass in successive years (Anon. 1987).

Grazing management based on the physiological status of the prairie grass plant (i.e. leaf regrowth stage) is more efficient than grazing management based on herbage accumulation or on set day rotations (Thom *et al.* 1990; Fulkerson and Donaghy 2001). For perennial ryegrass, the 2-leaf to 3-leaf stage of regrowth has been accepted as the optimal defoliation interval (Fulkerson and Donaghy 2001).

When perennial ryegrass plants are defoliated prior to the 2-leaf stage, there is insufficient time for replenishment of WSC reserves, which are depleted immediately following defoliation. Repeated defoliations before plants are physiologically 'ready' therefore results in reduced leaf regrowth, tillering and root growth (Donaghy and Fulkerson 1997, 1998; Rawnsley *et al.* 2002). In addition to the changes in stubble WSC concentration during regrowth, Fulkerson *et al.* (1998) suggest that there may

also be an imbalance in herbage mineral levels and the ratio of carbohydrates to protein when perennial ryegrass is grazed before the 2-leaf stage.

When perennial ryegrass plants are defoliated after the 3-leaf stage, leaf senescence and an increase in fibre concentration leads to increased rejection of herbage by grazing stock and therefore lower levels of DM utilisation. The optimal grazing intervals defined for perennial ryegrass pastures are the key to grazing management for the maintenance of a balance between pasture growth, persistence, herbage quality and utilisation (Fulkerson and Donaghy 2001). As species-specific grazing management is required to maximise the potential of perennial grass species, it follows that the optimal performance of prairie grass as a dairy pasture species would be similarly reliant on a customised optimal grazing interval.

In Chapters 3 and 4, a defoliation interval based on 4-leaf stage of regrowth was reported to favour prairie grass growth, persistence and herbage quality, in general agreement with Fulkerson *et al.* (2000). The aim of the present study was to further investigate morphological and physiological changes in prairie grass during regrowth to establish a basis for optimal defoliation management of prairie grass pastures.

5.2 Materials and methods

The experiment was conducted in a glasshouse at the Tasmanian Institute of Agricultural Research, Burnie, Australia (Latitude $-41^{\circ}04'S$), between May and November 2004. Three seeds of *Matua* prairie grass were planted in each of 385 polyvinyl bags (100 mm diameter x 280 mm depth), on May 5 2004. The bags contained a potting mixture composed of 50% *Pinus radiata* D. bark, 30% sand, 20% *Spaghnum* sp. moss and nutrients (Appendix A.2). The plants were arranged in the glasshouse at a density of 100 plants/m². Plants were watered daily via an underlying geotextile membrane capillary mat, to replace evapotranspiration losses. Glasshouse conditions were controlled to maintain day/night temperatures of 20/10°C. Once established, the weakest seedlings were removed to allow a single healthy seedling to reach maturity in each bag. At 56 days from germination and again prior to treatments being imposed, plants were fertilised with Osmocote® (Scotts Australia Pty. Ltd., New South Wales, Australia) at a rate equivalent to 40 kg N/ha.

5.2.1 *Determination of leaf stage*

Each leaf regrowth stage was defined as the time required for the production of one fully expanded leaf per tiller. Prairie grass maintains four to five live leaves per tiller, with a new leaf commencing growth when the previous leaf has reached approximately 75% of its full length. Thus, at any given time two prairie grass leaves are expanding, and measurement of 'leaf stage' is estimated by the amount of growth of the current expanding leaves.

5.2.2 *Experimental design*

Plants were arranged in a randomised complete block design, with five blocks each containing seven randomly allocated treatments. Each treatment consisted of a row of nine plants per block, resulting in 45 plants in total per treatment. Treatments consisted of one preliminary harvest (0) and six sequential harvests when each new leaf had regrown, up to the 6-leaf stage (1-6L). Buffer plants were placed around the minisward to minimise boundary effects. These plants were harvested but otherwise not included in analyses.

On June 30 2004 (55 days following sowing), all plants were defoliated to a stubble height of 50 mm to promote tillering. At the 4-leaf stage of regrowth, plants were again defoliated to 50 mm in preparation for the destructive harvesting regime.

5.2.3 *Destructive harvest regime and determination of DM yield*

At the second defoliation to 50 mm, the first pre-treatment destructive harvest was carried out (0). Sequential harvests then followed at each leaf regrowth stage, up to the 6-leaf stage.

Non-sheath leaf tissue (above 50 mm) was removed at each harvest event, and leaf DM yield per plant determined after drying samples for at least 24 hours at 60°C in a forced draught oven. Stubble tissue below 50 mm and roots were collected at each harvest event. Stubble and washed roots were dried for at least 24 hours at 80°C in a forced draught oven then weighed. Tiller DM yield and number per plant were also determined at each harvest interval. Harvests were consistently performed at three hours after sunrise, to negate the confounding effect of diurnal fluctuations in WSC

concentration (Fulkerson and Slack 1994a). Dried leaf, root and stubble samples were ground through a 1 mm sieve prior to chemical analyses.

5.2.4 *Differentiation in leaf material*

Leaf and tiller senescence as well as reproductive development proceeded as plants matured, and measures were taken to define differentiation in leaf material with plant growth. At the 5-leaf and 6-leaf stages, two subsamples from the harvested leaf material within each block were taken and one was separated into live and dead material, while the other was sorted into leaf and stem material.

5.2.5 *WSC analysis*

Root, stubble and leaf samples were analysed for WSC at New South Wales Department of Primary Industries Laboratories by Technicon Industrial Method number 302-73A, derived from the method outlined by Smith (1969; Appendix A.1).

5.2.6 *Herbage quality analyses*

Metabolisable energy: Leaf samples were analysed for DDM concentration using NIR Spectrometry at Hamilton FeedTEST Laboratories (Victoria Department of Primary Industries; Clarke *et al.* 1982; Appendix A.1).

Metabolisable energy values were calculated from predicted DDM values using the formula: $ME = 0.164 (DDM\% + EE)$, where EE = ether extract (% of DM), assumed to be 2% (Australian Fodder Industry Association 2002).

Minerals: P, K, Na, Mg and Ca concentrations of leaf samples were measured by inductively coupled plasma – atomic emission spectrometry (ICP-AES) at CSBP Soil and Plant Nutrition Laboratories (Western Australia; McQuaker *et al.* 1979; Appendix A.1).

Nitrogen (N): Leaf material was analysed for total N using a Leco FP-428 Nitrogen Analyser at CSBP Soil and Plant Nutrition Laboratories (Western Australia; Sweeney and Rexroad 1987; Appendix A.1). The CP concentration was calculated as $N \text{ concentration (mg/g DM)} \times 6.25$.

5.2.7 Statistical analyses

Pre-treatment DM values from defoliation event 0 were used as a co-variate. Differences between treatment (leaf regrowth stage) means were tested for the following variables: leaf, root and individual tiller DM yields, WSC, ME, CP, Ca, P, Ca:P, K, Na and Mg. Means were compared by ANOVA using the statistical package SPSS, and LSD, as defined by Steel and Torrie (1960). Regression (r^2) between WSC reserves and plant regrowth was tested using the statistical functions of EXCEL™.

5.3 Results

5.3.1 Changes in stubble and root WSC reserves with leaf regrowth

At defoliation (leaf regrowth stage 0) and throughout the subsequent regrowth cycle, the mean WSC concentration (% of DM) in the stubble was significantly greater ($P < 0.001$) than in the roots. Following defoliation, there was a significant ($P < 0.001$) decline in the stubble and root WSC concentrations. There was a significant ($P < 0.05$) increase in stubble WSC concentration between 1-leaf and 5-leaf stages of regrowth, while root WSC concentration initially significantly increased ($P < 0.001$) between the 1-leaf and 2-leaf stages, but then decreased ($P < 0.05$) between the 4-leaf and 5-leaf stages of regrowth (Figure 5.1).

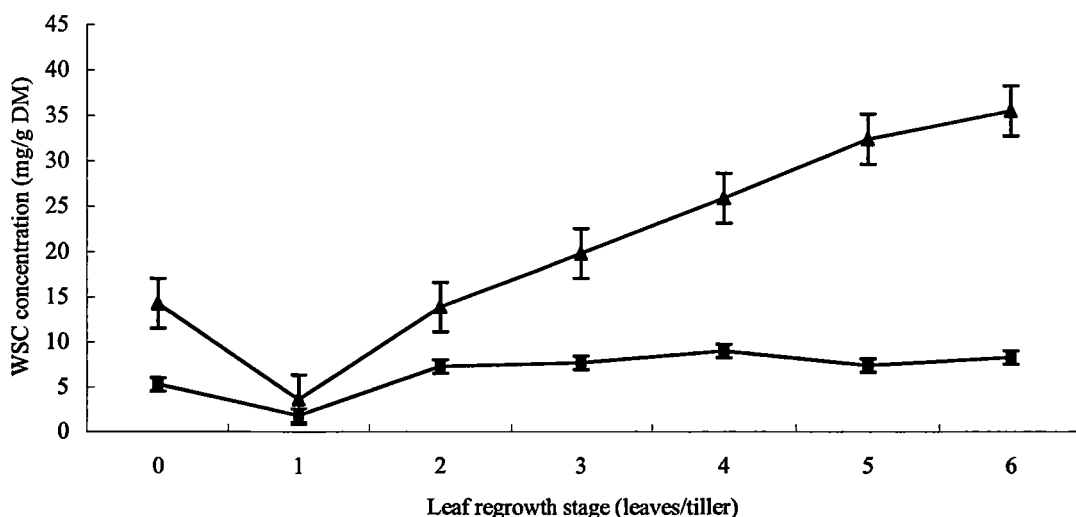


Figure 5.1 Changes in stubble (▲) and root (■) water-soluble carbohydrate (WSC) concentration (% of DM) with regrowth of prairie grass after defoliation. Vertical bars represent LSD ($P = 0.05$).

Total stubble WSC content (mg/tiller and mg/plant) decreased at the 1-leaf stage, and then returned to pre-defoliation levels by the 2-leaf stage of regrowth. Stubble WSC content was significantly higher ($P < 0.05$) at the 5-leaf and 6-leaf stages than at any previous regrowth stage (Table 5.1).

Table 5.1 Stubble water-soluble carbohydrate (WSC) content (mg/tiller and mg/plant) in relation to regrowth stage.

Leaf regrowth stage (leaves/tiller)	Stubble WSC (mg/tiller)	Stubble WSC (mg/plant)
0	8.41	63.07
1L	1.15	19.71
2L	8.34	66.38
3L	17.46	138.91
4L	20.33	139.35
5L	36.53	256.46
6L	49.05	370.45
LSD ($P = 0.05$)	13.20	89.17

5.3.2 Relationship between plant WSC levels and regrowth

There was a strong positive linear relationship between leaf, tiller and root DM yield at each leaf regrowth stage and stubble WSC concentration and content (% of DM and mg/tiller), as follows:

$$\begin{aligned}\text{Leaf DM/plant (g)} &= 0.1404 \text{ stubble WSC (\% of DM)} - 0.3226 \quad (r^2 = 0.83) \\ &= 0.0831 \text{ stubble WSC (mg/tiller)} + 0.9138 \quad (r^2 = 0.81)\end{aligned}$$

$$\begin{aligned}\text{Tiller DM (mg/tiller)} &= 2.7171 \text{ stubble WSC (\% of DM)} + 24.751 \quad (r^2 = 0.85) \\ &= 1.7186 \text{ stubble WSC (mg/tiller)} + 46.461 \quad (r^2 = 0.95)\end{aligned}$$

$$\begin{aligned}\text{Root DM/plant (g)} &= 0.0702 \text{ stubble WSC (\% of DM)} - 0.5019 \quad (r^2 = 0.75) \\ &= 0.0465 \text{ stubble WSC (mg/tiller)} + 0.0173 \quad (r^2 = 0.92)\end{aligned}$$

A positive relationship was found between tiller DM yield and root WSC concentration (% of DM), although the proportion of experimental variation (r^2) was only 0.40. No such relationship was found between root DM yield, leaf DM yield or

tiller number and root WSC concentration, or between tiller number and stubble WSC concentration or content.

5.3.3 *Changes in tillers per plant with regrowth*

Prior to commencement of defoliation treatments, there were 6.7 ± 0.4 tillers per plant and this remained relatively constant ($P > 0.05$) until the 3-leaf stage, after which tiller numbers significantly increased ($P < 0.05$) to 8.0 ± 0.4 at the 4-leaf and 5-leaf stages, and 9.4 ± 0.4 at the 6-leaf stage of regrowth.

5.3.4 *Changes in DM yield with regrowth*

Tiller DM yield (mg/tiller) significantly decreased ($P < 0.05$) following defoliation and increased at a significant ($P < 0.05$) and constant rate until the 3-leaf stage of regrowth. Tiller DM yield was significantly higher ($P < 0.05$) at the 5-leaf and 6-leaf stages than at any previous regrowth stage (Table 5.2). There was no significant ($P > 0.05$) difference in root DM yield (mg/plant) from defoliation until the 3-leaf stage, followed by a significant ($P < 0.001$) increase from the 4-leaf to the 6-leaf stage of regrowth (Table 5.2). Following defoliation, there was a steady and significant ($P < 0.05$) increase in leaf DM yield (mg/plant) with regrowth (Table 5.2). Leaf senescence was first measured at the 5-leaf stage, with 5% of leaf DM senescent, increasing to 9% at the 6-leaf stage of regrowth (Figure 5.2).

Table 5.2 Tiller dry matter (DM) yield (mg/tiller), root and leaf DM yield (mg/plant) before defoliation and at each corresponding leaf regrowth stage (leaves per tiller).

Leaf regrowth stage (leaves/tiller)	Tiller DM (mg/tiller)	Root DM (mg/plant)	Leaf DM (mg/plant)
0	58	293	1753
1L	42	161	377
2L	58	303	1099
3L	83	683	2204
4L	79	905	2820
5L	112	1592	4110
6L	133	2750	5772
LSD ($P = 0.05$)	13	518	498

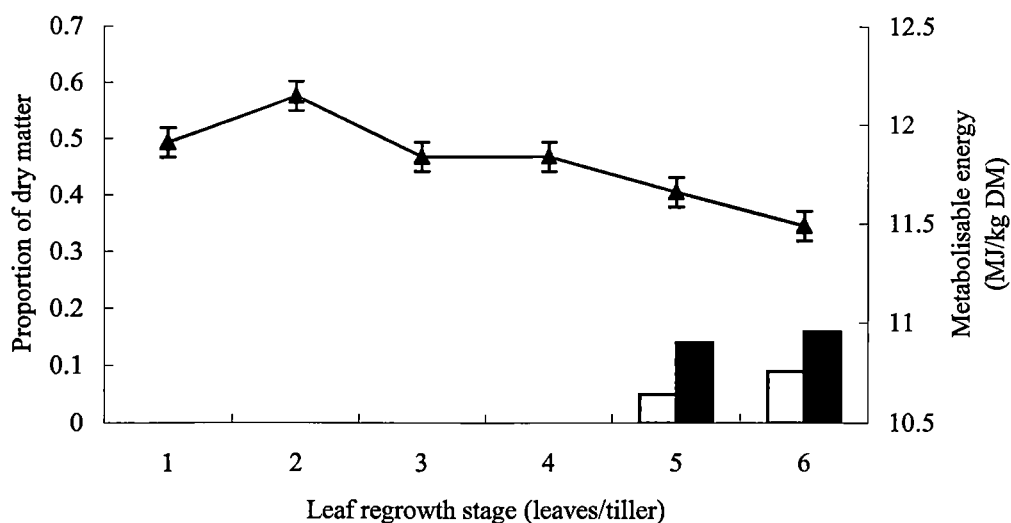


Figure 5.2 Changes in metabolisable energy concentration (MJ/kg DM) (▲) and the accumulation of senescent (□) and stem (■) (proportion of dry matter DM) material with regrowth of prairie grass after defoliation. Vertical bars represent LSD ($P = 0.05$).

5.3.5 Changes in herbage quality with regrowth

The ME concentration of the leaf decreased significantly ($P < 0.05$) with regrowth between the 4-leaf to the 6-leaf stage, with no significant ($P > 0.05$) difference between the 1-leaf, 3-leaf and 4-leaf stages (Figure 5.2). The stem material proportion of DM at the 5-leaf and 6-leaf stages of regrowth was 0.14 and 0.16 respectively (Figure 5.2).

There was a general decline in leaf CP, Ca, Mg, P and K concentrations with regrowth following defoliation. However, the decline was not constant, with a plateau effect evident between the 2-leaf or 3-leaf and 5-leaf stages (Table 5.3). The concentration of Na in the leaf significantly decreased ($P < 0.05$) between the 1-leaf and 2-leaf stages and significantly increased ($P < 0.05$) between the 3-leaf and 5-leaf stages of regrowth (Table 5.3).

Table 5.3 Crude protein (CP; % of DM) and mineral concentrations (mg/g DM) of prairie grass at each leaf regrowth stage, compared with the requirements (REQ) for a 600kg Friesian cow producing 23L milk per day (National Research Council 1989).

Leaf regrowth stage	CP	Ca	Mg	P	Na	K	Ca:P
1L	37.5	5.5	2.4	8.6	1.7	81.9	0.63
2L	27.7	4.4	1.8	6.1	1.4	62.2	0.72
3L	21.0	4.2	1.6	5.7	1.5	59.0	0.75
4L	20.0	4.4	1.6	5.2	1.8	55.8	0.84
5L	16.4	4.3	1.6	4.7	2.3	50.0	0.92
6L	14.1	3.9	1.4	4.0	1.9	41.8	0.98
REQ	18.0-20.0	5.4	2.0	3.4	1.2	9.0	1.60
LSD ($P = 0.05$)	2.0	0.4	0.1	0.6	0.1	3.4	0.13

5.4 Discussion

The current study presents quantitative evidence to indicate that the optimal defoliation interval for growth, persistence and herbage quality of prairie grass is the 4-leaf stage of regrowth. At this stage of plant development, increased WSC reserves coincide with a resumption of tillering and root growth. Herbage quality is also relatively high (ME above 11.80 MJ/kg DM), with concentrations of P, K and Na adequate to meet the needs of a highly producing dairy cow (National Research Council 1989). However, concentrations of Ca and Mg were insufficient to meet these requirements throughout the regrowth cycle.

Both the concentration of WSC and the level of replenishment following defoliation were greater in the stubble than in the root system, confirming that, as in ryegrass (Danckwerts and Gordon 1987; Fulkerson and Slack 1994a) and cocksfoot (Davidson and Milthorpe 1966b; Rawnsley *et al.* 2002), the stubble is the major storage site for WSC reserves in prairie grass. Immediately following defoliation, WSC replenishment commenced, resulting in significantly higher WSC reserves at the 5-leaf and 6-leaf stages than at any previous regrowth stage. In contrast to cocksfoot plants, in which WSC reserves were replenished to pre-defoliation levels by the 4-leaf stage (Rawnsley *et al.* 2002), prairie grass WSC reserves in this study were replenished to pre-defoliation levels by the 2-leaf stage of regrowth.

The strong positive linear relationship between stubble WSC reserves and the regrowth capacity of prairie grass confirms that WSC reserves play an important role in the entire plant regrowth cycle following defoliation. The importance of WSC reserves in the regrowth of cocksfoot (Davidson and Milthorpe 1966b; Rawnsley *et al.* 2002), perennial ryegrass (Davies 1965; Fulkerson and Slack 1994a; 1995; Donaghy and Fulkerson 1997; 1998), tall fescue (Booyesen and Nelson 1975; Volenec 1986) and timothy (Smith 1974) has been previously reported. However, the extent of reliance of ryegrass (Danckwerts and Gordon 1987; Fulkerson and Slack 1994a; Donaghy and Fulkerson 1997) and cocksfoot (Davidson and Milthorpe 1966a;b) plants on reserves in such studies has often been shown to be limited to several days post-defoliation.

While there was little difference in the strength of linear relationships between regrowth of leaves and stubble WSC content (mg/tiller) compared with WSC concentration (mg/g DM), there were stronger relationships between tiller DM yield and regrowth of roots with stubble WSC content compared with concentration. With prairie grass tillers weighing up to three times the mass of perennial ryegrass tillers (Chapter 3), the regenerative capacity of prairie grass is not only correlated to WSC content but also the size of the storage organ. Based on the figures from the current study, for any given WSC concentration, there is a significantly higher WSC content (mg/tiller) in prairie grass compared with perennial ryegrass.

Leaf growth had a higher priority for available energy than root growth and tiller initiation in the current study. This was evidenced by immediate leaf regrowth following defoliation, compared with significant root regrowth at the 3-leaf stage, and significant increases in tiller number at the 4-leaf stage of regrowth. This time sequence and overall priority for allocation of WSC reserves is almost identical to that found for perennial ryegrass (root regrowth occurring at the 1-leaf and tillering at the 2-leaf stage; Donaghy and Fulkerson 1998) and cocksfoot (root regrowth occurring at the 4-leaf and tillering at the 5-leaf stage; Rawnsley *et al.* 2002). Thus it appears evident that for a range of pasture grasses, a similar priority for energy reserve allocation exists, and this has ramifications for grazing management.

Despite the capability of prairie grass to immediately resume replenishment of energy reserves following defoliation, it is likely that defoliation prior to the 4-leaf stage of regrowth will not allow tiller initiation to occur. As perenniality of grasses depends on their capacity to replace dying tillers (Colvill and Marshall 1984; Marshall 1987), defoliation prior to the 4-leaf stage of regrowth may result in reduced persistence of prairie grass plants. The detrimental effect of frequent defoliation on the persistence of prairie grass is further exaggerated by the relatively low tiller density of this species compared with perennial ryegrass (Chapter 3). It is also important to note that the plants in the current study were defoliated at the 4-leaf stage of regrowth prior to treatments commencing – if they had been defoliated at an earlier leaf regrowth stage, the pattern of WSC reserve replenishment during the subsequent regrowth cycle may have differed considerably.

A reduction in root growth following defoliation has been previously reported for cocksfoot (Jacques and Edmond 1952; Davidson and Milthorpe 1966a; Evans 1973; Rawnsley *et al.* 2002) and perennial ryegrass (Jacques and Edmond 1952; Evans 1971; 1972; 1973; Fulkerson *et al.* 1993; Donaghy *et al.* 1997; Donaghy and Fulkerson 1997; 1998). In the current study, defoliation almost halved the root DM yield of prairie grass during the time it took to regrow one new leaf, supporting the findings of Evans (1972) and Donaghy and Fulkerson (1998) that root regrowth is highly sensitive to changes in WSC concentrations. While perennial ryegrass has been reported to resume root growth between the 1-leaf and 1.5-leaf stages (Fulkerson and Slack 1994a; Donaghy and Fulkerson 1998) and cocksfoot to resume root growth at the 4-leaf stage (Rawnsley *et al.* 2002), prairie grass resumed significant root growth at the 3-leaf stage of regrowth. Management that restricts root growth affects plant growth in general, due to the limitation placed on water and nutrient uptake (Davidson and Milthorpe 1966a; Clement *et al.* 1978), and therefore plant survival. From a root system perspective, defoliation of prairie grass prior to the 3-leaf stage of regrowth would therefore have a detrimental effect on plant survival.

The ME concentration of prairie grass remained above 11.80 MJ/kg DM until (and including) the 4-leaf stage, after which increased stem and senescent material combined to reduce the ME concentration with regrowth. Given the increased leaf

DM yield at the 5-leaf and 6-leaf stages, total ME yield (MJ/ha) would be substantially greater at the longer regrowth interval, but may not result in increased pasture utilisation in a grazing situation, due to increased rejection by stock because of the increased stem and senescent material.

The CP concentration decreased with regrowth, as was also reported in Chapter 4. The CP concentration of prairie grass met the requirements of a highly producing dairy cow until (and including) the 4-leaf stage, after which point CP concentrations fell below the requirements, possibly due to the increased stem to leaf ratio and increased levels of WSC reserves (Beever *et al.* 2000).

A decrease in the concentration of Ca in the leaf with increasing maturity is unusual and in contrast to that reported for perennial ryegrass (Wilman *et al.* 1994; Fulkerson *et al.* 1998), white clover (Wilman *et al.* 1994) and cocksfoot (Rawnsley *et al.* 2002). Combined with the more rapid decline in the concentration of P in the leaf, there was a 1.5-fold increase in the ratio of Ca to P in the leaf from the 1-leaf to the 6-leaf stage of regrowth. At no stage of regrowth did the Ca to P ratio approach the ratio of 1.6 recommended by National Research Council (1989) for a highly producing dairy cow. The concentration of Ca in the leaf only met these requirements at the 1-leaf stage of regrowth, while the concentration of P in the leaf was in excess of these requirements throughout the regrowth cycle. Calcium requirements in dairy cattle increase at the end of pregnancy and in the early stages of lactation (National Research Council 1989), and adequate Ca levels are also required during lactation to maintain Ca levels in milk. The low Ca concentrations observed in this study may not translate to Ca deficiencies for grazing animals in the field, as prairie grass would be sown with a companion legume (legumes generally contain more Ca than grasses; Whitehead 1972). Regular applications of superphosphate and lime to the pasture should maintain Ca levels (Grace 1989).

The decline in the concentration of Mg in the leaf was in contrast to the pattern of Mg accumulation reported for perennial ryegrass (Wilman *et al.* 1994; Fulkerson *et al.* 1998; Fulkerson and Donaghy 2001) but in agreement with that reported for

cocksfoot (Rawnsley *et al.* 2002). The concentration of Mg in the leaf of prairie grass did not approach the recommended 2.0 mg/g DM (National Research Council 1989) at any stage of the regrowth cycle. A low Mg concentration is one of the previously reported nutritional limitations of prairie grass (Thom *et al.* 1990; Fulkerson *et al.* 2000). However, the effect of low herbage Mg on milk production has been shown to be insignificant (Wilson and Grace 1978).

Leaf K concentrations declined with leaf regrowth stage, but were consistently higher than the recommended 9.0 mg/g DM by the National Research Council (1989) throughout the regrowth cycle, suggesting excess K availability in the potting mix and subsequent luxury uptake by plants. The pattern of Na accumulation in the leaf was somewhat unpredictable, but significantly increased between the 1-leaf and 6-leaf stages and remained in excess of the requirements of a highly producing dairy cow for the duration of the regrowth cycle. The high concentrations of P and Na in the current study contrast with a previous study (Crush *et al.* 1989), in which these minerals were identified as potential nutritional limitations for prairie grass compared with perennial ryegrass.

In conclusion, a defoliation interval based on the 4-leaf stage of regrowth enables adequate time for prairie grass to replenish WSC reserves, resume root growth and initiate new tillers, before the onset of significant leaf senescence, stem production and consequent reduction in herbage quality. These results confirmed that the tiller base is the primary storage organ for WSC reserves (Fulkerson and Slack 1994a) and that leaf growth has the highest priority for available energy after defoliation, followed by root growth and tiller initiation, as is the case for perennial ryegrass (Donaghy and Fulkerson 1998) and cocksfoot (Rawnsley *et al.* 2002).

While the pattern of WSC accumulation following defoliation has been demonstrated, the relationship between WSC and N reserves and defoliation interval requires further investigation and forms the basis of Chapter 6.

Chapter 6

The effect of defoliation interval on water-soluble carbohydrate and nitrogen energy reserves, regrowth of leaves and roots, and tillering:

Experiment 1. Cocksfoot

Experiment 2. Prairie grass

6.1 Introduction

Water-soluble carbohydrates located in plant stubble are utilised as an energy source to initiate new growth of perennial grasses until photosynthesis is sufficient to sustain plant respiration (White 1973). Water-soluble carbohydrate levels are affected by defoliation severity, as indicated by residual height of stubble (Troughton 1957; Davidson and Milthorpe 1966a; Wilson and Robson 1970), as well as the interval between defoliations (Davies 1965; Bell and Ritchie 1989; Hume 1991a; Fulkerson *et al.* 1994; Fulkerson and Slack 1995; Fulkerson and Donaghy 2001). Defoliation interval is generally of primary importance, followed by stubble height (Bell and Ritchie 1989; Fulkerson and Donaghy 2001).

The level of WSC reserves in plant stubble significantly influences the rate of regrowth following defoliation (Alberda 1966), affecting the rate of leaf growth, root growth and tillering. While the effect of WSC reserves on regrowth immediately following defoliation of pasture grasses is well documented, the impact of WSC reserves on herbage DM yield over a longer period has been questioned (Davies 1965; Fulkerson and Slack 1994a).

Cocksfoot maintains between four and five live leaves per tiller, with a 4-leaf to 5-leaf stage defoliation interval recommended to achieve an optimal nutritional balance (Rawnsley *et al.* 2002). Results of a glasshouse study conducted by Slack *et al.* (2000) showed that defoliation of prairie grass at the 4-leaf compared with the 1-leaf stage, led to greater WSC accumulation and therefore leaf and root growth throughout the following regrowth cycle (4-leaf stage of regrowth). In a field study in subtropical Australia, Fulkerson *et al.* (2000) also found that a grazing rotation

based on the 3.5 to 4-leaf regrowth stage favoured growth and persistence of prairie grass throughout the year.

There has been some debate regarding the relative contribution of WSC and N reserves to regrowth following defoliation. Sullivan and Sprague (1943), Alberda (1966), Gonzalez *et al.* (1989) assert that plant N reserves play a minor role in regrowth, while others have concluded that N compounds play an important role (Dilz 1966; Ourry *et al.* 1988; 1989a;b). The reliance of regrowth on N reserves and the relative importance of WSC and N reserves have not been conclusively proven.

The aim of the current studies was to utilise leaf stage based defoliation interval to verify WSC and N stubble and root reserve levels and to record their effect on regrowth of Kara cocksfoot (experiment 1) and Matua prairie grass (experiment 2) plants. The priority sequence for allocation of WSC reserves during the regrowth period was also investigated.

6.2 Materials and methods

The experiments were conducted in glasshouses at the University of Tasmania, Hobart, Australia, between July and December 2003 (experiment 1), and at the Tasmanian Institute of Agricultural Research, Burnie, Australia, between May and November, 2004 (experiment 2). In each experiment, three seeds were planted in polyvinyl bags containing a standard potting mixture. Plants were watered daily, to replace evapotranspiration losses, and were fertilised regularly with either Hoaglands® solution (experiment 1), or Osmocote® at a rate equivalent to 40 kg N/ha (experiment 2). Once established, the weakest seedlings were removed to allow a single healthy seedling to reach maturity in each bag.

6.2.1 Determination of leaf regrowth stage

Each leaf regrowth stage was defined as the time required for the production of one fully expanded leaf per tiller. Cocksfoot and prairie grass plants maintain four to five live leaves per tiller, with a new leaf commencing growth when the previous leaf has reached approximately 75% of its full length. Thus, at any given time two leaves are expanding, and measurement of 'leaf stage' is estimated by the amount of growth of the current expanding leaves.

6.2.2 *Experimental design*

Plants were arranged as a randomised complete block design. In experiment 1, there were 312 cocksfoot plants arranged in 52 by 6 rows and separated into four blocks. In experiment 2, there were 585 prairie grass plants arranged in 65 by 9 rows and separated into five blocks. Each row constituted a treatment within each block. Twelve treatments - consisting of three defoliation treatments and four harvest dates – and one row of pre-treatment plants were randomised within each block.

6.2.3 *Defoliation treatments*

Nine weeks after sowing, all plants were defoliated to a stubble height of 50 mm to promote tillering. At the 4-leaf stage of regrowth, plants were again defoliated to 50 mm, an event termed H_0 .

Defoliation treatments commenced from H_0 , with defoliation intervals of the 1-leaf (1L), 2-leaf (2L) and 4-leaf (4L) stages of regrowth. Plants were defoliated to a uniform stubble height of 50 mm at each event. Defoliation treatments ceased when the 1-leaf defoliation interval had been completed four times, the 2-leaf interval twice and the 4-leaf interval once. This event was termed H_1 .

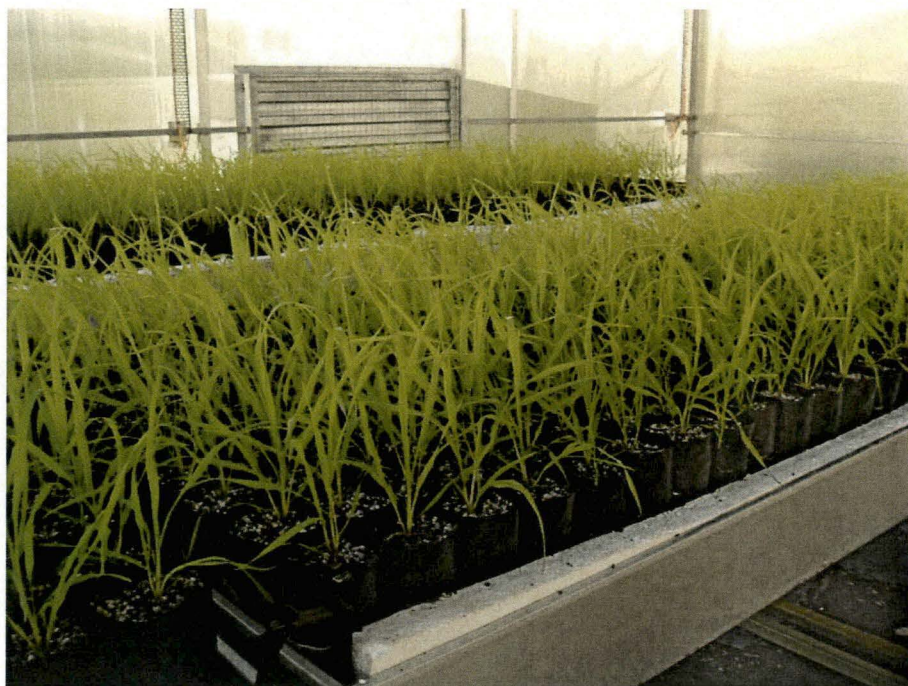


Plate 2 Experiment 2: Prairie grass plants prior to commencement of defoliation treatments.

6.2.4 Destructive harvesting and determination of DM yield

There were five destructive harvest events in these experiments (Figure 6.1). The first was carried out immediately prior to the commencement of treatments (H_0), with one row of plants per block destructively harvested. The second harvest was carried out at the cessation of defoliation treatments (H_1), for assessment of the immediate effect of the treatments. In experiment 1, the final three destructive harvests were carried out at 5 (H_2), 10 (H_3) and 24 days (H_4) following H_1 , to capture both the initial and lasting effects of defoliation interval on plant energy reserves and cocksfoot regrowth. Harvests H_3 and H_4 coincided with the 1.5-leaf and 3.5-leaf stages of regrowth, respectively. In experiment 2, the final three destructive harvests were carried out at the 1-leaf (H_2), 2-leaf (H_3) and 4-leaf stages of regrowth (H_4). At each harvest event from H_1 to H_4 , three rows of plants per block (one row per defoliation treatment) were destructively harvested.

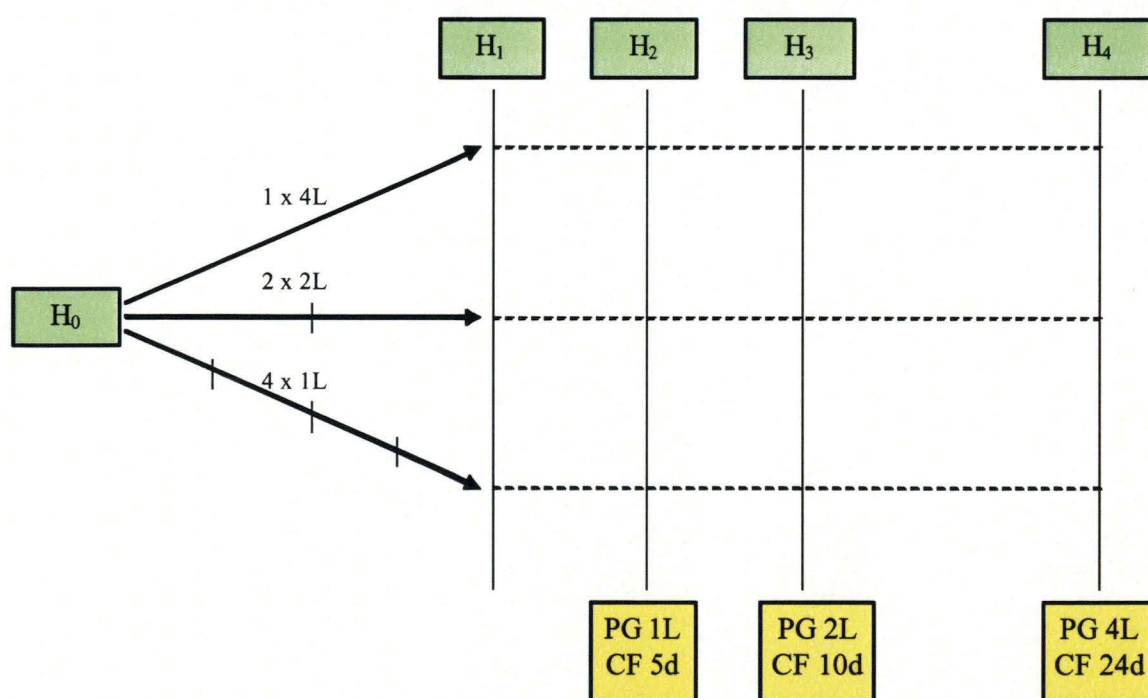


Figure 6.1 Diagrammatic representation of defoliation treatments (between H_0 and H_1) and destructive harvest regime (green boxes; H_0 - H_4) with corresponding leaf stages for prairie grass (PG 1-4L) and days for cocksfoot (CF 5-24d; yellow boxes).

At each harvest event, leaf tissue (above 50 mm) was removed and leaf DM yield per plant determined following drying of samples for 24 hours at 60°C in a forced draught oven. Root samples collected at the same time were stored at 2°C for up to

48 hours until they could be washed free of potting mix. Stubble and washed roots were immediately packed on ice for transportation to a freezer, frozen for 24 hours at -18°C , then freeze-dried and weighed. Tiller number per plant was also determined at each harvest interval. Harvests were consistently performed three hours after sunrise, to negate the confounding effect of diurnal fluctuations in WSC reserves (Fulkerson and Slack 1994a).

By H_4 in experiment 2, the leaves and tillers of many prairie grass plants from the 1-leaf stage treatment were either dead or did not provide a sample of sufficient size for analysis of WSC or N reserves.

6.2.5 *Determination of WSC*

Freeze-dried stubble and root samples were ground to pass through a 1 mm sieve in preparation for analysis of WSC content at New South Wales Department of Primary Industries Laboratories by Technicon Industrial Method number 302-73A, derived from the method outlined by Smith (1969; Appendix A.1).

6.2.6 *Determination of N*

Freeze-dried stubble and root samples were ground to pass through a 1 mm sieve in preparation for analysis of total N concentration. Ground samples were analysed for total N using a Leco FP-428 Nitrogen Analyser at CSBP Soil and Plant Nutrition Laboratories (Western Australia; Sweeney and Rexroad 1987; Appendix A.1).

6.2.7 *Tiller dynamics*

At H_0 , one tiller from each plant for treatments 1L/ H_4 , 2L/ H_4 and 4L/ H_4 was marked with a coloured wire loop. Its status [live (with or without a daughter tiller) or dead] was monitored at three day intervals in experiment 1 and every third week in experiment 2 for the duration of the experiments.



Plate 3 Experiment 1: Monitoring status of marked cocksfoot tillers following a defoliation treatment.

6.2.8 *Statistical analyses*

Means of all response variables were compared using an ANOVA two-way factorial design with replication using the statistical package SPSS (Version 11.5, SPSS Corporation, Illinois, USA), and LSD, as defined by Steel and Torrie (1960). At H_0 , the level of WSC and N reserves in plant stubble was compared with the level in plant roots using an ANOVA two-way factorial design without replication. Results are given in the text as the mean \pm s.e. Linear regression (r^2) between stubble WSC and N reserves at H_1 and plant regrowth at subsequent harvest events was tested using the statistical functions of EXCELTM.

Experiment 1. Cocksfoot

6.3 Results

6.3.1 *Effect of defoliation interval on WSC reserves*

At H₀, the mean WSC concentration (% of DM) of the stubble ($9.0 \pm 0.3\%$; mean \pm s.e.) was significantly higher ($P < 0.01$) than the mean WSC concentration of the roots ($4.3 \pm 0.5\%$).

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for stubble WSC concentration. The WSC concentration in stubble of cocksfoot plants defoliated at the 4-leaf stage was significantly greater ($P < 0.05$) than for plants defoliated at the 2-leaf and 1-leaf stages throughout the study (Table 6.1). Similarly, when converted to WSC content (mg/tiller), the 4-leaf stage defoliation resulted in significantly greater ($P < 0.001$) stubble WSC reserves than the 2-leaf and 1-leaf stage defoliations from H₁ through to H₄. There was no significant ($P > 0.05$) difference in stubble WSC concentration or content between the 2-leaf and 1-leaf stage treatments.

Table 6.1 Mean root water-soluble carbohydrate (WSC) concentration (% of DM) and stubble WSC concentration and content (mg/tiller) of cocksfoot, for plants defoliated four times at the 1-leaf stage (1L), twice at the 2-leaf stage (2L), or once at the 4-leaf stage (4L), at cessation of defoliation treatments (H₁), 5 days following H₁ (H₂), 10 days following H₁ (H₃) and 24 days following H₁ (H₄).

Leaf stage	Root WSC concentration (% of DM)				Stubble WSC concentration (% of DM)				Stubble WSC content (mg/tiller)			
	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄
1L	1.05	0.93	0.68	1.13	1.35	1.25	1.25	4.50	0.52	0.43	0.48	1.34
2L	1.60	1.13	0.95	1.55	2.50	1.65	1.83	5.33	1.11	0.80	0.68	2.00
4L	7.78	4.98	3.48	2.23	20.70	5.45	5.13	10.23	17.80	3.49	2.62	5.48
LSD ($P = 0.05$)	0.94				2.42				1.83			

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for root WSC concentration. Defoliation at the 4-leaf stage resulted in a significantly greater ($P < 0.05$) root WSC concentration than defoliation at the 2-leaf and 1-leaf stages at H₁, H₂ and H₃ (Table 6.1). At H₄, there was a significant ($P < 0.05$) difference in root WSC concentration between the 1-leaf and 4-leaf stage treatments

only. There was no significant ($P > 0.05$) difference between the 2-leaf and 1-leaf treatments during the regrowth period.

6.3.2 Relationship between plant WSC reserves and regrowth

There were stronger relationships between stubble WSC content at H_1 and subsequent regrowth than there were between stubble WSC concentration and regrowth, although r^2 values were similar.

There was a significant ($P < 0.001$) relationship between stubble WSC content at H_1 and leaf DM yield at H_2 (Table 6.2). At H_3 the r^2 value representing this relationship was also significant ($P < 0.01$), although not as significant as at H_2 . At H_4 there was no significant ($P > 0.05$) relationship between stubble WSC content at H_1 and leaf DM. The relationship between stubble WSC content at H_1 and root DM yield was significant ($P < 0.01$) at H_2 , H_3 and H_4 . The relationship between stubble WSC content at H_1 and tiller number was not significant at H_2 ($P > 0.05$), but was significant at H_3 ($P < 0.05$) and H_4 ($P < 0.01$), with relatively low r^2 values of 0.45 and 0.53.

Table 6.2 Proportion of experimental variation (r^2) explained for linear relationship between stubble water-soluble carbohydrate (WSC) content (mg/tiller) at the cessation of treatments (H_1) for cocksfoot and leaf dry matter (DM), root DM and tiller number, at 5 days following H_1 (H_2), 10 days following H_1 (H_3) and 24 days following H_1 (H_4). Asterisks indicate significance at * $P = 0.05$, ** $P = 0.01$ and *** $P = 0.001$.

Leaf stage	Stubble WSC (mg/tiller) at H_1		
	H_2	H_3	H_4
Leaf DM	0.75 (***)	0.64 (**)	ns
Root DM	0.61 (**)	0.83 (***)	0.61 (**)
Tiller No.	ns	0.45 (*)	0.53 (**)

6.3.3 Effect of defoliation interval on N reserves

At H_0 , the mean N concentration of the stubble ($3.5 \pm 0.1\%$; mean \pm s.e.) was significantly higher ($P < 0.01$) than the mean N concentration of the roots ($2.0 \pm 0.1\%$).

There was no significant ($P > 0.05$) defoliation interval by harvest event interaction for root N concentration (% of DM), stubble N concentration (% of DM) or stubble N content (mg/tiller).

Defoliation interval had a significant ($P < 0.01$) effect on stubble N content, with defoliation at the 1-leaf stage of regrowth resulting in a lower N content than defoliation at the 2-leaf or 4-leaf stage (Table 6.3). There was no significant ($P > 0.05$) difference in stubble N content between the 2-leaf and 4-leaf stages of regrowth. There was a significant ($P < 0.01$) decrease in stubble N content between H_1 and H_4 , from 1.37 to 0.92 mg/tiller, respectively.

Table 6.3 Mean root nitrogen (N) concentration (% of DM), stubble N concentration and stubble N content (mg/tiller) for cocksfoot, for plants defoliated four times at the 1-leaf stage (1L), twice at the 2-leaf stage (2L) or once at the 4-leaf stage (4L).

Leaf stage	Root N (% of DM)	Stubble N (% of DM)	Stubble N (mg/tiller)
1L	1.11	2.48	0.88
2L	1.17	2.60	1.13
4L	1.30	2.17	1.34
LSD ($P = 0.05$)	0.14	0.22	0.22

The effect of defoliation interval on root N concentration was significant ($P < 0.05$), with defoliation at the 4-leaf stage of regrowth resulting in significantly higher ($P < 0.05$) root N concentrations than defoliation at the 1-leaf stage (Table 6.3). There was no significant ($P > 0.05$) difference between the 2-leaf and 1-leaf stage treatments. Harvest event did not have a significant ($P > 0.05$) effect on root N concentration.

In contrast to this, defoliation at the 4-leaf stage resulted in a significantly lower ($P \leq 0.001$) stubble N concentration than defoliation at the 2-leaf and 1-leaf stages of regrowth (Table 6.3). There was no significant ($P > 0.05$) difference in stubble N concentration between the 2-leaf and 1-leaf stage treatments. Harvest event did not have a significant ($P > 0.05$) effect on stubble N concentration.

6.3.4 Relationship between plant N reserves and regrowth

The relationships between N levels and regrowth were weak and inconsistent (data not presented).

6.3.5 Effect of defoliation interval on DM yield

Root DM yield following H_1 was clearly related to defoliation interval prior to H_1 , with yield increasing with leaf regrowth stage (Figure 6.2). There were significant differences in root growth between plants defoliated at the 1-leaf and 4-leaf stages ($P < 0.001$) and 2-leaf and 4-leaf stages ($P < 0.01$) throughout the study. Root DM yield following defoliation at the 1-leaf stage was significantly lower ($P < 0.01$) compared with the 2-leaf stage at H_1 , H_3 and H_4 . There was no significant ($P > 0.05$) defoliation interval by harvest event interaction for root DM yield.

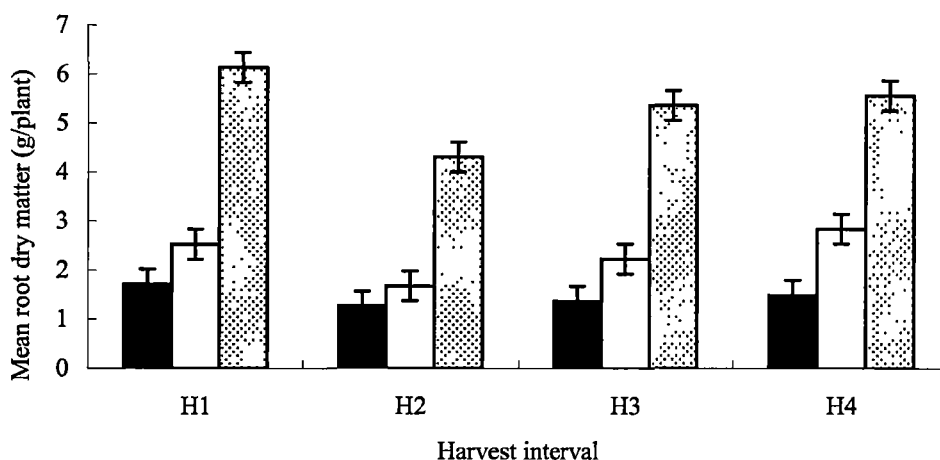


Figure 6.2 Mean root dry matter (DM) yield (g/plant) for cocksfoot plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (⋯), at cessation of defoliation treatments (H_1), 5 days following H_1 (H_2), 10 days following H_1 (H_3) and 24 days following H_1 (H_4). Vertical bars represent LSD ($P = 0.05$).

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for leaf DM yield. Leaf DM yield following H_1 was closely related to defoliation interval prior to H_1 , with yield increasing with leaf regrowth stage (Figure 6.3). Leaf DM yield of plants defoliated at the 1-leaf and 2-leaf stages was significantly lower

($P < 0.05$) compared with plants defoliated at the 4-leaf stage, with the exception of H₂.

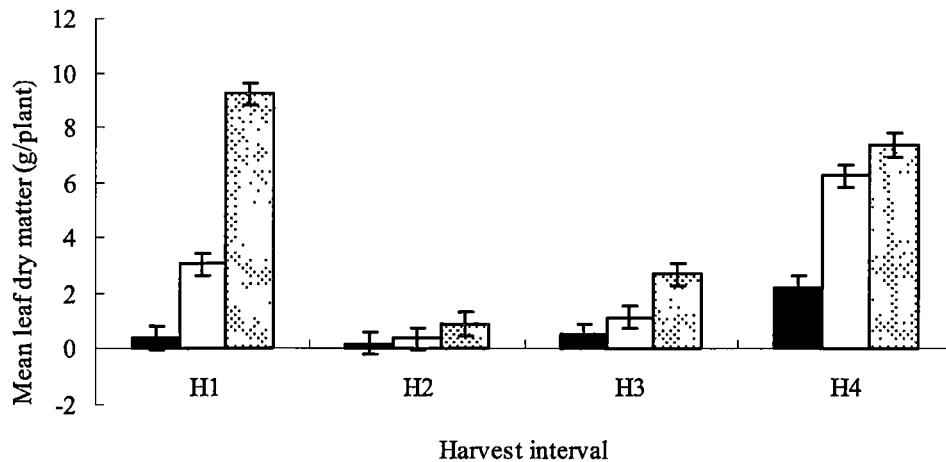


Figure 6.3 Mean leaf dry matter (DM) yield (g/plant) for cocksfoot plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (◻), at cessation of defoliation treatments (H₁), 5 days following H₁ (H₂), 10 days following H₁ (H₃) and 24 days following H₁ (H₄). Vertical bars represent LSD ($P = 0.05$).

The defoliation interval by harvest event interaction was not significant ($P > 0.05$) for tiller DM yield. Plants defoliated at the 4-leaf stage consistently maintained significantly heavier ($P < 0.001$) tillers than plants defoliated at the 2-leaf and 1-leaf stage (Figure 6.4), while the difference between the 2-leaf and 1-leaf stage was significant ($P < 0.05$) at H₁ only. Mean tiller DM yield significantly decreased ($P < 0.01$) between H₁ and H₄.

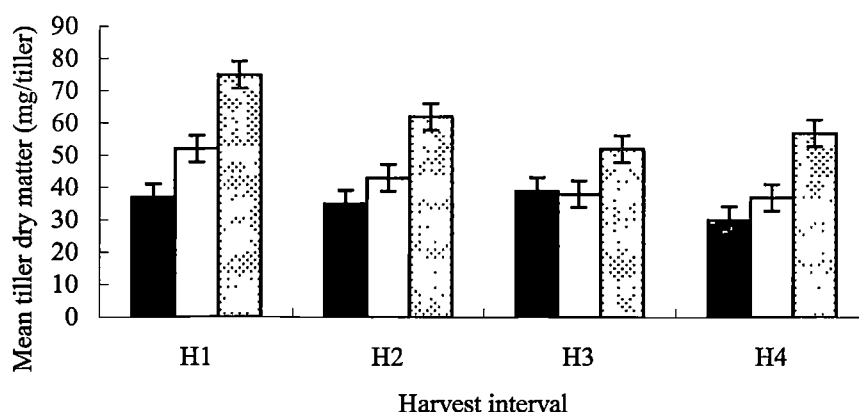


Figure 6.4 Mean tiller dry matter (DM) yield (mg/tiller) for cocksfoot plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (▨), at cessation of defoliation treatments (H₁), 5 days following H₁ (H₂), 10 days following H₁ (H₃) and 24 days following H₁ (H₄). Vertical bars represent LSD ($P = 0.05$).

6.3.6 Effect of defoliation interval on tiller dynamics

The mean number of tillers per plant at H₀ was 42 ± 2 (mean \pm s.e.). There was a significant ($P < 0.05$) defoliation interval by harvest event effect on tiller number per plant. The effect on tiller number was not observed until H₃, with the development of a significant ($P < 0.05$) difference in tiller number per plant between each leaf stage. By H₄ the plants repeatedly defoliated at the 1-leaf stage prior to H₁ had retained a mean of 42 ± 7 tillers per plant, while defoliation at the 2-leaf and 4-leaf stages resulted in a mean of 63 ± 4 and 83 ± 6 tillers per plant, respectively.

The lowest rate of tiller initiation was found in plants which were defoliated at the 1-leaf stage, with a significantly lower ($P < 0.001$) mean rate of 0.51 tillers initiated per marked tiller compared with rates of 1.20 and 1.08 for the 2-leaf and 4-leaf stages, respectively (Figure 6.5). There was no significant ($P > 0.05$) difference in tiller initiation between the 2-leaf and 4-leaf stage treatments.

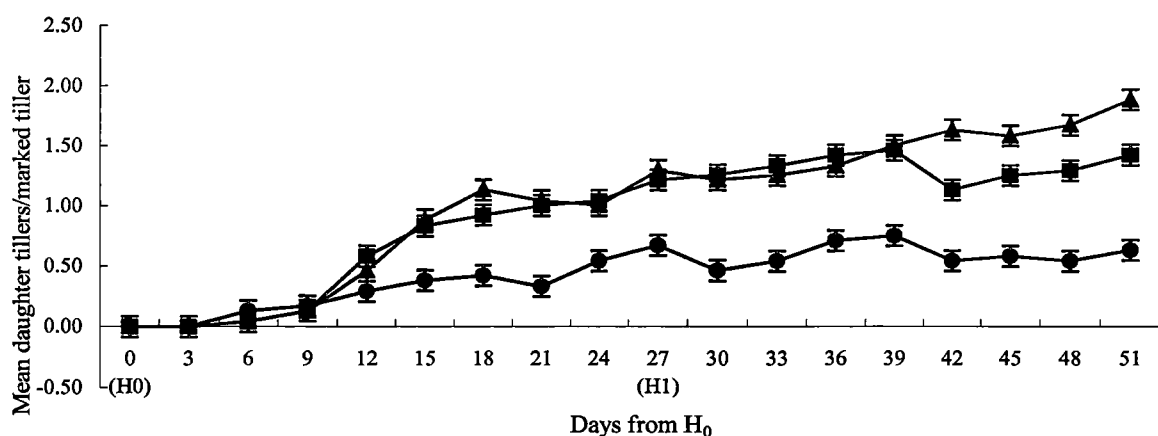


Figure 6.5 Mean number of daughter tillers initiated from each marked tiller, for cocksfoot plants defoliated four times at the 1-leaf stage (●), twice at the 2-leaf stage (▲) or once at the 4-leaf stage (■). Vertical bars represent LSD ($P = 0.05$).

Similarly, defoliation at the 4-leaf stage resulted in a significantly lower mean death rate of marked tillers than defoliation at the 2-leaf stage ($P < 0.05$), and the 1-leaf stage ($P < 0.001$). The mean death rate over the period of measurement for the 4-leaf stage was 0.08 tillers per marked tiller, compared with 0.11 and 0.12 for the 2-leaf and 1-leaf stage, respectively (Figure 6.6). There was no significant ($P > 0.05$) difference in tiller death rate between the 2-leaf and 1-leaf stage treatments.

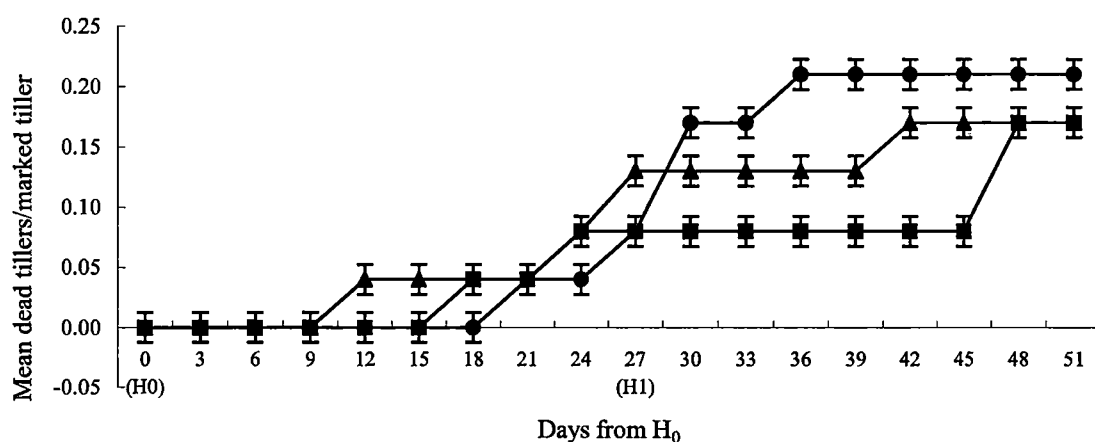


Figure 6.6 Mean number of dead tillers per marked tiller, for cocksfoot plants defoliated four times at the 1-leaf stage (●), twice at the 2-leaf stage (▲) or once at the 4-leaf stage (■). Vertical bars represent LSD ($P = 0.05$).

Experiment 2. Prairie grass

6.4 Results

6.4.1 *Effect of defoliation interval on WSC reserves*

At H₀, the mean WSC concentration of the stubble ($18.7 \pm 1.4\%$; mean \pm s.e.) was significantly higher ($P < 0.01$) than the mean WSC concentration of the roots ($6.4 \pm 1.4\%$).

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for both stubble WSC concentration (% of DM) and content (mg/tiller). The WSC concentration and content in stubble of prairie grass plants defoliated at the 4-leaf stage were significantly greater ($P < 0.001$) than for plants defoliated at the 2-leaf and 1-leaf stages throughout the study. Defoliation at the 2-leaf stage resulted in significantly greater ($P < 0.01$) stubble WSC concentration than defoliation at the 1-leaf stage, with the exception of H₂ where there was no significant ($P > 0.05$) difference between these treatments (Table 6.4).

Table 6.4 Mean root water-soluble carbohydrate (WSC) concentration (% of DM) and stubble WSC concentration and content (mg/tiller) of prairie grass, for plants defoliated four times at the 1-leaf stage (1L), twice at the 2-leaf stage (2L), or once at the 4-leaf stage (4L), at cessation of defoliation treatments (H₁), and at the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄).

	Root WSC concentration				Stubble WSC concentration				Stubble WSC content			
	(% of DM)				(% of DM)				(mg/tiller)			
	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄
1L	1.09	1.00	1.70	3.39	1.12	1.66	2.28	-	0.40	0.62	0.89	-
2L	5.28	1.62	3.24	8.53	11.38	3.78	6.81	35.62	6.83	2.28	4.71	39.61
4L	13.13	2.80	5.59	9.50	46.47	10.13	13.54	40.77	67.09	8.91	12.45	57.80
LSD ($P = 0.05$)	2.14				4.15				4.76			

Stubble WSC concentration remained stable between H₁ and H₃ for plants defoliated at the 1-leaf stage. For plants defoliated at the 2-leaf and 4-leaf stages, stubble WSC concentration decreased between H₁ and H₂, remained at similar levels at H₃ and then increased between H₃ and H₄ (Table 6.4).

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for root WSC concentration. Defoliation at the 4-leaf stage resulted in a significantly greater ($P < 0.001$) root WSC concentration than defoliation at the 2-leaf and 1-leaf stages at H_1 and H_3 . At H_2 , there was no significant ($P > 0.05$) difference between defoliation treatments, while at H_4 , defoliation at the 1-leaf stage resulted in a significantly lower ($P < 0.001$) root WSC concentration than less frequent defoliations (Table 6.4).

Root WSC concentration remained stable between H_1 and H_3 for plants defoliated at the 1-leaf stage, and increased between H_3 and H_4 . For plants defoliated at the 2-leaf and 4-leaf stages, root WSC concentration decreased between H_1 and H_2 , and increased between H_2 and H_4 (Table 6.4).

6.4.2 *Relationship between plant WSC reserves and regrowth*

There was a stronger linear relationship between stubble WSC concentration at H_1 and subsequent regrowth than there was between stubble WSC content and regrowth, although r^2 values were similar.

There was a significant ($P < 0.001$) positive linear relationship between stubble WSC concentration at H_1 and leaf DM, root DM, tiller DM and tiller number at H_2 , H_3 and H_4 (Table 6.5). There was also a significant ($P < 0.001$) relationship between root WSC concentration at H_1 and leaf DM, root DM, tiller DM and tiller number at H_2 , H_3 and H_4 , although r^2 values were generally lower than for the stubble WSC concentration relationships (Table 6.5). There was a significant ($P < 0.001$) relationship between stubble and root WSC concentration at H_1 and tiller initiation at H_4 , although r^2 values of 0.62 and 0.68 respectively, indicated a high level of variation around the relationship (data not presented).

Table 6.5 Proportion of experimental variation (r^2) explained for linear relationship between stubble and root water-soluble carbohydrate (WSC) concentration (% of DM) for prairie grass at the cessation of treatments (H_1) and leaf dry matter (DM), root DM, tiller DM and tiller number, at the 1-leaf (H_2), 2-leaf (H_3) and 4-leaf stages of regrowth (H_4).

	Stubble WSC % at H_1			Root WSC % at H_1		
	H_2	H_3	H_4	H_2	H_3	H_4
Leaf DM	0.95	0.88	0.63	0.87	0.86	0.66
Root DM	0.96	0.93	0.82	0.86	0.83	0.83
Tiller DM	0.89	0.70	0.64	0.83	0.60	0.69
Tiller No.	0.78	0.78	0.62	0.71	0.77	0.73

All r^2 values significant ($P < 0.001$)

6.4.3 Effect of defoliation interval on N reserves

At H_0 , the mean N concentration of the stubble ($3.7 \pm 0.1\%$; mean \pm s.e.) was significantly higher ($P = 0.001$) than the mean N concentration of the roots ($2.1 \pm 0.1\%$).

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for stubble N concentration (% of DM) and content (mg/tiller and mg/plant). In contrast to stubble WSC concentration, N concentration significantly decreased ($P < 0.001$) with increasing defoliation interval. Mean stubble N concentration also significantly decreased ($P < 0.001$) during regrowth between H_3 and H_4 (Table 6.6).

There was an increase in stubble N content (mg/plant) with increasing defoliation interval, with defoliation at the 4-leaf stage resulting in significantly higher ($P < 0.001$) stubble N content than more frequent defoliation, with the exception of H_1 , where there was no significant ($P > 0.05$) difference between the 4-leaf and 2-leaf stage treatments. There was also a significant ($P < 0.001$) difference in stubble N content between the 2-leaf and 1-leaf stage treatments throughout the study (Table 6.6).

Table 6.6 Mean root nitrogen (N) concentration (% of DM), stubble N concentration and stubble N content (mg/plant) for prairie grass, for plants defoliated four times at the 1-leaf stage (1L), twice at the 2-leaf stage (2L) or once at the 4-leaf stage (4L), at cessation of defoliation treatments (H₁), and at the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄).

	Stubble N concentration (% of DM)				Stubble N content (mg/plant)				Root N concentration (% of DM)				
	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄	H ₁	H ₂	H ₃	H ₄	Mean
1L	4.15	4.29	4.39	-	9.62	10.83	13.37	-	1.49	1.30	1.22	-	1.34
2L	2.94	3.42	3.42	1.70	13.10	14.73	16.10	24.64	1.58	1.56	1.56	1.15	1.47
4L	1.11	2.18	1.84	1.05	13.58	19.66	19.92	27.18	1.17	1.09	1.09	0.93	1.08
									Mean	1.41	1.34	1.29	1.04
LSD (<i>P</i> = 0.05)				0.62				2.12		LSD (<i>P</i> = 0.05)			0.17

The effect of defoliation interval on root N concentration was significant ($P < 0.001$), with defoliation at the 2-leaf stage of regrowth resulting in significantly higher ($P < 0.001$) root N levels than defoliation at the 1-leaf or 4-leaf stages (Table 6.6). The effect of harvest event on root N concentration was significant ($P < 0.001$), with N levels at H₄ significantly lower than at H₁, H₂ and H₃ (Table 6.6).

6.4.4 Relationship between plant N reserves and regrowth

There were stronger linear relationships between stubble N concentration at H₁ and subsequent regrowth than there were between stubble N content and regrowth.

There was a significant ($P < 0.001$) negative linear relationship between stubble N concentration at H₁ and leaf DM, root DM, tiller DM and tiller number at H₂, H₃ and H₄ (Table 6.7). There was also a significant ($P < 0.001$) relationship between stubble N concentration at H₁ and tiller initiation and tiller death rates at H₄, although r^2 values of 0.68 and 0.58 respectively, indicated a high level of variation around the relationship (data not presented).

Table 6.7 Proportion of experimental variation (r^2) explained for linear relationship between stubble and root nitrogen (N) concentration (% of DM) for prairie grass at the cessation of treatments (H₁) and leaf dry matter (DM), root DM, tiller DM and tiller number, at the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄). Asterisks are significant at * $P = 0.05$, ** $P = 0.01$ and *** $P = 0.001$.

	Stubble N % at H ₁			Root N % at H ₁		
	H ₂	H ₃	H ₄	H ₂	H ₃	H ₄
Leaf DM	0.93 (***)	0.92 (***)	0.77 (***)	0.59 (***)	0.57 (**)	0.27 (*)
Root DM	0.86 (***)	0.85 (***)	0.89 (***)	0.77 (***)	0.72 (***)	0.42 (**)
Tiller DM	0.89 (***)	0.78 (***)	0.79 (***)	0.58 (***)	0.49 (**)	ns
Tiller No.	0.72 (***)	0.63 (***)	0.76 (***)	0.54 (***)	0.59 (***)	0.28 (*)

The negative relationship between root N concentration at H₁ and root DM yield was significant ($P < 0.01$) at H₂, H₃ and H₄. The most significant ($P < 0.001$) of these relationships were found at H₂ and H₃ (Table 6.7).

6.4.5 Effect of defoliation interval on DM yield

There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for leaf, root and tiller DM yields.

Leaf DM yield following H₁ was closely related to defoliation interval prior to H₁, with leaf DM increasing with leaf regrowth stage (Figure 6.7). Leaf DM yield of plants defoliated at the 4-leaf stage was significantly higher ($P < 0.001$) compared with plants defoliated more frequently, while the difference between the 2-leaf and 1-leaf stage treatments was significant ($P < 0.001$) at H₁, H₃ and H₄. Leaf DM yield was significantly higher ($P < 0.001$) at H₄ than for earlier harvest events.

Root DM yield following H₁ was related to defoliation interval prior to H₁, with root DM increasing with leaf regrowth stage (Figure 6.8). Defoliation at the 4-leaf stage resulted in a significantly higher ($P < 0.001$) root DM yield than more frequent defoliation throughout the study. There was no significant ($P > 0.05$) difference between the 2-leaf and 1-leaf stage defoliation treatments. Root DM yield was significantly higher ($P < 0.001$) at H₄ than for earlier harvest events.

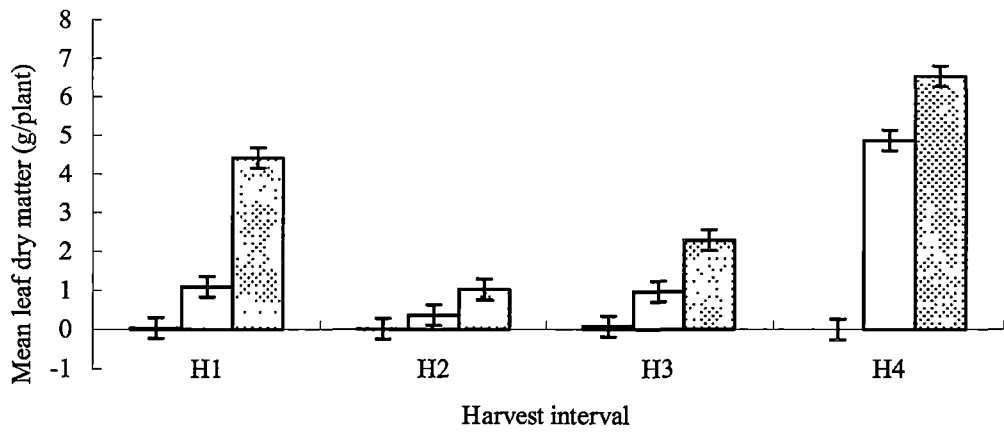


Figure 6.7 Mean leaf dry matter (DM) yield (g/plant) for prairie grass plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (⋯), at cessation of defoliation treatments (H₁), and the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄). Vertical bars represent LSD ($P = 0.05$).

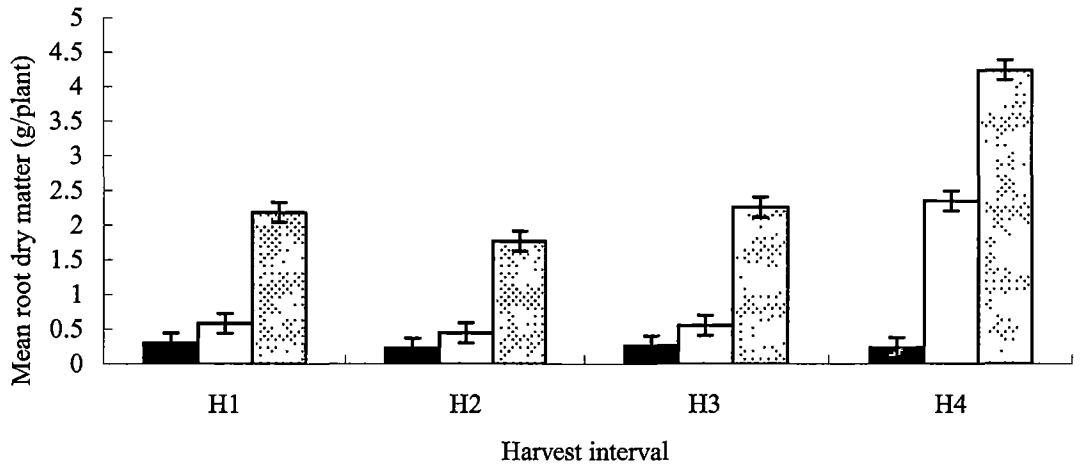


Figure 6.8 Mean root dry matter (DM) yield (g/plant) for prairie grass plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (⋯), at cessation of defoliation treatments (H₁), and the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄). Vertical bars represent LSD ($P = 0.05$).

Tiller DM yield significantly increased ($P < 0.001$) with increasing leaf regrowth stage (Figure 6.9). Tiller DM yield significantly decreased ($P < 0.001$) following defoliation at H_1 for all defoliation treatments, and significantly increased ($P < 0.001$) between H_3 and H_4 for the 2-leaf and 4-leaf defoliation treatments.

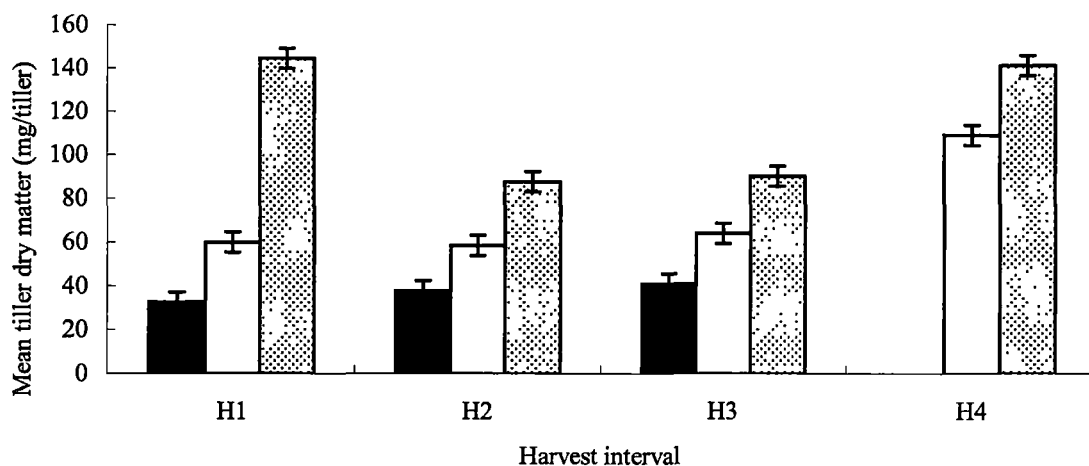


Figure 6.9 Mean tiller dry matter (DM) yield (mg/tiller) for prairie grass plants defoliated four times at the 1-leaf stage (■), twice at the 2-leaf stage (□) or once at the 4-leaf stage (▨), at cessation of defoliation treatments (H_1), and the 1-leaf (H_2), 2-leaf (H_3) and 4-leaf stages of regrowth (H_4). Vertical bars represent LSD ($P = 0.05$).

6.4.6 Effect of defoliation interval on tiller dynamics

The mean number of tillers per plant at H_0 was 6.8 ± 0.3 (mean \pm s.e.). There was a significant ($P < 0.001$) defoliation interval by harvest event interaction for tiller number per plant following defoliation treatments (Table 6.8). Defoliation at the 4-leaf stage resulted in a significantly higher ($P < 0.001$) tiller number per plant compared with defoliation at the 2-leaf and 1-leaf stages at H_2 , H_3 and H_4 . There was no significant ($P > 0.05$) difference in tiller number per plant for the 1-leaf and 2-leaf stage treatments at H_1 , H_2 , and H_3 , whereas tiller number per plant significantly increased ($P < 0.001$) for the 2-leaf stage treatment between H_3 and H_4 , resulting in 13.9 ± 0.8 tillers per plant. Tiller number per plant for the 4-leaf stage treatment significantly increased ($P < 0.001$) between H_1 and H_3 , and between H_3 and H_4 , resulting in 18.7 ± 0.8 tillers per plant (Table 6.8).

Table 6.8 Mean tiller number per plant, for prairie grass plants defoliated four times at the 1-leaf stage (1L), twice at the 2-leaf stage (2L) or once at the 4-leaf stage (4L), at cessation of defoliation treatments (H₁), and the 1-leaf (H₂), 2-leaf (H₃) and 4-leaf stages of regrowth (H₄).

	Tiller number/plant			
	H ₁	H ₂	H ₃	H ₄
1L	7.1	6.8	7.5	-
2L	7.5	7.4	7.5	13.9
4L	8.3	10.4	12.2	18.7
LSD ($P = 0.05$)				1.9

The rate of tiller initiation significantly increased ($P < 0.001$) with increasing leaf regrowth stage (Figure 6.10). Defoliation at the 1-leaf stage resulted in the lowest rate of tiller initiation of 0.04 tillers initiated per marked tiller, compared with rates of 0.38 and 1.11 for the 2-leaf and 4-leaf stages, respectively (Figure 6.10).

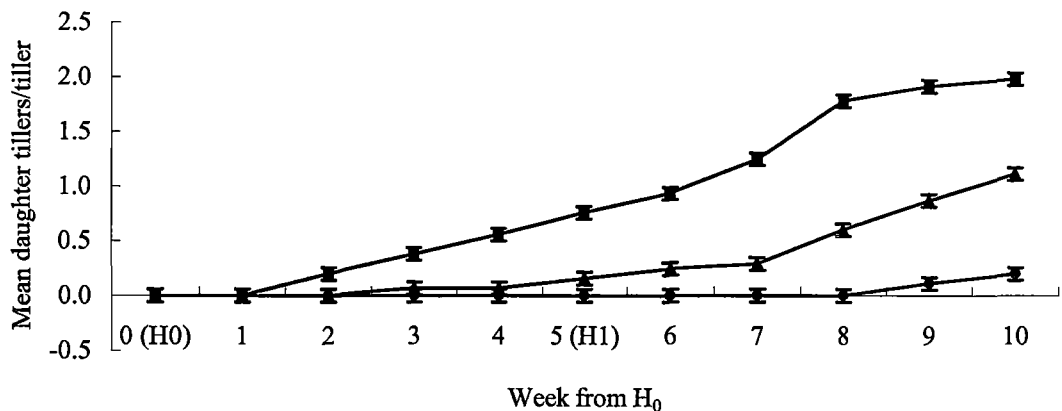


Figure 6.10 Mean number of daughter tillers initiated from each marked tiller, for prairie grass plants defoliated four times at the 1-leaf stage (●), twice at the 2-leaf stage (▲) or once at the 4-leaf stage (■). Vertical bars represent LSD ($P = 0.05$).

Defoliation at the 1-leaf stage resulted in a significantly higher ($P < 0.001$) mean death rate of marked tillers than defoliation at the 2-leaf and 4-leaf stages of regrowth (0.70 versus 0.06 and 0.04 dead tillers per marked tiller respectively; Figure 6.11). There was no significant ($P > 0.05$) difference in tiller death rate between the 2-leaf and 4-leaf stage treatments.

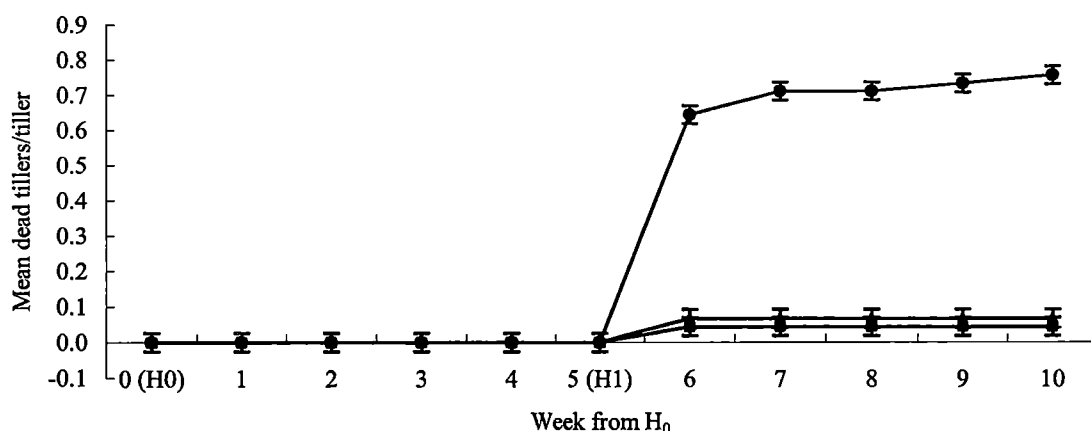


Figure 6.11 Mean number of dead tillers per marked tiller, for prairie grass plants defoliated four times at the 1-leaf stage (●), twice at the 2-leaf stage (▲) or once at the 4-leaf stage (■). Vertical bars represent LSD ($P = 0.05$).

6.5 Discussion

There were significantly greater concentrations of WSC and N in the stubble of cocksfoot and prairie grass plants compared with the roots, confirming the stubble as the primary site for energy storage, with roots playing a lesser role (Vartha and Bailey 1980; Fulkerson and Slack 1994a).

Defoliation interval had a marked effect on both plant stubble and root WSC reserves of both species, with more frequent defoliation resulting in reduced WSC reserves. Between H_1 and H_2 there was a dramatic decrease in both stubble WSC concentration and content for plants defoliated at the 4-leaf stage compared with other treatments, although WSC reserves at H_2 in plants defoliated at the 4-leaf stage still remained higher than for other treatments. This greater decline in WSC reserves was associated with significantly greater regrowth of leaves compared with the 1-leaf and 2-leaf treatments. The low level of WSC reserves at H_3 (1.5-leaf stage of regrowth for cocksfoot and 2-leaf stage of regrowth for prairie grass) in plants subject to 1-leaf and 2-leaf treatments indicated that these plants would be vulnerable to re-defoliation before the 2-leaf regrowth stage. Thus, a longer defoliation interval than the 2-leaf stage is required for adequate accumulation of plant energy reserves to support regrowth following defoliation of both cocksfoot and prairie grass plants.

Water-soluble carbohydrate reserves in cocksfoot plants from the 4-leaf stage treatment continued to decline at H₃, but remained higher than WSC reserves in plants from more frequently defoliated treatments, which were stable. This may reflect either greater WSC reserve utilisation for respiration in the larger 4-leaf treatment plants, or continued allocation of reserves for leaf growth and tiller initiation. By H₄ (3.5-leaf stage of regrowth), all cocksfoot plants had sufficient photosynthetic tissue to allocate carbohydrates to storage, reflected in an increase in WSC reserves.

Stubble WSC concentration at H₄ (4-leaf stage of regrowth) in prairie grass plants defoliated at the 1-leaf stage was less than 50% of WSC reserves prior to defoliation treatments. Further evidence of the severe effect of repeated defoliation at the 1-leaf stage on WSC reserves and subsequent regrowth was the death of 67% of plants in this treatment by H₄. The final stubble WSC concentration of plants defoliated at the 2-leaf and 4-leaf stages exceeded levels at H₀ by at least 90%, suggesting that defoliation of prairie grass at the 2-leaf stage does not have a lasting effect on WSC reserves, provided that this is followed by a longer recovery period.

Previous studies have found that root growth of perennial grasses has a lower priority for available energy than leaf growth (Jacques 1937; Donaghy and Fulkerson 1998). In support of this, leaves of both cocksfoot and prairie grass plants from all treatments regrew immediately following defoliation, whereas root growth only occurred at H₃ in the 2-leaf and 4-leaf stage treatments for cocksfoot, and in the 4-leaf stage treatment for prairie grass. The priority sequence for allocation of WSC reserves following defoliation was also evident in the relationship between regrowth parameters and stubble WSC concentration. The high r^2 values at H₂ and H₃ for leaf DM yield reflect plant dependence on WSC reserves to meet plant energy requirements until adequate photosynthetic tissue has been produced. This is consistent with previous studies by Troughton (1957), Davies (1965), Davidson and Milthorpe (1966b), White (1973), Hume (1991a), Fulkerson *et al.* (1994) and Fulkerson and Slack (1995).

For both species there was a stronger relationship between root DM and stubble WSC content at H₃ than between leaf DM yield and stubble WSC content, indicating partitioning of energy to root growth at this stage of regrowth. In plants defoliated at the 2-leaf and 4-leaf stages of regrowth, WSC reserves were then allocated to tillers, evident in an increased tiller number per plant. The priority sequence for allocation of WSC reserves in cocksfoot and prairie grass therefore followed the order of leaf growth, root growth and tillering during the regrowth period, following the same trend determined for perennial ryegrass by Donaghy and Fulkerson (1998).

Although there were significantly less WSC reserves stored in prairie grass roots than in the stubble, there were relatively strong relationships between root WSC concentration and regrowth parameters. The high r^2 values at H₂ and H₃ for the relationship between leaf DM yield and root WSC concentration indicate that WSC reserves are also mobilised from prairie grass roots in addition to the stubble, to meet plant energy requirements until adequate photosynthetic tissue has been produced. At H₄, there was a stronger relationship between root DM and root WSC concentration than between leaf DM yield and root WSC concentration, showing that energy stored in the roots had been allocated to root growth at this stage of the regrowth cycle. Root WSC concentration at H₄ in prairie grass plants defoliated at the 1-leaf stage was less than 53% of root WSC reserves prior to defoliation treatments, further indicating the severity of the effect of frequent defoliation on energy reserves and subsequent regrowth of prairie grass plants. The final root WSC concentration of plants defoliated at the 2-leaf and 4-leaf stages exceeded levels at H₀ by at least 33%.

The effect of defoliation interval on stubble N concentration (% of DM) in both species differed from the effect on stubble N content (mg/tiller for cocksfoot and mg/plant for prairie grass). Stubble N content (and root N concentration for cocksfoot) were aligned with patterns of WSC depletion and accumulation following defoliation, with significantly greater N content in plants defoliated at the 4-leaf stage of regrowth compared with plants defoliated at the 1-leaf stage. In contrast, defoliation at the 4-leaf stage of regrowth resulted in lower stubble N concentration than defoliation at the 2-leaf and 1-leaf stages.

There were no clear trends in N content on a mg/tiller basis for prairie grass, possibly due to the confounding effect of including newly initiated daughter tillers in energy calculations – an effect that was absolved through expression of N content on a mg/plant basis. Although energy reserve content (mg/tiller) is generally considered a more reliable basis for evaluating reserve energy levels than concentration (% of DM) (Smith 1974; Fulkerson and Slack 1995; Donaghy and Fulkerson 1998), the contrasting pattern of N reserve accumulation, when expressed as concentration, is worthy of attention. With mean tiller mass increasing and stubble N concentration decreasing with regrowth, it follows that tiller mass is entirely driving the positive relationship between stubble N content and leaf regrowth stage.

If stubble N concentration is used to evaluate energy reserve status, a trend becomes evident with higher N reserves associated with more frequent defoliation of both species. It is possible that accelerated N accumulation and storage in plant stubble was induced by more frequent defoliation, perhaps to substitute for low WSC reserves, as suggested by Davidson and Milthorpe (1965). Alternatively, assuming all plants absorbed the same amount of soil N, the lower growth resulting from frequent defoliation may have resulted in the accumulation of N reserves, in contrast to the diffusion of N in the larger herbage mass of less frequently defoliated plants. For cocksfoot, the latter argument is substantiated by the fact the relationships between stubble N levels (both N content and concentration) and regrowth following defoliation were weak and inconsistent. Thus, it appears that N reserves play a minor role in regrowth of well-fertilised cocksfoot plants following defoliation. For prairie grass, there were strong relationships between stubble N concentration and regrowth parameters from H₂ to H₄. Thus, it appears that N reserves may play an important role in regrowth of prairie grass plants following defoliation when WSC reserves are low, as has been argued for perennial ryegrass by Dilz (1966) and Ourry *et al.* (1988; 1989a;b).

Despite the strong relationship between N reserves and regrowth of prairie grass plants, the primary role of WSC reserves as the energy source for plant regrowth following defoliation was confirmed in the current study. While there was a 4-fold increase in stubble N concentration as a result of frequent defoliation, there was a 45-fold decrease in stubble WSC concentration. This compares with a 12% decrease in

stubble N concentration and a 15-fold decrease in stubble WSC concentration in cocksfoot plants. These results suggest that WSC reserves have a greater impact on plant regrowth relative to N reserves, and that the reserve status (and therefore regrowth) of prairie grass is more drastically affected by frequent defoliation than cocksfoot.

Defoliation interval had a marked effect on the regrowth capacity of cocksfoot and prairie grass plants, with defoliation at the 4-leaf stage resulting in greater rates of root and leaf DM accumulation in the subsequent recovery period, than defoliation at the 2-leaf or 1-leaf stages. The current studies showed that the critical defoliation interval in terms of influencing regrowth is the 2-leaf stage; defoliation at this interval likely to result in a satisfactory rate of regrowth provided that an adequate recovery period of regrowth is allowed. Leaf DM yield of both species had not significantly recovered by H₃, indicating that continual defoliation at the 2-leaf stage would be detrimental to pasture productivity. However, strategic defoliation of cocksfoot and prairie grass plants at the 2-leaf stage followed by implementation of a 3-leaf or 4-leaf defoliation interval is not likely to have an unfavourable long-term effect on leaf DM yields, as evidenced by the pattern of leaf DM yield at H₄.

Differences in tiller number per plant with regrowth can be explained by the patterns of daughter tiller initiation and tiller death, which reflect the effect of defoliation on energy reserves and in turn, plant persistence. After two defoliations at the 1-leaf stage (14 days following H₀) the capacity for cocksfoot plants to produce daughter tillers decreased in comparison to plants defoliated at the 2-leaf or 4-leaf stages, due to depleted WSC reserves. By H₁ a trend had established, with higher tiller death rates associated with more frequent defoliation, resulting in the previously mentioned differences in tiller number between treatments.

The effect of frequent defoliation on the tillering capacity of prairie grass was more extreme than for cocksfoot. By H₁, there was a significant difference between all treatments, with prairie grass plants repeatedly defoliated at the 1-leaf stage initiating fewer daughter tillers compared with plants in the 2-leaf stage treatment, and plants defoliated at the 2-leaf stage in turn initiating fewer daughter tillers compared with plants defoliated at the 4-leaf stage. At H₄, the effect of defoliation interval on

daughter tiller initiation was even more pronounced, and was again related to WSC reserves. Immediately following the cessation of defoliation treatments, the tiller death rate of prairie grass plants defoliated at the 1-leaf stage dramatically increased – resulting in the death of entire plants by the completion of the study.

The priority sequence for allocation of WSC reserves during the regrowth period followed the order of leaf growth, root growth and tillering for both cocksfoot and prairie grass. In prairie grass plants, WSC were mobilised from the roots in addition to the stubble, to meet requirements until adequate photosynthetic tissue had been produced. These studies showed that cocksfoot and prairie grass plants require a grazing rotation longer than the 2-leaf stage to maximise carbohydrate assimilation and therefore leaf, root and tiller DM yields, as well as tiller number and survival. Nitrogen energy reserves were found to play a minor role in the regrowth of cocksfoot plants following defoliation. There was a strong relationship between stubble N content and regrowth of prairie grass, with accelerated N accumulation and storage in plant stubble seemingly induced by more frequent defoliation, perhaps to substitute for low WSC reserves.

These experiments have focused on the effect of defoliation interval on plant WSC reserves and subsequent regrowth. While defoliation height is of secondary importance to defoliation frequency (Bell and Ritchie 1989; Fulkerson and Donaghy 2001), the WSC concentration gradient within cocksfoot and prairie grass stubble has not been previously studied and would be valuable knowledge in relation to the implementation of defoliation management regimes. Chapter 7 documents the storage locality and patterns of WSC accumulation in cocksfoot and prairie grass stubble.

Chapter 7

Water soluble carbohydrate gradients in the stubble of prairie grass and cocksfoot plants

7.1 Introduction

The recommended defoliation height for perennial ryegrass is 45-50 mm, which combined with defoliation between the 2-leaf to 3-leaf regrowth stages, maximises WSC accumulation and therefore the rate of plant regrowth (Fulkerson and Slack 1995). The importance of an appropriate defoliation interval to maximise the regrowth and persistence of cocksfoot and prairie grass has been established in this thesis, with results from field and glasshouse studies confirming the 4-leaf stage as the optimal time of defoliation for both species. The studies previously described in this thesis have adopted the recommended defoliation stubble height for perennial ryegrass (45-50 mm) for defoliation of prairie grass and cocksfoot plants, but the optimal defoliation height for these species is yet to be defined.

Although defoliation interval is generally of primary importance in the regrowth of pasture plants, and stubble height is of secondary importance (Bell and Ritchie 1989; Fulkerson and Donaghy 2001), stubble height can induce significant effects on plant regrowth and persistence. Fulkerson and Slack (1994b) assessed the effect of cutting height on production and persistence of perennial ryegrass and found that defoliation to 60 mm stubble height, as opposed to 120 mm, yielded 54% more edible DM and resulted in a 65% higher plant survival rate. Fulkerson and Slack (1994b) concluded that the 120 mm defoliation height provided shading that adversely affected ryegrass, while the 60 mm defoliation height allowed for sufficient reserves to support regrowth following defoliation. Detrimental consequences are reported to be associated with defoliation below a 50 mm stubble height, with depletion of stubble WSC reserves following defoliation leading to delayed regrowth and decreased plant persistence (Davidson and Milthorpe 1966a; Wilson and Robson 1970).

By providing a balance between maintenance of WSC reserves and minimisation of shading, defoliating grass plants at an optimal defoliation height maximises the rate

of plant regrowth and subsequent pasture productivity and persistence. The aim of the current glasshouse study was to investigate WSC reserve storage patterns in the stubble of Matua prairie grass and Kara cocksfoot plants throughout four distinct regrowth cycles.

7.2 Materials and methods

The experiment was conducted in a glasshouse at the Tasmanian Institute of Agricultural Research, Burnie, Australia (Latitude $-41^{\circ}04'S$), between December 2004 and October 2005. Three seeds were planted in each polyvinyl bag (100 mm diameter x 280 mm depth) on December 28 2004. The bags contained a potting mixture composed of 50% *Pinus radiata* D. bark, 30% sand, 20% *Spaghnum* sp. moss and nutrients (Appendix A.2). The plants were arranged in the glasshouse at a density of 100 plants/m², and watered daily via an underlying geotextile membrane capillary mat, to replace evapotranspiration losses. Glasshouse conditions were controlled to maintain day/night temperatures of 20/10°C. Once established, the weakest seedlings were removed to allow a single healthy seedling to reach maturity in each bag. Plants were fertilised bi-monthly with Osmocote® at a rate equivalent to 40 kg N/ha.

7.2.1 Experimental design

Plants were arranged in a randomised complete block design, with four replicates each containing eight randomly allocated treatments. Each treatment consisted of a row of nine plants per block, resulting in 36 plants in total per treatment. The treatments were each characterised by one of two species (prairie grass cv. Matua and cocksfoot cv. Kara) and one of four successive destructive harvests (H₁-H₄). Buffer plants were placed around the minisward to minimise boundary effects. These plants were harvested but otherwise not included in analyses.

7.2.2 Destructive harvest regime

On February 14 2005 (48 days following sowing), all plants were defoliated to a stubble height of 100 mm to promote tillering. At the 4-leaf stage of regrowth, plants were defoliated to 100 mm, an event termed H₁ (with determination of leaf stage for cocksfoot and bromes as described in Chapter 6). At H₁, one row of plants for each species per block was destructively harvested to ground level. The stubble was

immediately divided into 10 mm increments and samples were combined to produce one sample per row for each of the 10 mm increments. This harvest regime was repeated three times to investigate possible changes in WSC reserve storage patterns through four sequential regrowth cycles (H_1 - H_4). Immediately prior to each harvest event, numbers of vegetative and reproductive tillers per plant were recorded, and reproductive and vegetative tillers were separated at each harvest for individual analysis. Harvests were consistently performed three hours after sunrise, to negate the confounding effect of diurnal fluctuations in WSC reserves (Fulkerson and Slack 1994a). All stubble samples were frozen, freeze-dried and weighed.

7.2.3 *Determination of WSC*

Freeze-dried stubble samples were ground to pass through a 1 mm sieve in preparation for analysis of WSC content at New South Wales Department of Primary Industries Laboratories by Technicon Industrial Method number 302-73A, derived from the method outlined by Smith (1969; Appendix A.1).

7.2.4 *Statistical analyses*

Means were compared using an ANOVA three-way factorial design (WSC/segment by species by harvest) with replication using the statistical package SPSS (Version 11.5, SPSS Corporation, Illinois, USA), and LSD, as defined by Steel and Torrie (1960).

7.3 **Results**

7.3.1 *Vegetative tillers*

There were significant segment by species ($P < 0.001$) and species by harvest ($P < 0.001$) interactions for stubble WSC concentration (% of DM; Table 7.1). With the exception of the 0-10 mm segment, there was a significantly higher ($P < 0.001$) WSC concentration in the stubble of prairie grass compared with cocksfoot. For prairie grass, there was a significant ($P < 0.05$) increase in stubble WSC concentration between the 0-10 and 11-20 mm segments, stabilised WSC reserves between the 11-20 and 31-40 mm segments, and a significant ($P < 0.05$) decline in stubble WSC concentration between each segment in the range 31-40 to 51-60 mm. For cocksfoot, there was a significant ($P < 0.05$) decrease in stubble WSC concentration between

each segment in the range 11-20 to 31-40 mm. Levels of WSC reserves in cocksfoot stubble stabilised between 40 and 100 mm.

Table 7.1 Water-soluble carbohydrate (WSC) concentration (%) and content (mg/segment/tiller) in 10 mm segments of vegetative prairie grass and cocksfoot tillers and mean WSC concentration and content for each species at four sequential harvests (H₁-H₄).

Segment (mm)	WSC concentration (%)		WSC content (mg/segment/tiller)	
	Prairie grass	Cocksfoot	Prairie grass	Cocksfoot
0-10	30.59	27.36	5.38	11.79
11-20	46.15	29.29	6.58	7.13
21-30	46.37	20.04	5.54	3.36
31-40	43.16	12.73	4.38	1.57
41-50	38.14	10.59	3.40	1.10
51-60	33.61	9.46	2.70	0.84
61-70	29.81	9.40	2.25	0.83
71-80	26.72	10.11	2.05	0.86
81-90	23.49	10.85	1.60	0.84
91-100	21.64	11.49	1.16	0.59
LSD ($P = 0.05$)	4.27		1.38	
H ₁	34.71	13.15	3.24	2.23
H ₂	34.15	13.64	3.62	1.87
H ₃	30.53	9.48	3.20	1.29
H ₄	36.49	24.26	3.96	6.16
LSD ($P = 0.05$)	2.70		0.87	

The stubble WSC concentration in both prairie grass and cocksfoot was significantly lower ($P < 0.05$) at H₃ compared with the remaining harvests. For cocksfoot, stubble WSC concentration was significantly higher ($P < 0.05$) at H₄ than at any previous harvest (Table 7.1).

Stubble WSC content was generally higher for prairie grass compared with cocksfoot, as evidenced by a significant ($P < 0.01$) species effect and means of 3.50 and 2.89 mg/segment/tiller for these species, respectively. Significant ($P < 0.001$) segment and harvest effects represented the trends of decreasing stubble WSC content with

increasing segment height, and a higher WSC content at H₄ than at any previous harvest (Table 7.1).

7.3.2 Reproductive tillers

Only prairie grass exhibited reproductive growth, and at H₁ and H₄, reproductive tiller samples were of a sufficient size for determination of WSC reserves. There was significantly higher ($P < 0.001$) stubble WSC content at H₄ compared with H₁ (Table 7.2). There was a significant ($P < 0.01$) segment effect on stubble WSC content for reproductive prairie grass tillers, with WSC reserves decreasing with increasing segment height (Table 7.2). Mean WSC content was generally higher in reproductive prairie grass tillers than in vegetative tillers.

Table 7.2 Water-soluble carbohydrate (WSC) content (mg/segment/tiller) in 10 mm segments of reproductive prairie grass at two harvests (H₁ and H₄).

	WSC content (mg/segment/tiller)			
	H ₁	H ₄	Mean	LSD ($P = 0.05$)
0-10	6.94	14.66	10.80	2.85
11-20	5.88	10.23	8.05	
21-30	5.58	10.42	8.00	
31-40	6.36	10.08	8.22	
41-50	9.24	9.87	9.55	
51-60	7.03	11.03	9.03	
61-70	5.49	7.00	6.24	
71-80	7.71	7.68	7.70	
81-90	5.80	7.67	6.74	
91-100	4.54	5.21	4.87	
Mean	6.46	9.39		
LSD ($P = 0.05$)	1.28			

7.4 Discussion

Throughout the current study, WSC reserves (concentration and content) were higher in prairie grass tillers compared with cocksfoot tillers – a pattern that was also evident in Chapter 6 (Tables 6.1 and 6.4). Only prairie grass tillers became reproductive, with a higher WSC content and a less clearly defined decrease in WSC reserves with increasing stubble height than for vegetative prairie grass tillers.

A decrease in WSC reserves with increasing stubble height was observed for vegetative tillers of both species. However, the WSC concentration gradient was better defined for cocksfoot, with a clear decrease in WSC concentration between the 21-30 mm and 31-40 mm segments, and 77% of WSC content contained within the 0-30 mm stubble height range (0 mm representing the base). The WSC concentration gradient for prairie grass was not as distinct as for cocksfoot, with a relatively high WSC concentration throughout the 0-100 mm stubble height range. There was a trend for decreasing WSC concentration between the 31-40 mm and 41-50 mm segments, with 62% of WSC content contained within the 0-40 mm stubble height range. These results suggest that the previously adopted defoliation stubble height of 45-50 mm maintains over 60% of stubble WSC reserves and is therefore not detrimental to the persistence of these species.

The pattern of WSC reserve storage in cocksfoot stubble suggests that more severe defoliation to a height of 30 mm may be acceptable. As plants in this study were defoliated to a height of 100 mm, a further study that implements a range of defoliation heights, combined with the recommended defoliation interval of the 4-leaf stage is required to test the effects of a more severe defoliation regime on cocksfoot regrowth, production and persistence.

In terms of defoliation frequency, the relationship between N reserves and regrowth was shown in Chapter 6 to be non-existent for cocksfoot, but significant for prairie grass. The effect of this defoliation regime on N reserves of prairie grass would therefore also be of interest, given the possibility that proteins may be mobilised for growth and respiration following severe defoliation of pasture plants.

The pattern of WSC reserve storage in prairie grass suggests that this species is sensitive to severe defoliation, possibly due to its upright habit and lower tillering capacity (Hume 1991b). Prairie grass is also sensitive to frequent defoliation (Hume 1991a), as highlighted in Chapter 6, and the importance of careful defoliation management to maximise plant persistence must be emphasised. With this in mind, defoliation interval should be regarded as of primary importance, followed by defoliation height as of secondary importance (Bell and Ritchie 1989; Fulkerson and Donaghy 2001).

The conflict between pasture utilisation (optimised by more severe defoliation) and rate of regrowth (optimised by less severe defoliation) arises with discussion of defoliation height. As the regrowth of prairie grass is more sensitive to defoliation management, with a defoliation height of 45-50 mm required, short term utilisation of pasture must be sacrificed to a greater extent than for cocksfoot. However, in the long term, greater levels of pasture production and therefore utilisation are achieved when the rate of regrowth is maximised. As stated by Parsons and Chapman (2000), to optimise the long term utilisation of grass, it is necessary to strike a balance between the amount of leaf material that remains in the sward during a sequence of defoliations, regrowth that provides photosynthesis for growth, and the amount of leaf actually harvested to achieve a yield.

The variation in WSC accumulation between harvests may be explained by seasonal changes in light intensity and duration throughout the experimental period. While temperature, moisture and nutrient availability were constant variables, light intensity and duration were lower between H₁ and H₃ (late autumn and winter harvests) than at H₄ (mid-spring harvest). Increased light intensity and duration would have resulted in a higher photosynthetic capacity, which combined with stable respiration (due to constant temperature and moisture availability), resulted in greater WSC accumulation at H₄ than at previous harvests. Cocksfoot exhibited a more pronounced response to light than prairie grass.

In conclusion, these results suggest that the previously adopted defoliation stubble height of 45-50 mm is suitable to maintain WSC reserves at levels adequate for optimal regrowth and persistence of prairie grass and cocksfoot. While decreasing defoliation height to 30 mm may be acceptable for cocksfoot, prairie grass is more sensitive to defoliation severity, with defoliation below 45 mm not recommended.

Chapter 8

A comparison of the herbage quality and regrowth response of four cocksfoot and four brome cultivars, under leaf stage based defoliation management

8.1 Introduction

There is considerable evidence that prairie grass and cocksfoot are competitive alternatives to perennial ryegrass for the dairy industry in southern Australia in terms of productivity (Vartha 1977; Fraser 1982; DeLacy 1987; Crush *et al.* 1989; Mitchell 1997; Fulkerson *et al.* 2000) and herbage quality (Mitchell 1997; Lowe *et al.* 1999a; Fulkerson *et al.* 2000; Rawnsley *et al.* 2002). These findings were largely dependent on appropriate management of these alternative species. As well-recognised dairying cultivars over a 25-year period, the suitability of prairie grass cv. Matua and cocksfoot cv. Kara for the dairy industry in southern Australia has been further demonstrated in the studies previously described in this thesis.

The remaining potential limitations to use of Matua and Kara by dairy farmers, as identified in Chapters 3 and 4, include slow establishment of Kara in the field, high rates of seeding for Matua, and relatively high fibre levels for both cultivars compared with perennial ryegrass. While past and present breeding efforts for perennial ryegrass currently outweigh the attention given to further development of brome and cocksfoot lines, there is a range of more recently developed brome and cocksfoot cultivars selected for dryland production that may overcome the limitations of Matua and Kara outlined above.

Three of the more recent brome (Bareno, Gala and Tas 30J) and cocksfoot (Tekapo, Tas 2029 and Uplands) cultivars, which have neither been extensively tested nor accepted for use in dairying, were chosen to assess whether breeding and selection have resulted in significant advances in the productivity and herbage quality of cocksfoot and brome cultivars. Furthermore, one would expect the considerable genetic diversity within the brome (at a species level) and cocksfoot (at a sub species level) genomes to translate into agronomic differences. The brome cultivars were

chosen for comparison with Matua in terms of persistence and herbage quality, while the cocksfoot cultivars were chosen for comparison with Kara in terms of persistence, herbage quality, tiller density and seedling vigour.

The aim of the current glasshouse study was to investigate differences in establishment, productivity, herbage quality and response to infrequent and frequent defoliation, within and between the cocksfoot and prairie grass genera, through two distinct regrowth cycles.

8.2 Materials and methods

The experiment was conducted in a glasshouse at the Tasmanian Institute of Agricultural Research, Burnie, Australia (Latitude $-41^{\circ}04'S$), between December 2004 and August 2005. Three seeds were planted in each polyvinyl bag (100 mm diameter x 280 mm depth), on December 28 2004. Once established, the weakest seedlings were removed to allow a single healthy seedling to reach maturity in each bag. The bags contained a potting mixture composed of 50% *Pinus radiata* D. bark, 30% sand, 20% *Spaghnum* sp. moss and nutrients (Appendix A.2). The plants were arranged in the glasshouse at a density of 100 plants/m². Plants were watered daily via an underlying geotextile membrane capillary mat, to replace evapotranspiration losses. Glasshouse conditions were controlled to maintain day/night temperatures of 20/10°C. Plants were fertilised with Osmocote® at a rate equivalent to 40 kg N/ha in February and June 2005.

Emergence of seedlings (emergence of epicotyl) was monitored daily during the first two weeks from sowing, with the emergence date of the first seedling per pot recorded. From the third week from sowing, tiller number per plant was recorded on a weekly basis through to the eleventh week from sowing.

8.2.1 Experimental design

Plants were arranged within two randomised complete block designs, each with four blocks containing 16 randomly allocated treatments. Each treatment consisted of a row of four plants per block that were combined as one sample for analysis, resulting in 16 plants (or four samples) in total per treatment, per block design. The treatments were each characterised by one of eight cultivars (Table 8.1) and one of two

defoliation treatments (4-leaf stage of regrowth - identified as the optimal time of defoliation for both Kara and Matua, and the 2-leaf stage of regrowth - identified as a minimal, but adequate defoliation interval for cocksfoot). Plants were grouped in two block designs to separate plants destructively harvested at the first and second harvest events (H_1 and H_2). Buffer plants were placed around the minisward to minimise boundary effects. These plants were harvested but otherwise not included in analyses.

Table 8.1 Species, breeding company and release date of cultivars utilised in the current study

Species	Cultivar	Breeding company	Release date
<i>Dactylis glomerata</i>	Kara	NZ Grasslands Division	1980
<i>ssp. glomerata</i>			
<i>Dactylis glomerata</i>	Tekapo	NZ AgResearch	1990
<i>ssp. glomerata</i>			
<i>Dactylis glomerata</i>	Tas 2029	DPIWE* Tasmania	Not commercially released
<i>ssp. glomerata</i>			
<i>Dactylis glomerata</i>	Uplands	DPIWE Tasmania	Not commercially released
<i>ssp. hispanica</i>			
<i>Bromus willdenowii</i>	Matua	NZ Grasslands Division	1973
<i>Bromus valdivianus</i>	Bareno	NZ Agriseeds	1987
<i>Bromus stamineus</i>	Gala	NZ AgResearch	1992
<i>Bromus coloratus</i>	Tas 30J	DPIWE Tasmania	Not commercially released

* Department of Primary Industries, Water and Environment

A leaf stage based defoliation regime was utilised, with determination of leaf stage for cocksfoot and bromes as described in Chapter 6. On February 15 2005 (49 days following sowing), all plants were defoliated to a stubble height of 50 mm to promote tillering. At the 4-leaf stage of regrowth, plants were again defoliated to 50 mm in preparation for the destructive harvesting regime.

9.2.2 Destructive harvest regime and determination of DM yield

The second defoliation to 50 mm was regarded as the first pre-treatment defoliation (H_0). Treatments commenced after H_0 , and plants were defoliated to a uniform stubble height of 50 mm at each defoliation. When plants had been defoliated at the 2-leaf stage and 4-leaf stage twice and once, respectively, all plants in the first block

design were destructively harvested. This event was termed H₁. This process was repeated and when treatments coincided for the second time, all plants in the second block design were harvested. This event was termed H₂.

Non-sheath leaf tissue (above 50 mm) was removed at each defoliation and harvest event, and leaf DM yield per plant was determined after drying samples for at least 24 hours at 60°C in a forced draught oven. Stubble tissue below 50 mm was collected at each harvest event, then freeze-dried and weighed. Tiller DM and tiller number per plant were also determined at each harvest interval. Harvests were consistently performed at three hours after sunrise, to negate the confounding effect of diurnal fluctuations in WSC reserves (Fulkerson and Slack 1994a). Dried leaf and stubble samples were ground through a 1 mm sieve prior to chemical analyses.

8.2.3 *Determination of WSC*

Stubble samples were analysed for WSC at New South Wales Department of Primary Industries Laboratories by Technicon Industrial Method number 302-73A, derived from the method outlined by Smith (1969; Appendix A.1).

8.2.4 *Herbage quality analyses*

Leaf samples were analysed for DDM, ADF and NDF concentrations using NIR Spectrometry at Hamilton FeedTEST Laboratories (Victoria Department of Primary Industries; Van Soest and Wine 1967; Clarke *et al.* 1982; Appendix A.1).

Metabolisable Energy concentration (MJ/kg DM) was calculated using the following formula:

$$ME = (0.17 \times DDM) - 2 \text{ (Standing Committee on Agriculture 1990)}$$

Nitrogen: Leaf material was analysed for total N using a Leco FP-428 Nitrogen Analyser at CSBP Soil and Plant Nutrition Laboratories (Western Australia; Sweeney and Rexroad 1987; Appendix A.1).

Crude protein (%) was calculated using the following formula:

$$CP = N \text{ concentration} \times 6.25$$

Minerals: P, K, Na, Mg and Ca concentrations of leaf samples were measured by ICP-AES at CSBP Soil and Plant Nutrition Laboratories (Western Australia; McQuaker *et al.* 1979; Appendix A.1).

8.2.5 *Statistical analyses*

Statistical analyses were performed using the statistical package SPSS (Version 11.5, SPSS Corporation, Illinois, USA), and LSD, as defined by Steel and Torrie (1960). Means for days to emergence were compared using an ANOVA two-way factorial design (cultivar treatment by harvest event) with replication, and means for tiller number during establishment were compared using an ANOVA three-way factorial design (cultivar treatment by week of assessment by harvest event) with replication.

Means of DM, herbage quality and energy reserve response variables were compared using an ANOVA three-way factorial design (leaf stage treatment by cultivar treatment by harvest event) with replication. Pre-treatment leaf DM values from H_0 were used as a co-variate for comparison of DM means.

8.3 **Results**

8.3.1 *Days to emergence*

There was a significant ($P < 0.001$) difference between cultivars for days to seedling emergence. Of the brome cultivars, Bareno seedlings emerged significantly faster ($P < 0.001$; 5.1 days) than Matua seedlings, which emerged significantly faster ($P < 0.05$; 6.5 days) than Tas 30J (7.0 days) and Gala seedlings (7.2 days). Of the cocksfoot cultivars, Tekapo seedlings emerged significantly faster ($P \leq 0.001$; 5.9 days) than Uplands (6.9 days) and Tas 2029 seedlings (7.4 days), which in turn emerged significantly faster ($P < 0.05$) than Kara seedlings (8 days).

8.3.2 *Tiller number per plant*

There was a significant ($P < 0.001$) cultivar effect for tiller number per plant during establishment. Tas 2029 and Uplands exhibited a significantly higher ($P < 0.001$) rate of tiller initiation than Kara and Tekapo, with both cultivars attaining a mean 25.6 tillers per plant by 11 weeks from sowing. Matua and Gala exhibited a significantly lower ($P < 0.001$) rate of tiller initiation than Bareno and Tas 30J, with a mean 3.5 and 4.3 tillers per plant for Matua and Gala, respectively (Figure 8.1).

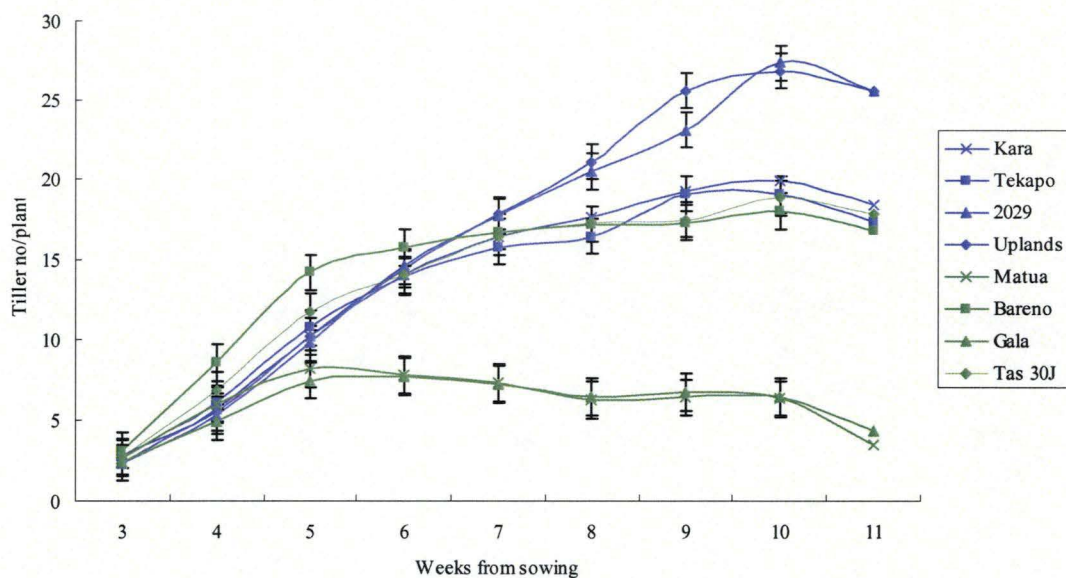


Figure 8.1 Mean tiller number per plant from 3 to 11 weeks following sowing for the eight cultivars assessed in the current study. Vertical bars represent LSD ($P = 0.05$).

There was a significant ($P < 0.001$) difference in tiller number per plant between cultivars once established (i.e. following H_0). There were significantly fewer ($P < 0.001$) tillers per plant for Matua (11.7) and Gala (11.6) than for Bareno (19.1) and Tas 30J (24.8). There was a significantly higher ($P < 0.001$) number of tillers per plant for Uplands (50.4) than for Tekapo (38.5) and Tas 2029 (38.8), which had a significantly higher ($P < 0.001$) number of tillers per plant than Kara (26.2). Defoliation interval and harvest event did not have a significant ($P > 0.05$) effect on mean tiller number per plant following H_0 .

8.3.3 Stubble WSC reserves

There was a significant ($P < 0.001$) cultivar effect on mean stubble WSC concentration (% of DM) and content (mg/tiller; Table 8.2). There was a significantly higher ($P < 0.001$) stubble WSC concentration and content in Matua and Gala than in Bareno, Tas 30J and all of the cocksfoot cultivars. There was a significantly higher ($P \leq 0.01$) stubble WSC concentration and content in Kara and Tas 2029 than in Tekapo and Uplands. Uplands had the lowest ($P < 0.01$) levels of WSC reserves of the cocksfoot cultivars. Defoliation at the 2-leaf stage resulted in a

significantly lower ($P < 0.001$) mean stubble WSC concentration and content than defoliation at the 4-leaf stage of regrowth (Table 8.2).

Table 8.2 Mean stubble water-soluble carbohydrate (WSC) concentration (% of DM), WSC content (mg/tiller), leaf dry matter (DM) yield (g/plant) and tiller DM yield (mg/tiller) for the cultivars assessed and for the 2-leaf stage (2L) and 4-leaf stage (4L) defoliation intervals.

		Stubble WSC concentration (% of DM)	Stubble WSC content (mg/tiller)	Leaf DM yield (g/plant)	Tiller DM yield (mg/tiller)
Cultivars	Kara	13.76	11.06	2.15	76.42
	Tekapo	9.43	4.83	1.91	48.65
	Tas	12.28	6.35	2.04	46.51
	2029				
	Uplands	7.01	1.85	1.93	24.35
	Matua	20.38	16.73	2.03	73.12
	Bareno	5.60	4.21	2.04	69.99
	Gala	21.40	21.36	1.97	85.89
	Tas 30J	6.16	3.35	1.91	50.56
	LSD ($P < 0.05$)	1.62	1.55	0.14	6.33
Defoliation interval	2L	6.04	3.18	2.52*	48.95
	4L	17.96	14.25	2.87*	69.92
LSD ($P < 0.05$)		0.81	0.77	0.10**	3.17

* Represents mean leaf DM yield at H₂

** Represents LSD for interaction between defoliation interval and harvest event

8.3.4 DM yield

There was a significant ($P < 0.05$) cultivar effect on mean leaf DM yield (Table 8.2). The leaf DM yield of Kara was significantly higher ($P < 0.01$) than the leaf DM yield of Uplands and Tekapo, with the leaf DM yield of Tas 2029 intermediate. There was no significant ($P > 0.05$) difference in leaf DM yield between the brome cultivars. There was a significant ($P < 0.001$) interaction between defoliation interval and harvest event. Defoliation at the 2-leaf stage resulted in significantly lower ($P < 0.05$) mean leaf DM yields than defoliation at the 4-leaf stage at H₂, while defoliation interval did not have a significant ($P > 0.05$) effect on leaf DM yield at H₁ (Table 8.2).

There was a significant ($P < 0.001$) cultivar effect on mean tiller DM yield (Table 8.2). Tiller DM yield for Kara was significantly higher ($P < 0.001$) than for Tekapo and Tas 2029, while the tiller DM yield for Tekapo and Tas 2029 was significantly higher ($P < 0.001$) than for Uplands. Tas 30J had the lowest ($P < 0.001$) and Gala had the highest ($P < 0.001$) tiller DM yield of the brome cultivars. Defoliation at the 2-leaf stage of regrowth resulted in significantly lower ($P < 0.001$) mean tiller DM yields than defoliation at the 4-leaf stage (Table 8.2).

8.3.5 *Herbage quality*

There was a significant ($P < 0.001$) cultivar effect on mean ME concentration (MJ/kg DM; Table 8.3). Tekapo and Uplands had significantly higher ($P \leq 0.01$) ME concentrations than Kara and Tas 2029, while Matua and Gala had significantly higher ($P < 0.05$) ME concentrations than Bareno and Tas 30J. Defoliation interval did not have a significant ($P > 0.05$) effect on ME concentration. The ME concentration of plants at H₁ was significantly higher ($P < 0.001$) than the ME concentration of plants at H₂ (Table 8.3).

There was a significant ($P < 0.001$) cultivar effect on mean ADF concentration (Table 8.3). The ADF concentration of Kara and Tas 2029 was significantly higher ($P < 0.001$) than for Uplands, which in turn had a significantly higher ($P < 0.001$) ADF concentration than Tekapo. Matua had the highest ($P < 0.001$) ADF concentration, followed by Gala, Bareno and Tas 30J. Defoliation at the 2-leaf stage resulted in a significantly lower ($P < 0.001$) mean ADF concentration than defoliation at the 4-leaf stage of regrowth (Table 8.3). The ADF concentration of plants at H₁ was significantly lower ($P < 0.001$) than the ADF concentration of plants at H₂ (Table 8.3).

There was a significant ($P < 0.001$) cultivar effect on mean NDF concentration (Table 8.3). The NDF concentration of Kara and Tekapo was significantly lower ($P < 0.001$) than for Uplands and Tas 2029. The NDF concentration of Matua and Gala was significantly lower ($P < 0.05$) than for Bareno and Tas 30J. Defoliation interval did not have a significant ($P > 0.05$) effect on mean NDF concentration. The NDF concentration of plants at H₁ was significantly lower ($P < 0.001$) than the NDF concentration of plants at H₂ (Table 8.3).

Table 8.3 Mean metabolisable energy (ME), acid-detergent fibre (ADF), neutral-detergent fibre (NDF) and crude protein (CP) concentrations for the cultivars assessed and for the 2-leaf stage (2L) and 4-leaf stage (4L) defoliation intervals.

		ME	ADF	NDF	CP
		concentration	concentration	concentration	concentration
		(MJ/kg DM)	(% of DM)	(% of DM)	(% of DM)
Cultivars	Kara	10.7	25.2	56.0	18.2
	Tekapo	10.9	23.1	55.3	21.9
	Tas	10.7	25.3	57.9	20.5
	2029				
	Uplands	10.9	24.5	58.1	22.3
	Matua	11.1	27.0	55.2	15.1
	Bareno	10.8	24.2	56.2	19.8
	Gala	11.2	25.9	55.0	16.0
	Tas 30J	10.9	23.6	58.0	21.8
LSD ($P < 0.05$)		0.2	0.6	1.0	0.8
Defoliation interval	2L	10.9	23.5	56.5	22.3
	4L	10.9	26.2	56.4	16.6
LSD ($P < 0.05$)		ns	0.3	ns	0.4
Harvest event	H ₁	11.0	24.3	55.6	19.8
	H ₂	10.8	25.4	57.4	19.1
LSD ($P < 0.05$)		0.1	0.3	0.5	0.4

There was a significant ($P < 0.001$) cultivar effect on mean CP concentration (Table 8.3). The CP concentration of Matua and Gala was significantly lower ($P < 0.001$) than for Bareno, Tas 30J and all cocksfoot cultivars, with Tas 30J containing the highest ($P < 0.001$) CP concentration among the bromes. The CP concentration of Tekapo and Uplands was significantly higher ($P < 0.001$) than for Kara and Tas 2029, with Kara containing the lowest ($P \leq 0.001$) CP concentration among the cocksfoot cultivars. Defoliation at the 2-leaf stage resulted in a significantly higher ($P < 0.001$) mean CP concentration than defoliation at the 4-leaf stage of regrowth (Table 8.3). The CP concentration of plants at H₁ was significantly higher ($P < 0.01$) than the CP concentration of plants at H₂ (Table 8.3).

There was a significant ($P < 0.001$) cultivar effect on mean P and K concentrations (Table 8.4). The P and K concentrations of Matua and Gala were significantly lower

($P < 0.001$) than for Bareno and Tas 30J. The P concentration of cocksfoot cultivars was within the range 5.6-6.9 mg/g DM, with Tekapo containing significantly higher ($P < 0.001$) P and K concentrations than Kara, Tas 2029 and Uplands. Plants defoliated at the 2-leaf stage had significantly higher ($P < 0.001$) mean P and K concentrations than plants defoliated at the 4-leaf stage of regrowth (Table 8.4).

Table 8.4 Mean phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) concentrations for the cultivars assessed and for the 2-leaf stage (2L) and 4-leaf stage (4L) defoliation intervals.

		P	K	Ca	Mg	Na
		concentration (mg/g DM)	concentration (mg/g DM)	concentration (mg/g DM)	concentration (mg/g DM)	concentration (mg/g DM)
Cultivars	Kara	5.69	31.33	5.42	3.70	3.05
	Tekapo	6.89	36.56	5.61	3.46	2.30
	Tas	5.59	30.78	6.69	3.05	5.48
	2029					
	Uplands	5.99	32.76	6.02	2.98	0.66
	Matua	3.76	26.71	7.30	2.22	6.49
	Bareno	7.00	35.84	8.09	2.74	0.80
	Gala	3.93	28.89	8.18	2.54	1.96
	Tas 30J	7.63	35.86	7.69	2.60	1.02
LSD		0.44	1.72	0.44	0.22	0.64
(P < 0.05)						
Defoliation interval	2L	6.24	36.16	6.24	2.93	2.60
	4L	5.38	28.53	7.51	2.91	2.84
	LSD	0.22	0.86	0.22	ns	ns
(P < 0.05)						

There was a significant ($P < 0.001$) cultivar effect on mean Ca and Mg concentrations (Table 8.4). Of the cocksfoot cultivars, Tas 2029 had a significantly higher ($P < 0.01$) Ca concentration than Kara, Tekapo and Uplands. Kara and Tekapo had a significantly higher ($P < 0.01$) Mg concentration than Tas 2029 and Uplands. Of the brome cultivars, Matua had a significantly lower ($P < 0.001$) Ca concentration than Bareno and Gala, with the Ca concentration of Tas 30J intermediate, while Matua had the lowest ($P < 0.05$) Mg concentration. The Ca concentration of the brome cultivars was significantly higher ($P < 0.01$) than the

cocksfoot cultivars and the Mg concentration of the cocksfoot cultivars was significantly higher ($P < 0.05$) than the brome cultivars. Defoliation at the 2-leaf stage resulted in a significantly lower ($P < 0.001$) mean Ca concentration than defoliation at the 4-leaf stage of regrowth (Table 8.4), while defoliation interval did not have a significant ($P > 0.05$) effect on Mg concentration.

There was a significant ($P < 0.001$) cultivar effect on mean Na concentration (Table 8.4). Tas 2029 had the highest ($P < 0.001$) Na concentration and Uplands the lowest ($P < 0.001$) Na concentration of the cocksfoot cultivars. Matua had the highest ($P < 0.001$) Na concentration and Bareno the lowest ($P < 0.001$) Na concentration of the brome cultivars. Defoliation interval did not have a significant ($P > 0.05$) effect on Na concentration.

8.4 Discussion

Kara and Matua are the most widely sown and utilised cocksfoot and brome cultivars for dairy pastures, and as such, are the industry standards to which newer cultivars have been compared. Since their commercial release (1973 Matua; 1980 Kara), there has been further selection and breeding within the cocksfoot and brome genera, for faster establishment, improved herbage quality, higher tiller density, and improved persistence under grazing. This study highlighted differences between four cocksfoot and four brome cultivars (including Kara and Matua) under leaf stage based defoliation management, through two plant regrowth cycles (terminating at H₁ and H₂).

Cocksfoot is relatively slow to establish compared with perennial ryegrass (Moot *et al.* 2000; Chapter 3) and although it is able to compete effectively with weeds and other pasture plants for resources once established (Borman *et al.* 1990), slow establishment continues to hinder farmer acceptance of this species for use in the dairy industry. Faster establishment was originally promoted as an attribute of Kara, but in the current study it was the slowest cultivar to emerge. Tekapo was the fastest emerging cocksfoot cultivar, showing that breeding has improved the establishment rate of cocksfoot cultivars. Of the four brome cultivars investigated, only Bareno exhibited faster emergence than Matua.

The cocksfoot cultivars Tas 2029 and Uplands (both selected for high tiller density) exhibited the most rapid rates of tiller initiation during establishment, and the brome cultivars Matua and Gala the slowest rates of tiller initiation, resulting in the highest and lowest tiller numbers, respectively, by the commencement of defoliation treatments and throughout the subsequent study. Higher rates of tillering of cocksfoot cultivars compared with brome cultivars may reflect relative persistence/survival capabilities.

While differences between cultivars in days to emergence and tiller initiation rates during establishment in the glasshouse are worthy of attention, they do not adequately represent establishment differences in the field. Further investigations into the elongation rates of seminal and adventitious root axes in relation to shoot development are required to provide valuable insight into seedling development and establishment rates of alternative grass species (Cornish *et al.* 1984; Aguirre and Johnson 1991).

The detrimental effect of frequent defoliation on the persistence of Matua (Chapter 6) is further exaggerated by relatively low tiller density, and it is possible that the higher tiller density of Bareno and Tas 30J would be beneficial in terms of improved persistence under grazing. Despite the low tiller density of Matua and Gala, these cultivars contained the highest WSC levels (both WSC concentration and content). Similarly, Kara had the lowest tiller density of the cocksfoot cultivars, but contained the highest WSC content. In agreement with previous studies on cocksfoot and prairie grass (Fulkerson *et al.* 2000; Slack *et al.* 2000; Chapters 3 and 6), more frequent defoliation of all cultivars resulted in reduced WSC assimilation and subsequent regrowth.

The effect of defoliation interval on WSC levels only translated to effects on leaf DM yields during the plants' second regrowth cycle, resulting in higher leaf DM yields for plants defoliated at the 4-leaf stage compared with the 2-leaf stage of regrowth at H₂. The higher leaf DM yield of Kara and Matua compared with the majority of newer cultivars reflects their regrowth capacity and suitability for intensive dairying systems.

From the commencement of treatments at H₀, tiller DM yield for plants defoliated at the 2-leaf stage was lower than for plants defoliated at the 4-leaf stage of regrowth, reflecting higher WSC reserve levels under less frequent defoliation. Of the cocksfoot cultivars, tiller DM yield was highest for Kara. While drought tolerance is a valuable attribute of the cocksfoot cultivars Tekapo, Tas 2029 and Uplands, breeding for summer growth (which has resulted in an increased number of smaller, finer leaved tillers compared with Kara) seems to have resulted in reduced annual DM yield.

Although not quantitatively measured, a high proportion of Matua and Gala plants were reproductive throughout the current study, compared with the remaining cultivars. Claims by breeders that the quality of bromes is not compromised when plants go to seed were verified by particularly high ME concentrations for these cultivars. The ME concentration of all cultivars in the current study was acceptable for dairy production, in the range of 10.7-11.2 MJ/kg DM.

Acid detergent fibre levels increased with defoliation interval, reflecting decreased digestibility of leaf material with age. The decreasing digestibility of successive leaves on a grass plant can be explained by the increasing proportion of sclerenchyma and vascular tissue with increasing leaf number on a tiller (Ducrocq and Duru 1997). This in turn may be related to an increase in the maximum length of the leaf blade with each successive leaf (Wilson 1976). Kara and Matua both had high concentrations of ADF, which translated to a lower ME concentration for Kara, but not for Matua. The low ADF concentration of Tekapo is a quality attribute that plant breeders should consider combining with the desirable regrowth characteristics of Kara, such as high leaf DM yield and rapid replenishment of WSC energy reserve levels.

The lower ADF concentration for plants defoliated at the 4-leaf stage of regrowth corresponded with lower CP concentrations. Only Matua and Gala had a lower mean CP concentration than the 18.0-20.0% required by lactating dairy cows (National Research Council 1989). The fact that Matua and Gala contained the lowest CP concentration and highest WSC levels of the cultivars assessed in this study is of interest, as an inverse relationship between CP and WSC has been recognised by

Buxton and Mertens (1995). This relationship can be explained by the stimulatory effect of N on growth and the subsequent use of WSC reserves in the development of structural material and in respiration. In Matua and Gala (cultivars that were highly reproductive), the lower CP concentration of stem compared with leaf blades (generally half) may have also contributed to this relationship.

The concentration of P in the leaf of all cultivars was in excess of the 3.4 mg/g requirement of a highly producing dairy cow, with the P concentration of Matua and Gala the lowest of all cultivars assessed. The concentration of K in the leaf decreased with increased defoliation interval and was the highest in Tekapo of the cocksfoot cultivars, and in Bareno and Tas 30J of the bromes. Throughout the study, the K concentration of all cultivars was above the recommended 9.0 mg/g DM (National Research Council 1989).

The increase in leaf Ca concentration with advancing plant development (leaf stage) was consistent with the pattern reported for perennial ryegrass (Wilman *et al.* 1994; Fulkerson *et al.* 1998), white clover (Wilman *et al.* 1994) and cocksfoot (Rawnsley *et al.* 2002). The Ca concentration of cocksfoot cultivars was considerably lower than in the brome cultivars, however, all cultivars possessed sufficient concentrations of Ca to meet the requirements of a highly producing dairy cow (5.4 mg/g DM; National Research Council 1989). Magnesium has been previously reported as a limiting nutrient in Matua prairie grass (Thom *et al.* 1990; Fulkerson *et al.* 2000), and in the current study, the brome cultivars possessed a lower leaf Mg concentration than the cocksfoot cultivars. However, the Mg concentration of all cultivars was above the recommended 2.0 mg/g DM (National Research Council 1989). The leaf Na concentration of Tas 2029 and Matua was higher than for the remaining cocksfoot and brome cultivars, respectively. Uplands, Bareno and Tas 30J failed to meet the Na requirements of a highly producing dairy cow (1.2 mg/g DM; National Research Council 1989). Sodium has been previously identified as a potential nutritional limitation for bromes compared with perennial ryegrass (Crush *et al.* 1989).

The improvements resulting from breeding and selection within the cocksfoot genera, measured in this study, included faster emergence of seedlings, higher tiller initiation

rates and tiller density, a lower ADF, higher CP and higher ME concentration. The newer cultivars had considerably lower leaf and tiller DM yields than Kara, with little variation in ME levels between cultivars. Results of the current study indicate that Kara would provide 7.5% more energy on a per hectare basis than the other cocksfoot cultivars assessed.

The improvements resulting from breeding and selection within the brome genera, measured in this study, included faster seedling emergence, a lower proportion of reproductive tillers, a lower ADF concentration and a higher CP concentration. The higher fibre levels for Matua and high proportion of reproductive tillers did not translate into a lower ME concentration; in fact, the energy content in Matua and Gala was higher than for all remaining cultivars. There were further similarities between Matua and Gala - the high WSC levels, leaf and tiller DM yields of these cultivars reflecting a strong regrowth response to defoliation.

The variation in productivity and herbage quality between cultivars in the current study indicated that some improvements have been made through breeding and selection within the cocksfoot and brome genera since the commercial release of Kara and Matua. However, the advantages of using the newer cultivars may not exceed the benefits of the original cultivars.

Chapter 9

Tasmanian dairy farmer perception of the herbage quality, palatability, dryland production and potential use of cocksfoot and prairie grass compared with perennial ryegrass

9.1 Introduction

Perennial ryegrass is the most commonly used pasture species on Tasmanian dairy farms, generally sown in a mixed sward with white clover (Mason 1993). Perennial ryegrass is often promoted as the highest herbage quality and most palatable and productive of the temperate grasses. However, as discussed in Section 2.5.2, there are serious limitations associated with the exclusive use of this species.

While the literature clearly shows that cocksfoot and prairie grass have great potential as dryland dairy pasture species in southern Australia, these species are generally perceived to be inferior to perennial ryegrass. The previous chapters in this thesis report on results from studies in which the morphology and physiology of cocksfoot and prairie grass are further investigated to determine their suitability as dairy pasture species. Management recommendations that maximise the productivity, herbage quality, persistence and utilisation of these species are made, but the importance of considering farmer perception in the process of extending the research results and on-farm adoption of innovative information is recognised by the author.

This chapter outlines a scoping study undertaken within the Tasmanian dairy industry by means of a survey, to establish the current and potential future use of perennial ryegrass, cocksfoot and prairie grass, and to evaluate quantitatively farmer perception of the herbage quality, palatability and dryland DM production of these species.

9.2 Methods

The results presented in this chapter are based on a questionnaire that was distributed to the 502 dairy farmers in Tasmania via the monthly TOPSTUFF newsletter (April 2005 edition), produced by the DPIWE.

The mail questionnaire was primarily chosen as a method of collecting information because, as specified by Moser and Kalton (1971), the survey had a clear purpose that could be explained briefly in writing, and the questions were straightforward. The author was aware that despite the economic advantage of using a mail questionnaire, the associated response rate could be as low as 10% (Alwin 1978).

Efforts were made to obtain greater cooperation by personalising the approach to the potential respondent (Dillman 1972). An informal letter with the author's photo was included in the preceding month's TOPSTUFF newsletter, to notify potential respondents of why and by whom the survey was being undertaken, and why they should take the time to reply. A reminder to respondents to complete and return the survey was then published in the newsletter for the month following distribution of the questionnaire. Consideration was also made of further factors that have been reported to favourably affect response rates – such as the farmers' positive affiliation with the DPIWE, subject matter of interest to the population and inclusion of a postage paid, return addressed envelope (Scott 1961).

An information sheet accompanied the questionnaire (Appendix A.3), to meet the requirements of the University of Tasmania Social Science Ethics Committee. The information sheet provided more detailed information about the purpose of the survey and assured the potential respondents of anonymity. The information sheet also provided the author's contact details, with an invitation to call or email about any questions relating to the study.

The questionnaire consisted of 12 pre-coded questions and a space left for comments (sample questionnaire follows). Inviting comments can act as an incentive, allowing respondents to include information other than that covered by simply answering the questions provided (Moser and Kalton 1971). The questions were carefully worded in language commonly used by the population and bold type was used to emphasise particular words, as suggested by Moser and Kalton (1971).

In the majority of questions, respondents were asked to choose between six response categories (5 scaled responses and an 'unsure' category), indicating various opinions about the herbage quality (termed feed quality in the survey as a better recognised

expression among farmers), palatability and production attributes of perennial ryegrass, cocksfoot and prairie grass. This scaled self-rating method has the merit that little effort is required from the respondent and that a measure of the respondent's position on the attitude continuum is provided (Moser and Kalton 1971). The closed form of questioning was chosen to ensure responses were relevant to the author's aims, and to provide data in a form that was easy to analyse (Alwin 1978). Data were entered into the database FileMaker Pro 7.0V1 and a statistical description of results follows (see Appendix A.4 for individual response summaries).

The questionnaire was as follows:

QUESTIONNAIRE

Please answer each question by circling the option that you consider to be closest to your opinion. Please keep in mind there are no right or wrong answers – the aim of this questionnaire is to find out what you think about these grass species.

Current pasture species on your farm

1. Is perennial ryegrass the dominant grass species sown on your farm?
YES NO
2. Have either cocksfoot or prairie grass been sown on your farm in the past?
YES NO UNSURE
- If yes, please circle which species: Cocksfoot Prairie Both

Feed Quality

3. How would you rate the feed quality of **cocksfoot**?
V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE
4. How would you rate the feed quality of **perennial ryegrass**?
V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE
5. How would you rate the feed quality of **prairie grass**?
V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

Palatability (animal acceptance)

6. How would you rate palatability of **perennial ryegrass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

7. How would you rate palatability of **prairie grass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

8. How would you rate palatability of **cocksfoot**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

Dryland Production

9a. How would you rate the **annual** dryland production of **prairie grass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

9b. How would you rate **summer to autumn** dryland production of **prairie grass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

10a. How would you rate the **annual** dryland production of **cocksfoot**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

10b. How would you rate **summer to autumn** dryland production of **cocksfoot**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

11a. How would you rate the **annual** dryland production of **perennial ryegrass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

11b. How would you rate **summer to autumn** dryland production of **perennial ryegrass**?

V. HIGH HIGH SATISFACTORY LOW V. LOW UNSURE

Future pasture species on your farm

12. Are you planning to sow cocksfoot or prairie grass on your farm during the next five years?

YES NO MAYBE

If yes, please circle which species: Cocksfoot Prairie Both

13. Are there any other comments you would like to make?

,

9.3 Results and Discussion

The completion rate of this survey was 38%, with 190 respondents returning fully answered questionnaires from a total sample of 502 Tasmanian dairy farmers. Given that it is common to receive responses to mail questionnaires from less than 10% of the targeted population, this was considered to be an excellent response rate and provides a high degree of confidence in the findings.

In general, there was a tendency for respondents to avoid the extreme ends of the answer scale, with the majority of respondents answering questions 3 to 11 between the ‘Low’ to ‘High’ continuum. According to Moser and Kalton (1971) this behaviour is a common occurrence with rating scales, and is termed the “error of central tendency”.

9.3.1 Current use of perennial ryegrass, cocksfoot and prairie grass

Perennial ryegrass was the dominant grass species currently used on the majority (97%) of dairy farms represented in this survey. Cocksfoot or prairie grass (predominantly cocksfoot) has been sown in the past on 68% of farms (Figure 9.1).

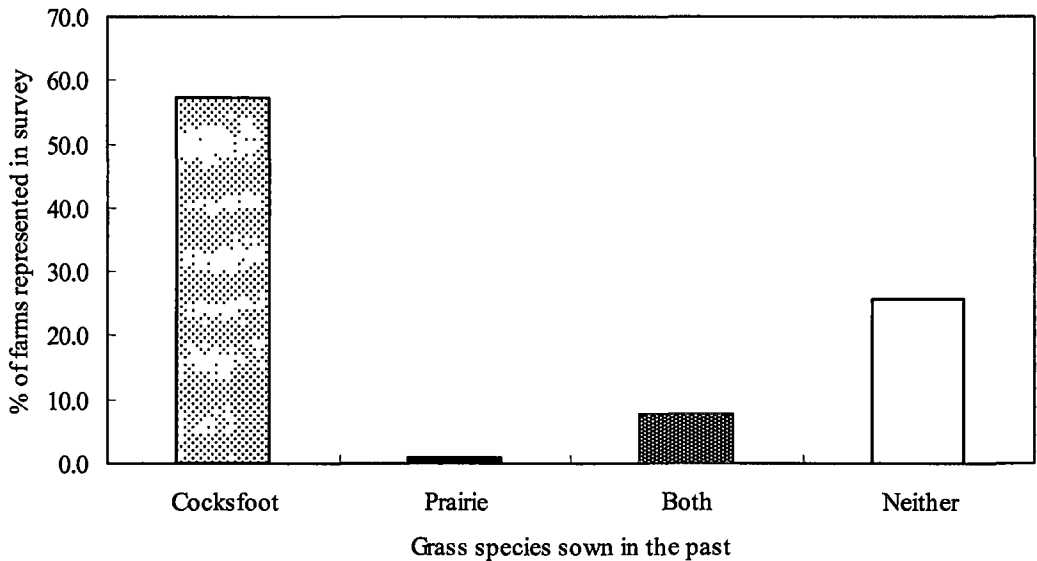


Figure 9.1 Percentage (%) of farms on which neither cocksfoot nor prairie grass have been sown in the past (□); and on which cocksfoot (▤), prairie grass (■) or both cocksfoot and prairie grass have been sown in the past (▨).

9.3.2 *Prairie grass attributes*

At least 60% of the respondents were uncertain about the attributes of prairie grass referred to in questions 5 (herbage quality), 7 (palatability) and 9 (dryland production), (Table 9.1). As indicated by responses to question 2 (current use of species, Figure 9.1), many farmers have never sown prairie grass on the farm, one commenting that he/she “(has) not used prairie grass and (has) no idea of its capability”.

Table 9.1 Percentage (%) of farmer responses for each answer category in relation to the herbage quality, palatability, annual and summer/autumn dryland production of prairie grass.

Prairie grass	Very high	High	Satisfactory	Low	Very low	Unsure
Herbage quality	2	10	14	9	3	62
Palatability	5	14	9	10	2	60
Annual production	0	7	17	7	2	67
Summer/autumn production	2	5	15	9	2	67

The most popular of the scaled response categories for questions 5 and 9 (both 9a and 9b) was ‘satisfactory’ – between 14 and 17% of respondents perceiving the quality and dryland production of prairie grass to be of a satisfactory standard. The best attribute of prairie grass according to farmer opinion was palatability, with 19% of respondents indicating that the palatability of prairie grass was either high or very high.

9.3.3 *Cocksfoot attributes*

The number of respondents who were unsure of cocksfoot attributes was fewer than for prairie grass, with less than 15% of dairy farmers indicating uncertainty about the herbage quality, palatability, annual and summer/autumn dryland production of cocksfoot (Table 9.2).

Table 9.2 Percentage (%) of farmer responses for each answer category in relation to the herbage quality, palatability, annual and summer/autumn dryland production of cocksfoot.

Cocksfoot	Very high	High	Satisfactory	Low	Very low	Unsure
Herbage quality	1	12	45	27	5	10
Palatability	1	16	46	23	5	9
Annual production	5	25	46	11	1	12
Summer/autumn production	5	29	41	12	2	11

Many farmers represented in this survey considered the herbage quality, palatability and dryland production of cocksfoot to be satisfactory (between 41 and 46% of respondents). Only 13% of respondents considered that the herbage quality of cocksfoot to be either of a high or very high standard, compared with 32% of respondents who were of the opinion that the herbage quality of cocksfoot was either low or very low. Similarly, 17% of respondents perceived the palatability of cocksfoot to be high or very high, compared with 28% of respondents who were of the opinion that the palatability of cocksfoot was either low or very low.

These responses suggest that the majority of farmers have a poor perception of cocksfoot as a potential dairy pasture species. Indeed, a number of farmers voluntarily provided comments at the end of the questionnaire stating that cocksfoot is “not as good quality as ryegrass” or that “cows prefer ryegrass” over cocksfoot. However, one farmer commented that “the quality and palatability of both cocksfoot and prairie grass can remain high provided they are grazed at the right intervals, if not they can be very low”, reflecting his/her grasp of the ability to largely control herbage quality and palatability through appropriate grazing management.

In contrast to farmers’ poor perception of herbage quality and palatability, more farmers thought that the annual and summer/autumn dryland production of cocksfoot was above satisfactory (30 and 34%, respectively) than below satisfactory (12 and 14%, respectively). A number of farmers commented that cocksfoot has been sown on infertile or dry parts of the farm, recognising that it can be a good feed source during summer/autumn and in areas where perennial ryegrass does not persist.

9.3.4 *Perennial ryegrass attributes*

The favourable view that Tasmanian dairy farmers have of perennial ryegrass attributes was evident both through the almost exclusive use of this species, and through responses to questions 4 (herbage quality), 6 (palatability) and 11a (annual production) (Table 9.3). However, the inability of this species to be highly productive under dryland conditions during summer/autumn was acknowledged by many respondents.

The herbage quality and palatability of perennial ryegrass was rated as high or very high by the majority of dairy farmers who responded to the survey (84% of respondents in both cases), almost five times the number of farmers who indicated that the herbage quality and palatability of cocksfoot can be maintained at this level.

Table 9.3 Percentage (%) of farmer responses for each answer category in relation to the herbage quality, palatability, annual and summer/autumn dryland production of perennial ryegrass.

Perennial ryegrass	Very high	High	Satisfactory	Low	Very low	Unsure
Herbage quality	23	61	16	0	0	0
Palatability	26	58	15	1	0	0
Annual production	6	35	46	8	2	3
Summer/autumn production	4	13	46	26	9	2

Annual dryland production of perennial ryegrass was rated as higher than for both cocksfoot and prairie grass, but fewer farmers (17% of respondents) thought that the summer/autumn dryland production of perennial ryegrass was above satisfactory – compared with 34% of respondents who thought that the summer/autumn dryland production of cocksfoot was above satisfactory (Table 9.2).

9.3.5 *Potential use of cocksfoot and prairie grass in the future*

In question 12, dairy farmers were asked whether they are planning to sow cocksfoot or prairie grass on their farms during the next five years, to which 52% answered ‘No’, 25% answered ‘Yes’ and 23% answered ‘Maybe’. Of the respondents who stated that they would consider sowing the alternative species on their farms, the majority indicated that they would use cocksfoot (Figure 9.2).

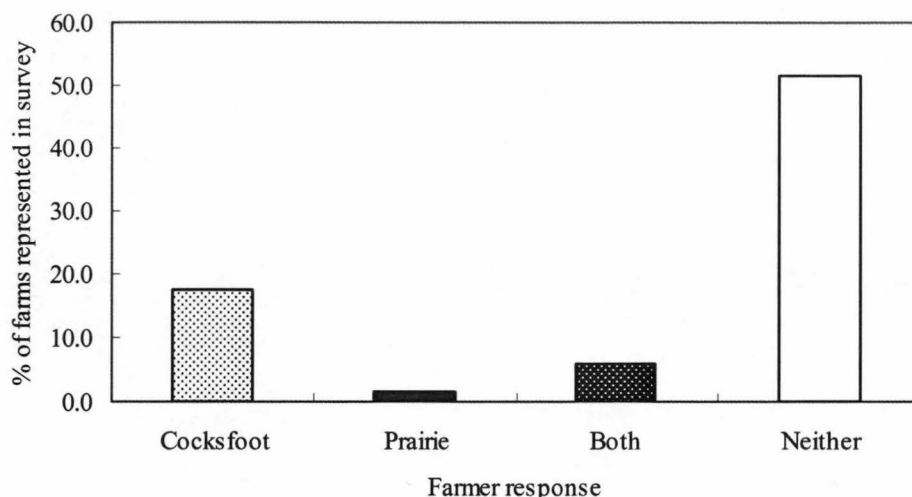


Figure 9.2 Percentage (%) of farms on which neither cocksfoot nor prairie grass will be sown during the next five years (\square); and on which cocksfoot (\square with dots), prairie grass (\blacksquare) or both cocksfoot and prairie grass (\square with cross-hatch) will be sown during the next five years.

9.3.6 Conclusions

Perennial ryegrass is currently the dominant perennial grass species utilised in Tasmanian dairy pastures. Farmer responses showed that the herbage quality, palatability and annual dryland production of perennial ryegrass are generally considered to be higher than for cocksfoot and prairie grass. However, the inability of this species to provide high levels of summer/autumn production under dryland conditions was acknowledged as a limitation by many respondents. While cocksfoot has been previously sown on 68% of respondents' farms, only 23% are planning to use it within the next five years – possible evidence that current management (presumably based on perennial ryegrass) has generally not resulted in acceptable pasture attributes for this species. The detrimental effect of such management on the productivity and herbage quality of cocksfoot is discussed in Section 2.6.1. Prairie grass has only been sown in the past on the farms of 9% of respondents and the uncertainty regarding the attributes of prairie grass showed that there is a lack of knowledge about this species among Tasmanian dairy farmers. The nature of responses to this survey highlight the importance of extension efforts within the Tasmanian dairy industry to communicate the positive potential role of cocksfoot and prairie grass in Tasmanian dairy pasture systems.

Chapter 10

General discussion

The results presented in this thesis have shown that cocksfoot and prairie grass are suitable alternatives to perennial ryegrass for the dryland dairy pastures of southern Australia. These results – which show that cocksfoot and prairie grass have comparable herbage quality and DM production to perennial ryegrass - challenge the negative perceptions that many Tasmanian dairy farmers have of these species. The performance of cocksfoot and prairie grass is dependent on appropriate defoliation management that takes into account the unique physiology of each species. In this thesis, leaf stage based defoliation management recommendations have been made for cocksfoot and prairie grass that optimise pasture production, persistence, herbage quality and hence, milk production.

This discussion follows the course of research undertaken in this thesis, as outlined below in Figure 10.1. Boxes to the right of the dotted line represent areas that were either indirectly measured or require further research.

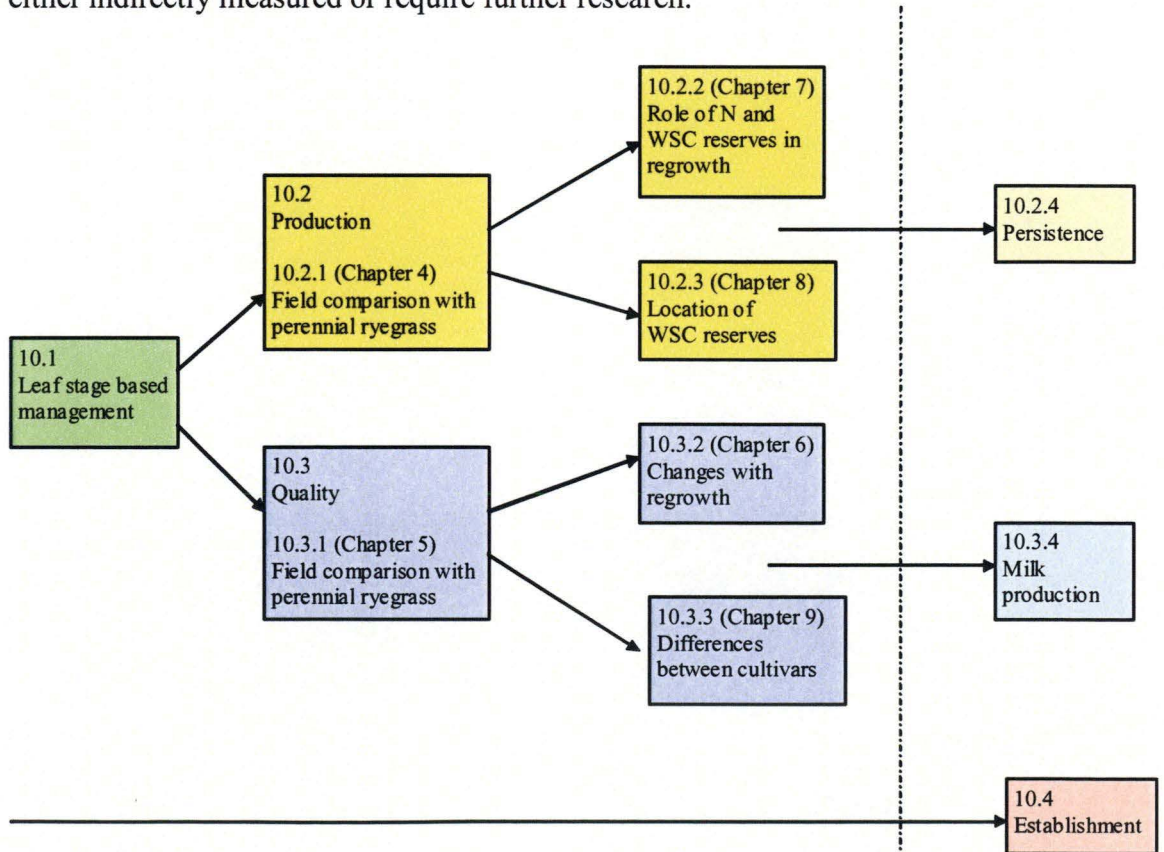


Figure 10.1 Flow chart depicting the course of research undertaken in this thesis.

10.1 Leaf stage based defoliation management

The effects of variables such as temperature and moisture on both WSC reserves and growth rates make it reasonable to base defoliation management on a physiological plant factor that indicates WSC reserve status and stage of plant regrowth. The number of fully expanded leaves per tiller (leaf stage) is an indicator that is readily distinguished in the field and glasshouse, signals the onset of senescence and is related to the degree of restoration of WSC reserves. Use of leaf stage to measure defoliation interval was pioneered by Fulkerson and Slack (1994a) and has increased in popularity during the past decade. Leaf stage based defoliation management was utilised throughout this project, in the investigation of the physiology underlying the production and herbage quality of cocksfoot and prairie grass.

The use of leaf stage as a generic measure of regrowth allows confidence in the relation of findings in the glasshouse to the field, as leaf appearance rate is primarily influenced by temperature and to a lesser extent moisture availability, and is independent of cultivar type and soil fertility (Mitchell 1953; Barker *et al.* 1985; Van Loo 1992). However, it is important to acknowledge that the effects of defoliation interval on plant regrowth parameters measured under ideal environmental conditions in the glasshouse are expected to be more drastic under field conditions that introduce limitations of moisture, nutrients and temperatures.

10.2 Production

10.2.1 Field comparison with perennial ryegrass

In the dryland field study outlined in Chapter 3, basing defoliation intervals on leaf stage enabled a comparison of the leaf appearance rates of the three species, with prairie grass exhibiting the most rapid leaf appearance rate, followed by cocksfoot and then perennial ryegrass. Despite low plant density and tiller number per plant, prairie grass out-yielded ryegrass and cocksfoot by at least 25%, reflecting its faster leaf appearance rate and larger leaves. Despite its slow establishment, DM yield of cocksfoot over the entire study period was equal to that of ryegrass.

Dry matter yield and WSC accumulation of cocksfoot and prairie grass increased with defoliation interval and the 4-leaf stage of regrowth was identified as the

optimal time of defoliation, in general agreement with Rawnsley *et al.* (2002; cocksfoot) and Fulkerson *et al.* (2000; prairie grass).

10.2.2 Role of N and WSC energy reserves

Total amount of WSC (or content) has been identified as a superior criterion than concentration of WSC for determining the importance of reserves for regrowth (Smith 1974; Booysen and Nelson 1975; Fulkerson and Slack 1995; Donaghy and Fulkerson 1998), hence the comparison of WSC content between perennial ryegrass, cocksfoot and prairie grass in Chapter 3. The field study confirmed that the regenerative capacity of perennial grasses is related to tiller size (which in turn is related to WSC, with WSC making up a proportion of DM), and is therefore larger for cocksfoot and prairie grass than perennial ryegrass. The higher WSC content of cocksfoot and prairie grass potentially contributes to the superior summer survival and production of these species.

Consistent with the results of the field study, defoliation interval was found to have a marked effect on both plant stubble and root WSC reserves in the glasshouse studies outlined in Chapter 6, with more frequent defoliation resulting in reduced WSC reserves. The critical defoliation interval for cocksfoot in terms of influencing regrowth (below which WSC reserve replenishment and hence regrowth were severely limited) was shown to be the 2-leaf stage, with defoliation at this interval only likely to result in a satisfactory rate of regrowth if a longer recovery period of regrowth was provided. Evidence of the severe effect of repeated defoliation at the 1-leaf stage on prairie grass WSC reserves and subsequent regrowth was the death of 67% of plants under this treatment. Results provided further confirmation that defoliation of cocksfoot and prairie grass plants at the 4-leaf stage of regrowth maximises WSC accumulation and therefore leaf, root and tiller DM yields, as well as tiller number and survival.

The priority sequence for allocation of WSC reserves in both cocksfoot and prairie grass during the regrowth period followed the expected order of leaf growth, root growth and tillering, which is consistent with the trend determined for perennial ryegrass by Donaghy and Fulkerson (1998).

The results of these studies confirmed that the stubble is the primary site for energy storage, with roots playing a lesser role. However, although there were significantly greater concentrations of WSC and N reserves in the stubble compared with the roots for both cocksfoot and prairie grass, high r^2 values for the relationships between root WSC concentration and regrowth parameters suggested that prairie grass plants utilised WSC reserves from the roots in addition to the stubble, to meet plant energy requirements until adequate photosynthetic tissue had been produced.

Historically, there has been some debate regarding the relative contribution of WSC and N reserves to pasture regrowth following defoliation. Nitrogenous energy reserves were found to play a minor role in the regrowth of cocksfoot plants following defoliation. For prairie grass, although WSC reserves were identified as the primary contributor to plant regrowth following defoliation, there was also a strong relationship between stubble N concentration and regrowth parameters, suggesting that accelerated N accumulation and storage in plant stubble may be induced by more frequent defoliation, perhaps to substitute for low WSC reserves as suggested by Davidson and Milthorpe (1965).

10.2.3 Location of WSC energy reserves

A decrease in WSC reserves with increasing stubble height was observed for vegetative tillers of both species in Chapter 7. However, the WSC concentration gradient was more pronounced for cocksfoot than for prairie grass, with a clear decrease in WSC concentration between the 21-30 mm and 31-40 mm segments, and with 77% of WSC content contained within the 0-30 mm stubble height range. The WSC concentration gradient for prairie grass was less apparent, with a relatively high WSC concentration throughout the 0-100 mm stubble height range. There was a decrease in WSC concentration between the 31-40 mm and 41-50 mm segments, with 62% of WSC content contained within the 0-40 mm stubble height range.

These results suggest that the previously adopted defoliation stubble height of 45-50 mm, which is the optimal defoliation management for perennial ryegrass, maintains over 60% of total stubble WSC reserves and is therefore not detrimental to the persistence of cocksfoot and prairie grass. While decreasing defoliation height to 30 mm may be acceptable for cocksfoot, prairie grass is more sensitive to defoliation

severity, with defoliation below 45 mm not recommended. Prairie grass is also sensitive to frequent defoliation (as highlighted in Chapter 6) and the importance of careful defoliation management to maximise plant persistence must therefore be emphasised.

10.2.4 Persistence

Poor persistence has been identified in the literature as a limitation of prairie grass as a dairy pasture species. In New Zealand, pasture pests including Argentine stem weevil and Hessian fly were reported to be partly responsible for the low survival rates of prairie grass. However, results presented in this thesis suggest that mismanagement of this species (frequency of grazing in particular) may have contributed to the poor persistence of prairie grass in the past. While persistence of prairie grass pasture over a number of years was not measured in this thesis, the effect of defoliation management on tiller dynamics was monitored in the glasshouse and summer survival of tillers was monitored in the field.

In Chapter 5, prairie grass immediately resumed replenishment of energy reserves and therefore leaf regrowth following defoliation, with WSC reserves replenished to pre-defoliation levels by the 2-leaf stage of regrowth. However, this glasshouse study showed that defoliation prior to the 4-leaf stage of regrowth does not allow sufficient time for tiller initiation to occur. Since perenniality of grasses depends on their capacity to replace dying tillers, defoliation prior to the 4-leaf stage of regrowth may result in reduced persistence of prairie grass plants.

Defoliation halved the root DM yield of prairie grass during the time it took to regrow one new leaf, indicating a high sensitivity of root regrowth to changes in WSC concentrations and also reflecting the mobilisation of WSC reserves from roots following defoliation. Prairie grass resumed significant root growth at the 3-leaf stage of regrowth. Management that restricts root growth affects plant growth in general, due to the limitation placed on water and nutrient uptake, and therefore also restricts plant survival. From a root system perspective, defoliation of prairie grass prior to the 3-leaf stage of regrowth would therefore have a detrimental effect on plant survival.

The detrimental effect of frequent defoliation on the persistence of prairie grass is further exaggerated by the relatively low tiller density of this species compared with perennial ryegrass, as identified in Chapter 3. In the field, low WSC reserves and an increased death rate of tillers contributed to a decreased growth rate for prairie grass during summer months and a reduced plant density during autumn. A defoliation regime that maximises WSC accumulation would alleviate this seasonal effect on plant persistence.

10.3 Herbage quality

10.3.1 Field comparison with perennial ryegrass

The perceived poor herbage quality of cocksfoot is a primary barrier to the use of this species on dairy farms, with responses to the survey in Chapter 9 clearly indicating that few dairy farmers believe that the herbage quality of cocksfoot can be maintained at a high standard. In the field study (Chapter 4), each species was defoliated at leaf stage based defoliation intervals, providing an objective comparison of changes in herbage quality with plant development. This revealed a statistically significant but not unacceptable difference in ME concentrations between cocksfoot and perennial ryegrass, challenging the common perception that cocksfoot should not be used in dairy pasture systems due to its unacceptable herbage quality. This perception is largely the result of studies in which management was based on perennial ryegrass (to the detriment of cocksfoot) or involved defoliation of the two grasses at exactly the same time. The higher NDF concentration of cocksfoot compared with perennial ryegrass suggests that intake of cocksfoot pasture may be limited by the less digestible nature of the herbage. As outlined in Section 10.3.3 however, possible differences in intake have not translated into differences in milk production between the species in a temperate environment.

The ME concentration of prairie grass was consistently lower than the ME concentration of both cocksfoot and perennial ryegrass (10.2-10.4 MJ/kg DM compared with 11.4-11.6 MJ/kg DM for ryegrass), reflecting a lower DDM (75.7-77.3% compared with 84.3-85.6% for ryegrass). Relatively high fibre and low CP concentrations (as a result of a high proportion of reproductive tillers and therefore stem material) limited the digestibility of prairie grass. However, the energy per

hectare of prairie grass exceeded the energy availability of both cocksfoot and perennial ryegrass by 9500 MJ/ha.

Cocksfoot maintained a higher CP concentration (mean 21.3%) than both perennial ryegrass (mean 12.9%) and prairie grass (mean 14.2%). The uncharacteristically low CP concentration for perennial ryegrass in relation to cocksfoot in this study may have resulted from the greater proportion of reproductive ryegrass tillers compared with cocksfoot (measured in plant material above the defoliation height of 45 mm) and emphasises the performance potential of cocksfoot under marginal growing conditions.

As defoliation interval increased, there was evidence of a trend for decreasing ME concentration for the three species, largely as a result of decreasing digestibility. The lower ME concentrations for plants defoliated at the 4-leaf stage of regrowth also corresponded with lower CP concentrations.

Results from this study have identified that the 4-leaf stage defoliation interval for prairie grass and cocksfoot, and the 2-leaf to 3-leaf stage for perennial ryegrass maximise DM production and WSC reserves. Although more frequent defoliation of prairie grass resulted in herbage with a higher herbage quality (lower fibre and higher CP concentrations), it would threaten plant persistence due to the exhaustion of WSC reserves. Although ME concentrations were higher for cocksfoot plants defoliated at the 2-leaf and 3-leaf stages compared with defoliation at the 4-leaf stage of regrowth, increased DM production with increased defoliation interval resulted in greater energy per hectare from plants defoliated at the 4-leaf stage of regrowth.

10.3.2 Herbage quality changes of prairie grass during regrowth

The results presented in Chapter 5 provide further evidence that the optimal defoliation interval for growth, persistence and herbage quality of prairie grass is the 4-leaf stage of regrowth. At this stage of plant development, increased WSC reserves coincided with a resumption of tillering and root growth. Herbage quality of prairie grass was higher than in the field (ME concentration above 11.8 MJ/kg DM), with concentrations of P, K and Na adequate to meet the needs of a highly producing

dairy cow. However, concentrations of Ca and Mg were insufficient to meet these requirements throughout the regrowth cycle.

The ME concentration of prairie grass remained above 11.8 MJ/kg DM until (and including) the 4-leaf stage, after which increased stem and senescent material combined to reduce the ME concentration. The ME concentrations for prairie grass in this glasshouse study were considerably higher than the ME concentrations measured in the field study, reflecting the advantageous effect of optimal water and nutrient application on herbage quality and indicating that a higher herbage quality for prairie grass may be achievable in the field under irrigation. Given the increased leaf DM yield at the 5-leaf and 6-leaf stages, total ME yield (MJ/ha) would be substantially greater at the longer regrowth interval, but may not result in increased pasture utilisation in a grazing situation due to increased rejection by stock because of the increased stem and senescent material. The CP concentration of prairie grass met the requirements of a highly producing dairy cow until (and including) the 4-leaf stage, after which point CP concentrations fell below the recommended 18.0-20.0%.

10.3.3 Herbage quality differences between cocksfoot and prairie grass cultivars

Kara and Matua are the most widely sown and utilised cocksfoot and brome dairy pasture cultivars, respectively, and were therefore utilised throughout this thesis to investigate the physiology and management of these alternative species. Since their release onto the commercial market (1980 Kara; 1973 Matua), there has been further selection and breeding within the cocksfoot and brome genera, and in Chapter 8, differences in establishment, productivity and herbage quality between four cocksfoot and four brome cultivars (including Kara and Matua) under leaf stage based defoliation management in the glasshouse were highlighted. While results suggest that the overall value of the newer cultivars to dairy pasture systems may not exceed the value of the original cultivars, further investigation in the field is required for conclusive evidence to this effect. The ME concentration of all cultivars in the current study was acceptable for dairy production, in the range of 10.7-11.2 MJ/kg DM.

The improvements resulting from selection and breeding within the cocksfoot genera included faster seedling emergence, higher tiller initiation rates and tiller density, lower ADF, higher CP and a slightly higher ME concentration. The newer cocksfoot cultivars had considerably lower leaf and tiller DM yields than Kara, however, and with little variation in ME concentrations between cultivars, Kara would provide far greater energy levels on a per hectare basis than the other cocksfoot cultivars assessed in this study.

The improvements resulting from selection and breeding within the brome genera included faster seedling emergence, a lower proportion of reproductive tillers, and therefore a lower ADF concentration and higher CP concentration. The higher fibre levels for Matua and high proportion of reproductive tillers did not translate into a lower ME concentration; in fact, the energy content in Matua (and Gala) was higher than for all remaining cultivars. Claims by breeders that the herbage quality of bromes is not compromised when plants go to seed were verified by particularly high ME concentrations for these cultivars.

10.3.4 Milk production

Although milk production was not measured in this thesis, recent research carried out in Tasmania at Elliott Research and Demonstration Station showed there was no significant difference in milk production per cow between herds grazing both irrigated and dryland cocksfoot, prairie grass and perennial ryegrass pastures (Donaghy *et al.* 2005). In fact, there was a slight trend for milk production from cows grazing prairie grass pastures to be higher than milk production from both cocksfoot and perennial ryegrass pastures. These findings, in combination with the work undertaken in this thesis, challenge the long-held belief in the Australian dairy industry that the herbage quality of alternative grasses is unacceptable, and that cows therefore find them unpalatable, or produce less milk per cow from these pastures compared with perennial ryegrass.

10.4 Establishment

The slow establishment of cocksfoot in the field was noted in Chapter 3 and is well recognised in the literature. Although this species is able to compete effectively with weeds and other pasture plants for resources once established, slow establishment

continues to hinder acceptance by dairy farmers. Faster establishment was originally promoted as an attribute of the cocksfoot cultivar Kara, but in the glasshouse study described in Chapter 8, it was the slowest cultivar to emerge, with the fastest emerging cocksfoot cultivar Tekapo highlighting advances through selection and breeding.

In terms of tiller initiation during establishment, the cocksfoot cultivars Tas 2029 and Uplands (both selected for high tiller density) exhibited the most rapid rates of tiller initiation, resulting in the highest tiller numbers by the commencement of treatments and throughout the subsequent study period. However, the establishment of cocksfoot plants in the glasshouse studies described in Chapters 6, 7 and 8 (regardless of cultivar) was relatively fast compared with establishment in the field, highlighting that light, temperature and sowing conditions significantly influence the rate of establishment.

While differences between cultivars in days to emergence and tiller initiation rates during establishment in the glasshouse are worthy of attention, they do not adequately represent establishment differences in the field. As suggested by Cornish *et al.* (1984) and Aguirre and Johnson (1991), further investigations into the elongation rates of seminal and adventitious root axes in relation to shoot development are required to provide valuable insight into seedling development and establishment rates of alternative grass species.

10.5 Implications

The work undertaken in this thesis has furthered our understanding of the physiology underlying the response of cocksfoot and prairie grass to defoliation. Investigations of the roles of N and WSC reserves during regrowth of these species have involved determination of the primary storage location for energy reserves, the priority sequence for allocation of WSC reserves and the relative contribution of N and WSC reserves to regrowth following defoliation. Changes in the physiology and herbage quality of prairie grass during regrowth have also been investigated and significantly contribute to the scientific knowledge underlying best management recommendations for this grass.

In terms of practical implications for the dairy industry, the DM yields and herbage quality of these alternative species have been shown to be favourable for dairy production and comparable with perennial ryegrass under leaf stage based defoliation management. Defoliation management recommendations have been made that provide an optimal balance between pasture yield, persistence and herbage quality.

While results in this thesis provide further support for the use of cocksfoot and prairie grass in the dairy pastures of southern Australia, the nature of responses to the farmer perception survey highlight the importance of extension efforts within the (Tasmanian) dairy industry to communicate the positive potential role of cocksfoot and prairie grass in dairy pasture systems.

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Appendices

A.1 Laboratory analysis procedures

Analysis of water-soluble carbohydrates

The concentration of WSC reserves was determined by cold extraction of plant material in a reciprocal shaker for one hour using 0.2% benzoic acid-water solution, and the hydrolysis of the cold water carbohydrates to invert sugar by 1 mol l⁻¹ hydrochloric acid. This was heated at 90°C, and the sugar was dialysed into an alkaline stream of potassium ferricyanide, again heated at 90°C, and then measured using an autoanalyser (420 nm) (Technicon Industrial Method number 302-73A, derived from the method outlined by Smith 1969).

Analysis of total nitrogen

Finely ground plant material was combusted at 950°C in oxygen using a Leco FP-428 Nitrogen Analyser. The released N from the sample was measured as it passed through a thermal conductivity cell (Sweeney and Rexroad 1987).

Analysis of minerals

Plant material was digested in nitric acid using a Milestone microwave and measurement was by inductively coupled plasma – atomic emission spectrometry (ICP-AES; McQuaker *et al.* 1979).

NIR analyses

Near Infra Red spectra were collected on all samples using a Foss-NIRSystems 5000 scanning monochromator in conjunction with Infracore International software. Near Infra Red calibrations for N were previously derived using the Kjeldahl method, for ADF and NDF using the method of Van Soest and Wine (1967) and ANKOM equipment, and for DDM using a pepsin-cellulase technique, with analytical values adjusted using a linear regression based on similar samples of known *in vivo* DDM (Clarke *et al.* 1982). Spectral outliers were analysed by the wet chemistry techniques described above.

A.2 Potting mix profile

In 1 m³ potting mix:

- 50% pine bark
- 30% sand (4 mm diameter)
- 20% *Spaghnum* sp. moss
- 1,000 g super phosphate
- 320 g potash
- 2,000 g Osmocote® plus (8-9 months)
15:9:12, N:P:K, plus micronutrients
Scotts Australia Pty. Ltd., NSW, Australia
- 1,000 g blood and bone
- 2,000 g lime
- 1,600 g dolomite
- 1,200 g SaturAid (wetting agent)
Active ingredient 15% propylene oxide-ethylene oxide block polymer
Debco Pty. Ltd., Victoria, Australia

A.3 Survey information sheet

Survey title

Farmer perception of the three pasture grasses: perennial ryegrass, prairie grass and cocksfoot.

What is the purpose of the survey?

The aim of this survey is find out which grass species are being used on farms and what dairy farmers see as the advantages and disadvantages of using particular pasture species. The survey is part of a PhD project that aims to create a greater understanding of how cocksfoot and prairie grass grow and to develop management guidelines. Knowing what influences a farmer's choice of grass species will be important information for further field and glasshouse studies and will assist in extension of results from the PhD project.

What is the time frame?

The survey will be sent out in March 2005 and information collected and analysed by July 2005.

Who is the questionnaire being sent to?

Tasmanian dairy farm owners, sharefarmers and managers (approximately 750) who receive the Targeting Our Profitability (TOP) newsletter.

What questions are being asked?

The questions address the opinions farmers have about the herbage quality, palatability (animal acceptance), and production of the three pasture species: perennial ryegrass, cocksfoot and prairie grass. A questionnaire will be mailed to each person with a postage paid, return-addressed envelope.

How will results remain confidential and anonymous?

Information gained from the questionnaires will be coded so that no names are used in the presentation of results. Questionnaires will be stored in a locked cabinet in the University of Tasmania.

How do participants give consent?

As results are confidential and subjects remain anonymous, the return of answered questionnaires to the sender is an indication of consent. If participants are not willing to participate, they simply do not answer or return the questionnaire provided.

When will information become available?

Information from this questionnaire as well as related research findings will be presented at DPIWE dairy discussion group meetings in late 2005, as advertised through the TOP newsletter.

Contact person: For further information about the study, please contact:

Lydia Turner

64 304 938; email - wilsonlr@utas.edu.au

A.4 Survey response summaries

N	No	VH	Very high
Y	Yes	H	High
U	Unsure	S	Satisfactory
C	Cocksfoot	L	Low
P	Praine grass	VL	Very low
B	Both		

Resp.	Q1	Q2a	Q2b	Q3	Q4	Q5	Q6	Q7	Q8	Q9a	Q9b	Q10a	Q10b	Q11a	Q11b	Q12a	Q12b
1	N	Y	C	S	H	U	H	U	S	U	H	S	S	H	S	N	
2	N	Y	B	L	VH	S	VH	S	VL	S	VL	H	L	S	VL	N	
3	N	Y	B	S	H	L	H	L	S	U	U	H	H	S	L	N	
4	N	Y	C	U	S	U	H	U	S	U	U	H	S	S	L	Y	C
5	N	N		U	S	U	H	U	U	U	U	U	U	S	S	N	
6	N	Y	B	H	H	H	H	VH	H	U	H	U	H	S	S	U	B
7	Y	Y	C	S	VH	L	VH	L	S	S	S	L	L	L	S	Y	B
8	Y	Y	C	S	H	L	H	S	S	S	S	H	S	H	H	N	
9	Y	Y	C	H	H	U	H	U	H	U	U	VH	H	VH	H	Y	C
10	Y	U		VL	H	U	H	U	VL	U	U	VL	VL	VL	S	N	
11	Y	Y	C	VH	VH	U	VH	U	VH	U	U	VH	VH	VH	VH	Y	C
12	Y	Y	C	S	H	U	H	U	S	U	U	L	L	S	L	U	C
13	Y	N		U	S	U	S	U	U	U	U	U	U	L	L	N	
14	Y	Y	C	S	H	S	H	S	S	H	S	H	H	H	L	Y	B
15	Y	Y	C	S	S	U	S	H	L	S	S	L	L	H	S	N	
16	Y	Y	C	S	H	U	H	U	S	U	U	S	S	S	S	Y	C
17	Y	Y	C	L	H	U	H	U	L	U	U	S	S	S	S	N	
18	Y	Y	C	L	H	U	VH	U	S	U	U	S	S	VH	S	N	
19	Y	N		L	H	U	H	U	L	U	U	S	L	L	S	N	
20	Y	N		L	H	U	H	U	L	U	U	U	U	VL	S	U	B
21	Y	Y	C	S	H	U	VH	U	L	U	U	H	S	S	VL	Y	C
22	Y	N		L	H	U	H	U	L	U	U	S	S	S	L	N	
23	Y	Y	C	S	H	L	H	L	L	L	L	S	S	S	S	N	
24	Y	N		L	H	L	H	L	L	L	L	L	L	H	H	N	
25	Y	Y	C	S	H	S	H	S	S	S	S	L	S	S	S	U	P
26	Y	N		S	H	H	S	S	S	S	S	S	S	S	L	Y	B
27	Y	Y	C	L	H	U	VH	U	S	U	U	S	H	S	S	N	
28	Y	Y	C	L	S	U	H	U	L	U	U	S	H	H	S	N	
29	Y	Y	C	L	S	U	S	U	S	U	U	S	S	S	S	N	
30	Y	Y	C	L	S	U	S	U	L	U	U	S	S	S	S	N	
31	Y	Y	C	VL	VH	U	H	U	VL	U	U	L	L	VH	VL	N	
32	Y	Y	C	L	S	U	S	U	L	U	U	L	L	S	L	N	
33	Y	Y	C	S	VH	S	VH	S	H	S	H	H	H	S	S	N	
34	Y	N		L	H	H	VH	H	L	S	U	U	U	L	S	U	P
35	Y	Y	C	S	H	U	H	U	L	U	U	S	S	H	H	N	
36	Y	Y	C	S	H	U	H	U	H	U	U	H	S	S	L	Y	C
37	Y	Y	C	S	H	L	S	L	S	L	L	H	H	H	S	Y	C
38	Y	U		H	VH	U	H	U	S	U	U	S	S	H	S	U	
39	Y	N		L	H	U	H	U	S	U	U	L	S	S	S	N	
40	Y	Y	C	L	H	U	H	U	L	U	U	S	S	H	S	N	
41	Y	Y	C	S	H	S	VH	S	S	L	S	S	S	H	L	N	
42	Y	N		L	H	S	S	U	VL	U	U	H	H	VH	VH	N	
43	Y	Y	C	S	H	U	H	U	S	U	U	S	S	H	H	N	
44	Y	Y	C	S	VH	S	VH	H	S	S	S	H	H	S	VH	N	
45	Y	Y	C	S	H	U	H	U	H	U	U	S	S	L	L	U	C
46	Y	Y	C	S	H	U	H	U	S	U	U	H	H	S	H	Y	C
47	Y	Y	C	S	H	U	H	U	S	U	U	S	S	S	L	N	
48	Y	N		L	H	L	S	L	L	U	U	S	S	H	L	N	
49	Y	Y	P	U	H	S	H	H	U	S	S	U	U	S	VL	Y	P
50	Y	U		S	H	H	VH	H	H	S	H	S	H	S	L	U	
51	Y	Y	C	S	H	U	H	U	S	U	U	H	H	S	S	U	P
52	Y	N		S	VH	U	VH	U	S	H	VH	S	VH	H	L	N	
53	Y	Y	B	H	VH	H	VH	H	H	U	U	H	S	H	S	Y	C
54	Y	N		U	VH	U	VH	U	U	U	U	U	U	S	S	N	
55	Y	Y		S	H	U	S	U	L	U	U	S	S	S	S	Y	P
56	Y	Y	C	S	H	U	H	U	S	U	U	U	U	S	S	U	B
57	Y	Y	C	S	VH	U	H	U	S	U	U	H	H	L	S	N	
58	Y	N		L	H	U	H	U	L	U	U	S	S	H	S	N	
59	Y	Y	C	H	VH	U	H	U	S	U	U	H	H	S	L	Y	C
60	Y	Y		S	VH	U	VH	U	L	U	U	S	S	H	S	N	
61	Y	N		L	H	VL	H	VL	L	S	S	S	S	S	L	N	
62	Y	Y	C	H	VH	U	VH	U	H	U	U	H	H	S	S	U	C
63	Y	Y	C	L	H	U	H	U	S	U	U	S	S	S	S	N	
64	Y	N		VL	H	VL	H	VL	VL	S	S	S	S	H	H	N	
65	Y	U		H	H	H	H	H	H	H	S	H	H	S	S	U	B
66	Y	N		L	H	U	H	U	L	U	U	L	L	L	S	N	
67	Y	U	C	S	VH	L	VH	L	S	L	L	S	S	H	S	N	
68	Y	Y	C	S	H	U	H	U	S	U	U	S	S	S	S	N	
69	Y	U	C	VL	H	U	VH	U	S	U	U	VL	VL	H	S	N	
70	Y	N		L	H	H	H	H	L	S	S	S	S	S	S	N	
71	Y	N		S	VH	U	H	U	S	U	U	S	S	H	H	N	
72	Y	Y	C	S	H	U	H	U	S	U	U	S	L	H	L	U	C
73	Y	Y		S	H	L	H	L	S	L	S	S	S	S	L	N	
74	Y	Y	C	S	H	U	VH	U	S	U	U	S	S	H	H	Y	C
75	Y	N		S	H	H	S	H	S	S	VL	S	S	S	L	N	
76	Y	Y	C	L	H	U	VH	U	L	U	U	S	S	U	S	N	
77	Y	Y	C	S	S	U	H	U	S	U	U	S	S	S	S	Y	C
78	Y	N		U	H	U	H	U	U	U	U	U	U	L	S	Y	B
79	Y	N		L	H	L	VH	S	VL	L	L	S	S	H	L	N	
80	Y	Y		H	VH	H	VH	VH	H	S	S	VH	VH	S	S	U	

Resp.	Q1	Q2a	Q2b	Q3	Q4	Q5	Q6	Q7	Q8	Q9a	Q9b	Q10a	Q10b	Q11a	Q11b	Q12a	Q12b
81	Y	Y	C	VL	H	U	VH	U	L	U	U	S	S	H	H	N	
82	Y	N		U	H	U	H	U	U	U	U	U	U	S	L	N	
83	Y	Y	C	S	H	U	VH	U	H	U	U	U	U	S	U	U	
84	Y	Y	C	S	S	L	H	L	S	L	U	H	H	H	S	Y	C
85	Y	U		S	VH	S	H	S	S	S	H	S	H	H	VH	U	
86	Y	Y	C	L	H	U	H	U	S	U	U	S	S	S	S	U	
87	Y	U		U	S	U	S	U	U	U	U	U	U	S	VL	N	
88	Y	Y	C	S	VH	S	L	S	S	U	U	L	S	VL	VL	N	
89	Y	Y	C	L	H	S	H	S	L	S	S	S	L	S	VL	N	
90	Y	Y	C	L	H	U	H	U	L	U	U	L	S	S	H	N	
91	Y	Y	C	S	VH	H	VH	H	S	H	VH	H	VH	H	H	Y	C
92	Y	Y	C	L	H	U	H	U	L	U	U	U	U	U	U	Y	
93	Y	Y	C	H	H	S	H	L	S	L	L	S	S	H	S	N	
94	Y	Y	C	S	H	H	H	H	S	S	S	S	S	H	L	U	C
95	Y	N		VL	H	VL	S	VL	VL	VL	VL	L	L	S	L	N	
96	Y	N		S	H	L	S	L	S	L	S	S	H	S	H	U	
97	Y	Y	B	H	H	H	H	H	S	H	VH	VH	H	H	L	Y	B
98	Y	N		S	VH	S	VH	S	S	L	S	S	H	VH	VH	U	
99	Y	N		S	H	H	H	H	S	H	S	S	S	H	S	N	
100	Y	N		S	H	U	H	U	S	U	U	S	S	H	S	N	
101	Y	Y	C	VL	H	VL	H	L	L	L	L	L	L	S	L	N	
102	Y	Y	C	L	H	U	H	U	S	U	U	H	H	S	S	Y	C
103	Y	Y	C	S	S	H	VH	H	S	S	S	S	H	H	S	Y	B
104	Y	N		U	H	S	H	H	L	S	L	H	H	H	S	Y	C
105	Y	Y	B	H	VH	VH	H	VH	H	VH	VH	VH	H	H	S	Y	B
106	Y	Y	C	H	VH	U	VH	U	H	U	U	H	S	S	S	Y	C
107	Y	Y	B	H	H	S	H	H	H	H	H	H	H	H	L	Y	B
108	Y	U		S	S	S	H	S	S	VL	H	L	H	S	H	Y	P
109	Y	Y	C	S	H	U	H	U	H	U	U	H	VH	VH	H	U	C
110	Y	U	C	U	H	U	H	U	U	U	U	U	U	U	S	N	
111	Y	Y	C	L	VH	U	VH	U	H	U	U	H	VL	H	S	N	
112	Y	Y	C	VH	VH	VH	H	VH	H	H	U	H	H	H	L	Y	C
113	Y	Y	C	L	H	U	H	U	L	U	U	S	S	S	S	U	
114	Y	Y	C	S	H	U	H	U	S	U	U	H	H	S	S	N	
115	Y	Y	C	S	H	VL	S	L	VL	VL	L	L	S	H	S	U	C
116	Y	N		S	H	U	H	U	S	U	U	S	S	H	H	N	
117	Y	Y	C	H	H	U	VH	VH	H	U	U	H	H	H	S	N	
118	Y	N		L	H	U	H	U	S	U	U	H	S	S	S	U	C
119	Y	Y	C	S	H	U	H	U	S	U	U	S	L	S	VL	U	C
120	Y	Y	C	S	VH	U	VH	U	S	U	U	S	H	VH	S	U	
121	Y	Y	C	S	H	S	H	H	H	S	L	S	S	H	S	N	
122	Y	Y	C	L	H	U	H	U	S	U	U	S	S	H	VL	U	B
123	Y	Y	C	L	H	U	H	U	L	U	U	S	S	S	L	N	
124	Y	Y	B	S	H	H	H	VH	S	S	S	S	H	S	VL	Y	C
125	Y	Y	B	L	H	L	H	L	L	H	S	S	H	H	H	U	
126	Y	Y	C	S	H	U	H	U	S	U	U	S	S	H	S	N	
127	Y	N		VL	H	U	H	U	L	U	U	S	S	H	S	N	
128	Y	N		L	H	H	H	H	S	S	L	S	S	H	L	U	P
129	Y	Y	C	U	S	U	S	U	U	U	U	U	U	VL	VL	Y	C
130	Y	Y	B	L	S	S	H	H	S	L	S	L	S	L	S	N	
131	Y	Y	C	VL	H	U	H	U	VL	U	U	H	H	H	H	U	
132	Y	N		S	H	L	H	L	S	S	L	S	S	S	H	N	
133	Y	Y	C	S	S	S	H	H	H	H	H	H	H	S	L	U	C
134	Y	Y	C	S	H	U	H	U	S	U	U	S	S	S	H	Y	C
135	Y	Y	C	S	VH	H	VH	H	H	U	U	S	H	H	S	Y	C
136	Y	Y	C	L	S	L	S	L	L	H	U	H	H	S	S	N	
137	Y	Y	C	L	VH	U	H	U	L	U	U	L	S	H	S	N	
138	Y	N		L	H	S	H	H	VL	U	H	L	S	S	H	N	
139	Y	Y	C	H	H	VH	VH	VH	VH	S	L	VH	S	H	L	Y	B
140	Y	Y	C	S	VH	U	VH	U	H	U	U	S	VH	VH	VH	N	
141	Y	Y	C	S	H	U	VH	U	H	U	U	H	H	S	L	U	C
142	Y	N		U	VH	VH	VH	VH	U	U	U	U	S	H	S	Y	C
143	Y	Y	C	S	H	U	H	U	S	U	U	S	S	S	S	Y	C
144	Y	Y	C	L	S	U	S	U	L	U	U	S	L	S	L	U	C
145	Y	N		L	VH	U	H	U	S	L	L	S	S	VH	VH	N	
146	Y	Y	C	S	H	U	H	S	S	U	U	H	H	U	S	Y	C
147	Y	Y		S	H	S	H	S	S	S	S	S	H	S	L	Y	C
148	Y	Y	B	S	H	L	VH	U	H	U	L	S	H	H	H	U	B
149	Y	N		L	H	S	H	S	L	S	S	L	L	H	S	N	
150	Y	Y	C	S	VH	U	VH	U	S	S	L	S	S	H	S	N	
151	Y	Y	C	S	H	U	H	U	H	U	U	S	H	S	L	Y	C
152	Y	N		L	S	L	S	L	L	S	S	L	L	S	S	N	
153	Y	Y	C	S	H	U	H	U	L	U	U	H	H	H	S	Y	B
154	Y	Y	B	S	VH	S	VH	VH	S	L	L	VH	S	L	L	N	
155	Y	Y	C	S	H	U	H	U	S	U	U	S	L	S	VL	N	
156	Y	U		H	H	H	H	H	H	H	S	H	H	H	S	U	C
157	Y	Y	C	S	H	U	H	U	S	U	U	S	L	S	S	U	C
158	Y	Y	P	H	H	H	S	H	S	U	U	H	L	S	VL	U	B
159	Y	Y	C	H	H	U	H	U	S	U	U	H	S	H	H	Y	C
160	Y	N		L	H	VL	H	VL	L	S	S	S	H	H	L	N	
161	Y	Y	C	S	H	U	H	S	S	U	U	S	VH	H	S	Y	C
162	Y	Y	C	L	VH	U	VH	U	S	U	U	L	L	H	S	N	
163	Y	Y	B	VL	VH	U	VH	S	VL	U	U	S	S	S	S	N	
164	Y	Y	C	H	S	U	VH	U	U	U	H	L	L	S	L	Y	B
165	Y	Y	B	S	VH	S	H	H	S	U	U	S	H	L	L	N	

Resp.	Q1	Q2a	Q2b	Q3	Q4	Q5	Q6	Q7	Q8	Q9a	Q9b	Q10a	Q10b	Q11a	Q11b	Q12a	Q12b
166	Y	Y	C	S	S	U	S	U	S	U	U	S	S	S	S	N	
167	Y	N		U	S	U	H	U	U	U	U	U	U	L	VL	U	
168	Y	N		L	H	U	H	U	U	U	U	S	S	H	H	N	
169	Y	Y	C	S	U	S	S	U	S	U	U	H	H	S	L	U	
170	Y	Y	C	S	H	U	H	L	S	U	U	H	H	S	S	U	C
171	Y	Y	C	H	VH	U	VH	U	H	U	U	VH	VH	S	VL	Y	C
172	Y	N		U	H	U	H	U	U	U	U	U	U	S	L	N	
173	Y	Y	C	S	VH	U	VH	U	S	U	U	H	H	L	S	N	
174	Y	Y	C	H	VH	U	VH	U	H	U	U	VH	VH	S	VL	Y	C
175	Y	N		L	H	U	S	U	L	U	U	S	S	U	L	U	
176	Y	Y	C	L	VH	U	VH	U	S	U	U	S	S	VH	S	N	
177	Y	N		H	VH	S	VH	H	H	U	U	U	U	L	VL	N	
178	Y	Y	C	L	H	U	H	U	L	U	U	U	U	U	U	U	
179	Y	Y	C	S	S	U	H	U	S	U	U	S	S	S	L	U	C
180	Y	Y	B	L	H	H	U	VH	L	H	H	L	L	H	L	N	
181	Y	Y	C	U	S	U	H	U	S	U	U	H	S	S	L	Y	C
182	Y	Y	C	U	H	U	VH	U	H	U	U	H	H	S	VL	U	
183	Y	N		U	S	U	S	U	U	U	U	U	U	S	S	N	
184	Y	Y	C	S	VH	U	H	U	S	U	U	H	H	H	L	Y	C
185	Y	Y	C	S	S	U	S	U	S	U	U	S	H	S	H	N	
186	Y	Y	C	S	VH	U	VH	U	L	U	U	S	H	H	L	N	
187	Y	Y	C	S	S	U	S	U	S	U	U	H	H	S	L	U	C
188	Y	N		S	S	U	H	U	S	U	U	S	H	L	S	N	
189	Y	N		U	S	U	S	U	U	U	U	U	U	S	U	N	
190	Y	Y	C	U	S	U	S	U	U	U	U	U	U	S	S	N	