Understanding constraints to cocksfoot (*Dactylis glomerata* L.) based pasture production

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This research examined the mechanisms by which temperature, water availability and nitrogen (N) affect the dry matter (DM) yield potential of cocksfoot (*Dactylis glomerata* L.) dominant pastures. The experiment was a split plot design with main plots of fully irrigated (I) or dryland (D), sub-plots of N fertiliser at 800 kg N/ha in 2003/04; and 1600 kg N/ha in 2004/05 (+N) or 0 kg N/ha (-N). The potential environmental yield of an established 8 year old cocksfoot dominant pasture was 21.9 t DM/ha/y from I+N pastures compared with 9.8 t DM/ha by I-N pastures and 15.1 t DM/ha/y by D+N pastures. The lowest yields were from dryland pastures with no N which produced 7.5 t DM/ha/y in 2003/03 and 5.0 t DM/ha/y in 2004/05.

The effect of seasonal temperatures on the DM production, when periods of water stress were excluded, was quantified using thermal time accumulated above a base temperature of 3°C as 7.0 kg DM/^{o}Cd/ha for N fertilised pastures and 3.3 kg DM/^{o}Cd/ha for pastures with no N.

The 2.5 t DM/ha difference in yields of D-N pastures in 2003/04 and 2004/05 was the result of the duration, extent and timing of the water stress period. In both years the critical limiting deficit (D_L) was calculated as 78 mm from the soil moisture deficit in the 0-0.8 m soil layers. Beyond D_L yield decreased at a rate of 1.45%/mm in +N and –N pastures, relative to fully irrigated control pastures.

Yields of D+N and D-N pastures were similar during periods of water stress with 0.4±0.1 t/DM/ha produced during the rotation ending 30/12/2003. This was less than from either the I-N (1.2 t DM/ha) or I+N (3.5 t DM/ha) pastures due to the reduction in

the amount of photosynthetically active radiation intercepted by the canopies of the dryland pastures. However, in the rotation ending 2/5/2004, after autumn rain alleviated drought conditions, yield of the D+N pasture was 2.1 t DM/ha compared with 1.7 t DM/ha by I+N pastures.

The effect of N on yield was described using a nutrition index which showed that as DM yield increased N% in the herbage declined. This is a function of the ratio between metabolic and structural N requirements rather than caused by ontogeny alone. Specific leaf N was determined at two harvests and appeared constant at a given point in time (1.0-1.6 g N/m^2 leaf). In contrast, specific pseudostem N increased from 0.8-1.0 g N/m^2 pseudostem at an NNI of 0.4 in –N pastures to 2.6-3.0 g N/m^2 pseudostem at an NNI of 1.2 in the +N pastures.

Differences between the yields of +N and –N pastures were caused by differences in radiation use efficiency (RUE) as determined by the linear relationship (R^2=0.76) between RUE and the nitrogen nutrition index (NNI).

In this thesis, empirical relationships for the effects of temperature, water availability and N were derived and the physiological mechanisms which underlie these descriptions were identified. These relationships provide clear and simple explanations of the effects of environmental variables on the productivity of cocksfoot based pastures which will enhance understanding of the benefits and limitations of cocksfoot, particularly in dryland farming systems.

Keywords: cocksfoot, *Dactylis glomerata*, leaf area index, nitrogen, orchardgrass, radiation interception, radiation use efficiency, temperature, water stress.

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List of Abbreviations

Abbreviation	Description	Units
AET	actual evapotranspiration	mm
ASMD	actual soil moisture deficit	mm
$ASMD_{Irr}$	actual soil moisture deficit for irrigation	mm
CP	crude protein	%, kg/ha or kg/ha/y
CV	coefficient of variation	%
D_L	critical limiting deficit	mm
LL	drained lower limit to extraction	% v/v or mm
DM	dry matter	g/m^2, kg/ha or t/ha
UL	upper limit	% v/v or mm
DWU_{max}	maximum daily water use	mm/d
EFV	extraction front velocity	mm/d
ELADP	ellipsoidal leaf angle distribution parameter	
ET	evapotranspiration	mm
GR_{max}	maximum growth rate	kg DM/ha/d
k	extinction coefficient	dimensionless
kl	diffusion constant	dimensionless
LA	leaf area	cm^2 or m^2
LAI	leaf area index	dimensionless
LAI_{adj}	adjusted leaf area index	dimensionless
LAI_{crit}	critical leaf area index (95% interception)	dimensionless
LAR	leaf appearance rate	leaves/d or leaves/^{o}Cd
LSD	least significant difference	
ME	metabolisable energy	MJ /kg DM or GJ /ha/y
n	number of paired values	
N%	nitrogen concentration	%
NNI	nitrogen nutrition index	dimensionless
N_{opt}	optimum nitrogen concentration	%
NUE	nitrogen use efficiency	kg DM/kg N
p	probability	
$P_{(I+R)}$	precipitation from rainfall and irrigation	mm
PAI	plant area index	dimensionless

Abbreviation	Description	Units
PAR	photosynthetically active radiation	MJ/m^2
PAWC	plant available water holding capacity	mm
$PAWC_S$	plant available water holding capacity (0-0.8 m)	mm
PET	potential evapotranspiration	mm
PSMD	potential soil moisture deficit	mm
PY	potential yield	t DM/ha/y
R^2	coefficient of determination	
R	transmitted photosynthetically active radiation	MJ PAR/m^2
RMSD	root mean square deviation	
R_o	incident photosynthetically active radiation	MJ PAR/m^2
R/R_o	fraction intercepted PAR	dimensionless
RUE	radiation use efficiency	g DM/MJ PAR intercepted
RY	relative yield	dimensionless
SEM	standard error of the mean	
SLN	specific leaf/lamina nitrogen	g N/cm^2
SLW	specific leaf/lamina weight	g DM/cm^2
SMD	soil moisture deficit	mm
SPN	specific pseudostem nitrogen	g N/cm^2
SPW	specific pseudostem weight	g DM/cm^2
SS_T	total sums of squares	
SWC	soil water content	mm
t	time	d
TAGR	temperature adjusted growth rate	kg DM/^oCd/ha
TAWC	total available waterholding capacity	mm
T_b	base temperature	^oC
T_{opt}	optimum temperature	^oC
Tr	regrowth duration	d
Tt	thermal time	^oCd
VPD	vapour pressure deficit	
VWC	volumetric water content	% v/v
WU	water use	mm
WU_{daily}	daily water use	mm/d
WUE	water use efficiency	kg DM/mm
Y	yield	kg/ha or t/ha

1 General Introduction

New Zealand's total land area exceeds 26.7M ha (Department of Statistics, 2003a). Of this 10.3M ha is used for sheep and beef production but, in 2002, only 1.5% of this was irrigated. About 1.6M ha for sheep and beef production is located in the Canterbury region where <2.0% is irrigated (Department of Statistics, 2003a, 2003b). The majority is managed under dryland conditions and therefore totally reliant on rainfall for pasture growth. In Canterbury, in an average year, potential evapotranspiration exceeds rainfall by 480 mm between September and April with annual pasture production consequently reduced by about 30% (MAF, 2000).

1.1 Dryland pastoral agriculture in New Zealand

Perennial ryegrass (*Lolium perenne*)/white clover (*Trifolium repens*) pastures have been the basis of pastoral agriculture in New Zealand for over 60 years (Mather *et al.*, 1995; Fletcher *et al.*, 1999). Their extensive use has lead to attempts to adapt both species to a wide range of climatic conditions (Caradus *et al.*, 1995) and productivity and persistence have been improved in areas with reliable rainfall and fertile soils (MacFarlane, 1990; Widdup and Turner, 1990).

However, on the east coast of New Zealand, pasture production declines in dryland systems because potential evapotranspiration is greater than rainfall from September–April (Rickard and Radcliffe, 1976; Cox, 1978). Therefore, dryland systems are designed to take advantage of the relatively short high growth season in spring. At other times of the year growth is constrained by i) low winter temperatures and ii) summer drought, which can completely halt growth. Drought is particularly severe on shallow free draining soils where both soil depth and texture limit the total available water holding capacity of the soil. The duration and intensity of summer droughts are variable and unpredictable (Hoglund and White, 1985; McKenzie *et al.*, 1990) which hampers management decision-making.

Limitations caused by topography, cost, and the quantity of water required to irrigate at the appropriate times to maintain growth means the majority of dryland pastures are unlikely to receive irrigation in the future. Consideration also needs to be given to the availability of water in irrigated systems which may be revoked by regional authorities when ground water levels reach a predetermined level. Thus, the financial cost

associated with the lack of production and persistence of the industry standard ryegrass/white clover pastures in summer dry regions has led to the realisation that alternative pasture species may be more suited to dryland systems (Woodman *et al.*, 1992).

1.2 The economic cost of drought conditions

The New Zealand economy is driven by primary production. In 2002, agricultural based exports from New Zealand had a value of $16.4B. Of this $7.1B was generated from the dairy industry and $5.1B from sheep and beef products which included wool. When combined, these industries accounted for 77% of the total agricultural export income (MAF, 2006).

Drought can have a large economic impact at both national and regional levels. Between 1997 and 1999 the east coast of New Zealand experienced a prolonged drought. This had a net impact on the Canterbury economy of $280M (MAF, 2000) almost half of which was attributed to reduced production from dryland pastoral systems. The drought caused farmers to feed out stored hay and silage that meant net farmgate losses totalled $214M over the drought period with additional social impacts on dryland pastoral regions and communities.

1.3 Potential to maximise production under dryland conditions

Globally, water is commonly the most critical limiting factor to crop/pasture production. Plants initiate a range of strategies ranging from reductions in canopy expansion under mild stress to eventual plant death (Brown, 1995). However, the extent, severity and duration of the stress period will determine which strategies are implemented for plant survival and will influence the extent of observed yield reductions (Jamieson, 1999). Regardless of these strategies, growth will not occur when there is no water available. Under these conditions, the ability of a plant to survive and recover after drought is of greater benefit in drought proofing a dryland farming system compared with the continued failure and death of ryegrass/white clover based pastures.

Cocksfoot (*Dactylis glomerata*) is the major dryland pasture grass used in New Zealand. It is drought tolerant, persistent and the main growth period occurs in summer (Charlton and Stewart, 2000). In Canterbury reported annual yields range from 7.5 t DM/ha to 28.6 t DM/ha. The lower yield (Stevens *et al.*, 1992) indicates an average year with no

N and dryland conditions whereas the high yield (Peri *et al.*, 2002a) was produced under non limiting water and N conditions. Cocksfoot can dominate white clover in mixed swards (Lee and Cho, 1985), to the point where pasture quality declines, as the vegetation becomes protein deficient (Moloney *et al.*, 1993). It has been shown that N fertility status of pastures affects grazing preference (Edwards *et al.*, 1993). This is particularly important for cocksfoot pastures which have been shown to be N deficient throughout the year (Peri *et al.*, 2002a). Furthermore, dryland cocksfoot pastures supplied with adequate N produced 80% more yield annually than pastures supplied with irrigation alone (Peri *et al.*, 2002a).

The failure of ryegrass/white clover in dryland systems has been widely reported and it is known that cocksfoot is persistent in summer dry regions. However, a lack of understanding of the impact of drought and N deficiency on cocksfoot yield means ryegrass/white clover pastures continue to be sown. By understanding the benefits and limitations to cocksfoot production in dryland systems pastoral production may be increased. This, in combination with a range of complementary pastures and forages suitable for the range of conditions dryland pastures experience annually will minimise the economic impact of drought.

1.4 Aim, objectives and thesis structure

The main aim of this thesis is to quantify the effects of temperature, water and nitrogen on the yield potential of cocksfoot pastures. The effect of each factor was assessed in relation to the potential yield determined with non limiting water and nitrogen during the 2003/04 and 2004/05 growth seasons in Canterbury, New Zealand. These relationships were then integrated into a multiplicative yield prediction model.

The thesis is structured in eight chapters (Figure 1.1). Chapter 2 reviews the literature and describes the agronomic and physiological reasons for yield variation. Techniques used to describe the effects of environmental variables in this thesis are also reviewed. Chapter 3 describes experimental design, environmental conditions, management, methods and analysis which were common to all four results chapters.

Within this thesis each chapter was designed to meet specific objectives:

Chapter 4 had two main objectives. The first was to quantify DM yield and quality of cocksfoot pastures with different levels of water and nitrogen. The second was to

account for seasonal temperature variation by describing DM production in relation to thermal time when pastures were fully irrigated but differed in the level of N fertility.

In Chapter 5, Objective 3 described the effect of water stress on dryland pasture production. This involved quantifying the critical limiting deficit beyond which DM production was compromised and the associated yield reductions were described. The rate of DM production in dryland and irrigated pastures described using thermal time will then be coupled with the critical limiting deficit to exclude periods of water stress. Objective 4 was to describe patterns of water extraction during known periods of water stress.

In Chapter 6 the fifth objective was to develop a nitrogen nutrition index to describe the effect of N deficiency on DM production and determine the radiation use efficiency of the pastures.

Objective 6 was to identify the mechanisms which compromised DM production when pastures were exposed to water stress and/or N deficiency (Chapter 7). These explanations provide the physiological basis for the empirical descriptions of DM production of pastures which are exposed to multiple stresses in a growth season.

In Chapter 8, Objective 7 was to integrate the relationships which described the effects of temperature, water stress and N deficiency on DM production into a simple multiplicative yield prediction model suitable for a range of environmental conditions. This chapter also discusses the main findings of the research and identifies the ways in which the insight gained can be applied in the future.

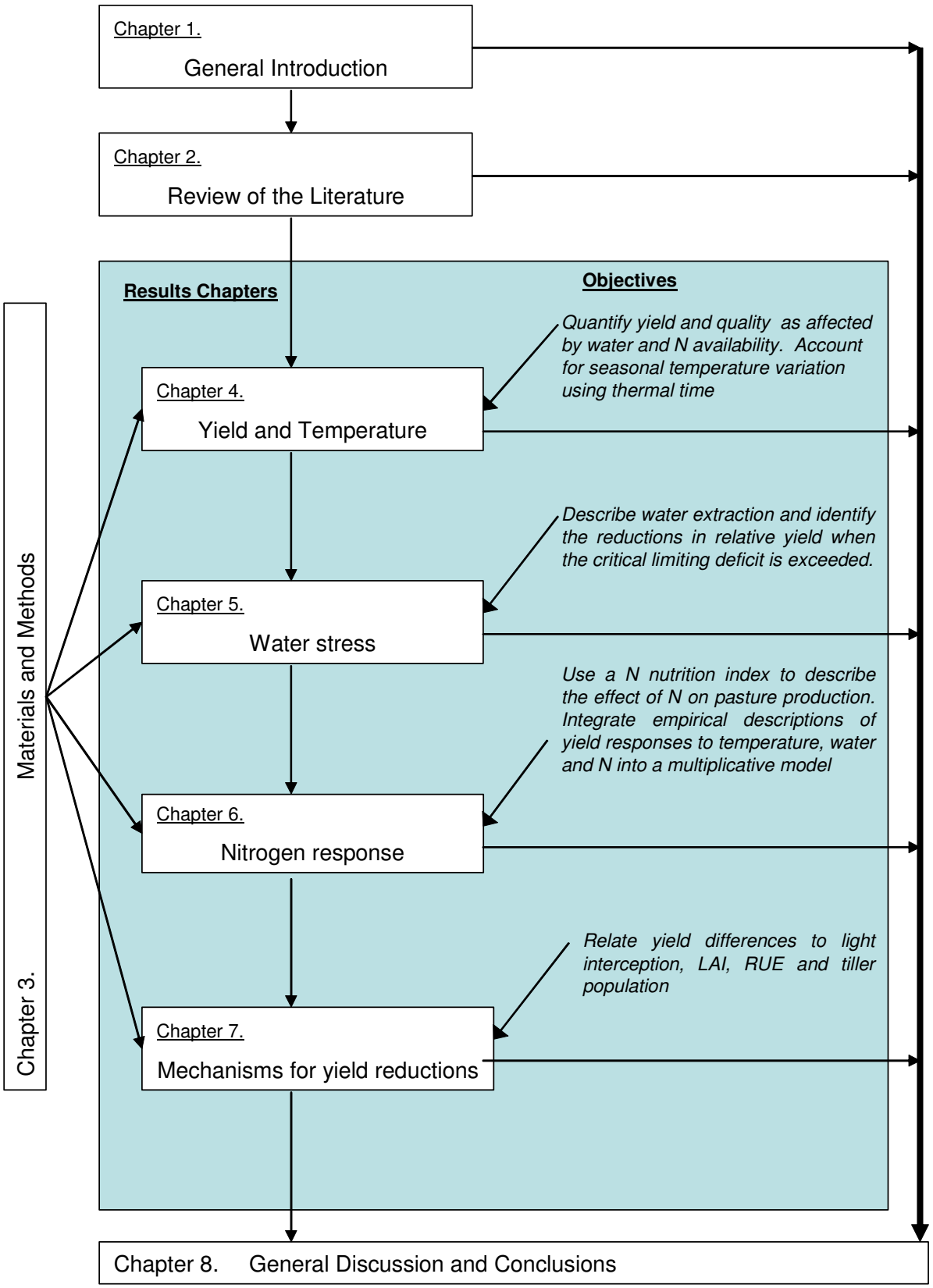

Figure 1.1 Flow diagram of thesis structure.

2 Review of the Literature

Dry matter (DM) production is the product of the amount of light intercepted by a crop/pasture and the efficiency with which that energy is used (Monteith, 1972; Biscoe and Gallagher, 1977; Monteith, 1977). This chapter reviews current literature to describe the effects of temperature, water and nitrogen on pasture production and describes the mechanisms which alter the factors which contribute to yield formation.

2.1 Yield formation

The formation of yield and its components (Equation 2.1) is primarily a function of the radiation environment and a set of environmentally mediated variables. However, responses may alter when the plant experiences stress conditions (Monteith, 1969, 1972; Biscoe and Gallagher, 1977; Monteith, 1977; Hay and Walker, 1989). For example, water stress restricts canopy expansion and reduces the amount of light intercepted by the crop/pasture (Hsiao, 1973; Belaygue *et al.*, 1996; Lecoeur *et al.*, 1996). In contrast, the amount of incident photosynthetically active radiation (PAR) cannot be manipulated and is determined by the location in which the pasture is grown.

Equation 2.1 $$\text{Yield} = R_o * R/R_o * RUE * H$$

Where R_o represents incident PAR, R/R_o is the fraction of PAR intercepted by the canopy, RUE is the radiation use efficiency of conversion of PAR to DM and H represents harvest index as a measure of utilised herbage in the form of grain, fruit or fibre with an economic value. For pastures this parameter is not usually considered because all DM is consumed or harvested (Thornley, 1998).

The amount of PAR intercepted by a canopy depends on factors which include cell expansion, leaf appearance rate (LAR), tillering propensity and canopy architecture (Biscoe and Gallagher, 1977; Hay and Walker, 1989). In contrast, RUE (Section 2.7.6) is an indirect measure of net photosynthesis and represents the efficiency with which a pasture uses intercepted light energy to produce DM (Monteith, 1972, 1977; Sinclair and Muchow, 1999b). This is strongly related to the N status of the pasture (Section 2.7) because over 50% of soluble plant N is directly associated with formation of the photosynthetic system (Sinclair and Horie, 1989). In particular, N is essential in the formation of proteins, nucleic acids, chlorophyll and Ribulose 1,5 biphosphate

carboxylase (Rubisco) (Novoa and Loomis, 1981). Rubisco alone accounts for up to 50% of the soluble protein in leaves of C3 plants (Schmitt and Edwards, 1981).

2.2 Potential yield (PY)

To determine the extent of yield reductions caused by any one factor it is essential to determine the potential yield when no factor is limiting. All crop and pasture species have the potential to produce a theoretical maximum yield when grown under optimum conditions (Alberda, 1962; Robson, 1981). This maximum potential yield (PY) is dependent on the environment in which the plants are grown (Mitchell, 1963; Monteith, 1972). Management decisions such as regrowth duration and environmental factors such as temperature, soil moisture, nitrogen and solar radiation are the main drivers (Thornley, 1998) behind differences in PY between seasons, years and environments.

The factors which control yield can then be altered sequentially to examine how each affects yield. By relating these factors to PY, environmental variables evaluated within one environment can be extrapolated to different environments. The potential for interactions among these variables additionally complicates understanding of the system. Therefore, when yield reductions occur variables must be quantified or the conclusions made may inaccurately identify the mechanism responsible (Jamieson *et al.*, 1998a) and empirical descriptions may not hold when applied to environments other than where they were developed.

2.2.1 Predicting the effects of environment and management on yield

Simulation models used to predict pasture production have a general form as shown in Equation 2.2 (McKenzie *et al.*, 1999). This relationship shows that yield is mainly a function of temperature (f(T)), soil moisture (f(W)), soil fertility (f(N)) and reproductive status (f(R)). The maximum growth rate (GR_{max}) or PY is required and then altered dependent on the expected responses to environmental variables by the functions. These vary between 0 and 1.0 where value of 1.0 means the factor does not limit growth. Values then decrease depending on the level of stress/deficiency. Any factor which returns a value of zero indicates that the extent of the deficiency/stress is sufficient to result in zero growth and the multiplicative nature of the functions then nullifies non limiting conditions in any other factor. In most cases, where irrigation is unavailable, the only factor which the farmer can alter is soil fertility.

Equation 2.2 $$GrowthRate = GR_{\max} * \int(T) * \int(W) * \int(N) * \int(R)$$

Therefore, if PY or GR_{max} are unknown it is impossible to determine the extent of yield reductions when the pasture/crop is exposed to a critical limiting factor. Unfortunately often published data, although agronomically or physiologically valuable, are insufficient to provide these parameters. For example, Rickard (1972) and Hayman and McBride (1984) did not explore the physiological basis of yield reductions caused by water stress. In this study, PY will be determined with non limiting water and N status (Sections 0, 4.3.1 and 4.4.1). Measurements of tiller population, light interception and leaf area index (LAI) will then allow the mechanism for any yield reductions to be identified and quantified. This will provide a physiological basis for the empirical descriptions.

Models have both theoretical and practical applications (Thornley, 1998) and can increase understanding of the mechanism involved or help to determine potential risk levels involved with on farm management decision-making. In this study, the growth rate will be described in thermal time to summarise the effects of temperature on growth processes. By combining GR_{max} and the temperature function (Equation 2.2) only one value is required. This value can be applied to any environment with a similar radiation environment and used as the basis of a yield prediction model which accounts for reductions in PY due to water stress or N deficiency.

2.3 Cocksfoot (*Dactylis glomerata*) use and yields in NZ

Cocksfoot (Figure 2.1) is a major pasture grass used in dryland pastoral environments in New Zealand. It is recommended for use in both flat dryland and hill country systems because of its moderate fertility requirement, persistence and drought tolerance (Kemp *et al.*, 1999; Charlton and Stewart, 2000). Further, animal health problems associated with perennial ryegrass (Fletcher *et al.*, 1999) are avoided because no harmful alkaloids are produced.

Floral initiation occurs when plants perceive a change from short to long days (Broue, 1973), measured by changes in the red: far red ratio, and cocksfoot is classified as a long day plant. There is usually a decline in growth rate at the time of maximum seedhead production regardless of the management strategies employed to minimise seedhead production. This is caused by a reduction in the number of vegetative tillers

present and indicates a change in partitioning priority associated with seed formation (Radcliffe and Baars, 1987).

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Figure 2.1 Generalised structure of a cocksfoot plant (Penn State University, 2006).

Stephens and Hickey (2000) reported peak production from a cocksfoot pasture occurred four years after establishment but measurements ceased after the fourth year. Seasonal production is generally lower than ryegrass in spring but this is offset by increased production in summer and autumn (Kemp *et al.*, 1999). In Canterbury, total annual DM production of dryland cocksfoot was 7.6 t DM/ha compared with 4.9 t DM/ha from ryegrass pastures (Stevens *et al.*, 1992). The difference in annual yield occurred because cocksfoot produced 131% more DM than ryegrass in summer and

74% more DM in autumn. In contrast, under non limiting conditions in Canterbury, a 10 year old cocksfoot dominant pasture was shown to produce a potential maximum yield of 28.6 t DM/ha/y (Peri *et al.*, 2002a).

2.3.1 Root growth and distribution

Cocksfoot roots form a dense fibrous mat in the top 0.25 m of the profile (Weaver, 1926; Ridley and Simpson, 1994). In New Zealand, Evans (1978) measured 16.0 m of cocksfoot roots in the top 0.20 m of the soil compared with 3.3 m in ryegrass or white clover treatments. The production of a more extensive root system increases the surface area for water and nutrient uptake. The small root system of white clover may be a major contributing factor to reduced production and persistence when sown in mixtures with cocksfoot (Lee and Cho, 1985). Both ryegrass and cocksfoot have been shown to extract water from similar soil depths (Evans, 1978). Therefore, the superior persistence and recovery of cocksfoot subjected to water stress may reflect differences between the species in i) the ability to access and extract soil moisture: ii) water use efficiency and/or iii) the mechanism used to recover from drought.

2.3.2 Pasture quality

Cocksfoot is considered to have low palatability (Charlton and Belgrave, 1992; Moloney, 1993; Moloney *et al.*, 1993; Charlton and Stewart, 2000; Peri, 2002). This reduces animal production because of reduced voluntary intake. However, it has been shown that crude protein (CP) content of the herbage on offer can influence grazing preference (Edwards *et al.*, 1993). They showed that when cocksfoot herbage had 5.1% N grazing preference by sheep was similar to five other grass species. Crude protein is calculated as N% x 6.25 (Nicol, 1987) so it is directly related to the N content of the herbage. In Canterbury, Peri *et al.* (2002b) showed cocksfoot pastures were nitrogen deficient throughout the year. In spring, CP was 27.0% in pastures fertilised with N compared with 18.7% in –N pastures. However, the efficiency of seasonal DM responses to N (kg DM/kg N applied) differed in magnitude. This was caused by increased DM production in +N pastures, which diluted the applied N (Section 2.7.3).

Nitrogen fixation by legumes is important in the success of pastoral agriculture in New Zealand. Legumes provide high quality feed and transfer N to the companion grass through urine or decomposition of root and shoot material (Haynes, 1980). Thus, maintenance of a high proportion of clover in the pasture will enhance pasture quality.

In mixed species pastures CP has been positively correlated with white clover content (Fraser and Kunelius, 1995). However, cocksfoot based pastures tend to become grass dominant over time. For example, Stevens *et al.* (1992) reported white clover content decreased from 19% in the first year to 4% in cocksfoot and 11% in ryegrass in the second year. Similarly, Lee and Cho (1985) reported cocksfoot was the most competitive grass sown in pasture mixes with white clover. Morhac *et al.* (1990) reported cocksfoot was the only species that persisted and remained productive beyond year eight but productivity of mixtures sown with white clover declined over time because of a decrease in clover content.

Mathieu and Besnard (1983) found cocksfoot based mixtures produced similar yields to grass monocultures only when >150 kg N/ha was applied. Peri *et al.* (2002b) hypothesised that there was potential to alleviate N deficiency in cocksfoot pastures by sowing an alternative legume with cocksfoot. Perennial legumes with taproots, which can access moisture from below the main uptake zone for cocksfoot, or winter active annual legumes, which have completed their lifecycle before the main DM production period for cocksfoot, may increase productivity and pasture quality. Both these options suggest cocksfoot yield could be improved by increasing N availability (Peri *et al.*, 2002b).

Metabolisable energy (ME) is also an important measure of pasture nutritive value (Figure 2.2) and represents the digestible energy which remains after losses of N in urine and eruption of methane (Nicol, 1987). Pasture ME usually ranges between 8-12 MJ ME/kg DM (Nicol, 1987) and varies seasonally (Stockdale, 1999). The ME of pastures in late winter/early spring (Figure 2.2) are at the higher end of this range because simple sugars accumulate in the vacuole and temperature limitations restrict movement of sugars to developing organs (Nicol, 1987). Factors which affect ME include botanical composition; leaf stem ratio; disease incidence and seasonal patterns of energy accumulation as affected by changes in solar radiation and temperature (Doyle *et al.*, 2005).

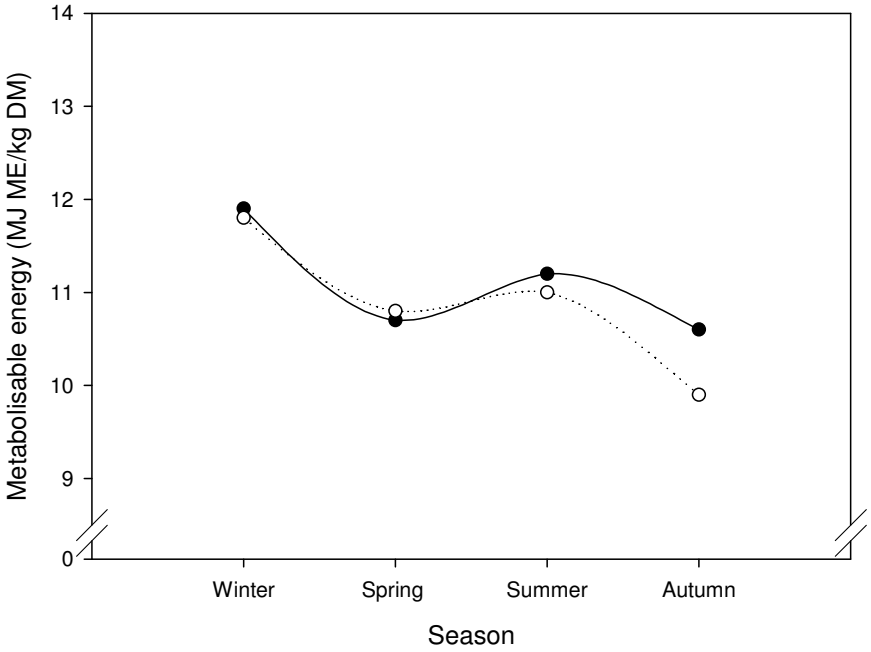

Figure 2.2 Seasonal changes in the metabolisable energy content (MJ ME/kg DM) of lamina (●) and pseudostem (○) of irrigated ryegrass (Stockdale, 1999).

2.4 Effects of temperature

Pasture growth rates vary in temperate environments because of seasonal variation in temperature, soil water and nutrient availability, pests and diseases and solar radiation receipts (Monteith, 1972; Biscoe and Gallagher, 1977). Interpretation may be further complicated by seasonal or stress induced changes in partitioning between roots and shoots (Caradus and Evans, 1977; Ridley and Simpson, 1994) which are not usually measured in the field. After canopy closure, solar radiation receipts will be the main factor responsible for DM production but prior to canopy closure, temperature will affect the rate at which the canopy expands (Radcliffe and Baars, 1987). At Winchmore, in Canterbury, mean daily growth rate (Figure 2.3) of an irrigated ryegrass based pasture was 5 kg DM/ha/d in winter and 49 kg DM/ha/d in summer. Baars and Waller (1979) concluded that regrowth of ryegrass pastures following defoliation was strongly correlated with management and temperature. Early work showed that soluble carbohydrate levels of leaves which were still in the expansion phase after defoliation (i.e. they had not fully emerged from the leaf sheath) affected canopy expansion and initial growth rates (Davidson and Milthorp, 1966). However, in the field this probably

reflects higher N content in rapidly differentiating tissue at the base of the expanding leaf (Gastal and Nelson, 1994).

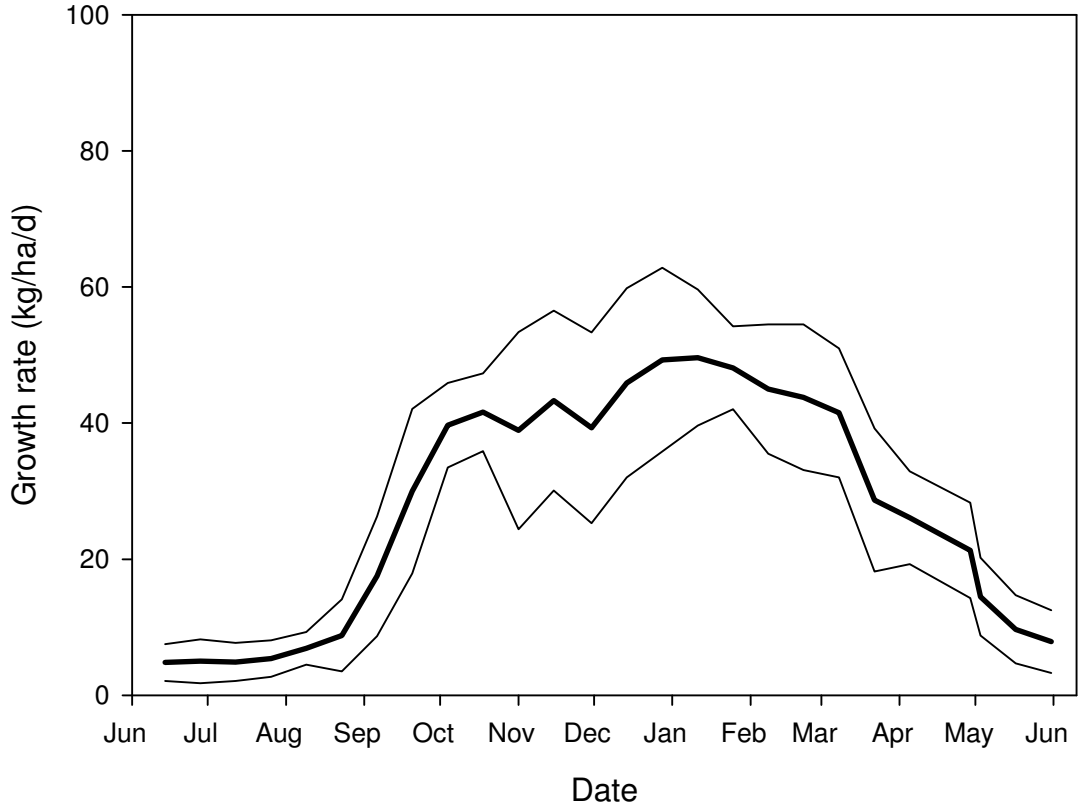

Figure 2.3 Mean daily growth rates of an irrigated ryegrass based pasture at Winchmore, Canterbury. Data are 13 year average ± standard errors. Redrawn from Rickard and Radcliffe (1976).

The temperature effect represents optima and minima for the different biochemical and photochemical processes within the plant. The response observed may be the additive result of the various processes, particularly enzyme activity, which have different temperature requirements (Falk *et al.*, 1996). Two of the most important processes affected by temperature are i) the rate of photosynthesis which influences RUE (Biscoe and Gallagher, 1977) and ii) leaf appearance rate which affects light interception.

2.4.1 Photosynthesis responses to temperature

Woledge and Dennis (1982) reported the photosynthetic rate of ryegrass and white clover at 15ºC was double the rate measured at 5ºC. Both species had similar photosynthesis rates and responded similarly to temperature. Therefore, intercepted light was not utilised as efficiently at temperatures outside the optimum and yield was

below potential (Brown, 1995). Additionally, photosynthesis declines as leaf age increases and is less efficient when leaf appearance rate declines (Woledge, 1979).

At sub optimal temperatures, photosynthetic rate is reduced. In field grown cocksfoot, Peri *et al.* (2002b) showed leaf photosynthesis was optimum between 19-23°C. This was comparable to the 20-22°C optimum range reported in controlled environments (Mitchell and Lunacus, 1962; Eagles, 1967). Peri *et al.* (2002b) reported every 1°C drop below 19°C caused the rate of photosynthesis to decline by 6% from the maximum of 27.4 μmol $CO_2/m^2/s$. When temperatures exceeded 23°C, photosynthesis also declined but at a rate of 8%/^{o}C. Stomatal resistance was not associated with reductions in photosynthesis which supported the conclusions of Nie *et al.* (1992). Decreases in photosynthesis at temperatures below optimum were hypothesised to be caused by changes at the chloroplast level probably associated with a decline in enzyme activity which catalyses reactions (Falk *et al.*, 1996).

2.4.2 Leaf development and appearance

In grasses and cereals leaf appearance rate (LAR) is a function of cell division and expansion processes and represents emergence of mature leaf cells from within the pseudostem. These are pushed out by expansion of younger leaf cells closer to the apical meristem. Expansion processes continue after emergence from the leaf sheath, but at a slower rate than prior to leaf emergence, until final cell size is achieved (Hay and Walker, 1989).

MacAdam *et al.* (1989) showed that leaf expansion in tall fescue (*Festuca arundinacea*), was a function of epidermal cell elongation which was synchronised with mesophyll division. Nitrogen increased leaf extension rates because of increased cell differentiation (Section 2.7). Durand *et al.* (1999) reported the maximum leaf extension rate of tall fescue was increased by temperature. At 24°C leaf extension of leaves 1 and 2 was 60-75% faster than at 14°C. At 24°C leaf extension of leaves 3 and 4 was more than double that measured at 14°C. This probably represented the time required for cells to cross the elongation zone and attain their maximum size as shown previously for cereals (Ben-Haj-Salah and Tardieu, 1995). In addition, division and expansion processes appeared to be synchronised with the position of the cell in the elongation zone rather than cell age (Ben-Haj-Salah and Tardieu, 1995).

2.4.3 Accounting for variation in daily temperature

Thermal time (Tt) is widely used to standardise rates of leaf appearance and describe development, germination and emergence requirements for a range of crops including cereals, grain legumes, brassicas (*Brassica* spp.) and pasture species (Baars and Waller, 1979; Lopez-Castaneda and Richards, 1994; Atkinson and Porter, 1996; Wilson and Robson, 1996; Wu *et al.*, 1997; Collie and McKenzie, 1998; Jamieson *et al.*, 1998b; Olivier and Annandale, 1998; Jame *et al.*, 1999; Moot *et al.*, 2000; de Ruiter, 2001). This method of describing phenology and developmental status of the plant allows extrapolation of results to other environments and is often used in simulation models, particularly to predict canopy development and crop maturity. In this study, Tt will be calculated (Equation 2.3) with the method described by Jones and Kiniry (1986). Temperature is interpolated into eight 3-hour intervals to account for diurnal temperature fluctuations throughout a day.

Equation 2.3

$$\mathbf{Tt_{daily} = t_{range\_fract} * diurnal\ range}$$

$$\mathbf{T_{range\_fract} = 0.92 + 0.0114 * P - 0.07 * P^2 + 0.005 * P^3}$$

$$\mathbf{Diurnal\ range = T_{max} - T_{min}}$$

Where P is the period (1-8) for each interval during the day and the sum of P 1-8 gives daily Tt (Tt_{daily}). These are then summed to determine accumulated Tt for a known regrowth cycle.

2.4.4 Using thermal time (Tt) to describe growth and development

Leaf appearance rate is generally constant in thermal time (Tt) so as temperature declines it takes longer to accumulate the Tt necessary to meet phyllochron and plastochron requirements (Hay and Walker, 1989). These Tt requirements accumulate above a base temperature (T_b) which is species specific. The consistency of this relationship is a result of the coordination of processes, which include leaf initiation and elongation (Skinner and Nelson, 1994).

Species differ in plastochron and phyllochron requirements for leaf initiation and emergence due to two main factors. These are either i) a difference in T_b or ii) different phyllochron values. For example, both white and Caucasian (*T. ambiguum*) clovers have similar phyllochrons but white clover has a T_b of 1°C and Caucasian clover has a T_b of 5°C (Black *et al.*, 2003). Therefore, leaf appearance is slower for Caucasian clover because it takes longer to accumulate the required Tt (Black *et al.*, 2003). This causes

differences in canopy development and the amount of light intercepted by the canopy particularly during establishment or following defoliation.

In a temperate environment where the optimum temperature (T_{opt}) is seldom exceeded, relationships described with Tt will show more systematic variation if an incorrect T_b is used (Bonhomme, 2000). To ensure the appropriate T_b for a temperate C3 species is used, Tt is iteratively accumulated above a range of T_b from 0-10°C. The T_b which results in the lowest coefficient of variation (CV%) across the range indicates the most appropriate base temperature (Draper and Smith, 1998). Secondly, the regression of the relationship between temperature and Tt is calculated. The combination of both criteria allows the appropriate T_b to be identified.

Thermal time can also be used to summarise growth processes (de Ruiter, 2001). Spring growth of tall fescue and cocksfoot has been described previously in relation to Tt accumulation (Lemaire and Salette, 1982). Relationships for vegetative and reproductive growth were calculated. However, the switch between vegetative and reproductive phases was made when seedheads were visible and would not account for changes in partitioning which occur when plants perceive a change in daylength (Section 2.3). Subsequently, Lemaire *et al.* (1982) showed predictions of tall fescue production during this period were improved using a heliothermic index. This did not improve predictions for cocksfoot pastures. The authors concluded that Tt alone provided an inaccurate summary of growth because it did not account for changes in LAR, expansion, tiller production and senescence across years. In this study, growth will be summarised with Tt, but measurements will be made on an established cocksfoot pasture for a two year period. This may help identify limitations of this approach.

Accumulated Tt has also been applied as a predictive tool in New Zealand. Using a T_b of 4°C, Hutchinson *et al.* (2000) successfully described long-term (1950-1961) DM production (Radcliffe, 1974) of a mixed species pasture. However, this did not account for seasonal rainfall distribution and associated periods of water stress. In the field, factors other than temperature influence the rate of DM production. Unfortunately, the relationships presented in the literature often exclude periods when either water or N are the main constraints to pasture production. This study will describe and explain the effect of these factors in reducing DM yield. Unifying relationships for temperature, water stress (Section 2.6) and N deficiency (Section 2.7) will be combined to develop a

yield prediction model for field grown cocksfoot pastures suitable for a range of conditions. This will allow a more accurate description of DM production typical in dryland pastoral systems.

2.5 Physiological Responses to Water Stress

Limited water availability is often the most critical limiting factor affecting plant growth and survival (Hsiao, 1973). Plant processes vary in the level of sensitivity to deficit development and the time scale over which plant characteristics and processes are affected (Sinha, 1987; Brown, 1995). Responses to water stress vary among species and between environments but initiation of strategies to reduce water loss inevitably lead to reductions in yield and productivity due to the balance between water supply and plant demand (Jamieson, 1999).

In the field soil moisture deficits (SMD) develop gradually and the extent, frequency and severity of water stress determine the response initiated (Hsiao, 1973; Brown, 1995; Jamieson, 1999). In dryland pastures differences in the quantity and distribution of rainfall and soil type can result in large annual yield differences. In Canterbury, dryland ryegrass based pastures produced 3.1-13.0 t DM/ha/y. Annual yield was lowest on shallow stony soils and highest on deep free draining soils (Hayman, 1984; Hayman and McBride, 1984). A secondary effect of moisture stress can be reduced N availability because the majority of soil N is held in the topsoil, once the uppermost layer of the profile dries N deficiency may be observed even if adequate water is extracted from lower in the soil profile (Garwood and Williams, 1967).

In summer, on a given day, an unstressed crop can transpire >5 mm of soil moisture which may be 1-10 times greater than the water held in plant tissues (Hsiao, 1973; Jamieson, 1986; Brown, 1995; McKenzie *et al.*, 1999). Johns (1978) reported soil evaporation and crop transpiration by a pasture accounted for 3% and 97% of water used, respectively. However, this depends on transpiration demand, which is determined by LAI prior to full canopy closure. Premature leaf senescence in response to water stress may reduce transpiration demand after critical LAI (95% interception). For example, after being exposed to drought for 26 d green foliage cover decreased by 24% and by 50% for ryegrass and white clover, respectively (Johns, 1978).

2.5.1 Leaf and canopy expansion are affected by water stress

A comprehensive understanding of the physiological basis of the yield reductions due to water stress is necessary to determine the mechanism causing yield reductions. After canopy closure, DM production is a result of the quantity of PAR intercepted and RUE (Sections 2.5.3 and 2.7.6). These two factors are modified by physiological responses to water deficits. Initially, effects of water stress on cell expansion and division will have a greater effect on DM production than changes in RUE (Hsiao, 1973). Under mild water stress reduced leaf water potential causes a progressive decline in cell turgor pressure. Cell expansion is reduced causing the formation of smaller leaves (Hsiao, 1973; Dale, 1988; Hay and Walker, 1989) and less light is intercepted if LAI is below critical (95% interception) (Johns, 1978) .

In ryegrass, water stress inhibited tiller production, enhanced tiller death and reduced leaf appearance and extension rates (Baker *et al.*, 1985). In Manawatu, Korte and Chu (1983) reported that reduced DM production by water stressed ryegrass pastures was initially caused by a decrease in individual tiller weight but, as the duration of the stress period increased, reductions in tiller weight and tiller density caused an 86% reduction in yield compared with unstressed controls. Norris (1982) showed when the potential soil moisture deficit (PSMD) was >100 mm that the growth rate of water stressed ryegrass plants was 1.4 g m^2/d compared to 4.0 g m^2/d when irrigated to maintain the PSMD at <50 mm. In contrast, under the same conditions irrigated cocksfoot produced 4.0 g m^2/d compared with 3.0 g m^2/d when water stressed. The leaf extension rate of both species declined by 40% compared with irrigated plants but dryland cocksfoot had 19.2 tillers/plant compared with ryegrass which had 9.6 tillers/plant. Therefore, cocksfoot probably intercepted more PAR than ryegrass under dryland conditions. Unfortunately direct measurements of the soil moisture deficit were not made and differences between the extent of stress the plants were exposed to were not quantified. This may be important because Evans (1978) measured almost 400% more roots than ryegrass in the top 0.2 m soil layer which would indicate a potentially greater surface area for root water uptake.

In ryegrass, the main factor affecting the rate of tiller production, under water stress, was a reduction in leaf appearance rate (Van Loo, 1992) of mother tillers because tiller buds were in direct competition with expanding leaves for substrates (Marshall, 1987). Reduced LAR by mother tillers was probably caused by reduced cell expansion which

reduced the rate at which mature leaf cells emerged from the pseudostem. In addition to smaller individual cell size, reductions in tiller production and premature leaf senescence can limit water loss and increase plant survival under drought conditions (Burch and Johns, 1978; Norris, 1982). Thus, all three factors can limit canopy expansion.

Reductions in canopy expansion rate or increased rates of leaf senescence also reduces the area available for gas exchange (Johns, 1978). In a pot experiment, Burch and Johns (1978) reported the LAI of white clover decreased from 2.0 to 0.8 after drought was imposed for 18 d. Johns (1978) showed that withholding water for 28 d caused white clover LAI to decrease from 1.5 at a relative water content (measured at midday) of ~90% to 0.5 when relative water content was ~55% while ryegrass LAI declined from 1.4 to 0.8 at a relative water content of about 65% after 28 d. A decline in canopy expansion and increased rates of leaf senescence were the main cause of reduced canopy photosynthesis rather than reduced radiation use efficiency.

2.5.2 Renewal of growth processes after drought

Under prolonged water stress, pasture species have different mechanisms to ensure survival. For example, cocksfoot survival after drought induced summer dormancy resulted from the production of new leaves from previously sterile buds formed in the previous season (Knight, 1965). In contrast, tall fescue recovery depended on the level of endophyte infection and tiller density (West *et al.*, 1993). Barker *et al.* (1985) showed after drought conditions were alleviated, compensatory growth from previously water stressed ryegrass pastures resulted in higher yields than from fully irrigated pastures. This was similar to the results reported by both Horst and Nelson (1979) and Korte and Chu (1983).

In tall fescue, the compensatory production was a result of expansion of cells formed during mild stress which were then able to complete expansion (Durand *et al.*, 1995). Cell division is less sensitive to water stress than cell expansion (Hsiao, 1973) so there may be a number of unexpanded cells which can continue expansion when water stress is alleviated. Similarly, in dicot species, the ability of cell expansion to continue depended on whether the cells were primarily experiencing division or expansion when water stress was imposed (Alves and Setter, 2004). As a result, yields of previously

water stressed plants may exceed that of their irrigated controls upon re-watering due to faster canopy regeneration.

In the absence of water stress cocksfoot tiller production was suppressed at LAI >3.0 (Simon and Lemaire, 1987). This is because of reductions in the red: far red ratio perceived at the tiller bases. However, if the rate of tiller production equals the rate of tiller senescence changes in tiller population may not be observed (Sanderson and Elwinger, 2002). After defoliation, tiller production may be stimulated as the amount of red light at the base of the sward increases due to the removal of leaf area (Sanderson *et al.*, 1997; Sanderson and Elwinger, 2002) and this may also occur on completion of the reproductive phase.

2.5.3 Canopy expansion measurements in pastures

Light interception and canopy development data provide information for estimating DM production because PAR provides the energy to drive photosynthesis. When any factor (water stress, defoliation, disease, nitrogen) compromises canopy expansion yield is reduced (Hay and Walker, 1989). After canopy closure, if no factor is limiting, energy availability should not limit photosynthesis (Hay and Walker, 1989).

Although non destructive measurements of light interception can be made easily (DELTA-T Devices Ltd., 1999; Wilhelm *et al.*, 2000), practical application in pastures is problematic and comparisons are often confounded by differences in methodology (Faurie *et al.*, 1996; Castro and Fetcher, 1999; Nouvellon *et al.*, 2000; Sinoquet *et al.*, 2000). In addition, there is no differentiation between light intercepted by green and non green pasture components (DELTA-T Devices Ltd., 1999; Wilhelm *et al.*, 2000). In this study, LAI was measured from destructive harvests and used to calibrate non destructive *in situ* measurements (Section 7.2.1). This will overcome problems which occur when the inbuilt calculations fail to match canopy reality. In addition, non destructive measurements will account for interception by residual biomass.

2.5.4 Photosynthesis inhibition due to water stress

As the extent and duration of the water stress period increases, photosynthesis is also inhibited (Hsiao, 1973; Brown, 1995). When stomata close to minimise evaporative water loss, CO_2 assimilation declines because both processes share much of the same pathway through leaf cavities (Jamieson, 1986, 1999). Stomatal movement in response

to water stress is the main mechanism that regulates transpiration losses, especially after canopy closure. Basically, plant water loss is reduced because stomata close when soil water supply is incapable of meeting demand. Gas exchange is reduced as CO_2 cannot enter the leaf, O_2 cannot escape and photorespiration increases due to reduced CO_2 concentrations within the leaf.

This reduces gross photosynthesis as carbon fixed by the Calvin cycle is consumed during photorespiration and no ATP is generated (Monteith, 1972; Campbell, 1996) and DM production is reduced or ceases (Hsiao, 1973; Johns, 1978). Evaporative cooling is reduced and the heat load experienced by the plant increases (Hay and Walker, 1989; MacFarlane, 1990) which causes maintenance respiration to increase (Section 2.7.6). In addition, reduced N uptake as the soil dries can cause N deficiency (Stark and Firestone, 1995). Reductions in nitrate reductase activity are mirrored by an increase in the breakdown of chloroplast proteins within the plant. When exposed to prolonged drought the breakdown of these proteins can decrease photosynthesis by limiting the amount of photosynthetic enzymes present (Cornic and Massacci, 1996).

In the field, photosynthesis by an established cocksfoot sward was not limited by soil moisture when predawn leaf water potential was -0.1 – 1.2 bar (Peri *et al.*, 2002b). This was equivalent to soil volumetric water content (VWC) of 27-30% in the 0-0.5 m soil layer. Beyond this, the rate of photosynthesis declined from the maximum rate of 27.4 μmol $CO_2/m^2/s$ at a rate of 8%/mm down to -14.0 bar. Between -14.0 and -16.0 bar, a constant negative rate of photosynthesis occurred which indicated respiration exceeded carbon gain (Peri *et al.*, 2002b).

2.6 Describing water extraction and use

Empirical descriptions (Equation 2.4) have been used to determine the extent of yield reductions due to water stress. Subsequently, yield predictions can be made (Equation 2.5) using PY and the measured yield (Y) of the stressed crop (McAneney *et al.*, 1982). This approach does not explain why yield reductions occur, it simply generates a stress factor based on the relationship created between actual evapotranspiration (AET) and potential evapotranspiration (PET).

Equation 2.4 $$\frac{Y}{PY} = \frac{AET}{PET}$$

Equation 2.5 $PY = Y * (AET / PET)$

More recently, macroscopic mechanistic approaches have been developed to describe the movement of water between soil and plants. However, they tend to focus on either the plant or the soil and as such there is little information relating the functional relationship between the two because of narrow disciplinary boundaries (Hopmans and Bristow, 2002). As a result empirical descriptions are usually used to describe the boundaries between soil-plant and plant-atmosphere. These relationships are not well understood and the empirical descriptions further complicate understanding due to a poor biological and physiological basis. Although empirical descriptions may be suitable for non-stressed conditions they may fail when resources become limiting (Hopmans and Bristow, 2002).

2.6.1 Measurement of soil water content (SWC)

Non-destructive measurements of soil water content are made with a neutron probe and results are then converted to mm of water stored in a given layer (0.1 or 0.2 m slices) of the soil. The probe must be calibrated for different soil types to reduce the noise from elements other than hydrogen. It is also unsuitable for taking measurements in the top 0.2 m because of neutron leakage from the soil surface. Thus, time domain reflectometry (TDR) can be used to determine volumetric water content in the top 0.2 m of the soil. Soil type affects the proportion of total soil moisture available for plant use and this must be quantified by determining the upper and lower limits (Section 2.6.4) of each slice of the profile (Ghildyal and Tripathi, 1987; Jury *et al.*, 1991).

2.6.2 Describing changes in soil water content and water extraction patterns during growth

Passioura (1983) showed the relationship between roots and the yield of water-limited crops could be analysed using Equation 2.6. Here the quantity of water used (WU in mm) is multiplied by the water use efficiency (WUE in kg DM/mm) of the crop (Tanner and Sinclair, 1983). However, the success of this method depends on whether WU is based on transpiration, AET or PET.

Equation 2.6 **DM yield = WU*WUE**

When precipitation inputs from rainfall (R) and/or irrigation (I) are insufficient to replace water depleted from the profile soil moisture deficits develop (Penman, 1971). Initially, the changes in soil moisture content are a result of the crop water and energy balance. The water balance (Equation 2.7) shows the change in soil water content (ΔSWC) depends on the balance between evapotranspiration (ET) losses and precipitation from rainfall and irrigation (P_{R+I}).

Equation 2.7 $\Delta SWC = P_{R+I} - ET$

Both rainfall and irrigation are easily measured but ET values depend on complex relationships between weather, surface and soil factors (French and Legg, 1979). These are described by Equation 2.8, where PET is potential evapotranspiration (mm); Δ is the slope of saturation water vapour pressure against temperature (mb/K) at a known air temperature; γ is the psychometric constant (mb/K), H is the net radiation ($J/m^2/d$); *p* is the density of water (kg/m^3) and λ is the latent heat of vaporisation (J/kg) at a given air temperature (French and Legg, 1979).

Equation 2.8 $$PET = \frac{1000\Delta H / p\lambda + \gamma + E_a}{\Delta + \gamma}$$

When water is non-limiting for growth, soil moisture deficits calculated by this method are reasonably accurate (French and Legg, 1979). However, when plants are exposed to water stress most of the assumptions used to calculate the extent of the soil moisture deficit may be violated. This will cause PET to overestimate AET in water stressed crops (Tanner and Sinclair, 1983) because PET is purely a measure of atmospherically driven demand (French and Legg, 1979; Moir *et al.*, 2000; Hopmans and Bristow, 2002).

Garwood and Sinclair (1979) showed, for a range of pastures, PET prior to harvest was 2.9 mm/d which overestimated AET by 21%. After the harvest PET was 3.5 mm/d compared with AET of 0.8 mm/d. Because PET does not account for differences in the total available waterholding capacity of the soil (TAWC) or plant demand, soil moisture deficits calculated using PET will continue to increase until rain or irrigation is applied whereas AET will increase and then plateau when growth slows/ceases because there is i) low demand and/or ii) insufficient plant available water for growth to continue (French and Legg, 1979; Moir *et al.*, 2000; Hopmans and Bristow, 2002).

2.6.3 The Monteith Framework

Monteith (1986) proposed a framework for analysing the effects of water extraction on crop yields based on the relationship between SWC and time (t) as initially proposed by Passioura (1983) which describes the exponential pattern of water extraction within a given soil layer. The ET component of Equation 2.7 is the minimum of demand, set by available energy, or supply, set by soil and root factors (Jamieson, 1999). Therefore, in the supply-limited phase, which characterises much of dryland pastoral production, daily changes in the maximum supply rate are determined by the amount of water in the soil and an uptake coefficient that is determined by soil factors and root length density (Jamieson and Ewert, 1999). These last two can be combined into a single coefficient designated kl where 'k' is a diffusion constant and 'l' represents root length density. As a result, in the supply limited phase (Equation 2.9), the change in SWC in any one day can be described.

Equation 2.9 $\Delta SWC = kl*(SWC_i - LL)$

Where LL is the drained lower limit to extraction also referred to as the permanent wilting point (Section 2.6.4), and SWC_i is the soil moisture content at the beginning of the day. As SWC_i declines, the ΔSWC also reduces on a daily basis. Therefore, extraction of soil moisture within a given soil layer declines exponentially after roots begin extraction. This is because it becomes more difficult for plants to extract water as the soil dries (Passioura, 1983; McLaren and Cameron, 1996). Integration of Equation 2.10 gives the time course of soil moisture extraction through a period with no precipitation.

Equation 2.10 $SWC = SWC_i*\exp(-kl*(t - t_c))$

Where t_c is the time (d) that supply limitations started, and SWC_i is the SWC on that day. The generalised pattern of extraction (Figure 2.4) shows a stable SWC when water demand is below supply. The other soil property of interest is DUL, the value of SWC when drainage has just ceased, because the difference between this and the drained lower limit (LL) defines the plant available waterholding capacity (PAWC) of any given soil layer.

Figure removed for copyright compliance

Figure 2.4 An example of the change in soil water content in a particular soil layer, and fitted curve. The arrow indicates the time (tc) when roots begin water extraction (Thomas *et al.*, 1995).

2.6.4 Drained Upper and Lower Limits to soil water extraction

The drained upper limit (DUL) and lower limit (LL) of each slice of the soil profile (Figure 2.5) allow the soil to be described in terms of water holding and storage capacity. The DUL (or field capacity) occurs when drainage to lower levels slows to 1 mm/d after a saturation event and differs between soil layers and soil types because of textural differences (Reid *et al.*, 1984). The LL (or permanent wilting point) is found when plants are observed to be visibly stressed by drought or when no further water has been extracted (Passioura, 1983). After the soil profile is split into predefined layers and DUL and LL are identified the 'Monteith framework' (Monteith, 1986) can be applied.

Figure removed for copyright compliance

Figure 2.5 Mean maximum (■) and minimum (□) soil water contents observed at each measured soil depth, averaged over dryland treatments at six rates of N. Bars are standard errors. Full lines (-) correspond to laboratory water contents determined at water potential of -0.05 and 0.50 MP, respectively (Singh *et al.*, 1998).

2.6.5 The root system and maximum depth of water extraction

The depth and density of the root system determines the volume of soil that can be exploited for water. This represents the 'l' component of Equation 2.9 and causes differences in PAWC between species and soil type (Ghildyal and Tripathi, 1987; Jury *et al.*, 1991). The permeability of root surfaces and root axil resistances may also impede the ability of the plant to extract water (Passioura, 1983).

Garwood and Sinclair (1979) reported dryland cocksfoot pastures had 50% more roots in the top 0.1 m of the profile than irrigated cocksfoot but total root length density was 13% less than that of dryland ryegrass (0-0.6 m). Relative to dryland ryegrass which produced 2.3 t DM/ha, cocksfoot produced 15% less DM (Garwood *et al.*, 1979) but had 35% less total root biomass (Garwood and Sinclair, 1979). The soil was a sandy loam of 0.8 m depth above parent material at Hurley, and stand age at the time of measurement was 2 years. In contrast, Evans (1978) reported ryegrass had 15% less total root length density than cocksfoot (0-1.4 m). This resulted in the production of 4.9 t DM/ha by ryegrass which was 60% less than the 12.1 t/ha produced over the same period by cocksfoot pastures. The soil was a sandy loam of 4.0 m depth above parent material on a river terrace in Palmerston North, New Zealand and stand age at the time

of root measurements was 8-10 months. Both Garwood and Sinclair (1979) and Evans (1978) reported significant reductions in root length density with increasing soil depth.

This inconsistency between measurements which show cocksfoot has a i) dense, shallow root system or ii) a dense, deep root system has lead to contradictory claims that the success of cocksfoot in dryland systems is due to access to soil moisture at depth or rapid use of rainfall infiltrating the topsoil. However, Weaver (1926) and Ridley and Simpson (1994) support the claim that cocksfoot has a dense, shallow root system (Section 2.3.1). The majority of soil water uptake by most pasture species with adventitious roots occurs from the topsoil even if roots penetrate to greater soil depths. Newman (1969) stated that deeper roots will be important in aiding plant survival even though water uptake from depth is less than from the topsoil.

2.6.6 Extraction Front Velocity (EFV)

Water extraction by an annual crop starts in the uppermost soil layer, indicated by a sudden reduction of water in a given layer, at time t_c (Figure 2.4). Over time extraction from lower layers, at progressively greater t_c, indicates the downward movement of the extraction front. The slope of the linear regression of t_c in different soil depths over time (Figure 2.6) is defined as the EFV (mm/d) (Monteith, 1986; Singh *et al.*, 1998). This semi-mechanistic approach has been widely used to describe water extraction and use for a range of annual crops in different environments (Passioura, 1983; Jones *et al.*, 1986; Robertson *et al.*, 1993b, 1993a; Thomas *et al.*, 1995; Singh *et al.*, 1998). Robertson *et al.* (1993a; 1993b) reported incomplete water extraction at depth was a result of fewer roots and a lack of time to extract water before the crop reached maturity. Root growth within a layer continued until 60-80% of the plant available water was extracted and uptake per unit root length declined. This caused an exponential decline in kl. Singh *et al.* (1998) stated the EFV was decreased by irrigation because water supply from upper layers was sufficient to meet demand.

Figure removed for copyright compliance

Figure 2.6 The change in relative water content at different depths of the soil profile over time. The fitted line represents the logarithm of relative water content (p) plotted against time. A difference in water content corresponding to p = 0.69 is equivalent to 6.9 cm on the apparent depth scale. The diagonal line is the estimated position of the extraction front. Open points precede the apparent onset of extraction (t_c) in a given layer, thus the slope of the line represents the extraction front velocity (EFV) (Singh *et al.*, 1998).

Brown (2004) has shown that an established lucerne stand, grown on a deep (>2 m) Wakanui silt loam soil, had an extraction pattern similar to that found in annual crops. Consequently, root death and regeneration may influence annual EFV patterns by perennial crops or pastures. An established perennial pasture with a developed root system t_c in lower soil layers may show an extraction pattern for the profile which initially represents water demand. This would indicate extraction of water from multiple soil layers due to the balance between demand and the maximum extractable water supply from a given soil layer. Extraction from multiple layers may occur when initial demand exceeds supply from the uppermost soil layer. Currently there are no published data relating to the behaviour of established perennial pasture grasses using this approach and published literature has not applied the technique to crops grown on shallow soils (<1 m over parent material).

2.6.7 The Critical Limiting Deficit (D_L)

The previous section described the patterns of water extraction but the extent of yield reductions caused by water stress was not explained. Penman (1971) showed that yield reductions occurred when crops/pastures experienced water stress at levels exceeding a site and species-specific critical limiting deficit (D_L). It was proposed that the reduction in yield would be proportional to the amount by which the maximum deficit exceeded the D_L. If a species can extract more water from a given layer or extracts water from greater depths it gains a competitive advantage. This is reflected as a greater D_L.

This approach was used by Martin (1984) and assumed that at D_L growth ceased until rainfall or irrigation were applied. Rickard *et al.* (1986) suggested a negative curvilinear relationship between DM yield and soil moisture deficits beyond D_L. This relationship would reflect the balance between soil water supply and plant demand because plant growth declines as the soil dries (Hansen *et al.*, 1980). However, the ability to fit the curve depends on collection of sufficient data. The coefficient of determination (R^2) for the relationship between actual and predicted yields increased from 0.70 using the Penman relationship to 0.85 using the negative curvilinear relationship (Rickard *et al.*, 1986).

In this study, the D_L will be identified for dryland pastures and the reduction in relative yield described with the method of Penman (1971). The stability of this relationship will be investigated over a two year period using the measured soil moisture deficit. This will allow the potential yield losses associated with water stress to be estimated for different years which may have different environmental conditions. The rate of yield reduction beyond D_L will then be used to create a water stress function to be included in a multiplicative yield prediction model suitable for describing yield loss during periods of water stress.

2.6.8 Water use efficiency (WUE)

Water use efficiency can be defined in several ways and care must be taken when interpreting/extrapolating WUE from the literature (Moir *et al.*, 2000; Martin *et al.*, 2006). Most published WUE is based on above ground yield and partitioning to the roots is not accounted for. These values do not account for changes in root: shoot ratios or seasonal changes in partitioning which may occur in perennial pasture species, such as lucerne (Teixeira, 2005). However, in the field measuring root yield of a pasture with

a fibrous root system is difficult and root material may be lost when samples are washed. In this study, WUE is defined as the slope of the regression between above ground DM yield and the amount of water (mm) used to produce that yield.

The physiological basis for differences between species in WUE is a result of the net photosynthetic ability of the plant under non-limiting conditions. As CO_2 diffuses into the leaf it is captured and fixed as it dissolves in the wet cell wall surface. However, during the process of gas exchange transpiration occurs and photosynthetic cells can dehydrate. The extent to which this occurs depends on the balance between water supply and demand (Hsiao, 1973; Passioura, 1983; Turner, 1986) and the degree of stomatal control (Turner, 1986).

Increased WUE has been reported when plants are exposed to mild water stress (Silcock and Wilson, 1981). This efficiency gain reflects a change in the amount of water associated with evaporative loss and can differ between species and environment (Section 2.6.7). As a result, transpiration efficiency (Tanner and Sinclair, 1983) can be used to determine WUE rather than calculations based on ET. Yield will not increase unless more water is used for transpiration rather than in the soil evaporation component of ET. When PET is used to quantify ET, changes in WUE may reflect the inaccuracy of PET under water stressed conditions (Section 2.2.1). In this study, WUE will be calculated using Equation 2.11, where ET is transpiration (mm) which may be either potential or actual water use.

Equation 2.11 $$WUE = \frac{DM}{ET}$$

Water demand is affected by factors which include solar radiation, temperature, windspeed and humidity (French and Legg, 1979). When the vapour pressure deficit increases, transpiration increases but there is no associated increase in the rate of photosynthesis. Effectively, WUE decreases because the atmospheric conditions extract more water to produce the same quantity of DM. Conversely, under conditions of high humidity (low VPD), WUE increases because the gradient between internal and external water vapour concentrations is reduced (Tanner and Sinclair, 1983; Jamieson *et al.*, 1984; Turner, 1986).

Brown *et al.* (2007) demonstrated a variable and inconsistent relationship between the reciprocal of transpiration efficiency and VPD. This caused variation in the transpiration efficiency coefficient and use of a constant value resulted in over-prediction of ET by

>300 mm/y. It was proposed that transpiration demand could be determined with an energy balance equation. Linear regressions were fitted between transpiration and intercepted radiation within individual regrowth cycles. The slopes of the regressions were then plotted against mean regrowth VPD and this explained 75% of the observed variation. The slope of this relationship gave an estimate of the transpiration coefficient.

2.7 Nitrogen Metabolism

Nitrogen (N) is the most limiting of all plant nutrients required for growth (Grindlay, 1997; Azam, 2002). Soils generally contain ≤10% of total soil nutrients, including N, in a plant available form. Deficiency symptoms of any plant nutrient result when i) soil nutrient content is low, ii) low quantities of the required nutrient are in a plant available form, or iii) when the rate of replacement of the required nutrient in solution is inadequate to meet plant demand (Novoa and Loomis, 1981; McLaren and Cameron, 1996).

Nitrogen is an essential component of the photosynthetic apparatus particularly chlorophyll, Rubisco and proteins but also stimulates cell division and tillering. It is an essential component of amino acids which are precursors to protein formation and is required for the formation of enzymes and co-enzymes (Hay and Walker, 1989; McLaren and Cameron, 1996). The net effect of N supply on these factors results in changes in both leaf area and photosynthesis (Novoa and Loomis, 1981).

2.7.1 Nitrogen and canopy development

In contrast to water stress (Section 2.5) insufficient N also inhibits cellular division. This affects the maximum attainable leaf size through reduced cell number (Gastal and Nelson, 1994) but does not affect the final size of individual mature cells. In tall fescue, N increased the number of epidermal cells produced by 22% compared with low N plants (Volenec and Nelson, 1983). MacAdam *et al.* (1989) showed that N application increased the time required for individual epidermal cells to attain their final size by 25%. Due to the coordination between epidermal cell size and mesophyll division this delay allowed 40% more mesophyll cells to be produced. In *Lolium* and *Fustuca*, N application increased primordia initiation, leaf emergence and extension rates, and delayed leaf senescence. Specific leaf area (g DM/cm^2) of individual leaves was

reduced by N application (Wilman and Mohamed, 1981). Furthermore, N effects on leaf extension may be greater than effects on leaf appearance rate (Belanger, 1998).

In contrast, stimulation of tiller production by N application (Baker and Younger, 1987) is the main cause of increased leaf number per unit area. Harris *et al.* (1996) reported that N application doubled tiller population and Ackmal and Janssens (2004) showed N application increased tillers/plant by 13.6% compared with water alone which increased tiller numbers by 5.6%. In ryegrass, water stress had a greater effect on yield reductions than N deficiency. This contradicts the response of cocksfoot to water and N where, annually, N had a greater effect on DM yield than water (Peri *et al.*, 2002b). Whether N or water produces the greatest response will depend on the extent of water and N stresses experienced by the pasture at the time of measurement.

2.7.2 Nitrogen and photosynthesis

At least 50-75% of soluble N is associated with formation of photosynthetic components (Horst and Nelson, 1979; Field and Mooney, 1986) and within individual leaves the distribution of N containing compounds varies with distance from the ligule. In tall fescue, total leaf N decreased by >50% from 0 mm to 150 mm from the ligule in both +N and –N treatments. The majority of N was located primarily in the leaf region associated with rapid cell division. Rubisco content increased with increasing distance from the ligule. There was no Rubisco 0-25 mm from the ligule but rapid synthesis after this point resulted in 4.5-6.0 µg/mm in +N plants compared with 1.5-2.0 µg/mm in –N plants 125 mm from the ligule. Furthermore, leaf elongation rate of +N plants was 1.5-5.0 times greater than that of the –N treatments (Gastal and Nelson, 1994). MacAdam (1989) showed N application increased the number of mesophyll division cycles completed and these represented 46-54% of the cross sectional leaf area compared with epidermal cells with accounted for 20-28% of area. Total cross sectional leaf area of +N treatments was 27-38% greater than those of –N treatments (Rademacher and Nelson, 2001).

In cocksfoot, it was shown that with leaf N concentrations of 5.2-5.9% photosynthesis was not affected by N deficiency. However, there was a linear decline in photosynthesis when leaf N% fell below 5.2%. Between 2.6-5.2% N, photosynthesis decreased 11.5% from the potential maximum of 27.4 µmol $CO_2/m^2/s$ for every 1% decrease in leaf N. When leaf N was between 2.6-1.5% N photosynthesis declined at a faster rate of 41%

per 1% decrease in leaf N concentration (Peri *et al.*, 2002b). As mesophyll cells are the main site where chlorophyll is located (Campbell, 1996) N application would increase the efficiency of light capture and in combination with increased Rubisco content this would explain the increase in photosynthetic rate responsible for increased DM yield (Peri *et al.*, 2002b).

2.7.3 Describing the decline in N% during growth

Leaf senescence is generally a function of accumulated Tt following the attainment of final leaf size. This can be modified by source:sink relationships, water stress and plant nutrition. Degradation of chloroplasts during senescence (Section 2.5.4) is a major source of N redistribution within the plant. In wheat (*Triticum aestivum*), the decline in total RNA and soluble proteins began after full leaf size was attained (Crafts-Brandner *et al.*, 1998). The reduction in soluble proteins was paralleled by a reduction in Rubisco activity and N deficiency accelerated the rate of senescence. Rubisco degradation during senescence explains the decrease in soluble proteins as they are translocated out of the leaf, following proteolysis, to developing sinks.

In this study, the response of cocksfoot monocultures to N fertility will be described and the mechanism of yield reductions explained. Agronomic approaches, such as pasture DM response (kg DM/kg N applied), are of limited use as they are specific to the environment in which they were collected, show large variation and are dependent on timing of application and form of N fertiliser used (Novoa and Loomis, 1981; Smith *et al.*, 2000). Smith *et al.* (2000) reported application of 50 kg N/ha to mixed species pasture in early spring gave 1.5-9.0 kg DM/kg N in 1998 compared with 6.0-23.0 kg DM/kg N in 1999. In October/November responses were 4.0-20.0 kg DM/kg N and 3.2-20.0 kg DM/kg N in February/March. Risk (1982) reported DM responses of 3.0-15.0 kg DM/kg N and autumn applications showed more variability than spring applications due to reductions in soil temperature. As a result it is generally advised that N applications should not be made when 10 cm soil temperatures are likely to drop below 5°C during the projected growth period.

Nitrogen content declines during a regrowth period and previously this has been attributed to ontogeny or phenological variation (Lemaire *et al.*, 2007). To provide a unifying relationship which adequately describes the extent of N deficiency in a way that is stable and suitable for a range of different environments, this study will apply a

nitrogen nutrition index (NNI) (Lemaire *et al.*, 1989). This involves the creation of an N dilution curve (Figure 2.7), from a pasture not limited by water stress or N deficiency, and describes the reduction in herbage N% with increasing DM (t DM/ha) production (Equation 2.12).

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Figure 2.7 Examples of the decline in nitrogen concentration as biomass yield increases for some C3 and C4 crops (Belanger and Gastal, 2000).

Equation 2.12 $\mathbf{N\% = a(DM)^{-b}}$

The 'a' coefficient is the non limiting N% required for a 1.0 t/ha yield. The 'b' coefficient describes the rate of decline in N% as DM yield increases (Belanger and Gastal, 2000). These relationships are usually generated from sequential harvests within a defined regrowth cycle. For cocksfoot, the form of this relationship was $N\%=4.8(DM)^{-0.32}$ (Lemaire *et al.*, 1989). This relationship adequately describe the N dilution in mixed species pastures (Duru *et al.*, 1997). Greenwood *et al.* (1990) proposed that a common 'b' coefficient of 0.34 for both C3 and C4 species could be applied during vegetative growth. However, more recently evidence has been presented that indicates the relationship may be species specific (Justes *et al.*, 1994; Lemaire *et al.*, 2007). In this study, the relationship will be generated from a fully irrigated cocksfoot pasture supplied with non limiting N.

The reduction in N% over time was proposed to be caused by an increase in the ratio of structural to non structural N within the plant over time (Caloin and Yu, 1984) because the N requirement for metabolic compounds is greater than that required for structural growth. Over time, the amount of standing biomass increases and N required for structural material represents a greater proportion of total plant N (Lemaire and Gastal, 1997). This causes a decrease in the ratio of metabolic to structural N (Greenwood *et al.*, 1990; Lemaire and Gastal, 1997; Belanger and Gastal, 2000; Jamieson and Semenov, 2000). Regardless of these factors, for a specified species the N dilution approach has shown a stable relationship between N% and DM yield in a range of environments (Lemaire *et al.*, 2007).

2.7.4 Specific leaf nitrogen (SLN)

In grasses, newly formed leaf tissue emerges from the pseudostem when the majority of expansion and division processes are complete. Unfortunately, this complicates separation of structural and metabolic N pools (Lemaire and Gastal, 1997). The structural N component is associated with cell wall formation and therefore specific leaf N should be constant regardless of N supply, provided that N is above the critical threshold where N dilution occurs to maintain leaf area (Jamieson and Semenov, 2000). In contrast, metabolism and storage N pools are associated with cell division and synthesis of photosynthetic apparatus. Nitrogen associated with cell division will be highest in differentiating meristematic tissue which is surrounded by leaf sheaths of older emerged leaves. In this study, SLN and specific pseudostem N (g N/m^2) will be determined at two harvest dates in early spring to exclude periods of water stress. This will provide novel information on partitioning of N in vegetative cocksfoot.

It has been proposed that specific leaf N can be treated as a constant (Jamieson and Semenov, 2000). In the model for wheat, leaf N was set at 1.5 g N/m^2 whereas the stem fraction could range from 0.3-1.5% N. Plant N requirements are determined by the N necessary to maintain a critical N concentration in new leaves and remaining tissue is available to store N in excess of current plant requirements (Grindlay, 1997). This stored N, particularly in the form of Rubisco, is then available for remobilisation when required (Novoa and Loomis, 1981). However, under N deficient conditions, newly formed leaves will have a lower specific leaf area to maintain a critical N concentration (Jamieson and Semenov, 2000). Furthermore, in dense canopies, N content tends to be

higher in the uppermost canopy layers due to remobilisation of soluble N from shaded leaves (Lemaire *et al.*, 1991; Grindlay, 1997).

Recently, Lemaire *et al.* (2007) examined the relationships between LAI, DM yield and N% of a range of C3 and C4 crops which excluded periods of water stress and N deficiency. This work confirmed that 'a' and 'b' parameters for the relationship between N% and yield (Equation 2.12) were species specific but stable across environments. The relationship between N% and LAI was stable for a species within a known environment and critical specific leaf nitrogen was 1.4-2.7 g N/m^2 (Lemaire *et al.*, 2007). Relationships could not be extrapolated because of compensation between stem N and leaf N as LAI increased and the relationship cannot currently differentiate between structural and metabolic N requirements.

A theoretical model has been proposed to account for partitioning between structural and metabolic N during vegetative grass growth (Sheehy *et al.*, 1996). The model separated leaf N and photosynthetic N pools and allowed for reversible fluxes and accounted for remobilisation of soluble N during leaf senescence but no validation with an independent data set was conducted. Despite the fact this was proposed 10 years ago, there is still little pertinent published data to describe these N pools in perennial pasture grasses.

2.7.5 Using a nitrogen nutrition index (NNI) to describe the extent of N deficiency

The NNI is calculated as measured N% divided by the optimal N concentration for a known DM yield derived from the N dilution curve. The extent of N deficiency experienced by the pasture is quantified by a ratio which varies from 0-1.0. A value of 1.0 indicates N is non limiting and values ≥1.0 represent luxury consumption (Justes *et al.*, 1994) which gives no additional increase in DM yield. Values <1.0 indicate DM production is compromised by N deficiency (Belanger and Gastal, 2000). Most literature describing NNI excludes periods of water stress due to the intrinsic link between water availability and mineral nutrition.

In a regrowth period, non limited DM yields (NNI = 1.0) in tall fescue and timothy (*Phleum pratense*) pastures were achieved with N applications of 140-160 kg N/ha but when no N was applied the NNI dropped to a minimum value of 0.4 which indicated available N was only able to provide 40% of the N needed for non limited DM

production (Lemaire and Maynard, 1997). In annual ryegrass (*Lolium multifloram*) N applications ≤100 kg N/ha were insufficient for non limited production in a 70 d regrowth cycle. Applications of 250 kg N/ha had maximum NNI values of 1.5-1.6 which indicated luxury consumption. There was no yield benefit from rates >150 kg N/ha (Marino *et al.*, 2004) but excess N stored may be remobilised for future growth (Novoa and Loomis, 1981).

The effect of N nutrition on various crop growth processes for tall fescue and timothy (Figure 2.8) explains the close relationship between RUE and leaf extension (Belanger and Gastal, 2000). In timothy it was shown that N application more than doubled leaf length per tiller (Belanger, 1998) which increased the amount of light intercepted by the canopy. However, the relationship between LAI and NNI was more sensitive to changes in environmental conditions than the relationship between N% and DM yield caused by an increase in the proportion of total N allocated to structural material (Lemaire *et al.*, 2007).

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Figure 2.8 Example of the expected response to changes in the index of N nutrition, or NNI, for photosynthesis, leaf extension and radiation use efficiency (Belanger and Gastal, 2000).

2.7.6 Radiation Use Efficiency (RUE)

Net photosynthesis (P_{net}) represents total respiration (R_T) loss from gross photosynthetic (P_g) output (Equation 2.13). Total respiration is the combined product of growth respiration (R_G) and maintenance respiration (R_M) (McCree and Troughton, 1966; McCree, 1970). Both R_G and R_M are affected by biomass yield but R_G is associated with photosynthesis and is highly dependent on temperature. Maintenance respiration represents the quantity of substrate required to maintain standing biomass with no net yield gain. For example, R_M will be proportionally greater for a 3.0 t DM/ha yield than a 1.0 t DM/ha yield. In addition, plants experiencing higher temperatures, through reduced evaporative cooling, will have proportionately higher R_M losses than unstressed plants (McCree, 1970; Biscoe and Gallagher, 1977).

Equation 2.13 $$P_{net} = P_g - R_T$$

Net photosynthesis can be summarised using RUE. There is a linear relationship between DM yield and intercepted PAR under non-limiting conditions, the slope of which is RUE (Monteith, 1972, 1977; Sinclair and Muchow, 1999b). Radiation use efficiency is usually based on above ground biomass production and interpreting results can be difficult because of the different methods used. For example, some published RUE values are based on total intercepted radiation whereas others are based on intercepted or absorbed PAR (Sinclair and Muchow, 1999b). Furthermore, RUE differs between species and metabolic groups because of different pathways for CO_2 assimilation and the variation in energy requirements for the production of carbohydrates, proteins and lipids (Monteith, 1972; Sinclair and Muchow, 1999b).

The amount of PAR intercepted by a canopy is dependent on LAI and canopy architecture, particularly the extinction coefficient (k) as a measure of light penetration into the canopy. Nitrogen is necessary in the formation of many compounds (Section 2.7). If structural N is a constant proportion of total biomass (Jamieson and Semenov, 2000), N deficiency will primarily cause reductions in the metabolic N pool (Section 2.7.4). This may cause remobilisation of excess N stored as Rubisco, or result in a reduction of chlorophyll and Rubisco per unit lamina area. Therefore, N deficiency may reduce leaf N associated with photosynthetic apparatus to the extent that RUE may be reduced (Biscoe and Gallagher, 1977; Hay and Walker, 1989).

The severity of water stress is an important factor in interpreting RUE especially in dryland systems. Singh and Sri Rama (1989) showed that when the level of extractable water was >30% RUE was independent of soil water content. However, as the fraction of extractable water declined below this critical value there was an exponential reduction in RUE. There has also been criticism of RUE results generated from cumulative data sets (Demetriades-Shah *et al.*, 1992). In this study, RUE was calculated from an annual cumulative data set but to address these concerns the RUE of individual regrowth cycles over a two year period were determined and compared with the annual RUE to identify if RUE from cumulative data gave an accurate representation of the non cumulative data set. This will be conducted on treatments not compromised by water stress or N deficiency.

Yunusa *et al.* (1995) reported RUE of 1.95 for ryegrass and 2.34 g DM/MJPAR for lucerne pastures. Khaiti and Lemaire (1992) showed RUE of an establishing (<1 year) lucerne stand varied seasonally. In late summer RUE was about 3.8 g DM/MJ PAR compared with 1.2 g DM/MJ PAR in late winter. In tall fescue RUE was determined using total (root and shoot) DM by Belanger *et al*. (1994) to account for seasonal variation in partitioning priorities. It was shown that shoot RUE was 1.9 g DM/MJ PAR in spring, 1.3 in summer and 1.1 in autumn. Calculating RUE based on total DM removed some but not all of the seasonal RUE variation. This study determines RUE of an established perennial pasture and calculation of regrowth RUE will allow identification of any seasonal variation.

2.8 Conclusions

Based on this literature review the following conclusions can be drawn:

- Seasonal yield variation within and between environments is primarily due to temperature which affects canopy expansion and photosynthetic rate. Other factors which affect the seasonal distribution of DM production include: solar radiation receipts, pests and disease, water availability and nutrition.
- Water stress primarily reduces the amount of light intercepted before photosynthesis is inhibited.
- Nitrogen deficiency reduces the metabolic N pool rather than structural N. Reductions in chlorophyll and Rubisco formation reduce gross photosynthesis and radiation use efficiency.
- To predict DM yield the potential production can be determined under non limiting conditions and then modified according to the magnitude of water and nitrogen stresses based on their underlying physiological mechanisms.

The aim of the current research is to describe relationships between yield and the main factors influencing yield, namely temperature, water and N. These descriptions will then be used to identify underlying physiological mechanisms and integrated into a simple multiplicative yield prediction model as a first step in estimating yield in a range of environments.

3 Materials and Methods

The following chapter describes methodology and analysis procedures common to all results chapters. Data presented in this thesis (Chapters 4, 5, 6 and 7) compared production from cocksfoot monocultures with two levels of irrigation and two levels of fertiliser nitrogen. Specific measurements are also described within the relevant results chapter.

3.1 Site

The experiment was conducted in Block H18 of the Horticultural research area (HRA) at Lincoln University, Canterbury, New Zealand (43º 38'S and 172º 28'E, 11 m a.s.l.).

3.2 Meteorological Conditions

Meteorological data were measured at the Broadfields meteorological station, located 2 km north of the site. Long-term monthly data are means for the period 1975-2002. The long-term average annual rainfall is 624 mm. Mean annual air temperature is 11.4ºC, ranging from a daily minimum of 6.1ºC in July to a maximum of 21.9ºC in January. Generally, within this environment, Penman potential evapotranspiration (PET) exceeds rainfall from September to April with a long-term (1975-2002) average annual potential soil moisture deficit of 400 mm.

3.2.1 Rainfall and Potential Evapotranspiration (PET)

For the experimental period (2003-2005) annual (1 January to 31 December) rainfall totalled 466 mm, 645 mm and 411 mm, respectively compared with a long term average of 624 mm. However, seasonal distribution did not follow long term patterns, particularly in 09/2003, 12/2003, 08/2004 and 12/2004 (Figure 3.1a). Monthly PET (Figure 3.1b) followed the long term trend with a minimum monthly PET of 30-45 mm in June/July and a maximum of 120-175 mm in December/January. Annual PET was 1091 mm, 1043 mm, 1027 mm for 2003, 2004 and 2005, respectively.

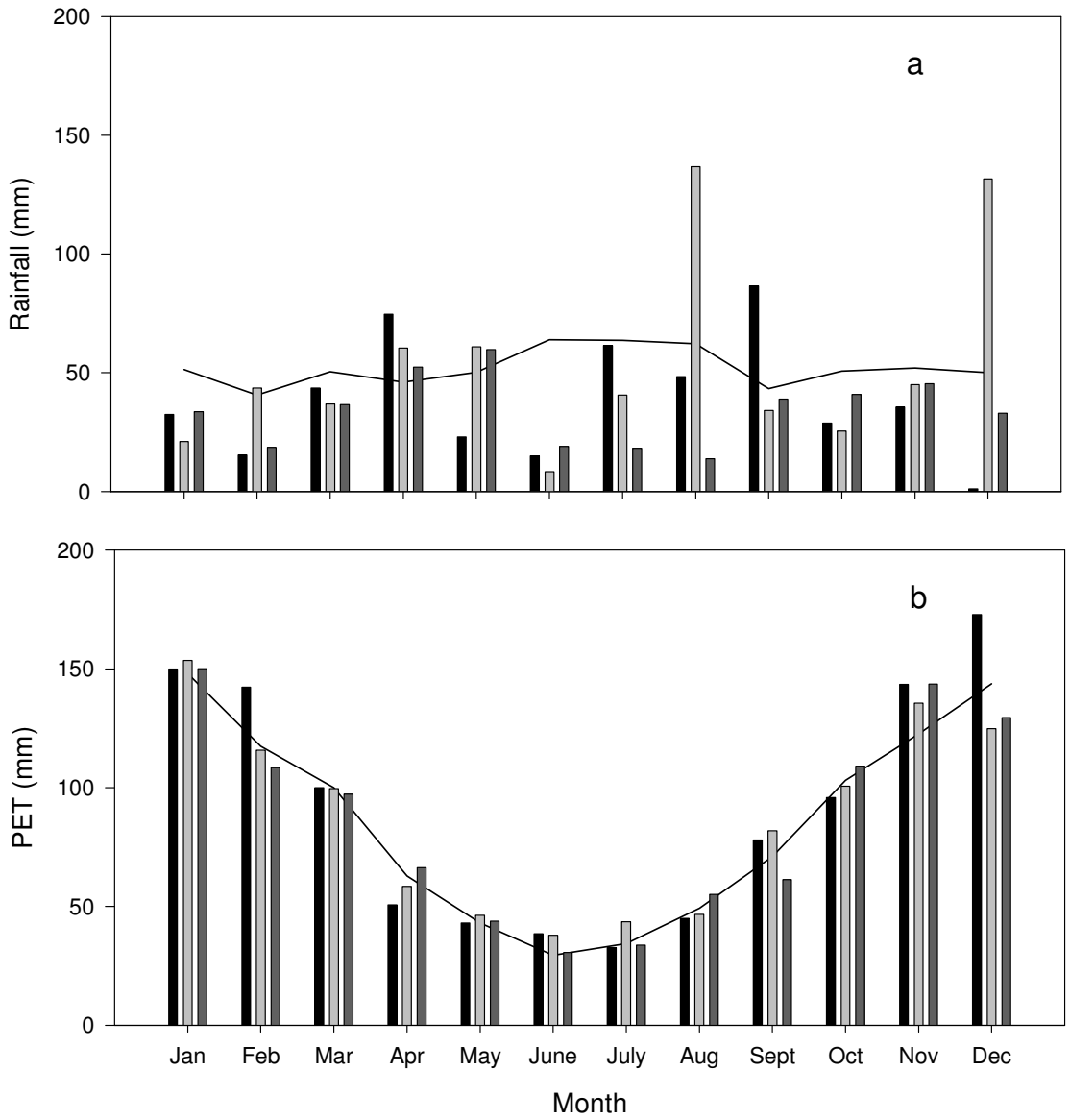

Figure 3.1 Meteorological data for 2003 (■), 2004 (■), 2005 (■) and long-term (1975-2002) monthly (a) rainfall and (b) potential evapotranspiration (PET) data (—) from the Broadfields meteorological station located 2 km north of the experiment.

3.2.2 Mean Air Temperature and Total Solar Radiation

Mean monthly air temperature and total solar radiation followed the long term trend. Monthly temperature was highest in January 2004 (17.9ºC) and the minimum was 5.2ºC in July 2004 before increasing in the spring (Figure 3.2a). Total solar radiation was highest in December 2003 (783 MJ/m^2) and lowest (121 MJ/m^2) in June 2004 (Figure 3.2b).

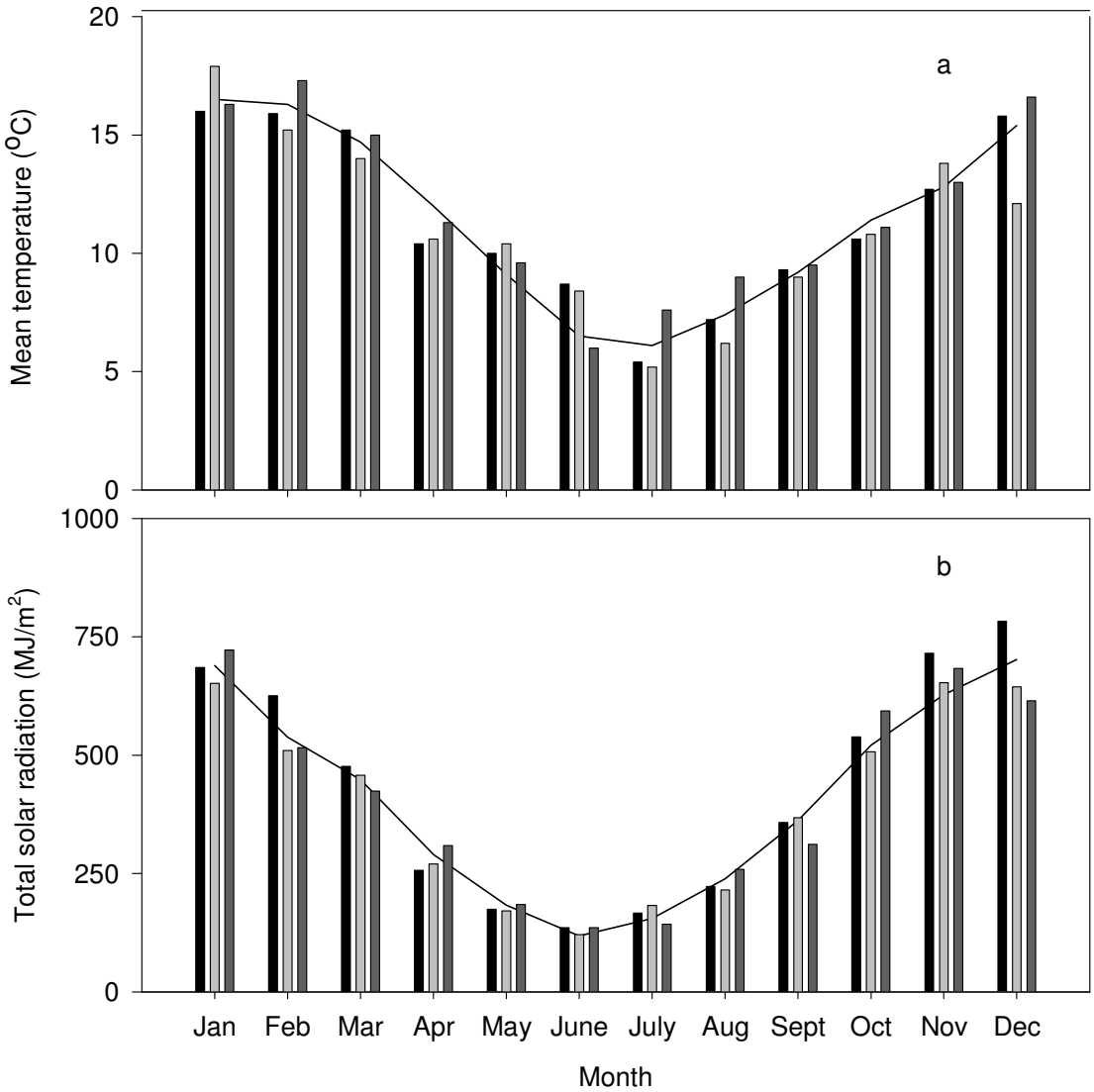

Figure 3.2 Meteorological data for 2003 (■), 2004 (■), 2005 (■) and long-term (1975-2002) monthly (a) mean air temperature and (b) total solar radiation data (—) from the Broadfields meteorological station located 2 km north of the experiment.

3.2.3 Vapour pressure deficit (VPD) and Windrun

Vapour pressure deficit was calculated daily as the difference between vapour pressure and the saturated vapour pressure at air temperature calculated using wet and dry bulb temperatures. Further details on the calculations are presented in Jenson *et al.* (1990). From 09/2003 to 10/2005 the maximum average monthly vapour pressure deficit was 1.0 kPa in January 2004 and February 2005 and a minimum of 0.4 kPa in August 2004 (Figure 3.3a). Wind run was highest in December 2003 (12 800 km) and was 7 800 km in June 2005 (Figure 3.3b).

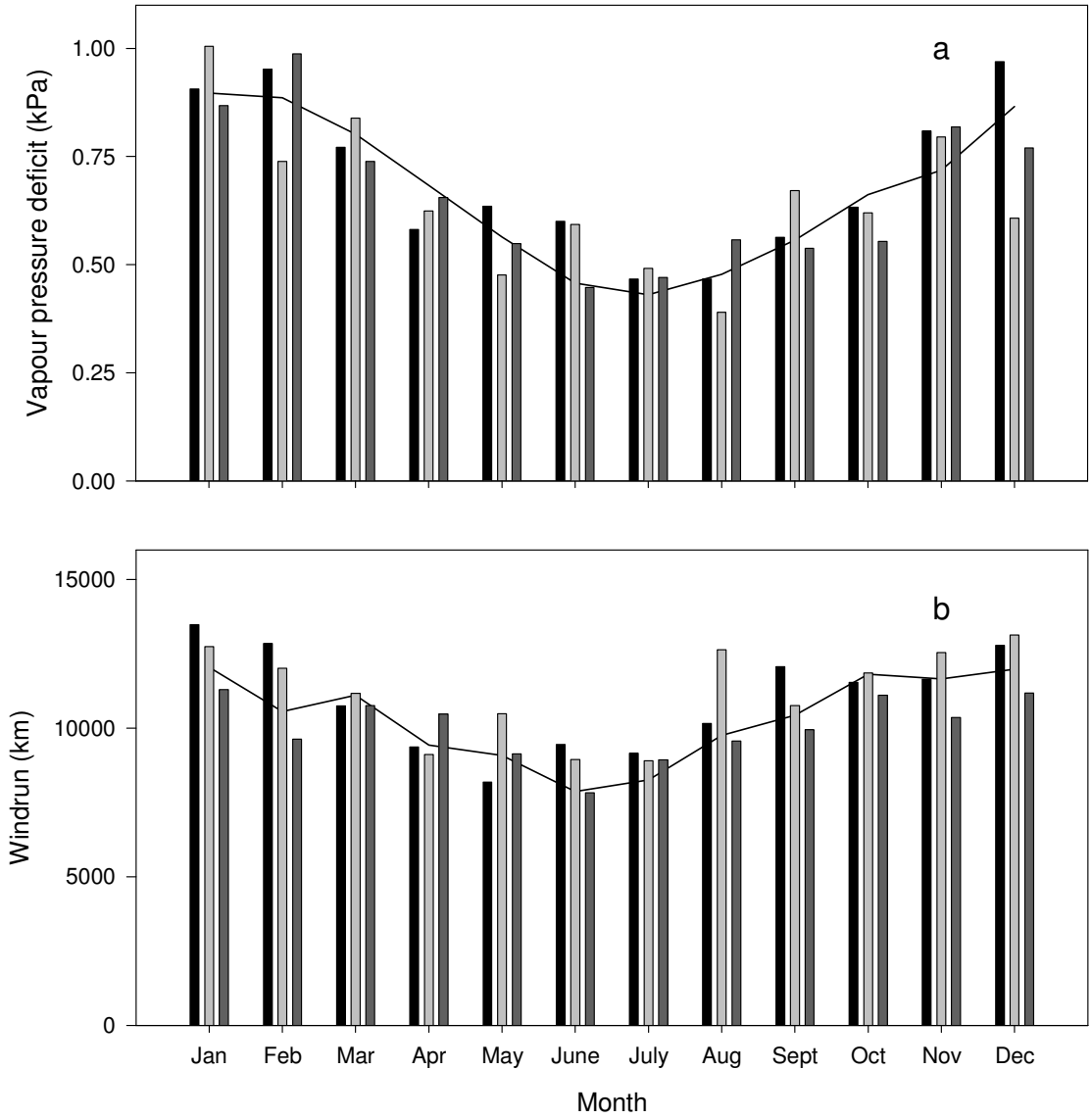

Figure 3.3 Meteorological data for 2003 (▇), 2004 (..), 2005 (..) and long-term (1975-2002) monthly (a) vapour pressure deficit and (b) windrun (—) from the Broadfields meteorological station located 2 km north of the experiment.

3.3 Soil

The site was flat and the soil was a variable depth Templeton silt loam (Udic Ustochrept, USDA Soil Taxonomy) soil overlying alluvial gravels (Cox, 1978; U.S.D.A., 1984; Watt and Burgham, 1992). Soil parent material was sandy and silty alluvium (Gyamtsho, 1990; Watt and Burgham, 1992). Generally, these soils have a weakly developed silt loam top soil of 0.2-0.3 m overlying subsoil layers that range from silt loam to sand in texture and are typically free draining (Watt and Burgham, 1992). The plant available water holding capacity (PAWC) of soils in this series is 100-

120 mm/m (Webb, 1989a, 1989b; Webb *et al.*, 2000). Depth to gravels at an adjacent site (Block H17) was variable, ranging from 0.6-1.5 m (Gyamtsho, 1990), which is typical of soils formed on a floodplain. However, site specific data were unavailable for Block H18.

3.4 Site History

The site was sown in 03/1995 with 'Grasslands Wana' cocksfoot in combination with white clover (*T. repens*), red clover (*T. pratense*) or subterranean (sub) clover (*T. subterraneum*). The current experiment was initiated on 30/09/2003. Only minimal amounts of white and sub clovers were present at this time (<2%). The main dicot species was dandelion (*Taraxacum officinale*) and the main monocot weed was *Poa annua*.

3.4.1 Environmental conditions during the measurement periods

Environment conditions reported below are for the two annual growth seasons over which measurements were made. Measurements in the first growth season (2003/04) were made between 30/09/2003 and 05/10/2004. In the second growth season (2004/05) measurements were made between 6/10/2004 and 17/10/2005 when the experiment was terminated.

3.4.1.1 Rainfall, PET and Irrigation

Rainfall totalled 515 mm in 2003/04 (30/9/2003-5/10/2004) compared with 523 mm in 2004/05 (6/10/2004-17/10/2005). Total irrigation applied was 447 mm in 2003/04 and 256 mm in 2004/05. Irrigation dates and application rates are detailed in Appendix 1. In 2003/04, PET totalled 1109 mm and 1052 mm in 2004/05.

3.5 Experimental Design

A split plot experiment with three replicates (Plate 3.1) was established on an eight year old established cocksfoot pasture, at site H18, on 30/09/2003. Irrigation was the main plot (Section 3.5.1) and nitrogen (Section 3.5.2) was the subplot treatment (Table 3.1). Plots were 6.0 x 6.3 m.

Table 3.1 Treatment details of the cocksfoot potential yield experiment located in H18, Lincoln University, Canterbury, New Zealand. Unless stated otherwise in figure captions symbols shown below are used to differentiate pastures.

Treatment	Irrigation Level	Nitrogen level	Nomenclature	Symbol
1	Fully Irrigated (I)	+N	I+N	●
2	Fully Irrigated (I)	- N	I-N	○
3	Dryland (D)	+N	D+N	▼
4	Dryland (D)	- N	D-N	▽

Plate 3.1 Experiment site on 08/09/2004. Replicates run east-west and caps for neutron probe access tubes are central in each plot.

3.5.1 Irrigation

Irrigation was applied to maintain the soil moisture deficit above 50 mm in the top 0.5 m of the profile by a removable overhead sprinkler system. Irrigation scheduling was based on the actual soil moisture deficit (ASMD) measured with Time Domain Reflectometry (TDR) (0-0.2 m) (Trace Systems, Model 6050X1, Soil Moisture Equipment, Santa Barbara, California, USA) and neutron probe (0.2-2.3 m) (Troxler Electronic Industries Inc., Triangle Research Park, North Carolina, USA) (Section

3.6.3) using Equation 3.4. Flow meters were installed to measure actual irrigation application as flow rates varied dependent on demand placed on the system. Dates and amounts of irrigation applied are outlined in Appendix 1.

3.5.2 Nitrogen

In the 2003/04 season a total annual application of 800 kg N/ha/y was applied in eight split applications of 100 kg N/ha at the beginning of active regrowth periods. If rainfall occurred within the first 4 d of the regrowth cycle, N was applied as urea (46,0,0,0) to all +N treatments. When rainfall did not occur within the first 4 d of the rotation, irrigation (15-25 mm) was applied to the I+N treatment to dissolve N. No irrigation was applied at any time to D+N treatments and N applications were deferred until rainfall occurred. Nitrogen application rates were increased to 1 600 kg N/ha/y, applied in 11 split applications in 2004/2005. This was comparable to non limiting N applications applied by Peri *et al.* (2002a) and Donohue *et al.* (1981). Applications were one application of 100 kg N/ha followed by an increase to 150 kg N/ha for the subsequent 10 rotations.

3.5.3 Soil Fertility

In response to soil test results (Table 3.2) super phosphate and lime (Table 3.3) were applied, prior to (26/06/2003) the establishment of the experiment (30/9/2003) to increase fertility levels.

In 2003, soil cores were taken using a systematic sampling procedure across the entire site to a depth of 75 mm. In 2004, samples were bulked across treatments but in 2005 two replicated samples were taken to allow analysis. Eight soil cores were taken from each plot to a depth of 75 mm in 2004 and 2005. 'Pseudo' total N was used to measure the total soil N pool. Tests are total Kjeldahl N which involves soil sample digestion by sulphuric acid. The term 'pseudo' refers to N recovery, as the method recovers about 93% of total soil N. The remainder are nitrates which are not readily extractable by sulphuric acid (Searle, 1984). Nitrogen percentage is converted to kg N/ha using Equation 3.1:

Equation 3.1 $$N\ (kg/ha) = N\% * BD * d * 1000$$

Where BD is bulk density of the soil layer measured and d is layer depth in cm.

Table 3.2 Soil test results (0-75 mm) from pure cocksfoot monocultures at H18, Lincoln University, Canterbury, New Zealand.

Year	Treatment	pH (H_2O)	Olsen P (µg/ml)	SO_4^-S (µg/g)	Ca^{2+}	K^+	Mg^{2+}	Na^+
					---------(meq/100g)--------			
2003		5.6	14	7	7	13	16	9
2004	I+N	6.3	19	2	9	6	15	5
	I-N	6.6	21	5	9	7	16	7
	D+N	6.0	30	6	8	7	13	6
	D-N	6.5	26	4	8	9	16	7
2005	I+N	5.3	17	3	6	4	9	6
	I-N	6.8	20	6	10	7	17	8
	D+N	5.3	27	3	7	4	10	7
	D-N	6.7	27	5	9	9	17	8
	Effect	N	ns	ns	N	N	ns	ns
	Significance	***			*	*		

Note: Treatment acronyms were given in Table 3.1. Soil samples were analysed using Ministry of Agriculture and Fisheries Quicktest (MAF QT) procedures. Significance levels are; ns= non significant, * $p \leq 0.05$, ** $p \leq 0.01$ and *** $p \leq 0.001$ and relate to replicated soil tests taken in 2005. Numbers with the same letter are similar at the $p \leq 0.05$ level.

Table 3.3 Basal and maintenance fertiliser applications to the cocksfoot potential yield experiment at Lincoln University, between 25/06/2003 and 10/10/2005 in response to soil test results.

Date	Fertiliser	Nutrient content	Rate
25/06/2003	Lime		5.0 t/ha
	Single Superphosphate	(0,9,0,11)	400 kg/ha
29/10/2004	Potassium sulphate	(0,0,42,12)	100 kg/ha

3.5.4 Weed Control

Herbicides were applied to control broadleaf weeds and annual grasses to maintain the experimental area as a cocksfoot dominant monoculture. Dates, application rates and active ingredients are detailed in Appendix 2.

3.6 Biological Measurements

3.6.1 DM Production

3.6.1.1 Destructive sampling

Regrowth periods were ~25-35 d during active growth and extended to a maximum of 52 d over winter or during drought periods. Dry matter cuts were taken from a 0.2m^2 quadrat with a set of electric shears to a residual pasture height of 3.0 cm. The area harvested at the end of the previous rotation was avoided by dividing the plots into four 'strata' (Cayley and Bird, 1996) and moving sequentially around the plot. After cutting, samples were stored in a cooler at 4°C and samples were processed within 48 h of harvest. Plots were then mown to a residual cutting height of 3.0 cm with a ride on mower and herbage was removed.

3.6.1.2 Non-destructive sampling

A pasture capacitance probe (Mosaic Systems Ltd, Palmerston North, New Zealand) was used to determine pasture production non-destructively within a regrowth period from 01/2004 onwards. Measurements were made every 7-14 d when conditions were suitable. Destructive harvests were used to make paired comparisons for probe calibrations at the end of each regrowth period. A regression between probe readings and harvested DM allowed DM to be estimated (Vickery *et al.*, 1980; Vickery, 1981; Vickery and Nicol, 1982).

3.6.2 Botanical composition

Botanical composition was measured at every destructive harvest by dissecting a subsample taken randomly from the bulk using a quartering technique (Cayley and Bird, 1996). Subsamples of ~50 g freshweight were sorted into sown grass, other grasses, dicot weeds and senesced fractions. If leaf or stem was ≥50% dead it was included in the senesced fraction. The bulk and botanical composition samples were then dried in a forced draft oven at 50-60ºC until samples reached a constant weight.

3.6.2.1 Tiller population and Reproductive Status

Cocksfoot tiller population above cutting height was estimated by removing ~20 tillers (≥2 leaves) from the destructive bulk samples. Tillers were then oven dried at 50-60ºC

and weighed allowing tiller DM above cutting height to be calculated using Equation 3.2 during the vegetative phase. When the pasture became reproductive Equation 3.3 was used to differentiate between vegetative and reproductive tiller structures to calculate total tiller population above cutting height.

Equation 3.2 $$T_{pop} = CF\ DM / V_{DWT}$$

Equation 3.3 $$T_{pop} = ((CF\ DM * V_f) / V_{DWT}) + ((CF\ DM * R_f) / R_{DWT})$$

Where T_{pop} is total tiller population (tillers/m^2), CF DM is cocksfoot DM (g/m^2) V_{DWT} is vegetative tiller DM, V_f is fraction of vegetative tillers, R_f is fraction of reproductive tillers and R_{DWT} is reproductive tiller DM. The reproductive status of the pasture was measured because samples sent for nutritional analysis contained reproductive structures during this developmental phase and this may have influenced pasture quality measurements.

3.6.3 Soil water content

3.6.3.1 Access tube installation

Neutron probe access tubes were installed to a depth of 2.3 m in each plot. Due to soil type it was necessary to spike the access holes using a post hole driver as it was impossible to auger through alluvial gravels which occurred below ~0.6 m. Measured soil moisture was compared with gravimetrically determined soil moisture to ensure installation method did not affect measurement of actual soil moisture. Destructive samples were made within 0.5 m of the access tube, to a depth of 0.6 m, to allow a calibration with neutron probe measurements (Appendix 3).

3.6.3.2 Measurements

Soil moisture was measured by TDR (Section 3.5.1) with stainless steel rods (0.2 m length) within 0.2 m of the neutron probe access tube. Volumetric soil moisture content below 0.2 m was measured with a neutron probe at 0.2 m intervals to 2.3 m every 7-14 d under suitable conditions. The probe was calibrated for a Templeton silt loam soil and this same calibration has been used previously to measure soil moisture in soils of the Wakanui series in Canterbury (Brown, 2004; Teixeira, 2005).

3.6.4 Actual soil moisture deficit for irrigation ($ASMD_{Irr}$)

The $ASMD_{Irr}$ was calculated to determine water use and irrigation requirements to maintain the soil moisture deficit above 50 mm in the top 0.5 m of soil with Equation 3.4:

Equation 3.4 $$ASMD_{Irr} = ASMD_{i-1} + AET - P_{(R+I)}$$

Where $ASMD_{i-1}$ is the ASMD on the previous day (mm) from 0-0.5 m, AET is actual evapotranspiration and P is precipitation including inputs from rainfall (R) and Irrigation (I). Calculations for $ASMD_{Irr}$ were not permitted to exceed field capacity and excluded runoff and drainage. This calculation was used purely for irrigation scheduling and differs from the ASMD calculated based on the maximum extraction depth ($ASMD_{Ext}$) which is described in Section 5.2.1.

3.6.5 Nutritional and foliar analysis

Nutritional analysis was conducted on green cocksfoot samples retained after botanical separations. Samples were ground in a mill to pass through a 1 mm stainless steel sieve (Cyclotec Mill, USA) and near infrared spectroscopy (NIR) was used to determine N% and ME after a cross calibration was generated between NIR measurements and wet chemistry techniques. The calibration is presented in Appendix 4. Data were not collected from any other pasture components.

Crude protein (CP) was calculated using Equation 3.5 and ME was calculated with Equation 3.6. Analyses were conducted by the Animal and Food Sciences Group, Lincoln University using a Foss NIR Systems 5000 Rapid Content Analyser.

Equation 3.5 $$CP = N\% * 6.25$$

Equation 3.6 $$ME = DOMD * 0.16$$

3.7 Calculations

3.7.1 Mean daily growth rate

Daily growth rates (kg DM/ha/d) were calculated at end of rotation harvests by dividing total DM yield (kg DM/ha) by regrowth cycle duration (d).

3.7.2 Thermal time accumulation and base temperature selection

Appropriate base and optimum temperatures for growth were derived by minimising the coefficient of variation (CV) (Section 2.4.4). Base temperatures (T_b) between 0 and 10°C were evaluated. After the base was identified the optimum temperature was altered, above the base, in 1°C increments from 20-30°C. Thermal time was calculated following the method of Jones and Kiniry (1986) where a modified sinusoidal curve was fitted to mean daily air temperature above T_b (Section 2.4.3 and Equation 2.3). This method calculates Tt at three hourly intervals which are then integrated over a calendar day.

3.8 Statistical Analysis

Statistical analysis was conducted in GENSTAT (version 8.2) (Lawes Agricultural Trust, IACR, Rothamsted, U.K.) as a split plot design with irrigation as the mainplot and nitrogen the subplot. Comparison of annual yields was conducted as a split-split plot design using year as a repeated measure. When significant, means were separated using Fishers protected least significant difference (LSD) at the α=0.05 level. When interactions occurred means were separated using the most conservative interaction LSD.

3.8.1 Linear Regression

Linear regression was used to account for seasonal temperature effects by performing a linear regression between accumulated DM production and accumulated Tt. Regressions were fitted to data from each plot and slopes were analysed by ANOVA. A similar procedure was used to determine water use efficiency (Chapter 5) and radiation use efficiency (Chapter 7).

Details of other analysis techniques are described in the relevant results chapter.

4 Agronomic performance of cocksfoot (Dactylis glomerata) monocultures

4.1 Introduction

Annual DM yields of cocksfoot, in Canterbury, range from 7 to >28 t DM/ha (Stevens *et al.*, 1992; Peri *et al.*, 2002a). The lower value represents a typical yield under grazed dryland conditions and the upper extreme was considered the environmental maximum when neither water nor nitrogen limited pasture growth (Section 2.3). The difference between values indicates that cocksfoot based pastures usually produce substantially less than their potential.

In this chapter, the first objective was to quantify the agronomic performance and quality of cocksfoot pastures in response to water, nitrogen and temperature. The ultimate aim is to produce unifying relationships that explain these responses. Of these, temperature induces a seasonal effect that cannot be manipulated, but its impact can be assessed in relation to thermal time (Objective 2). Severe summer moisture deficits will restrict pasture growth but cocksfoot has been shown previously to produce more DM than ryegrass in dry summer and autumn periods in Canterbury (Stevens *et al.*, 1992). Similarly, the aggressive growth habit of cocksfoot, when sown with legumes such as white clover, leads to a decrease in the clover component (Lee and Cho, 1985; Moloney, 1991). This can cause pastures to become nitrogen deficient which has the effect of restricting leaf/canopy photosynthesis and pasture production (Peri *et al.*, 2002a; Peri *et al.*, 2002b) and decreasing pasture palatability (Edwards *et al.*, 1993). The impact of water and N on pasture production will be quantified in this chapter and investigated fully in Chapters 5, 6 and 7.

4.2 Materials and Methods

This chapter reports the agronomic results for a total of 22 regrowth periods between 30/09/2003–17/10/2005. Experimental design, management details including soil test results, biological measurements and thermal time accumulation were presented in Sections 3.5.3, 3.6 and 3.8.

4.2.1 Statistics

Analysis was conducted in Genstat 8.2 (Section 3.8). Total DM was analysed as a split-split plot with year as a repeated measure. Growth rates were analysed for each regrowth cycle using the split plot design. To account for temperature effects on mean daily growth rates, temperature adjusted growth rates (TAGR, kg DM/^{o}Cd/ha) were derived by regression, through the origin, of accumulated DM against accumulated thermal time (Tt) for irrigated treatments using air temperature. The procedure for identification of the appropriate base temperature to summarise growth was described in Section 3.7.2. Where interactions were significant but F ratios were an order or two of magnitude less than first order effects, the interaction is shown and the main cause of systematic error attributed to the first order effect. Means were separated by Fishers protected LSD ($p \leq 0.05$) when significant.

4.3 Results

4.3.1 Dry matter yield

There was a three way interaction ($p \leq 0.05$) between Irrigation, Nitrogen and Year (I*N*Y) for total annual DM yield (Figure 4.1). Total treatment yields (t DM/ha/y) were similar between years for the I+N (21.9), I-N (9.8) and D+N (15.7) treatments. However, D-N treatments produced more DM in 2003/04 (7.5) than in 2004/05 (5.0). Despite the interaction, the main effect of N was dominant and accounted for 79% of the total sums of squares (SS_T) compared with <1% for the I*N*Y interaction.

In 2003/04, total accumulated DM was 22.6 t DM/ha/y for the I+N pasture 10.5 for I-N, 15.1 for D+N and 7.5 for D-N pastures. The yield ratios were therefore 0.46, 0.67 and 0.33 of the potential maximum determined from the I+N pasture. In 2004/05, total DM yield was 21.1 t DM/ha/y from the I+N pasture. The yields of I-N (9.1), D+N (16.4) and D-N pastures (5.0) resulted in similar yield ratios (0.43, 0.77 and 0.24) to the previous year.

The reduction in yield of D+N pastures relative to I+N occurred 65 days earlier in 2003/04 (21/11/2003) than in 2004/05 (31/01/2005). The timing of the yield reduction was similar for D-N relative to I-N pastures in both years. The cause of the yield reduction in dryland pastures is explained by water stress in Section 5.3.3.

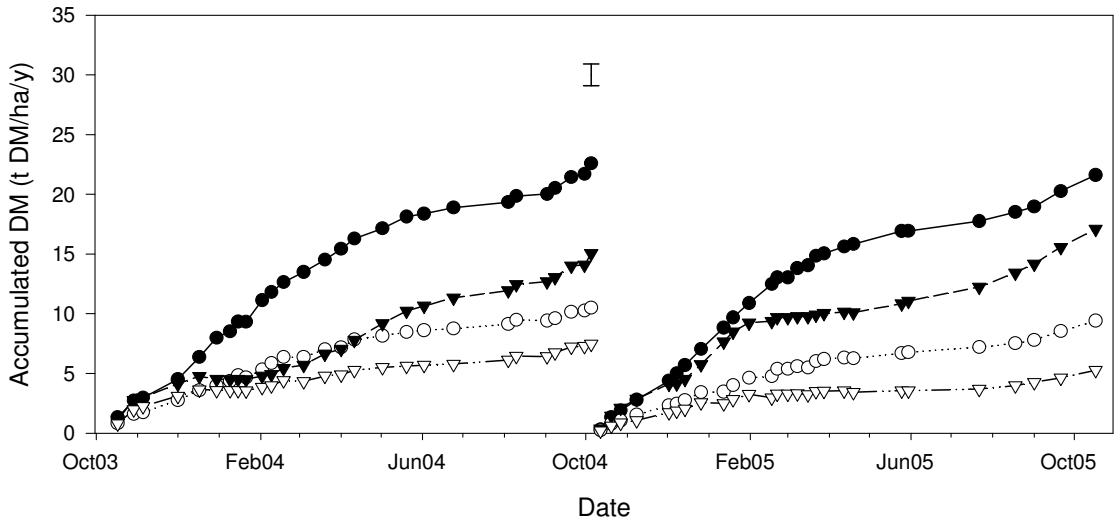

Figure 4.1 Accumulated DM production of 'Grasslands Wana' cocksfoot, at Lincoln University, Canterbury, New Zealand, against time. Treatments are I+N (●), I-N (○), D+N (▼) and D-N (∇) in two years. The error bar is the LSD ($p \leq 0.05$) for the three way interaction (I*N*Y) on total annual DM production. Treatment acronyms were given in Table 3.1.

4.3.2 Mean daily growth rates

Mean daily growth rates of I+N pastures give an indication of variation in potential throughout the year as affected by temperature. As expected, this showed a distinct seasonal response and increased from 12-16 kg DM/ha/d in winter to >75 kg DM/ha/d in spring and summer (Figure 4.2). However, there were also declines in growth rates in late spring of both years which corresponded to the reproductive phase (Section 4.3.3.4). Full details of total DM yields for individual regrowth cycles and treatment effects are given in Appendix 5 (2003/04) and Appendix 6 (2004/05).

The I-N pastures also had the lowest growth rates in winter (8-10 kg DM/ha/d) with maximum growth rates (45-55 kg DM/ha/d) earlier in the growing season (Oct/Nov). There were I*N interactions in summer/autumn caused by low growth rates from dryland pastures. Specifically, in the December 2003 rotation, I+N pastures produced 124 kg DM/ha/d, compared with 43 kg DM/ha/d from I-N pastures and only 16±2 kg DM/ha/d from D+N and D-N pastures. A similar interaction occurred in April 2005, when I+N pastures produced 54 kg DM/ha/d or more than double that produced by the I-N pastures (24 kg DM/ha/d) but both D+N and D-N pastures produced 8±2 kg DM/ha/d.

In 2003/04, the highest growth rate (95 kg DM/ha/d) of D+N pastures occurred in spring (October) and then declined to 8-9 kg DM/ha/d during summer, which was only half the growth rate produced in winter (16-23 kg DM/ha/d). The D-N pastures produced a maximum of 68 kg DM/ha/d (Oct 2003) and declined to 3-5 kg DM/ha/d in winter.

4.3.3 Botanical composition and reproductive status

4.3.3.1 Green cocksfoot

Annually, the amount of green cocksfoot harvested was affected by year ($p \leq 0.001$) (Figure 4.3). In 2003/04, green cocksfoot DM comprised 76% of total yield whereas in 2004/05 cocksfoot made up 83% of total yield. There was also an I*N interaction ($p \leq 0.05$) which showed that the D-N pastures contained less cocksfoot (72%) then I+N, I-N or D+N (83, 80 and 82%, respectively). The amount of green cocksfoot was affected by I*N interactions in the summer and autumn. For example in the 30/12/2003 rotation, the interaction was caused by D+N and D-N pastures which had similar

amounts of green cocksfoot DM (52±0.05%) compared with I+N (62%) and I-N (72%) (data not presented).

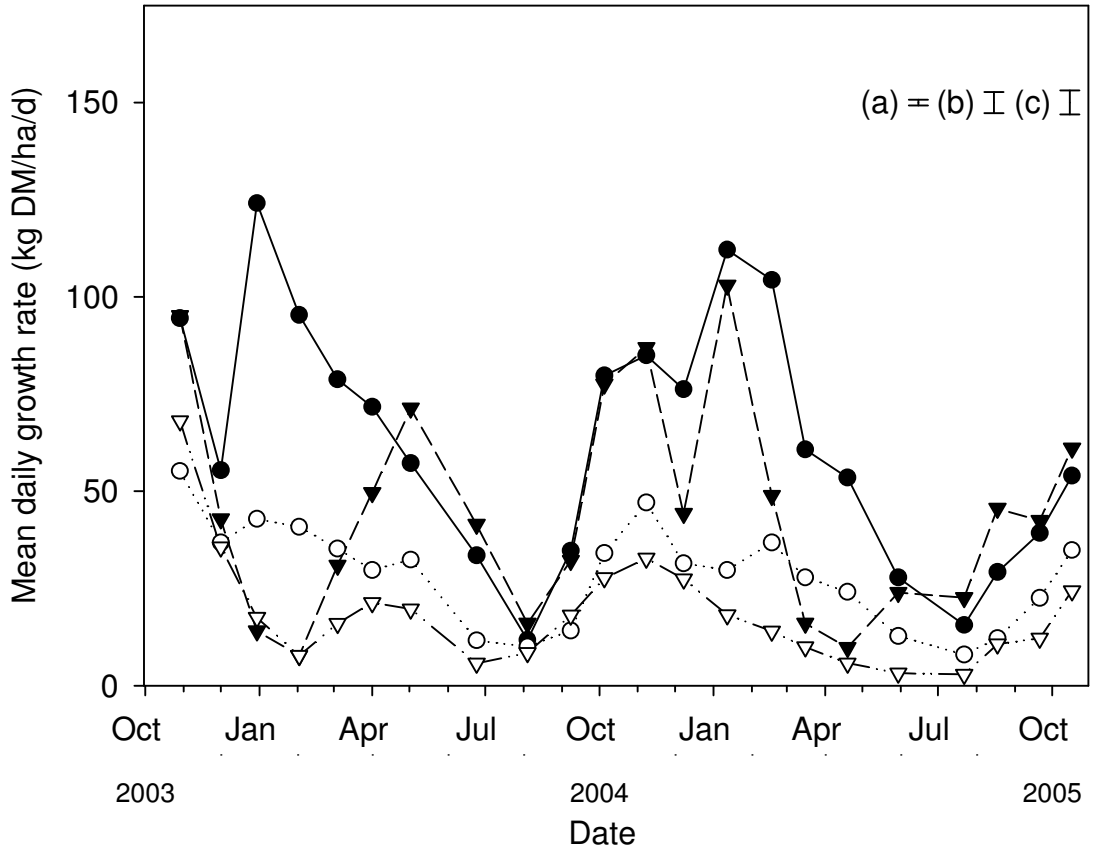

Figure 4.2 Daily growth rates of 'Wana' cocksfoot monocultures under I+N (●), I-N (○), D+N (▼) and D-N (▽) treatments. Error bars are maximum SEM for (a) I effects, (b) N effects or (c) I*N interactions. Treatment acronyms were given in Table 3.1.

4.3.3.2 Weed species

Weed grasses (6%) mainly *Poa annua*, volunteer white clover (<0.1%) and dicot weeds (<0.1%) contributed minimally to total annual DM yield throughout the experiment and were unaffected by the treatments.

4.3.3.3 Senesced material

Annually, the amount of dead material was affected by three two way interactions. The I*N interaction ($p \leq 0.05$) occurred because dead material in D–N pastures was 6.5% higher than in D+N pastures, while I–N treatments contained 3% more dead material than I+N. The I*Y interaction ($p \leq 0.05$) showed that dead material in 2004/05 was 6%

and 2% lower for irrigated and dryland pastures respectively than that measured in 2003/04. The N*Y interaction ($p \leq 0.05$) showed there was 6% less dead material in +N treatments in 2004/05 than 2003/04 but –N treatments had a 3% reduction in dead matter between 2003/04 and 2004/05. In the 30/12/2003 rotation, there was less ($p \leq 0.05$) dead material in irrigated pastures (10±6%) compared with 35±3% in dryland pastures. In addition, there was also less ($p \leq 0.05$) dead material (18±14%) in +N pastures than –N pastures (27±11%) (data not presented).

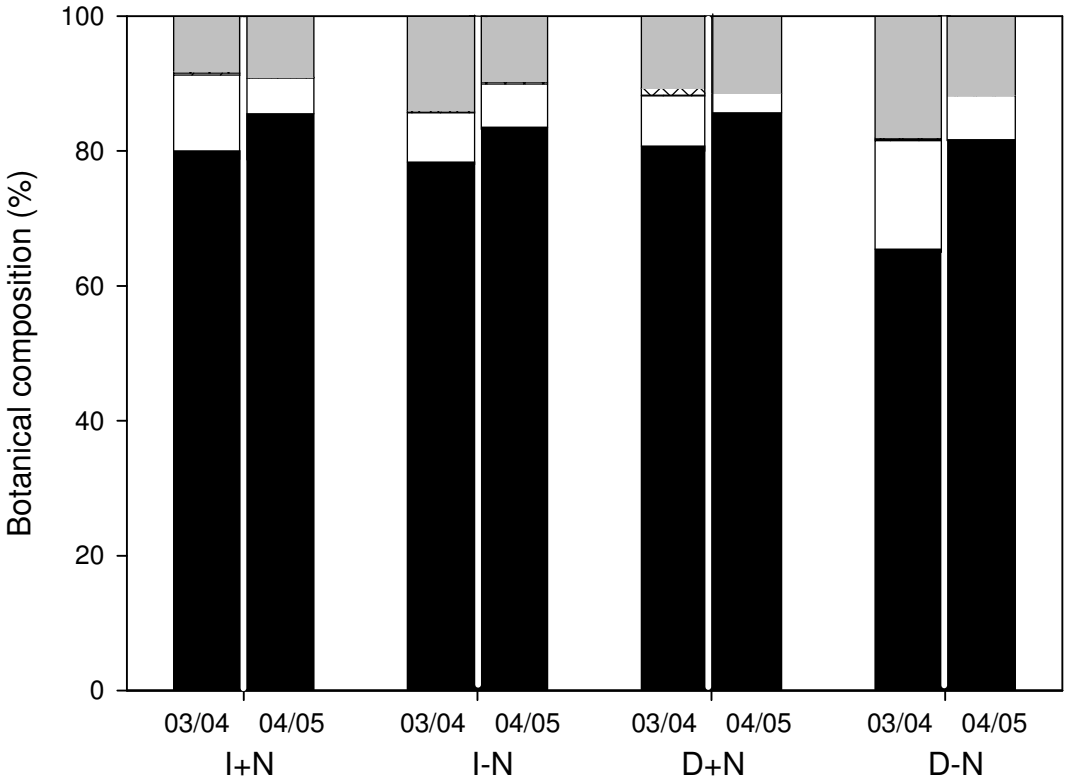

Figure 4.3 Botanical composition of 'Wana' cocksfoot pastures at Lincoln University, Canterbury, New Zealand in 2003/04 (03/04) and 2004/05 (04/05). Components are cocksfoot (■), weed grasses (□) dicot weed (⊠) and dead material (▒). See text for treatment effects. Treatment acronyms were given in Table 3.1.

4.3.3.4 Reproductive material

Reproductive status of the pasture was measured at every destructive harvest where cocksfoot seedheads were present but treatments had no effect on status. In 2003/04, reproductive tillers represented 17% of total tillers on 1/12/2003 and 1% on 17/12/2003. In 2004/05, reproductive tillers were present at harvests on 8/11/2004 (16%), 8/12/2004 (14%) and 12/1/2005 (7%). Tiller population is discussed further in Chapter 7.

4.3.4 Crude protein (CP) yield

Crude protein (CP) yield was determined from green harvested cocksfoot. There was an N*Y interaction ($p \leq 0.001$) which resulted from a 30% increase in annual CP yield (t CP/ha/y) between 2003/04 (3.2) and 2004/05 (4.2) from +N pastures compared with 1.0±0.32 from –N pastures (Table 4.1). As expected, the main effect on CP was caused by N and represented 86% of SS_T compared with 3% for the interaction.

Regrowth cycle CP yields (kg CP/ha) in 2003/04 and 2004/05 are shown in Figure 4.4. The I+N pasture CP ranged from 300-500 kg CP/ha except in winter or when no N was applied. In comparison, the CP yield of the I-N pastures ranged from 167 kg CP/ha (2/5/2004) to 73 kg CP/ha (4/8/2004). The CP yield of the D+N pastures ranged from 30 kg CP/ha to 550 kg CP/ha whereas the D-N pastures ranged from 21-134 kg CP/ha. In the summer/autumn, I*N interactions occurred because CP yield of D+N and D-N pastures were not different.

Table 4.1 Annual crude protein (CP) yield (t CP/ha) of a 'Wana' cocksfoot monoculture grown at Lincoln University, Canterbury, New Zealand in 2003/04 and 2004/05.

Treatment	2003/04	2004/05
I+N	3.7	4.7
I-N	1.2	1.3
D+N	2.7	3.8
D-N	0.6	0.6
Effect	N*Y	
Significance	***	
LSD ($p \leq 0.05$)	0.2	

Note: Treatment acronyms were given in Table 3.1. Levels of significance are: 0.05 (*), 0.01 (**), and 0.001 (***).

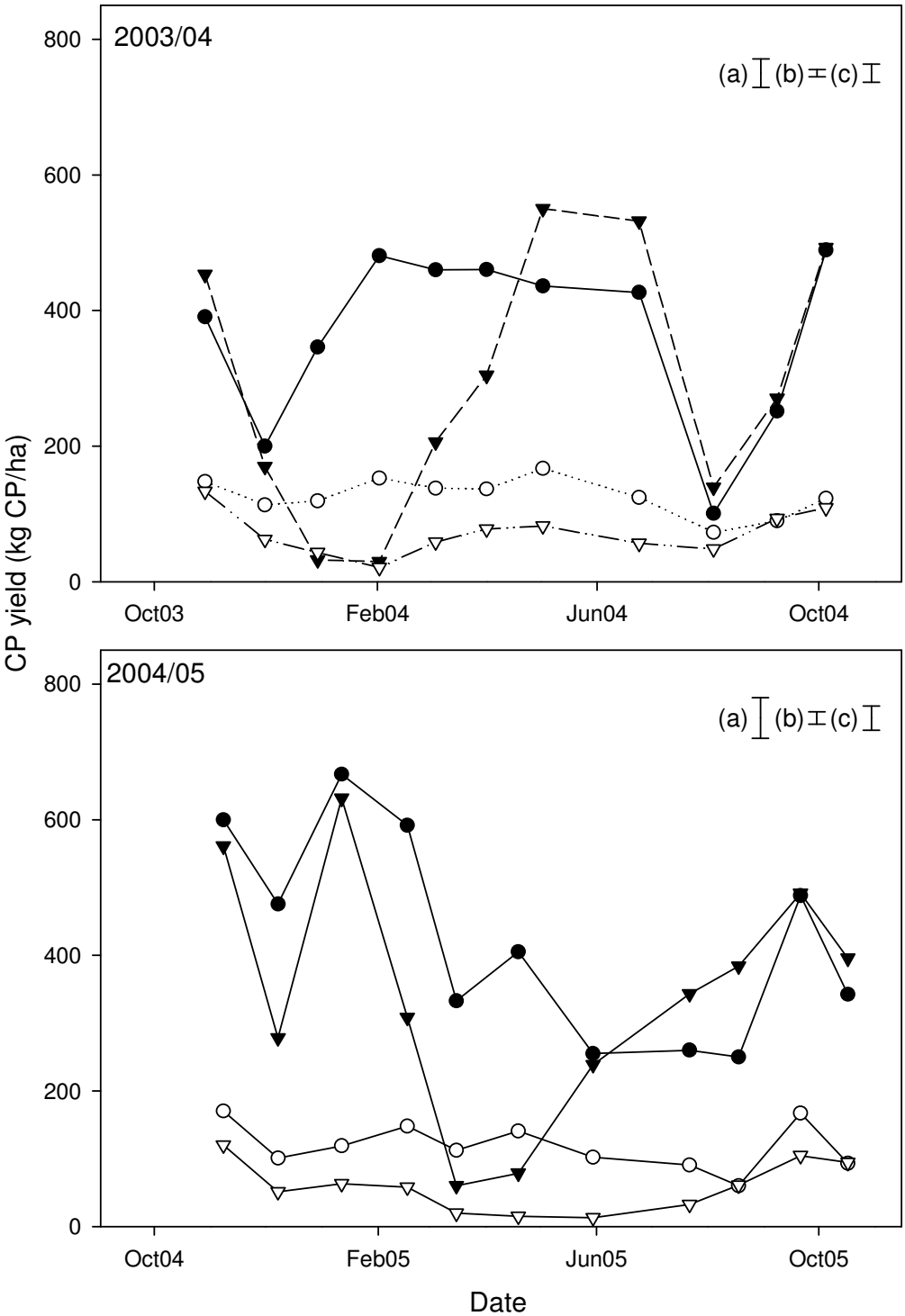

Figure 4.4 Crude protein (CP) yield (kg CP/ha) of 'Wana' cocksfoot in 2003/04 (top) and 2004/05 (bottom) for I+N (●), I-N (○), D+N (▼) and D-N (▽). Error bars are maximum SEM for (a) N effects, (b) I effects and (c) I*N interactions in each season. Treatment acronyms were given in Table 3.1.

4.3.5 Metabolisable Energy (ME) yield

Annual ME yield (GJ ME/ha) was affected by an N*Y interaction ($p \leq 0.01$) with similar values for the –N pastures in 2003/04 (72) and 2004/05 (66) but a 7% increase for +N pastures between 2003/04 (172) and 2004/05 (183) (Table 4.2). Despite the interaction, N was the main cause of observed differences and represented 83% of SS_T compared with <1% for the interaction. Over two years, cocksfoot ME ranged from a minimum of 10.2 MJ ME/kg DM to a maximum of 12.4 MJ ME/kg DM (Figure 4.5). In most cases, there were no treatment differences in winter, but N affected ME content in the summer. There was less variation in 2004/05 than in the first year but ME yield tended to be higher over winter and, in D+N pastures, in the autumn.

Table 4.2 Annual metabolisable energy (ME) yield (GJ/ha) of a 'Wana' cocksfoot monoculture grown at Lincoln University, Canterbury, New Zealand in 2003/04 and 2004/05.

Treatment	2003/04	2004/05
I+N	202	204
I-N	91	86
D+N	143	161
D-N	53	45
Effect	N*Y	
Significance	**	
LSD ($p \leq 0.05$)	10.0	

Note: Treatment acronyms were given in Table 3.1. Levels of significance are: 0.05 (*), 0.01 (**), and 0.001 (***).

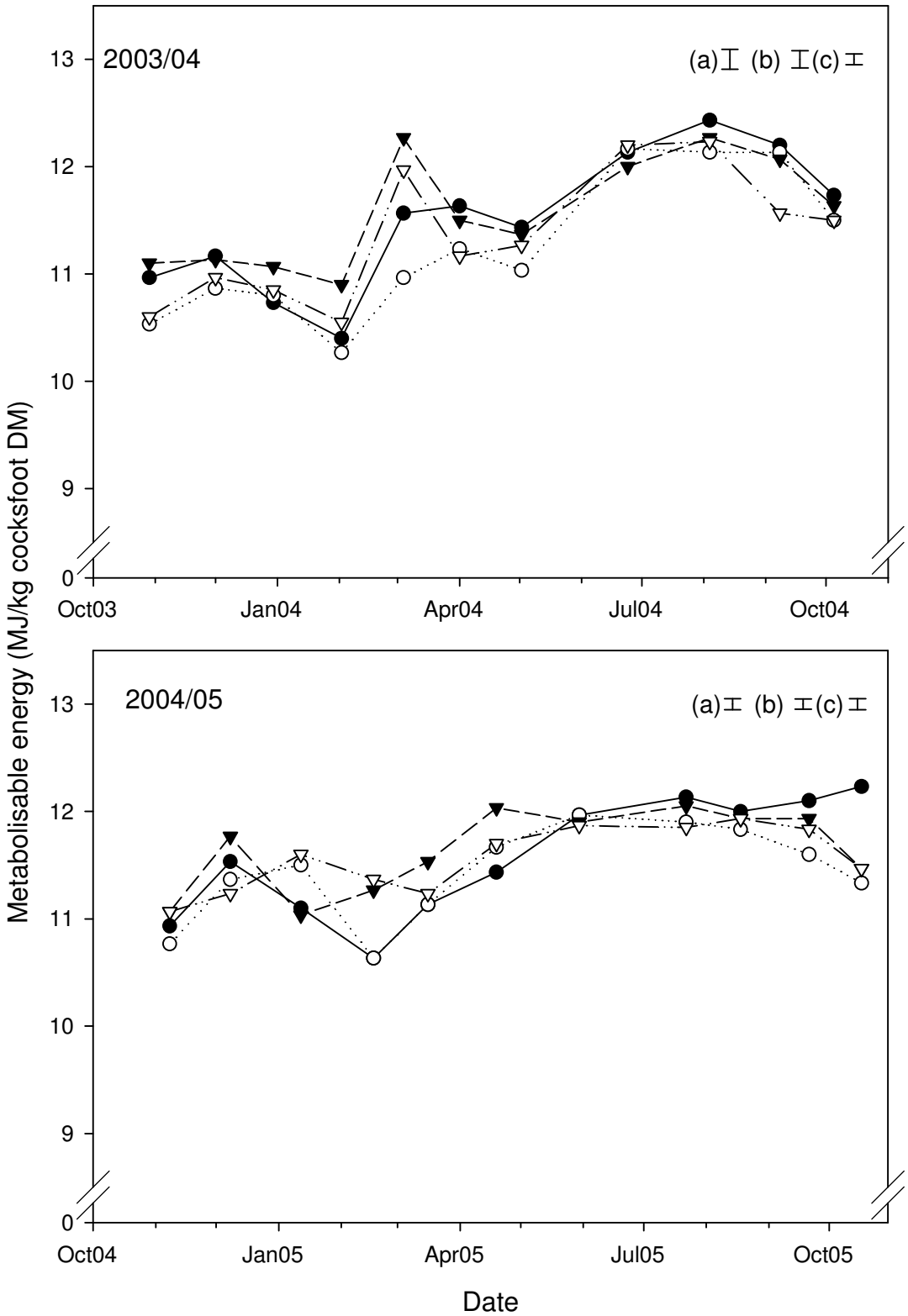

Figure 4.5 Metabolisable energy (ME) content (MJ/kg DM) of green 'Wana' cocksfoot dry matter (DM) at Lincoln University, Canterbury, New Zealand in 2003/04 (top) and 2004/05 (bottom) for I+N (●), I-N (○), D+N (▼) and D-N (∇) pastures. Error bars are maximum SEM for (a) I effects, (b) N effects and (c) I*N interactions in each season. Treatment acronyms were given in Table 3.1.

4.3.6 Analysis of seasonal temperature effect using thermal time

Thermal time was accumulated for 19 individual regrowth cycles of the I+N treatment, and base temperatures were altered in 1°C increments from 0-10ºC (Figure 4.6). Three rotations in 2003/04 were excluded from the analysis because no N was applied. The base temperature which corresponded to the lowest CV, and which had the slope closest to zero, was 3°C. Changing the optimum temperature above the base only changed the slope from 0.1-0.2 and the CV increased from 0.33-0.34. Because of the lack of change an optimum temperature, 23ºC was selected as T_{opt} (data not shown). This was within the temperature range of 19-23°C required for maximum cocksfoot leaf photosynthesis (Peri, 2002).

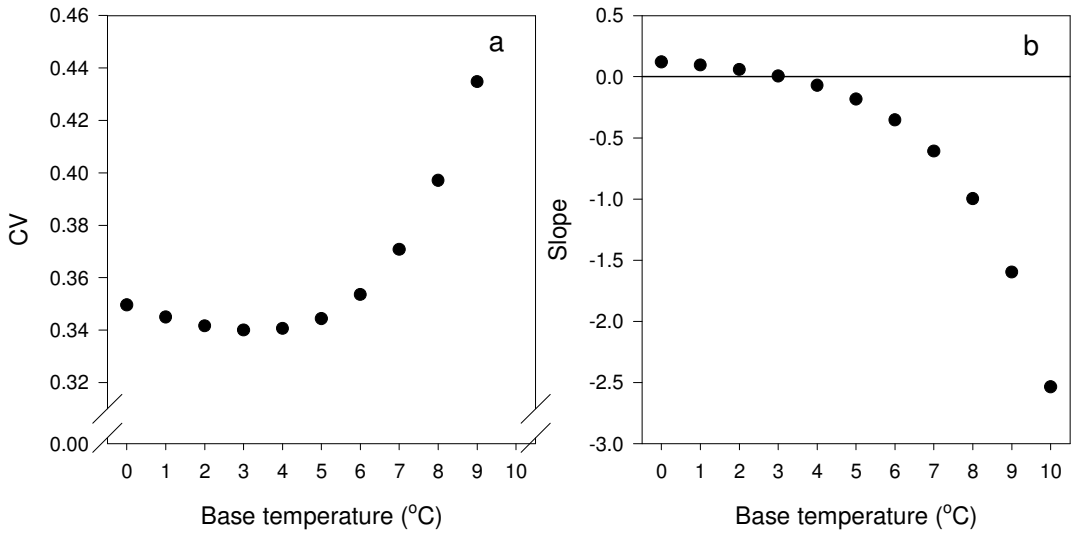

Figure 4.6 Coefficient of variation (CV) (a) and slope (b) at base temperatures from 0-10ºC used to identify the base temperature for 'Grasslands Wana' cocksfoot growth from the I+N treatment as an indicator of environmental potential.

To explain the seasonal variations in pasture growth rates the impact of temperature was summarised through accumulated Tt (Moot *et al.*, 2000) calculated with this base temperature of 3ºC and the optimum of 23ºC (Figure 4.7). The TAGR of the I+N pastures increased ($p \leq 0.001$) at a near constant rate of 7.2 kg DM/ºCd/ha above T_b. For I-N pastures the rate was 3.2 kg DM/ºCd/ha, 56% lower than that of I+N pastures. Reasons for this difference are explained in Chapters 6 and 7. For both treatments there was an indication of systematic variation around the regression which showed the

TAGR overestimated DM production in autumn/winter and underestimated production in spring/summer. The slopes of dryland pastures were compared with those of irrigated pastures. Data from dryland pastures are described and related to water availability in Section 5.3.3.

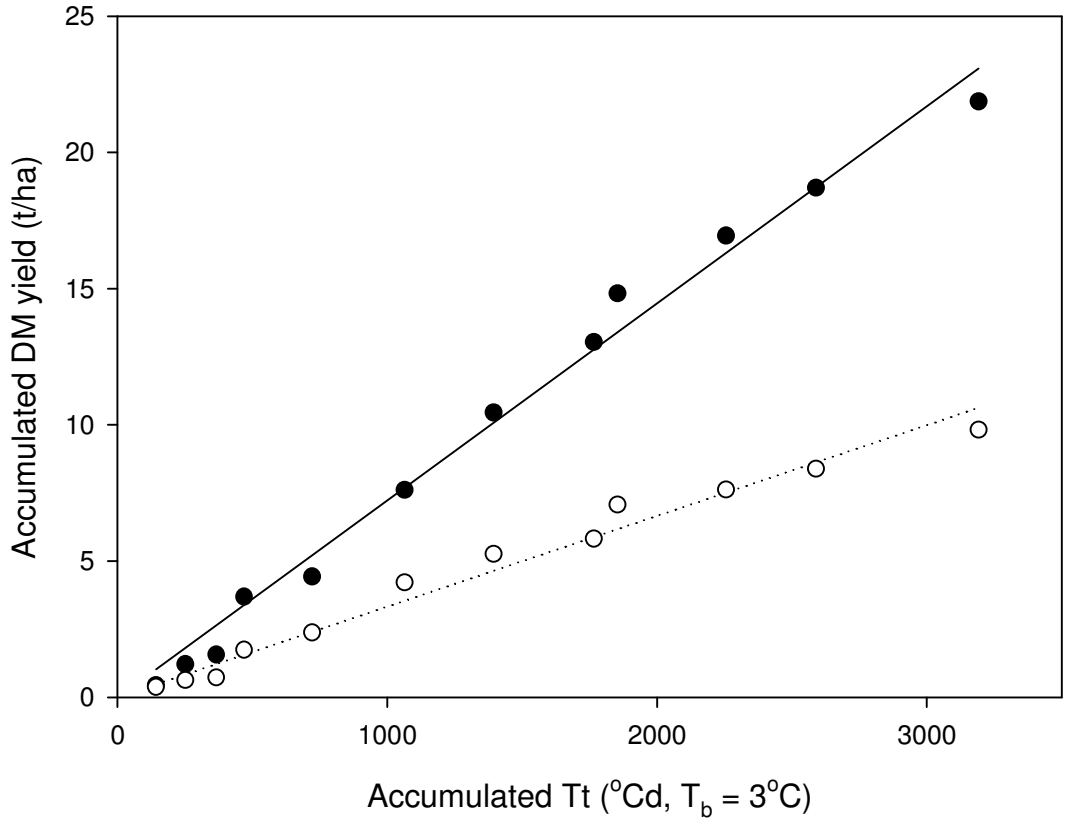

Figure 4.7 Dry matter (DM) accumulation of I+N (●) and I-N (○) pastures against accumulated thermal time (Tt) with a base temperature of 3ºC for a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury New Zealand. Regression of I+N (—) is y = 0 + 7.2x (± 0.1) (R^2=0.97) and I-N (····) is y = 0 +3.2x (± 0.1) (R^2=0.95) with standard error of the slope is given for each regression. Values are the two year average accumulated from end of rotation harvests. Treatment acronyms were given in Table 3.1.

4.4 Discussion

The first objective of this results chapter was to quantify the yield and quality of cocksfoot pastures in response to temperature, water availability and N nutrition. Objective 2 was to account for the seasonal effects of temperature using Tt.

4.4.1 Dry matter production

The maximum yield attained within this environment was 21.9 t DM/ha/y (Figure 4.1) In 2004/05, D-N pastures produced 5.0 t DM/ha/y which was 23% of the environmental potential and similar to yields consistently reported for cocksfoot pastures in dryland Canterbury (Stevens *et al.*, 1992). This confirms previous work which has also shown N was the most limiting factor to cocksfoot pasture production in this environment (Peri *et al.*, 2002a).

The maximum yield was comparable to the potential (Section 2.2) estimated for perennial ryegrass pastures in Canterbury (Mitchell, 1963) and was consistent with irrigated lucerne stands (25 t DM/ha/y) but exceeded that of either chicory (*Cichorium intybus*) or red clover (18 t DM/ha/y) in the same region (Brown *et al.*, 2005). This confirmed that although cocksfoot is generally perceived to be a drought tolerant species suited to low-moderate fertility conditions (Section 2.3) it is capable of high yields when neither water or N limit productivity. In addition, these results show that, if irrigation is available, sufficient N is required to allow DM production to accumulate at potential rates and this will also directly increase the quality of feed on offer (Sections 4.3.4, and 4.4.2).

Pastures receiving irrigation alone yielded <50% of the potential maximum but were comparable to yields reported by Hayman and McBride (1979) for irrigated ryegrass pastures in Canterbury (6.3-13.0 t DM/ha/y). McBride (1994) also reported irrigation increased pasture yield by 44% (6.7 to 11.9 t DM/ha/y), averaged over a 34 year period which is similar to the 40% reported by Peri (2002a) and the response to irrigation in 2003/04 reported here. However, in 2004/05 irrigation increased yield by 82% compared with the control (D-N) pastures because water stress occurred two months later in 2004/05 than 2003/04 (Section 5.4.1). This meant that after autumn rains alleviated water stress, pastures experienced higher temperatures, and thus accumulated

more Tt, in 2003/04 than 2004/05. This is confirmed by the growth rates which decreased in late summer/autumn and continued to decline in winter (Figure 4.2).

The D+N pastures produced at least double the yield of the control pastures (D-N) in both years (Section 4.3.1). Peri (2002) also reported N increased yield by 155% at a comparable N rate to that used in 2004/05 which supports the contention that N was the main factor affecting yield. Yields of D+N deviated from I+N earlier (December) in 2003/04 than 2004/05 (February) and when considered the lack of growth rate response of the D-N pastures in 2004/05 shows that the timing of the delay is important and affects annual DM production. In 2003/04, autumn rains (Section 3.4.1 and Figure 3.1) alleviated drought conditions (Section 5.3.3) while temperatures were higher than those experienced in the second year when the drought occurred leading into decreased winter temperatures (Figure 3.2). Therefore, as photosynthesis rates are highest at temperatures from 19-23°C there was more potential production (Peri, 2002). Control yields (D-N) were less than those reported by Peri (2002) under grazing (9.2 t DM/ha/y) but similar to the 7.6 t DM/ha/y reported by Stevens *et al.* (1992) and others (Sections 2.3 and 2.5). The annual yield variation, both within and between regions, shows the impact of year to year variation caused by water stress. However, the timing, extent and duration of the drought period will ultimately determine the reduction in dryland pasture production (Jamieson, 1999) and this will be investigated further in Chapter 5.

4.4.2 Pasture quality

Nitrogen was also the main cause of difference in pasture quality (Table 4.1) but CP yield was 30% higher in the second year from +N pastures and was comparable to those reported for lucerne (4.6-4.4 t CP/ha/y) by Brown (2004). However, to achieve comparable values large quantities of N were applied to cocksfoot (800 and 1 600 kg N/ha/y in 2003/04 and 2004/05, respectively), whereas lucerne had no applied N and produced CP yields as a result of biological N fixation, the extraction and utilisation of soil N reserves and utilisation of N returns from grazing livestock. The –N pastures produced annual CP yields of only 0.9 and 1.0 t CP/ha/y because they were totally reliant on the soil N. A nitrogen nutrition index was generated (Section 6.3) to quantify the effect of various levels of N nutrition. In individual regrowth cycles, cocksfoot CP of DM ranged from a minimum of 11.8% (D-N) to a maximum of 43.2% (I+N) over the two years and this corresponds to leaf N% of 1.8 and 6.9, respectively.

Annual ME yield increased by 7% (Table 4.2) between 2003/04 and 2004/05. The increase in ME yield was associated with a corresponding increase in green cocksfoot material harvested in 2004/05 (Section 4.3.3). Annual ME, from the +N treatments was >170 GJ/ha/y which was comparable to annual ME consumption reported for irrigated lucerne (191), chicory (141) and red clover (140) (Brown, 2004). However, both CP and ME of –N pastures was less than half those of +N treatments. The ME of green cocksfoot material ranged from 10.2-12.4 MJ ME/kg DM (Section 4.3.4) over the two years. These values represent the quality of green cocksfoot herbage above cutting height and do not include contributions from any other pasture component or residual biomass. Thus, these values may be taken as the annual minima and may have been higher if quality had been determined from total DM. However, this may indicate that reported reductions in cocksfoot pasture quality and associated poor palatability (Edwards *et al.*, 1993) may be a reflection of an increase in the proportion of senesced material of low N content relative to total DM (Section 2.3.2). As expected, there were seasonal variations in pasture ME (Figure 4.5). Pasture ME was lower in late spring and summer compared to autumn and winter. The reasons for these seasonal quality variations were reviewed in Section 2.3.2.

4.4.3 Mean daily growth rates

Growth rates of the I+N pastures ranged from 12-124 kg DM/ha/d, which were similar to the minimum and maximum reported in Finland (14-140 kg DM/ha/d) and consistent with the maximum (130-154 kg DM/ha/d) from France (Rinne, 1978; Lemaire *et al.*, 1982). In New Zealand, ryegrass dominant pastures produce daily growth rates that range seasonally from 5-90 kg DM/ha/d (Baars *et al.*, 1991) and it has been shown that ryegrass growth rates are lower (35 kg DM/ha/d) than cocksfoot in the summer (65 kg DM/ha/d) (Radcliffe and Baars, 1987). Moloney *et al.* (1993) also reported that the seasonal production pattern was lowest in the winter and highest in the summer, and cocksfoot production exceeded that of ryegrass in summer.

There was a seasonal response of daily growth rates to mean regrowth air temperature which was hysteretic (data not presented). The response showed higher growth rates occurred in spring and summer (excluding the reproductive phase) compared with corresponding growth rates at similar temperatures in autumn and winter. This has been shown for ryegrass/white clover pastures using 100 mm soil temperatures (Radcliffe and Baars, 1987). Cocksfoot is a long day plant (Section 2.3) and reproductive

development is initiated by the change from increasing to decreasing photoperiod (Broue, 1973). Therefore, the hysteretic response may indicate a change in partitioning priority associated with the reproductive phase. Hysteresis has been shown in some spring wheat cultivars with reduced final leaf number as photoperiod increased compared with leaf numbers at corresponding daylengths as photoperiod decreased (Brooking *et al.*, 1995). When the pasture entered the reproductive phase growth rates decreased which was similar to the response of reproductive ryegrass pastures. This short term decline in response to a change in development occurs as seedheads mature and is usually associated with a reduction in vegetative tiller population (Anslow, 1966). This occurs under non limiting conditions even if management minimises reproductive status of the pasture (Radcliffe and Baars, 1987).

The period of peak production for cocksfoot occurs in summer (Charlton and Stewart, 2000) and generally happens later than in ryegrass pastures (Radcliffe and Baars, 1987). The main cause is the different temperature optima of the two species for photosynthesis (Kemp *et al.*, 1999; Peri, 2002). This shows the benefit of cocksfoot, under non limiting conditions, where production peaks after the reproductive phase is completed and growth rates are higher than ryegrass in summer and autumn (Radcliffe and Baars, 1987). In contrast, at low temperatures, the predominant effect of temperature is to reduce leaf appearance and extension rates which are a function of thermal time accumulation (Section 2.4). Consequently, at low temperatures it takes longer to accumulate the number of heat units required for leaf appearance and extension (McKenzie *et al.*, 1999) and photosynthetic rate also declines with reduced air temperature (Peri *et al.*, 2002b).

Growth rates of D+N pastures were similar to potential except in summer/autumn (Section 4.3.2). Water is required for nutrient uptake from the soil so if there is insufficient water (Section 5.3.3), even when N is not a limitation to growth, DM production will only proceed at the rate allowed by the most limiting factor (water). In summer/autumn growth rates were lower than those in winter which showed drought can have a greater affect on productivity of cocksfoot pastures than low winter temperatures. After February rainfall in 2003/04 (Section 3.4.1.1), daily growth rates of D+N were higher than those in the I+N pastures (Figure 4.2). This could be a result of cell expansion of leaves initiated under stress conditions as cell expansion is the first

process affected by water stress and cell division can continue even if there is insufficient water for expansion (Hsiao, 1973).

The recovery after drought (Section 2.5.2) may depend on the development stage of the leaf at the time the stress is imposed. It has been shown that leaves, which have been initiated but have not entered the phase of rapid cell proliferation when water stress occurred, can expand without showing any affect on final leaf size after rewatering, other than the delay caused by the stress (Durand *et al.*, 1995; Alves and Setter, 2004). This is probably the cause of compensatory growth following drought (Horst and Nelson, 1979; Kramer, 1983).

4.4.4 Botanical composition

Nine years after establishment, cocksfoot was the dominant species in the pastures (Section 4.3.3) and represented 91% of harvested green herbage over the two growth seasons. The persistence of cocksfoot has lead to its recommendation as a component in seasonally water stressed dryland pastoral systems. The lack of unsown species similarly shows cocksfoot does not allow invasive weed species to encroach into the environment. Annually, the proportion of senesced material was highest in the D-N pastures (21%) and lowest in I+N pastures (10%).

4.4.5 Accounting for seasonal temperature variation

Thermal time was used to summarise cocksfoot growth (Section 4.3.6). The I+N pasture yield increased at a rate of 7.2 kg DM/^{o}Cd/ha (Figure 4.7) above a T_b of 3°C. This was 56% higher than that calculated for I-N which produced 3.2 kg DM/^{o}Cd/ha. This means that at any given temperature when moisture was sufficient the +N pastures were producing DM at twice the rate of –N or control pastures. The Tt concept allows extrapolation of results to other years and environments as long as total solar radiation receipts are similar to those reported here (5038±24 MJ/m^2/y) (Sections 2.4.4 and 3.2) and water stress is avoided. Validation will be required in regions with different solar radiation receipts because, above T_b, plants with similar leaf area will produce more DM when solar radiation receipts are 20 MJ/m^2/d than at 2 MJ/m^2/d. The systematic variation around the regressions was probably associated with remobilisation and/or partitioning which is similar to other perennial species such as lucerne (Teixeira, 2005) and asparagus (*Asparagus officinalis* L.) (Wilson *et al.*, 2002). Seasonal changes in root formation and/or regeneration have been shown previously for both perennial ryegrass

and cocksfoot (Caradus and Evans, 1977; Ridley and Simpson, 1994) which may also explain the systematic variation observed when Tt was used to summarise growth of above ground biomass.

Both the T_b and T_{opt} identified for growth were close to the those identified for photosynthesis by Peri *et al.* (2002b). Although selection of the optimum was somewhat arbitrary, within a temperate environment selection of an incorrect T_b will have a greater affect in producing systematic error (Bonhomme, 2000) than an incorrect T_{opt} because there are fewer days above T_{opt} in the course of a growing season (Section 2.4.3). This shows the dependence of DM production on i) photosynthesis as the main biophysical process contributing to DM yield and ii) thermal time on the rate of leaf appearance/extension which influences the quantity of light intercepted by the pasture.

Furthermore, this approach may allow production in other regions to be estimated (Table 4.3). Based on the TAGR relationships generated for I+N and I-N pastures, long term (1971-2000) annual temperature data from NIWA (National Institute of Weather and Atmospheric Research) were used to estimate potential and N limited production in different regions throughout NZ assuming a non limiting water supply. Mean monthly air temperatures were multiplied by the appropriate TAGR and days in each month. These were then summed to estimated annual yields for different regions. This indicates that although cocksfoot is generally perceived to be a drought tolerant species (Rumball, 1982) it is performing well below potential in most regions throughout New Zealand either due to insufficient soil moisture or N deficiency.

Table 4.3 Estimated annual yields of cocksfoot pastures under N sufficient and N deficient conditions at several New Zealand sites assuming non limiting water, based on long term meteorological data summaries (1971-2000), using a base temperature of 3°C to accumulate thermal time and temperature adjusted growth rates (TAGR) of 7.2 and 3.2kg DM/°Cd/ha as calculated in Figure 4.7.

Location	Latitude and Longitude	Mean annual temperature (°C)	Potential yield (t DM/ha)	N limited yield (t DM/ha)
Kaitaia	35°08'S and 173°17'E	15.7	33.4	14.8
Napier	39°30'S and 176°56'E	14.5	30.2	13.4
Blenheim	41°38'S and 173°57'E	12.9	26.0	11.6
Christchurch	43°33'S and 172°47'E	12.1	23.9	10.6
Alexandra	45°14'S and 169°25'E	10.8	20.5	9.1
Invercargill	46°24'S and 168°24'E	9.9	18.1	8.1

4.5 Conclusions

This chapter presented the results necessary to meet Objectives 1 and 2 (Sections 1.4 and 4.1). Based on these results, the following conclusions can be made:

- Cocksfoot pastures can produce 21.9 t DM/ha annually when neither water nor N are limiting. In spring, before soil moisture limited pasture production, -N pastures produced only half the DM of +N pastures. In dryland systems this is the critical period when DM production is required to meet livestock demand.

- Nitrogen was the main factor which affected crude protein and ME. Crude protein was a maximum of 4.7 t CP/ha/y (I+N) compared with a minimum of 0.6 t CP/ha/y from D-N pastures. The ME ranged from 204 GJ ME/ha/y (I+N) to 45 GJ ME/ha/y from D-N pastures. Annual differences were caused by the timing of drought conditions and the increase in N application rate between years.

- Growth rates were highly dependent on variation in seasonal temperatures. Under non limiting moisture conditions I+N pastures produced 7.2 kg DM/^{o}Cd/ha compared with 3.2 kg DM/^{o}Cd/ha for I–N pastures above a base temperature of 3°C.

The following chapter will describe the effect of water stress on DM production of dryland pastures. Nitrogen deficiency will be examined in Chapter 6.

5 Describing reduced DM production by dryland pastures

5.1 Introduction

Chapter 4 showed cocksfoot pastures produced between 5.0 and 21.9 t DM/ha/y dependent on water and nitrogen availability. Yields of I+N and I-N pastures were then described in relation to thermal time to account for the seasonal effects of temperature. There were consistent linear relationships for irrigated pastures, but the linearity failed in dryland pastures.

Objective 3 of this research was to quantify the extent of yield reductions caused by water stress (Section 1.4). In this chapter, the soil moisture conditions that reduced pasture growth in dryland pastures are investigated. Specifically, the critical limiting deficit (D_L) (Penman, 1971) is calculated (Section 2.6.7). This is used to determine the extent of yield reductions in response to the development of the actual soil moisture deficit (ASMD). The yields of dryland pastures are also explained in relation to the quantity of water used and water use efficiency (Section 2.6.8). Objective 4 was to apply the 'Monteith framework' (Monteith, 1986) to describe water extraction (Section 2.6.3) by dryland pastures.

5.2 Materials and Methods

Experimental design and management details were presented in Section 3.4. Details related to biological measurements, which contain details on soil moisture measurement and the irrigation schedule, were presented in Section 3.6. Briefly, soil water measurements were made at 33 dates in 2003/04 and 36 dates in 2004/05. This section describes methods used to describe the effects of water availability on DM yield. The theory and relevant literature on water use and extraction were presented in Section 2.6.

5.2.1 Actual soil moisture deficit (ASMD)

The ASMD (0-0.8 m) was calculated with Equation 5.1 and differs from Equation 3.4 (Section 3.6.4) which was used to trigger irrigation applications based on soil water content in the 0-0.5 m soil layer. Criteria which resulted in the exclusion of changes in

soil moisture content at soil depths >0.8 m from calculation of the ASMD are described fully in Section 5.2.7.

Equation 5.1 $$ASMD = ASMD_i + AET - P_{(R+I)} - D$$

Where $ASMD_i$ is the sum of the ASMD (0-0.8 m) on the previous day (mm), AET is sum of actual evapotranspiration (0-0.8 m) between sequential measurements and P is precipitation which includes inputs from both rainfall (R) and irrigation (I) and excludes drainage (D) losses to soil depths >0.8 m.

5.2.2 Water use (WU)

Water use (WU) was calculated from Equation 5.2 as the sum of WU (mm) from 0-1.2 m soil depths. Changes in soil water content in the 0.8-1.2 m soil layers occurred during known periods of water stress (Section 5.3.3, Figure 5.3). In this study, the-main objective is to explain limitations to cocksfoot growth. However, water extracted from the 0.8-1.2 m soil layers probably contributed to pasture survival and subsequent recovery (Sections 5.2.1 and 5.2.7), but minimally to measured DM yield, and were therefore included in calculations of water use.

Equation 5.2 $$WU = P_{(R+I)} - (SMC_i - SMC_t)$$

Where SMC_i was the soil moisture content (SMC) at the previous measurement and SMC_t was the SMC on the current day. These were summed to determine both annual and regrowth cycle WU.

5.2.3 Water use efficiency (WUE)

Water use efficiency (kg DM/mm) was determined from the slope of linear regression, forced through the origin, fitted to the relationship between accumulated DM yield and cumulative water use (mm) calculated from Equation 5.2. The regressions were fitted to annual DM yields and also to DM production within each individual regrowth cycle. Water use efficiency was not calculated for the first rotation (ending 29/10/2003) as soil moisture measurements were not initiated until two weeks into the regrowth cycle.

5.2.4 Upper (UL) and lower limits (LL) to plant water extraction

The measured DUL (% v/v) and LL (% v/v) to water extraction were calculated to determine the plant available waterholding capacity (mm) in each soil layer of dryland

pastures (Section 2.6.4). The difference between DUL and LL was used to describe the plant available waterholding capacity (PAWC) for each 0.2 m soil layer (Equation 5.3).

Equation 5.3 $$PAWC = (UL-LL)*d$$

Where PAWC is the plant available waterholding capacity (mm) and d is layer depth (m).

In this study, the UL for each soil layer was defined as the maximum volumetric soil moisture content (VWC). This may have differed from the upper limit (UL) used to describe patterns of water extraction described in Section 5.2.5.2 when the soil was not fully wet at the start of the extraction period analysed. The lower limit (LL) to water extraction within individual soil layers was identified as the lowest measured VWC during known periods of water stress as the actual soil moisture deficit increased. The consistency of LL measurements in dryland pastures indicated it was likely that the minimum VWC was close to the LL, particularly in the 0-0.8 m soil layers. For example, the LL identified in known periods of water stress from dryland pastures was 6.8±0.5% in the 0-0.2 m soil layer; 8.2±0.1% in the 0.2-0.4 m soil layer and 8.2±0.1% in the 0.4-0.6 m soil layer.

It has been reported that measured LL in soil layers where the SWC does not change but extraction continues in lower soil layers provides an adequate description of field derived LL, provided there are no precipitation inputs (Ritchie, 1981). However, when the lowest measured VWC is used to identify LL, values may not be accurate because of incomplete extraction (Dardanelli *et al.*, 2004). This may be caused by either i) precipitation inputs which increase the VWC in upper soil layers and reduce the need for extraction at depth or ii) insufficient root length density within the lower soil layers (Section 2.3.1).Therefore, for crops/pastures managed under dryland conditions where rainfall occurs during the measurement period, the LL may not be equal to the lower asymptote of the exponential curve between VWC and time (d) (Dardanelli *et al.*, 2004).

Section 5.3.3 will show water extraction in individual soil layers beneath a dryland pasture reached a plateau prior to autumn rainfall. Generally, the majority of plant roots have been shown to be distributed in soil layers which showed an exponential decrease in VWC during periods with no precipitation inputs (Passioura, 1983; Dardanelli *et al.*, 2004). The description of exponential soil water extraction is described in Section 5.2.5

and reviewed in Section 2.6. The LL of irrigated pastures was unable to be determined because the experiment was ongoing and irrigation (Section 3.5.1) ensured the ASMD did not exceed 50 mm in the top 0.5 m of the profile. However, it was unlikely to differ from that of the dryland pastures as the soil/pasture combinations of the four pastures were the same in both growth seasons.

5.2.5 Patterns of water extraction

When neutron probe access tubes were installed (Section 3.6.3.1) it was observed that depth to alluvial gravels occurred between 0.6-0.8 m in all pastures. It was hypothesised that root water extraction may have been limited by i) a lack of plant available water at lower soil depths or ii) because root penetration was impeded because of soil textural change. The practical implication of both factors is a reduction in PAWC. Templeton silt loam soils generally have 0.5-0.7 m of silt loam/sandy loam textured fine material overlying gravels (Cox, 1978; Webb *et al.*, 2000). In this study, the increase in the proportion of stones present at depths >0.6-0.8 m meant the volume of the soil available to store soil moisture was reduced compared with soil layers between 0-0.8 m.

5.2.5.1 Period of analysis

In 2003/04, equations were fitted to the relationship between VWC and time (d) for the period between 30/9/2003-21/1/2004 (96 d) at which time the maximum soil moisture deficit was measured. In addition, rainfall in December 2003 was only 1.2 mm (Section 3.2.1) which made this the most appropriate period to describe water extraction patterns. The LL used for curve fitting was the lowest recorded VWC during the analysis period because the asymptote of the equations was less than the minimum VWC. The maximum VWC for the period was used as DUL. Previous literature supports the use of VWC at the start of extraction when the soil is not fully wet (Meinke *et al.*, 1993). This will have no effect on kl or t_c as the amount of water extracted depends on the PAWC of the soil layer at the time of extraction. In 2004/05, water extraction patterns were not analysed because of above average rainfall in 12/2004, 04/2005 and 05/2005 (Sections 3.4.1.1 and 5.3.2).

5.2.5.2 The model of water extraction

The pattern of water extraction within individual 0.2 m soil layers of dryland pastures was described by the 'Monteith framework' (Monteith, 1986) (Section 2.6). This

involved fitting exponential models (Passioura, 1983) to describe the change in VWC over time (Equation 5.4). The original model (Equation 2.10) has been modified by the inclusion of a switch (Brown, 2004) to keep VWC constant prior to the start of extraction (t_c). Models were fitted to 12 soil layers (0.2 m/layer) between 0-2.3 m for all replicates of the D+N and D-N pastures.

Equation 5.4 $$\mathbf{VWC = LL + PAWC * (Exp(-kl\ (t-t_c)))}$$ **when ($t>t_c$)**

The model coefficients describe the extraction decay constant (kl) and t_c for each soil layer. Where t_c is the day extraction begins in a soil layer during a growth season.

Models which had R^2 >0.75 were accepted to accurately describe water extraction within a soil layer. This was the same criteria as that used previously when describing water extraction by annual crops and taprooted forages (Section 2.6.3). Models were also fitted to water extraction in the 0-0.2 m soil layer, whereas it is usually discarded for this type of analysis (Meinke *et al.*, 1993). Inclusion of the 0-0.2 m layer enabled description of the maximum number of coefficients (kl and t_c) to be described for this soil/pasture combination. Pasture species such as cocksfoot, perennial ryegrass and white clover have all been shown to have the majority (72-81%) of their total root length in the 0-0.2 m soil layer (Sections 2.3.1 and 2.6.5) whereas no roots were present at depths >1.5 m (Evans, 1978). In contrast, annual crops and taprooted forages can extract water from ≥1.3 m by the end of the season (Section 2.6.3).

5.2.6 Plant available waterholding capacity of the soil ($PAWC_S$)

Equation 5.5 converts the difference between DUL and LL in the 0-1.2 m soil layers to mm of plant available water. There was no evidence to indicate LL (0-1.2 m) would differ between irrigated and dryland pastures. Therefore, the mean LL of D+N and D-N pastures was used as the LL for the I+N and I-N pastures (Section 5.2.4). The $PAWC_S$ of the soil (0-1.2 m) was 172.6 mm and was unaffected ($p \leq 0.25$) by treatment. Inclusion of soil layers between 0.8 and 1.2 m depths represented 20.6±2.4 mm of plant available water included in this total.

Equation 5.5 $$\mathbf{PAWC_S = \sum(DUL-LL) * maximum\ extraction\ depth\ (mm)}$$

5.2.7 Statistics

As reported the DM yields of pasture with or without N differed (Section 4.3.1). Therefore, relative yield reductions of the two dryland pastures were determined separately based on a maximum set from their respective irrigated crops. Thus, yields from the I+N pasture were used to define the potential for the D+N pastures. Similarly, yields from the I-N pasture yield were used as the non water limited maximum for the D-N pastures.

The critical limiting deficit (D_L) (Penman, 1971) (Section 2.6.7) was identified by fitting broken stick models (Draper and Smith, 1998) to the relationship between relative yield and the ASMD (Equation 5.6). The model with the highest R^2, and which accounted for the most variation compared with the initial linear regression, was then used to explain reductions in relative yield. For this procedure, the ASMD was increased by adding changes in soil water content from each successive soil layer until all measured soil layers (0-2.3 m) were included.

Equation 5.6 $$\textbf{Relative yield} = 1 - (C * (ASMD - D_L))$$

Where C is the rate of reduction in relative yield (%/mm) and D_L is the critical limiting deficit beyond which yield reductions occur.

Results showed the R^2 increased from a minimum of 0.69 with the initial linear regression to a maximum of 0.85 for –N and 0.98 for +N pastures based on an ASMD calculated from changes in soil moisture content in the 0-0.8 m soil layer. Inclusion of changes in soil moisture content in soil layers >0.8 m caused the R^2 to decline from these maximum R^2 values. Therefore, to describe yield reductions, the ASMD was based on the soil moisture deficit calculated from changes in the soil water content from the 0-0.8 m soil depth. It is important to note that this differs from the depths from which water use and water use efficiency were calculated outlined in Section 5.2.2.

The temperature adjusted growth rates (TAGR) of dryland pastures were compared with irrigated pastures (Section 4.3.6) by ANOVA of slopes against thermal time (Tt) accumulation for pre- and post-stress periods (before and after D_L was exceeded) across all treatments. Where significant, treatment means were separated using Fishers' protected LSD at the $\alpha = 0.05$ level. Where interactions occurred the most conservative LSD was used to separate means.

Three stage broken stick models (Draper and Smith, 1998) were fitted to the relationship between accumulated DM production and Tt for water stressed pastures. The model was used to determine the delay caused by water stress as indicated by the plateau in accumulated DM yield compared with irrigated pastures. The model with the lowest correlation coefficient, compared with the initial linear regression, identified the period when soil moisture availability was the main factor which compromised DM production (Draper and Smith, 1998).

For comparisons across years, WU and WUE were analysed using a split-split plot design with year as a repeated measure. This analysis was conducted to determine annual variation in WU which is primarily a function of the environmental variables of temperature, VPD, solar radiation and PET (French and Legg, 1979). Within individual regrowth cycles, WU and WUE were analysed using a split plot design with irrigation as the main plot and N as the sub plot treatment.

Exponential models of water extraction, described by Equation 5.4, were fitted by non-linear regression in SYSTAT 9 for the D+N and D-N pastures. Irrigated pastures were not included in the analysis. Models were fitted to the relationships between VWC and time (d) for the water stressed period, described in Section 5.2.5, for dryland pastures in each 0.2 m layer of the soil profile between 0-2.3 m (n=72). At all soil depths >0.8 m models consistently failed (R^2 <0.75) so only data for the 0-0.2, 0.2-0.4, 0.4-0.6 and 0.6-0.8 m soil depths are presented. The –kl and t_c coefficients determined by curve fitting to describe water extraction pattern by D+N and D-N pastures were then analysed by ANOVA with a split plot design using N as the mainplot and soil depth as the subplot in Genstat 8.2.

5.3 Results

5.3.1 Plant available waterholding capacity of the soil ($PAWC_S$)

The $PAWC_S$ which contributed to growth was 152±3.8 mm (0-0.8 m) and was similar for all pastures. An example of the soil moisture profile under a D+N pasture (plot 1, replicate 1) is shown in Figure 5.1. At soil depths between 0.8 and 1.2 m, volumetric water content declined during periods of water deficit (Section 5.3.3, Figure 5.3) and provided access to an additional 20.6±2.3 mm of water. The low DUL at soil depths >0.8 m corresponded to the depth to alluvial gravels.

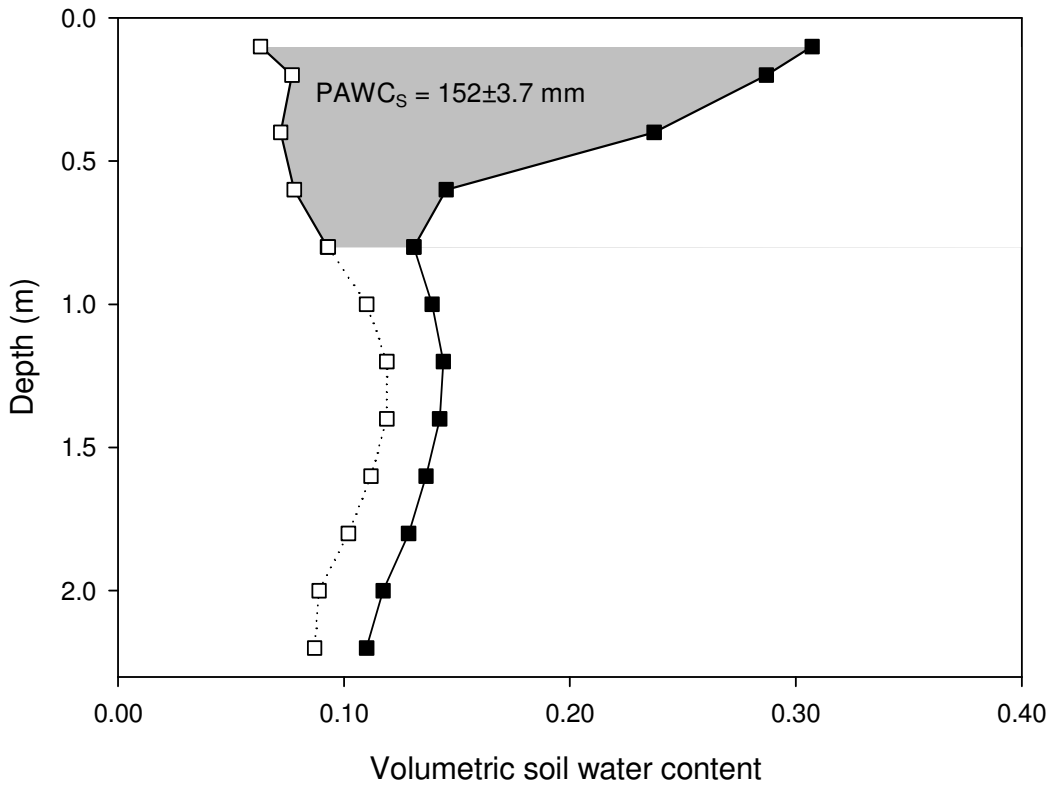

Figure 5.1 Drained upper (■) (DUL) and lower (□) (LL) limits of an eight year old 'Grasslands Wana' cocksfoot monoculture grown on a Templeton silt loam soil at Lincoln University, Canterbury, New Zealand. Data are for a D+N pasture (plot 1, replicate 1). The shaded area represents the plant available waterholding capacity of the soil ($PAWC_S$) within soil layers (0-0.8 m) which were used to calculate the actual soil moisture deficit for yield reduction and text is $PAWC_S$±SEM (mm). An additional 20.6±2.3 mm was extracted from the 0.8-1.2 m soil layers.

5.3.2 The actual soil moisture deficit (ASMD)

At the start of each growth season (30/9/2003 for 2003/04 and 6/10/2004 for 2004/05) the ASMD (0-0.8 m) was 28±11 mm and increased to 81±11 mm before irrigation was initiated. The ASMD of irrigated pastures was consequently reduced and maintained at 44±34.5 mm in 2003/04 and 38±26.3 mm in 2004/05. The ASMD of dryland pastures reached a maximum of 137±2.5 mm in 2003/04 (Figure 5.2). Dryland pastures showed the main period of recharge occurred from 2000-3000°Cd, or from 30/3/2004-2/9/2004, when there was 317 mm of rain. In 2004/05, a total of 85 mm of rain fell between 15/12/2004 and 27/12/2004. This decreased the ASMD of dryland pastures to a similar value to the irrigated pastures. The ASMD in dryland pastures then increased to a maximum of 129±0.4 mm on 22/3/2005, or 1925°Cd accumulated above a T_b of 3°C since the beginning (6/10/2004) of the 2nd growth season. The main recharge period occurred from 2100-2800°Cd (14/4/2004-18/8/2004), when 161 mm of rain fell. The discussion (Sections 5.4.1 and 5.3.6) will address the reason for using thermal time as the explanatory variable instead of date.

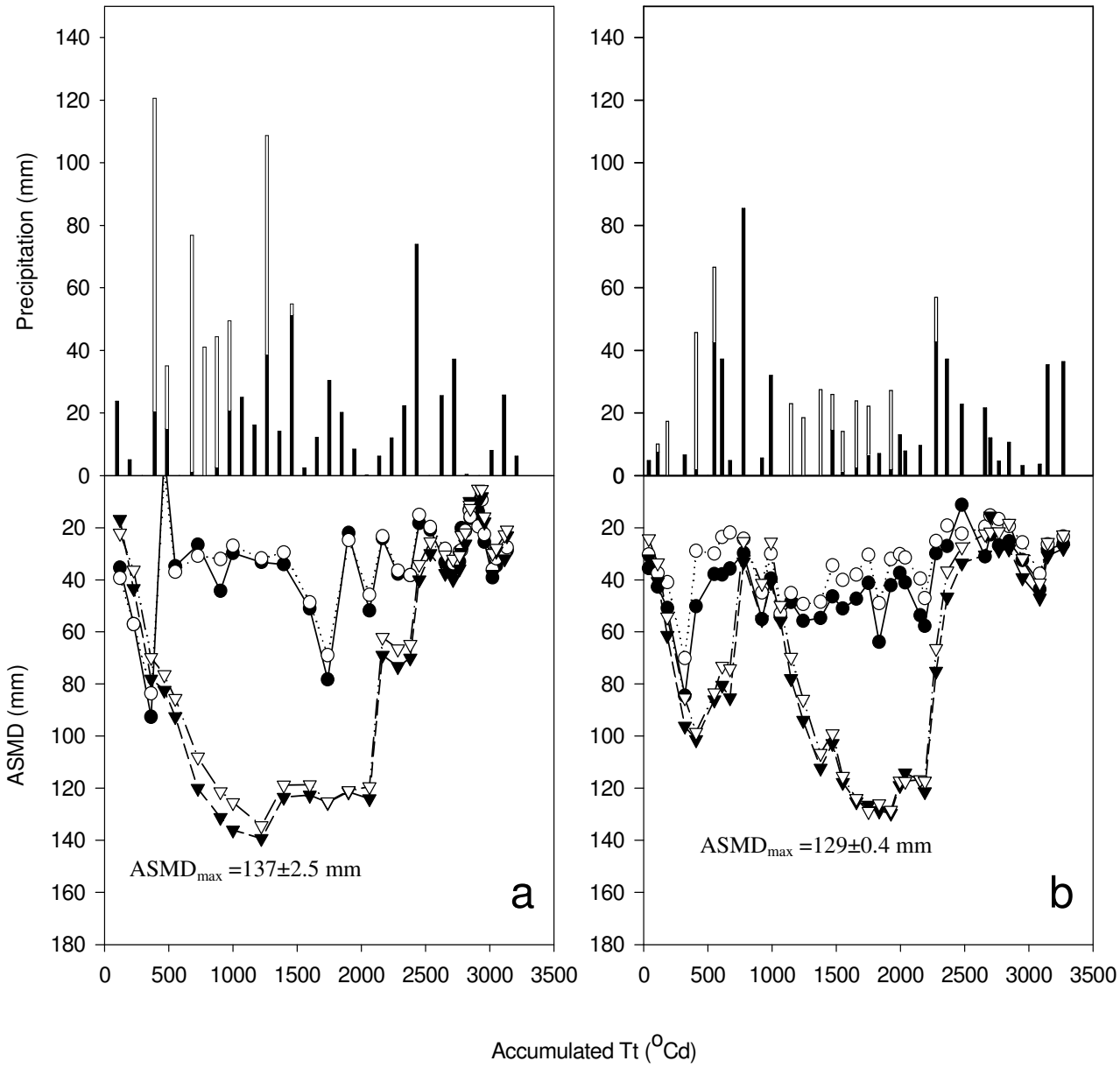

Figure 5.2 Precipitation (top) including rainfall (■) and irrigation (□) in (a) 2003/04 and (b) 2004/05 and actual soil moisture deficit (ASMD) (mm) (bottom) from 0.0-0.8 m soil depth for I+N (●), I-N (○), D+N (▼) and D-N (▽) treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. The mean maximum ASMD ($ASMD_{max}$) of D+N and D-N pastures in 2003/04 and 2004/05 is shown. In 2003/04, thermal time was accumulated (T_b=3°C) between 30/9/2003-5/10/2004 and between 6/10/2004-17/10/2005 in 2004/05. Treatment acronyms were given in Table 3.1.

5.3.3 Water extraction patterns

Figure 5.3 shows the pattern of water extraction of a D+N pasture (replicate 1, plot 1) at six depths in the profile (0.0-1.2 m). Table 5.1 summarises the kl and t_c parameters from curve fitting procedures to describe soil water extraction.

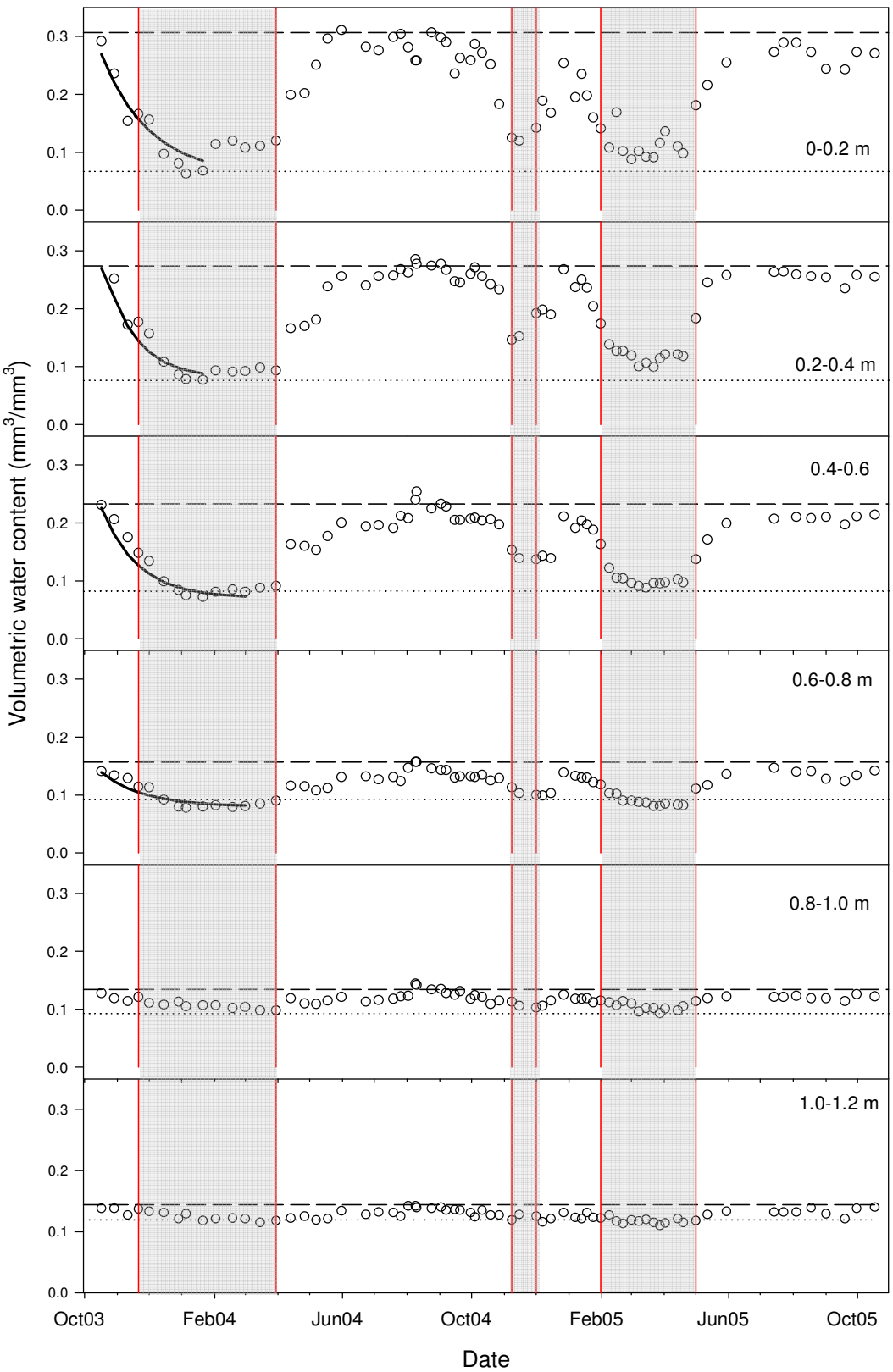

Figure 5.3 Water extraction patterns in the top six 0.2 m layers (0.0-1.2 m) below a D+N pasture (plot 1, rep 1) applied to an eight year old 'Grasslands Wana' cocksfoot monoculture on a Templeton silt loam soil at Lincoln University, Canterbury, New Zealand. Shaded areas indicate known periods of water stress when the actual soil moisture deficit was >78 mm. Dashed lines (- -) indicate the measured upper limit and dotted lines (····) represent the measured lower limit to extraction.

For the period of analysis, layer depth affected ($p \leq 0.01$) the LL (mm^3/mm^3) to extraction. In the 0-0.2 m soil layer the LL was 0.068 compared with 0.084±0.005 in the 0.2-0.4 and 0.4-0.6 m soil layers and 0.104 at 0.6-0.8 m soil depths. The PAWC was different ($p \leq 0.001$) in all four soil layers (0-0.8 m) and decreased from a maximum of 0.228 (0-0.2 m) to 0.055 in the 0.6-0.8 m soil layer and was unaffected by N level. The extraction decay constant (-kl) was unaffected by treatment and was 0.032. The start of extraction (t_c) was also affected ($p \leq 0.01$) by layer depth with extraction initiated in the 0.6-0.8 m soil layer 37 d into the analysis period, on 5/11/2003 which was 18 days after extraction began to decrease VWC in the 0-0.2 m soil layer.

Table 5.1 Coefficients to describe the pattern of water extraction by D+N and D-N pastures for the 0-0.2, 0.2-0.4, 0.4-0.6 and 0.6-0.8 m soil depths with R^2>0.75 in 2003/04 between 1/12/2003 and 21/1/2004 when the maximum soil moisture deficit was reached.. Where the –kl is the extraction decay constant and t_c is the time until extraction began within a soil layer. The lower limit (LL) was the minimum measured volumetric water content (mm^3/mm^3) for the extraction period and PAWC is the difference between /the volumetric water content on 17/10/2003 and LL (mm^3/mm^3).

Year	Pasture	Soil layer (m)	LL	PAWC	-kl	t_c (d)	R^2
2003/04	D+N	0-0.2	0.068	0.228	0.032	19	0.95
		0.2-0.4	0.076	0.193	0.034	22	0.98
		0.4-0.6	0.084	0.137	0.032	25	0.97
		0.6-0.8	0.106	0.057	0.035	39	0.91
	D-N	0-0.2	0.68	0.227	0.029	21	0.95
		0.2-0.4	0.092	0.159	0.037	27	0.96
		0.4-0.6	0.083	0.123	0.036	31	0.97
		0.6-0.8	0.102	0.053	0.017	35	0.84
		Effect	Depth	Depth	NS	Depth	
		Significance	**	***		**	
		LSD	0.015	0.035		6.7	

Levels of significance are: 0.05 (*), 0.01 (**), and 0.001 (***). Treatment acronyms were given in Table 3.1.

5.3.4 Water use (WU)

Annually, the amount of water used (0-1.2 m) was affected ($p \leq 0.001$) by an I*Y interaction (Table 5.2). Irrigated pastures used 757 mm in 2003/04 compared with 651 mm in 2004/05 and dryland pastures used 377 mm in 2003/04 and 435 mm in 2004/05.

Table 5.2 Annual water use by a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand.

	Water Use (mm)	
Treatment	2003/04	2004/05
I+N	735	651
I-N	778	650
D+N	387	440
D-N	366	429
Effect	I*Y	
Significance	***	
LSD ($p \leq 0.05$)	35.0	

Treatment acronyms were given in Table 3.1.

Mean daily water use (WU_{daily}) of all pastures were similar in rotations ending 4/8/2004; 5/10/2004; 22/7/2005; 18/8/2005; 21/9/2005 and 17/10/2005 (Figure 5.4). Irrigated pastures showed a seasonal variation and had a maximum WU_{daily} of 5.8 mm/d in December 2003 and a minimum of 1.1 mm/d in June 2004. In comparison, dryland pastures had a maximum WU_{daily} of 3.1 mm/d (21/9/2005) and a minimum of 0.7 mm/d (2/5/2004). The WU_{daily} of dryland pastures was consistently lower than that of irrigated pastures from December to May in both growth seasons. The timing of the maximum differences of WU_{daily} between irrigated and dryland pastures was in December and January rotations of the 2003/04 growth season compared with rotations ending 19/4/2005 and 30/5/2005 in the second growth season.

In the first rotation of both growth seasons there was an effect ($p \leq 0.05$) of N on WU_{daily}. In the 29/10/2003 rotation, +N pastures used 1.8 mm/d compared with 1.4 mm/d by –N pastures. Similarly, in the 8/11/2004 rotation, +N pastures used 2.9 mm/d compared with 2.5 mm/d by –N pastures ($p \leq 0.01$). Subsequently, irrigation was the main cause of differences in WU_{daily} until July in each year. For example, in the 2/2/2004 rotation, irrigated pastures used 4.0 mm/d ($p \leq 0.001$) compared with 0.7 mm/d by dryland

pastures. For reference Figure 5.4 also shows mean daily potential evapotranspiration for each regrowth cycle which generally overestimated actual water use by all pastures.

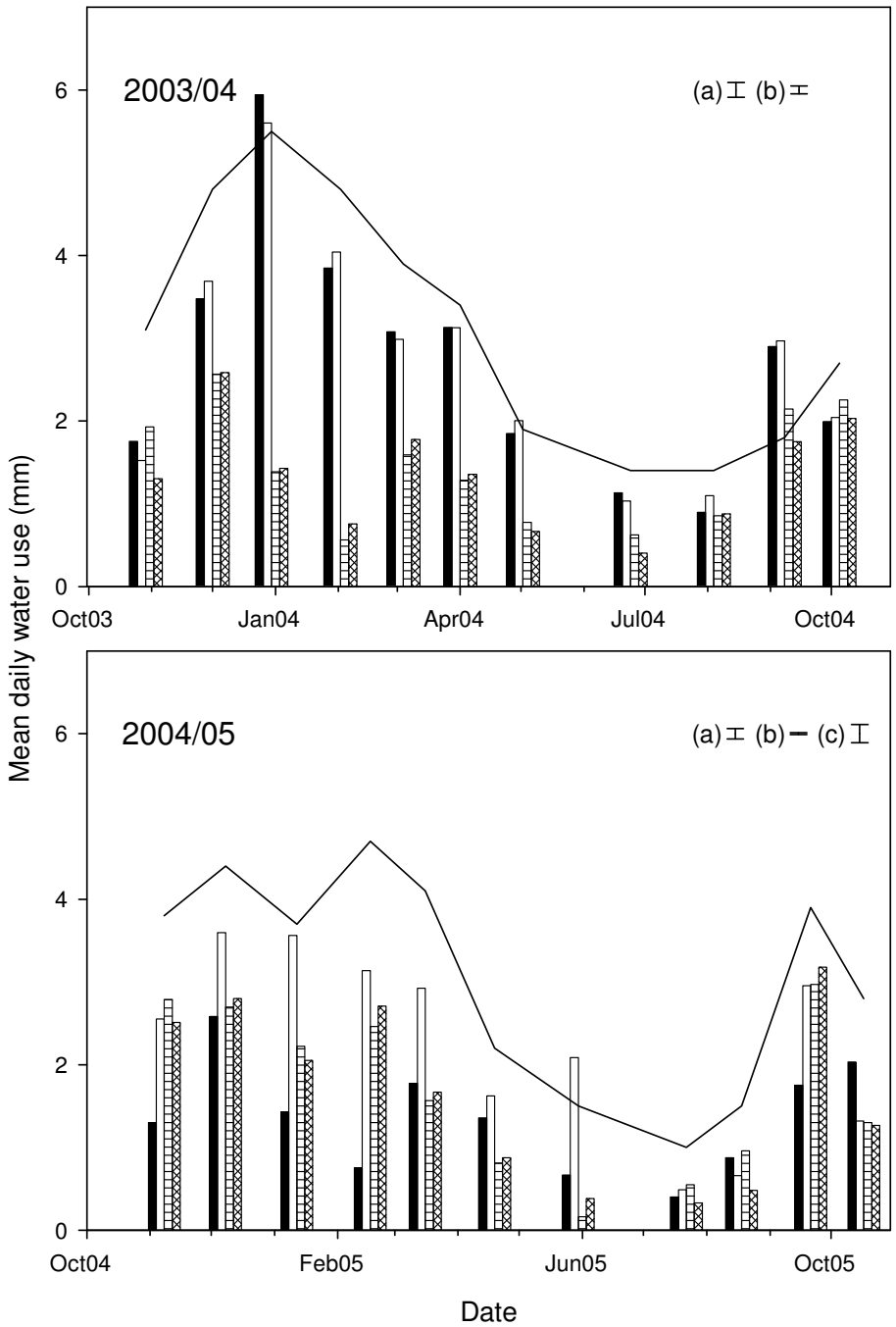

Figure 5.4 Mean daily water use (mm/d) of I+N (■), I-N (□), D+N (▤) and D-N (▩) 'Wana' cocksfoot pastures at Lincoln University, Canterbury, New Zealand in 2003/04 (top) and 2004/05 (bottom). The solid line (—) is average daily Penman potential evapotranspiration (PET) for each regrowth period. Error bars are maximum SEM for (a) I, (b) N and (c) I*N effects. Treatment acronyms were given in Table 3.1.

5.3.5 The critical limiting deficit (D_L)

To account for the effect of water on pasture yields, the D_L (Penman, 1971) was identified from data collected during periods when the ASMD was increasing. The D_L was identified using a broken stick approach (Sections 2.6.7 and 5.2.7) using mean treatment data (Figure 5.5). Measurements when soil water recharge occurred through rainfall were excluded because soil moisture was not measured daily.

Analyses showed the D_L was 83 and 73 mm for +N and –N treatments, respectively. However, there is no reason to expect the D_L to differ between dryland treatments, and there is a distinct lack of data around the point of inflexion which makes it difficult to accurately determine this. When the point of inflexion was averaged to a D_L of 78 mm the rate of reduction in relative yield (RY) was similar at 1.45% DM/mm for both treatments when ASMD $>D_L$. This rate of yield reduction was similar in both years despite a two month difference in the timing of the maximum ASMD (Figure 5.2).

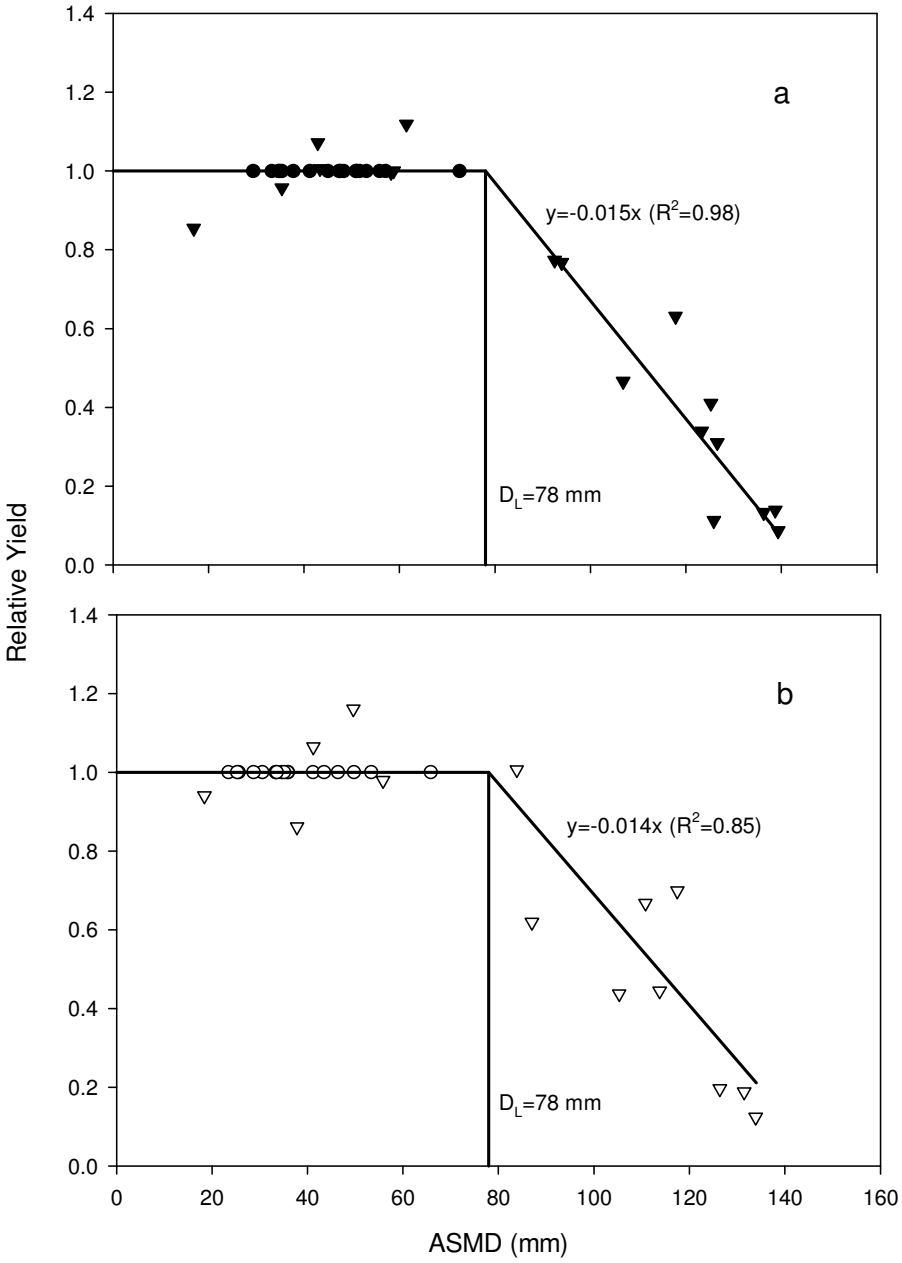

Figure 5.5 Decrease in relative yield of (a) D+N (▼) relative to I+N (●) and (b) D-N (∇) relative to I-N (○) for 'Wana' cocksfoot pasture at Lincoln University, Canterbury, New Zealand during periods when the actual soil moisture deficit was increasing. Treatment acronyms were given in Table 3.1.

5.3.6 Expected yield loss of dryland pastures

Based on the measured periods of moisture stress (Section 5.4.1), the effect of time lost on DM production by dryland pastures, compared to their respective irrigated control pastures, can be estimated. To do this the time beyond D_L, quantified in Tt, was multiplied by the appropriate TAGR (7.2 or 3.2 kg DM/^{o}Cd/ha) from Figure 4.7. Dry

matter produced during the deficit period was then subtracted. This is appropriate because rainfall during the deficit period is available for growth even if it did not appear to decrease the ASMD to <78 mm because soil moisture was not measured daily.

The difference between estimated and measured yields is then added to annual DM production of dryland pastures and compared with yields from their respective irrigated control pastures. These are summarised in Table 5.3. For example, in 2003/04, when the actual soil moisture deficit was >78 mm, the D+N pastures produced 2.9 t/ha and the D-N pastures produced 1.8 t/ha. This was 24% and 35% of estimated yields for the same period if soil moisture had not limited growth. After this production was subtracted from the estimated yield loss caused by water stress it was shown that predicted yields for dryland pastures were within 3-11% of the yields of their respectively irrigated control pastures.

Table 5.3 Effect of lost time, caused by water stress, on the annual yield of dryland pastures. Where (A) is thermal time (Tt) accumulated when the actual soil moisture deficit (ASMD) was >78 mm and (B) is the predicted yield for the period of water stress. For +N pastures: B=A*7.2 kg DM/^{o}Cd/ha and for –N pastures B=A*3.2 kg DM/^{o}Cd/ha. (C) is the measured yield of dryland pastures when ASMD >78 mm, (D) is the annual yield of the dryland pastures and D+(B-C) is the estimated annual yield of dryland pastures if soil moisture was non limiting to DM production. Annual yields of the irrigated control pastures are shown for reference.

	+N		-N	
	2003/04	2004/05	2003/04	2004/05
(A) Tt (T_b=3°C)	1597	1265	1547	1265
(B) Predicted yield (t/ha)	11.5	9.1	5.1	4.1
(C) Measured yield (t/ha)	2.8	2.1	1.8	1.0
(D) Dryland yield (t/ha/y)	15.1	16.4	7.5	5.0
D+(B-C)	23.8	23.4	10.8	8.1
Yield of irrigated control pasture (t/ha/y)	22.6	21.2	10.5	9.1

Data were then reanalysed by ANOVA (I*N*Y*stress_period) to compare TAGR of all pastures in the main pre- and post-water stress periods with the periods when ASMD > D_L (78 mm) excluded (Figure 5.6). These results showed N deficiency caused ($p \leq 0.001$) most of the differences in TAGR. The +N pastures produced 7.0 kg DM/^{o}Cd/ha compared with 3.3 kg DM/^{o}Cd/ha by –N pastures. These values show that the rate of DM accumulation prior to D_L, and then after rainfall alleviated water stress, were

comparable to those calculated under non limiting moisture conditions for I+N (7.2) and I–N (3.2) (Section 4.4.5). This was similar to the model describing time lost for DM production when D_L was exceeded (Penman, 1971). The effect of N on the TAGR of +N and –N pastures is described in Chapter 6.

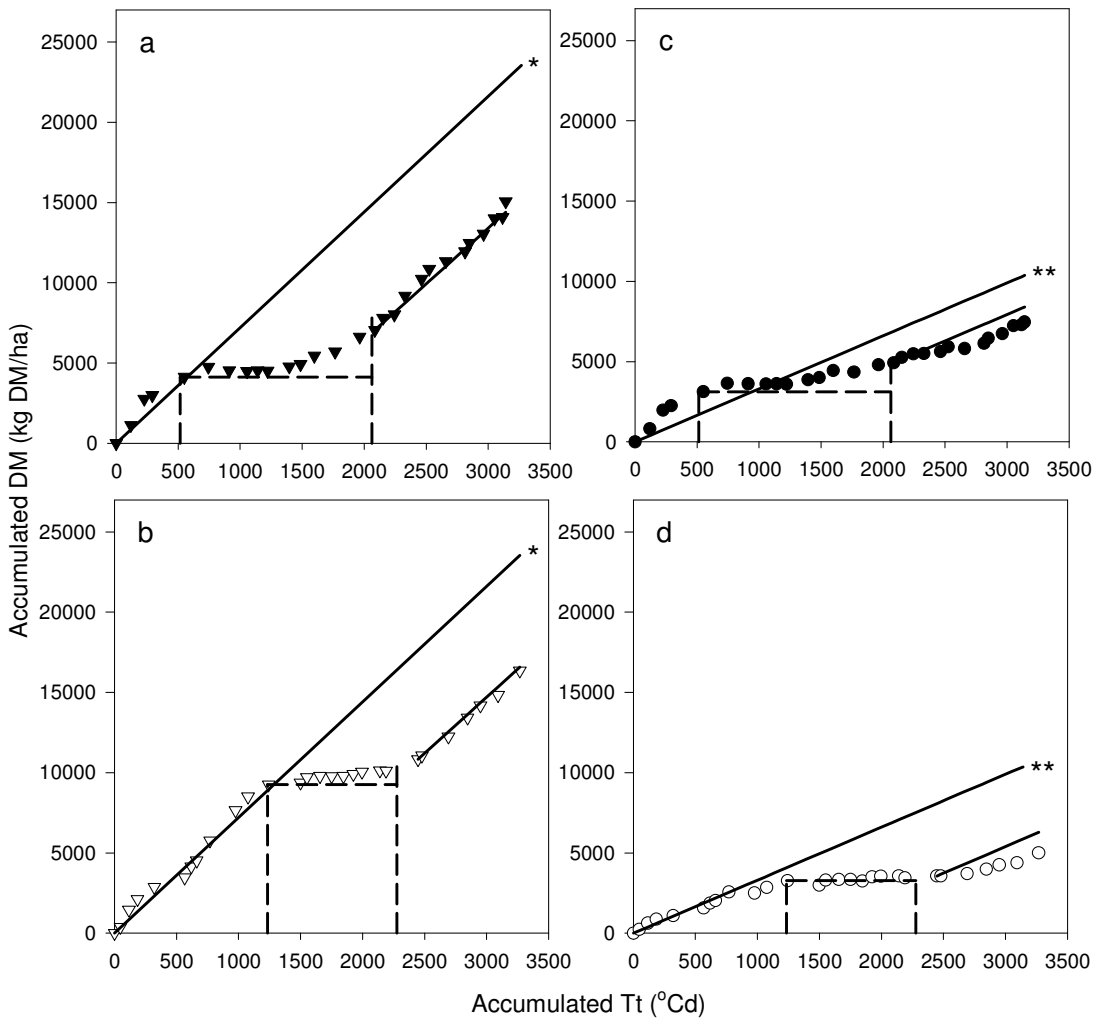

Figure 5.6 Dry matter production of D+N pastures in (a) 2003/04 (▼)and (b) 2004/05 (▽) and D-N pastures in (c) 2003/04 (●)and (d) 2004/05 (○). Solid lines shown by * and ** represent TAGR of I+N (y = 7.2x) and I-N (y = 3.2x) shown in Figure 4.7. Thermal time is accumulated above a base temperature of 3°C. Dashed vertical lines represent the period during which the critical limiting deficit (78 mm) was exceeded by dryland pastures. Slopes of dryland pastures excluding the drought period were 7.0 and 3.3 kg DM/°Cd/ha for +N and -N pastures, respectively. Treatment acronyms were presented in Table 3.1.

5.3.7 Water use efficiency (WUE)

Annual WUE (kg DM/mm) of each pasture was determined from the regression between accumulated DM yield (Section 4.3.1) and cumulative annual WU (Section 5.3.3) (Figure 5.7). The I*Y interaction ($p \leq 0.01$) was caused by the similar WUE of 22.6±0.53 kg DM/mm from irrigated pastures in 2003/04 and 2004/05 and dryland pastures in 2004/05 compared with 30.1 kg DM/mm by dryland pastures in 2003/04. The N*Y interaction ($p \leq 0.05$) occurred because the WUE of –N pastures was 18.5 kg DM/mm in 2003/04 compared with 12.5 kg DM/mm in 2004/05. In contrast, the WUE of +N pastures was 33.5±0.20 kg DM/mm and similar in both years. Despite the interactions, the main effect of N was dominant and represented 83% of SS_T compared with 4% for the I*Y interaction and 2% for the N*Y interaction.

Within individual regrowth cycles, WUE of I+N pastures ranged from 11.9-46.8 kg DM/mm compared with 4.8-26.6 kg DM/mm from the I-N pastures (Figure 5.8). The D+N pastures produced a maximum of 81.2 kg DM/mm in the rotation ending 24/6/2004 (Section 5.3.5), and a minimum of 12.8 kg DM/mm in the 16/3/2005 rotation. The WUE of 81.2 kg DM/mm was unusual and corresponded to a DM yield from the D+N pasture of 2.2 t DM/ha (Appendix 5). Conservatively, if the harvest had cut below the residual pasture height of 3.0 cm and caused an additional 500 kg DM/ha to be measured WUE for this period would have decreased to 62 kg DM/mm which is still greater than WUE from all other pastures. Rainfall for the regrowth period in question totalled 69 mm. It is possible that rainfall may have been underestimated as it was not measured on site. Alternatively, there may have been a calculation error associated with the drainage function which could not be identified as soil moisture was not measured daily. The WUE of the D-N pastures ranged from 6.9 to 30.6 kg DM/mm over the two years.

Nitrogen affected WUE of the pastures in 11 of the 21 regrowth cycles. For example in the rotation ending 8/11/2004, the +N pastures had a WUE of 33.1 kg DM/mm compared with ($p \leq 0.001$) 17.6 kg DM/mm in the –N pastures. Interactions between irrigation and N affected WUE in 7 of the 21 rotations. In the rotation ending 30/12/2003, an I*N interaction ($p \leq 0.01$) showed that I+N pastures had a WUE of 21.7 kg DM/mm compared with 14.8±0.60 kg DM/mm in dryland pastures and 8.2 kg DM/mm in the I-N pastures. Irrigation affected WUE in the rotation ending 19/4/2005

when irrigated pastures had a WUE of 28.2 kg DM/mm compared with ($p \leq 0.05$) 12.9 kg DM/mm in dryland pastures.

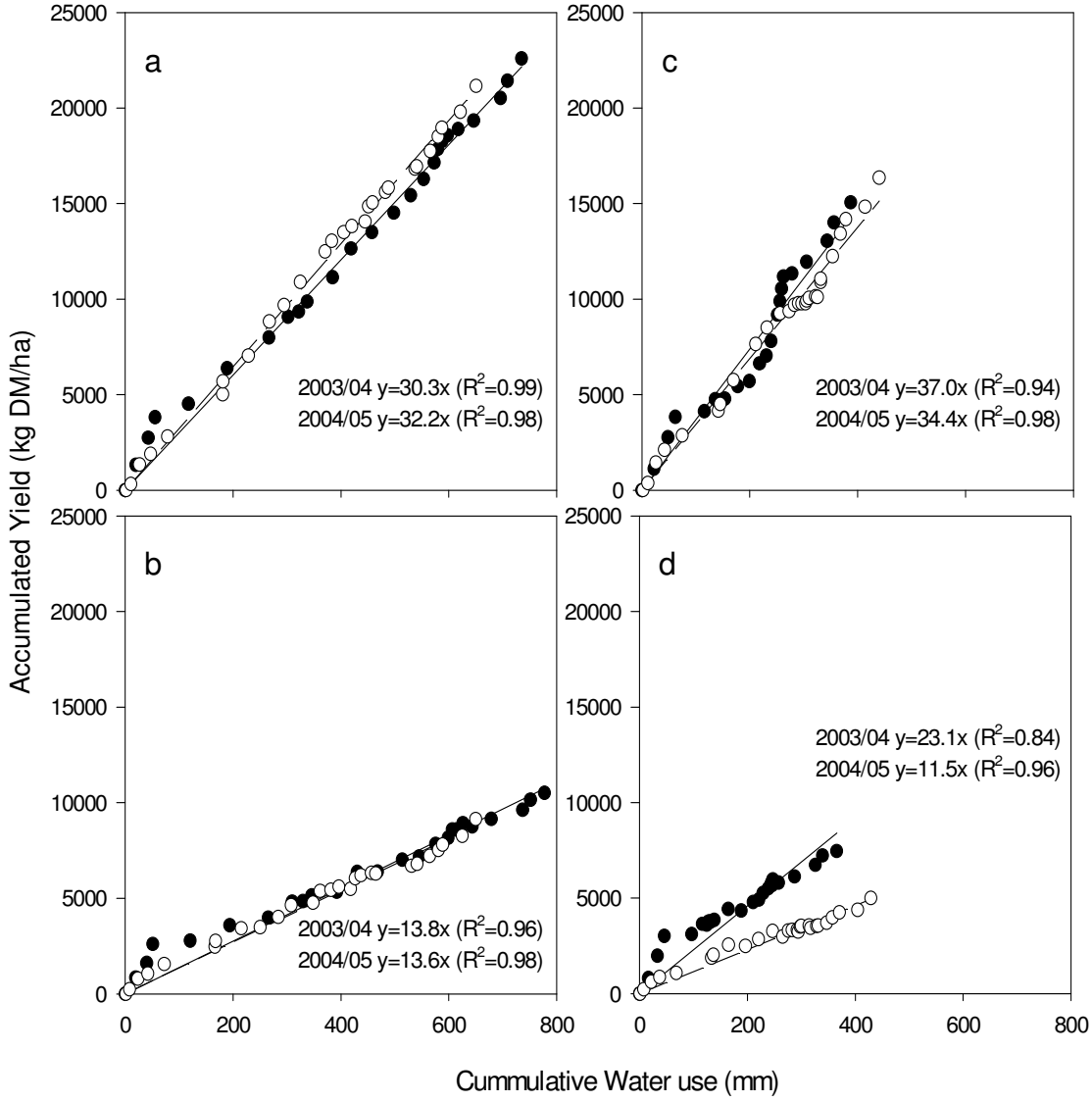

Figure 5.7 Relationship between accumulated yield (kg DM/ha) and cumulative annual water use (mm) of cocksfoot monocultures at Lincoln University, Canterbury, New Zealand for (a) I+N, (b) I-N, (c) D+N and (d) D-N pastures in 2003/04 (●) and 2004/05 (○). Regressions are for 2003/04 (—) and 2004/05 (- -) for each treatment forced through the origin. Treatment acronyms were given in Table 3.1.

Anomalies occurred in WUE calculations for D+N pastures in rotations ending 2/5/2004 (95 kg DM/mm) and 30/5/2005 (160 kg DM/mm) and these were excluded from the analysis (not shown). Specifically, these WUE may indicate either an upward or lateral movement of water, calculation errors associated with the drainage function or errors associated with rainfall data which was not collected at the experiment site. There is

evidence to support upward water movement in all soil layers >1.2 m indicated by the difference between UL and LL shown in Figure 5.1. Soil moisture was not a limitation to growth in these rotations so the WUE of the I+N pastures was used to estimate water used but not accounted for in calculations. The estimated amount of water used which was unaccounted for was 46 mm for the rotation ending 2/5/2004 and 42 mm for the rotation ending 30/5/2005, and these values were comparable to the difference between UL and LL at soil depths >1.2 m which was equivalent to 42 mm

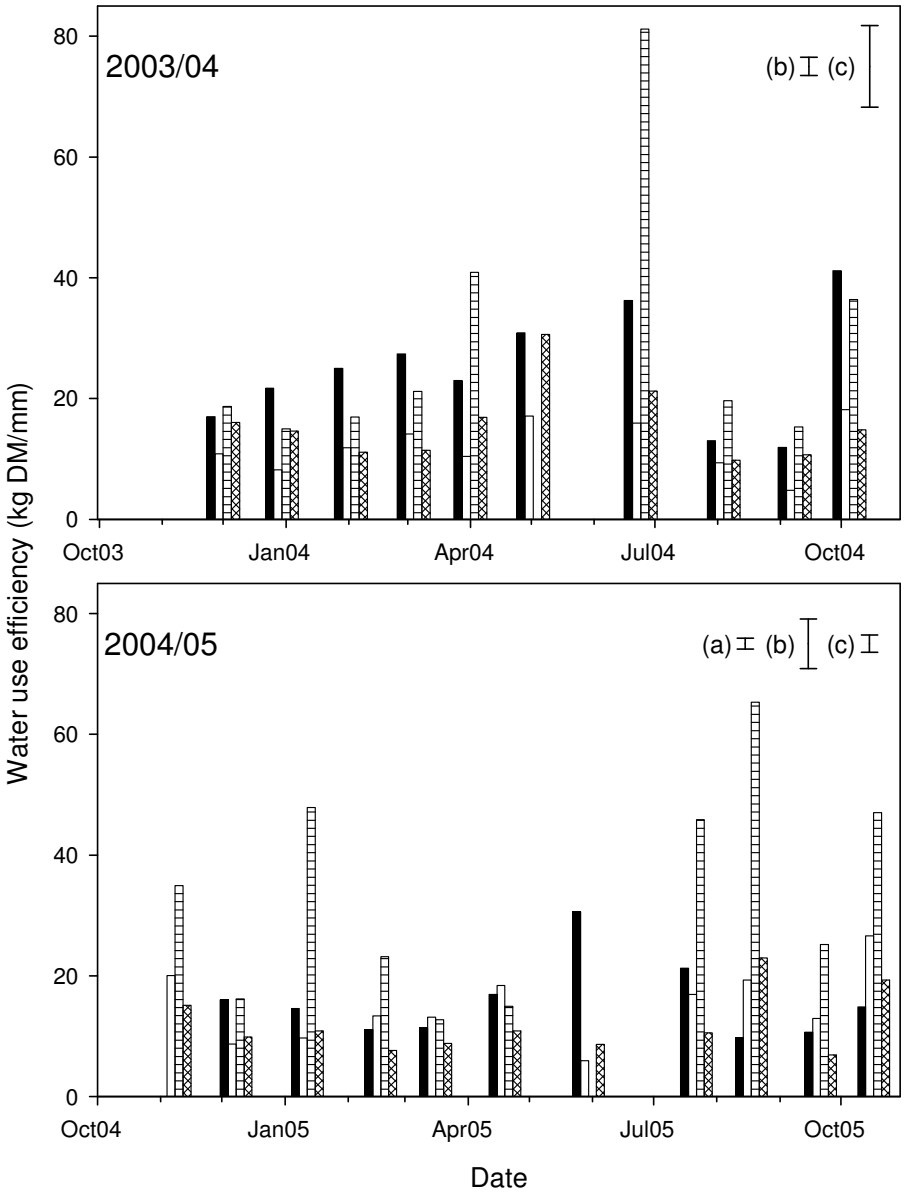

Figure 5.8 Water use efficiency (WUE) of cocksfoot monocultures (kg DM/mm) at Lincoln University, Canterbury, New Zealand for I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures in 2003/04 (top) and 2004/05 (bottom). Arrows indicate rotations where no N was applied to I+N or D+N pastures in 2003/04. Error bars are the maximum SEM for (a) I, (b) N and (c) I*N effects. Treatment acronyms were presented in Table 3.1.

5.4 Discussion

The aim of this chapter was to describe the differences in DM production of dryland pastures reported in Chapter 4 in relation to soil moisture availability. Specifically Objective 3 (Section 1.4) was to describe the expected reduction in RY when D_L was exceeded and involved re-analysis of the TAGR to include all four pastures and excluded periods of water stress when the ASMD exceeded D_L. Water use and water use efficiency were also described. Objective 4 was to describe water extraction patterns during a known period of water stress until the maximum soil moisture deficit was measured in the 2003/04 growth season.

5.4.1 Yield reductions and the critical limiting deficit (D_L)

The effect of water stress on DM yield was investigated separately for D+N and D–N pastures because –N pastures always produced lower yields than +N pastures (Section 4.3.2) due to N deficiency (Section 6.3.5). The D_L was used to quantify the delay caused to DM production in relation to temperature adjusted growth rate (TAGR) relationships which used Tt to account for seasonal temperature variations (Section 4.3.6). It was shown that beyond a D_L of 78 mm (Figure 5.5) yield of the D+N and D-N pastures consistently decreased at a rate of 1.45% DM/mm relative to their respective irrigated control pastures. Therefore, at any known ASMD beyond D_L, the extent of yield reductions below potential can be quantified. For example, at an ASMD of 100 mm, which is 22 mm beyond D_L, the yield would be 31% below potential. This allows a functional relationship to be generated for inclusion in a DM production model (Section 8.6). Table 5.3 showed that, when actual production of dryland pastures exposed to water stress was accounted for, predicted annual yields were within 3-11% of those measured in the irrigated control pastures (Section 5.3.6).

The development of the ASMD was described in relation to accumulated Tt (Figure 5.2). This was done to allow the potential yield losses caused by water stress to be quantified by coupling the TAGR and D_L (Section 5.3.6). It was shown that in 2003/04 the D+N pastures exceeded D_L for a total of 1597ºCd (465-2062ºCd) or 130 days between 21/11/2003-30/03/2004. In 2004/05, both D+N and D-N pastures initially exceeded D_L for 23 d (8/11/2004-1/12/2004) or 230ºCd (320-550ºCd) before the rainfall stimulated pasture growth and reduced the ASMD to <78 mm. The ASMD again exceeded D_L for a total of 1035ºCd (1243-2278ºCd) or 90 d from 31/1/2005 to

1/5/2005. The ASMD reached a maximum of 137±2.5 mm in 2003/04 and 129±0.4 mm in 2004/05 and did not exceed the calculated PAWC of the soil (Section 5.2.6). Re-analysis of TAGR when periods of water stress were excluded showed +N pastures had a common TAGR of 7.0 kg DM/^{o}Cd/ha. For –N pastures a common TAGR of 3.3 kg DM/^{o}Cd/ha was found and this was less than half that of the +N pastures. The effects of N on growth will be described in Chapters 6 and the mechanisms responsible for these differences are identified and explained in Chapter 7.

In this experiment, direct measurement of soil moisture allowed the ASMD to be determined for this site/pasture combination and was successfully used to explain the expected loss in DM production when D_L was exceeded. This was not affected by differences in the timing of water stress between years. By extrapolating the regression between relative yield and the ASMD (0-0.8 m) to the x axis the plant available soil moisture was determined as 147±3.0 mm. When combined with the D_L of 78 mm this indicated that yield was compromised by water stress when 53±1% of the total soil moisture (0-0.8 m) had been extracted. A limitation of this approach is that D_L values are specific for a known soil/crop combination and cannot be assumed to be constant (French and Legg, 1979) because of differences in rooting depth and soil waterholding capacity (Section 2.6.7). Previously, the D_L has been described in relation to the potential soil moisture deficit (PSMD) calculated using potential evapotranspiration (PET). Previous analyses conducted in Canterbury have accurately described reductions in RY (Martin, 1984; Rickard *et al.*, 1986) in relation to development of water stress quantified using PET. Actual measurements of soil moisture are not required and this approach has provided an accurate description for reductions in RY when D_L is exceeded (Section 2.6.7). In addition, the D_L accounts for periods when PET deviates from actual evapotranspiration because supply is not able to meet pasture demand (Section 2.6.3).

Soil water content decreased in all soil layers between 0-1.2 m during known periods of water stress (Section 5.3.3) and this was comparable to the >1.1 m extraction depth reported by both Evans (1978) and Parry *et al.* (1992). However, inclusion of water used from the 0.8-1.2 m soil depths did not increase the R^2 of broken stick models fitted to the relationship between the actual soil moisture deficit and relative yield. In this study, the total DM yields reported refer to DM production above a 3.0 cm residual cutting height. It is likely that water used from the 0.8-1.2 m soil depths contributed to

survival during drought but it is not known whether it contributed to root growth which was not measured.

5.4.2 Water use efficiency (WUE)

Differences in the annual WUE were predominantly caused by N, which represented 83% of the total sums of squares. The +N pastures had an annual WUE of 33.5±3.38 kg DM/mm which was more than double the 15.5±4.00 kg DM/mm by –N pastures (Section 5.3.7). The I-N pastures used the same amount of water as I+N pastures but produced only 45% of the yield produced by I+N pastures (Section 4.3.1). This was described by the difference in WUE (Sections 5.3.7 and 5.4.2) which showed WUE of the –N pastures was 54% less than that of the +N pastures (Figure 5.7). Nitrogen affects WUE indirectly because photosynthetic capacity is increased (Peri, 2002) relative to N deficient pastures. Although annual WU was similar for irrigated pastures, within a growth season, the efficiency with which that water is used will be intrinsically linked to the increase in RUE caused by N fertiliser (Chapter 7).

As expected, the I*Y interaction showed the WUE of dryland pastures in 2003/04 was 30.1 kg DM/mm compared with 22.6 kg DM/mm for irrigated pastures (2003/04 and 2004/05) and dryland pastures in 2004/05. Increased WUE has been reported (Silcock and Wilson, 1981) in response to water stress (Section 2.6.8). When water is not a limitation to growth more than 90% of the water extracted from the soil is released as water vapour and does not directly contribute to photosynthate production. When soil water supply is insufficient to meet pasture demand stomata close and there is a decrease in gaseous water loss from stomata. This in turn causes an apparent increase in WUE as more DM is produced, per unit water extracted from the soil, because of a decrease in the proportion of water released into the atmosphere (Section 2.6.8). Photosynthesis is also compromised because CO_2 assimilation and gaseous water loss through the leaves of C3 species share a common pathway through the leaf cavities (Jamieson, 1999), but stomatal closure occurs after cell expansion is affected (Hsiao, 1973).

Nitrogen application was the primary cause of differences in WUE in 11 of the 21 rotations (Figure 5.8). This reinforced the need to alleviate N deficiency when water is not a limitation to growth in order to use available water efficiently, regardless of whether the pasture is managed under irrigated or dryland conditions. In tall fescue, it

has been shown that N delays the time until epidermal cells reach their final length which allows an increased number of mesophyll division cycles to occur (MacAdam *et al.*, 1989). After rainfall alleviated water stress, expansion of cells which had not been able to expand previously due to insufficient water availability (Section 2.5.2) may have increased the amount of light intercepted by D+N pastures compared with I+N pastures. This will be investigated fully in Chapter 7.

For rotation ending 2/5/04 rainfall recorded on 6/4/2004 was 20% greater from a manual rain gauge 0.5 km from the experimental area compared with Broadfields data (Section 3.2.1) of 42.2 mm on the same day. Even though the higher rainfall from the manual rain gauge was used to recalculate WUE (Section 5.3.7), it is likely that rainfall was underestimated and subsurface water flow may have occurred. At an adjacent site, overland water flow was observed due to a blocked drain but no overland flow observed at the experiment site. In the rotation ending 30/5/2005, it was more likely that the cause of the anomaly was a result of errors in the drainage function. Using the WUE of the I+N pastures in these same two rotations the amount of water which was unaccounted for was estimated based on DM production.

Relative humidity affects water use because more DM is produced per unit AET under low VDP compared with high VPD conditions (Sinclair and Muchow, 1999a). This is caused by the gradient between soil and atmospheric moisture content through the plant. Low VPD, or high humidity, means less water is transpired relative to high VPD conditions to produce the same amount of DM. However, there were two main reasons WU, and therefore WUE, were not normalised for vapour pressure deficit (VPD) in this study. The first was that seasonal changes in VPD mirrored seasonal variation in temperature and WU was not compared across different environments. Use of VPD normalised WU or WUE would be important when comparing a range of environments. The second reason was because there is no relevant VPD normalised data published in the literature specifically related to cocksfoot based pastures.

5.4.3 Quantifying water use by cocksfoot pastures

As expected, because there was above average summer rainfall in 2004/05 which is the peak production period for cocksfoot, dryland pastures used 15% more water annually in 2004/05 compared with 2003/04 (Table 5.2). In contrast, irrigated pastures used 15% less water in 2004/05 compared with 2003/04. This could not be explained by annual

variation in either accumulated Tt (3192±76°Cd) or total solar radiation receipts (5038±24 MJ/m^2) (Section 3.2). In summer (Dec-Mar) irrigation applications were 77% greater in 2003/04 than the 155 mm applied in the summer of the 2004/05 growth season (Appendix 1) due to above average rainfall in 12/2005. Although total yields of the I+N (21.9 t/ha/y) and I-N (9.8 t/ha/y) pastures were statistically similar both growth seasons (Section 4.3.1), DM production in 2004/05 was about 10±3% lower than that measured in 2003/04.

Mean daily WU of irrigated pastures showed seasonal variation and ranged from a maximum of 5.6 mm/d by the I+N pastures in summer to 1.1 mm/d in winter. This seasonal variation generally mirrored the seasonal variation in both PET (Figure 5.4) and temperature (Figure 3.2). As expected, potential evapotranspiration generally overestimated AET. This would be expected as PET is a measure of atmospherically driven demand (French and Legg, 1979) but it still gives a good indication of water use grown in non limited conditions.

In comparison, WU_{daily} of dryland pastures was only about half that of the irrigated pastures and ranged from 3.1 to 0.7 mm/d (Figure 5.4). Daily water use in dryland pastures was highest when soil moisture was non limiting but decreased as the ASMD increased (Figure 5.2) or as temperatures declined in winter. Parry *et al.* (1992) reported mean daily water use of 2.7 mm/d between November to January of the first growth season. This was comparable to WU_{daily} by dryland pastures in 2004/05 in the corresponding months but less than the mean daily water use of irrigated pastures.

5.4.4 Validating the 'Monteith framework'

Most literature to date (Section 2.6.3) has applied the 'Monteith framework' (Monteith, 1986) to describe the exponential rate of water extraction (Passioura, 1983) at different soil depths by annual crops (Section 2.6.3). Recently, this framework has been shown to accurately describe the behaviour of lucerne (Brown, 2004) but it has not been applied to an established pasture nor has it been used on a shallow soil. As the pastures were managed under dryland conditions curves were only fitted to the relationship between VWC and time between 30/9/2003 and 21/1/2004 after which autumn rainfall begin to reduce the soil moisture deficit. Exponential models of extraction accurately (R^2=0.84-0.99) described root water extraction (0-0.8 m) by dryland cocksfoot pastures (Figure 5.3 and Table 5.1).

Based on the soil moisture profiles under the pastures it is likely that a combination of i) reduced water storage capacity at depth caused by an increase in stones present and ii) reductions in root length density at depth resulted in a decline in plant available water with increasing soil depth. It has been shown previously that cocksfoot, perennial ryegrass and white clover have all been shown to have 72-81% of their total root length present in the 0-0.2 m soil layer whereas no roots were present at depths >1.5 m (Evans, 1978). Root hairs attached to fibrous roots are the main sites for water and nutrient uptake by plants and, under field conditions, accurate determination of root biomass is difficult, and was not determined in this experiment.

It was shown that neither N or soil depth affected the extraction decay constant (kl) during the analysis period (Table 5.1). Results showed the fraction of water available on a daily basis was 0.032. This was comparable to the –kl reported for lucerne at similar soil depths by Brown (2004) on a deeper soil with the same parent material. However, these results indicate that the proposed use of a constant kl of 0.096 proposed by Dardanelli *et al*. (2004) based on analysis of soil water extraction patterns for a range of annual crops grown in different soils does not apply to water extraction by cocksfoot pastures or lucerne Specifically, the rate of water extraction would be overestimated for species which have more conservative water use (Dardanelli *et al.*, 1997).

The kl were comparable to those reported for grain sorghum (Robertson *et al.*, 1993b, 1993a) at similar soil depths. However, the kl was slightly lower than those reported for sunflower (Meinke *et al.*, 1993). The kl is a function of root length density and this may indicate that annual crops i) have more roots present for soil water extraction or ii) differences in soil type/environment. Annual crops may make a greater investment in roots because the reproductive phase is more important for species survival than for perennial species which can initiate other strategies, which includes summer dormancy, to survive drought conditions. Alternatively, it may show that cocksfoot is unable to extract the soil moisture as efficiently as sunflower or it has a lower water demand. The 0-0.2 m layer was included for this analysis. Generally this layer is not included in this type of analysis because of the noise associated with small rainfall events during the measurement period which reduces the R^2 values and can prevent parameters being accurately identified (Meinke *et al.*, 1993). To increase confidence in these results, especially the kl and t_c parameters, it would be necessary to measure soil moisture more

frequently and reduce the noise associated with infiltration events through the use of rainshelters.

Previous analyses using the 'Monteith framework' have been conducted on annual crops which show a stable VWC because there is no root system present prior to sowing/germination. Recent analyses of taprooted forage crops, such as lucerne (Brown, 2004), have also shown a stable VWC at the start of the growth season. This is because lucerne is dormant over winter months and temperature limits the rate of leaf appearance. In comparison, cocksfoot has been shown to have a 3°C base temperature for growth (Sections 4.3.6 and 4.4.5) and can produce more DM relative to crops with higher T_b. The stable VWC prior to the start of exponential water extraction reported in the literature also corresponds to a period when soil moisture recharge occurs as rainfall exceeds PET (Figure 3.1) and the system is demand limited because temperature is the main limitation to production. Therefore, in cocksfoot pastures, water is necessary for DM production at a time when other crops analysed by this method either i) haven't been sown, ii) haven't germinated or iii) are in a winter dormant phase where minimal growth occurs. It may be possible that a stable VWC, particularly in the 0-0.2 m soil layer, may not occur in a pasture/crop which has an established but shallow root system and some degree of winter activity. If rainshelters had been used and pasture water demand was met solely by water extraction from the 0-0.2 m soil layer an extraction front velocity may not be determined. However, it is likely that an EFV will not be observed until demand exceeds supply from that layer and water is extracted from greater depths in the profile.

5.5 Conclusions

In this chapter, the results presented meet the requirements outlined in Section 1.4 for Objectives 3 and 4. Based on the results, the following conclusions can be made:

- Dryland pasture production was reduced by 1.45% DM/mm when the ASMD exceeded the critical limiting deficit of 78 mm.
- By coupling the TAGR (Chapter 4) with the thermal time beyond D_L, DM yield differences between yields of irrigated and dryland pastures were explained. In 2003/04, water stress in the D+N pastures resulted in a yield loss equivalent to 8.7 t/ha/y.
- When periods of water stress were excluded +N pastures had a common TAGR of 7.0 kg DM/^{o}Cd/ha compared with 3.3 kg DM/^{o}Cd/ha for –N pastures.
- Daily water use varied seasonally in irrigated pastures and was a maximum of 5.8 mm/d in summer and 1.1 mm/d in winter.
- Extraction models were used successfully to describe the pattern of water extraction in the 0-0.8 m soil layers. The extraction decay constant was 0.032 and was not affected by N or soil depth.

The Chapter 6 will describe the effect of N on DM yields and Chapter 7 will explain the cause of yield differences by describing differences in light interception and RUE caused by N and water availability.

6 Describing how nitrogen affects DM production of cocksfoot pastures

6.1 Introduction

Chapter 4 showed that irrigated pastures with high rates of N fertiliser produced 21.9 t DM/ha or more than twice the 9.8 t DM/ha produced when only irrigation was applied. In Chapter 5 temperature adjusted growth rates (TAGR) and the time the actual soil moisture deficit exceeded the critical limiting deficit (D_L) were coupled to show that the TAGR of dryland pastures were similar to those of the irrigated pastures when water was non limiting. However, the actual TAGR was affected by nitrogen status being 7.0 kg/^{o}Cd/ha (T_b=3°C) in both +N pastures compared with 3.3 kg/^{o}Cd/ha in the –N pastures.

This chapter describes these yield differences by quantifying the effect of N on these cocksfoot pastures. Yield responses to applied nitrogen fertiliser, N use efficiency (NUE) and a N nutrition index (Lemaire *et al.*, 1989) were used to quantify the difference in DM yield (Objective 5, Section 1.4). The extent of yield reductions caused by N deficiency was then estimated. The mechanisms which caused these differences in DM production are quantified further in Chapter 7, where the effects of water and N availability are described in relation to canopy expansion and radiation use efficiency.

6.2 Materials and Methods

This chapter describes the agronomic results presented in Chapter 4 in relation to nitrogen availability and utilisation. Experimental design and management details including soil test results and biological measurements were presented in Sections 3.4 and 3.6. The extent and effects of water stress were described in Chapter 5.

6.2.1 DM response (kg DM/kg N) and N recovery

The DM response (kg DM/kg N) was calculated separately for the I+N and D+N pastures. To do this the yield of the I+N pastures was compared with the yield from irrigated no N pastures and similarly the yield of the D+N pastures was compared with dryland no N pastures. Differences in DM yields of the +N pastures and their respective

control pastures were divided by the rate of N applied (kg N/ha) annually and for individual regrowth cycles (Section 3.5.2). Three rotations in 2003/04 (1/12/2003, 24/6/2004 and 4/8/2004) were excluded from the analysis because no N applications were made.

Nitrogen recovery was compared for the green cocksfoot component of all four pastures by calculating the amount of N (kg N/ha) removed in herbage at the end of each rotation (Equation 6.1). This was summed to determine annual N removed by all four pastures from fertiliser N and/or soil N. The difference in N recovered between +N and –N pastures indicated the extent of deficiency when no fertiliser N was applied. It also allowed the recovery of applied fertiliser N (kg N/ha) to be determined for the +N pastures.

Equation 6.1 **N recovery (kg N/ha) = N% * green cocksfoot DM yield**

6.2.2 Development of a nitrogen dilution curve and N nutrition index

A N dilution curve (Equation 2.12) was developed using data from the I+N pastures (Lemaire *et al.*, 1989) to describe the pattern of decline in N% of the green cocksfoot herbage as DM yield increased. The ideas and literature related to this were reviewed in Section 2.7.3. The dilution curve should only be applied to the vegetative growth of the pasture when there is no leaf senescence (Lemaire *et al.*, 1997). In this experiment the curve was fitted to N% data derived only from green cocksfoot herbage. Other pasture components, which contributed 17-28% of total annual yield (Section 4.3.3), were excluded. The benefit of the relationship between DM yield and N% is that variation in N response between site, season and year are eliminated and the relationship can be applied over a range of environments (Lemaire *et al.*, 2007).

6.2.3 Specific leaf N (SLN) and specific pseudostem N (SPN)

A subsample of green cocksfoot was taken from the bulk sample (Section 3.6.1) to determine specific leaf N and specific pseudostem N (Section 2.7.4). From this subsample, cocksfoot was separated into either 1) lamina (ligule to leaf tip) after emergence from the leaf sheath or 2) leaf pseudostem (below the ligule) which contained newly formed leaves in the centre of the pseudostem which had not yet been exposed to light. Data were from two replicates of each treatment at a mid rotation

harvest on 1/9/2005 and at the end of the following rotation on the 17/10/2005.These early spring samples were taken when soil moisture was non limiting. This effectively doubled the replication of the N treatments because soil moisture was not a factor. Lamina and pseudostem surface area were measured by taking a digital image of the components on a scaled template. Images were then processed in QUANT (Vale *et al.*, 2003) following the methodology of Teixeira (2005) to determine green surface area of the cocksfoot component. Samples were then oven dried and weighed.

The nitrogen nutrition index (NNI) of the pastures was compared with specific leaf N and specific pseudostem N to separate the structural N (leaf) from the storage and metabolism N held in the pseudostem. This procedure was conducted to determine if the hypothesis that leaf N is constant, as proposed for annual crops (Jamieson and Semenov, 2000), held for cocksfoot. Nitrogen associated with storage and metabolism components of total plant N may be subject to change dependent on N availability. This would be identified by an increase in specific pseudostem N as newly formed leaves complete cell differentiation prior to emergence from the leaf sheath. In contrast, if there is a linear relationship between NNI and specific leaf N then the structural N component, associated with cell wall formation, is responsible for the change in N nutrition. In tall fescue, Rubisco formation was almost completed by the time leaves appeared from the leaf sheath (Gastal and Nelson, 1994) and Rubisco may be associated with storage of N in excess to plant requirements (Novoa and Loomis, 1981).

Both specific leaf weight (SLW) and specific pseudostem weight (SPW) were calculated as g DM/m^2 of green surface area. Each component was ground (Section 3.6.5) and sent for N analysis by the Kjeldahl procedure (Kjltec Auto 1030 Analyser, Tectator, Sweden). Specific leaf N and specific pseudostem N (g N/m^2) were calculated by multiplying specific weights by the N% in each component. These were then correlated with the NNI determined from the cocksfoot subsample used for botanical composition and N%. This sample included leaf lamina and pseudostem material.

6.2.4 Statistics

Analyses were conducted in Genstat 8.2. Nitrogen responses were calculated as additional yield of I+N over I-N pastures and D+N over D-N pastures (Section 6.2.1). This was analysed on an annual basis as a split-plot design with N as the mainplot and year as the subplot and also within individual regrowth cycles by one way ANOVA

with irrigation level as the treatment. Where significant, treatment means were separated using Fishers' LSD at the $\alpha = 0.05$ level.

Nitrogen recovery was calculated as total N (kg/ha) removed in green cocksfoot herbage minus N recovered in their respective control pastures (I-N or D–N) as determined from nutritional analysis. The N use efficiency was determined as green cocksfoot DM produced per kg N recovered in herbage removed for all four pastures. This was analysed as a split-split plot design with year as a repeated measure. The N use efficiency of individual regrowth periods was analysed as a split plot design. This analysis did not include N in any other pasture component or soil N reserves. At the end of the experiment soil tests were conducted in each treatment to quantify the soil N status (Appendix 7).

The N dilution curve was fitted to data from the I+N pasture, as an indicator of the non limited yield, in Systat 9 (version 9.01) (SPSS Inc.). Data were from both mid and end of rotation harvests for a total of 19 regrowth cycles. Three rotations in 2003/04 when N was not applied were excluded from the analysis. The NNI was calculated and analysed in Genstat 8.2 (Section 3.8) as a split plot design for each individual harvest date with irrigation as the mainplot and N as the subplot.

A broken stick model (Draper and Smith, 1998) was used to quantify the extent of yield reductions due to N deficiency. The model was fitted to the relationship between relative yield (RY) and NNI when water was not a limitation to DM production (Equation 6.2) to allow the extent of yield reductions caused by N deficiency to be predicted. The form of the model was:

Equation 6.2 $$RY = 1 + (r * (NNI - t_n) * (NNI < t_n))$$

Where 'r' is the slope or rate of reduction in relative yield per unit decrease in NNI and 't_n' is the NNI value at which relative yield declines. The model was modified by the inclusion of a switch ($NNI < t_n$).

6.3 Results

6.3.1 DM responses (kg DM/kg N) to applied N fertiliser

The overall DM response of I+N and D+N pastures to applied fertiliser N was affected ($p \leq 0.001$) by an I*Y interaction (Figure 6.1). This was caused by a 10 kg DM/kg N DM response by the D+N pastures in 2003/04, compared with 7 kg DM/kg N in 2004/05. In contrast, the I+N pastures produced 15 kg DM/kg N in 2003/04 but only 8 kg DM/kg N in 2004/05. The rate of applied N in 2004/05 was double that applied in 2003/04 and the diminished response in the second year reflects the typical decline in DM responses as N rates are increased.

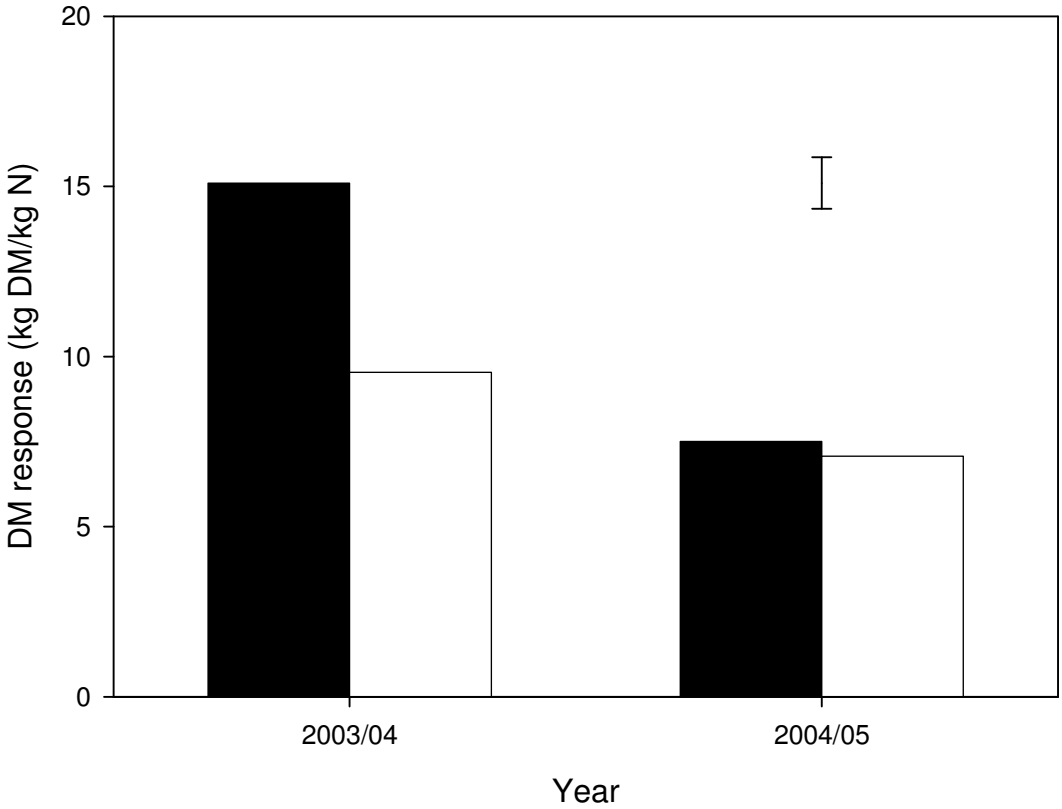

Figure 6.1 Annual N response (kg DM/kg N applied) in 2003/04 and 2004/05 of irrigated and dryland treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. Responses are for I+N (■) pastures where I-N was the control, and D+N pastures (□) where the D-N pasture was the control. Error bar is the LSD ($p \leq 0.05$) for the I*Y interaction. Treatment acronyms were presented in Table 3.1.

Within individual regrowth cycles, the DM response of I+N pastures in 2003/04, ranged from 7 to 23 kg DM/kg N (Figure 6.2a). The D+N pastures produced a maximum

response of 13 kg DM/kg N in the rotation ending 5/10/2003 and a minimum of -1 kg DM/kg N in the 30/12/2003 rotation. The nominally negative response occurred because 0.4 t DM/ha was produced by the D+N pasture compared with 0.5 t DM/ha from the D-N pastures (Appendix 5).

In 2004/05 (Figure 6.2b), the level of DM response to applied N was generally lower than in 2003/04. Both the I+N and D+N pastures produced a maximum response of 19 kg DM/kg N in the 12/1/2005 regrowth cycle. In contrast, the lowest response of the irrigated +N pasture was 2.6 kg DM/kg N in winter (07/2005) compared with 1.0 kg DM/kg N for the dryland +N pastures in March and April rotations 2005. The lower responses by D+N pastures corresponded to the drought periods in 2003/04 and 2004/05 when the ASMD exceeded the D_L of 78 mm (Section 5.4.1). However, after rainfall, the DM response of the D+N pastures in winter/spring 2005 was greater than that of the I+N pastures. This indicates uptake of additional N from the current application and from that applied in the previous rotations when water stress had compromised the growth response.

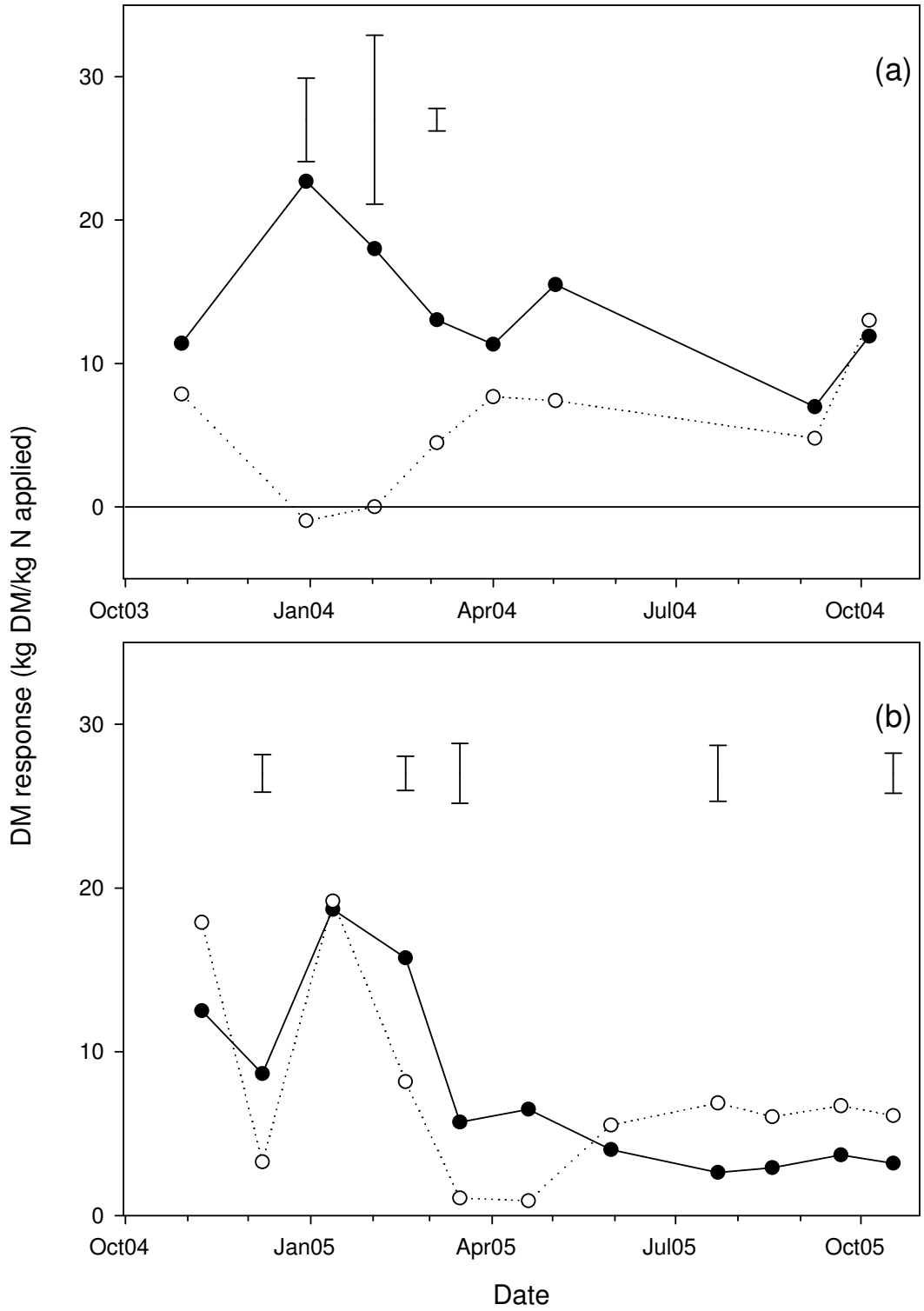

Figure 6.2 Dry matter response (kg DM/kg N applied) to applied N within individual regrowth cycles in (a) 2003/04 and (b) 2004/05 of irrigated and dryland treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. In 2003/04, rotations ending 1/12/2003, 24/6/2004 and 4/8/2004 were excluded because N was not applied. Responses are for I+N (●) pastures with I-N as the control, and D+N pastures (○) where the D-N pasture was the control. Error bars are the LSD ($p \leq 0.05$) for I effects. Treatment acronyms were given in Table 3.1.

6.3.2 Nitrogen recovery by green cocksfoot

Nitrogen recovery (kg N/ha) in the cocksfoot herbage was affected ($p \leq 0.001$) by an N*Y interaction which showed 215±25 kg N/ha was recovered from the –N pastures in both growth seasons (Table 6.1). In contrast, 786 kg N was recovered from +N pastures in 2004/05 compared with 708 kg N/ha in 2003/04.

In 2003/04, an addition 550 kg N/ha was removed in green cocksfoot herbage by the I+N pasture in excess of soil mineral N supply as quantified by the I-N pasture. Therefore 65% of the 800 kg N/ha/y applied was accounted for. In comparison, the D+N pastures recovered 52% of applied N, after N removed by D-N pastures was accounted for. In 2004/05, the I+N pastures recovered 619 kg N/ha more than the I-N pasture. The D+N pastures recovered 574 kg N/ha more N than D-N pastures. These recovery values are only valid for green harvested cocksfoot herbage and excludes for N in roots, residual biomass below 3.0 cm, N in other pasture components or remaining soil N reserves. In addition, it has been shown previously that DM responses may occur up to six months after N applications are made (Peri *et al.*, 2002a).

Table 6.1 Amount of N recovered in green cocksfoot DM (kg N/ha) from I+N, I-N, D+N and D-N treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand.

Treatment	2003/04	2004/05
I+N	802	871
I-N	282	252
D+N	615	702
D-N	196	128
Effect	N*Y	
Significance	***	
LSD ($p \leq 0.05$)	45	

The LSD ($p \leq 0.05$) is for the N*Y interaction term. Treatment acronyms were given in Table 3.1.

6.3.2.1 Soil N levels

Results of soil N tests at the end of the experiment (Appendix 7) showed mineral N, at soil depths between 0-0.6 m, totalled 95 kg N/ha and was independent of treatment. Soil depths >0.6 m were not sampled as alluvial gravels prevented sampling. Nitrogen

fertiliser application affected both ammoniacal-N ($p \leq 0.01$) and nitrate-N ($p \leq 0.01$) levels which are the two most readily available forms of plant available N (McLaren and Cameron, 1996). Ammoniacal N (0-0.6 m) was 8.0 μg/g in the +N pastures compared with 2.9 μg/g in the –N pastures. Average nitrate N (0-0.6 m) was 81.1 μg/g in +N pastures compared with 9.8 μg/g in the –N pastures.

A nitrogen budget was calculated to account for N removed by herbage in 2004/05 plus soil N remaining at the end of the experiment (Table 6.2). Soil bulk density was only determined for the 0-0.2 m layer so ammoniacal-N (ppm) and nitrate-N (ppm) could only be quantified as kg N/ha for the 0-0.2 m soil layer. This was achieved by converting values to percentages and converting to kg N/ha using Equation 3.1 (Section 3.5.3). An additional 174 kg N/ha for I+N and 300 kg N/ha for D+N pastures could be accounted for if soil bulk density from the 0-0.2 m soil layer was extrapolated to the 0.2-0.6 m soil depths to account for contributions from ammoniacal-N and nitrate-N. In contrast, this would add only 10±1.5 kg N/ha to the N recovered from the –N pastures.

Table 6.2 A N balance of cocksfoot pastures which includes N remaining in the soil profile at the end of the experiment. Mineral N (kg N/ha) is determined from 0-0.6 m soil depths. Ammoniacal-N and Nitrate-N represent plant available N present in the 0-0.2 m soil layer. Herbage N values represent N removed in harvested green cocksfoot in the 2004/05 growth season. Total N (kg/ha) represents the sum of N accounted for at the end of the 2004/05 growth season.

Pasture	Herbage N (kg N/ha)	Mineral N (kg N/ha)	Ammoniacal-N (kg N/ha)	Nitrate-N (kg N/ha)	Total N (kg/ha)
I+N	871	105	29	147	1152
I-N	252	103	9	4	368
D+N	702	84	28	199	1013
D-N	128	90	6	96	320

Note: Nitrogen removed by harvested weed grasses, dicot weeds and dead material was not measured and is not included in the N balance. Nitrogen held in the residual biomass (0-30 cm) was not determined and was also excluded. Treatment acronyms were given in Table 3.1.

There was equivalent to 28 kg ammoniacal-N/ha in the 0-0.2 m soil depth of the +N pastures compared with 7.4 kg ammoniacal-N/ha in the –N pastures. Nitrate N was 173 kg/ha in +N pastures compared with 50 kg/ha in the –N pastures in 0-0.2m. In 2004/05, green cocksfoot recovered 39% of applied N fertiliser (Section 6.3.2). When soil N at the end of the experiment was included, the amount of N accounted for increased to

49%. The amount of N accounted for by the D+N pastures increased from 36% to 43% when soil N was included.

As expected, Figure 6.3 shows that N recovery within individual regrowth cycles by D+N pastures deviated from that of I+N pastures during periods of water stress. In comparison, N recovery by the D-N pastures was generally lower than that in I-N pastures throughout summer, autumn and winter months. In 2003/04, I*N interactions occurred at all harvests between 30/12/2004-2/5/2004 and in the rotation ending 4/8/2004. N application affected N recovery in the five remaining rotations. In 2004/05, N application affected N recovery in the green cocksfoot component of the pastures in all eight of the remaining rotations.

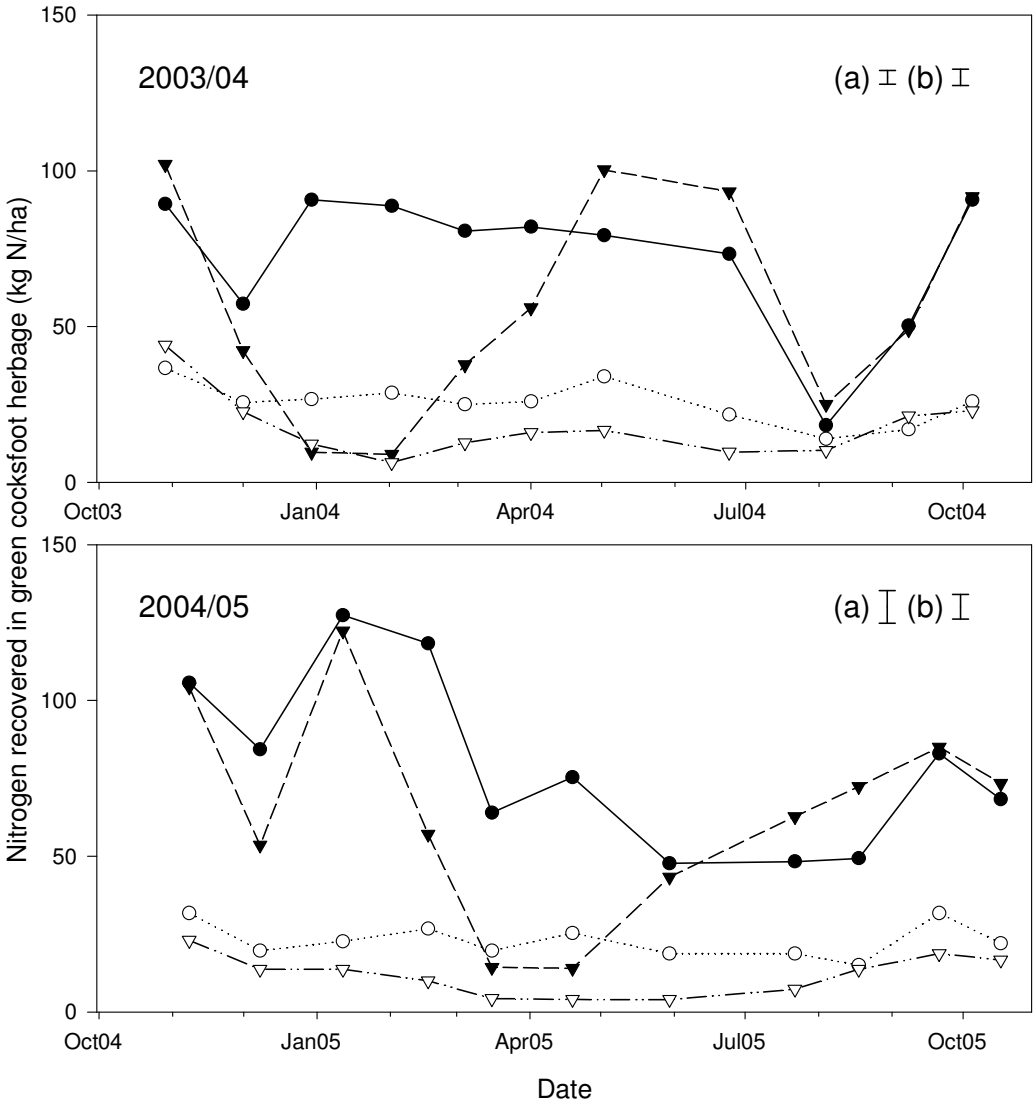

Figure 6.3 Nitrogen recovered (kg N) in green cocksfoot herbage from in 2003/04 (top) and 2004/05 (bottom) by green cocksfoot herbage from I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand in (a) 2003/04 and (b) 2004/05. Error bars are maximum SEM for (a) N effects and (b) I*N interactions. Treatment acronyms were given in Table 3.1.

6.3.3 Nitrogen use efficiency (NUE)

The annual NUE, based on N recovered and including the contribution of soil mineral N for the +N pastures, in the cocksfoot component of the pastures was affected by two first order interactions (Table 6.3). Despite the interactions described below the main effect of N represented 90% of SS_T compared with 1% for the I*Y and 3% for the N*Y interactions. The N*Y interaction ($p \leq 0.001$) showed the NUE of +N pastures decreased from 27.1 kg DM/kg N in 2003/04 to 24.2 kg DM/kg N in 2004/05. In comparison, the NUE of –N pastures increased from 37.0 kg DM/kg N in 2003/04 to 38.8 kg DM/kg N

in 2004/05. The I*Y interaction ($p \leq 0.001$) was caused by the small but significant decrease in annual NUE. The NUE of irrigated pastures was 31.2 kg DM/kg N in 2003/04 and decreased to 30.1 kg DM/kg N in 2004/05. In contrast, dryland pastures had an NUE of 32.1 kg DM/kg N in 2003/04 and this increased to 32.8 kg DM/kg N in 2004/05.

Table 6.3 Nitrogen use efficiency (kg DM/kg N recovered) of green cocksfoot DM from I+N, I-N, D+N and D-N treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand.

Treatment	2003/04	2004/05
I+N	27.7	24.1
I-N	36.2	36.1
D+N	26.4	24.2
D-N	37.7	41.4

Effect	I*Y	N*Y
Significance	***	***
LSD ($p \leq 0.05$)	0.34	0.30

The LSD ($p \leq 0.05$) values are for the I*Y and N*Y interaction terms respectively. Treatment acronyms were given in Table 3.1.

The NUE determined for individual regrowth cycles is shown in Figure 6.4 and indicated that NUE of –N pastures tended to be greater than that of +N pastures. There was also a tendency for the D-N pasture to have an increased NUE, relative to I-N pastures when subjected to periods of moisture stress but this was not as obvious in the D+N pastures. In addition, all pastures appeared to use N more efficiently in the production of DM in spring/summer than in winter months when temperature was the main constraint to DM production.

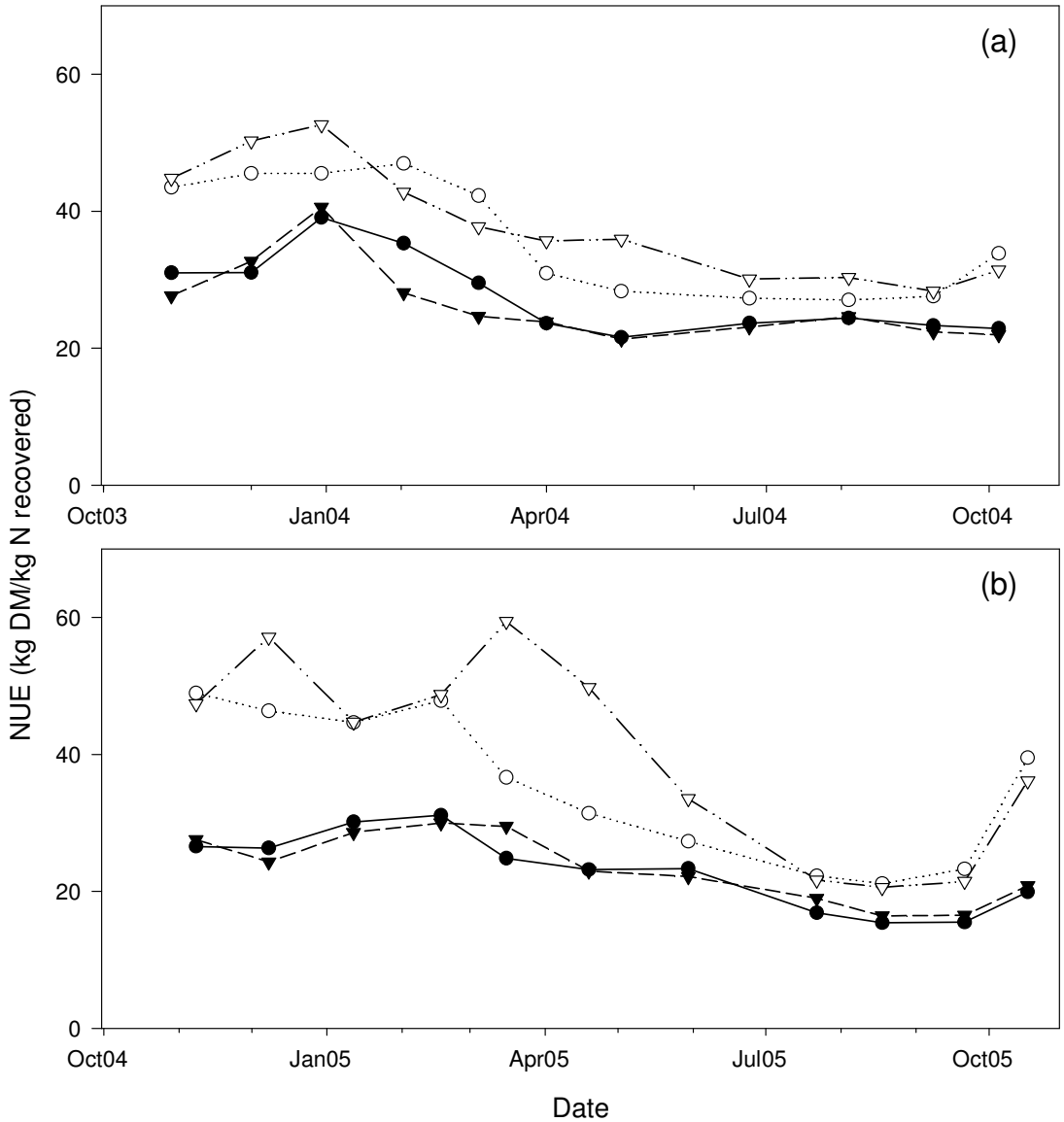

Figure 6.4 Nitrogen use efficiency (NUE) of green cocksfoot herbage from I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand in (a) 2003/04 and (b) 2004/05. Treatment acronyms were given in Table 3.1.

6.3.4 Development of a nitrogen dilution curve for cocksfoot

The cause of the difference between the initial TAGR of I+N (7.2 kg DM/^{o}Cd/ha) and I-N (3.2 kg DM/^{o}Cd/ha) pastures (Section 4.3.6) was investigated by creation of a N dilution curve (Lemaire *et al.*, 1989) for I+N pastures. This provides an indicator of the decrease in N% as standing biomass increases under non limiting conditions. The form of the relationship was $4.8x^{-0.35}$ (R^2 = 0.65) (Figure 6.5). Standard errors were 0.16 and 0.05, respectively.

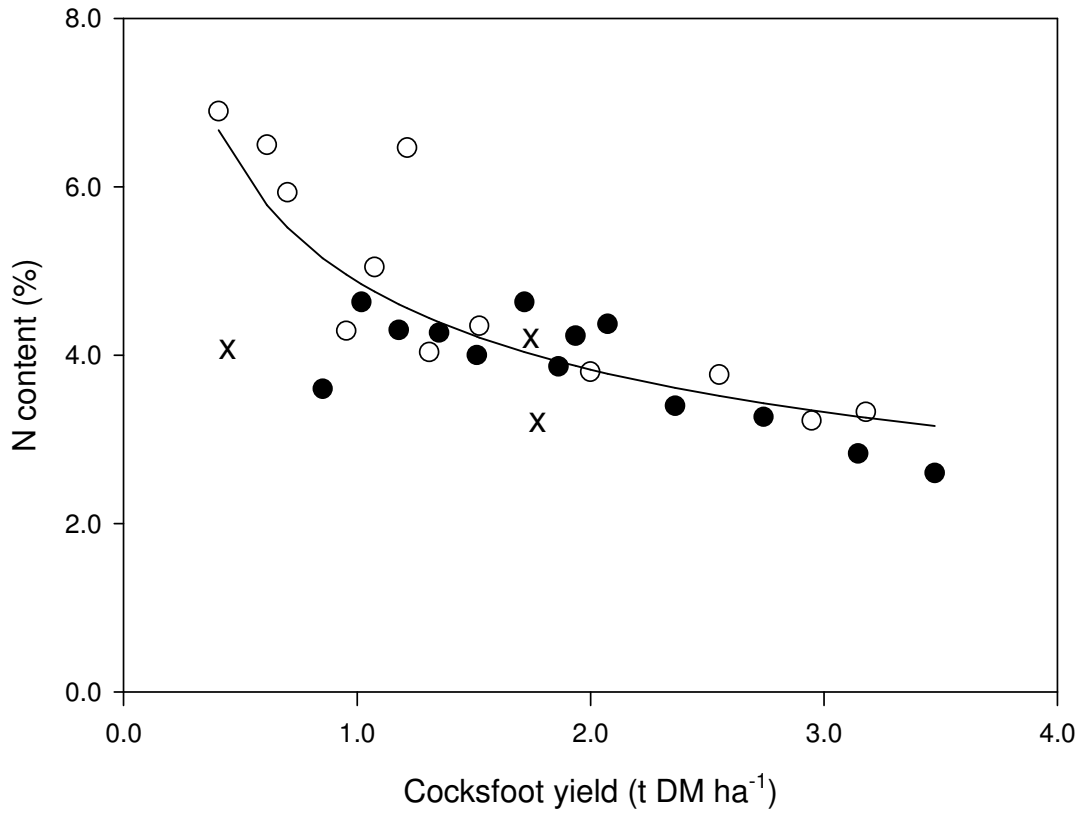

Figure 6.5 Nitrogen content (%) against DM yield of harvested green 'Wana' cocksfoot herbage above cutting height for I+N pastures grown at Lincoln University, Canterbury, New Zealand. The parameters of the model were $y = 4.8x^{-0.35}$ (R^2=0.65) fitted to data from 2003/2004 (●) and 2004/2005 (○). Standard errors were 0.16 and 0.05, respectively. Three harvests in 2003/2004 where N was not applied were not included in the analysis but are shown for reference (X). Treatment acronyms were given in Table 3.1.

6.3.5 Creation of a nitrogen nutrition index (NNI)

The N dilution curve was used to develop the nitrogen nutrition index (NNI) to quantify the yields of I-N, D+N and D-N pastures relative to I+N pastures. To do this the ratio between measured N% (N_{act}) of green harvested cocksfoot herbage and optimum N% (N_{opt}) from the fitted curve (Figure 6.5) was calculated. The analysis showed that I–N and D-N pastures were consistently N deficient (NNI<1.0). In contrast, the D+N pastures were N deficient in summer and autumn (<0.6) but when rainfall alleviated water stress conditions D+N pastures recovered to have an NNI that were similar to or greater than those of the I+N pastures (Figure 6.6).

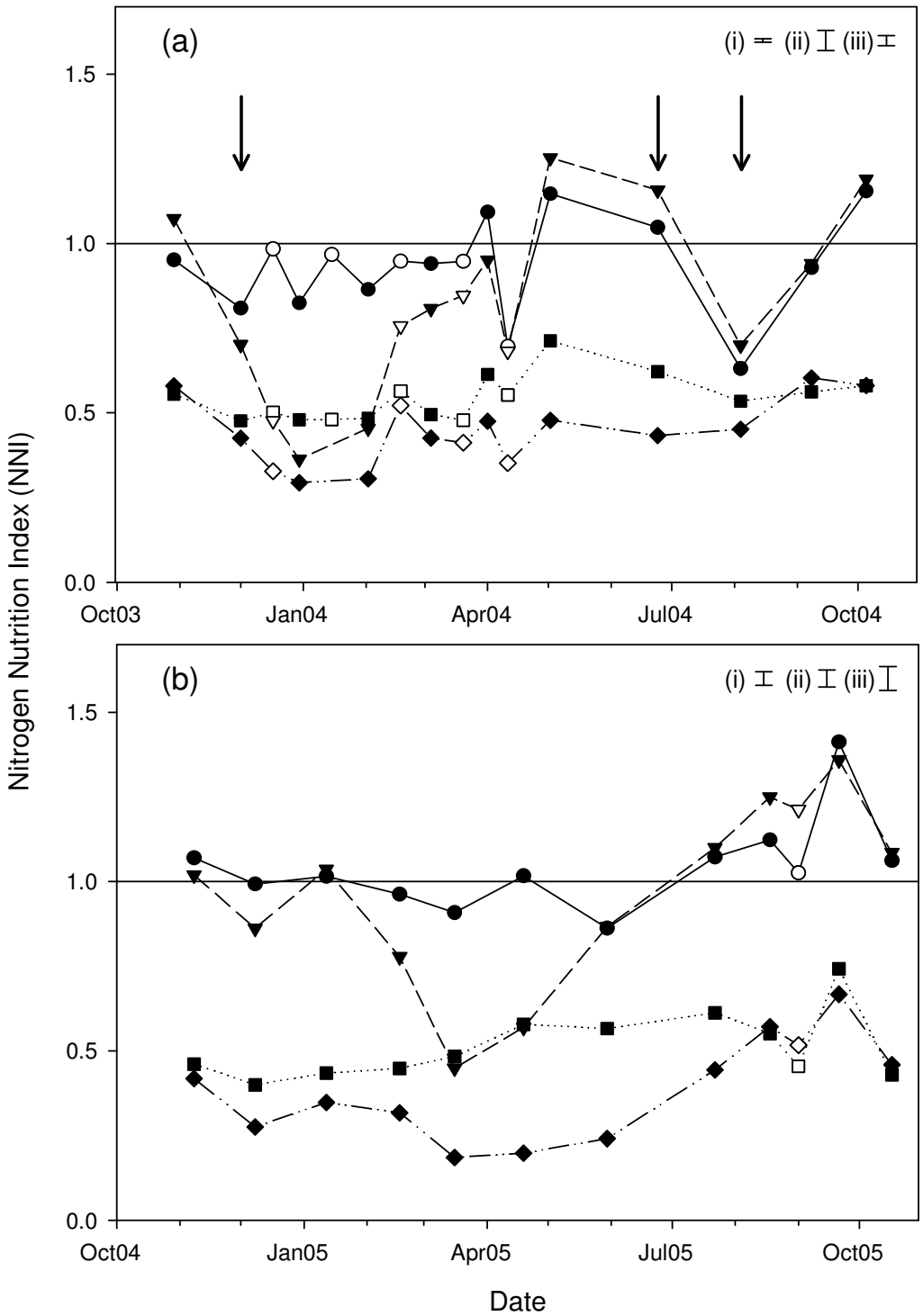

Figure 6.6 Nitrogen nutrition index (NNI) over time in 2003/04 (a) and 2004/05 (b) for I+N (●,○), I-N (■,□), D+N (▼,▽) and D-N (◆,◇) treatments imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. Closed symbols represent end of rotation harvests and open symbols are mid rotation harvests. Arrows indicate three rotations in 2003/04 when no N was applied to I+N or D+N pastures. The line indicates the optimal NNI (1.0) at, or above which, N is non limiting to DM production. Error bars are maximum SEM for (i) I, (ii) N and (iii) I*N effects. Treatment acronyms were given in Table 3.1.

In 2003/04, the average NNI, across all harvests, was 0.9 for I+N pastures (Figure 6.6a). The primary cause of an annual NNI <1.0 was because the N application rate (100 kg N/ha) in the summer months, was insufficient for maximum growth within a four week regrowth cycle. In addition, the NNI was <1.0 at the end of two of the three regrowth cycles when N applications were not made (1/12/2003 and 4/8/2004). The annual NNI of the I-N pastures was 0.5 and 0.8 for D+N pastures. The annual NNI of the D-N pastures was 0.4. By definition, N application was the main cause of differences in the NNI for 11 of the 15 harvests. At these times +N pastures consistently had a higher NNI than –N pastures which were, on average, 42% lower than the NNI of the +N pastures.

Of the four remaining harvests in 2003/04, there were I*N interactions on 17/12/2003 and 30/12/2003. On 17/12/2003 the NNI of the I+N pasture was 1.0 and this was greater ($p \leq 0.05$) than the NNI of I-N and D+N pastures which were similar at 0.5±0.02. The NNI of the D-N pasture was the lowest at 0.3. By the end of rotation harvest two weeks later (30/12/2003) the NNI of the D+N pasture was 0.4 and was similar to both the 0.3 in the D-N pasture and the 0.5 in the I-N pastures. However, the NNI of the D-N and I-N pastures were different ($p \leq 0.05$). At this time the I+N pastures had an NNI of 0.8 which was greater than all other pastures but below the expected optimum of 1.0. This indicated that the N application rate of 100 kg N/ha for rotations during the peak production period for cocksfoot was insufficient for non limited growth. This was the basis for the decision to increase the N application rates for the 2004/05 growth season (Section 3.5.2).

In the subsequent regrowth cycle (2/2/2004), both I and N affected ($p \leq 0.01$) the NNI but the interaction was not significant. At this harvest, the NNI of the irrigated pastures was 0.66±0.17 compared with 0.40±0.07 in dryland pastures. In addition, the N effect showed an NNI of 0.65±0.18 in +N pastures compared with 0.4±0.08 in the –N pastures. The primary cause of the N effect was an increase in the NNI of the D+N pastures after rainfall alleviated water stress conditions. This allowed previously unavailable N to be accessed and used in the production of DM.

Irrigation affected the NNI at three of the 15 harvests and consistently occurred in association with N effects. Another I*N interaction occurred in the rotation ending 24/6/2004. At this time all pastures had a different ($p \leq 0.05$) NNI. The D-N pasture had the lowest NNI of 0.4 compared with 0.6 for I-N and 1.03 for I+N pastures. The D+N

pasture had the highest NNI of 1.2 which was above the optimal value of 1.0 and indicates uptake of N in excess of pasture requirements.

In 2004/05, the average NNI was 1.0 for I+N pastures, which indicates the increased N application ensured N levels were always above optimum (Figure 6.6b). The NNI was 0.5 for I-N pastures which was comparable to the 2003/04 growth season. In contrast, the NNI of the D+N pasture was 1.0 and 19% higher than in 2003/04. The D-N pasture had an average NNI of 0.4. The main effect of N was significant on the NNI for 10 of the 12 harvests. The irrigation treatment affected NNI on four harvest dates. Irrigation affects were always associated with significant N effects but interactions were not significant. The NNI of dryland pastures was 20-55% lower than that in irrigated pastures in the rotations ending 17/2/2005, 16/3/2005 and 19/4/2005. In these same rotations the NNI of –N pastures was 51-56% lower than those of the +N pastures. Subsequently, in the rotation ending 30/5/2005, there was an I*N interaction when I+N and D+N pastures had an NNI of 0.9 which was higher ($p \leq 0.05$) than the 0.6 in I-N and 0.2 in D-N pastures. The I*N interactions on 24/6/2004, 30/5/2005 and 22/7/2005, represented 4-9% of the total sums of squares (SS_T), compared with 75-90% for the main effect of N.

6.3.6 Relationship between NNI and SLN or PSN

Figure 6.7a shows SLN at the mid and end of rotation harvests. The SLN was 1.6±0.15 g N/m^2 at the mid rotation harvest on 1/9/2005 for all treatments. For the end of rotation harvest on 17/10/2005, the SLN was 1.0±0.14 g N/m^2 and also stable for all treatments. In comparison, SPN increased as the NNI increased (Figure 6.7b). The –N pastures had an average SPN of 1.2±0.25 g N/m^2 averaged over the two measurement dates, compared with 2.7±0.13 g N/m^2 in +N pastures.

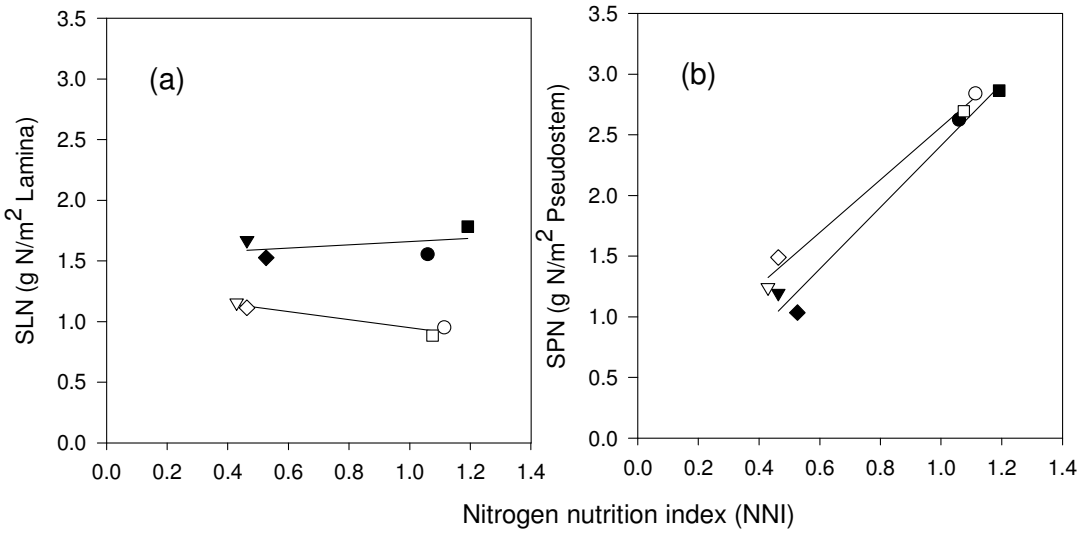

Figure 6.7 Specific leaf N (SLN) (a) and specific pseudostem N (SPN) (b) against nitrogen nutrition index (NNI) of I+N (●,○), I-N (■,□), D+N (▼,∇) and D-N (◆,◇) pastures imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. Closed symbols represent the mid rotation harvest on 1/9/2005 and open symbols are an end of rotation harvest on 17/10/2005. Regressions for SLN (a) were y = 1.5 + 0.1x (R^2=0.18) on 1/9/2005 and y = 1.28 - 0.3x (R^2=0.93). Regressions for SPN (b) were y = -0.13 + 2.5x (R^2=0.97) at 1/9/2005 and y = 0.4 + 2.2x (R^2=0.99) at 17/10/2005. Each data point is the mean of two replicates. Treatment acronyms were given in Table 3.1.

6.3.7 Measured N concentration (N%)

The annual N%, averaged over all harvest dates and including mid rotation harvests, was affected ($p \leq 0.001$) by an N*Y interaction (Table 6.4). This showed that the mean N% of the –N pastures was 3.2±0.1% in 2004/05 and this was 13% higher than the 2.8±0.1% N in 2003/04. In comparison, the N% of the +N pastures was 26% higher in 2004/05 (4.8± 0.05%) than in 2003/04 (3.8± 0.05%).

Over the two years, the N% of green cocksfoot herbage in the I+N pastures ranged from a minimum of 2.6% at the end of rotation harvest on 30/12/2003 to a maximum of 6.9% at the mid rotation harvest on 01/09/2005 (Figure 6.8). The N% of the I-N pastures ranged from a minimum of 2.1% (17/12/2003) to 4.5% in the rotation ending 22/7/2005. The D+N pastures had a minimum N content of 2.5% (30/12/2003) and a maximum of 6.8% (1/9/2005) and D-N pastures ranged from 1.7% N (16/3/2005) to 4.9% N (18/8/2005). Although –N pastures consistently had lower N concentrations than +N pastures, N% was highest in all pastures in early spring. Also, dryland pastures tended

to have lower N% than their respective irrigated treatments in summer/autumn. In addition, at every mid rotation harvest N% was higher than that measured at the end of that regrowth cycle.

Table 6.4 Mean annual N% of green cocksfoot DM from I+N, I-N, D+N and D-N treatments applied to a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand.

Treatment	2003/04	2004/05
I+N	3.8	4.9
I-N	2.9	3.3
D+N	3.9	4.8
D-N	2.7	3.1
Effect	N*Y	
Significance	***	
LSD ($p \leq 0.05$)	0.1	

Treatment acronyms were given in Table 3.1.

Over the two growth seasons, the N application affected the N% for 21 of the 27 measurement dates, whereas irrigation affected N% at four harvests. These irrigation effects only occurred in association with N effects but the interaction term was not significant. There were I*N interactions for harvests made on 17/12/2003, 8/12/2004, 19/4/2005, 18/8/2005 and 21/9/2005. The I*N interaction at the mid rotation harvest on 17/12/2003 showed that cocksfoot in the I+N pasture had an N% of 3.9 compared with 2.0% in the D-N pastures. The interaction was a result of similar N% from the I-N and D+N pastures which was 2.65±0.05%.

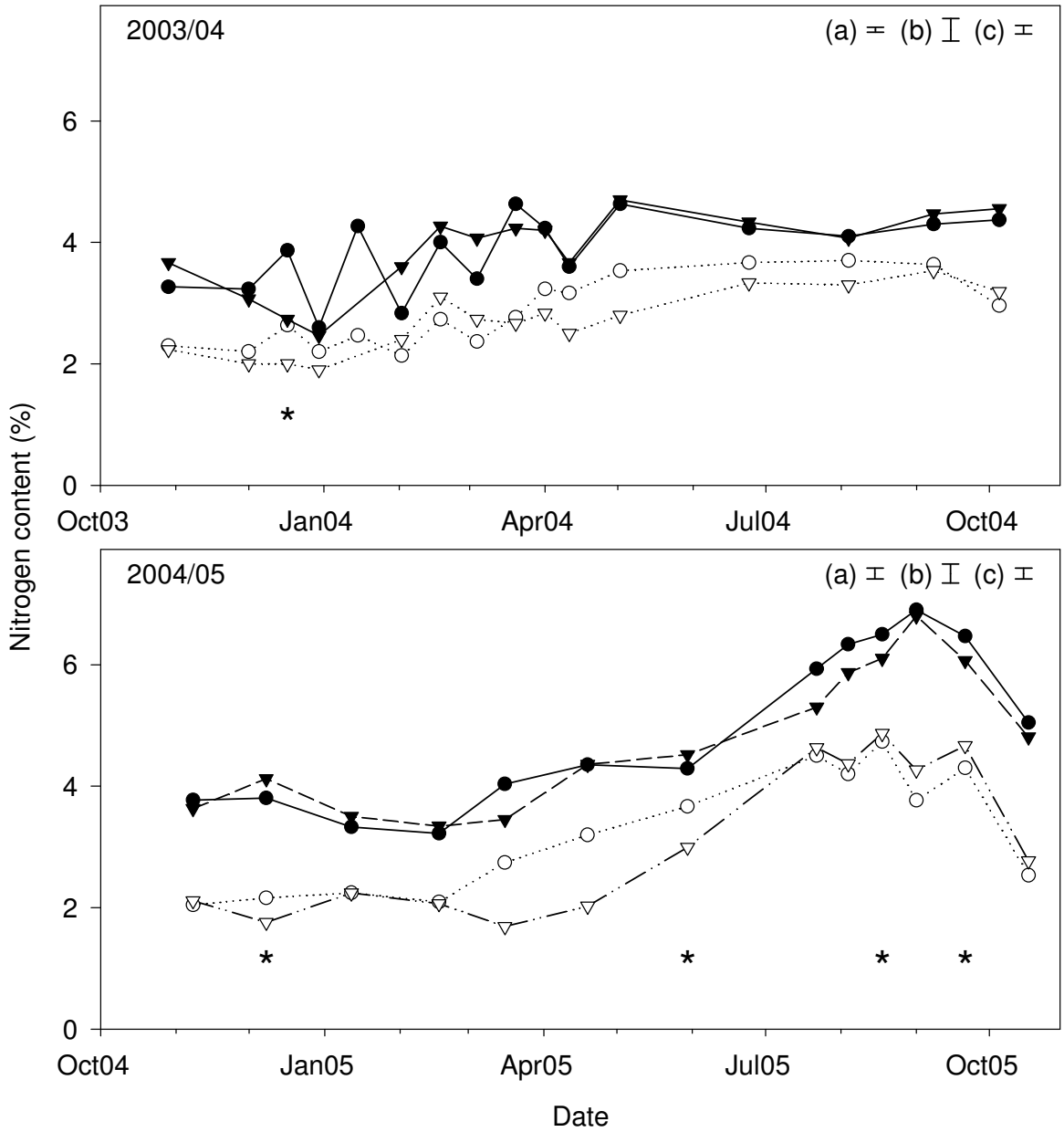

Figure 6.8 Measured N concentration (%) in green cocksfoot herbage in I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand in 2003/04 (top) and 2004/05 (bottom). Error bars are maximum SEM for (a) I, (b) N and (c) I*N effects. An asterisk (*) indicates harvests where I*N interactions occurred. Treatment acronyms were given in Table 3.1.

6.4 Discussion

The aim of this chapter was to describe the cause of the differences in DM yields of irrigated and dryland pastures (Chapter 4 and 5) which had different levels of N nutrition. Objective 5 was to create a NNI (Sections 2.7.3 and 2.7.5) for cocksfoot pastures to determine the extent of N deficiency.

6.4.1 The N dilution curve

The N dilution curve for the I+N pasture (Figure 6.5) explained >65% of the variation between N% and DM yield. Based on this relationship, the critical N concentration for a 1.0 t/ha yield, when N was not a limiting factor, was 4.8% and the dilution coefficient was -0.35 and a non limited yield of 3.5 t DM/ha should have a critical N% of 3.1%. The form of this curve was comparable to the general relationship for C3 species of $y = 4.8x^{-0.34}$ reported for a range of C3 crop and pasture species (Lemaire *et al.*, 1989; Greenwood *et al.*, 1990; Belanger and Gastal, 2000). The dilution curve and NNI (Sections 2.7.3 and 2.7.5) are suitable for vegetative growth. This was a suitable analysis for the current study because N concentrations were determined purely from the green cocksfoot herbage removed at harvest, typical of the situation in a rotationally grazed pasture. The ability of this relationship to eliminate variations caused by site and season (Lemaire *et al.*, 2007) makes it a robust approach for extrapolating results compared with a basic agronomic approach in which DM response curves are used to determine the optimum rate of N fertiliser required.

The rates of N fertiliser applied are not commercially recommended. By using the N dilution curve and measured DM yields of the green cocksfoot component of the I+N and D+N pastures the amount of N required for the DM produced was estimated. For example, in the 2003/04 growth season the accumulated annual yield of the green cocksfoot component was 17.9 (I+N), 8.2 (I-N), 12.3 (D+N) and 4.6 t DM/ha/y by D-N pastures. To achieve these yields with non limiting N, the quantity of nitrogen recovered in herbage should have totalled 709, 430, 539 and 292 kg N/ha/y. For the I-N pasture where 282 kg N/ha/y was recovered (Table 6.1) from a green herbage yield which totalled 7.6 t DM/ha this indicates an additional 148 kg N/ha/y would have been required to produce the same yield when unlimited by N deficiency. For the I+N pastures annual N applications could have been reduced by 93 kg N/ha/y assuming all

applied N fertiliser was used in the production of the DM yield measured. However, this does excluded N held in residual biomass (0-3.0 cm).

In 2004/05, accumulated green cocksfoot herbage totalled 18.1 (I+N), 7.6 (I-N), 14.0 (D+N) and 3.9 t DM/ha/y by D-N pastures. To produce these yields under non limiting N conditions annual N in required in green herbage should have totalled 707, 406, 591 and 255 kg N/ha/y respectively. Specifically, in the rotation ending 12/1/2005 green cocksfoot contributed 3.2 t DM/ha by I+N pastures and 2.9 t DM/ha by D+N pastures. Actual N required for these yields, which were not produced during a period of water stress, were 102 kg N/ha and 96 kg N/ha. This indicated N fertiliser application were about 50% more than was required for the DM yields produced above a 3.0 cm residual cutting height.

6.4.2 The extent of N deficiency in cocksfoot pastures

After quantifying the optimum N requirements for a given DM yield (Figure 6.5), determined under non limiting N conditions, an NNI was calculated to determine the extent of N deficiency the pastures were exposed to. The I+N pastures had an average NNI of 1.0, across the two growth seasons (Figure 6.6). This is expected because the N dilution curve, which was comparable to that previously reported (Lemaire *et al.*, 1989; Greenwood *et al.*, 1990), was derived from this pasture. In the I-N pastures, the NNI averaged 0.5. This was consistent with the difference in TAGR calculated previously (Section 5.3.6). Specifically, after the period of water stress was accounted for, it was shown that +N pastures produced 7.0 kg DM/^{o}Cd/ha but the TAGR of –N pastures was 3.3 kg DM/^{o}Cd/ha. Thus, the difference between the annual NNI of the I+N and I-N pastures accurately described the differences in TAGR of +N and –N pastures when water stress was not the main limitation to pasture production. The mechanism responsible for these differences will be addressed in Chapter 7.

The NNI showed that the I+N and D+N pastures were similar when soil moisture did not limit dryland pasture production (Figure 6.6). However, when the D_L of 78 mm was exceeded (Section 5.4.1), the NNI of the D+N pastures was below 1.0. This is expected because water and N uptake are intrinsically linked which can make it difficult to attribute results to an individual factor (Stark and Firestone, 1995). If soil moisture is the critical limiting factor to growth, regardless of soil N status, growth can only continue at the water limited rate. Furthermore, as the soil dries, symptoms of N

deficiency may be observed because nutrient supply from solution is unable to meet plant demand (Section 2.5.4).

6.4.3 Partitioning the NNI

The NNI was then related to specific leaf N (Figure 6.7a) for measurements taken in early spring of 2005 when soil moisture was non limiting. The SLN of emerged leaves was constant (1.3-1.5 g N/m^2 leaf) over a range of NNI values, at a given point in time, but declined as the regrowth duration increased. This was probably associated with the duration of growth which differed for the two sampling dates. The mid rotation harvest on 1/9/2005 occurred 12 d after mowing whereas the end of the following rotation on 17/10/2005 occurred after 27 d. As a result there were probably a greater proportion of newly emerged leaf tips at the mid rotation harvest compared with the end of rotation harvest.

Peri *et al.* (2003) reported N% of field grown cocksfoot leaves decreased from 5.8% (10 d regrowth) at a rate of 0.04%/d during a 60 d rotation. This was probably a result of an increase in the proportion of total plant N allocated to structural and non photosynthetic material (Caloin and Yu, 1984) for the period from leaf tip emergence to the end of leaf extension. This is in agreement with the proposed behaviour of wheat (Jamieson and Semenov, 2000) where leaf N is hypothesised to be a constant proportion of total N associated with structural formation of cell walls. Subsequently, remobilisation and translocation of mobile nutrients, which includes N, to other plant parts (Whitehead, 1995) increases as individual leaves age (Peri *et al.*, 2003).

Specific pseudostem N was related to the NNI and a linear relationship was observed (Figure 6.7b). The change in NNI was associated with a greater quantity of total plant N. This was probably associated with metabolic N being dominant in the main region associated with cell differentiation of newly developing leaves within the leaf sheath (Gastal and Nelson, 1994). This was consistent with the literature as an increase in SPN is associated with an increase in available N for use in metabolism and storage and changes in NNI are associated with the storage component of total N (Jamieson and Semenov, 2000). The increased SPN of +N treatments may have represented an increase in Rubisco formation prior to leaf lamina emergence from the leaf sheath. In tall fescue it has been shown that the majority of total leaf N is present within 25 mm of the ligule (Section 2.7). Sequential use of leaf N occurs with N used in differentiation

then recycled to form Rubisco. It has also been reported that the majority of Rubisco was formed prior to lamina emergence from the pseudostem (Gastal and Nelson, 1994). The results shown in Figure 6.7 support these ideas and indicated cocksfoot behaved in a similar manner. It is important that further work is conducted to ensure the relationships for SPN, and SLN, with the NNI accurately describes the partitioning of N reported here because measurements were made at only two harvest dates during the course of the experiment.

6.4.4 Estimating the expected yield reductions caused by N deficiency

To predict expected yield losses caused by N deficiency the NNI was compared with DM yields of the green cocksfoot component of the pastures. As expected, Figure 6.9a shows that yield of the green cocksfoot component generally showed a linear increase as the NNI increased from 0.33 to 1.0 (R^2=0.84) up to a critical yield of 1171 kg DM/ha. Over 50% of soluble N is directly associated with formation of photosynthetic apparatus (Section 2.7.2) and N also stimulates tiller production (Baker and Younger, 1987). Therefore, increased photosynthetic efficiency in combination with increased canopy interception due to more leaves per unit area would contribute to an increase in DM production as N availability increased. For this analysis, the group of circled values were excluded.

The DM yields of the green cocksfoot component in the –N pastures did not exceed 1 400 kg DM/ha in any regrowth period, even when irrigated. This yield corresponded to a NNI of 0.6 in the D-N pasture and only occurred in early spring, prior to the development of water stress. Seasonally, this was the period of highest N recovery (Figure 6.3) and N concentration (Figure 6.8) of cocksfoot herbage in the –N pastures. It is likely that this resulted from a flush of N into the system from mineralisation as soil temperatures increased and stimulated soil microbial activity (McLaren and Cameron, 1996).

The -N pastures (circled values) within the range of 600-1400 kg DM/ha did not show the same DM response when water was not a limitation to pasture production and they produced more DM than was expected based on the NNI. These values occurred between November and February which is the peak production period for cocksfoot. It is likely that this shows N dilution occurred to maintain leaf area (Jamieson and Semenov, 2000) during periods when temperature and soil moisture were non limiting

for growth but N was below optimum. The behaviour of the I-N pastures during this period suggests the relationships presented in Section 6.3.6 are unlikely to be constant for the range of conditions pastures are exposed to throughout a growth season and confirms the need for further work to develop a unifying relationship to explain potential variation in specific leaf/pseudostem N. Recently, Lemaire *et al*. (2007) summarised critical SLN for a range of C3 and C4 species which ranged from 1.4-2.0 g N/m^2 but no critical SLN was reported for cocksfoot. It is important that further work is conducted to identify the critical SLN for cocksfoot. Peri *et al*. (2002b) showed that cocksfoot leaf photosynthesis was non limitied by N when ≥5.2%. Photosynthesis was 70% of optimum at 2.6-5.2% leaf N. When leaf N% was <2.6% photosynthesis was only 25% of leaves which contained non limiting N.

The expected yield reduction caused by N deficiency was determined from the relationship between relative yield (RY) and the NNI (Figure 6.9b). The form of the relationship was Relative yield = 1+(1.08*(NNI-1.0)) (R^2=0.81). Standard errors were 0.04 and 0.03, respectively. This relationship allowed the loss in DM production caused by N deficiency to be estimated. For example, a yield of 700 kg DM/ha with a NNI of 0.5 would have produced only 46% of the potential yield of 1 522 kg DM/ha. Furthermore, the relationship does not need information on time of year or regrowth duration to estimate yield losses. If a pasture had a NNI of 0.8 and a yield of 700 kg DM/ha then 78% of the potential yield (875 kg DM/ha) was produced. Data from periods when pastures were exposed to water stress were excluded from the analysis. During these times water was the main factor limiting production and the rate of yield reduction during this period has already been successfully described in relation to the D_L in Section 5.3.5. Pastures which consumed N in excess of the optimum N required for a known yield, which occurred in the D+N pastures after rainfall alleviated water stress, and I+N pastures with NNI <0.9 when N applications were insufficient for non limited growth in 2003/04 were also excluded.

It is important to state that the minimum NNI for growth has been proposed as 0.2 (Lemaire and Gastal, 1997) which is comparable to the x intercept shown in Figure 6.9b. The NNI is an instantaneous method of determining the extent of N deficiency and linearity between RY and the NNI has been shown to hold only when the NNI is constant (Lemaire and Gastal, 1997). The relationship would probably have been improved if an average regrowth NNI had been determined. This may have removed

some of the observed variability. Unfortunately, only end of rotation harvests were made during periods when soil moisture was non limiting.

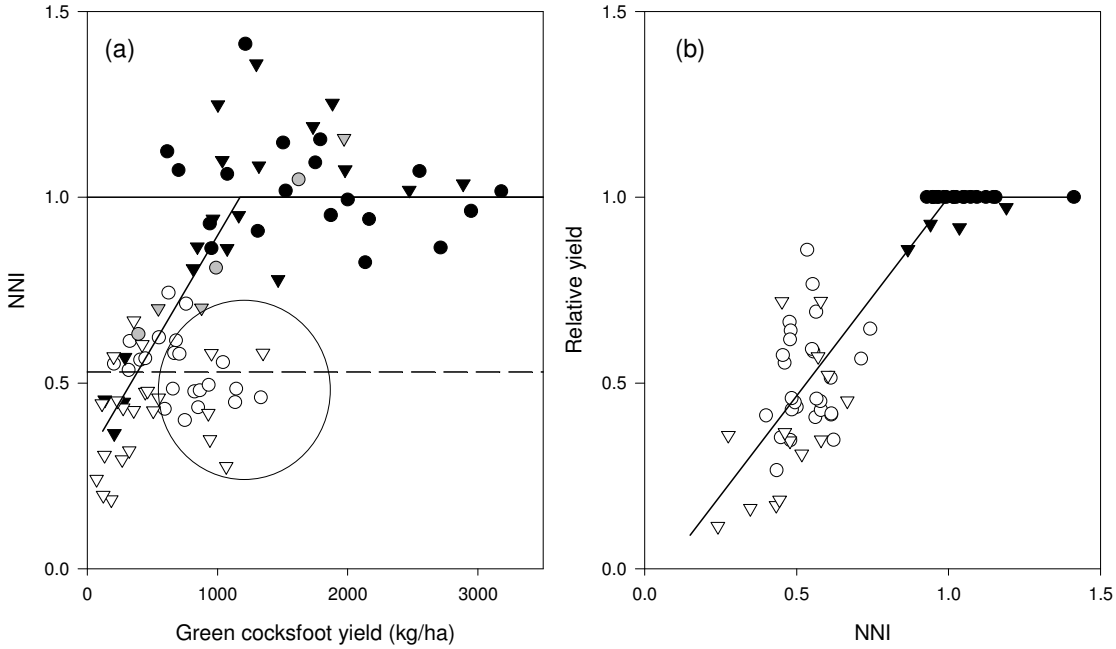

Figure 6.9 Relationship between (a) the nitrogen nutrition index (NNI) and measured green cocksfoot yield (kg DM/ha) and (b) relative yield and the NNI for I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures at Lincoln University, Canterbury, New Zealand. Grey symbols (a) represent regrowth cycles where no N application was made to +N pastures. Circled values (a) represent non water limited yields of –N pastures in spring/summer. Lines represent the mean annual NNI of the I+N pasture (—) of 1.0 and the I-N pasture (- -) of 0.5. The form of the broken stick model (b) was Relative yield = 1+(1.08*(NNI-1.0)) (R^2=0.81). Standard errors were 0.04 and 0.03. Treatment acronyms were given in Table 3.1.

6.4.5 N content of cocksfoot pastures

The actual N% of cocksfoot was higher in 2004/05 than 2003/04 in both +N and –N pastures (Table 6.4). In +N pastures this was caused by a doubling of the N application rate in 2004/05 because the NNI indicated I+N pastures were N deficient in summer months of 2003/04. In addition, rainfall in December 2004 was 132 mm compared with 1 mm in December 2003 (Figure 3.1). This allowed more DM production from D+N and D-N pastures in summer of the second growth season compared with 2003/04 (Figure 4.2). Mineralisation of soil organic matter is microbially mediated. As the soil dries microbial activity declines, nitrification slows and less plant available N is available (McLaren and Cameron, 1996). The N% (Section 6.3.7) of –N pastures, averaged over the two growth seasons was 3.0% compared with 4.3% in the +N pastures. It has been shown that leaf N concentrations <5.2% reduced the photosynthetic capacity of cocksfoot pastures (Peri *et al.*, 2002b). The 3.8% in the +N pastures in 2003/04, which included leaf and pseudostem, was probably sufficient to ensure photosynthesis was at least 90% of potential.

6.4.6 DM responses to applied fertiliser N

Table 6.4 shows the DM response of the I+N pasture in 2004/05 was only half that of 2003/04. This probably occurred because of the doubling of the N application rate in 2004/05. In 2004/05, the rate of N applied annually was comparable to that applied to Peri *et al.* (2002a; 2002b) and others but only half this amount was applied in 2003/04. These rates are not commercially recommended but were applied to ensure that N was not a limitation to production. Comparable N rates have previous been reported for individual regrowth cycles and annual application rates for a range of pasture species (Donohue *et al.*, 1981; Mathieu and Besnard, 1983; Belanger *et al.*, 1994; Belanger, 1998; Marino *et al.*, 2004). This allowed potential production of I+N pastures to be determined and allowed the extent of reductions caused by biophysical factors to be quantified. However, the main limitation of this purely agronomic approach is that results are subject to variation caused by site, season and species (Lemaire *et al.*, 2007). This means that results cannot be extrapolated beyond the specific conditions under which they are collected. Figure 6.2 showed the I+N pastures response to N fertiliser showed a seasonal variation caused by temperature and confirms DM responses to applied N vary seasonally (Section 2.7.3). In contrast, the N response of the D+N pasture declined over summer and this corresponded to the period when the growth was

compromised by insufficient soil moisture quantified by the time beyond D_L (Section 5.4.1).

6.4.7 N recovery and NUE

Table 6.1 showed that I-N soils supplied 29-34% of the N required for non N limited yields, as indicated by recovery relative to the I+N pasture. In comparison, the D-N soils supplied 18-32% of that required for optimum dryland yield indicated from N recovery from D+N pastures. This further accentuates the large effect N deficiency has on cocksfoot production shown here and supports the conclusions of Peri *et al.* (2002a).

Figure 6.3 showed the amount of N recovered in green cocksfoot herbage for individual rotations was affected by I*N interactions during periods of water stress. For example, in the rotation ending 30/12/2003 N recovery in green herbage was 55 kg N/ha for I+N and 19 kg N/ha for I-N. In contrast, dryland pastures contained 5 kg N/ha. In this rotation, irrigated pastures used a similar amount of water (Section 5.2.2) even though total DM yields were 3.5 (I+N) and 1.2 t DM/ha (I-N) (Appendix 5). This indicates that when water is non limiting to production, though either rainfall or irrigation, DM production could be doubled if sufficient N is available and water in the production of that DM would also be used more efficiently. The dryland pastures produced total DM yields of < 0.5 t/ha in the same rotation which shows that regardless of N availability at this time, water was the main constraint to DM production. This is probably a combined effect of reduced canopy light interception as cell expansion is compromised (Hsiao, 1973) and stomatal closure which increases photorespiration and causes a reduction in net photosynthesis (Biscoe and Gallagher, 1977; Brown, 1995). This can be indirectly estimated by calculating radiation use efficiency and is affected by water availability (Singh and Sri Rama, 1989). After autumn rainfall the N uptake of the D+N pastures exceeded that of I+N which shows luxury uptake of N which was previously unavailable due to insufficient water uptake from the topsoil (Garwood and Williams, 1967) where the majority of N is located (Appendix 7).

Inclusion of soil N levels after the experiment ended (Section 6.3.2.1) allowed 43-49% of applied N in 2004/05 to be accounted for. Soil tests (Table 6.2) did not show any difference in mineral N content of the pastures (0-0.6 m) and was 95 kg N/ha. This would be typical of a system under cut and carry management as biomass was removed from the pastures at harvest. If the bulk density determined for the 0-0.2 m layer was

used to estimate the contribution of ammoniacal-N and nitrate-N at 0.2-0.6 m soil depths the amount of N accounted for increased to 59% in the I+N pastures and 62% in the D+N pastures. Visual observation of the site 14 months after the final N application (November 2006) showed +N pastures were still producing higher yields than the –N pastures. Therefore, N which was unaccounted for at the end of the experiment was still contributing to increased pasture production in +N pastures. Responses to applied N have been reported to occur up to six months after application (Peri *et al.*, 2002a).

The NUE was consistently greater in –N pastures than in +N pastures. This suggests that N was diluted by the pasture to maintain leaf area rather than initiating mass export of soluble N from leaves (Jamieson and Semenov, 2000). By maintaining leaf area at below optimum N concentrations the quantity of light intercepted would be unchanged but the efficiency with which the energy was used to produce DM would decline. Under extreme stress conditions leaf area would be sacrificed by initiating premature senescence of older leaf tissue which would have then been imported into developing leaves of smaller size. This will be examined in detail in Chapter 7 from light interception measurements and destructive leaf area determinations. Alternatively, internal remobilisation of N by the –N pastures to maintain leaf N in leaves at the top of the canopy may have occurred (Lemaire and Gastal, 1997; Lemaire *et al.*, 1997).

6.5 Conclusions

From this chapter the following conclusions can be made:

- Specific leaf N was 1.3-1.5 g N/m^2 and constant across treatments, at a given point in time, and was associated with structural N as a constant proportion of total N. In contrast, specific pseudostem N increased from 1.0 to 1.7 g N/m^2 as the NNI increased from 0.4 to 1.2 and indicated that +N pastures had more N for cell differentiation and storage than –N pastures.

- Relative yield decreased at a rate of 1.08% per unit NNI below a value of 1.0 when water was not the main limit to DM production.

- The NNI showed –N pastures were N deficient at all times. In contrast, D+N pastures were N deficient during periods when the actual soil moisture deficit exceeded the critical limiting deficit of 78 mm.

In Chapter 7 the effects of both N and soil moisture will be used to identify the mechanism which resulted in yield differences. This will be achieved by explaining the effects of treatments on the quantity of light intercepted and the efficiency with which the light energy was used to produce DM.

7 Mechanisms which reduce DM production by cocksfoot pastures

7.1 Introduction

Chapter 4 showed the differences in DM production of cocksfoot monocultures caused by different water and nitrogen treatments. These yields were then described in relation to seasonal temperature, soil moisture (Chapter 5) and nitrogen (Chapter 6). To determine the mechanisms responsible for these yield differences investigations of canopy light interception (R/R_o) and radiation use efficiency (Monteith, 1972, 1977) are required. Initially, both R/R_o and RUE need accurate measurement of the light environment. The methodology to do this is poorly defined for established pastures so this is explored in detail in the Materials and Methods (Section 7.2).

The aim of this chapter is to provide the physiological basis for descriptions of yield responses presented in the previous results chapters (Objective 6, Section 1.4). Results of destructive calibrations to calculate LAI are presented. The quantity of PAR intercepted above ground level, RUE, tiller population and specific leaf weight (SLW) are used to examine the mechanisms responsible.

7.2 Materials and Methods

Experimental design, management details including soil test results were presented in Section 3.4. Section 3.6 described biological measurements and included descriptions of measurements to determine tiller population and reproductive status of the pasture. The extent of water stress was described in Chapter 5 and the effect of N nutrition of the pastures was described in Chapter 6. Section 6.2.3 described calculations for specific leaf weight (SLW) and specific pseudostem weight (SPW).

7.2.1 Measurement of the light environment

In most cases, the non destructive equipment used to measure light interception and estimate leaf area index (LAI) was designed for use in annual crops where the growth season is relatively short and there is no residual biomass. However, evaluation of three methods of light interception in maize (*Zea mays*) showed all equipment underestimated

actual LAI (Wilhelm *et al.*, 2000). Furthermore, in forests and discontinuous canopies, the effect of clumping causes inaccurate estimates of LAI (Jonckheere *et al.*, 2004; Weiss *et al.*, 2004). Calibrations between destructive and estimated LAI can allow readings to be adjusted to account for these errors.

Light interception from perennial pastoral systems is not widely available, and of that data, much is a result of short term experiments which are either made in establishing swards or in controlled environments with pots or micro swards (Brougham, 1960; Faurie *et al.*, 1996). This is probably because direct measurement of canopy parameters is difficult in short swards (Welles and Cohen, 1996; Nouvellon *et al.*, 2000; Jonckheere *et al.*, 2004). In addition, the accuracy of the estimate of LAI depends on how closely model assumptions built into the equipment match canopy reality (Welles and Cohen, 1996) and there is a co-dependence of LAI estimates on R/R_o for non destructive *in situ* measurements of LAI.

The extinction coefficient (k) is the negative slope of the relationship between $Ln(R/R_o)$ and LAI. In this study, values are reported as positive numbers which is consistent with the literature (Goyne *et al.*, 1993). The use of a constant k is not ideal. This is because k depends on the angle of the incoming beam of light and changes throughout the day and seasonally. However, it has proven to be a satisfactory way to estimate canopy architecture and is used in many simulation models. In pasture, it has also been shown that interception may be underestimated during early growth and overestimated at the end of the growing season (Nouvellon *et al.*, 2000). Regardless of the issues associated with pastures alone, it is important in any system where light interception is measured and used to separate treatment effects, that the data is an accurate representation of the canopy. This section describes the reasons for equipment selection, measurements and the results of calibrations conducted to generate accurate and independent variables to be used in an established perennial cocksfoot pasture.

7.2.2 Choice of equipment to measure light interception

Incident and transmitted photosynthetically active radiation measurements were made with a Sunscan plant canopy analyser (Delta-T Devices Ltd, Burwell, Cambridge, U.K.) after measurements channels were installed at ground level in the pasture (Section 7.2.3). This equipment was used to record the main measurements of the light environment. A benefit of the Sunscan was that measurements of transmitted PAR are

the mean calculated from 64 photodiodes evenly spaced along a 1 m long below canopy sensor. This reduces the need for multiple measurements and reduced disruption of the canopy when placed in the channel.

The LAI2000 canopy analyser (LI-COR, Lincoln, Nebraska, USA) was used on five dates to confirm the *k* used by the Sunscan. Canopy analyser measurements were made with a 12º view cap to exclude the operator and measurements were not made in the first two weeks of regrowth. One above canopy measurement was made followed by five sequential below canopy readings at ground level, under uniform overcast conditions. For the purposes of cross calibration, canopy analyser readings were taken within 12 h of Sunscan measurements. Mean tilt angles for each of the five view rings were reanalysed using the LAI2000 C2000 programme.

7.2.3 Fractional radiation interception

Radiation intercepted by the canopy was measured using the Sunscan fitted with a BF2 beam fraction sensor (Delta-T Devices Ltd, Burwell, Cambridge, U.K.). This allows simultaneous measurement of photosynthetically active radiation (PAR) both above (incident) and below (transmitted) the canopy. Fractional intercepted PAR (PAR_i) was calculated using Equation 7.1:

Equation 7.1 $$\mathbf{PAR_i = R/R_o}$$

Where R is transmitted PAR and R_o is incident PAR in MJ PAR/m^2.

Below canopy measurements were made at ground level. Metal channels (1.0x0.04x0.03 m) were installed in a representative area of each plot. Within 24 h of harvest, measurements were made to quantify light interception by residual biomass. On the 6 of 22 occasions when this was not possible, due to rain or equipment failure, interpolation of the daily rate of increase between the next two sequential measurements was extrapolated back to the start of the rotation to estimate light interception by residual biomass.

At each measurement date the Sunscan was used to make five simultaneous readings of above and below canopy PAR levels and the average was taken. System settings were a leaf absorption parameter of 0.85 and an ellipsoidal leaf angle distribution parameter (ELADP) of 1.0 indicating a canopy tending towards randomness (k = 0.57). Because the ELADP varied from the start to the end of the regrowth period this default setting of

1.0 was maintained for the two years of measurements to describe the relative change between treatments and regrowth cycles. In addition, it was impractical to determine canopy structure/ ELADP at each of the measurement dates because of the time involved to process samples.

Replicated, destructive measurements of plant area index (PAI) were made from 9 of the 28 destructive harvests over a two year period. The PAI was determined as neither the canopy analyser or the Sunscan differentiate between pasture components, particularly green and non green material (Jonckheere *et al.*, 2004). To do this a subsample was separated into pasture components (Section 3.6.1) and cocksfoot was further separated into lamina and pseudostem. Surface area was measured from a digital image on a scaled template as previously described in Section 6.2.3. Samples were then oven dried and weighed. The PAI was calculated based on the resulting botanical composition data (Section 3.6.2).

7.2.4 Calibration Results

The relationship between Sunscan estimated LAI and PAI (Figure 7.1) showed that the Sunscan tended to underestimate LAI >8.0. This was mainly because of two measurements made in I+N pastures where PAI exceeded 12.0. The relationship shown has been inverted to allow PAI to be predicted from non destructive determinations of LAI. The adjusted LAI (LAI_{adj}) values identified the critical LAI as 4.1 (Figure 7.2). From this point forward any data of canopy development is presented as LAI_{adj} which estimates actual PAI including green and non green pasture components to ground level.

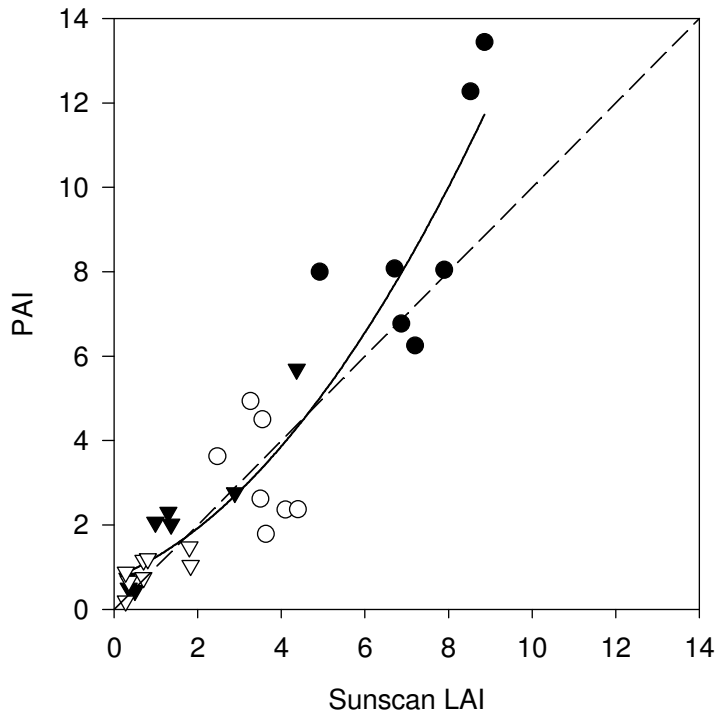

Figure 7.1 Relationship between Sunscan leaf area index (LAI) and plant area index (PAI) for I+N (●), I-N (○), D+N (▼) and D-N (▽) treatments imposed on a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. Form of the fitted line, when forced through the origin, is $y = 0.79x + 0.06x^2$ ($R^2 = 0.87$). The dashed line (--) represents the 1:1 line. Treatment acronyms were presented in Table 3.1.

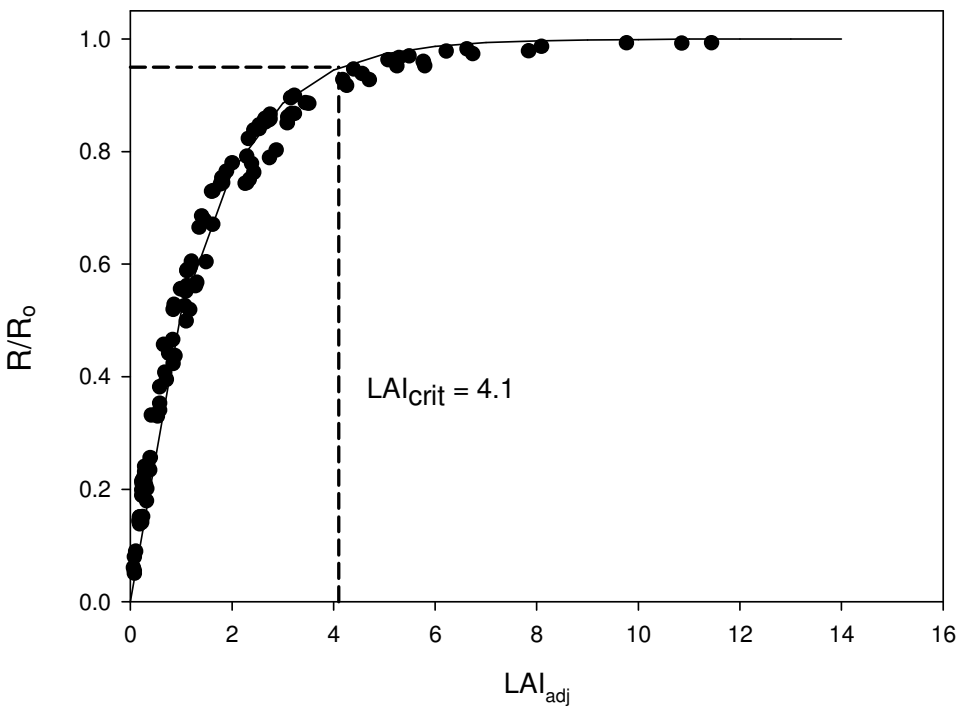

Figure 7.2 Relationship between adjusted Sunscan leaf area index (LAI_{adj}) and fractional PAR interception (R/R_o) in a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand. Form of the fitted line, when forced through the origin, was $y = 1\text{-}\exp(-0.72x)$ ($R^2 = 0.99$). The critical LAI ($LAI_{crit} = 4.1$) when 95% incident of PAR was intercepted.

7.2.5 The extinction coefficient (*k*)

The Sunscan *k* value of 0.57 was validated independently with the canopy analyser and found to be 0.57±0.004.

7.2.6 Radiation use efficiency (RUE)

Radiation use efficiency (RUE) was calculated from the slope of the regression, through the origin, of total harvested DM yield against accumulated intercepted PAR. Annual RUE data for 2003/04 was for a partial year (17/12/2003-5/10/2004). Data for 2004/05 was for the full growth season (6/10/2004-17/10/2005).

7.2.7 Relationship between RUE and NNI

The regression between RUE and the NNI (Sections 6.2.2 and 6.3.5) was used to explain differences in RUE of the four pastures using mean treatment data for all four pastures. Measurements made during periods of water stress were excluded.

7.2.8 Statistics

Analyses were conducted in Genstat 8.2 (Section 3.8). Both the total quantity of intercepted annual PAR (MJ/m^2) and the slopes of linear regressions used to determine RUE were analysed as split plot designs with irrigation as the main plot and N as the subplot. This was necessary because data from 2003/04 were for a partial growth season (17/12/2003-5/10/2004) and therefore not directly comparable to the 2004/05 growth season.

In 2004/05, annual RUE was analysed as a split-split plot design with irrigation as the main plot, N as the subplot and stress_period as the sub-sub plot (Section 5.2.7). This allowed comparison of RUE in the pre- and post water stress periods by excluding measurements made when the soil moisture deficit exceeded 78 mm in dryland pastures.

Within each individual regrowth cycle, the quantity of intercepted PAR, RUE, tiller population, tiller weight, SLA and SLW were analysed using a split plot design. Where significant means were separated at the α=0.05 level. Interactions were separated using the most conservative LSD.

Non linear regression and appropriate curve fitting procedures were used for calibrations related to canopy development presented in Sections 7.2.1 and 7.2.4. A

broken stick model (Section 5.2.7) was fitted to the relationship between relative LAI and the actual soil moisture deficit to explain the effect of water stress on canopy expansion. The rates at which relative LAI declined were determined separately for D+N and D-N pastures based on a maximum set from their respective irrigated crops. Thus, LAI_{adj} from the I+N pasture were used to define the potential for the D+N pastures. Similarly, LAI_{adj} from the I-N pasture was used as the non water limited maximum for the D-N pastures.

7.3 Results

7.3.1 Quantity of PAR intercepted by pastures

In 2003/04, an I*N interaction ($p \leq 0.01$) indicated all pastures intercepted different amounts of PAR for the year between 17/12/2003 and 5/10/2004. The I+N pasture intercepted 1593 MJ/m^2 compared with 1308 MJ/m^2 by I-N pastures, 955 MJ/m^2 for D+N and 832 MJ/m^2 for D-N pastures (Table 7.1). The interaction term represented 2% of the total sums of squares (SS_T) compared with 84% for the main effect of irrigation. In 2004/05, the total PAR intercepted between 6/10/2004 and 17/10/2005 was affected ($p \leq 0.05$) by irrigation being 2065 MJ/m^2 for dryland pastures and 2228 MJ/m^2 for irrigated pastures.

Table 7.1 Total intercepted PAR (MJ PAR/m^2) of cocksfoot monocultures at Lincoln University, Canterbury, New Zealand. Data for 2003/04 are based on data collected from 01/12/2003-05/10/2004 and 2004/05 data were for the period 06/10/2004-17/10/2005.

	Year	
Treatment	2003/04	2004/05
I+N	1593	2250
I-N	1308	2207
D+N	955	2136
D-N	832	1994
Effect	I*N	I
Significance	**	*
LSD ($p \leq 0.05$)	111.4	159.7

Treatment acronyms were given in Table 3.1.

In 2003/04, the quantity of PAR intercepted (MJ/m^2) by the pastures was affected by I*N interactions in 4 of the 8 regrowth cycles (Figure 7.3). For example, in the rotation ending 30/12/2004, the I*N interaction ($p \leq 0.001$) occurred because I+N pastures intercepted 334 MJ/m^2, compared with 151 MJ/m^2 for the I-N pastures and a consistent 54±2 MJ/m^2 for both dryland pastures. A similar pattern of means separation occurred in the rotation ending 02/02/2004 ($p \leq 0.01$). In contrast, the I*N interaction ($p \leq 0.05$) in the rotation ending 2/5/2004 showed that I+N pastures intercepted 125 MJ/m^2; 89 MJ/m^2 was intercepted by the D-N pastures and 112±4 MJ/m^2 was intercepted by I-N and D+N pastures. There was no effect of treatment on the amount of PAR intercepted by the pastures in rotations ending 4/8/2004 and 8/9/2004.

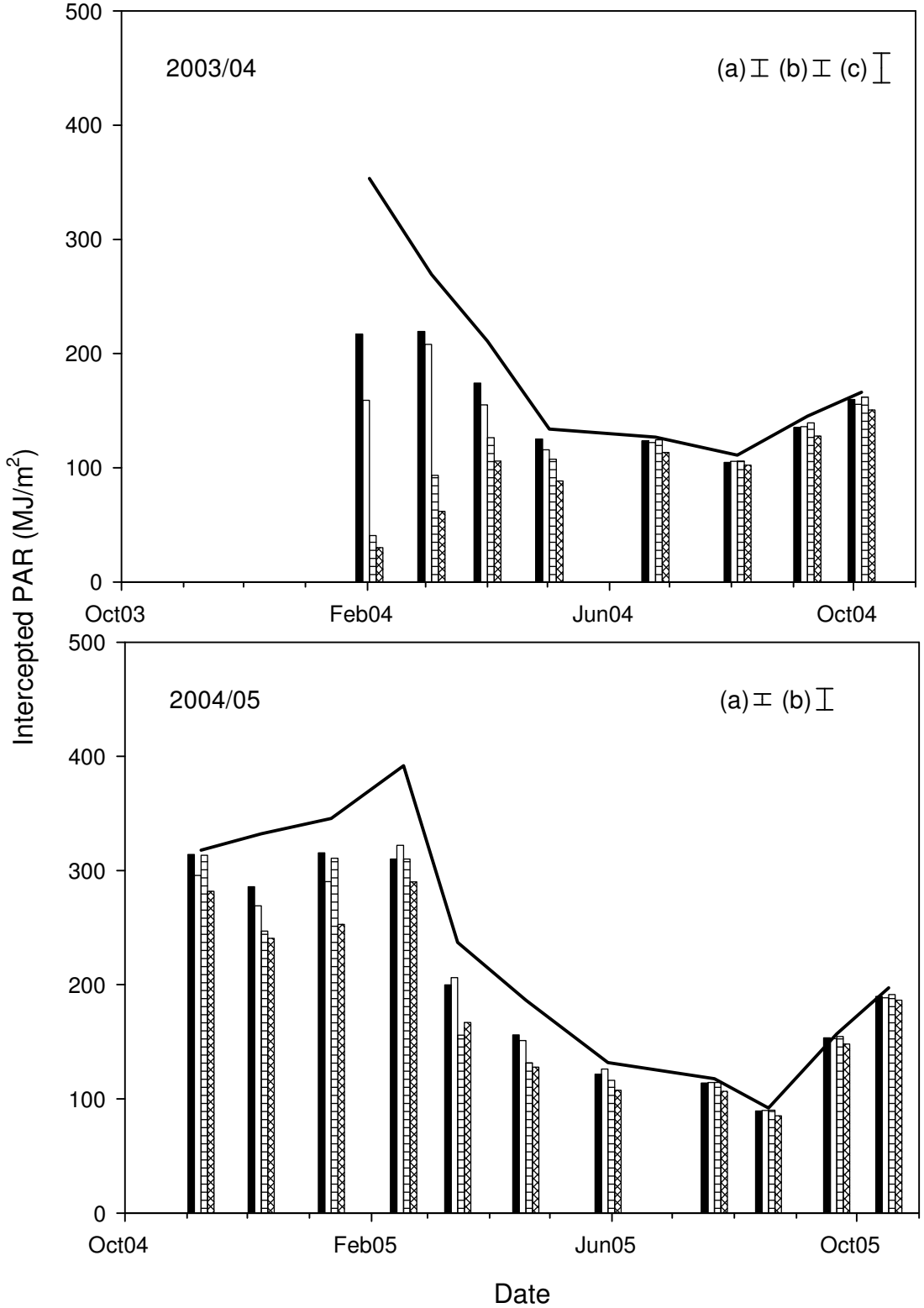

Figure 7.3 Quantity of PAR intercepted by cocksfoot monocultures at Lincoln University, Canterbury, New Zealand in 2003/04 (top) and 2004/05 (bottom) throughout individual regrowth periods for I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures. The solid line (—) represents total incident PAR receipts for each regrowth cycle. Error bars are maximum SEM for (a) I and (b) N and (c) I*N interactions. Treatment acronyms were presented in Table 3.1.

In 2004/05, irrigation increased the total amount of PAR intercepted in 5 of the 11 regrowth cycles. When responses to irrigation occurred, dryland pastures consistently intercepted less PAR than the irrigated pastures. For example, in the rotation that ended on 8/12/2005, irrigated pastures intercepted 278 MJ/m^2 compared with 244 MJ/m^2 by dryland pastures. Nitrogen increased the quantity of PAR intercepted in the two rotations ending 8/11/2004 ($p \leq 0.01$) and 12/1/2005 ($p \leq 0.05$). In the 8/11/2004 regrowth cycle, the +N pastures intercepted a total of 314 MJ/m^2 compared with 289 MJ/m^2 by the –N pastures. The amount of PAR intercepted by all pastures in rotations ending 17/2/2005, 22/7/2005, 18/8/2005, 21/9/2005 and 17/10/2005 were unaffected by treatment. For reference, Figure 7.3 also shows the total incident PAR receipts for each individual regrowth cycle. In the rotation ending 2/2/2004, total incident PAR was 353 MJ/m^2. Of this, the I+N pastures intercepted 61% of incident PAR, compared with 45% by the I-N pastures, 12% by D+N and 9% by the D-N pastures. In comparison, in the rotation ending 2/5/2004, all pastures intercepted >90% of incident PAR.

7.3.2 Leaf area index

By the end of every regrowth cycle the LAI_{adj} of I+N pastures was ≥4.1 (LAI_{crit}) and ranged from 4.1-11.8. In contrast, the I-N pastures had LAI ≥4.1 in 16 of the 19 rotations. The maximum end of rotation LAI of the D+N pastures over two growth seasons was 12.6 and the minimum was 0.3. The D+N pastures reached LAI_{crit} in 13 of the 19 rotations and the D-N pastures had LAI >4.1 in three regrowth cycles. The minimum LAI_{adj} (0.2) for the dryland pastures occurred within the first two months after channels had been installed and canopies may still have been recovering. The timing of installation also coincided with the period of water stress experienced by the dryland pastures. During this time several measurements made in dryland pastures indicated interception was nil. Plate 7.1 was taken on 15/1/2004 and shows that there was little green material in the dryland pastures at this time.

In the rotation ending 2/2/2004, an I*N interaction ($p \leq 0.001$) showed the I+N pasture had an LAI_{adj} of 10.0 compared with 3.0 in the I-N pasture; 0.3 in the D+N pasture and 0.2 in the D-N pasture (Figure 7.4). However, the I*N interaction ($p \leq 0.05$) on the 24/6/2004, showed the LAI_{adj} of I+N and D+N pastures was 11.1±1.10 compared with 4.6 in the I-N pasture and 2.8 in D-N pastures. There was no effect of treatment on LAI_{adj} of the pastures in rotations ending 8/09/2004 or 5/10/2004.

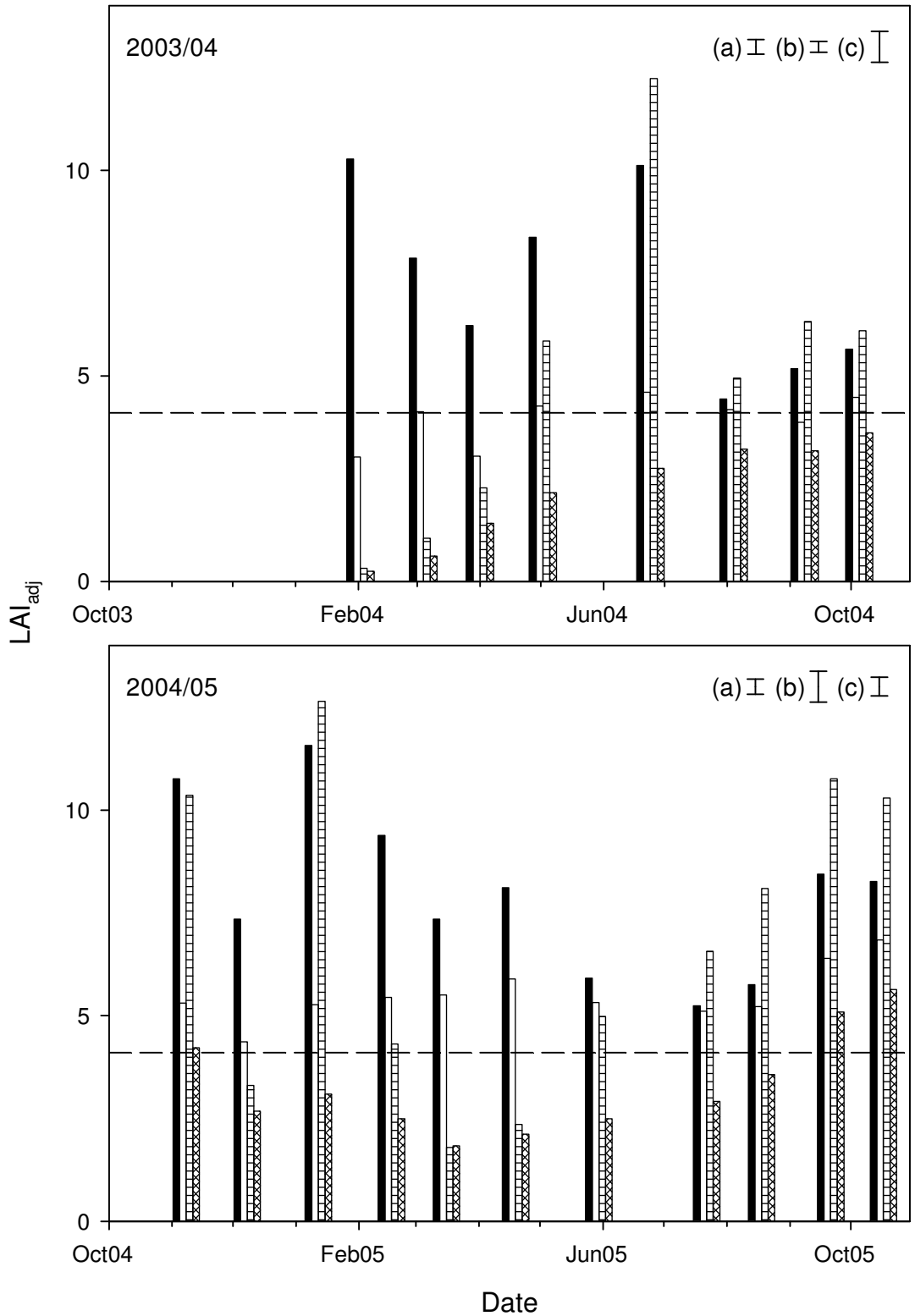

Figure 7.4 Adjusted leaf area index (LAI_{adj}) at the end of individual regrowth cycles by I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures in 2003/04 (top) and 2004/05 (bottom) at Lincoln University, Canterbury, New Zealand. Error bars are maximum SEM for (a) I, (b) N and (c) I*N interactions. Treatment acronyms were presented in Table 3.1.

In 2004/05, N affected LAI_{adj} in 7 of the 11 regrowth cycles whereas in the rotations ending 16/3/2004, 19/4/2004 and 30/5/2004 irrigated pastures had higher ($p \leq 0.05$) LAI_{adj} than dryland pastures. An I*N interaction ($p \leq 0.05$) occurred in the rotation ending 22/7/2004, when D-N pastures had an LAI_{adj} of 2.9 compared with 5.6±1.0 in I+N, I-N and D+N pastures. Nitrogen was the cause of differences in LAI_{adj} in the three subsequent rotations.

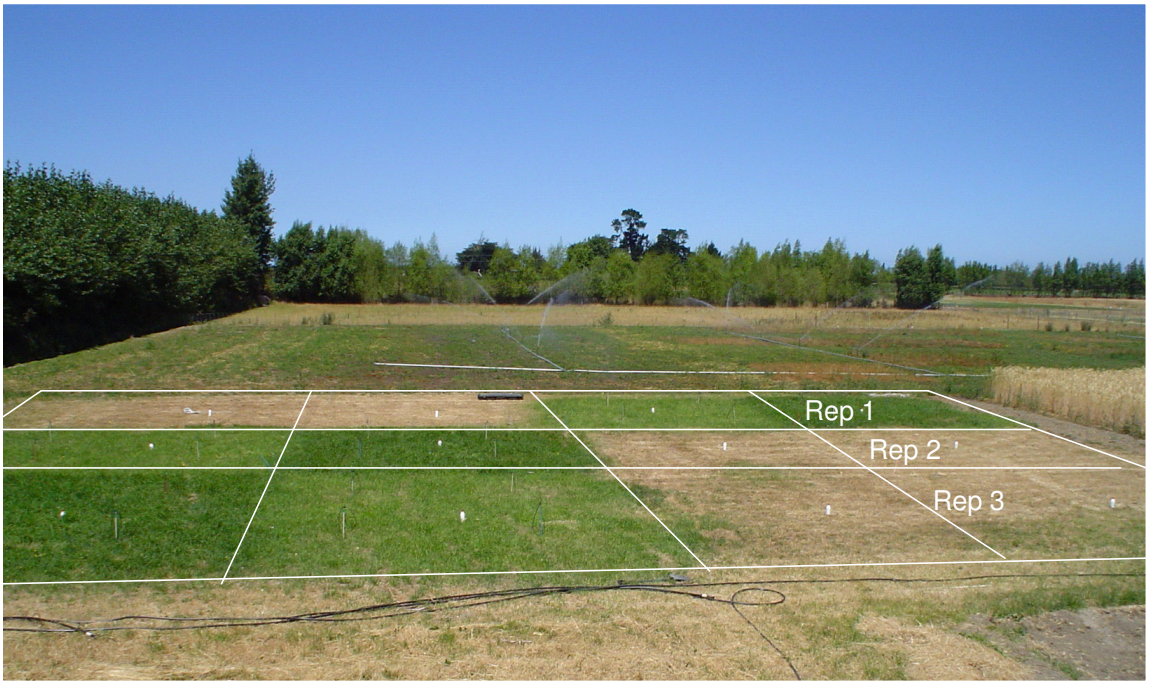

Plate 7.1 Experiment site at Block H18, Lincoln University, Canterbury, New Zealand on 15/01/2004. Replicates run left to right and caps for neutron probe access tubes are central in each plot.

7.3.3 Quantifying the effect of water stress on LAI_{adj}

Figure 7.5a showed that LAI_{adj} of D+N pastures, relative to I+N pastures, declined at a rate of 1.97%/mm beyond an ASMD of 87mm. In comparison, the LAI_{adj} of D-N pastures (Figure 7.5b) declined at a rate of 1.41%/mm when the ASMD exceeded 67 mm. A t-test showed there was no difference in the rate of reduction, which was an average of 1.69%/mm. However, the point of inflexion differed ($p \leq 0.05$) between +N and –N pastures. In -N pastures, LAI_{adj} declined when the ASMD was >67 mm but in +N pastures the ASMD beyond which LAI_{adj} declined > 87 mm.

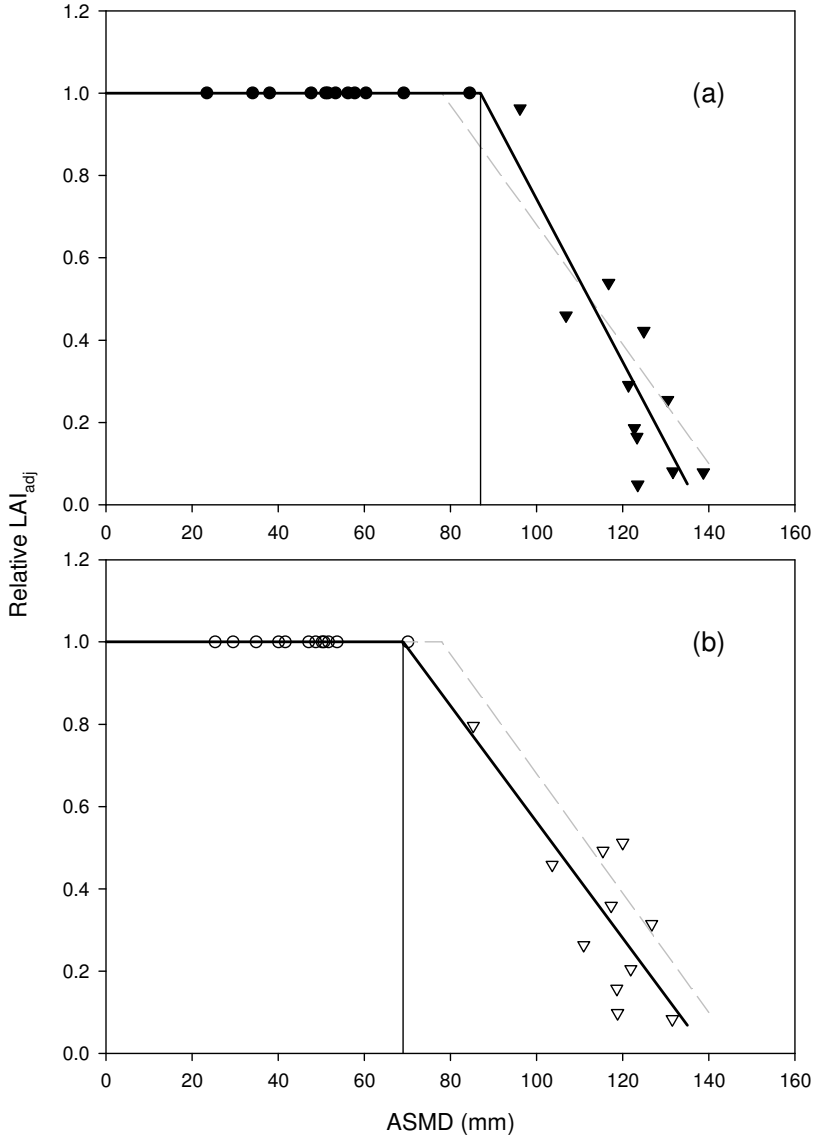

Figure 7.5 Relationship between leaf area index (LAI_{adj}) and the actual soil moisture deficit (ASMD) for (a) (a) D+N (▼) relative to I+N (●) pastures and (b) D-N (▽) relative to I-N (○) pastures at Lincoln University, Canterbury, New Zealand. The form of the broken stick model in (a) was: Relative LAI_{adj} = 1 + ((87mm*-0.0197)*(ASMD>87 mm)) (R^2 = 0.94). Standard errors of the parameters were 5.0 and 0.0026, respectively. The model in (b) had the form of Relative LAI_{adj} = 1 + ((67 mm*-0.0141)*(ASMD>67 mm)) (R^2 = 0.94). Standard errors of the parameters were 5.0 and 0.0016, respectively. The grey dashed line (- -) represents the rate at which relative yield decreased in response to water stress (Figure 5.5). Treatment acronyms were given in Table 3.1.

7.3.3.1 Tiller dynamics

In 2003/04, total tiller population (tillers/m^2) above cutting height was strongly affected by either irrigation or N but no I*N interactions occurred (Figure 7.6). Irrigated pastures had more ($p \leq 0.05$) tillers than dryland pastures in rotations ending 1/12/2003,

30/12/2003 and 2/2/2004, which corresponded to the period beyond D_L (Sections 5.3.6 and 5.4.1). The extent of differences declined after autumn rainfall alleviated water stress (Sections 3.4.1.1 and 5.3.2). Subsequently, +N pastures consistently had more tillers than –N pastures. In 2004/05, +N pastures contained a greater tiller population than –N pastures in 5 of the 9 regrowth cycles. Tiller population in rotations ending 8/12/2004, 17/2/2005, 16/3/2005 and 17/10/2005 were unaffected by treatment.

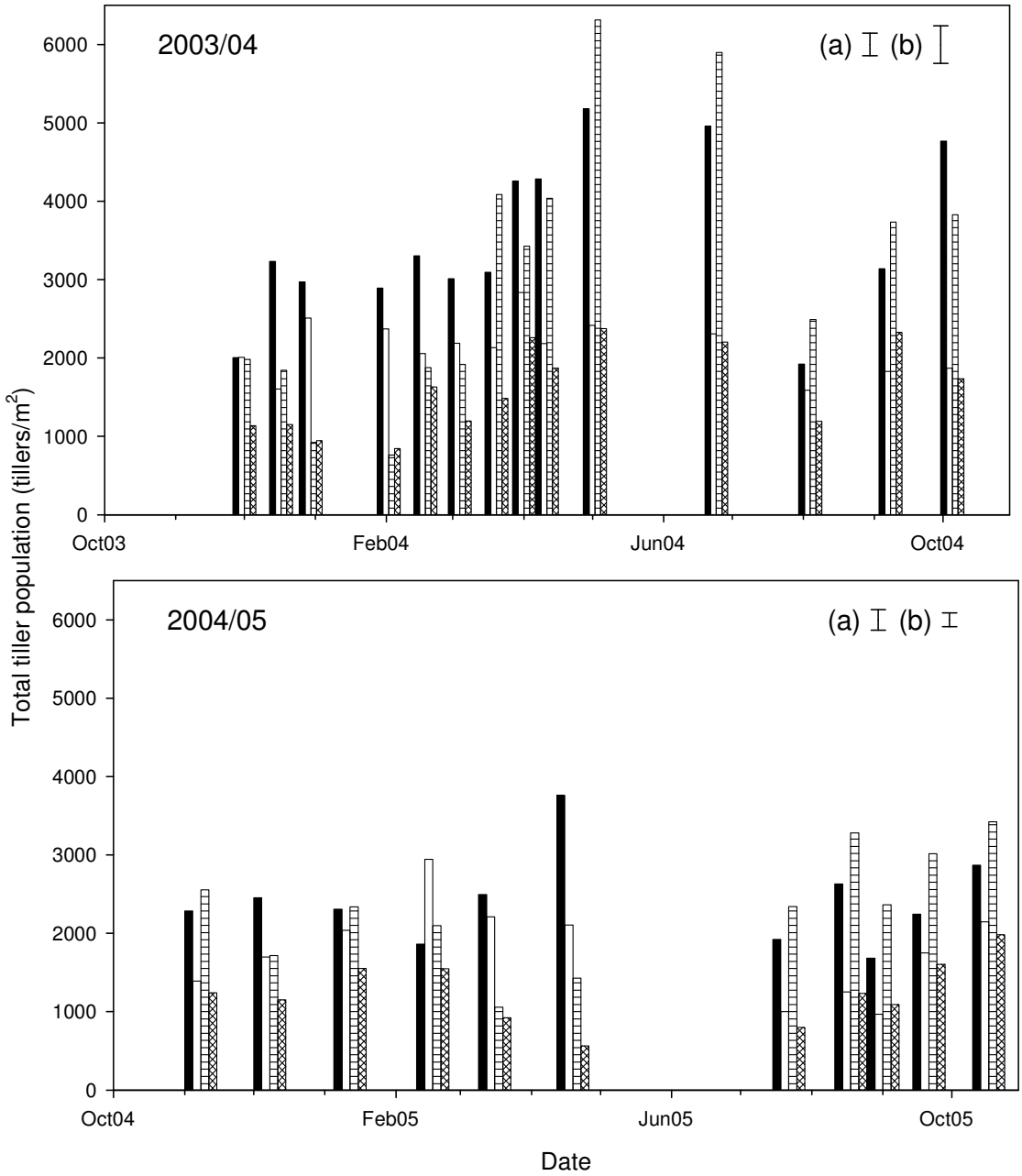

Figure 7.6 Total tiller population (tillers/m^2) of I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures at Lincoln University, Canterbury in 2003/04 (top) and 2004/05 (bottom). Error bars are the maximum SEM for (a) I and (b) N effects. Treatment acronyms were presented in Table 3.1.

7.3.3.2 Vegetative tiller weight

In 2003/04, vegetative tiller weight (g/tiller) was affected by treatment at four harvests (Figure 7.7). An I*N interaction ($p \leq 0.01$) occurred in the rotation ending 30/12/2003 when vegetative tiller weight was 0.03 g /tiller in the I-N and D-N pastures compared with 0.07 g/tiller in the I+N pastures and 0.02 g/tiller in the D-N pastures. In the rotation ending 4/3/2004, irrigation affected ($p \leq 0.05$) vegetative tiller weight which was 0.06 g/tiller in irrigated pastures compared with 0.04 g/tiller in dryland pastures. At the end of the subsequent regrowth cycle (1/04/2004) vegetative tillers in +N pastures ($p \leq 0.001$) weighed 0.04 g/tiller compared with 0.02 g/tiller in –N pastures. There was no effect of treatment in rotations ending 1/12/2003, or rotations between 2/5/2004 -5/10/2004.

In 2004/05, rotations ending 8/11/2004, 8/12/2004, 18/8/2005 and 17/10/2005 were unaffected by treatment. In the 12/1/2005 rotation vegetative tillers in the +N pastures ($p \leq 0.001$) weighed 0.11 g/tiller compared with 0.04 g/tiller in –N pastures. Irrigation affected ($p \leq 0.05$) tiller weight in rotations ending 16/3/2005 and 19/4/2005. At both dates tillers in the dryland pastures weighed 0.02 g/tiller compared with 0.04 g/tiller in the irrigated pastures.

At no time when reproductive tillers were present (Section 4.3.3), over the two growth seasons, did treatment affect either reproductive tiller number or reproductive tiller weight (Table 7.2).

Table 7.2 Reproductive tiller dry weight (g DM/tiller) and reproductive tiller population (reproductive tillers/ m^2) of a 'Wana' cocksfoot monoculture at Lincoln University, Canterbury, New Zealand.

Date	Reproductive tiller weight (g/tiller)	SEM	Reproductive tillers (tillers/m^2)	SEM
01/12/2003	0.12	0.31	80	7.8
08/11/2004	0.10	0.37	150	7.8
08/12/2004	0.12	0.36	65	8.1
12/01/2005	0.12	0.46	55	10.2

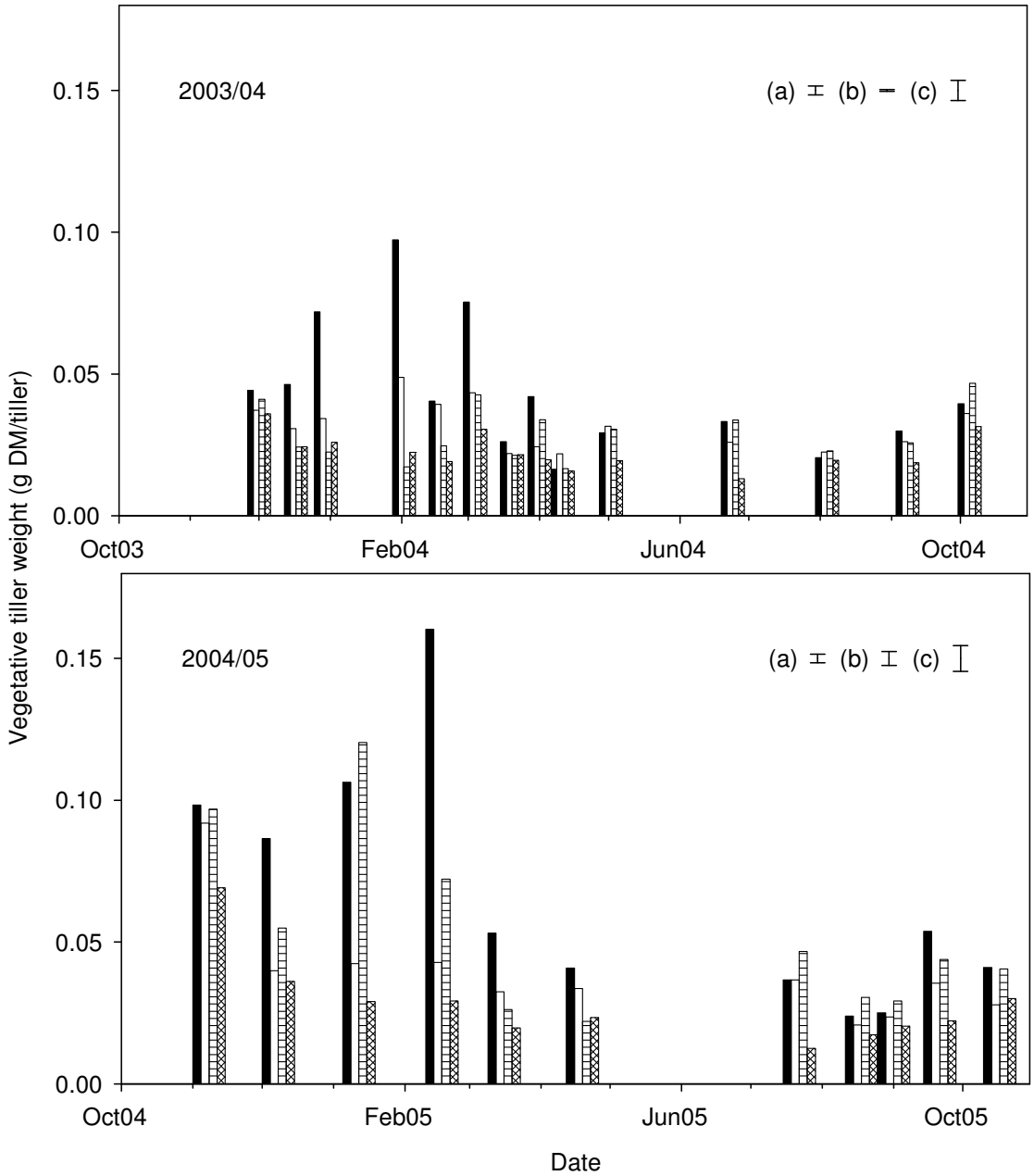

Figure 7.7 Vegetative tiller weight (g DM/tiller) of I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures at Lincoln University, Canterbury in 2003/04 (top) and 2004/05 (bottom). Error bars are the maximum SEM for (a) I, (b) N and (c) I*N interactions. Treatment acronyms were presented in Table 3.1.

7.3.3.3 Specific leaf weight (SLW)

Specific leaf weight (g DM/m^2) of the green cocksfoot component of the I+N pastures was 26.3±2.35g/m^2 at all seven measurement dates whereas the SLW of the I-N pastures ranged from 27.4 to 43.5 g/m^2 (Figure 7.8). Specific leaf weight of cocksfoot in the D+N pastures was between 22.8 and 55.8 g/m^2 and 28.0-50.0 g/m^2 in the D-N

pastures. An I*N interaction ($p \leq 0.01$) occurred on 17/10/2003 when all pastures had different SLW. Despite the interaction, the main effect of irrigation accounted for 85% of the total sums of squares compared with 11% for the interaction term. The minimum was 28.6 g/m^2 in the I+N pastures and a maximum of 55.8 g/m^2 in the D+N pastures. Irrigation was the cause of different ($p \leq 0.05$) SLW at harvests made on 30/12/2003 and 2/2/2004 whereas, N was the main factor which affected ($p \leq 0.05$) specific leaf weight at the harvest on 4/3/2004.

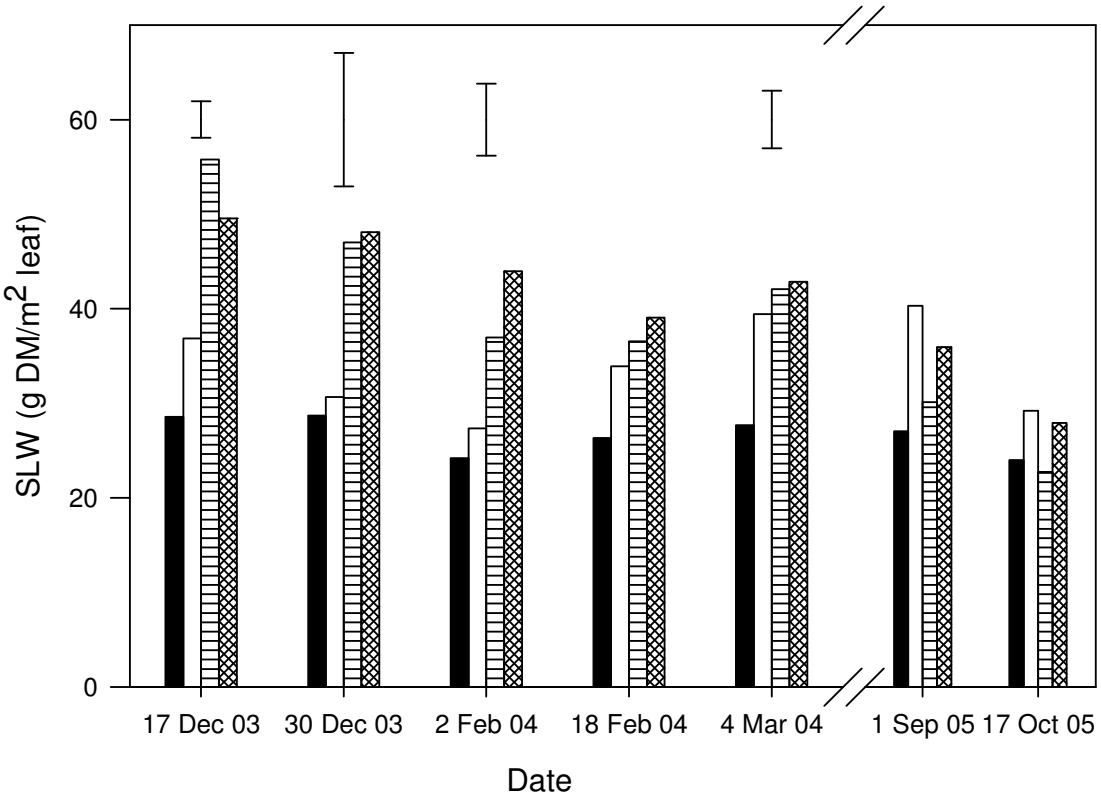

Figure 7.8 Specific leaf weight (SLW) of I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures at Lincoln University, Canterbury. Error bars are the LSD ($p \leq 0.05$) for the I*N interaction (17/12/2003), irrigation (30/12/2003 and 2/2/2004) and nitrogen effects (4/3/2004). Treatment acronyms were presented in Table 3.1.

7.3.4 Effect of water stress on total tiller population

As the actual soil moisture deficit increased total tiller population declined (Figure 7.9). Initially, the +N pastures were able to support a greater ($p \leq 0.05$) total tiller population than –N pastures. The +N pastures had an intercept of 4000±350 tillers/m^2 (R^2=0.83) compared with 2600±270 tillers/m^2 (R^2=0.74) for –N pastures. The reduction in tiller numbers of +N pastures as the ASMD increased was 21 tillers/m^2/mm compared with

13 tillers/m^2/mm in the –N pastures. A t-test showed no difference in the rate of tiller reduction as the ASMD increased and was 17±4 tillers/m^2/mm for both the +N and –N pastures.

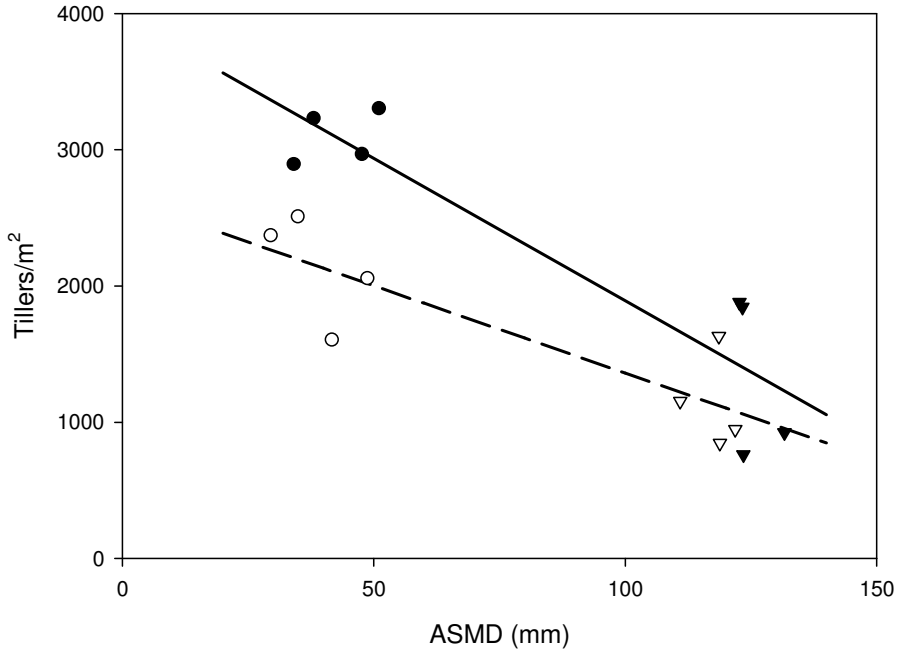

Figure 7.9 Relationship between total tiller population (tillers/m^2) of I+N (●), I-N (○), D+N (▽) and D-N (▼) pastures and the actual soil moisture deficit (ASMD) at Lincoln University, Canterbury, New Zealand. The solid line (—) represents the regression of +N pastures (●,▼) where y = 4000(±350) -21x (±350) (.The dashed line (- -) represents regression of –N pastures (○,▽). Treatment acronyms were given in Table 3.1.

7.3.5 Radiation use efficiency (RUE)

In 2003/04, annual RUE of the +N pastures was of 1.18±0.03 g DM/MJ PAR ($p \leq 0.001$) compared with 0.53±0.04 g DM/MJ PAR in the –N pastures (Table 7.3). In 2004/05, N was the main cause ($p \leq 0.001$) of different RUE when the soil moisture deficit was <78 mm. The +N pastures had an RUE of 0.90 g DM/MJ PAR intercepted compared with 0.36 g DM/MJ PAR by the –N pastures (Figure 7.10). There was insufficient data in the 23 d period between 8/11/2004 and 1/12/2004 to determine if RUE was also compromised by water stress.

Table 7.3 Annual radiation use efficiency (g DM/MJ PAR) of a 'Wana' cocksfoot monoculture grown at Lincoln University, Canterbury, New Zealand in 2003/04. Regressions used to calculate RUE are presented in Figure 7.10.

Treatment	2003/04
I+N	1.15
I-N	0.57
D+N	1.21
D-N	0.50
Effect	N
Significance	***
LSD ($p \leq 0.05$)	0.071

Note: Treatment acronyms were given in Table 3.1. Levels of significance are: 0.05 (*), 0.01 (**), and 0.001 (***).

7.3.6 Regrowth RUE

To determine if the annual RUE calculated from cumulative data was an accurate representation of RUE of individual regrowth cycles the relationship between yield (g/m^2) and intercepted PAR (MJ/m^2) for each individual regrowth period were calculated using data from the I+N pasture. Specifically, this was done because of the strong correlation between cumulative data which has been criticised previously (Demetriades-Shah *et al.*, 1992). Figure 7.11 shows that RUE determined from regression ($p \leq 0.001$) of non cumulative data was 1.04±0.04 g DM/MJ intercepted PAR (R^2=0.84).

In 2003/04, RUE of the I+N pastures ranged from 0.6-1.6 g DM/MJ PAR (Figure 7.12). The minimum occurred in the rotation ending 4/8/2004 when no N fertiliser was applied (Section 6.3.5). The RUE of the I-N pasture ranged from 0.4-0.7 g DM/MJ PAR compared with D+N pastures which had RUE between 0.4-1.5 g DM/MJ PAR. The RUE of the D-N pasture was 0.2-0.7 g DM/MJ PAR. An I*N interaction ($p \leq 0.05$) in the rotation ending 02/02/2004, indicated RUE of I+N pastures was 0.9 g DM/MJ PAR compared with 0.5±0.09 g DM/MJ PAR in I-N, D+N and D-N pastures. Nitrogen was the main cause of different RUE in 6 of the 8 rotations.

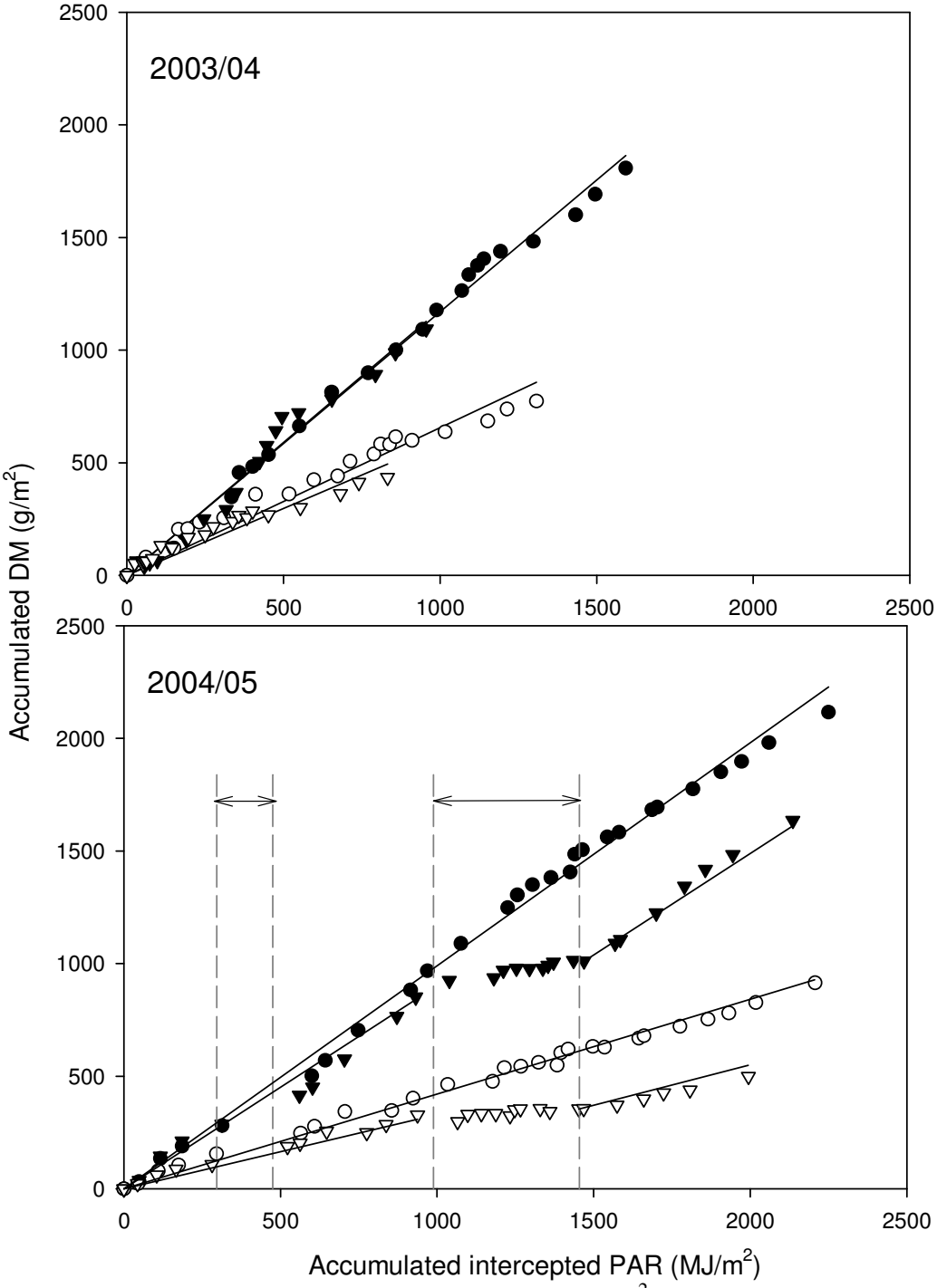

Figure 7.10 Relationship between accumulated DM (g /m^2) and accumulated intercepted photosynthetically active radiation (MJ /m^2) by I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures in 2003/04 (top) and 2004/05 (bottom) at Lincoln University, Canterbury, New Zealand. Slopes of the regressions for 2003/04 were presented in Table 7.3. In 2004/05, dashed lines indicate the periods of water stress when the critical limiting deficit of 78 mm was exceeded. When periods of water stress were excluded, the form of the regression for +N pastures was y = 0.90x (±0.017) (R^2=0.99). The form of the regression for the –N pastures was y = 0.0.35x (±0.025) (R^2=0.98). Treatment acronyms were given in Table 3.1.

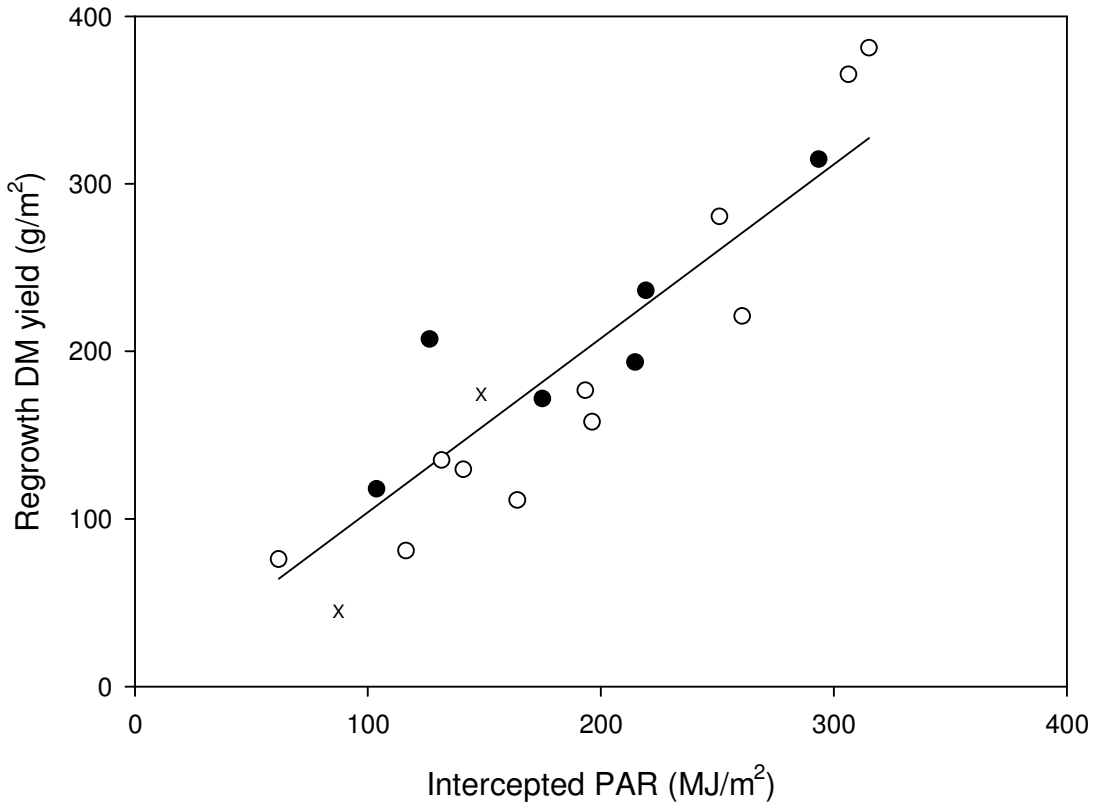

Figure 7.11 Relationship between DM yield (g/m^2) and intercepted PAR (MJ/m^2) of the I+N pastures in 2003/04 (●) and 2004/05 (○) pastures at Lincoln University, Canterbury, New Zealand. Rotations in 2003/04 when no N fertiliser was applied (ending 24/6/2004 and 4/8/2004) were included in the regression and are shown with X symbols. Each point represents one of 19 rotations made over two growth seasons and is the mean of three replicates. The form of the regression, forced through the origin, is y = 1.04x (±0.04) (R^2=0.84). Treatment acronyms were given in Table 3.1.

In 2004/05, N was the primary cause of differences in RUE for 9 of the 11 regrowth cycles. The RUE of the I+N pasture was between 0.7-1.2 g DM/MJ PAR compared with 0.3-0.7 g DM/MJ PAR in the I-N pastures. The RUE of D+N pastures was 0.2-1.2 g DM/MJ PAR and 0.1-0.5 g DM/MJ PAR in D-N pastures. In the rotation ending 12/1/2005, the RUE of the +N pastures ($p \leq 0.001$) was 1.1±0.01 compared with 0.3±0.05 g DM/MJ PAR in the –N pastures. An I*N interaction ($p \leq 0.05$) in the rotation ending 17/2/2005 showed the RUE of the I-N and D+N pastures was 0.4±0.06 g DM/MJ PAR, compared with 1.1 for I+N and 0.1 for D-N pastures.

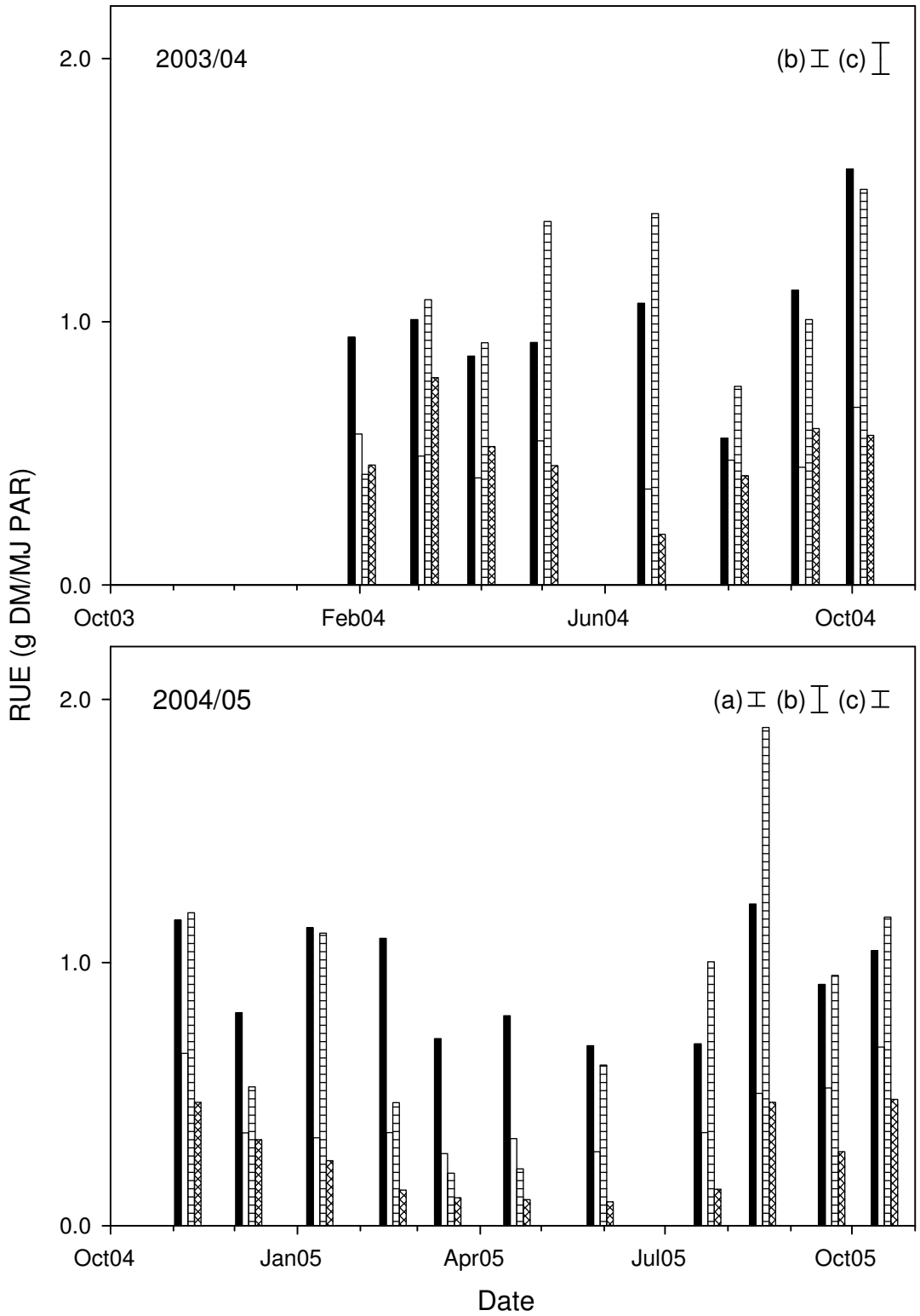

Figure 7.12 Radiation use efficiency (RUE) for individual regrowth cycles of I+N (■), I-N (□), D+N (▤) and D-N (▩) pastures at Lincoln University, Canterbury, New Zealand in 2003/04 (top) and 2004/05 (bottom). Error bars are the maximum SEM for (a) I, (b) N and (c) I*N interactions. Treatment acronyms were presented in Table 3.1.

7.3.7 The relationship between NNI and RUE

The effect of N deficiency on RUE was explained by the regression ($p \leq 0.001$) between RUE and the nitrogen nutrition index (Figure 7.13). The form of the regression was RUE=-0.23 +1.26*NNI (R^2=0.80). In the 4/8/2004 rotation, when no N was applied, the I+N pasture was N deficient with an NNI <1.0 and this was associated with the lowest measured RUE from the I+N pastures.

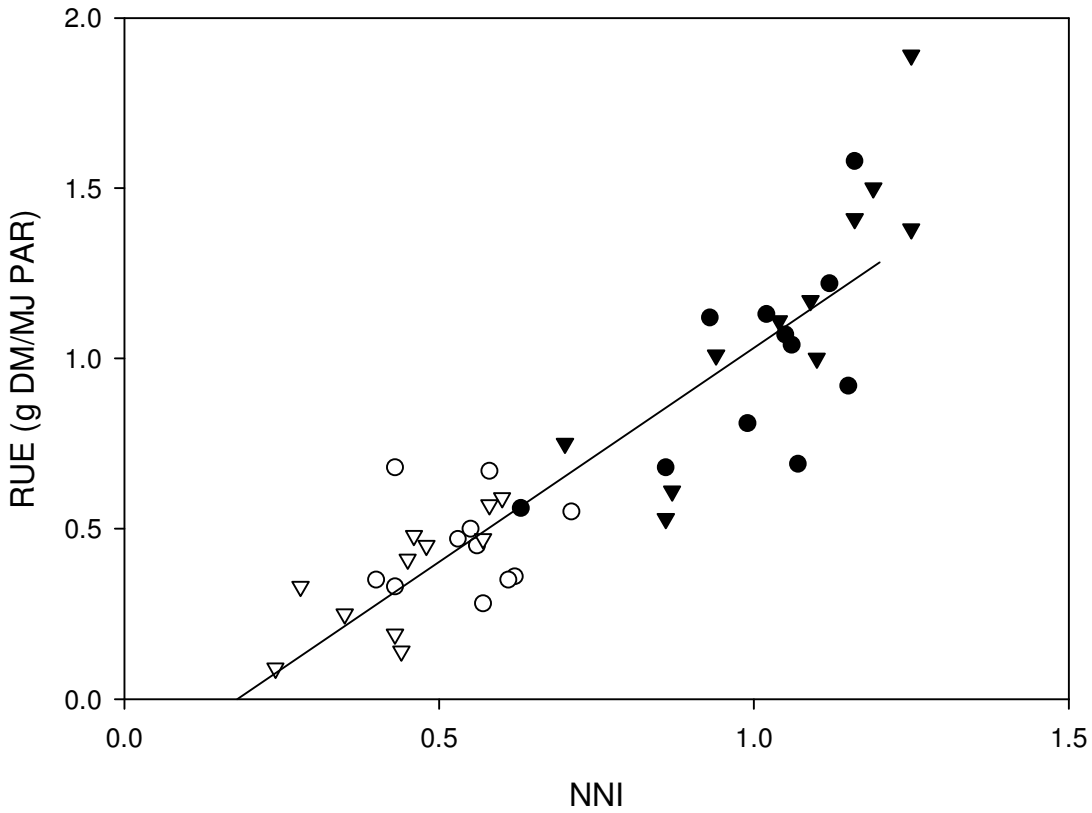

Figure 7.13 Relationship between RUE and NNI for I+N (●), I-N (○), D+N (▽) and D-N (▼) pastures. Data from periods of water stress were excluded from the analysis. Form of the regression was RUE=-0.23+1.26*NNI (R^2=0.80). Standard errors of parameters were 0.08 and 0.10, respectively. Treatment acronyms were presented in Table 3.1.

7.3.7.1 Relationship between yield and total tiller population

When N was the only factor affecting DM production, there was a relationship (R^2=0.80) between cocksfoot yield and total tiller population (Figure 7.14). The form of the regression was y =-0.80(±68.7) + 0.35(±0.025)x.

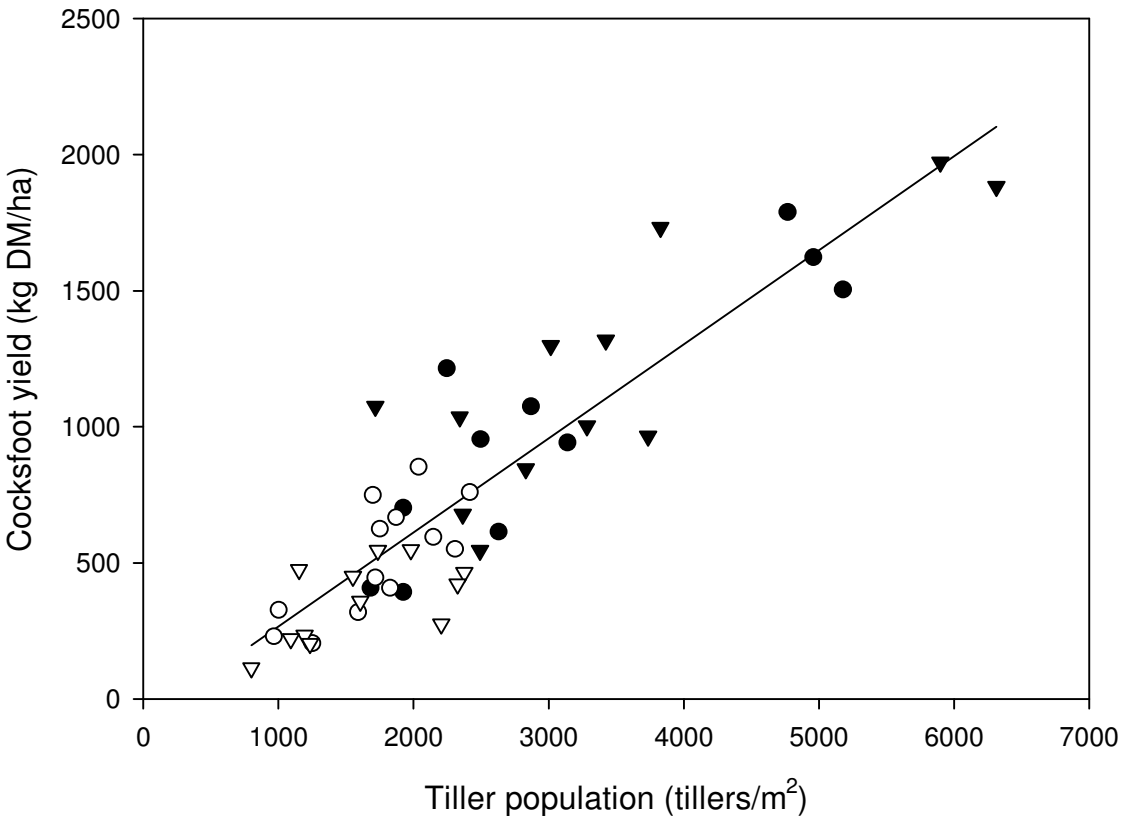

Figure 7.14 Relationship between cocksfoot yield and total tiller population of I+N (●), I-N (○), D+N (▽) and D-N (▼) pastures at Lincoln University, Canterbury, New Zealand. Form of the regression was y=-0.80 + 0.35x (R^2=0.80). Standard errors were 68.7 and 0.025, respectively. Treatment acronyms were presented in Table 3.1.

7.4 Discussion

The main aim of this chapter was to identify the mechanisms which caused the differences in DM yields reported in Chapter 4. Section 7.4.1 identifies the mechanisms responsible for reduced DM production of cocksfoot pastures during periods of water stress. In Section 7.4.2, periods of water stress are excluded to identify the physiological basis for yield differences between the +N and –N pastures.

7.4.1 How did water stress affect DM production by cocksfoot pastures?

7.4.1.1 Canopy expansion and water stress

The mechanism which reduced canopy PAR interception of dryland pastures was identified by relating LAI_{adj} to the actual soil moisture deficit (Figure 7.5) during periods when the ASMD was increasing. The relationship indicated that LAI_{adj} of dryland pastures, relative to their respective irrigated control pastures, decreased at a rate of 1.69±0.28%/mm. The point of inflexion was 87 mm for +N pastures compared with 67 mm for the –N pastures. The mean inflexion point for the relationship between LAI_{adj} and the ASMD was a mean of 77±10 mm.

Although the inflexion points differed, there was a distinct lack of data at the point of inflexion. This was similar to the situation when relative yield was related to the ASMD (Figure 5.5) but the mean point of inflexion and the rate at which LAI_{adj} declined were comparable to those reported in Section 5.3.5 to describe relative yield reductions in pastures exposed to water stress (-1.45%/mm beyond a D_L of 78 mm). The maximum measured ASMD was 139.5 mm in the 2003/04 growth season and the reduction in relative LAI_{adj} (Figure 7.5) showed canopy expansion, and consequently yield reductions (Section 5.3.5), were compromised when ~55% of plant available water had been extracted. This was comparable to the inflexion point beyond which relative yield reductions were reported by Penman (1971) and Anwar *et al*. (2003) for dicot crop species.

The reduction in LAI_{adj} resulted in reduced light interception by dryland pastures annually (Table 7.1) and within individual regrowth cycles when the actual soil moisture deficit exceeded D_L (Figure 7.3). Figure 7.4 showed I+N pastures achieved the critical LAI of 4.1 in all rotations. In contrast, the LAI_{adj} of the D+N pastures was <4.1 when the critical limiting deficit was exceeded. Light interception by dryland pastures

was reduced when LAI was below 4.1 and this would also reduce the area available for gas exchange (Johns, 1978).

7.4.1.2 Effect of water stress on individual leaf size

Specific leaf weights (Figure 7.8) determined when the ASMD >78 mm in 2003/04 showed that dryland pastures had SLW of between 40.5 and 52.7 g DM/m^2 at harvests made on 17/12/2003, 30/12/2003 and 2/2/2004. In contrast, the SLW of cocksfoot leaves in irrigated pastures were 25.8 to 32.7 g DM/m^2. This indicated the production of smaller and thicker leaves in dryland pastures and supports the conclusion that as plant available water becomes more difficult to extract, turgor pressure declines (Section 2.5.1) and cell expansion is compromised (Hsiao, 1973; Dale, 1988; Hay and Walker, 1989). Harvests on 17/12/2003, 30/12/2003 and 2/2/2004 showed that vegetative tiller weight in dryland pastures were similar but lower than those measured in either I-N or I+N pastures (Figure 7.7).

7.4.1.3 Water stress affected tiller population

Figure 7.9 showed that as the ASMD increased the total tiller population declined at a rate of 0.05%/mm. Further work is required to gather information on the change in tiller numbers at soil moisture deficits between 50 and 100 mm due to the lack of data linking the two distinct groups of tiller populations from irrigated and dryland pastures. This work would confirm if the linear decrease shown accurately describes the change in tiller numbers as the ASMD increases. In addition, collection of additional data could identify if the decrease in tiller population was predominantly caused by suppressed tiller production or because of premature senescence.

The responses of tiller population and SLW (Section 7.4.1.2) as the ASMD increased support the literature reviewed in Section 2.5.1. The data presented in this chapter showed as the ASMD increased beyond D_L, specific leaf weight increased; tiller population decreased and there were reductions in individual tiller weight. These mechanisms decreased canopy expansion, relative to irrigated control pastures, and less PAR was intercepted (Table 7.1 and Figure 7.3). Other authors (Korte and Chu, 1983; Baker *et al.*, 1985; Van Loo, 1992) have also reported reduced DM production was caused by inhibition of tiller production; reductions in individual tiller weight and reduced leaf size.

7.4.2 How did pasture N status affect the yield of cocksfoot pastures?

7.4.2.1 Prediction of yields from the effect of N nutrition on RUE

The mechanism responsible for differences in the yield of +N and -N pastures, when soil moisture was not the main limitation to growth, was a result of differences in RUE. The exclusion of periods of water stress is important when comparing RUE because Singh and Sri Rama (1989) reported that RUE was only independent of soil water content when the level of extractable water was >30%. This study showed there was (R^2=0.80) linear relationship between RUE of all four pastures and the nitrogen nutrition index (Figure 7.13). Based on Equation 2.1 (Section 2.1), which showed DM production was a function of RUE and the quantity of PAR intercepted by the pasture, the relationship between RUE and the NNI can be used to estimate DM production within individual regrowth cycles.

For example, in the rotation ending 8/9/2004, all pastures intercepted 134±6 MJ PAR/m^2 (Figure 7.3), even though the tiller population was 3440 tillers/m^2 in +N pastures compared with 2060 tiller/m^2 in –N pastures (Figure 7.6). The NNI of the +N pastures was 0.88 compared with 0.53 in –N pastures (Section 6.3.5, Figure 6.6). Using these figures for interception and NNI predicted yield of the +N pasture was 1179 kg DM/ha compared with 590 kg DM/ha by –N pastures. Observed total DM yields were 1136±43 kg DM/ha by the +N pastures ($p \leq 0.05$) compared with 437±67 kg DM/ha by –N pastures (Appendix 5). Therefore, yield predictions were within 4-8% of observed values. There is potential to further strengthen the relationship shown in Figure 7.13 by using an NNI determined from a bulked subsample rather than an NNI calculated from the green cocksfoot component. Lambert and Peeters (2005) used a similar approach to explain differences in RUE of ryegrass pastures over a range of sites, growth seasons and N levels but methodology differences do not allow direct comparison.

7.4.2.2 Nitrogen applications stimulated tiller production

Figure 7.14 showed a linear relationship (R^2=0.80) between DM yield and total tiller population. The relationship showed that, when N was the main limitation to pasture production, +N pastures generally contained more total tillers than –N pastures. This is important for two main reasons. Firstly, N has been shown to stimulate tiller production (Harris *et al.*, 1996; Ackmal and Janssens, 2004), when the LAI is below critical LAI (Simon and Lemaire, 1987; Sanderson *et al.*, 1997; Sanderson and Elwinger, 2002).

Thus, the canopies of +N pastures can intercept more PAR as there are more leaves per unit ground area (Baker and Younger, 1987). Secondly, when LAI exceeds 4.1, the surface area available for gas exchange is increased (Johns, 1978). This can increase the potential net rate of canopy photosynthesis thereby resulting in greater DM production by +N pastures. Figure 7.4 showed that, when the ASMD < D_L, +N pastures had higher LAI_{adj} than –N pastures. However, Figure 7.3 showed that the increased LAI_{adj} of +N pastures, compared with –N pastures, did not generally result in the interception of more PAR within a given regrowth cycle. Consequently, the main cause of increased DM production was because of a greater surface area for gas exchange and photosynthesis. Similar values of PAR interception by +N and –N pastures probably reflect the inherent difficulty associated with measuring light interception in perennial pastures where a residual biomass remains after cutting/grazing. Commonly, the residual biomass intercepted >70% of PAR when measured within 24 hours of mowing and additional limitations which include the inability of the equipment to differentiate between green and non green pasture components was thoroughly discussed in Section 7.2.1.

Over 50% of plant N is associated directly with photosynthesis (Horst and Nelson, 1979; Field and Mooney, 1986) and strong relationships have been shown with N content (Section 2.7) for species which include cocksfoot (Peri *et al.*, 2002b). Nitrogen is essential in the formation of chlorophyll, the majority of which is present within mesophyll cells (MacAdam *et al.*, 1989). These are the main centres for PAR capture and conversion of light energy to the chemical energy required to drive photosynthesis (Campbell, 1996). Therefore, if –N pastures intercepted the same quantity of PAR as +N pastures but were N deficient, chlorophyll content would likely be reduced and less PAR intercepted by leaf surfaces is converted to chemical energy per unit area. Nitrogen is an essential component of Rubisco and N deficiency may limit carbon assimilation (Novoa and Loomis, 1981; Evans, 1996). Furthermore, storage of N in excess to current plant requirements in the form of Rubisco (Novoa and Loomis, 1981; Grindlay, 1997), which represents the metabolic N pool (Jamieson and Semenov, 2000) may be expressed as additional leaf area when plant N demand exceeds supply (Section 6.3.6).

7.4.2.3 Radiation use efficiency of pastures with sufficient N and water

Figure 7.11 showed that RUE of the I+N pasture determined with non cumulative data from 19 rotations over two growth seasons gave a RUE of 1.04±0.04 g DM/MJ PAR and accounted for 84% of the observed variation. Therefore, under non limiting water

and N conditions, annual RUE gave an accurate representation of RUE within individual regrowth cycles. This strong relationship addresses concerns related to the use of correlations between cumulative data sets (Demetriades-Shah *et al.*, 1992) and supports the conclusions of other authors (Section 2.7.6) who have justified its use as a simple and robust procedure to determine system productivity under non limiting conditions of water and nitrogen. There was some evidence of systematic variation around regressions for annual RUE (Figure 7.10) which may reflect seasonal variation in partitioning to below ground biomass (Caradus and Evans, 1977; Ridley and Simpson, 1994). However, root DM yields were not determined during this study.

Radiation use efficiency (Monteith, 1972, 1977) is an indirect measure of net canopy photosynthesis and relates the capture of light energy to the amount of DM produced (Section 2.7.6). Published values differ depending on species, stress and the method of calculation (Sinclair and Muchow, 1999b). These factors make comparison of data from different experiments difficult. It is important to note that the RUE's calculated here are only about half that of published values (Section 2.7.6). In this experiment, pastures were not cut to ground level and the interception of PAR by the residual was measured after mowing. Therefore, the intercepted PAR values reported indicate PAR used in the production of harvested DM but assumed that light intercepted by the residual was used for subsequent growth.

In the present study, the –N pastures were completely reliant on soil N reserves and the associated rate at which mineral N was made available through microbial activity. Based on the results of soil N tests (Section 6.3.2.1) it was shown that the majority of mineral N was contained in the 0-0.2 m soil layer and N recovery in green herbage declined when dryland pastures were exposed to water stress, relative to irrigated pastures. It has been shown previously that, when the microbial population is not substrate limited, activity declines as the soil dries (Tate and Terry, 1980; Orchard and Cook, 1983; Fisher and Gosz, 1986; Stark and Firestone, 1995). Recently, relationships between crop N uptake, DM production and canopy expansion have been reported. It was proposed that N uptake rate was a function of soil N supply and N fertiliser inputs (Lemaire *et al.*, 2007).

It is recommended that further information on root yields of established pastures is collected. This would allow any seasonal patterns of assimilate partitioning between roots and shoots, as reported for lucerne (Khaiti and Lemaire, 1992; Teixeira, 2005), to

be quantified. However, care must be taken as pasture species tend to have fibrous root systems and separation of these fine roots from field samples may underestimate root biomass if all roots are not recovered. Assuming no water stress or N deficiency it is likely that the rate of root death would equal the rate of root regeneration to maintain equilibrium within an established perennial pasture. However, partitioning may be modified when the pasture is exposed to stress conditions which could cause increased root exploration of the soil to access resources (Sections 2.5 and 2.6.5). This would cause an apparent decrease in shoot RUE as more assimilates were partitioned to the roots. However, results presented in Chapter 5 did not show any evidence to support increased root exploration for water during the period when the critical limiting deficit was exceeded.

7.5 Conclusions

Based on the results presented in this chapter the following conclusions can be made:

- Water stress reduced LAI_{adj} at a rate of 1.69%/mm when the actual soil moisture deficit was >77±10 mm. This was comparable to the relationship between relative yield and the ASMD which showed yield in dryland pastures decreased by 1.45%/mm beyond a critical limiting deficit of 78 mm. The consistency indicates the main cause of yield differences between irrigated and dryland pastures was caused by reduced light interception.

- The reduction in LAI_{adj} during periods of water stress represented a decrease in total tiller population, which declined at a rate of 0.5%/mm in both +N and –N pastures.

- In addition, specific leaf weight was 26.3±2.35g/m^2 in I+N pastures whereas specific leaf weight in D+N pastures ranged from 22.8 g/m^2 when water was non limiting to a maximum of 55.8 g/m^2 when pastures experienced water stress. This showed water stress caused the production of smaller and thicker leaves which also reduced canopy light interception.

- The cause of yield differences between +N and –N pasture was explained by the linear relationship (R^2=0.80) between regrowth RUE and the nitrogen nutrition index for all pastures when water was non limiting. The relationship indicated a pasture with sufficient N (NNI=1.0) would have an RUE of 1.03 g DM/ MJ PAR compared with 0.40 g DM/MJ PAR in pastures with an NNI of 0.5.

8 General Discussion

8.1 Introduction

The main aims of this thesis (Chapter 1) were to quantify and explain the effects of temperature, water availability and N nutrition on the yield of cocksfoot pastures. The underlying assumption was that greater understanding of the benefits and limitations to cocksfoot productivity can lead to increased production from dryland farming systems. To investigate this, four treatments with contrasting amounts of water and nitrogen were imposed on an eight year old 'Wana' cocksfoot dominant pasture (Sections 3.4 and 0).

Dry matter production, pasture quality, water use and light interception were measured for two growth seasons (2003-2005). The effects of temperature, water and nitrogen were quantified and the mechanisms which caused yield differences identified. This chapter discusses results in relation to previously published work (Chapter 2) to develop unifying relationships and increase understanding of cocksfoot pasture production. Areas for future research will also be identified. Additionally, Objective 6 was to integrate the relationships between yield and temperature (Chapter 4), water availability (Chapter 5) and N nutrition into a multiplicative yield prediction model (Objective 7, Section 1.4).

8.2 Pasture yields

Annual yields ranged from 5.0-21.9 t DM/ha (Chapter 4). The environmental optimum was lower than the 28.6 t DM/ha/y previously reported (Peri *et al.*, 2002a) but comparable to the estimated potential production for the region described by Mitchell (1963). The potential environmental yield was lower than that reported by Peri *et al.* (2002a) who implemented 60 d regrowth durations so pastures intercepted more PAR before they had to re-establish their canopies. In addition, in this study the management aimed at minimising seedhead production whereas the management of Peri *et al.* (2002a) resulted in lodging during the reproductive phase. The minimum yield determined from the D-N pastures was within the expected range for dryland pastures in Canterbury (Section 2.3).

The seasonal pattern of DM production in irrigated pastures was due to changes in mean daily growth rates and was comparable to previous patterns in Canterbury (Rickard and Radcliffe, 1976) reported in Section 2.4. The seasonal variation is typical of most temperate environments and followed seasonal temperature fluctuations (Figure 3.1). In irrigated pastures, mean daily growth rates ranged from a minimum of 8 kg DM/ha/d in winter to a summer maximum of 124 kg DM/ha/d. The maximum was comparable to those reported in the literature (Rinne, 1978; Lemaire *et al.*, 1982). The predominant effect of decreased temperatures is through reduced daily rates of leaf appearance, which are generally constant in accumulated Tt (Section 2.4.2). Furthermore, reductions may occur from reduced enzyme activity which catalyses reactions associated with photosynthesis (Section 2.4.1). These were not measured directly, but there is sufficient evidence in the literature to support these conclusions. For example, in wheat and barley, photosynthesis declined as temperature decreased. This was a result of reduced Rubisco specificity at low temperatures (Bunce, 1998).

8.3 Temperature

Seasonal temperature variation was characterised using Tt (Sections 4.3.6 and 4.4.5). Initial analysis showed the I+N pasture produced 7.2 kg DM/^{o}Cd/ha and I-N pastures produced 3.2 kg DM/^{o}Cd/ha. Further analysis showed that when periods of water stress were excluded (Section 5.3.6), the +N pastures produced 7.0 kg DM/^{o}Cd/ha but a separate relationship was necessary for N deficient pastures. The –N pastures produced 3.3 kg DM/^{o}Cd/ha when not limited by water stress. The annual values were comparable to those determined in Southland using a T_b of 0°C (Hutchinson *et al.*, 2000). However, they were only about half those reported by Lemaire and Salette (1982) whose values were determined for the period from the last autumn defoliation to the first spring defoliation using mean air temperature and a T_b of 3°C (Section 2.4.4).

The base (3°C) and optimum (23°C) temperatures for growth were close to the minima (2°C) and optima (19-23°C) identified for photosynthesis in cocksfoot (Peri *et al.*, 2002b). These values represent a range of temperature requirements for specific biochemical pathways within the plant (Falk *et al.*, 1996). The consistency of results for both +N and –N pastures across seasons and years (Section 5.3.6) show that these relationships are transferable. From them the potential production in environments with similar radiation receipts could be estimated when water is not limiting growth. Further validation is necessary if these relationships are to be applied in environments with

different patterns or quantities of seasonal/annual radiation receipts. But the strong relationship between radiation and temperature (Fletcher and Moot, 2007) may also allow this to be predicted.

8.4 Water availability

Pastures that received irrigation only produced less than half the yield of I+N pastures but this was 31-96% more than the D-N pastures which experienced water stress (Chapter 4). The D+N pastures produced 72% of the environmental potential yield as a result of growth during periods when soil moisture was available. When soil moisture limited growth production of D+N and D-N pastures was similar.

The extent of yield reductions due to water stress was described with the critical limiting deficit (Penman, 1971) in Chapter 5. Over 80% of the observed variation was accounted for. Other authors (Martin, 1984; Rickard *et al.*, 1986) have modified this model to describe yield reductions due to water stress but they based their measurements on PET. In this study, the actual soil moisture deficit (ASMD) was used and the model accurately described yield reductions in both 2003/04 and 2004/05 despite the two month difference in the timing of the maximum soil moisture deficit and variation in the distribution of summer rainfall between years.

Following the alleviation of water stress by autumn rains there was evidence of compensatory growth in dryland pastures, particularly D+N pastures in 2003/04. This phenomenon has been reported for crops and pastures previously (Horst and Nelson, 1979; Kramer, 1983). It is probably due to the rapid expansion of cells which were formed during the stress period but which were unable to expand (Section 2.5.2). It has been reported that if cells are in the differentiation zone (Alves and Setter, 2004) and have not begun rapid expansion (Durand *et al.*, 1995) they continue to expand when rewatered to achieve similar cell size to those found in unstressed plants.

By coupling the temperature adjusted growth rates with D_L, the plateau observed in dryland pasture production was described and the estimated production losses quantified. The combination of these two descriptions explained that the difference in yield of the D-N pasture across years was due to timing of the drought and a subsequent

reduction in Tt accumulation after water stress was alleviated. Model estimates were consistently within 1-12% of measured yields (Section 5.3.6).

Water extraction patterns were accurately described with the exponential water extraction model (Passioura, 1983; Monteith, 1986) in the 0-0.8 m soil depths but failed at soil depths > 0.8 m during periods when the soil moisture deficit was increasing (Section 5.3.3). This method of describing water extraction has not previously been applied to an established perennial pasture grass nor has it been applied to a shallow soil (0.6-0.8 m overlying parent material). This study has shown that water extraction can be successfully described by this method and the 0-0.2 m layer can be included in the analysis (Section 5.3.3) Due to insufficient measurement frequency and rainfall during the main extraction period an extraction front velocity was not able to be identified. Further work with more frequent measurements and rainshelters may allow this coefficient to accurately be described for an established perennial pasture grown on a shallow free draining alluvial soil. However, because the study was conducted on a pasture with an established root system, it is possible that extraction from multiple soil layers may occur when water available from one layer is insufficient to meet plant demand. Because perennial pastures have an established root system it is expected that stable soil water contents will only be observed when supply exceeds plant demand (e.g. winter months). Subsequently, supply limitations will limit the rate of DM production during periods when no precipitation decreases the ASMD.

8.5 Nitrogen status

Nitrogen deficiency caused greater yield reductions annually than water stress (Section 4.3.1). The annual N concentration of the +N pastures differed between 2003/04 (3.8%) and 2004/05 (4.8%) as a result of an increase in the N fertiliser application rate (Section 3.5.2) combined with differences in the timing of the water stress period (Section 5.3.2). This was reflected in annual differences in the DM response to N fertiliser (Figure 6.1). Above average rainfall in December 2004 meant there was adequate water for growth in the D+N pastures during the peak summer production period and growth was not compromised until the ASMD increased beyond the D_L of 78 mm in 02/2005. Reduced N recovery (Figure 6.3) by D+N pastures during periods of water stress was primarily a result of lower daily growth rates (Figure 4.2) rather than a decrease in N% (Figure 6.5).

The main cause of reduced yield by the I-N pastures was lower RUE (Section 7.3.5 and Figure 7.10). This was a result of N deficiency, quantified with a NNI (Section 6.3.5) which showed, annually, I-N pastures able to access less than half the N required for a non limited yield. The strong relationship between the NNI and RUE was shown graphically in Figure 7.13 and explained 79% of the observed variation from 19 rotations over a two year period. Nitrogen is directly involved in cell differentiation and can stimulate tillering (Section 2.7), particularly after defoliation or if water stress is alleviated, when light penetrates into the base of the canopy. Figure 7.4 showed that LAI_{adj} of the D+N pastures was similar to that of the D-N pastures when the critical limiting deficit was exceeded. After autumn rainfall reduced the soil moisture deficit the LAI_{adj} of the D+N pastures was able to exceed that of the I+N pasture whereas LAI_{adj} of D-N pastures never exceeded that of the I-N pasture. The increased rate of canopy expansion by D+N pastures after the water stress period ended was a result of an increase in total tiller population (Figure 7.6) and supports reports in the literature that +N pastures were able to re-establish their canopies more rapidly than –N pastures (Section 2.5.2).

The –N pastures had average annual N% of 2.8 in 2003/04 and 3.2% in 2004/05 (Table 6.4). The NUE indicated that –N pastures produced more DM per unit N than the +N pastures (Figure 6.4). This suggests dilution of leaf N occurred (Jamieson and Semenov, 2000) which would have compromised leaf photosynthesis but maintained leaf area. Nitrogen concentrations in the –N pastures confirmed previous work which showed that cocksfoot pastures were N deficient throughout the year (Peri *et al.*, 2002a) and shows that increased N nutrition of cocksfoot pastures will result in increased yields during periods when soil moisture is not limiting.

The extent of yield reductions caused by insufficient N was described using a NNI which has been shown to accurately describe the extent of N deficiency (Chapter 6) and is not subject to confounding by other environmental factors (Lemaire *et al.*, 2007). This removes the variability associated with agronomic descriptions of DM responses to N application which are specific to the environment in which they were determined (Sections 2.7.3 and 2.7.5). In annual crops, this ratio between measured N% and optimum N% allows remedial N applications to be made to alleviate N deficiency. In pastures, often no remedial action can be made because of the duration of the regrowth

period. However, it does allow the N requirement for the subsequent regrowth cycle to be determined (Belanger and Gastal, 2000).

In 2003/04, the average NNI of the I+N pastures was 0.93 (Section 6.3.5) and in summer months application of 100 kg N/ha was insufficient to prevent the NNI from dropping below 1.0 by the end of the rotation. It has been shown previously that 100 kg N/ha was insufficient for spring regrowth of annual ryegrass (Marino *et al.*, 2004). Applications of 150 kg N/ha were non limiting to pasture productivity and there was no yield benefit when >150 kg N/ha N was applied. However, luxury uptake of excess N at N fertiliser rates >150 kg /ha was probably stored for future growth (Section 2.7.5). In addition, it has been reported that grass monocultures required 150 kg N/ha to produce yields comparable to grass/clover mixes (Mathieu and Besnard, 1983). The I-N pastures which had an NNI of 0.54, all of the N accessed by the pasture was sourced from soil N reserves. Due to water stress, the NNI of the D+N pastures deviated from that of the I+N pastures but still had an annual NNI of 0.82 compared with 0.44 in D-N pastures.

8.6 Modelling DM production by incorporating a function for NNI

A multiplicative model (Section 2.2.1, Equation 2.2) was created to predict yields (McKenzie *et al.*, 1999) when pastures were exposed to different temperature, soil moisture availability and N nutrition. Models were evaluated by regression of predicted (P) against observed (O) yields. Functions for temperature, water and N were evaluated separately and then combined into a multiplicative model. The model which accounted for the most variation as described by reductions to the R^2 compared to the initial model was selected. The initial model calculated yield by multiplication of thermal time by the TAGR of 7.0 kg DM/^{o}Cd/ha within each regrowth period. Root mean square deviations (RMSD) of the models were calculated using Equation 8.1 to determine the accuracy of predictions (Wilson *et al.*, 1995; Jamieson *et al.*, 1998a). Statistical accuracy was determined by calculating the RMSD as a percentage of the mean observed value.

Equation 8.1 $$RMSD = \left[\frac{\sum (O-P)^2}{n} \right]^{0.5}$$

Where *n* is the number of paired values used in the prediction.

The model (Equation 8.2) was created to predict production of green cocksfoot DM, not total DM yield. This model used the temperature adjusted growth rate of the +N pastures (7.0 kg DM/^{o}Cd/ha) which was not different for I+N or D+N pastures when periods of water stress were excluded (Sections 5.4.1 and 5.3.6). The water function (f(W)) then reduced by 1.45%/mm of actual soil moisture deficit (AMSD) when the critical limiting deficit of 78 mm was exceeded (Section 5.3.5) based on the ASMD on the day the destructive harvest was made. For example, at the highest measured ASMD of 140 mm, 62 mm beyond the D_L, gave a value of 0.1 and indicated yield was only 10% of potential due to water stress. A value of 1.0 indicated soil moisture was non limiting to production when the ASMD was <78 mm.

The nitrogen function ($f(N_{NNI})$) ranged from 0-1.0 where an NNI of 1.0 indicated N was sufficient for non limited DM production and then decreased at a rate of 1.08% per 1% decline in the NNI (Figure 6.9b). The reproductive phase (f(R)) was accounted for by an increased spring TAGR (R=1.0) prior to the reproductive phase (data not shown) which was probably associated with either a change in partitioning priority associated with seedhead development (Section 2.1) or possible remobilization of reserves as has been shown in other perennial species (Wilson *et al.*, 2002; Teixeira, 2005). This function was set at 1.0 when temperatures began to increase after winter, and corresponded to an increasing photoperiod. The R function was switched to 0.8 after the reproductive phase was completed which corresponded to a decline in photoperiod. Unlike McKenzie *et al.*, (1999) partitioning values were fixed and did not decline over time within the reproductive phase. This decision accounted for the slight hysteretic response observed in TAGR with photoperiod (data not presented). The form of the full model was:

Equation 8.2 $$\textbf{Yield} = \textbf{TAGR} * (T_{air} - T_b) * Tr * f(W) * f(N_{NNI}) * f(R)$$

Where TAGR was 7.0 kg DM/^{o}Cd/ha; T_{air} was the mean regrowth air temperature; T_b was the base temperature (3°C) for thermal time accumulation (Section 4.3.6); Tr is the regrowth duration (d); W represented the water function (Section 5.4.1) and varied from 0-1.0; N_{NNI} was the nitrogen function and also varied from 0-1.0. The R function represents the reproductive phase and indicates DM production during vegetative growth was 20% lower than during reproductive development (McKenzie *et al.*, 1999).

The root mean square deviation (RMSD) was calculated to determine the effects of each function as a weighted measure of how accurately model predictions match measured

cocksfoot production. Because the NNI was calculated from the green cocksfoot biomass, observed yields were for the cocksfoot component not total DM yield. The RMSD was 66.4 kg DM/ha when only the TAGR was used to predict yield (Table 8.1). This used data for all four pastures with a total of 114 paired comparisons. When the full model (Figure 8.1) was used to predicted cocksfoot DM yield (n = 110) the RMSD decreased to 4.7 kg DM/ha (Figure 8.1).

Generally, RMSD <20% indicate that model predictions are an accurate representation of observed values and model improvements are associated with a reduction in the RMSD. It is important to state that validation with an independent data set is required as a good relationship would be expected when the model is created from the observed data. The best prediction of DM yield was given by the multiplicative model which included functions for water and N, but excluded the reproductive function, with a RMSD of 4.6 kg DM/ha (Table 8.1). The regression accounted for 70% of the observed variation between observed and predicted yields. The model which included the reproductive function had an RMSD of 4.7 kg DM/ha and accounted for 75% of the observed variation. Both models showed the RMSD was 5% of the mean observed values which contributed to the RMSD. However, for individual pastures, the inclusion of the reproductive function did not behave in a consistent manner. The RMSD of the I+N pasture decreased from 8.5 to 0.6 kg DM/ha (n=29) and from 4.0 to 0.3 kg DM/ha in I-N pastures (n=29). In contrast, the RMSD of the D+N pastures increased from 3.3 to 7.3 kg DM/ha (n=28) and from 0.1 to 1.3 kg DM/ha (n=28) for the D-N pastures.

Figure 8.1 shows the relationship between predicted and observed cocksfoot DM yields for models which exclude or include the reproductive (R) function. Although the RMSD indicated the best simulation occurred when the R function was excluded it can be seen that inclusion of the R function reduced the scatter surrounding the regression. However, this also resulted in the slope decreasing from 1.0 to 0.9 and indicated predictions underestimated yields by 10%. A t-test of the slopes indicated a difference at the $p \leq 0.05$ level. It is possible that the inclusion of the R function increased the RMSD for dryland pastures, but not irrigated pastures. This suggests there may have been an interaction between water stress and partitioning priority during the reproductive phase. There is large variability associated with harvest index due to the plasticity associated with yield components which tend to be self compensating (Donald, 1968). Alternatively, a ceiling yield may have been reached where the rate of DM production

may have been matched by the rate of senescence in +N pastures not exposed to water stress. This was not an objective of the current experiment and the associated lack of appropriate data means this could not be determined. As a result further work is needed to generate either i) a phenological sub model, rather than a empirical switch, to quantify the extent of stress the pasture is exposed to during the reproductive phase or ii) the ceiling yield is determined.

Table 8.1 Model evaluations showing the progression of the selection of the most appropriate model to predicted cocksfoot DM production. Where TAGR is the temperature adjusted growth rate (7.0 kg DM/^{o}Cd/ha) above a base temperature (T_b) of 3°C. T_{air} is the mean air temperature during the measurement period and Tr is the regrowth duration (d). f(W) represents the water function, $f(N_{NNI})$ is a N function based on NNI, and f(R) is the reproductive function. Linear regression coefficients are results of regression between predicted (P) and observed (O) DM yields for slope, correlation coefficient (R^2) and regression significance. SE_{OBS} is the estimated standard error of the observations from the regression. Root mean square deviations (RMSD) were determined from a total of 114 paired samples for models which did not include N functions and from 110 paired samples for models that included N functions. RMSD (% observed) is the RMSD as a percentage of the mean observed values.

Model	Linear Regression					RMSD (kg DM/ha)	RMSD (% observed)
	Slope	R^2	Significance	SE_{OBS}	Comment		
$TAGR*(T_{air}-T_b)*Tr$	1.36±0.09	N/A	***	1119	Residual variance exceeded variance of response variate. Evidence of systematic variation.	66.4	7.4
$TAGR*(T_{air}-T_b)*Tr*f(W)$	1.25±0.07	N/A	***	847	Residual variance exceeded variance of response variate.	58.7	6.5
$TAGR*(T_{air}-T_b)*Tr*f(N_{NNI})$	1.08±0.04	0.55	***	435		15.2	1.7
$TAGR*(T_{air}-T_b)*Tr*f(W)*f(N_{NNI})$	1.00±0.03	0.70	***	364		4.6	0.5
$TAGR*(T_{air}-T_b)*Tr*f(W)*f(N_{NNI})*f(R)$	0.90±0.02	0.75	***	288		4.7	0.5

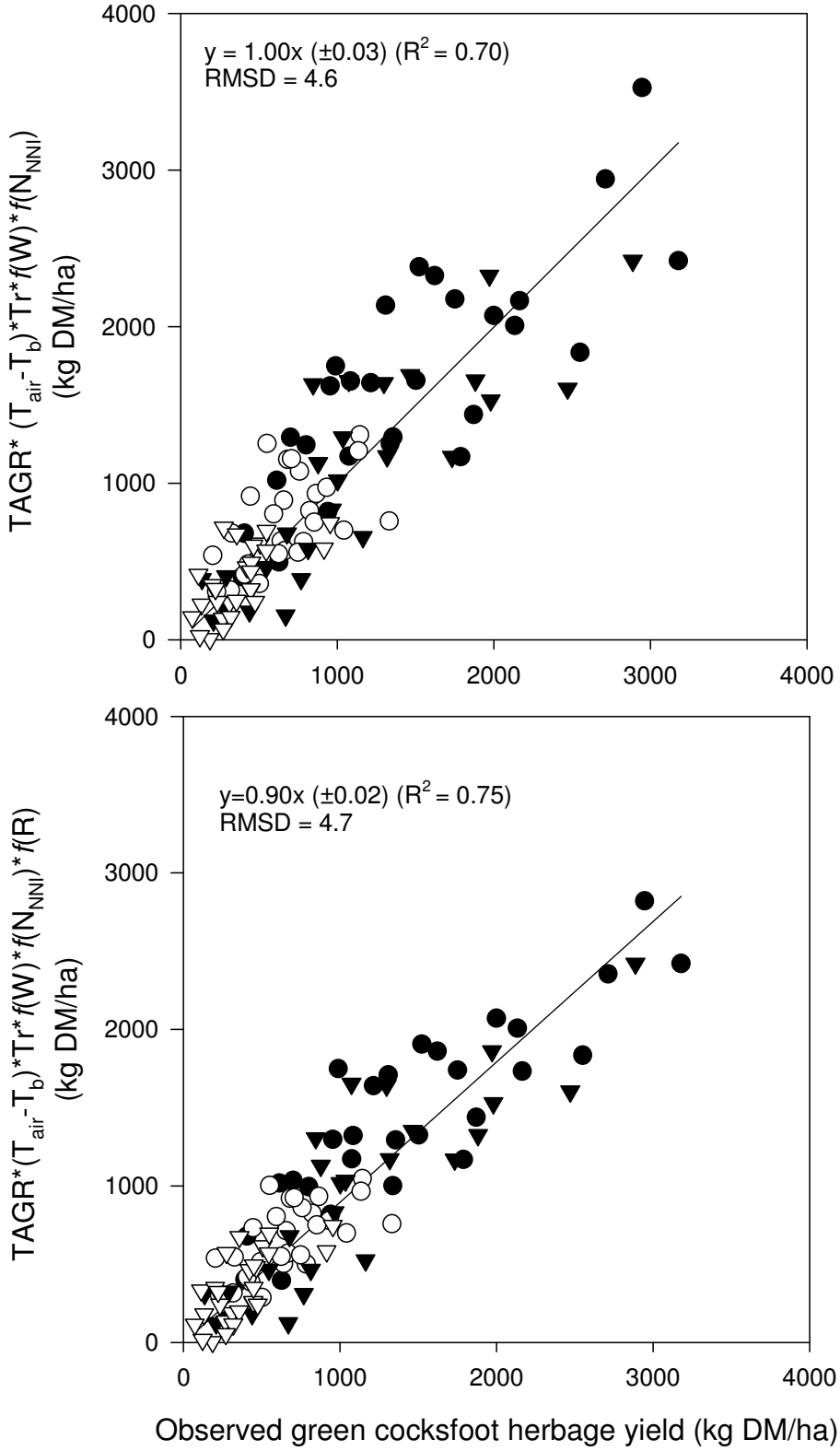

Figure 8.1 Relationship between predicted and measured cocksfoot yield (kg DM/ha) of I+N (●), I-N (○), D+N (▼) and D-N (▽) pastures at Lincoln University, Canterbury, New Zealand. Predictions which exclude the reproductive function (top) and predictions which include a function for reproductive status (bottom) are shown. Text represents the form for the linear regression, forced through the origin and associated RMSD. Treatment acronyms were given in Table 3.1.

The rate at which relative yield decreased because of N deficiency was described using the NNI (Figure 6.9) and the description was then incorporated into a multiplicative model which included the temperature adjusted growth rate (7.0 kg DM/^{o}Cd/ha, Section 5.3.6) and D_L function to successfully predict DM production of cocksfoot monocultures (Section 8.6). The best model tested explained 75% of the variation between observed and predicted yields (Table 8.1 and Figure 8.1). The reproductive function increased the accuracy of predictions in irrigated pastures but not dryland pastures. This was expected due to the inherent variability associated with yield component plasticity (Donald, 1968). Further work is needed to determine if there is an interaction between the timing of the stress period and reproductive status of the pasture and an accurate method for describing the interaction.

8.7 Mechanisms responsible for yield reductions

It was shown that the mechanism which caused yields of D+N pastures to deviate from potential during water stress was primarily due to a reduction in LAI_{adj} (Figure 7.4). Cellular expansion is the most sensitive plant process (Hsiao, 1973) affected by the development of soil moisture deficits (Section 2.5). Canopy expansion slows and decreases the area available for gas exchange. Figure 7.5 showed the rate at which relative LAI_{adj} declined was comparable (1.69%/mm) to the rate of yield reduction beyond D_L (Figure 5.5) which was 1.45%/mm. This was caused by a reduction in tiller population (Figure 7.9) in combination with a reduced specific green area during periods of drought. Therefore, canopy expansion slows, and less PAR is intercepted because of the formation of smaller thicker leaves on fewer tillers per unit area.

Differences in RUE were successfully explained by correlation with the NNI (Section 7.2.7). Nitrogen is essential for photosynthesis and >50% of soluble N is associated with the formation of photosynthetic apparatus. Deficiency can reduce cell differentiation resulting in the production of smaller leaves due to cell number limitations (Sections 2.7.1 and 7.4.2.2) whereas N in excess to requirements can also be stored as Rubisco for future use (Novoa and Loomis, 1981). A breakdown of the NNI indicated that lamina N, appeared to be a constant fraction of total N whereas pseudostem N was higher in +N pastures (Section 6.3.6). This supports the proposal that leaf N is constant (Sheehy *et al.*, 1996; Jamieson and Semenov, 2000) and associated with the structural component of total plant N whereas pseudostem N represents the metabolism and storage N components (Caloin and Yu, 1984). The majority of N in

developing leaves is held in the site of cell differentiation closest to the apex and the majority of Rubisco is formed prior to the emergence of mature leaf tips from within the pseudostem. Further work is needed to confirm these results due to the limited data set however, currently these data appear to support previous literature (Jamieson and Semenov, 2000; Lemaire *et al.*, 2007) stating that structural and metabolic N pools must be quantified to accurately describe N cycling and use within the plant.

8.8 Implications for dryland farming systems

These results show that cocksfoot pasture production will slow/cease during periods of water stress which are a characteristic of dryland farming systems on the east coast of New Zealand. If there is no water available for growth, maintaining production in a dryland farming system during this period this would only be accomplished by the inclusion of a taprooted species, such as lucerne, which can access water from deeper in the soil. However, there is potential to maximise cocksfoot production in the early spring, and in autumn after drought conditions are alleviated by rainfall, by increasing the N nutrition of the crop.

The rates of fertiliser N applied in this study are not recommended and it is important that an appropriate companion legume, which can survive and persist in mixtures with cocksfoot is identified. As cocksfoot production peaks in summer months (Lemaire *et al.*, 2007), the best strategy for improving the N fertility of cocksfoot based pastures is likely to come from inclusion of an annual legume such as subterranean clover (*T. subterranuem*). Due to the highly competitive acquisition of water and soil N from the dense cocksfoot root system (Stevens *et al.*, 1992), a species which is rarely in direct competition for resources with cocksfoot will be a more appropriate choice.

In early spring, yield and quality of the cocksfoot will be improved predominantly through N returns in urine from grazing animals which select a high clover diet prior to setting seed. This increases crude protein content (Section 4.3.4) and will make the pasture more acceptable to grazing livestock relative to N deficient pasture which has low preference (Garwood and Williams, 1967; Evans, 1978; Garwood and Sinclair, 1979; Lee and Cho, 1985). The increased liveweight gain associated with selection of a high clover diet during lambing and lactation will mean lambs will reach sale weights faster and be sold before drought conditions result in the use of conserved feed. It has been shown previously the decline in clover content over time decreases animal

production (Edwards *et al.*, 1993). A legume with an annual life cycle may also benefit cocksfoot in moist summers due to the decomposition of residual root and shoot biomass which would release N to the associated grass.

8.9 Recommendations for future research

The results chapters highlighted several areas which require further clarification to complement the results presented here. These include:

a) In this study, the I-N pastures produced less than half the yield of the I+N pastures. Pastures grown on soils with lower natural levels of soil N reserves may show different results. Therefore, the N limited rate of DM production (3.3 kg DM/^{o}Cd/ha) is likely to be specific to this site/pasture combination and may differ at different sites.

b) The model showed that inclusion of a reproductive function increased the accuracy of predictions in irrigated but not water stressed pastures (Section 8.6). It is important to identify any potential interactions between water availability and reproductive status. In addition, the reproductive factor was subjective and was not an objective of the current study. This function could be confirmed/altered using more detailed descriptions of changes in partitioning priority associated with development changes.

c) The critical limiting deficit was identified as 78 mm (Section 5.3.5) and is specific to this site/pasture combination. For the model to be applied in different environments the D_L must be determined for the site/pasture combination in that environment. The use of rainshelters and increased measurement frequency may further increase the accuracy of the D_L particularly if more data were collected at the time the point of inflexion occurred.

d) The NNI provided adequate descriptions of the effect of N on DM production. Limited data indicated that specific leaf N was reasonably stable (Sections 6.3.5 and 6.3.6). It is important that more data is collected to separate the structural and metabolic N pools (Papadopoulos *et al.*, 2001). This should include periods when water stress limits production to quantify the behaviour of pastures when exposed to multiple stresses to provide more robust descriptions as it is hypothesised that I-N pastures diluted leaf N during the summer months to maintain leaf area.

8.10 Conclusions

The research presented in this thesis has provided a range of unifying relationships, some of which are suitable for extrapolation to other environments. Specific conclusions include:

- Cocksfoot pastures produced 21.9 t DM/ha when neither water nor N were limiting. Both water and N availability caused reductions below potential but N deficiency was the main cause of reduced DM production.
- Seasonal temperature variation was accounted for using thermal time. When periods of water stress were excluded +N pastures produced 7.0 kg DM/^{o}Cd/ha compared with 3.3 kg DM/^{o}Cd/ha by –N pastures.
- When subjected to water stress both D+N and D-N pastures had similar growth rates which showed that, regardless of N nutrition status, water availability was the main causal factor responsible for decreased yields in the summer/autumn period.
- The critical limiting deficit for this pasture/soil combination was 78 mm beyond which yield declined by 1.45%/mm.
- During periods of water stress differences in the yields of irrigated and dryland pastures were caused by slower canopy expansion. This reduced the amount of light intercepted by the pastures due to a reduction in tiller population and an increase in specific leaf area in dryland pastures.
- The primary mechanism which caused different yields between +N and –N pastures was different RUE. This was strongly correlated with the NNI and represented differences in the photosynthetic capacities of the pastures

9 Acknowledgements

So this is it – most likely to be the first and most commonly read page of this thesis as everyone who helped checks I remembered to mention their names. I can only hope there are no glaring errors…

Firstly, thanks to my Mum and Dad. After a slow start onto the path of continued education I think I'm done. I can't think of any other programs I could enrol in so I guess this means I'll have to go out and get a real job. Thanks for all your support and cleaning, cooking and mowing the lawns when you were in town. To my sister Emma, I realise I was never going to be able to con you into helping with the field work. It isn't the same offering a bag of cocksfoot as payment for help and I think I would have had more success if I'd stuck with the potatoes. As for Damian, well he left the country to avoid helping with the potatoes so it's logical that he would stay away to avoid helping when I start research into pasture production.

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10 List of Publications

Mills, A., Moot, D. J., Lucas, R. J., Jamieson, P. D. and McKenzie, B. A. 2005. Potential yield of cocksfoot (*Dactylis glomerata*) monocultures in response to irrigation and nitrogen. In: *Utilisation of grazed grass in temperate animal systems. Proceedings of a satellite workshop of the XX International Grassland Congress, 3 - 6 July 2005, Cork, Ireland*. Wageningen Academic Publishers: The Netherlands. p 163.

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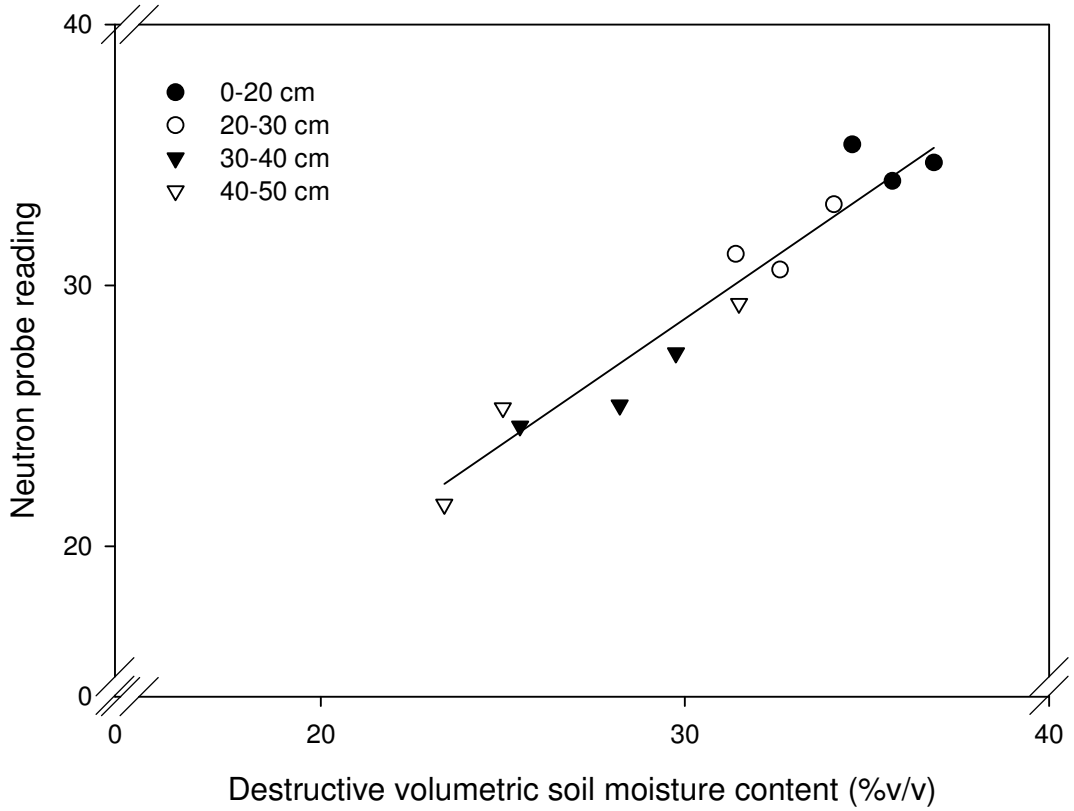
12 Appendices

Appendix 1 Dates and amounts of irrigation applied.

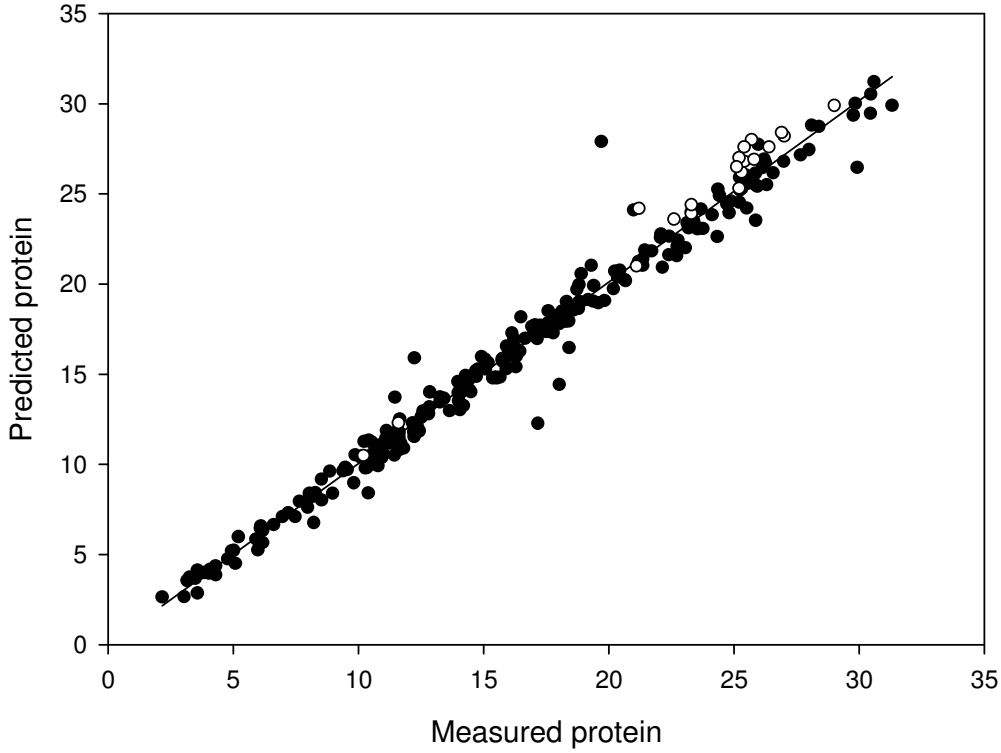
Date	Irrigation applied (mm)	Annual total
21/11/2003	100	
2/12/2003	17	
8/12/2003	24	
13/12/2003	34	
20/12/2003	41.9	
27/12/2003	33.7	
4/01/2004	41.0	
6/01/2004	7.5	
18/01/2003	43.0	
24/01/2004	28.7	
5/02/2004	3.0	
6/03/2004	15.9	
8/03/2004	22.7	
14/03/2004	31.3	
3/04/2004	3.5	447.2 mm
13/10/2004	2.5	
23/10/2004	17.1	
9/11/2004	14.2	
11/11/2004	8.5	
12/11/2004	20.8	
21/11/2004	23.8	
18/01/2005	9.8	
20/01/2005	7.6	
21/01/2005	5.6	
25/01/2005	18.3	
1/02/2005	10.8	
2/02/2005	16.6	
13/02/2005	11.3	
19/02/2005	12.7	
24/02/2005	21.3	
6/03/2005	15.3	
18/03/2005	25.2	
21/04/2005	14.2	255.7

Appendix 2 Herbicide applications, rates and active ingredients (ai content) made during the duration of measurements to an experiment to determine the potential yield of 'Wana' cocksfoot monocultures at Lincoln University, Canterbury, New Zealand.

Date	Herbicide	Rate	Active Ingredient	ai content
30/09/2003	2,4-DB	6.0 L/ha	4-(2,4-dichlorophenoxy) butyric acid	400 g/L
10/02/2004	Banvel	2.0 L/ha	dicamba	200 g/L
27/02/2004	Spinnaker	0.4 L/ha	imazethapyr	240 g/L
06/05/2004	Versatill	0.3 L/ha	clopyralid	300 g/L
12/07/2004	Nortron	4.0 L/ha	ethofumesate and ethylene glycol	500 g/L and 80 g/L
04/05/2005	Banvel	2.0 L/ha	dicamba	200 g/L
10/05/2005	Nortron	4.0 L/ha	ethofumesate and ethylene glycol	500 g/L and 80 g/L



Appendix 3 Calibration between destructive gravimetric soil moisture content in four soil layers and corresponding TDR (0-20 cm) and neutron probe measurements.



Appendix 4 Calibration used for NIR determinations of crude protein. Data set consists of 251 pairs of observed and predicted values (●) for the semi independent data set. Independent values (○▼) were added at the start of analysis to confirm the accuracy of the calibration in use for green cocksfoot samples. These independent samples represent green vegetative material (lamina and petiole/leaf sheath) for ryegrass, white clover, sub clover and balansa clover pastures taken from a site adjacent to the experiment on which this thesis is based. Cocksfoot samples were taken from the experimental site. The form of the regression was y = 0.999x (R^2 = 0.98) for the initial data set. Inclusion of the independent data changed the regression to y = 0.992x (R^2 =0.98) which was not different from the initial regression for the calibration data.

Note: The NIR calibration used equations generated by WinISI software (Infrasoft International) using a modified partial least squares regression. Of the total 251 paired samples, 240 were used to create the equation. The remainder were screened as potential outliers. The calibration dataset includes a range of species, stages of maturity, and quality. Species represented in the data set include, but were not limited to, ryegrass, cocksfoot, fescue, white clover, red clover, balansa clover, Caucasian clover, kale, rape, swede, lucerne. Samples for cereals which included triticale and oats only represented vegetative development before grain formation.

Samples were from both monocultures and mixed species pastures and represented bulked samples which included various amounts of senesced matter and weed species such as dock, dandelion and yarrow. The wide range gives a robust calibration, able to give reliable predictions for a wide range of unknowns. A similar procedure was used to determine the relationship between measured and predicted values for metabolisable energy determinations by NIR.

Appendix 5 DM production of individual regrowth cycles in Year 1 (30/9/2003-5/10/2004) of cocksfoot monocultures. Treatments are irrigated (I) or dryland (D) as the mainplot and + Nitrogen (+N) or – nitrogen (-N). Data in bold indicate end of rotation harvests. Data in normal font indicates a destructive mid rotation harvest. Comments indicate the rate of N applied to +N treatments at the start of that rotation and the irrigation period.

	Date	I+N	I-N	D+N	D-N	Effect	Significance	LSD ($p \leq 0.05$)	Comments
2003/04	17/10/2003	1326	844	1121	812	N	0.007	214.4	
	29/10/2003	2741	1601	2760	1974	I*N	0.47	412.5	100 kg N/ha
									No N applied
	1/12/2003	1772	1177	1371	1140	N	0.004	195.6	Irrigation initiated mid rotation
	17/12/2003	1862	811	628	530	I*N	0.005	298.3	
	30/12/2003	3474	1202	393	490	I*N	≤0.001	219.6	100 kg N/ha
	15/1/2004								
	2/2/2004	3146	1347	254	254	I*N	0.002	470.2	100 kg N/ha
	18/2/2004	1513	1046	663	568	I	0.021	417.5	
						N	0.019	206.1	
	4/3/2004	2362	1058	926	479	I*N	≤0.001	369.9	100 kg N/ha
	20/3/2004	1019	629	933	451	N	0.015	296.4	
	1/4/2004	1936	803	1339	575	I	0.017	234.4	100 kg N ha
						N	≤0.001	207.1	
	11/4/2004	853	654	762	348	N	0.044	294.0	Irrigation ceases
	2/5/2004	1717	971	2141	591	I*N	0.05	402.2	100 kg N/ha
	24/6/2004	1743	604	2156	297	N	≤0.001	474.9	No N applied
	4/8/2004	445	382	610	320	N	0.02	131.4	No N applied
	8/9/2004	1179	480	1093	614	N	0.023	457.8	100 kg N/ha
	5/10/2004	2073	885	2016	720	N	≤0.001	333.8	100 kg N/ha

Treatment acronyms were presented in Table 3.1.

Appendix 6 DM production of individual regrowth cycles in Year 2 (6/10/2004-17/10/2005) of cocksfoot monocultures. Treatments are irrigated (I) or dryland (D) as the mainplot and + Nitrogen (+N) or – nitrogen (-N). Data in bold indicate end of rotation harvests. Data in normal font indicates a destructive mid rotation harvest. Comments indicate the rate of N applied to +N treatments at the start of that rotation and the irrigation period.

	Date	I+N	I-N	D+N	D-N	Effect	Significance	LSD ($p \leq 0.05$)	Comments
2004/05	8/11/2004	2805	1555	2867	1079	N	≤0.001	463.2	Irrigation initiated
									100 kg N/ha
	8/12/2004	2210	912	1284	794	I*N	0.012	847.6	150 kg N/ha
	12/1/2005	3812	1010	3500	618	N	≤0.001	729.6	150 kg N/ha
	17/2/2005	3652	1289	1713	489	I	≤0.001	103.5	150 kg N/ha
						N	≤0.001	606.3	
	16/3/2005	1578	724	417	257	I*N	0.005	332.7	150 kg N/ha
	19/4/2005	1766	795	324	191	I	0.016	569.0	Irrigation ceases
									150 kg N/ha
	30/5/2005	1113	509	957	127	N	≤0.001	299.2	150 kg N/ha
	22/7/2005	810	416	1178	150	I*N	0.01	710.8	150 kg N/ha
	18/8/2005	759	317	1185	278	N	0.002	275.1	150 kg N/ha
	1/9/2005	460	272	751	263	I*N	0.027	213.1	
	21/9/2005	1295	744	1401	400	N	0.007	423.2	150 kg N/ha
	17/10/2005	1350	871	1526	610	I*N	0.008	306.4	150 kg N/ha

Treatment acronyms were presented in Table 3.1.

Appendix 7 Soil bulk density (g/mL), Total N (%), Total C (%), C:N ratio, ammoniacal-N (ppm), nitrate-N (ppm) and anerobic mineral N (kg/ha) of cocksfoot pastures at Lincoln University, Canterbury, New Zealand. Samples were taken on 18/10/2005 which was immediately after the final harvest (17/10/2005) of the 2004/05 growth season.

Pasture	Soil depth	Bulk density (g/mL)	Total N (% w/w)	Total C (% w/w)	C:N ratio	Ammoniacal-N (ppm)	Nitrate-N (ppm)	Anaerobic Mineral N (kg/ha)
I+N	0-0.2 m	0.84	0.19	1.9	10.0	17.0	87.7	72.3
	0.2-0.4 m		0.10	1.0	9.0	3.8	52.5	20.3
	0.4-0.6 m		0.05	0.4	8.7	3.8	47.4	12.0
I-N	0-0.2 m	0.78	0.17	1.9	11.3	5.4	2.8	80.3
	0.2-0.4 m		0.09	0.9	10.0	2.1	0.6	15.7
	0.4-0.6 m		0.04	0.4	10.3	1.8	<0.5	7.0
D+N	0-0.2 m	0.88	0.19	1.9	10.3	15.6	112.8	57.7
	0.2-0.4 m		0.09	0.9	9.7	4.2	97.3	18.7
	0.4-0.6 m		0.04	0.4	8.7	3.6	88.7	8.0
D-N	0-0.2 m	0.90	0.16	1.9	11.3	3.5	53.5	62.3
	0.2-0.4 m		0.08	0.9	11.7	2.3	0.9	18.0
	0.4-0.6 m		0.04	0.4	10.0	2.2	0.6	9.3

Treatment acronyms were presented in Table 3.1.