TILLER DYNAMICS AND LEAF GROWTH PROCESSES OF THE PERENNIAL RYEGRASS CULTIVARS ‘ELLETT’ AND ‘GRASSLANDS RUANUI’ AS INFLUENCED BY ENVIRONMENTAL FACTORS

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of the requirements for the degree of
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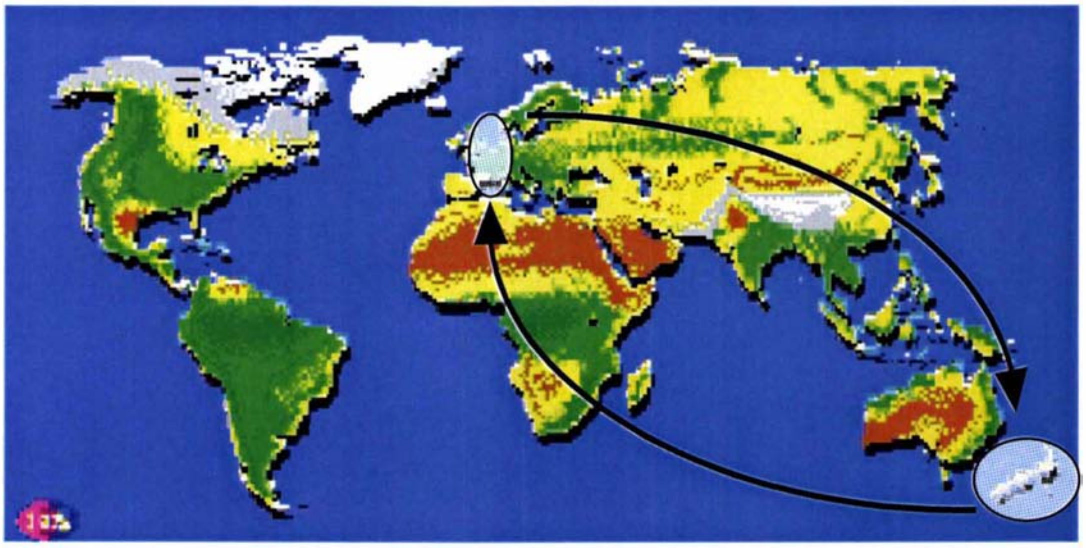

Et
Pour le diplôme de Docteur en Sciences Agronomiques
de l'Institut National Polytechnique de Lorraine,
Nancy, France

1996-1999

I dedicate this thesis to my parents,

Leila BAHMANI,
my mother and best friend

and

Nacer BAHMANI,
my father and source of guidance

ABSTRACT

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ABSTRACT

In New Zealand, perennial ryegrass (*Lolium perenne*) is considered the most important and cheapest feed source for dairy cows. The profitability of dairy farming is reliant on the quality, persistence and productivity of perennial ryegrass dominant pastures. However, research shows some 'modern' perennial ryegrass cultivars derived from the Mangere ecotype do not persist under intensive dairy cow grazing. Other research suggested that 'Ellett', a representative of 'modern' ryegrass cultivars, had a different perennation strategy from the older cultivar 'Grasslands Ruanui', used previously. The objectives of this study were (i) to compare the sward productivity, tiller dynamics and flowering behaviour of the perennial ryegrass cultivars 'Ellett' and 'Grasslands Ruanui' under different nitrogen and irrigation treatments and (ii) to determine the morphological and tillering responses of 'Ellett' and 'Grasslands Ruanui' ryegrasses when grown in different light environments.

A field experiment at the No 5 Dairy of the Dairying Research Corporation (Hamilton, New Zealand) was conducted from April 1996 to April 1998 to assess the sward productivity of 'Ellett' and 'Grasslands Ruanui' ryegrasses, and their tiller dynamics and flowering behaviours under two levels of nitrogen and irrigation. This field experiment was rotationally grazed by dairy cows stocked at 3.2 cows per hectare.

Results showed 'Ellett' had a greater tiller weight and lower tiller density than 'Grasslands Ruanui', which was reflected in higher average yields in spring (3220 vs 2788 kg DM/ha) and summer (2125 vs 1844 kg DM/ha) for 'Ellett' and 'Grasslands Ruanui', respectively. Because of different sward structures 'Ellett' tended to 'pull' more than did 'Grasslands Ruanui' during grazings in summer and autumn, but this did not appear to have greatly influenced the yield comparisons between cultivars. No significant differences in the proportions of white clover, weeds and other grass species were observed between 'Ellett' and 'Grasslands Ruanui' swards. 'Ellett' and 'Grasslands Ruanui' ryegrasses had similar herbage accumulation responses to nitrogen and irrigation; pre-grazing herbage mass, tiller weight and botanical composition were generally affected by these treatments. Overall, nitrogen fertiliser increased herbage accumulation and tiller density, but tiller weight responses were restricted to the second winter and autumn. Irrigation increased herbage accumulation and tiller density in summer and autumn, but did not significantly affect tiller weight.

Seasonal tillering patterns for both cultivars were similar and were characterised by high tiller populations in summer followed by a rapid decline in early autumn and then a recovery or tillering 'flush'. This pattern was more pronounced in the second year than the first. 'Grasslands Ruanui' had a higher total tiller number than 'Ellett', regardless of nitrogen and irrigation treatments. From a sward stability diagram developed in Chapter 5, a population index (P_t/P_0) was defined as reflecting population changes over time via changes in tiller birth and survival rates. 'Ellett' had a higher population index (P_t/P_0) in winter (June 1997) than did 'Grasslands Ruanui' as 'Ellett' had a higher birth rate than did 'Grasslands Ruanui'. This suggests 'Grasslands Ruanui' was more dormant in winter than was 'Ellett'.

The ryegrass cultivars when treated with nitrogen had different tiller turnovers in autumn (March 1997) and late spring/early summer (December 1997) giving rise to a significant cultivar × nitrogen interaction. The autumn (March 1997) population index of 'Grasslands Ruanui' (0.704 without nitrogen) decreased when treated with nitrogen (0.627) whereas the 'Ellett' population index (0.788 with nitrogen) increased, compared to the no nitrogen treatment (0.677). The opposite trend was observed between cultivars during the post-flowering period (December 1997) with a higher population index for 'Grasslands Ruanui' (1.129) compared with a lower population index for 'Ellett' (0.996) when both cultivars were treated with nitrogen. Spring differences in tiller population index between cultivars were linked to their flowering behaviour (see Chapter 5 and 6). 'Ellett' had a higher percentage of reproductive tillers than did 'Grasslands Ruanui', regardless of environmental factors, and these differences were stronger in the second year (1997/98), despite there being no clear differences in tiller turnover between 'Ellett' and 'Grasslands Ruanui' during the pre- and post-flowering periods. Moreover, 'Ellett' had a tendency to produce more reproductive tillers in response to nitrogen whereas 'Grasslands Ruanui' favoured vegetative tillering, especially after the establishment year. Due to an acceleration of leaf area expansion, as tiller number increased in response to nitrogen, the half-life of ryegrass tillers was reduced for the tillers tagged in September 1996 and June 1997.

Irrigation increased total tiller number for both cultivars in January 1997 and February 1998 but tiller populations declined in March 1998 with 'Grasslands Ruanui' losing more tillers than 'Ellett' (see Chapter 5). Reproductive tiller number averaged across cultivars increased with irrigation in November and December 1996 but decreased in October 1997. Both ryegrass cultivars had similar responses to irrigation with respect to reproductive and vegetative tillering, except in December 1996 and January 1997, when 'Grasslands Ruanui' had more vegetative tillers than did 'Ellett' (see Chapter 6).

To characterise the morphological traits affecting vegetative tillering of 'Ellett' and 'Grasslands Ruanui' ryegrasses, an experiment during vegetative growth with different light environments (control and shade treatments, see Chapter 4), was carried out at INRA, Lusignan, France from February to May 1998. To study the relationship between leaf size and tillering, the morphogenesis of 'Ellett' and 'Grasslands Ruanui' were compared with short- and long-leaved perennial ryegrasses ('SL' and 'LL', respectively) resulting from divergent selection in France based on lamina length. Results from this experiment, after imposing thirty three days of light treatment, showed that ryegrass genotypes had different leaf morphology and tillering. 'Ellett' had longer leaves, higher tiller weight and lower tiller number than 'Grasslands Ruanui' regardless of light environments. Differences between genotypes in leaf length were attributable mainly to higher leaf elongation rate in the two long-leaved genotypes ('Ellett' and 'LL') compared with short-leaved types ('Grasslands Ruanui' and 'SL'), as leaf elongation duration (LED) did not differ significantly between genotypes. 'Grasslands Ruanui' maintained greater site filling and a similar leaf appearance rate to 'Ellett' in both light environments, offering an explanation for the higher tiller number per plant for 'Grasslands Ruanui' than for 'Ellett'. However, 'LL' had a higher tiller number per plant than 'SL', because of a higher leaf appearance rate, although this difference decreased during the experiment under the control treatment as 'SL' tended to have a higher site filling ratio than 'LL'. When shaded, differences in tiller number between 'LL' and 'SL', were more mediated by the leaf appearance rate than site filling.

With regard to the relationship between leaf growth characteristics and tillering, these results show genotypes with high LER and long lamina length, even though associated with reduced site filling in both light environments, do not necessarily have low tiller number per plant.

To describe post-flowering tillering in a dense canopy of 'Ellett' and 'Grasslands Ruanui' ryegrasses, before and after removal of the seed-head, a second controlled light experiment was carried out at INRA, Lusignan, France (see Chapter 6), from October 1997 to July 1998. Results of this experiment after imposing the different light treatments (near full light and shading) for forty five days showed that 'Ellett' had a higher proportion of reproductive tillers than did 'Grasslands Ruanui' during the summer of the establishment year, regardless of light environment (34 % vs 25 %, respectively). These results were in agreement with previous field observations (Chapter 6). Shading reduced the proportion of reproductive tillers produced by both cultivars compared with the full light treatment. Vegetative tiller weight of both cultivars was similar under both light treatments whereas shading reduced reproductive tiller weight by 40 % for 'Ellett' and 43 % for 'Grasslands Ruanui' compared with full light.

From the results obtained in field and controlled light experiments, it was concluded that an explanation of the tiller dynamics pattern for 'Ellett' and 'Grasslands Ruanui' could be related to their morphological characteristics (see Chapter 7 and 8). Thus, to assist with the understanding of the seasonal tillering patterns of 'Ellett' and 'Grasslands Ruanui' ryegrasses in different environments, a conceptual approach was proposed, using the morphological ceiling leaf area (MCLA) as an agronomic indicator regulating tiller density.

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CHAPTER ONE

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INTRODUCTION

CHAPTER 1: INTRODUCTION

1.1 Background

The New Zealand dairy industry earns 21% of the national export income (New Zealand Dairy Board, Annual Report, 1998), and 90% of the dairy production is obtained from North Island flat and rolling country in the regions of Northland, Auckland, Waikato, Bay of Plenty and Taranaki. The dairy system is based on a low-cost feed source, mixed pasture, dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*), which is intensively grazed all year round by dairy cows.

Missionaries and settlers introduced ryegrass seed into New Zealand, early in the nineteenth century. Ryegrass ecotypes that have developed over long periods in particular environments are often used by plant breeders as a source of parent material for new cultivars. Up until 1975, an ecotype from Hawke's Bay (named 'Grasslands Ruanui' in 1964) that developed under sheep grazing, was the most widely used. Since 1975, the Mangere ecotype from South Auckland, which developed under cattle grazing, has been extensively used. Cultivars such as 'Ellett', 'Yatsyn 1', 'Grasslands Nui', 'Dobson' and 'Bronsyn' have been derived from this ecotype, and are representatives of the "modern" perennial ryegrass. 'Ellett' and 'Grasslands Nui' were the first of the modern perennial ryegrasses to be commercialised. Plants of these cultivars were more erect with larger leaves than 'Grasslands Ruanui' (Corkill et al., 1981; Easton 1983) and with a higher yield potential (Armstrong 1977, Goold 1982). Other features of the new selections were better tolerance of summer drought and crown rust (*Puccinia coronata*), and superior responses to autumn rain and nitrogen fertiliser (Easton 1983; Hunt and Easton 1989). However, concerns have been expressed by farmers (Edgecombe 1988) and researchers (Thom et al., 1998a) as to the poor persistence of "modern" ryegrass cultivars in dairy pastures. Increasing stocking rate and associated increased cow damage (e.g. severe summer grazings, pugging in winter/early spring), dry summers and insect damage, have also contributed to pasture deterioration.

Ryegrass persists in pastures either through reseeding or tillering; the latter method predominates in moist-temperate dairy pastures (Matthew et al., 1993). Work by Matthew (1992) and Matthew et al. (1993) suggested that 'Ellett' ryegrass had a different perennation strategy from 'Grasslands Ruanui'. 'Ellett' ryegrass was more dependent on survival of daughter tillers produced at the base of tillers that had flowered while 'Grasslands Ruanui' was more dependent on surviving vegetative tillers. However, this tentative suggestion was made from separate experiments and in different years. Tiller studies by Korte (1986) showed that perennation through the survival of vegetative tillers predominated in the first year after the sowing of 'Grasslands Nui', and that daughter tiller production by flowering tillers was more important in the second year.

L'Huillier (1987) showed for rotationally grazed dairy pastures containing modern ryegrasses, that summer tiller density was low (2000-6000 tillers/m^2) because of poor survival of vegetative tillers. If modern ryegrasses do rely on daughter tiller production by reproductive tillers that develop in October/November, they are likely to be vulnerable to stress post-flowering (early summer) when turnover of tillers may reach 70% (Matthew et al., 1989). Stresses common at this time are lack of moisture (Thom et al., 1986b) and nitrogen (Harris et al., 1996). For example, Harris et al. (1996) showed that tiller density of ryegrass in dairy pastures was more than doubled in nitrogen treated areas in January (9950 tillers/m^2) compared with those untreated (4750 tillers/m^2).

The possibility that ryegrasses from different ecotypes have different perennation strategies requires confirmation, especially since there may be implications with regard to their persistence in dairying systems under different climatic and management conditions. A gap also exists in the literature with regard to agronomic, ecological and morphological comparisons between 'Grasslands Ruanui' and 'Ellett', the latter being the first cultivar produced from the Mangere ecotype. A description of the morphological characteristics of both ryegrass cultivars is necessary for a better understanding of their tillering behaviour.

1.2 Objectives

This study therefore sought to:

(i) Characterise the morphological traits affecting the tillering of 'Ellett' and 'Grasslands Ruanui' ryegrasses (in the absence of light competition and with a shade treatment).

(ii) Compare the tiller population demography of 'Ellett' and 'Grasslands Ruanui' ryegrasses to identify possible differences in perennation strategies likely to influence their persistence under intensive dairy cow grazing, and with nitrogen fertiliser and irrigation treatments.

(iii) Determine the effects of irrigation and nitrogen fertiliser on seasonal tillering patterns and sward productivity of pastures containing 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars.

1.3 Thesis structure

The thesis is presented in eight chapters. This introductory chapter is followed by a review of literature (Chapter 2). Chapter 3 reports on a field study of the productivity of 'Ellett' and 'Grasslands Ruanui' swards with different nitrogen and irrigation treatments under dairy cow grazing. Chapter 4 describes the morphological characteristics of 'Ellett' and 'Grasslands Ruanui' ryegrasses and how these relate to tillering. The seasonal tillering patterns of the two ryegrass cultivars and the effects of different nitrogen and irrigation treatments are described in Chapter 5. The perennation strategies of 'Ellett' and 'Grasslands Ruanui' are discussed in the Chapter 6. A conceptual approach regarding the interpretation of the tiller dynamics pattern in relation to the morphological characteristics is presented in Chapter 7. The final chapter (Chapter 8) presents a summary of the main results along with suggestions for possible future work and a discussion of the implications for the pastoral industry in New Zealand.

The chapters of this thesis are not chronologically linked. The results of the field experiment carried out at the Dairying Research Corporation in Hamilton, New Zealand from April 1996 to April 1998, are reported in Chapters 3, 5 and 6. Two controlled environment experiments were completed from April to July 1998, at the Forage Plant Ecophysiology and Forage Plant Breeding Stations, INRA, Lusignan, France. The first of these experiments characterised the morphological traits of 'Ellett' and 'Grasslands Ruanui' ryegrasses in relation to tillering under different light environments, while plants were in the vegetative phase of growth (Chapter 4). The second experiment characterised the tillering patterns of the two ryegrass cultivars under different light environments, while plants were at the reproductive growth stage, and is described in Chapter 6. Chapter 7 summarises the theories used to study 'Ellett' and 'Grasslands Ruanui' sward productivity, persistence and plant morphology in different environments, which lead to the development of a conceptual approach to aid the understanding of the perennial ryegrass tiller dynamics pattern. A general conclusion including a synthesis of the main results, some suggestions for further work and practical information for the pastoral industry in New Zealand, are presented in Chapter 8.

The thesis is presented as a series of chapters involving papers that have already been published (Chapter 3, first year results of the field experiment) or submitted to journals for publication (Chapter 4 and Chapter 6).

CHAPTER TWO

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LITERATURE REVIEW

CHAPTER 2: LITERATURE REVIEW

2.1 Introduction

The grasslands of New Zealand, which were established by man on previously forested land, are for the most part recently created plant communities. Over 150 years ago, the European settlers introduced many grass species into New Zealand, but only a few of these are extensively cultivated in pastures. Perennial ryegrass and white clover became the most important components of pastures (Harris 1968; Belgrave et al., 1990) and are extensively used by dairy farmers as a cheap feed source for cows. The warm temperate climate of the Waikato region of New Zealand usually allows sufficient ryegrass growth to meet cow requirements, the main exceptions being when dry summers or autumns occur. Nevertheless, researchers (Thom et al., 1993; Thom et al., 1998a) have raised the issue of the poor persistence of perennial ryegrass under intensive rotational cow grazing.

In a ryegrass sward, persistence is determined by tiller population dynamics, essential elements of which are rates of tiller initiation and tiller death, which together result in a continuous change in the population. The persistence of a plant, or its perenniality, is often determined by seasonal factors associated with flowering. The expression of perenniality is assured, if tillers arising while conditions are still favourable for flowering, remain vegetative. These tillers which are few in number, have the time and resources to develop strongly before winter starts (Langer 1963). Knowledge of tillering mechanisms, environmental influences on tiller dynamics in a sward and the flowering behaviour of ryegrass are essential to the understanding of sward persistence or perenniality.

This chapter summarises knowledge of the relationship between morphogenesis of the grazed plant and tillering, and the influence of environmental factors on this relationship. A review is made of perennation strategies reported from previous tiller dynamics studies, both for different grass species, and for different cultivars within the perennial ryegrass species. This is followed by a review of the different methods used to study tiller population dynamics of grass plants. Finally, the origins of the perennial ryegrass cultivars chosen for this study will be outlined.

2.2 Growth of perennial ryegrass

2.2.1 Tillers: the units of growth

As the name implies 'perennial ryegrass' is a long-lived perennial capable of producing many tillers. This species belongs to the *Poaceae* family, with a diploidl chromosome number of 14.

The ryegrass tiller in the vegetative condition comprises a single shoot with an extremely short stem bearing leaves at its nodes in two opposite ranks. The point of attachment of each leaf to the shoot apex is called a 'node' and the stem tissues separating one node from the next is called the 'internode'. The true stem segments separated by the nodes are called phytomers (Fig. 2.1). The phytomers are differentiated from a common apical meristem (Langer 1979; Robson et al., 1988). A phytomer is usually defined as consisting of a leaf blade and sheath, the internode, the node, and the associated axillary bud below the point of sheath attachment (Briske 1991) (Fig. 2.1).

Apart from producing its own leaves, the true stem may also branch to form 'tillers'. Every time the apical meristem produces a new leaf, it also produces an axillary bud which is located on the opposite side of the internode and so in the axil of the previous leaf (Jewiss 1993) (Fig. 2.2). Hence there is a tiller bud at every node. Each of these is a potential site for a new tiller (Jewiss 1972). When buds initiate and become externally visible above the subtending leaf sheath, they are referred to as tillers.

When an axillary bud becomes active, its apex produces its own leaves and secondary tillers can form from the buds in the axils of these. The process can be repeated many times, giving rise to a hierarchy of tillers, and the increased total number of tillers per plant was exponential, as long as the process remained unrestricted

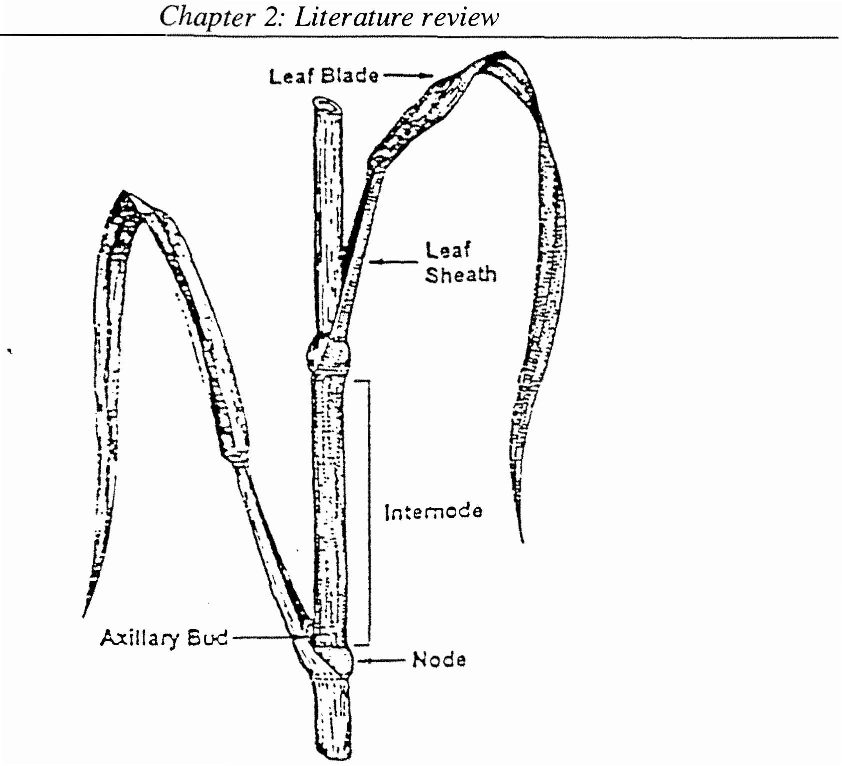


Figure 2.1. Illustration of a grass phytomer. The phytomer is the basic unit of the grass plant and consists of a leaf blade and sheath, the internode the node, and the associated axillary bud below the point of sheath attachment (after Briske 1991).

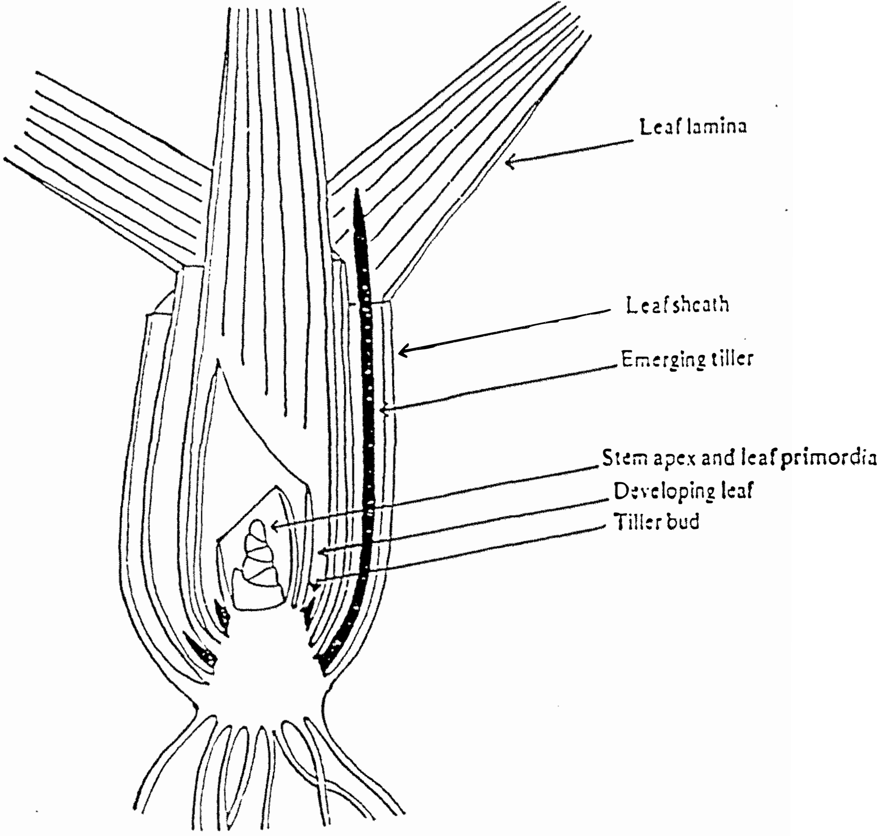


Figure 2.2. Enlarged diagrammatic longitudinal section of a vegetative grass showing position of stem apex and production of leaves and tillers from leaf primordia and buds, respectively (after Jewiss 1972).

(Langer 1963). Tillers on the main stem (T.P.) are referred to as primary tillers (T_1, T_2,...), shoots produced by them are called secondary tillers ($T_{1.1}$, $T_{1.2}$, $T_{2.1}$,...) (Fig. 2.3); these in turn give rise to tertiary tillers, and so on, denoting successive orders. This process is called 'tillering'.

Reproductive growth occurs in spring. After the inductive requirements of winter temperatures and/or short days have been satisfied, the terminal meristem shows a characteristic change in development, which foreshadows inflorescence production. The critical daylength ranges from 8 to 13 hours in different ryegrasses (Cooper 1951; Ryle and Langer 1963). Early flowering types, are particularly sensitive to air temperature in March and April while late flowering types are sensitive to air temperature in April and May in the United Kingdom (Northern hemisphere).

The first sign of reproductive development is an acceleration of leaf primordia production and lengthening of the shoot apex (Jewiss 1993). Instead of the normal single ridge indicating a developing leaf, new primordia begin to show a double ridge (Fig. 2.4). This double ridge is the morphological indication of progress towards flowering. The terminal meristem itself commits to reproductive development. This altered differentiation of primordia means leaf production eventually ceases on that tiller. Hence, a reproductive tiller is by definition annual. Further development is accompanied by internode extension, which elongates the true stem and so lifts the developing inflorescence up through the sheath tube (Parsons and Chapman 1999, Fig. 2.4). Once stem extension has begun, cutting or grazing will remove the terminal meristem and any expanded leaves which remain. Further regrowth is then only possible from tiller buds below the cutting height in the axils of old leaves. Consequently, perennation depends on the production of new vegetative tillers, which replace senescent and reproductive tillers.

2.2.2 Relationship between the morphogenesis and tiller density of grazed plants

As described above, leaves are produced sequentially at the individual tiller level. This arises because each successive phytomer follows a pre-programmed series of developmental stages from primordium to mature organ and finally senescence (Silsbury 1970). The leaf production determines the number of axillary buds available to develop into tillers or branches. This lead to the concept of 'site filling' defined as the

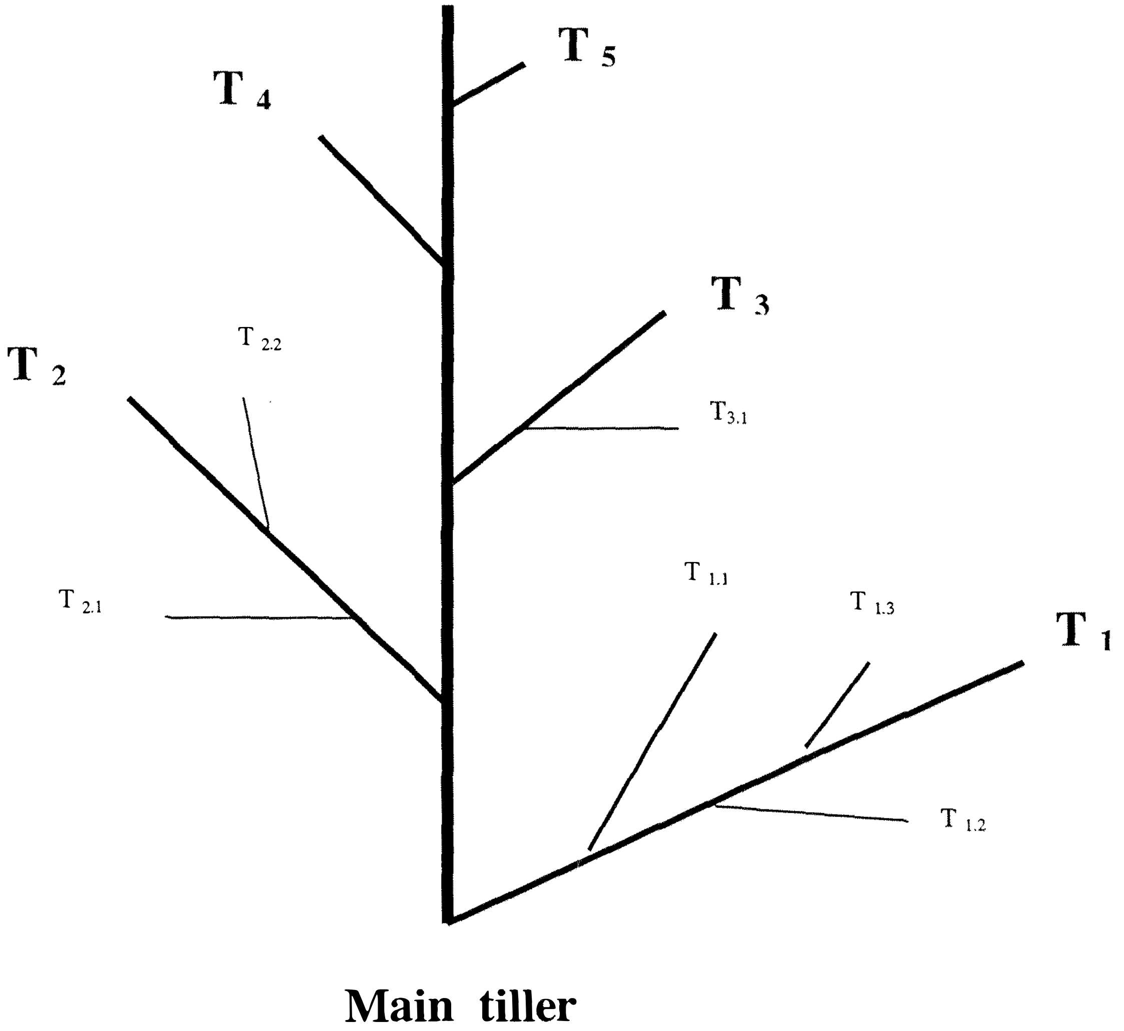


Figure 2.3. Tiller hierarchy on a perennial ryegrass plant.

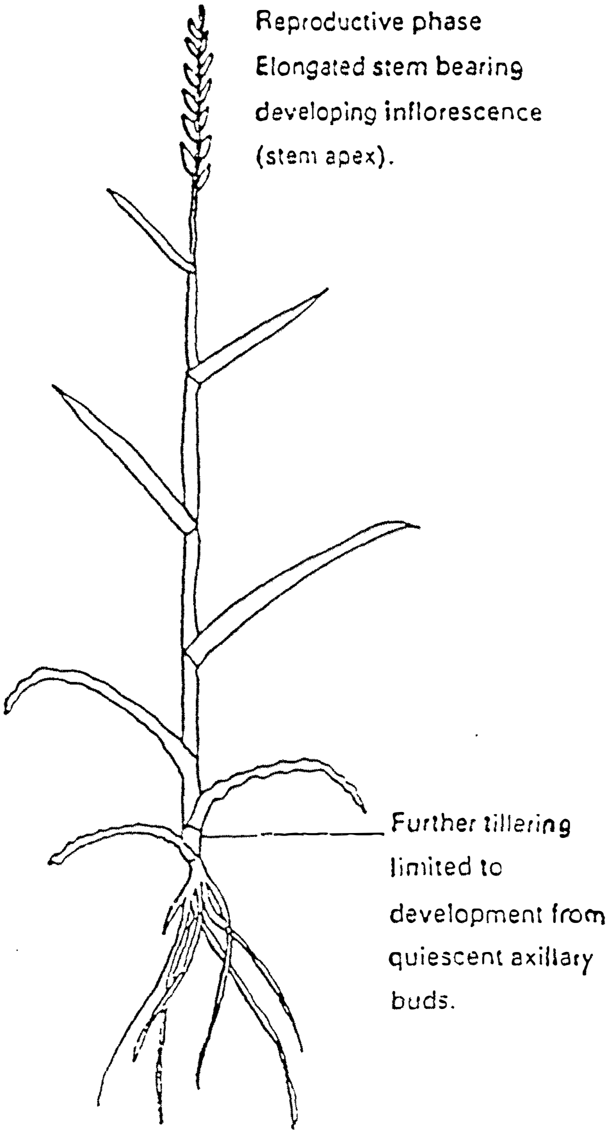


Figure 2.4. The morphology of a temperate region perennial ryegrass plant at the flowering stage (after Jewiss 1972).

rate of development of daughter tillers in relation to the leaf appearance rate (Davies 1974). The nodal structure of phytomer development also allows root appearance to be related to leaf and tiller development (Hunt and Thomas 1985; Matthew et al., 1991; Yang et al., 1998). As Chapman and Lemaire (1993) have proposed, plant morphogenesis can be described by the components of leaf turnover since, for vegetative plants, only leaves are produced (Fig. 2.5). Leaf tissue turnover depends on three main characteristics, which are genetically determined (Chapman and Lemaire 1993):

- **Leaf appearance rate (A_L)** is the inverse of the phyllochron. The phyllochron is defined as the time interval between the appearance of two successive leaves and is expressed in growing degree-days per leaf. A_L has a central role in shoot morphogenesis and potential tiller production (Davies 1974).

- **Leaf elongation rate (LER)** is the cumulative effect of cell elongation (Durand et al., 1999). It is expressed in mm or cm per growing degree-day.

- **Leaf life-span** measures the duration of a mature leaf, expressed in growing degree-days.

The leaf appearance rate, the leaf elongation rate and the life-span of leaves are closely interrelated and the combination of these elementary morphogenetic variables determine the three main structural characteristics of the sward (Fig. 2.5):

- **Final leaf size** is the product of LER and the duration of the elongation period for a single leaf. Robson (1967) and Dale (1982) showed that this period was proportional to the leaf appearance interval giving a proportionality between final leaf size and the ratio LER/A_L.

- **Tiller density** is related to the leaf appearance rate (A_L) through the determination of the potential number of tiller bud sites and site filling, which together define rate of tiller appearance (TAR) (Davies 1974). The equilibrium between TAR and tiller death rate determines the tiller density of grazed swards.

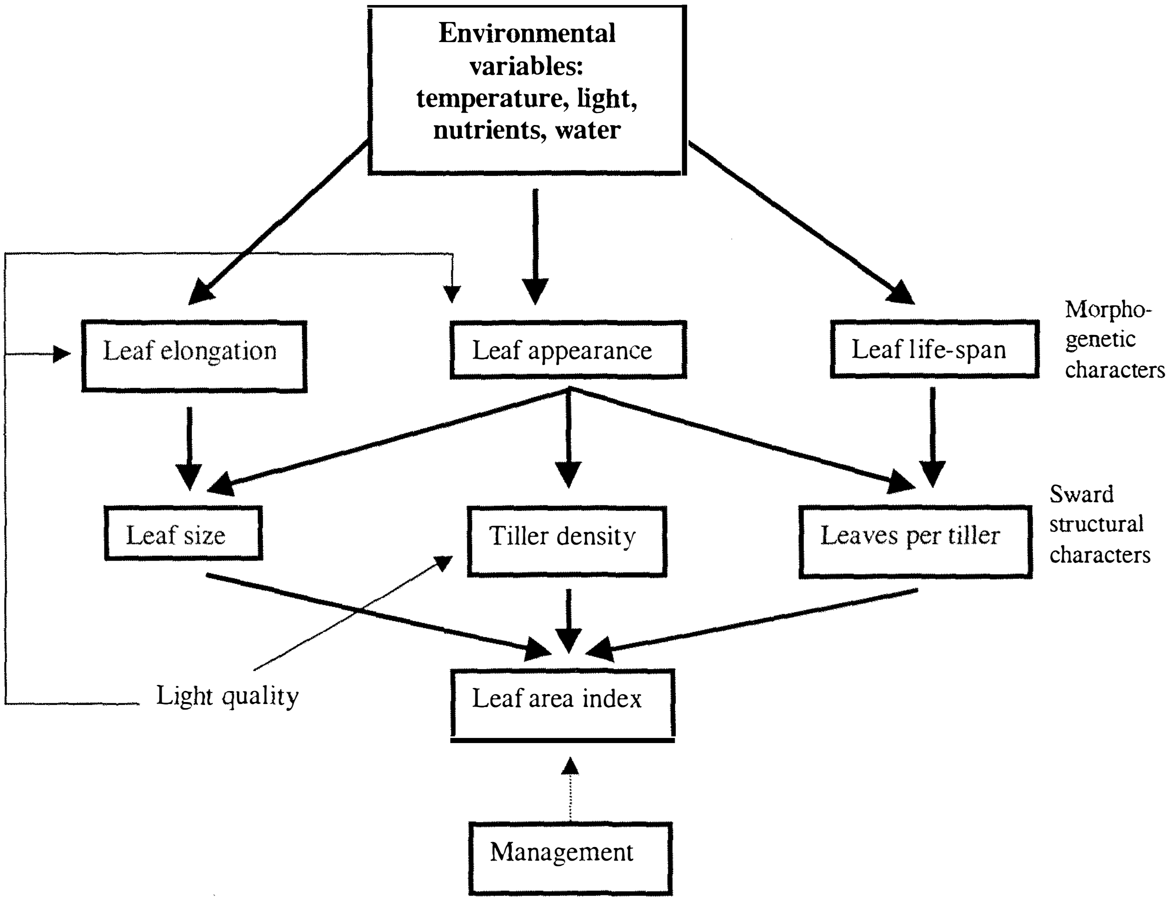


Figure 2.5. The relationship between the main morphogenetic characteristics of grasses and sward structural components (after Lemaire and Chapman 1996).

- **Number of green leaves per tiller** is the product of leaf life-span and A_L. In seedlings, the A_L of the first five or six leaves is higher than that of subsequent leaves (Parsons and Chapman 1999). But thereafter, the number of live leaves per tiller falls to a number that remains constant throughout the life of the plant, e.g. in perennial ryegrass at around 3 leaves per tiller (Davies 1981). Leaves continue to be produced, but each time a new leaf appears, the oldest leaf on that tiller dies (Hunt 1965). For most species A_L is more or less constant under controlled and field conditions over most of the growth period (Silsbury 1970). The phyllochron of perennial ryegrass equalled 110 growing degree-days per leaf when the base temperature was 0°C (Davies and Thomas 1983).

Leaf area index (LAI) of the sward is determined by the product of leaf size, leaf number per tiller, and tiller density, assuming that the leaf area/leaf length ratio for a given genotype is constant. The LAI of a sward was defined by Thomas (1980) as the green leaf area per unit area of ground.

2.2.3 Environmental effects on the morphological characteristics of ryegrass in relation to tiller dynamics

The morphological characteristics described above (Fig. 2.5) are influenced by environmental variables like temperature, light, nutrient supply (especially nitrogen) and soil water status, which will therefore modify tiller dynamics and hence the equilibrium between tiller initiation and the rate of tiller death.

2.2.3.1 Temperature

Temperature is the dominant environmental determinant of leaf growth. Peacock (1975a, b) showed that LER in perennial ryegrass responds to change of temperature at the meristematic zone near the shoot apex, rather than to the general soil or air temperature. For most temperate grasses, the response of LER to temperature is near exponential in the range 0-12°C of average daily temperature and linear above these values until the optimum was reached at about 20-25°C, depending on species (Lemaire and Chapman 1996). Leaf extension rate strongly decreased when temperatures were above the optimum values. Many authors have noted that the response of LER to temperature shows seasonal differences (Peacock 1975c; Parsons and Robson 1980). In association with the transition from vegetative to reproductive growth, leaves extend faster in spring at a given temperature than in autumn, which results in a higher potential growth (Gastal et al., 1992). In grasses, A_L is linearly related to temperature (Langer 1954; Davies and Calder 1969; Peacock 1975b). For maize (*Zea mays*), this relationship is linear for a range in average daily temperature of 8-34°C (Jones and Kiniry 1986). Therefore leaf size, as determined by the LER/A_L ratio, increased as temperature increased. Moreover, the appearance of successive leaves on a tiller, and at a faster rate with higher temperature, also increased the number of potential sites for the appearance of new tillers, and so tiller number per plant. Nevertheless, Mitchell (1953) suggested that the filling of lateral tiller buds in perennial ryegrass decreased at high temperature, and other authors (Langer 1979; Ryle 1964) have noted that the optimum temperature for tillering is lower than that for leaf production.

2.2.3.2 Light

Light plays an important role in leaf growth and tiller production. Indeed, Mitchell (1953) showed that total light energy received affects tiller production in perennial ryegrass through increased site number, arising from increased A_L, and in the site filling of these buds. In response to low light stress, plants often increased leaf area to maximise light interception and changed physiological processes to enhance the efficiency of carbon utilisation (Sanderson et al., 1997). When shaded, leaf length and leaf area per tiller increased mainly through increased LER (Gautier et al., 1999) while leaf width remained unaffected (Sanderson and Nelson 1995). Allard et al. (1991) showed that for shaded tall fescue (*Festuca arundinacea*), leaf area increased because of increased duration of leaf elongation, which probably resulted in a decreased A_L due to shading. The plant also produced thinner new leaves with a lower specific leaf weight than those produced in bright light (Allard et al., 1991; Kephart et al., 1992). For an individual perennial ryegrass plant, simulated shading drastically decreased tillering (Mitchell and Coles 1955) through a reduction of A_L and site filling (Gautier et al., 1999). In a dense sward, light was almost extinguished at the base of the plant when LAI reached a value of 3, which slowed down and suppressed tillering (Simon and Lemaire 1987). However, before light intensity was severely decreased in a closed grass canopy, the phytochrome pigments perceived a reduction in the ratio of red (R) to far-red (FR) light at the bud level, and this light quality response caused tillering inhibition (Casal et al., 1985, 1987). Many factors can cause tiller mortality but carbon starvation resulting from competition for light seemed to be the most important (Ong and Marshall

1979). When shaded, a plant allocated carbohydrate to older tillers at the expense of developing new tillers (Davies and Thomas 1983). Experimental evidence showed that young tillers were first to die as a result of being overtopped and shaded by mature tillers (Ong 1978b). Lemaire and Chapman (1996) suggested that in shaded canopies some initiated tiller buds abort before they emerge.

2.2.3.3 Nitrogen

Nitrogen application strongly stimulated leaf growth and tiller production in grass swards (Harris et al., 1996; McKenzie 1998). Gastal and Bélanger (1993) reported that nitrogen fertilisation improved dry matter yield by speeding up leaf area expansion and increasing light interception, rather than by increasing canopy photosynthesis. The increased area of leaves on existing tillers under nitrogen treatment was mainly due to increased leaf elongation rate through a higher rate of cell division (Gastal et al., 1992; Gastal and Nelson 1994). Leaf appearance rate was unaffected by nitrogen application in tall fescue swards under cutting (Lemaire 1988; Lemaire and Culleton 1989) or when continuously grazed by sheep (Mazzanti et al., 1994). Harris et al. (1996) showed that pre-grazing ryegrass tiller density in dairy pastures was consistently higher with 200 kg N/ha (6295 tillers/m^2) or 400 kg N/ha (6673 tillers/m^2), than without nitrogen (4072 tiller/m^2). The positive effect of nitrogen on tiller appearance rate was not due to a higher rate of production of bud sites since A_L was only slightly changed, but was mainly due to an increase in the degree of site filling which was considered as maximum when nitrogen nutrition was optimal (Lemaire and Chapman 1996). Conversely, nitrogen deficiency can lead to low values of site filling (Lemaire 1985), and suppressed tiller appearance rate, even if sward LAI is low. Faster growth of the ryegrass tiller population, stimulated by nitrogen, reduced the time taken to reach the LAI at which tillering was reduced or inhibited due to self-shading by leaves (Simon and Lemaire 1987; Van Loo 1992; Lemaire and Chapman 1996). When sward LAI was above 3, young tillers died first, which resulted in a drastic decrease in tiller density (Simon and Lemaire 1987). So the positive effect of nitrogen on tiller density observed during the earlier part of a regrowth period can be totally offset and transformed into a negative effect when cutting or grazing interval is long, allowing a high herbage accumulation. Conversely, reduced nitrogen nutrition decreased tiller density and increased assimilate allocation to roots (Bélanger et al., 1992; Van Loo 1992).

2.2.3.4 Water

In dense ryegrass swards, rotationally grazed by dairy cows in summer/autumn, irrigation (235 mm) increased dry matter yield by 1.5 tonne DM/ha compared with unirrigated swards (Thomson 1996). In summer, plants are often subjected to water stress, which can be defined as an imbalance between the evaporative demand on the plant and the ability of the plant to meet that demand from the soil (Parsons and Chapman 1999). Water stress severely reduced dry matter yield by limiting leaf area development (Slatyer 1974; Ludlow and Ng 1977; Ludlow et al., 1980). Van Loo (1992), in a hydroponic glasshouse experiment at low and normal water potentials, measured leaf area expansion of perennial ryegrass in terms of leaf elongation rate, leaf appearance rate, specific leaf area and tillering. He observed that tiller number per plant was limited by water stress principally by a reduction in leaf appearance rate. Site filling did not change consistently when ryegrass plants had a low water potential (Van Loo 1992). Also, in the field with established swards, reduced tiller density under dry conditions was attributable mainly to a lower leaf appearance rate (Norris 1982; Barker et al., 1985). Responses observed during drought can also be associated with a high soil temperature (Davies and Thomas 1983), reduced mineral availability to the shoot (Gales 1979) as a consequence of dry upper soil layers, and damage caused by severe grazing and/or pulling by animals (Thom et al., 1986a).

2.2.4 Effects of grazing management on leaf growth in relation to ryegrass tiller population dynamics

Grass plants have a rapid turnover of leaf tissue and any material which remains unharvested, soon dies. Therefore, to maintain a high production potential, the grass crop has to be harvested soon after reaching ceiling herbage mass (Brougham 1958). Repeated defoliation over the seasons reduced the leaf area and light interception of the canopy, interrupted canopy photosynthesis and so reduced the capacity for the production of new leaves (Parsons 1988). Leaf regrowth and restoration of leaf area depend mainly on reserves of carbohydrate in the early stages (Davidson and Milthorpe 1966a, b).

The equilibrium between tiller appearance and tiller death, which determines the tiller population in the field, is strongly dependent on the LAI of a sward. The LAI varies according to sward defoliation regime. Swards continuously grazed by sheep at a low LAI (e.g. 2) or to low height (e.g. 3 cm) are characterised by a large number of small tillers. Ryegrass tiller density changed through the grazing season reaching 30-50 000 tillers/m^2 in mid summer and around 20 000 tillers/m^2 in winter (Grant et al., 1983; Parsons et al., 1983). By contrast, swards continuously defoliated at a greater height (e.g. 9 cm) and hence at a greater LAI (e.g. 4.0), developed fewer, much larger tillers (10 000 to 25 000 tillers/m^2) in summer (Parsons 1988). Swards rotationally or intermittently grazed by animals have a different LAI, dependent on the frequency and the defoliation height of the grass sward. Simon and Lemaire (1987) demonstrated that in an intermittently defoliated sward, tiller density increased after severe defoliation until a LAI of 3-4 was reached and then began to decline. Under severe and frequent defoliation, grass plants adapt their morphology to tolerate defoliation by reducing leaf and tiller size. Smaller tillers are less susceptible to grazing since they are closer to the ground. For a given LAI, the plant has the flexibility or plasticity to avoid grazing by increasing tiller density and decreasing tiller size. In this case, LAI may be maintained if a compensatory increase in tiller density was achieved. This process is the reverse of that defined by the self-thinning rule (Yoda et al., 1963).

Lemaire and Chapman (1996) have suggested that genotypes with high A_L (e.g. perennial ryegrass) have a high number of small tillers and those with low A_L (e.g. tall fescue) have a low number of large tillers. For example, Mazzanti et al. (1994) showed that at a LAI of 3.0 tall fescue swards generated 4-6000 large tillers/m^2 while perennial ryegrass developed 10 000-15 000 much smaller tillers/m^2. Then, to the extent that such relationships are typical, tiller size and density are inversely correlated. Yoda et al. (1963) found for several plant species that logarithmic plots of weight against shoot density showed a –3/2 slope (or –1/2 for the equivalent relationship between herbage mass and shoot density, according to Weller, 1987). It has been assumed that defoliated swards also follow this relationship (Bircham and Hodgson 1983; Lambert et al., 1986; Davies 1988; Xia 1991). This relationship defines a 'size/density compensation line', and may define a line of constant LAI (Sackville Hamilton et al., 1995; Matthew et al., 1995). Therefore, swards plotted to the right (e.g. above) an arbitrarily positioned size/density compensation line will have a higher LAI and swards plotted to the left (e.g. below) a lower LAI (Matthew et al., 1996). Decreasing leaf area with increasing defoliation intensity in continuously grazed swards, violates the constant leaf area assumption of –3/2 size/density compensation (Matthew et al., 1996). Consequently, increased tiller density across a series of swards of differing defoliation intensity, was usually slightly less than that needed to maintain a constant LAI, resulting in empirical size density compensation slopes more like –5/2 (Matthew et al., 1995), rather than the –3/2 of classical self-thinning.

2.3 Tiller demography of grass swards

2.3.1 Previous studies

The pattern of persistence of perennial grass plants is referred to tiller dynamics, and can be described as the balance between tiller birth and death rates. The usual methodology used in tiller dynamics studies has been to monitor the survival of marked tillers and the birth of new tillers within fixed quadrats (Langer et al., 1964), or sometimes by repeated destructive harvest of pre-selected plants (Silsbury 1964). Some published tiller dynamics studies of grasses are described in Table 2.1. It emerges from Table 2.1 that the pattern of tiller dynamics shows seasonal variation (often linked with reproductive growth in spring) and responds to fertiliser (Ito et al., 1989) or defoliation regimes (Jewiss 1966), with differing species responses.

Common to all the studies listed in Table 2.1, to a greater or lesser degree, was a period of intensive tiller turnover associated with reproductive growth, and little effect of the grazing management imposed. Fig. 2.6 (from Jewiss 1966) illustrates tiller turnover for timothy (*Phleum pratense*) and meadow fescue (*Festuca pratensis*). Both species showed increased tiller death rates (indicated by a steeper decline in numbers within individual cohorts) in June of each year, regardless of management applied. Perennation in timothy relied almost totally on new tillers produced in May and June (Northern hemisphere) whereas meadow fescue had more tillers born earlier in the season (February to April) and some of these survived to the following season, especially under more frequent defoliation (Fig. 2.6c and 2.6d).

Korte (1986) also observed a high tiller turnover during late spring early summer in ‘Grasslands Nui’ perennial ryegrass (Fig. 2.7a), and associated data on tiller

Table 2.1. Major grass tiller dynamics studies

Authors	Year	Measurement period	Latitude or location	Species	Treatment and type of experiment	Analytical method
Langer	1956	Oct 1951 to Oct 1953	51.30 N	*Phleum pratense*	Potted plants	Seasonal death rates of each cohort
Silsbury	1964	Jun 1958 to Jun 1959	35 S	*Lolium perenne* *Lolium rigidum*	Field study	ANOVA on tiller number per plant
Langer et al. and Jewiss	1964 1966	Jun 1957 to Oct 1959	51.30 N	*Phleum pratense* *Festuca pratensis*	Simulated hay and frequent cutting	ANOVA on tiller appearance and death rates
Davies	1988			*Lolium perenne* *S24, S203, RVP, S22* *Lolium × multiflorum* (hybrid)	4 defoliation regimes and 3 cross over treatments in second year	No statistical analysis
Colvill and Marshall	1984	Jul 1975 to Jul 1977	53 N	*Lolium perenne* S23	Field plot, cut post-flowering each year	Classification of tillers into primary, secondary, tertiary and quaternary
Korte	1986	Sep 1977 to Sep 1979	41 S	*Lolium perenne* Grasslands Nui	Field experiment, frequent mowing and infrequent mowing at 95% light interception	Exponential decay curves fitted
Garwood	1969	Two experiments Exp 1: From spring 1956 to spring 1957 Exp 2: From spring 1958 to spring 1959	Hurley Berks, Britain	*Lolium perenne* S23 and S24 *Dactylis glomerata* *Phleum pratense*	Field experiment, two levels of irrigation (+Irr and –Irr)	ANOVA on new and dead tillers

Table 2.1 (Cont.)

Ito et al.	1989	May to Nov 1979 May to Nov 1980	38 N	*Dactylis glomerata*	Defoliations: 9 frequent and 5 infrequent per season. Low and high N and P applications	No evidence, paper in Japanese
Matthew	1992	Oct 1989 to Apr 1991	41 S	*Lolium perenne* Grasslands Ruanui		No statistical analysis
Hernandez-Garay	1995	Sep 1992 to Apr 1993 Sep 1993 to May 1994	41 S	*Lolium perenne* Grasslands Nui		ANOVA on tiller appearance and tiller death rates
McKenzie	1997b	Sep 1992 to Oct 1994	30 °24'S	*Lolium perenne* Ellett	3 grazing frequencies and defoliation height in an incomplete factorial combination plus continuous grazing by sheep	Plots of % tillers surviving. Treatments compared at each sampling date by ANOVA
Bluett et al.	1999	Sep 1996 to Mar 1997	41 S	*Lolium perenne* Aries HD Yatsyn 1	2 cultivars replicated 3 times	Exponential decay curves fitted to tiller survival data and ANOVA of tiller death rate
Pakiding and Hirata	1999	May 1996 to May 1998	32 N	*Paspalum notatum* Bahiagrass	Rotationally grazed by cattle	Exponential decay curves fitted Tiller appearance and death rates analysed by ANOVA

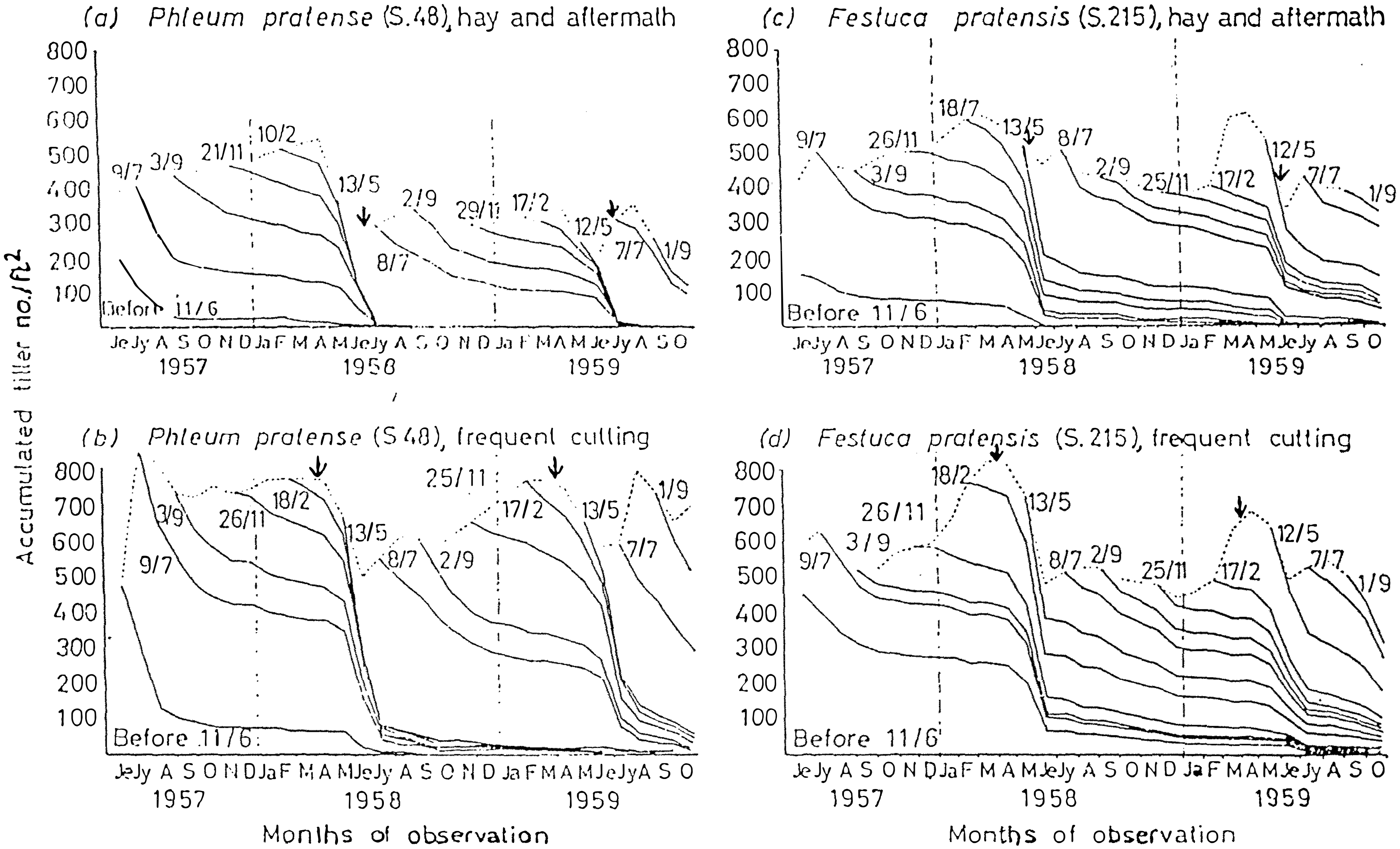
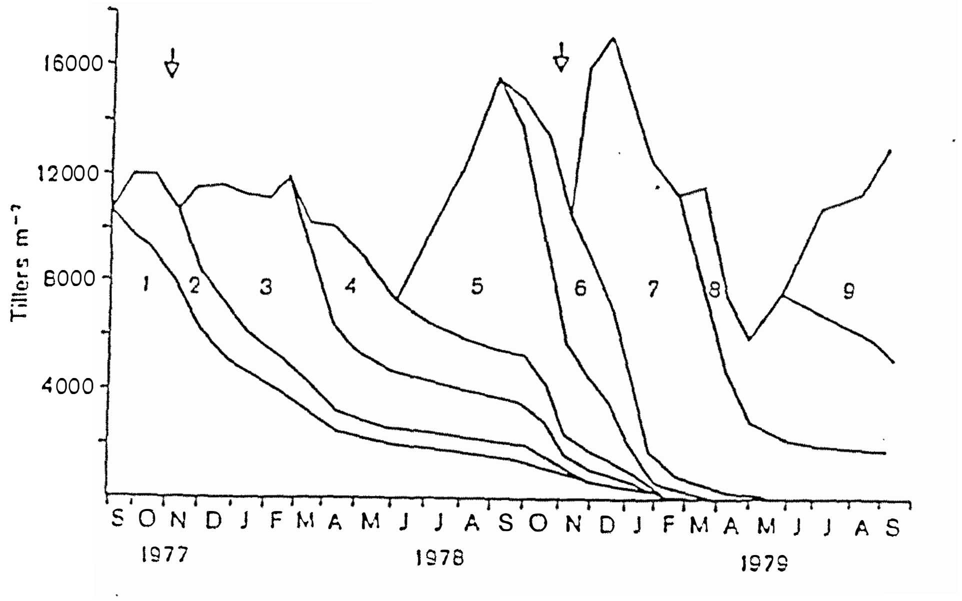


Figure 2.6. Life history of tillers of *Phleum pratense* and *Festuca pratensis* under hay and aftermath, and frequent cutting systems of management. Dates of first observation on tillers arising in alternate months, and numbers of those present in successive months; arrows indicate dates of first cut in each year (after Jewiss 1966). Note: 100 tillers/ft^2 equals 1076 tillers/m^2.

(a)



(b) Tiller natality (————) and mortality (— — —) for the same sward.

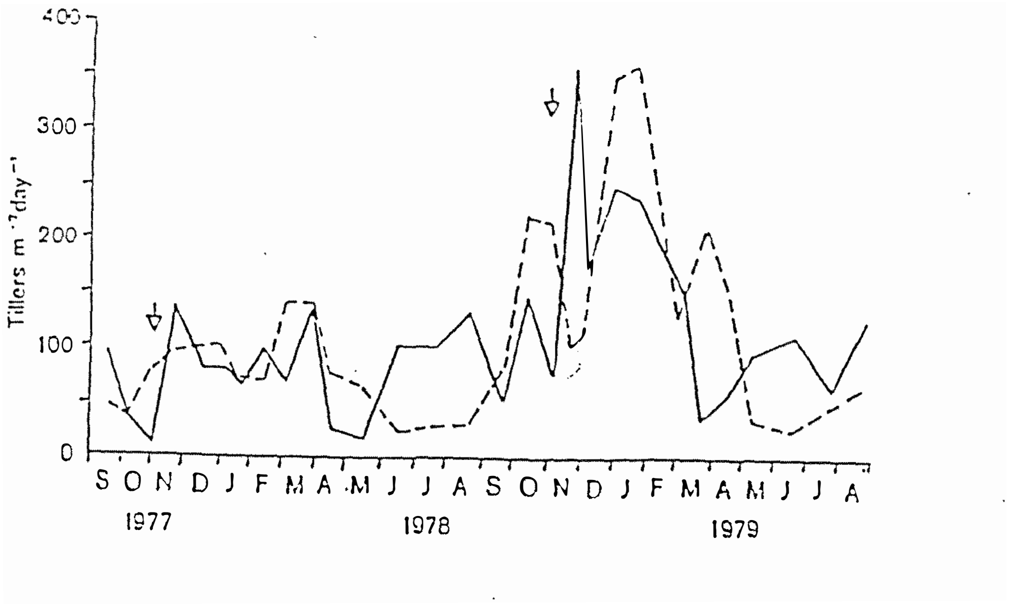


Figure 2.7. (a) Tiller age-cohort survival diagram showing tiller population density by age categories for a 'Grasslands Nui' ryegrass sward over 2 years at Palmerston North (after Korte 1986). Arrows indicate defoliation of the main crop of reproductive tillers.

appearance and death (Fig. 2.7b) clearly showed high tiller turnover during December/January of the second year rather than the establishment year. Other studies of perennial ryegrass, showing evidence of a similar tiller turnover include Garwood (1969), Colvill and Marshall (1984), L'Huillier (1987), Davies (1977) and Hernandez-Garay et al. (1993; 1997).

For 'Ellett' ryegrass, a cultivar related to 'Grasslands Nui', the majority of the new tillers produced in spring originated from the base of flowering tillers decapitated by grazing (Matthew 1992). However, only a slight increase in tiller turnover in spring was observed by Matthew (1992) when studying 'Grasslands Ruanui' ryegrass. Based on these different patterns of tiller turnover, Matthew et al. (1993) proposed the existence of different perennation strategies in perennial ryegrass cultivars:

(i) Reproductive pathway in which perennation is by production of daughter tillers from flowering tillers

(ii) Vegetative pathway in which perennation is by tillering from surviving non flowering tillers

Matthew et al. (1993) also indicated that tall fescue was more dependent on the vegetative pathway whereas prairie grass (*Bromus willdenowii*) was more dependent on the reproductive pathway. The relevance of the distinction between vegetative and reproductive pathways is that it highlights the possibility that axillary buds of *both* vegetative and reproductive tillers may contribute to post-flowering tiller production, and that it is helpful to identify the balance between these two processes. Silsbury (1964) and later Jewiss (1981), have noted that axillary buds on flowering tillers were of importance to perennation. Silsbury's studies were carried out under "Mediterranean" climate conditions in Adelaide and this raises the question as to whether or not climate was a factor in the responses observed.

At flowering, species like timothy (Jewiss 1966, Fig. 2.6) and Italian ryegrass (*Lolium multiflorum*) (Davies 1977) have a very high turnover. This would be consistent with a high proportion of tillers flowering and being replaced by new vegetative tillers.

For *Phleum pratense* swards either cut to simulate hay and aftermath management (Fig. 2.6a) or cut frequently (Fig. 2.6b) the new vegetative tiller population, appearing between June and September formed the greater proportion of the sward for most of the year, and ensured perennation of that sward (Langer et al., 1964; Jewiss 1966). This pattern was repeated as an annual cycle since tillers did not survive more than one year.

Festuca pratensis differed in perennation strategy from *Phleum pratense.* In *Festuca pratensis,* pre-flowering tillers were important to perennation (Fig. 2.6c and 2.6d) and the degree of tiller replacement during the flowering period differed with management. *F. pratensis* replaced only about one third of its tiller population under frequent cutting (Fig. 2.6d), but approximately two thirds of the population under infrequent cutting (Fig. 2.6c). Another difference between P. *pratense* and *F. pratensis* was that in the latter some tillers survived more than 3 years (Jewiss 1966).

Thus, it is clear from previous studies that different species (and even cultivars within species) have differing perennation strategies. In addition, tiller age-cohort survival diagrams from studies by Colvill and Marshall (1984) and Korte (1986) indicated that the vegetative pathway predominated in the first or establishment year of perennial ryegrass swards, and that the reproductive pathway predominated in the second year with a faster tiller turnover.

In perennial ryegrass, Matthew (1992) also observed an effect similar to that noted above in Jewiss' (1966) data for timothy, in that laxer, less frequent defoliation tended to increase the proportion of flowering tillers compared with frequent grazing. However, in other cases frequent or severe grazing increased tiller death and turnover rate. Indeed, infrequent defoliation of perennial ryegrass swards with a low proportion of flowering tillers decreased tiller death rate in summer under subtropical conditions, whereas frequent and intensive defoliation increased tiller death rate (McKenzie 1997a). Finally, the time of heading of grass species is of considerable interest in swards as it determines the pattern of growth and regrowth over spring and summer. Different defoliation or grazing managements during the pre- and post-flowering periods may therefore result in a different tiller dynamics pattern.

A seasonal tiller population increase in late winter early spring and a corresponding decrease in autumn can also be seen in Korte's (1986) data (Fig. 2.7a). This probably represents a general response of the tiller population to seasonal fluctuations in environmental conditions, as a similar seasonal trend in tiller population was found by Davies (1988) when results from several experiments were averaged. The autumn tiller decline was often followed by a 'tillering flush' under cutting (Garwood 1969; Davies 1988; Korte 1986) or grazing (Chapman et al., 1983; Korte et al., 1984; Hernandez-Garay et al., 1993, 1997; Matthew 1992). Korte and Chu (1983) showed that the 'tillering flush' in autumn was more pronounced in perennial ryegrass swards exposed to drought over the previous summer. Water stress allowed tiller initiation to continue but deterred tiller emergence. In autumn, when soil water availability increased, a rapid expansion of dormant tillers was observed (Korte and Chu 1983). In contrast, L'Huillier (1987) did not observe a tillering flush in autumn. However, rainfall during the 1984/85 summer was above the long term (75 year) average and L'Huillier (1987) suggested lack of inhibition of tiller appearance in summer could have reduced the autumn flush of tiller appearance. In contrast to the autumn tillering patterns observed by L'Huillier (1987), a high tiller appearance and a low tiller death were reported by McKenzie (1997a) for perennial swards under different frequency or intensity of sheep grazing in the subtropics. McKenzie (1997a) suggested that differences between the autumn tillering pattern observed in New Zealand (L'Huillier 1987) and South Africa might be partly due to the animal grazing regime since sheep grazed pastures generally showed a high tiller appearance (Chapman et al., 1983). Another possible explanation, however, could be reduced ryegrass vigour associated with high summer temperatures in the subtropics.

2.3.2 Methodology for the study of tiller dynamics in grass swards

As shown in the previous section, the sward tiller population includes populations of tillers from different age classes. The tiller population also changes with season depending on the number of births and deaths in particular environments and under different grazing managements. To quantify tiller dynamics changes, such relationships need to be represented mathematically.

2.3.3 Methods used in previous studies

A further point that arose from the review of previous tiller dynamics studies (Table 2.1) was the lack of development of analytical methodology for tiller age-cohort data. Four types of data analysis were found in the studies listed in Table 2.1. Some conclusions were argued from visual inspection of the data (Jewiss 1966; Matthew 1992; Hernandez-Garay 1995) or from seasonal changes (Korte 1986; McKenzie 1997a, b). In the ecological literature, an integral part of population dynamics analysis was the determination of survival probability and birth rates for different tiller age classes. Some studies (Korte 1986; Pakiding and Hirata 1999; Bluett et al., 1999) fitted an exponential decay curve to the surviving tiller number in each age-cohort and calculated the tiller half-life, or the time taken for half the tillers in a population to die. This gives an estimate of the average survival probability of an age-cohort without taking into account the seasonal variation. A recent study (McKenzie 1997b) generated the survival probability for the tiller population at two monthly intervals while Pakiding and Hirata (1999) calculated survival probability for seasonal groups of age-cohorts.

A comparison of tiller longevity between seasonal age-cohorts can identify tiller age groups which contribute less to perennation because they are short-lived. Spring tillers of Korte (1986), (age-groups 5 and 6 in Fig. 2.7a), fall into this category. Bluett et al. (1999) fitted an exponential decay curve to compare the survival and reproductive development of 300 tillers of 'Aries HD' and 'Yatsyn 1' ryegrass cultivars from September 1996 to March 1997. Results from this analysis did not show any significant differences in the cultivar patterns of tiller survival, and the tiller death rates of the cultivars were similar to those found by Korte (1986) for 'Grasslands Nui'. Alternatively, comparisons between species can reveal fundamental differences in tiller longevity. For ryegrass, tiller longevity ranged from 36 to 143 days (Korte 1986) and for Bahiagrass from 321 to 902 days (Pakiding and Hirata 1999). Post-flowering tillers were identified as important for perennation since they lived longer (Langer et al., 1964; Korte 1986; McKenzie 1997a, b). None of these studies quantify the differences in perennation strategy that appear to exist between timothy and meadow fescue. To fully appreciate differences in perennation strategies it would be desirable to have a more complete analysis of survival and birth probabilities than has been carried out to date. Published agronomic interpretations of tiller dynamics data are mainly based on intuitive comments (Jewiss 1966). In the next section, possibilities for a more complete analysis will be explored.

2.3.4 Opportunities to develop methodology for describing tiller population dynamics

In the simplest sense, the dynamics of a plant population can be described by the following equation:

$$N_{(t+1)} = N_t + B - D \qquad (1)$$

where:

$N_{(t)}$ and $N_{(t+1)}$ are the population at the time t and t+1, respectively, and B and D are the number of births and deaths. The equation shows that population size (N) changes between time t and a later time t + 1 as a result of births (B) and deaths (D). Fig. 2.8 shows an example of dynamics of a Bahiagrass tiller population under cattle grazing over two years (Pakiding and Hirata 1999). The balance of births and deaths every month determined the extent of the population increase or decrease giving an indication of the population size and hence its persistence. For example, the population size of perennial ryegrass after two years of observations decreased (Garwood 1969; L'Huillier 1987) whereas the population size of *Agrostis stolonifera* increased (Bullock 1996). Studies, which show the contribution of births and deaths to longer term change in population size, include those of Korte (1986), Ito et al., (1989); Matthew (1992), Hernandez-Garay et al. (1993), Hernandez-Garay (1995) and McKenzie (1997a).

The tiller population changes can be expressed in different ways. One of the mathematical frameworks suitable for describing simultaneous effects of births and deaths on a tiller population is matrix algebra (Leslie 1945). The method has more commonly been applied to animal populations (Usher 1972), but it has also been applied to tiller populations of *Carex bigelowii* (Callaghan 1976) for the quantitative description of tiller demography in swards. Leslie's (1945) approach (sometimes referred to as a Leslie matrix) used a transition matrix, which defined survival and birth coefficients for each age group in a population. This matrix, is multiplied by a column vector containing the numbers in each age group within the population, producing a second column vector predicting the new population age structure one unit of time later

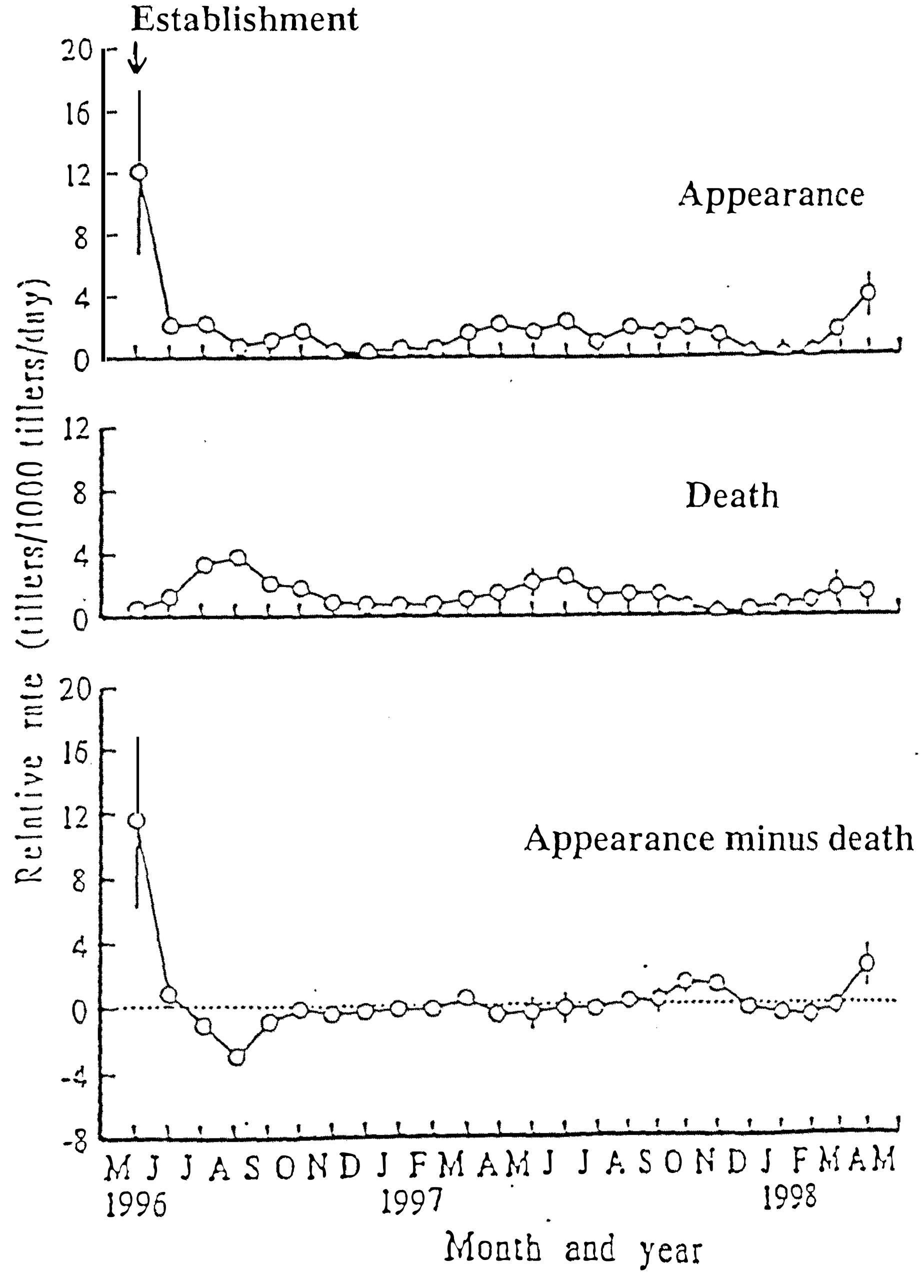


Figure 2.8. Relative tiller appearance rate or birth rate, death rate and their balance (appearance rate minus death rate) of Bahiagrass (*Paspalum notatum* Flügge) pasture under cattle grazing in Japan (after Pakiding and Hirata 1999).

$$\underset{\lambda}{\begin{bmatrix} B1,1 & B2,1 & B3,1 & B4,1 \\ S1,2 & \bullet & \bullet & \bullet \\ \bullet & S2,3 & \bullet & \bullet \\ \bullet & \bullet & S3,4 & S4,4 \end{bmatrix}} \times \underset{\mathbf{N}_{(\mathbf{t})}}{\begin{bmatrix} n_{1,(t)} \\ n_{2,(t)} \\ n_{3,(t)} \\ n_{4,(t)} \end{bmatrix}} = \underset{\mathbf{N}_{(\mathbf{t+1})}}{\begin{bmatrix} n_{1,(t+1)} \\ n_{2,(t+1)} \\ n_{3,(t+1)} \\ n_{4,(t+1)} \end{bmatrix}}$$

Bi : probability of birth from age-group i at time t into age group 1 at time t+1.

Sij : probability of survival from age group i at time t into age group j at time t+1.

n1....n4 : numbers in the 4 age classes at times t and t+1, respectively.

Figure 2.9. Transition probability matrix of birth and survival coefficients (λ) for predicting the population age structure at time t+1 with observed age class structure in the population ($N_{(t)}$) at time t.

(Fig. 2.9). The relationships illustrated in the Fig. 2.9 can be expressed mathematically as follows:

$$\lambda \times N_t = N_{(t+1)} \qquad (2)$$

where:

λ is the Leslie transition matrix of birth and survival coefficients and N the size of the population including the different age groups at different times (t and t+1). Fig. 2.9 illustrates a simple case of 4 age groups in the population. A coefficient, $S_{4,4}$, not included in Leslie's (1945) model, was used by Usher (1972) to provide for continued survival of the oldest age group. That is, with the coefficient included $n_{4,(t)}$ represents the number of individuals four time periods old and older (Fig. 2.9). Without this coefficient, all individuals surviving until the beginning of the fourth time period disappear at the end of that period (C. Matthew and N.R. Sackville Hamilton, unpublished). In fact, the appropriate size of the transition matrix will depend on the length of life of an individual tiller and the number of age classes deemed to be present in the population. In a hypothetical case where tillers lived no longer than one year, division of 12 age cohorts would be a convenient way to record monthly observations of births and deaths.

The matrix model is able to completely describe tiller survival diagrams such as these in Fig. 2.6 and 2.7 but there are practical difficulties. This approach would require not only survival probabilities of tagged tillers but also the probability for each age group of forming a daughter tiller, and all these data would be needed for each time step in a simulation. This would require a very intensive field measurement programme. As far as the writer is aware, only the study of Black (Matthew et al., 1999) has produced such data. Because seasonal variation is much more important than variation between age-cohorts, one way to simplify the problem is to reduce the population to two age classes, existing and new tillers (C. Matthew and N.R. Sackville Hamilton, pers. comm.) and this approach is developed further in Chapter 5.

A different approach has recently been applied to the sward dynamics of white clover. This was the dynamical systems model based on differential equations for rate processes (Louie et al., 1998). As applied to clover, this model used the meristem as the unit of population, because it was the meristem where the key growth processes occurred (Brock et al., 1988; Harris 1993). By using the tiller as the growth unit instead of the meristem, this model could be adapted to describe the perennial ryegrass sward dynamics under field conditions.

Even though the Leslie matrix model gives a precise description of the tiller population demography using the birth and survival rates of each tiller age-group, it is not mechanistic and does not explain the reasons for seasonal fluctuation in tiller number. Such a model, which can take into account the effects of environmental factors and grazing management on the tiller dynamics of perennial ryegrass, is not yet developed and is beyond the scope of this thesis. What is attempted in later chapters, however, is to identify sensitive stages in a life cycle of tillers, information from which management strategies can be developed.

2.4 History of ryegrass cultivar usage in New Zealand

Perennial ryegrass was the most important 'English' grass introduced to New Zealand in the nineteenth century (Corkill 1949). Settlers and missionaries sowed seeds of perennial ryegrass in most 'bush burn' mixtures to establish new pasture for livestock. Climate, farming practices, type and topography of soils, disease and pest resistance changed the structure and the performance of ryegrass populations introduced to New Zealand. Two ryegrass populations adapted to New Zealand environments have been identified as ecotypes (Levy and Davies 1929, 1930; Cumberland and Honore 1970). The Hawke's Bay/Poverty Bay and Mangere ecotypes are often used by plant breeders as a source of parent material for the creation of new ryegrass cultivars. 'Ellett' and 'Grasslands Ruanui', the ryegrass cultivars which were chosen for this study, originated from the Mangere and Hawke's Bay ecotypes, respectively.

2.4.1 'Grasslands Ruanui' selection

From 1870 to 1920, superior perennial ryegrass populations were found in the Hawke's Bay and Poverty Bay regions, where soil and climate particularly suited perennial ryegrass. In succeeding years, a new line of ryegrass varieties were developed by selecting within the improved populations that had been identified by the Grasslands Division, DSIR, Palmerston North (Easton 1983). A perennial ryegrass originating from the Hawke's Bay ecotype, which was selected for increased leaf production, persistence and resistance to crown rust (*Puccinia coronata*), was first certified in 1936 and was named 'Grasslands Ruanui' in 1964 (Corkill et al., 1981; Easton 1983). In 1964 seven clones were chosen as the parents of 'Grasslands Ruanui' ryegrass after a recurrent selection programme over at least 30 years. It was reported in the late 1950's that 'Grasslands Ruanui' had high levels of endophyte. However, 'Grasslands Ruanui' seed has since lost its endophyte because of storage under inappropriate temperature and humidity conditions (Easton 1983; Fletcher et al., 1996).

2.4.2 'Ellett' selection

A ryegrass population in the Mangere area in the south Auckland region of New Zealand, showing superior summer growth to other pastures in this district, was identified by the farmer, Mr Trevor Ellett. The ryegrass in this pre-1900 sown pasture had undergone natural selection over time, on a naturally fertile soil which was prone to drought. During the 1950's and 60's, it was common practice to add annual (or biennial) Italian ryegrass (*Lolium multiflorum*) to the seeds mixture to provide extra winter feed (Duder 1976). The origin of the pasture mixture sown on Mr Ellett's farm was unknown (Duder 1976). Ryegrass tillers were taken from Mr Ellett's property in 1962 and the production of this ryegrass type under dry conditions, its resistance to crown rust and palatability were measured at Palmerston North, New Zealand (Easton 1983). The plants in this population were more erect with larger leaves and tillers than were 'Grasslands Ruanui' plants (Corkill et al., 1981; Easton 1983).

In the early 1970's, Trevor Ellett offered Arthur Yates and Company Ltd the opportunity to harvest seed from his farm, capitalising on the natural selection that had taken place. Seeds off plants harvested from the silage paddock on Mr Ellett's farm (Duder 1976) were multiplied and marketed as 'Mangere ryegrass'. However, in 1980, following the introduction of a formal quality assurance programme, the name was changed to 'Ellett' perennial ryegrass. A new ryegrass cultivar, bred by the Grasslands Division, DSIR, Palmerston North from the 1962 selection from the Mangere ecotype was certified and released as 'Grasslands Nui' in 1975. It was not realised at the time that 'Ellett' was the only variety with a consistently high level of infection with the endophyte (*Neotyphodium lolii*), conferring insect resistance. The relationship between the ryegrass endophyte and protection at the plant from insect attack, particularly from Argentine stem weevil (*Listronotus bonariensis*), was published in 1982 (Prestidge et al., 1982).

CHAPTER THREE

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PRODUCTIVITY OF 'ELLETT' AND 'GRASSLANDS RUANUI' SWARDS UNDER NITROGEN AND IRRIGATION TREATMENTS AND WHEN GRAZED BY DAIRY COWS

CHAPTER 3: PRODUCTIVITY OF 'ELLETT' AND 'GRASSLANDS RUANUI' SWARDS UNDER NITROGEN AND IRRIGATION TREATMENTS AND WHEN GRAZED BY DAIRY COWS

Some results from the first year of this field experiment were published in the **Proceedings of the New Zealand Grasslands Association 59: 117-124** (Appendix 3.1).

3.1 Introduction

Ecotypes that have evolved from mixed ryegrass populations, subjected over long periods to particular conditions of climate, soil and management are often used by plant breeders as sources of parent material for the breeding of new ryegrass cultivars. Up until 1975, an ecotype from Hawke's Bay (initially released as 'New Zealand certified' perennial ryegrass in 1936 and renamed 'Grasslands Ruanui' in 1964) was the most widely used in New Zealand. Since 1975, the Mangere ecotype from south Auckland, which is geographically quite distinct from the Hawke's Bay ecotype, has been extensively used. 'Ellett' and 'Grasslands Nui' were the first perennial ryegrasses from the Mangere ecotype to be commercialised and are considered to be the first of the 'modern' ryegrasses.

'Ellett' plants are more erect with larger leaves and upright tillers compared with plants of 'Grasslands Ruanui' (Corkill et al., 1981; Goold 1982; Easton 1983). 'Ellett' was higher yielding than 'Grasslands Ruanui' under most conditions (Hunt and Easton 1989), and was more resistant to summer drought and had a faster response to the autumn rains (Corkill et al., 1981). Goold (1982) reported that 'Ellett' produced 16 to 28% more total dry matter than 'Grasslands Ruanui' on peat soils when 21 cuts were made from September 1976 to September 1979. 'Ellett' outyielded 'Grasslands Ruanui'

(Longhurst et al., 1999) because of higher winter (Corkill et al., 1981) and autumn (Goold 1982; Easton 1983) production leading to reduced weed, clover and other grass production (Cumberland and Honore 1970; Goold 1982). Thus, in the 1980's, 'Ellett' and 'Grasslands Nui' became the recommended improved cultivars for dairying regions. However, the superior summer/autumn performance of 'Ellett' over 'Grasslands Ruanui,' recorded in trials before 1982 has now been partly attributed to 'Ellett' having consistently higher endophyte levels, conferring insect resistance (Hunt and Easton 1989; Thom et al., 1998a). However, a recent 3 year study in the central Waikato region showed that 'modern' ryegrasses had reduced persistence over time under intensive dairy cow grazing (Thom et al., 1998a).

Rotationally grazed dairy pastures containing 'modern' ryegrasses have low tiller density in summer because of poor survival of vegetative tillers (L'Huillier 1987). Animal treading (Edmond 1966), drought (Korte and Chu 1983), nutrient stress and hard grazing (Brougham 1960, 1961; Harris and Brown 1971; Hughes and Jackson 1974) were most often responsible for pasture deterioration under intensive dairying. Ryegrass growth during summer is enhanced by nitrogen application on pastures, which consistently increased tiller density (Harris et al., 1996). The utilisation of nitrogen fertiliser by perennial ryegrass can be enhanced by irrigation, when this was sufficient to account for soil water deficits at the time of cutting or grazing and application of fertiliser (Garwood et al., 1980). During dry periods, irrigation has also increased ryegrass growth (Hopewell 1960; Holmes and Wilson 1987). However, some studies showed that irrigation did not improve the survival or greatly increase the yield of 'modern' ryegrass cultivars in the Waikato (Thom et al., 1986b; Thomson 1996). Grazing management (Harris 1978) and seasonal weather differences (Thomson 1996) could possibly influence the effect of irrigation on pasture growth. However, there are few published data describing agronomic or ecological comparisons between 'Ellett', the first of the 'modern' ryegrass cultivars, and its predecessor, 'Grasslands Ruanui'.

3.2 Objectives

A field experiment was carried out with the objective of comparing the productivity and persistence of 'Ellett' and 'Grasslands Ruanui' ryegrasses under different nitrogen and irrigation treatments, and when intensively grazed by dairy cows. Grass productivity was measured as herbage accumulation, and a study of tiller dynamics (see Chapter 5) provided a framework for the assessment of persistence. The productivity of 'Ellett' and 'Grasslands Ruanui' ryegrasses in swards is reported in this chapter.

3.3 Materials and methods

3.3.1 Site

The trial was located at the Dairying Research Corporation, Hamilton, New Zealand (latitude 37° 47' south, longitude 175° 19' east, altitude 40 m a.s.l). The region is classified as warm temperate with an average air temperature of 13°C and an annual rainfall of 1276 mm (Fig. 3.1). The soil was a fertile but poorly drained, Te Kowhai clay loam (Typic Ortho Gley or Typic Ochraqual) (Singleton 1991; Hewitt 1998), previously supporting intensive dairying and receiving regular maintenance dressings of potassic superphosphate. Soil pH in April 1996 was 5.8.

3.3.2 Trial design and treatments

The trial design was a 2 × 2 × 2 split-plot factorial with main (6 × 12 m) plots of the endophyte-free perennial ryegrass cultivars 'Ellett' and 'Grasslands Ruanui' randomly arranged in four blocks (Fig. 3.2). The ryegrass cultivars were direct-drilled (10 kg/ha) on 24 April 1996, following spraying with 1.44 kg a.i. of glyphosate (Roundup® herbicide, 36 % glyphosate) plus Pulse penetrant.

Nitrogen fertiliser was applied as urea (30 kg N/ha) to half of the plot area (randomly chosen) following each grazing, with a total of 240 kg N/ha applied from September 1996 to May 1997, and 180 kg N/ha from October 1997 to April 1998 (Table 3.1). Muriate of potash was applied on 26 October 1997 at 100 kg/ha (50 kg K/ha).

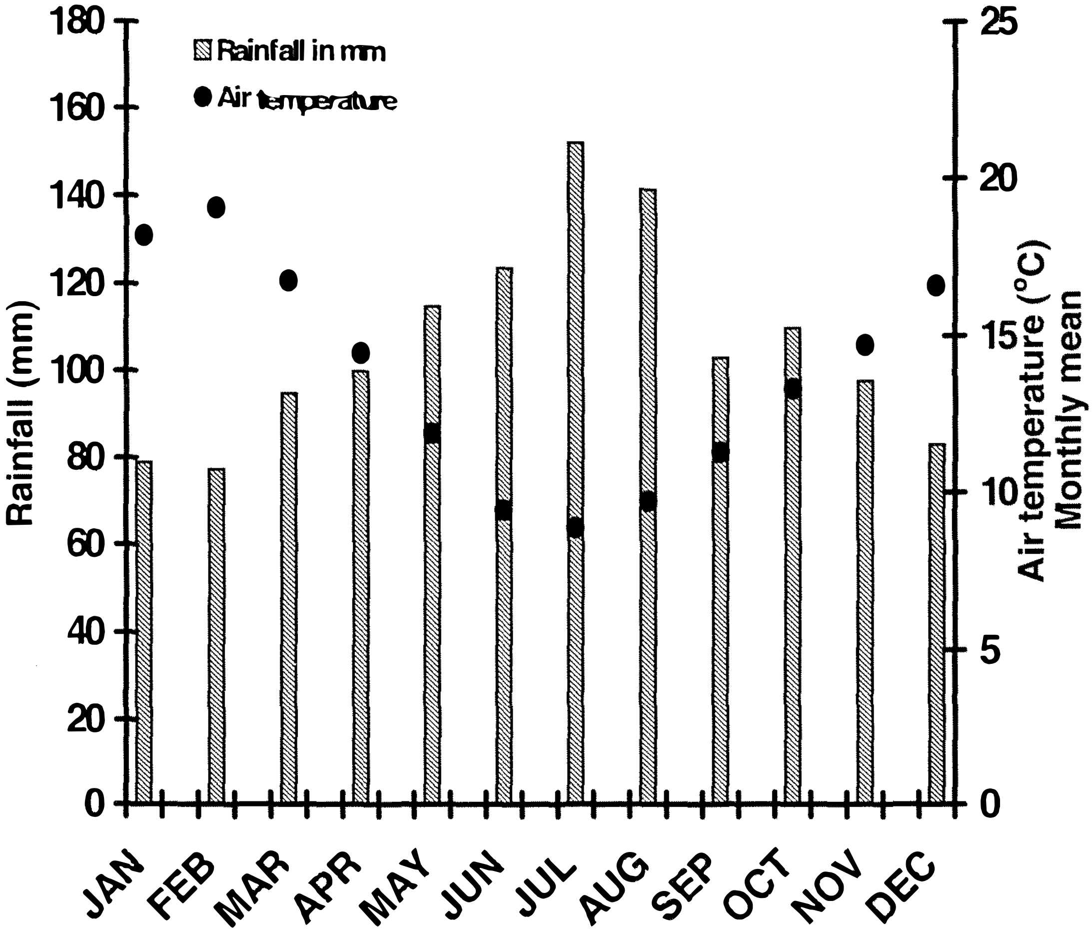


Figure 3.1. Rainfall distribution and mean monthly air temperature averaged over the last 10 years. Data recorded at the Ruakura Climatological Station, 2 km north-west of the trial site.

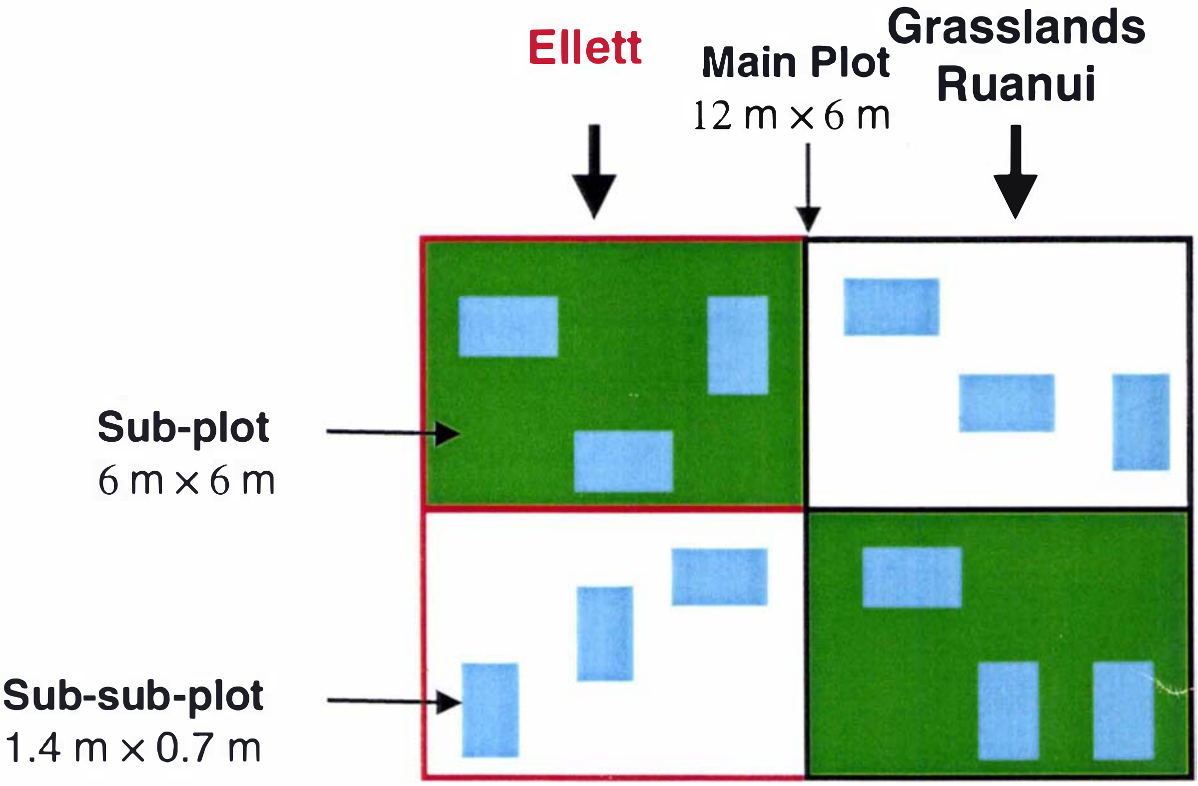


Figure 3.2. Representation of one replicate or block of the trial design. Nitrogen fertiliser was applied to green areas (sub-plot) and water was applied to blue areas (sub-sub-plot). White areas received no irrigation and no nitrogen. The trial had four replicates.

Table 3.1. Grazing dates and schedule of insecticide, nitrogen and irrigation water applications over spring, summer and autumn, with amounts of water applied at each date.

Date				
Grazing	**Insecticide**	**Nitrogen** [a]	**Irrigation**	**Amount of water applied in mm per sub-sub-plot**
24-Sep-96	26-Sep-96	25-Sep-96		
24-Oct-96		25-Oct-96		
21-Nov-96	29-Nov-96	22-Nov-96	26-Nov-96	22
21-Dec-96		24-Dec-96	11-Dec-96	27
			24-Dec-96	34
17-Jan-97		21-Jan-97	10-Jan-97	23
			16-Jan-97	24
			21-Jan-97	20
			03-Feb-97	36
28-Feb-97			11-Feb-97	27
			14-Feb-97	19
			25-Feb-97	23
	18-Mar-97	10-Mar-97	17-Mar-97	23
09-Apr-97		11-Apr-97	27-Mar-97	22
20-May-97		23-May-97		
30-Jul-97				
06-Oct-97	09-Oct-97	09-Oct-97		
07-Nov-97		11-Nov-97	27-Nov-97	26
11-Dec-97		12-Dec-97	16-Dec-97	29
			24-Dec-97	36
			30-Dec-97	23
20-Jan-98		23-Jan-98	05-Jan-98	30
			08-Jan-98	25
			22-Jan-98	13
			30-Jan-98	32
			02-Feb-98	25
			09-Feb-98	29
			16-Feb-98	27
			20-Feb-98	23
15-Mar-98		17-Mar-98		
07-Apr-98		16-Apr-98		

Colour code : **Spring**; **Summer**; **Autumn**; **Winter**.

[a] 30 kg N/ha at each date.

Triple superphosphate was applied on 23 May 1997 at 375 kg/ha (79 kg P, 4 kg S). Insecticide (Miral 5G, 0.5 kg of isazophos/ha) was applied after four grazings from September 1996 to October 1997 to control Argentine stem weevil (*Listronotus bonariensis*) (Table 3.1). The trial was sprayed with a herbicide (2,4 D B at 1.5 litres/ha) on 10 September 1997 to control weeds, and another more selective herbicide (Nortron 500 SC) was used on 15 April 1997 to control *Poa annua* and to reduce competition with white clover.

In addition, sub-sub-plots (three 0.98 m^2 randomly located plots within each sub-plot) were irrigated from November 1996 to March 1997, and from November 1997 to February 1998 (Table 3.1), using a metal frame to prevent run-off and reduce subsurface water movement (Plate 3.1). Frames were inserted 2-3 cm into the soil on the plot margins and were removed after the applied water had soaked into the soil. Irrigation took place when the moisture level was between field capacity and wilting point. Thom (1984) reported a soil water content of 60 % (dry weight basis) at field capacity and 28 % at wilting point for a Te Kowhai clay loam supporting a ryegrass/white clover pasture on the same farm. Soil water content was monitored weekly in sub-sub-plots in spring (from November) and autumn and every second day in summer, using a Time Domain Reflectometer (TDR) with probes inserted to 150 mm. The difference between the soil water content at field capacity and the average TDR water content was used to estimate the irrigation water needed to return the soil to near field capacity. This value was converted to the irrigation requirement in millimetres by multiplying by the TDR probe length (150 mm) and then to litres to be added to each sub-sub-plot, by multiplying by the plot area (0.98 m^2). The water status of irrigated and non-irrigated areas located between replicates were also monitored using probes permanently installed to 15 cm depth. In spring 1996, summer 1996/97, autumn 1997, spring 1997 and summer 1997/98 22, 233, 45, 26 and 292 mm of irrigation water, respectively, were applied (Table 3.1).

Dairy cows, at a farm stocking rate of 3.2 cows/ha, grazed the trial for the first time on 24 September 1996, and at intervals of 29 days (spring 1996), 33 days (summer 1996/97), 39 days (autumn 1997), 70 days (winter 1997), 33 days (spring 1997), 47 days (summer 1997/98) and 23 days during autumn 1998. The trial was grazed by a mixed herd of Friesian and Jersey dairy cows (Plate 3.2) when pasture cover ranged

Plate 3.1. The author applying water to a sub-sub-plot within an 'Ellett' ryegrass main plot during January 1997.

from 1700 to 3000 kg dry matter per hectare (DM/ha). Cows were taken off the trial after one day of grazing or when the post-grazing pasture residual was 1400 kg DM/ha as estimated by the farm manager.

3.3.3 Sward measurements

3.3.3.1 Herbage mass

Pre- and post-grazing herbage mass on each sub-plot and sub-sub-plot were estimated by taking 40 readings with a calibrated pasture probe (Plate 3.3) in the former and 5 readings in the latter. An air reading was taken with the probe before and after the collection of each data set. Pre- and post-grazing probe readings were converted to herbage mass in kg DM/ha according to the seasonal calibration equations (Table 3.2) of L'Huillier and Thomson (1988).

3.3.3.2 Ryegrass tiller density

Two fixed steel frames (20 x 5 cm) were positioned at random across drill rows within each sub-plot and another in two of the three sub-sub-plots. The number of perennial ryegrass tillers in each fixed frame was counted before and after each grazing to estimate the percentage of tillers lost or 'pulled' during grazing. Only tillers with one or more fully emerged leaf were counted. Different plastic circular frames were used for the tiller dynamics study (Chapter 5).

3.3.3.3 Ryegrass tiller weight

A sample of 100 tillers from separate plants, were located at random positions on drill lines in all sub-plot and sub-sub-plots, and were cut to ground level before each grazing. Tillers with less than one fully emerged leaf were not sampled. The tillers were oven dried for 36 hours at 95°C before weighing.

3.3.3.4 Botanical composition

The frequency of occurrence of perennial ryegrass, other grasses, white clover, weeds, dead material and bare ground were estimated using point analysis (Radcliffe and Mountier 1964) (Plate 3.4). The point analysis frame was made up of 10 spring-loaded needles suspended 50 to 100 mm above the sward surface. Each needle was independently depressed and the number of times each plant species was touched by the

Plate 3.2. Jersey and Friesian cows grazing the field trial in April 1997. Farm stocking rate was 3.2 cows per hectare.

Plate 3.3. DRC technician estimating the post-grazing herbage mass of pasture with a capacitance probe in March 1998.

Table 3.2. Seasonal calibration equations used to convert capacitance probe readings of pasture yield to kg dry matter per hectare (L'Huillier and Thomson 1988).

Season	Equation
Winter-early spring (before stem growth) June - mid October	$9.9 \times \text{CMR}^{(\dagger)} + 600$
Late spring-early summer (during stem growth) mid October - mid January	$9.5 \times \text{CMR} + 1200$
Mid Summer mid January – February	$13.8 \times \text{CMR} + 1240$
Early Autumn (before autumn rain) March – mid April	$12.7 \times \text{CMR} + 1020$
Late Autumn (after rain starts) Mid April - May	$10.4 \times \text{CMR} + 990$

† Corrected Meter Reading
CMR = average air reading – (probe reading/number of readings)

Plate 3.4. Estimation of the frequency (%) in pasture of perennial ryegrass, other grasses, white clover, weeds, dead material and bare ground using the point analysis method of Radcliffe and Mountier (1964).

needle point as it passed through the sward was recorded (bare ground was recorded if no herbage was touched). Data were collected from 3 random positions of the point analysis frame within each sub-plot and one random position within each sub-sub-plot. Botanical composition (% frequency of each species) was assessed every two months from September 1996 to March 1997 and from November 1997 to March 1998.

3.3.4 Data analysis

3.3.4.1 Herbage accumulation

Herbage accumulation between each grazing (1) and the total herbage accumulation over the experimental period (2) were calculated as follows:

$$\text{HA (kg DM/ha)} = (\text{HMF}_i - \text{HMI}_i) \qquad (1)$$

$$\text{Total HA (kg DM/ha)} = \sum_{i=1}^{n} (\text{HMF}_i - \text{HMI}_i) \qquad (2)$$

where:

HA = herbage accumulation; HMF = herbage mass before a grazing; HMI = herbage mass after the previous grazing; i = 1...n denotes successive regrowth cycles between grazings (Table 3.1) over the 2 year experiment.

3.3.4.2 Assessment of ryegrass pulling

Post-grazing tiller densities were compared with pre-grazing tiller densities to estimate tiller losses during grazings. Ryegrass pulling, expressed as the percentage of ryegrass tillers pulled (removed by cows during grazings) was calculated as follows:

$$\text{Pulling (\%)} = (\text{TDF} - \text{TDI})/\text{TDF} \times 100$$

where:

TDI = tiller density post-grazing; TDF = tiller density pre-grazing.

3.3.4.3 Statistical analysis

The data were analysed as a split-split plot ANOVA using the model in Genstat 5 (Rothamsted Experimental Station). Cultivar was the main plot, nitrogen the sub-plot and irrigation the sub-sub-plot. Sub-sample measurements were averaged to provide the plot mean for the analysis. A repeated measure analysis in SAS (1989, version 6) was used to compare data between seasons. No data transformations were necessary, except for some botanical data, which were square-root-transformed before analysis.

The model used was:

$$y_{jklm}=\mu+b_j+c_k+e''_{jk}+n_l+(cn)_{kl}+e'_{jkl}+i_m+(ci)_{kl}+(ni)_{lm}+(cni)_{klm}+e_{jklm}.$$

where:

y_{jklm} is the observation on the j^{th} replicate, on the k^{th} cultivar, on the l^{th} nitrogen level and the m^{th} irrigation level

μ is the overall mean

b_j is the effect of the j^{th} replicate, $j=1,2,3,4$

c_k is the effect of the k^{th} cultivar, $k=1,2$

e''_{jk} is the error term for the cultivar main plot stratum

n_l is the effect of the l^{th} nitrogen treatment, $l=1,2$

$(cn)_{kl}$ is the cultivar by nitrogen interaction term

e'_{jkl} is the error term for the nitrogen sub-plot stratum

i_m is the effect of the m^{th} irrigation treatment, $m=1,2$

$(ci)_{kl}$ is the cultivar by irrigation interaction term

$(ni)_{lm}$ is the nitrogen by irrigation interaction term

$(cni)_{klm}$ is the cultivar by nitrogen by irrigation interaction term

e_{jklm} is the residual error term

3.4 Results

3.4.1 Climate

The annual cycle is defined as from April to March. Weather data obtained from the Ruakura Climatological Station, 2 km from the trial site, showed that total rainfall during the first year (1996/97) was 7 % higher than the 10 year average (1369 mm vs 1276 mm), whereas the second year (1997/98) was 25 % below the 10 year average (958 mm vs 1276 mm). The seasonal rainfall pattern also varied from the 10 year average and in each of the two years of the trial (Fig. 3.3).

Dry months occurred in each of the two summers (December to February) of the trial (Fig. 3.3). Summer 1996/97 was the most extreme with no rain for 23 days in January and 20 days in February 1997 with total rainfall of only 27 and 36 mm, respectively. The number of rain days during the second summer (1997/98) was similar to the first (1996/97) but total rainfall in February 1998 was 168 % higher than in February 1997. Total summer rainfall was 28% and 18% below average (239 mm) for 1996/97 and 1997/98, respectively. The monthly average air temperature in December, January and February was close to or slightly below the 10 year average during summer 1996/97 (Fig. 3.4). However, air temperature in December 1997 was 2.2 °C (13.5 vs 15.7 °C) and 3.1 °C (13.5 vs 16.6 °C) lower than in December 1996 and the 10 year average, respectively. February was the warmest month in each year with the maximum monthly air temperature averaging 24.6 and 26.8 °C in 1997 and 1998, respectively.

Autumn 1996 (April to May) and 1997 (March to May) were wetter than average (323 vs 215 mm; 327 vs 310 mm) but the beginning of autumn 1998 (March) was slightly below average (86.4 vs 94.8 mm). Winter 1997 (June to August) was drier than average (239 vs 417 mm) whereas rainfall in winter 1996 was similar to average (419 vs 417 mm). Total rainfall in spring (September to November) 1996 and 1997 was 6% (292 vs 310 mm) and 12 % (273 vs 310 mm) lower than the 10 year average, since rainfall was low in October 1996 (67 mm) and 1997 (71 mm) compared with the average (110 mm). Winter 1998 was cold with 47 frosts (grass minimum temperature < -1 °C) compared to 26 in winter 1997 and the 10 year average of 29. There were 9 (1996) and 12 (1997) heavy frosts (< -5 °C) over the winters. July was the coldest

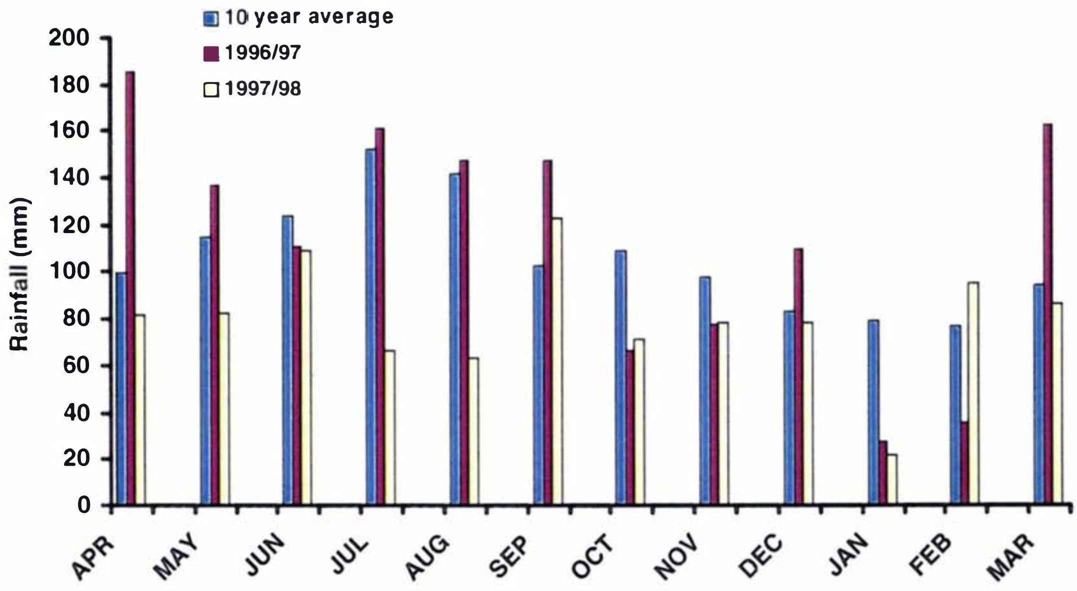


Figure 3.3. Rainfall distribution for the 2 years (1996/97, 1997/98) of the experiment compared with the 10 year average.

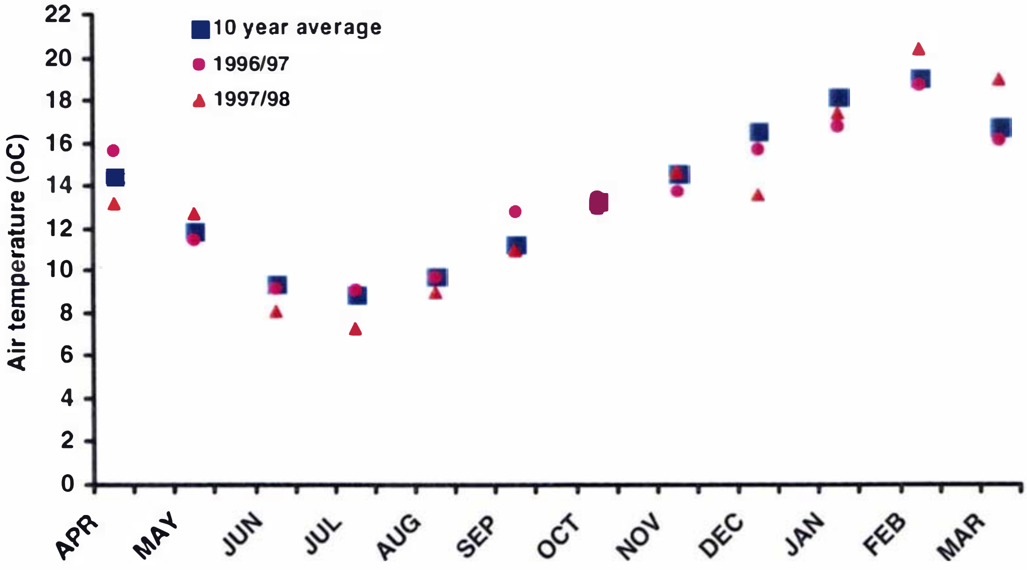


Figure 3.4. Monthly air temperature for the 2 years (1996/97, 1997/98) of the experiment compared with the 10 year average.

month with the maximum air temperature averaging 13.5 °C and 13.2 °C for 1996 and 1997, respectively.

3.4.2 Herbage accumulation and pre-grazing herbage mass

3.4.2.1 Herbage accumulation

Total herbage accumulation over the whole trial period for 'Ellett' was 13 % greater than 'Grasslands Ruanui' ($P<0.084$). 'Ellett' outyielded 'Grasslands Ruanui' by 20 % (2168 vs 1806 kg DM/ha, SED=79*), 18 % (3706 vs 3151 kg DM/ha, SED=31***) and 11 % (2082 vs 1882 kg DM/ha, SED=42*) over summer 1996/97, spring 1997 and summer 1997/98, respectively (Fig. 3.5).

Ryegrass herbage accumulation was the highest on average in spring (3004 kg DM/ha) and the lowest in winter (428 kg DM/ha) ($P<0.05$), regardless of the treatments imposed. Differences in seasonal herbage accumulation between the first (1996/97) and the second year (1997/98) of the trial were not significant, except for spring when herbage accumulation was 25 % higher in 1997 than in 1996 ($P<0.05$).

There were no significant interactions between cultivar and nitrogen or cultivar and irrigation treatments (Fig. 3.7, Fig. 3.9). Total herbage accumulation was increased by 30 % with nitrogen compared to the no nitrogen treatment (Fig. 3.6). Ryegrass herbage accumulation in response to nitrogen fertiliser was strong and consistent for each season except in spring 1996 following the establishment ($P<0.06$). Water applied in late spring (November) and autumn (March) 1997 (Table 3.3) did not have a significant effect on ryegrass herbage accumulation for either cultivar. Herbage accumulation increased by 25 % ($P<0.05$) and 14 % ($P<0.001$) during summer 1996/97 and 1997/98, and 12 % in autumn 1998 ($P<0.05$) in response to irrigation (Fig. 3.8). However, irrigation decreased herbage accumulation by 18.5 % during the first autumn (1997) compared to the no irrigation treatment ($P<0.05$). The irrigation response was greatest in February 1997 and January 1998 when ryegrass yield increased by 85 % (1110 vs 600 kg DM/ha, SED=114***) and 45 % (1082 vs 748 kg DM/ha, SED=87***), respectively. The autumn 1998 response was a carryover effect (Fig. 3.8), since no irrigation water was applied (Table 3.3).

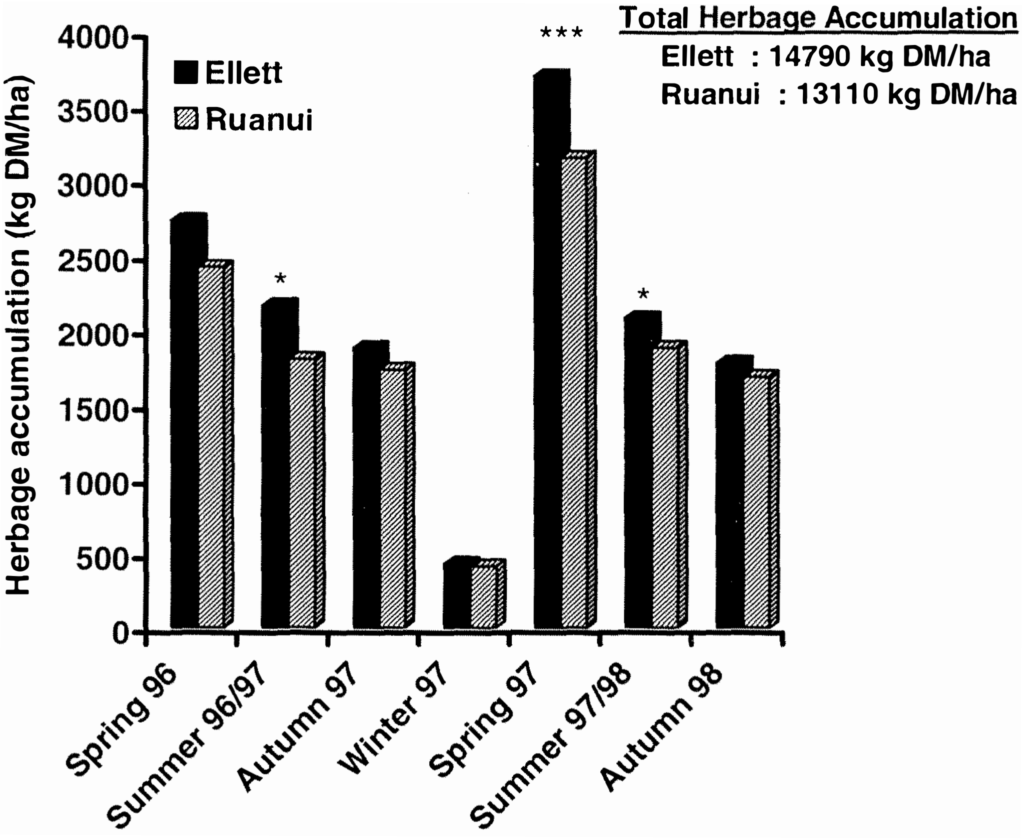


Figure 3.5. Herbage accumulation on 'Ellett' and 'Grasslands Ruanui' ryegrass swards over 2 years (spring 1996 to autumn 1998), across nitrogen and irrigation treatments.

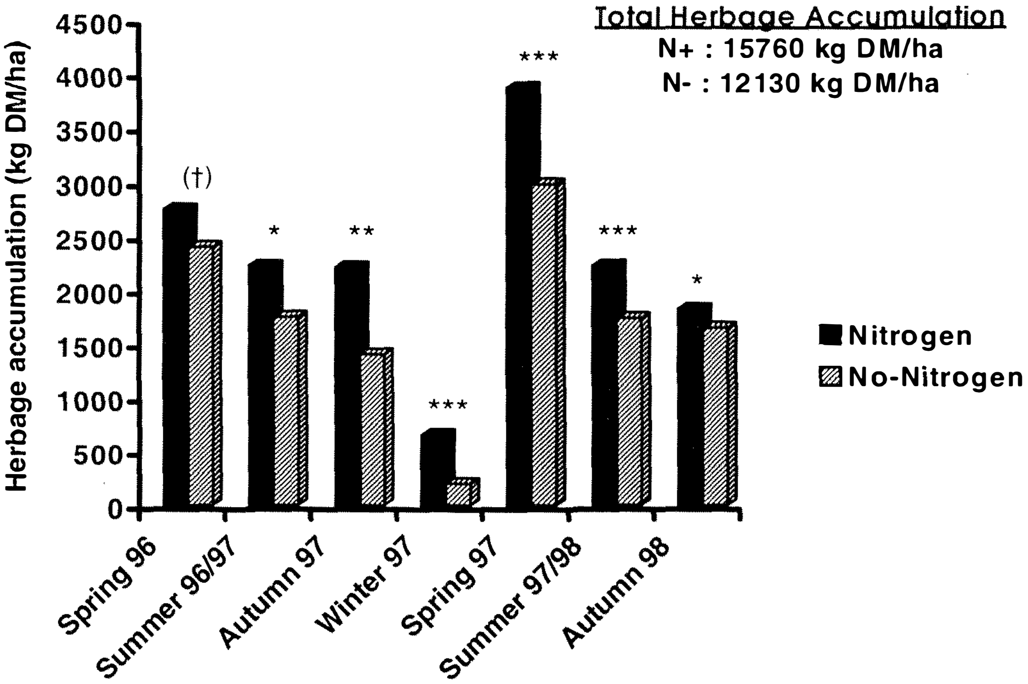


Figure 3.6. Main effect of nitrogen on herbage accumulation over the 2 years of the field trial.

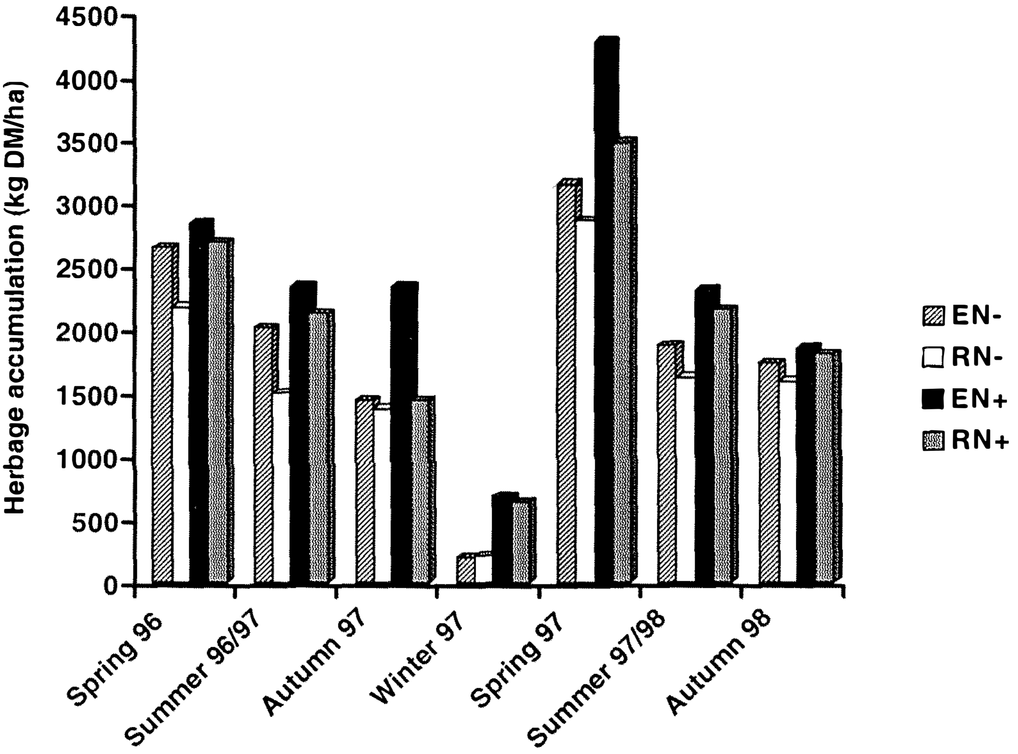


Figure 3.7. Effect of nitrogen on herbage accumulation of 'Ellett' and 'Grasslands Ruanui' ryegrass swards over 2 years of the field trial. Ruanui (RN+) and Ellett (EN+) with nitrogen; Ruanui (RN-) and Ellett (EN-) without nitrogen.

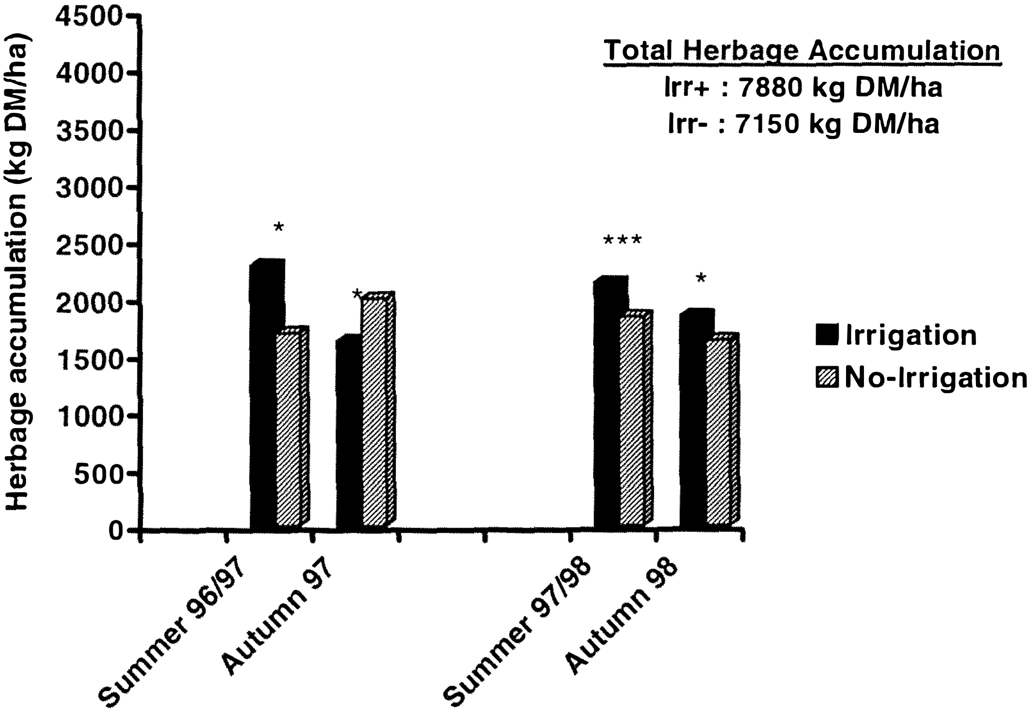


Figure 3.8. Main effect of irrigation on herbage accumulation over summer and autumn for the 2 years of the field trial.

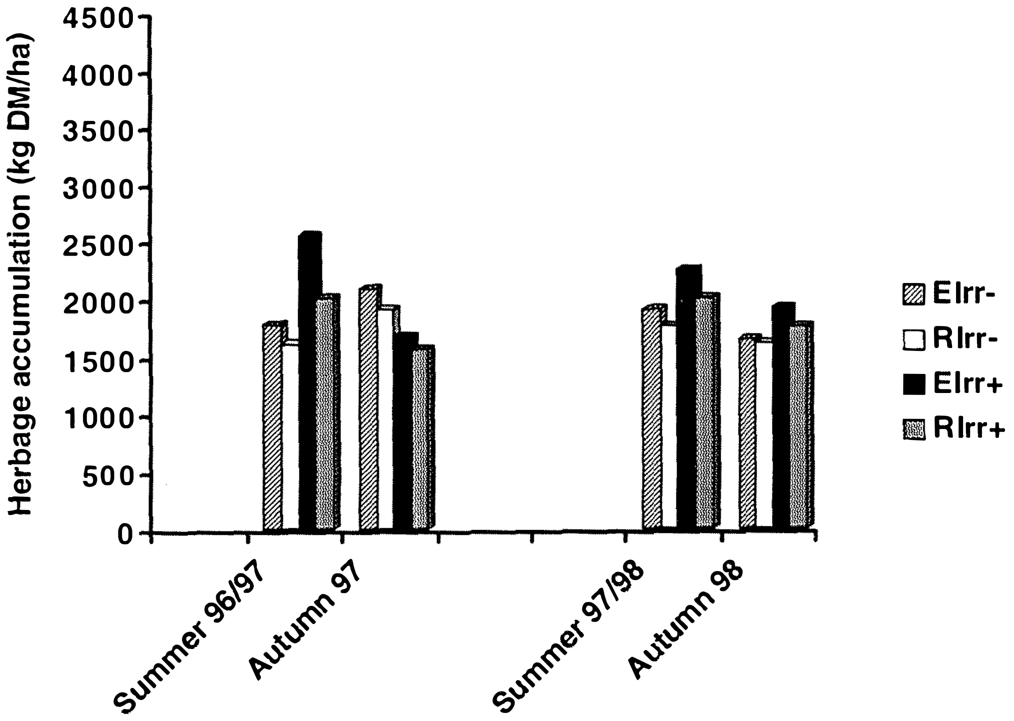


Figure 3.9. Effect of irrigation on herbage accumulation of 'Ellett' and 'Grasslands Ruanui' ryegrass over 2 years of the field trial. Ruanui (RIrr+) and Ellett (EIrr+) with irrigation; Ruanui (RIrr-) and Ellett (EIrr-) without irrigation.

3.4.2.2 Pre-grazing herbage mass

'Ellett' plots had a higher average pre-grazing herbage mass than did 'Grasslands Ruanui' over every season, but differences were only significant in spring 97 and summer 1997/98 (Table 3.4). Pre-grazing herbage mass response to nitrogen was strong and consistent for each season, but failed to reach significance in spring 96. Summer irrigation increased average pre-grazing herbage mass by 6% ($P<0.05$) and 4% ($P<0.01$) in 96/97 and 97/98 (Table 3.4). Average pre-grazing herbage mass was greater in non-irrigated than in irrigated plots in spring 96, autumn 97, winter 97 and spring 97 (Table 3.4). However, only 22 and 26 mm of water was applied in spring 96 and spring 97, respectively, and no irrigation water was applied in winter 97 (Table 3.3). There was no significant interactions between cultivar and nitrogen or cultivar and irrigation treatments.

3.4.3 Pre-grazing tiller density

'Ellett' swards had a lower pre-grazing tiller density than did 'Grasslands Ruanui' during each season, but differences between cultivars were not significant in spring 1997 and autumn 1998 ($P>0.10$) (Table 3.5). Pre-grazing ryegrass tiller density was lower in the first than the second year for each season ($P<0.05$). The lowest ryegrass tiller density was observed during spring of both years and the highest in the winter and summer of the second year of the trial. The main effect of nitrogen on pre-grazing tiller density was strong and consistent (Table 3.5), with a greater response to nitrogen by 'Grasslands Ruanui' than 'Ellett' as shown by a significant interaction between cultivar and nitrogen treatments from spring 1997 to autumn 1998 (Table 3.5). Irrigation had no significant effects on ryegrass pre-grazing tiller density. There was no significant interaction between cultivars and irrigation treatments.

3.4.4 Ryegrass pulling

No significant differences in ryegrass pulling were observed between 'Ellett' and 'Grasslands Ruanui' except in summer 1996/97 and autumn 1997. The average percentage removal of tillers by cows during summer grazings in 1996/97 was slightly higher for 'Ellett' than 'Grasslands Ruanui' (11 % vs 7 %, SED=1.49†). The greatest summer differences in tiller removal between 'Ellett' and 'Grasslands Ruanui' were observed in plots receiving nitrogen fertiliser and no irrigation (17 % vs 5 %,

Table 3.3. Comparison of the monthly rainfall with the amount of water applied per sub-sub-plot during 1996/97 and 1997/98.

	1996/97		**1997/98**	
Month	**Rainfall (mm)**	**Irrigation (mm)**	**Rainfall (mm)**	**Irrigation (mm)**
November	78	22	79	26
December	110	61	79	88
January	27	67	22	100
February	36	105	96	104
March	163	45	86	–
Total	414	300	362	318

Colour code : **Spring**; **Summer**; **Autumn**.

Table 3.4. Effects of nitrogen and irrigation on average pre-grazing herbage mass (kg DM/ha) of 'Ellett' and 'Grasslands Ruanui' ryegrass swards over different seasons.

	Season						
Treatments	**Spring 96**	**Summer 96/97**	**Autumn 97**	**Winter 97**	**Spring 97**	**Summer 97/98**	**Autumn 98**
Cultivars							
Ellett	3002	2540	2801	1749	2963	2702	2964
Ruanui	2867	2388	2638	1722	2736	2597	2938
SED[a]	195.4	105.1	127.3	106.3	20.0	18.9	87.2
Signif.[b]	NS	NS	NS	NS	***	*	NS
Nitrogen							
N+	3009	2553	2952	1975	3088	2781	3022
N-	2861	2375	2487	1495	2611	2518	2880
SED	97.4	54.2	92.9	42.4	59.8	44.3	34.3
Signif.	NS	*	***	***	***	***	**
Irrigation							
Irr+	2795	2537	2639	1575	2683	2704	2998
Irr-	3074	2391	2800	1896	3016	2595	2904
SED	63.2	67.0	74.1	35.7	57.5	30.8	46.4
Signif.	***	*	*	***	***	**	(†)

(†) P=0.067; * $P<0.05$; ** $P<0.01$; *** $P<0.001$; NS not significant;
[a] Standard error of the difference between pairs of means;
N+, N fertiliser; N- no N fertiliser;
Irr+, irrigation; Irr- no irrigation.
[b] Signif. = Significance

Table 3.5. Effects of nitrogen and irrigation on pre-grazing tiller density (tillers/m^2) of 'Ellett' and 'Grasslands Ruanui' ryegrass swards over different seasons.

	Season						
Treatments	**Spring 96**	**Summer 96/97**	**Autumn 97**	**Winter 97**	**Spring 97**	**Summer 97/98**	**Autumn 98**
Cultivars							
Ellett	5123	5895	7625	9703	7414	10413	8242
Ruanui	8170	9349	10980	13491	10223	14730	11116
SED[a]	370.4	1164.0	851.3	1536.6	1349.1	1095.4	1710.1
Signif.[b]	**	†	*	†	NS	*	NS
Nitrogen							
N+	7257	8814	12095	14297	10823	15009	12486
N-	6035	6431	6509	8897	6814	10133	6872
SED	628.5	888.1	1875.3	2195.1	915.3	1540.5	1039.7
Signif.	NS	*	*	*	**	*	**
Cultivar x N							
EN-	5025	5267	6181	8631	6691	10353	7572
EN+	5221	6523	9069	10775	8138	10472	8913
RN-	7046	7595	6838	9163	6938	9913	6172
RN+	9294	11104	15122	17819	13509	19547	16059
SED	729.5	1464.1	2059.4	2679.5	1630.3	1890.3	2001.4
Signif.	NS	NS	NS	NS	*	*	**
Irrigation							
Irr+	7154	8145	9148	11684	8966	14117	8542
Irr-	6139	7099	9456	11509	8672	11025	10816
SED	614.5	687.0	1687.2	2196.6	1407.5	1899.9	1778.6
Signif.	NS	NS	NS	NS	(†)	NS	NS

(†) $P<0.10$; * $P<0.05$; ** $P<0.01$; NS not significant; [a]Standard error of the difference between pairs of means; N+, N fertiliser, N- no N fertiliser; Irr+, irrigation; Irr- no irrigation. [b] Signif. = Significance.

SED=3.58*). Ryegrass pulling was higher in autumn 1997 for 'Ellett' when nitrogen fertiliser was applied than when it was not applied (16 % vs 5 %, SED=2.14*).

3.4.5 Ryegrass tiller weight

'Ellett' ryegrass consistently had a greater tiller dry weight than did 'Grasslands Ruanui', regardless of nitrogen and irrigation treatments (Table 3.6). On average, spring tiller weight was higher than in other seasons ($P<0.05$). Ryegrass tiller weight was usually higher with the addition of nitrogen fertiliser, but differences only reached significance in winter 1997 ($P<0.01$) and autumn 1998 ($P<0.05$) (Table 3.6). Irrigation generally had no effect on tiller weight except in autumn 1998 despite no water being applied (Table 3.3, 3.6). There were no significant interactions between cultivar and nitrogen or cultivar and irrigation treatments.

3.4.6 Botanical composition

The average ryegrass frequency was the lowest in spring with a wide range (28 % to 59 %) across cultivar, nitrogen and irrigation treatments. No differences in frequency were detected between ryegrass cultivars except in spring 1996 when 'Grasslands Ruanui' plots had a higher frequency of dead material than 'Ellett' (22 % vs 18 %, SED=0.22***) (Appendix 3.2).

Perennial ryegrass remained the dominant sward species over the two years of the field experiment (Fig. 3.10 and 3.11). There were no significant interactions between cultivar and nitrogen or cultivar and irrigation treatments. Ryegrass frequency was greater in the nitrogen treated than in the untreated plots from summer 1996/97 through to autumn 1998 ($P<0.05$). White clover was only present from summer 1997/98 to autumn 1998, and tended to have a frequency inversely related to that of ryegrass. The nitrogen treated plots, which maintained the most ryegrass, had lowest frequency of white clover ($P<0.05$) (Fig. 3.10b). As for white clover, the frequency of dead material was lower in nitrogen treated than in the untreated plots in spring 1996 (18 % vs 22 %, SED=1.23*) and 1997 (17 % vs 25 %, SED=1.72**). Hits on *Poa* were the highest in spring for both years and when nitrogen fertiliser was applied ($P<0.05$). Weed content in the sward was the highest in autumn 1997. Nitrogen fertiliser significantly reduced the weed content of the plots in summer 1996/97 ($P<0.05$).

Table 3.6. Effects of nitrogen and irrigation on tiller dry weight (mg) of 'Ellett' and 'Grasslands Ruanui' ryegrass over different seasons.

	Season						
Treatments	**Spring 96**	**Summer 96/97**	**Autumn 97**	**Winter 97**	**Spring 97**	**Summer 97/98**	**Autumn 98**
Cultivars							
Ellett	88.2	59.6	40.6	48.9	85.6	54.9	37.9
Ruanui	54.9	41.9	26.3	37.9	68.3	41.4	29.9
SED[a]	4.70	5.77	1.12	3.66	2.94	1.18	2.86
Signif.[b]	**	(†)	***	(†)	**	**	(†)
Nitrogen							
N+	73.0	51.0	33.4	49.8	80.5	49.3	37.9
N-	70.1	50.6	33.4	37.0	73.4	46.9	30.0
SED	7.16	1.98	1.25	2.90	5.49	2.20	2.68
Signif.	NS	NS	NS	**	NS	NS	*
Irrigation							
Irr+	68.3	49.4	32.6	41.3	76.1	46.6	35.7
Irr-	74.8	52.2	34.4	45.6	77.8	49.6	32.1
SED	3.57	2.48	1.49	2.05	5.06	1.78	1.50
Signif.	(†)	NS	NS	(†)	NS	NS	*

(†) P=0.057; * P<0.05; ** P<0.01; *** P<0.001; NS not significant;

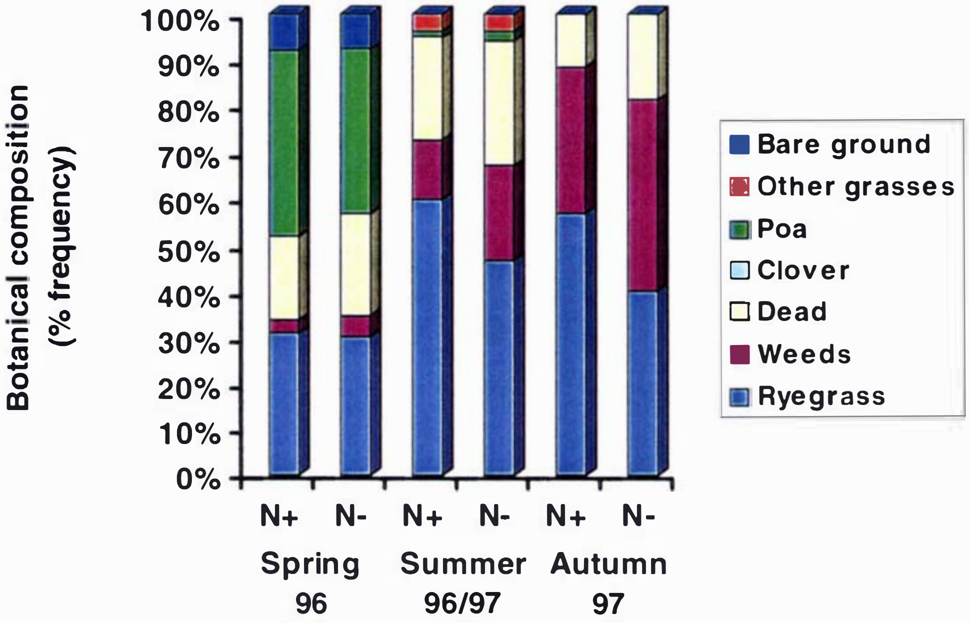
[a] Standard error of the difference between pairs of means;

N+, N fertiliser, N- no N fertiliser;

Irr+, irrigation; Irr- no irrigation.

[b] Signif. = Significance

(a)



(b)

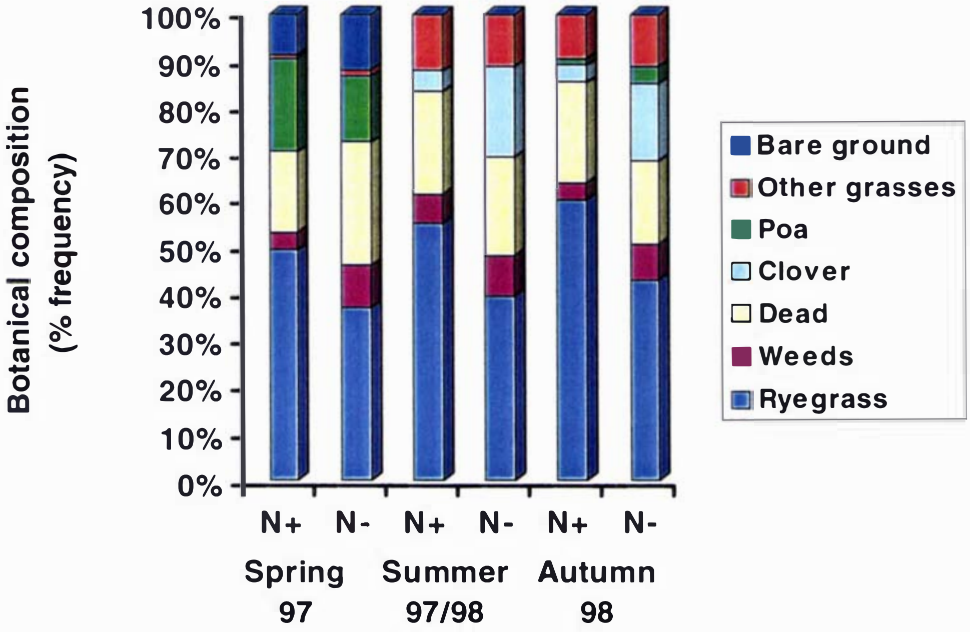
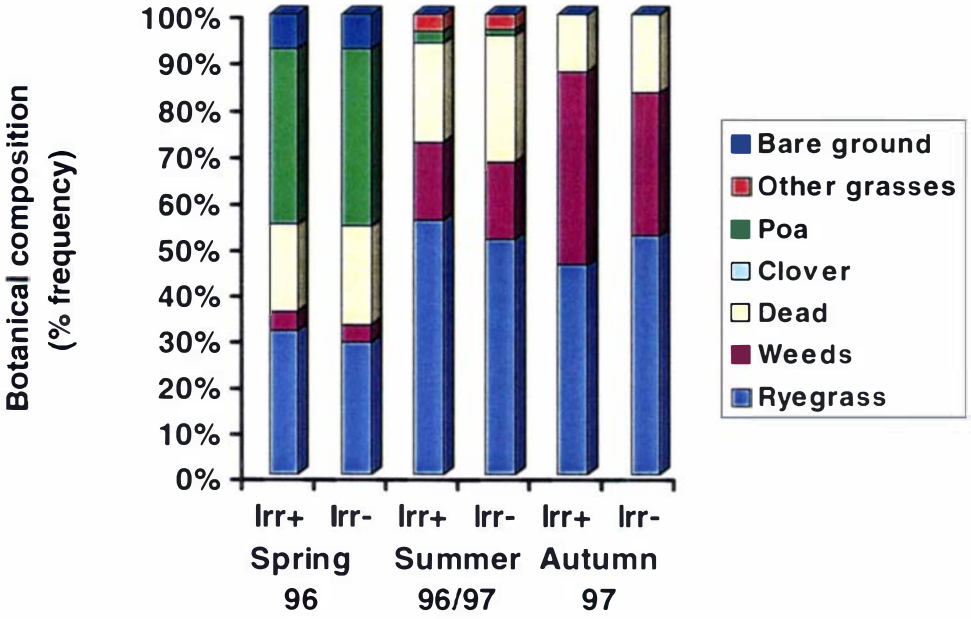


Figure 3.10. Effect of nitrogen (N) fertiliser on the botanical composition of the swards in (a) the first and (b) the second year of the trial.

(a)



(b)

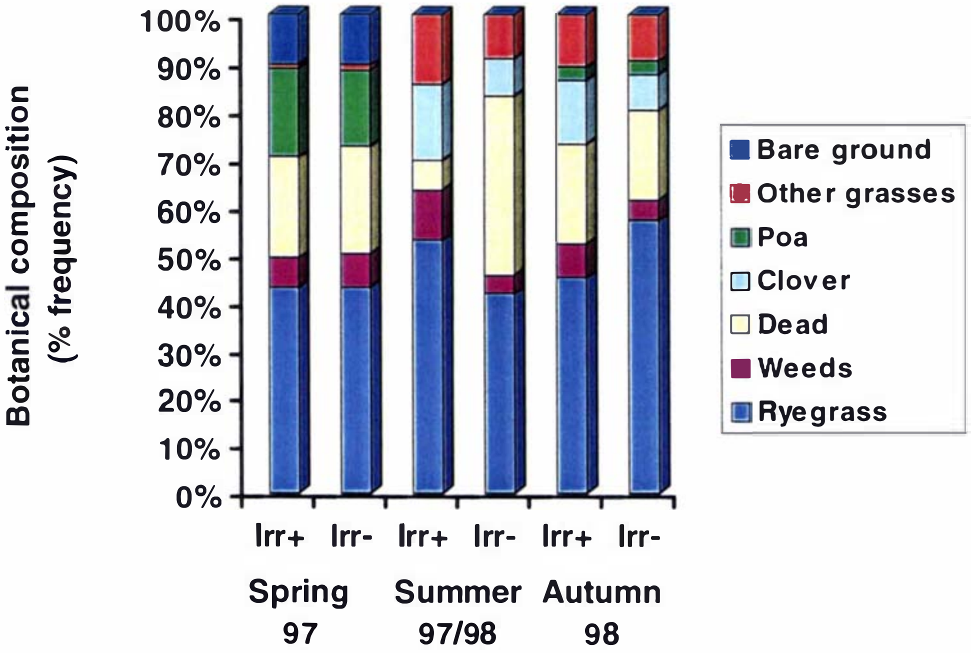


Figure 3.11. Effect of irrigation (Irr) on the botanical composition of the sward in (a) the first and (b) the second year of the trial.

The frequency of ryegrass in both summers and white clover in summer 1997/98 and autumn 1998, was greater in irrigated than in non-irrigated plots ($P<0.05$) (Fig. 3.11a, b). Irrigated plots had a different botanical composition over the second summer (1997/98) compared with the first (1996/97), with a lower frequency of dead material (6 % vs 21 %) and ryegrass (50 % vs 54 %) and a higher content of white clover (15 % vs 0 %), weeds (10 % vs 16 %) and others grasses (14 % vs 4 %) ($P<0.05$) (Fig. 3.11a, b). Irrigated plots had a higher frequency of ryegrass (50 % vs 39 %, SED=2.63***), white clover (15 % vs 7 %, SED=2.29**) and other grasses (14 % vs 9 %, SED=2.29*) and a lower frequency of dead material (6 % vs 35 %, SED=2.83***) during the second summer than did the non-irrigated plots (Fig. 3.11b).

The frequency of dead material was also lower, and the frequency of weeds higher, in irrigated compared with non-irrigated plots in autumn 1997 (11 % vs 16 %, SED=1.52** and 38 % vs 28 %, SED=3.02**, respectively).

3.5 Discussion

3.5.1 Seasonal growth of perennial ryegrass

Tiller density increased going from spring to summer over both years of the trial (Table 3.5), but tiller size decreased (Table 3.6). These changes reflect the transition from reproductive growth in spring towards more vegetative growth in summer. During flowering in late spring, a large portion of total plant dry weight was contributed by reproductive tillers and seed-heads, with a reduced proportion of smaller vegetative tillers (Korte 1986). Hernandez-Garay et al. (1997) also showed average perennial ryegrass tiller weight increased during the reproductive period. The tiller density increase during the transition from reproductive growth to vegetative growth can be linked to high tillering rates in December in both grazed (Chapman et al., 1983; Korte et al., 1984; L'Huillier 1987; Da Silva et al., 1993; Da Silva 1994) and cut swards (Korte 1986).

However, the optimal management at the time of the transition from a lower tiller number (mainly reproductive tillers) to a larger number of mainly vegetative tillers, remains a matter for debate. It is clear that it is possible to target a higher herbage mass, in which case the potential tiller density increase moving into summer is lessened by a higher leaf area index (larger tiller size) (Table 3.6), but tillering later in summer appears to be enhanced. Alternatively, it is possible to target a lower herbage mass during the transition from reproductive to vegetative growth and as a consequence promote tillering after flowering. The latter strategy has been recommended by Brock and Hay (1993).

Pre-grazing herbage mass decreased from autumn to winter (Table 3.4) whereas tiller density increased (Table 3.5). However, adult tiller weight did not significantly change (Table 3.6). Because incident photosynthetically active radiation and daily average ambient temperature decreased going from autumn to winter, the leaf area index (LAI) of ryegrass swards also tended to decrease as the plants produced shorter leaves (Lemaire and Chapman 1996). Parsons and Chapman (1999) reported that pastures at a low LAI characteristically developed large numbers of small tillers. It has also been demonstrated from the size/density compensation concept, that pastures at a lower herbage mass will develop small tillers or shoots, and the population density will correspondingly increase (Matthew et al., 1996).

3.5.2 Effects of nitrogen and irrigation on ryegrass growth

Nitrogen fertiliser strongly increased seasonal herbage accumulation, pre-grazing herbage mass and tiller density, with less influence on tiller weight. These results have been confirmed by a large number of trials showing that additional nitrogen stimulates pasture growth (O'Connor and Cumberland 1973; Ball and Field 1982; Holmes 1982; O'Connor 1982; Harris and Clark 1996). Application of nitrogen fertiliser in late autumn had a carryover effect on winter herbage production. Periods of nitrogen shortage have been identified in dairy pastures in autumn/early winter and late winter/early spring (O'Connor 1982). Nitrogen applied at a minimum rate of 25 kg N/ha on a mixed ryegrass/white clover pasture during these periods increased pasture dry matter production (O'Connor 1982), which agrees with our observations.

Despite possible losses of nitrogen by volatilisation under dry and warm conditions, nitrogen fertiliser applied in summer can stimulate ryegrass growth. Harris and Clark (1996) showed this was possible for a ryegrass/white clover pasture grown with an application at 200 or 400 kg N/ha, and grazed intensively by dairy cows in northern New Zealand. Lack of moisture can inhibit macro- and microbiological activity in soil which is necessary to decompose vegetative or animal organic matter such as dung. Because the decomposition of organic matter in summer is influenced by low soil moisture, high air temperature and low earthworm activity, the ryegrass growth response to nitrogen observed was probably due to the nitrogen fertiliser (60 kg N/ha) applied. On the contrary, ryegrass growth in winter 1997, expressed as herbage accumulation (Fig. 3.6), pre-grazing herbage mass (Table 3.6), tiller density (Table 3.4) and tiller weight (Table 3.5) was higher in the nitrogen treated than in the untreated plots, despite no nitrogen being applied. Therefore, the nitrogen application in autumn 1997 may have stimulated ryegrass growth in the following winter. This positive effect of nitrogen on ryegrass growth could also be partly due to the effects of urine and/or dung deposited by dairy cows during grazings. Lemaire and Culleton (1989) also observed that tall fescue increased tillering in winter in response to nitrogen fertiliser applied after the last cut in autumn.

The effect of irrigation on herbage accumulation was greatest in summer and autumn 1998. The two components of yield, tiller density and tiller weight were slightly increased or were unaffected by irrigation. However, these small differences translated into a significant effect of irrigation on pre-grazing herbage mass in summer (Table 3.4). Herbage accumulation response to irrigation was smaller in the second summer compared with the first (Fig. 3.8) and more water was applied in the second (292 mm) than the first year (233 mm) (Table 3.3), although the average rainfall was higher during summer 1997/98 (197 mm) than in 1996/97 (173 mm), and differences in average daily temperature in February were large (24.6 °C in 1997; 26.8 °C in 1998). Work conducted by Hopewell (1960) in the Waikato, showed an average pasture response to irrigation (290 mm irrigation water applied per year) of 36%, or an extra 4.2 tonnes DM/ha/year. The lack of pasture growth in the Waikato over summer could be explained by the sensitivity of ryegrass to high temperature. Thomson (1996) noted that summer temperatures were often in excess of the maximum for ryegrass growth (25°C) (Cooper and Tainton 1968) limiting the growth response to irrigation, as was the case during the second year of this trial. Severe grazings may also reduce the growth of pasture over summer (Thom et al., 1986b) and the ability of ryegrass to respond to irrigation (Thomson 1996). The autumn herbage accumulation response to irrigation in 1998 reflects a carry-over effect from the preceding summer, since no water was applied during this period.

Nitrogen stimulated tillering by producing a large number of small tillers, reducing the overall average tiller weight despite the fact that the weight of adult tillers was also increased by nitrogen application. This suggests that the two components of yield, tiller density and tiller weight were not influenced the same way by environmental factors. According to Chapman and Lemaire (1993), tiller density is a sward structural characteristic that is influenced by environmental factors and sward botanical composition, whereas tiller weight is a genotypic character that is mostly influenced by frequency and intensity of defoliation.

Nitrogen and irrigation treatments had a consistent effect on the botanical composition of the sward. Increased tillering of perennial ryegrass in response to nitrogen fertiliser, partly caused by reduced content of white clover and weeds over the second summer and autumn, supports the findings of Ball and Field (1982), O'Connor (1982), Davies (1992), and Harris and Clark (1996). More *Poa* was observed in nitrogen treated plots in spring confirming previous reports (Wells 1974; Hagger and Squires 1979; Ball and Field 1982; Thom et al., 1986a). Ryegrass was more responsive to nitrogen fertiliser than was white clover, leading to shading of white clover and suppression of its growth (O'Connor 1982). In contrast to nitrogen, irrigation increased the content of white clover and ryegrass in summer 1997/98 and autumn 1998, but decreased the dead material content in both summers. However, white clover frequency was low (< 1 %) over the first summer. Other researchers have noted that the white clover content of swards sown with grass was increased by irrigation (Harris 1978; Brock and Hay 1993; Hutchison et al., 1995) and have shown the ability of white clover to respond to irrigation because of reduced sensitivity to high temperature (Davies 1992) compared with perennial ryegrass. Thom et al. (1986b) and Thom et al. (1998b) confirm the current results of increased frequency of dead material in dairy pastures in summer.

3.5.3 Productivity of 'Ellett' and 'Grasslands Ruanui' swards

Total herbage accumulation over the entire field experiment was greater for 'Ellett' than 'Grasslands Ruanui' swards. 'Ellett' outyielded 'Grasslands Ruanui' because of its higher spring-summer production which contrasts with others reports

(Corkill et al., 1981; Goold 1982; Easton 1983) showing that differences were due to the superior autumn-winter production of 'Ellett' over 'Grasslands Ruanui'. Morphological differences also made an important contribution to the observed herbage accumulation differences between the two cultivars.

Both cultivars seemed to respond the same way to nitrogen and irrigation with respect to herbage accumulation and tiller weight, since no interaction between cultivar and nitrogen or cultivar and irrigation treatments were observed. However, 'Grasslands Ruanui' showed a greater tillering response to nitrogen than 'Ellett', particularly in the second year of the trial (Table 3.5). Since sward tiller population density is defined as the equilibrium between tiller birth and death rate, differences between 'Grasslands Ruanui' and 'Ellett' could possibly be explained through these components with 'Grasslands Ruanui' having a higher tiller birth rate and a lower tiller death rate than does 'Ellett'. Tiller dynamics aspects of these responses will be discussed in Chapter 5.

3.5.4 Tiller loss during grazing (pulling)

Losses of ryegrass plants or tillers have often been associated with cattle grazing in summer-autumn (Plate 3.5) (Hughes and Jackson 1974; Thom et al., 1986a). 'Ellett' ryegrass lost more tillers by pulling during summer-autumn grazings than did 'Grasslands Ruanui'. Thom et al. (1998a) has also shown low tolerance to pulling of some ryegrass cultivars, which like 'Ellett', originate from the Mangere ecotype. Morphological and genotypic differences in tiller size between the two cultivars may contribute to differences in pulling. 'Ellett' plants have larger leaves (Easton 1983) and more upright tillers than those of 'Grasslands Ruanui', making them more easily accessible to dairy cows and possibly easier to pull. Thom et al. (1996) also showed that leaf shear strength affects pulling, but shear strength measurements were not carried out in the current trial.

The highest pulling levels were observed when nitrogen fertiliser was applied without irrigation, confirming other research (Tallowin et al., 1986; Fulkerson et al., 1993); increased ryegrass pulling was associated with low soil moisture levels, as was the case in the 1996/97 summer, and use of nitrogen fertiliser.

Plate 3.5. Ryegrass clumps (arrowed) pulled from the sward by dairy cows during grazing of the field experiment in April 1997.

Since 'Ellett' outyielded 'Grasslands Ruanui' during summer, when tiller losses due to pulling were highest, it appears that 'Ellett' was able to compensate for the increased tiller losses associated with increased susceptibility to pulling. Lack of an effect of pulling on yielding ability of ryegrass cultivars has also been reported by Thom et al. (1996).

3.5.5 Methodology

3.5.5.1 Nitrogen treatment

A quantitative analysis of plant nitrogen status may have shown differences in nitrogen use efficiency between 'Ellett' and 'Grasslands Ruanui' cultivars. The diagnosis of the nitrogen status in crops through the nitrogen dilution curve as developed by Lemaire (1997), could have helped define the optimum nitrogen fertilisation management for 'Ellett' and 'Grasslands Ruanui' ryegrass swards.

If the objective had been to quantify nitrogen status and nitrogen use efficiency, the dilution curve of Lemaire (1997) could have been used. However, the objective here was to test whether tiller dynamics (Chapter 5) was sensitive to addition of N fertiliser.

3.5.5.2 Pasture probe assessments of herbage mass

Pre- and post-grazing herbage mass were estimated using the electronic pasture probe. This tool is often used in grassland research and farming in New Zealand to estimate accumulation of pasture dry matter, but its reliability remains a matter of debate. The functioning of the pasture probe depends on sward conditions and in particular moisture levels (Jones and Haydock 1970; Johns 1972; Angelone et al., 1980; L'Huillier and Thomson 1988). Herbage mass can be overestimated when pasture is wet. The calibration equations used to convert probe readings to kg DM/ha (L'Huillier and Thomson 1988) in the current trial were derived from non-irrigated sites on intensive dairy farms in Waikato and Taranaki. Limitations of trial design (small size of sub-sub-plots) precluded the derivation of separate calibration equations for the irrigated sub-sub-plots, by taking herbage cuts to ground level. Possible errors resulting from this methodology were minimised by restricting measurements to when herbage was dry, and when this was not possible, by carefully waxing the lower portion of the probe. Others factors such as the presence of dead herbage material and the effects of sward structure (Campbell et al., 1962; Jones and Haydock 1970) could have also affected the meter reading and hence the assessments of herbage mass. Thomson (1983) has demonstrated that the capacitance meter (probe) was insensitive to dead herbage mass and has suggested that probe estimates could be improved by combining it with a visual estimate of dead and dry matter content.

The pasture probe may take into account differences in sward structure between species and cultivars within a species through the detection of the capacitance change, which is related to sward surface area. However, there can be calibration differences between different sward types. For example, it was shown from an unpublished study at the former Taranaki Agricultural Research Station, that the assessment of herbage mass in tall fescue, using the calibration equation for a perennial ryegrass sward, underestimated herbage mass (N. Thomson, personal communication). Since 'Ellett' has a larger tiller size than 'Grasslands Ruanui' and in that respect may behave somewhat like tall fescue, it is possible that the pasture probe underestimated the herbage mass of 'Ellett' compared with 'Grasslands Ruanui'. Although assessment of possible bias in capacitance meter estimation of herbage mass based on unpublished results with tall fescue is speculative, the available evidence suggests the difference in herbage production between cultivars would more likely have been underestimated than overestimated. If this was the case, then 'Ellett' would have shown an even larger herbage accumulation difference than was shown in Figure 3.5. However, 'Ellett' herbage accumulation was always higher than 'Grasslands Ruanui', confirming previous observations (Goold 1982; Longhurst et al., 1999).

The main advantage of the pasture probe over other methods of estimating herbage mass is that it is non-destructive and fast.

3.6 Summary

3.6.1 Differences in productivity and yield components between cultivars

- Total herbage accumulation for 'Ellett' (14 790 kg DM/ha over the field trial period) was 13 % greater than for 'Grasslands Ruanui' reflecting differences in spring and summer pasture production.

- 'Ellett' swards consistently had a higher weight per tiller and a lower tiller density than 'Grasslands Ruanui'.

- There were no differences observed in the frequency of white clover, weeds and other grass species in 'Ellett' and 'Grasslands Ruanui' swards.

- 'Ellett' tended to 'pull' more than 'Grasslands Ruanui' during grazings in summer and autumn. Tiller pulling did not eliminate the yield advantage of 'Ellett' over 'Grasslands Ruanui'.

3.6.2 Nitrogen and irrigation effects on productivity and yield components

- 'Ellett' and 'Grasslands Ruanui' cultivars had similar responses to nitrogen and irrigation for herbage accumulation, pre-grazing herbage mass, tiller weight and botanical composition.

- 'Grasslands Ruanui' pre-grazing tiller density was much higher than that for 'Ellett' when nitrogen was applied in the second year of the field trial, giving rise to a significant cultivar × nitrogen treatment interaction.

- Nitrogen fertiliser increased herbage accumulation and tiller density of both cultivars. Increased tiller weight in response to nitrogen only occurred in the winter and autumn of the second year of the trial.

- Nitrogen fertiliser changed the botanical composition of the sward by increasing the frequency of *Poa* in spring and by decreasing the frequency of white clover, weeds and dead material in summer. Irrigation also changed the botanical composition of the sward by increasing the frequency of white clover and weeds, and decreasing the amount of dead material in summer.

- Irrigation increased total herbage accumulation and tiller density in summer 1996/97, 1997/98 and autumn 1997 but tiller weight was only slightly affected.

CHAPTER FOUR

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MORPHOLOGICAL AND TILLERING RESPONSES OF ‘ELLETT’ AND ‘GRASSLANDS RUANUI’ RYEGRASSES WHEN GROWN IN DIFFERENT LIGHT ENVIRONMENTS

CHAPTER 4: MORPHOLOGICAL AND TILLERING RESPONSES OF ‘ELLETT’ AND ‘GRASSLANDS RUANUI’ RYEGRASSES WHEN GROWN IN DIFFERENT LIGHT ENVIRONMENTS

This chapter forms the basis of a paper accepted for publication in the **Crop Science** journal.

4.1 Introduction

Breeding for high yield through selection or chromosome doubling has led to a tendency in swards of modern cultivars for a lower density of larger tillers (Hunt and Easton 1989; Van Loo 1992). As reported by Easton (1983) ‘Ellett’ plants have larger tiller size and lower tiller number than ‘Grasslands Ruanui’ plants in a dense grazed sward. It has been observed by researchers and farmers that ‘modern’ ryegrasses such as ‘Ellett’, ‘Yatsyn 1’ and ‘Grasslands Nui’ do not persist under intensive dairy grazing (Thom et al., 1998a). Persistency of a perennial ryegrass depends on the equilibrium between the relative rate of tiller initiation and tiller death (Langer 1963). Breeding for increasing tiller size may therefore have restricted tillering ability of the selected genotypes.

In forage grasses, leaf appearance rate (A_L), leaf elongation duration (LED), leaf elongation rate (LER), final leaf length and tiller appearance rate (A_T) are all interdependent (Fig. 4.1). In particular, A_L controls both number of tiller buds produced and LED. As A_L decreased, LED increased (Robson 1967) and the number of tiller buds produced decreased, since there is only one tiller bud in the axil of each leaf. Consequently, a low A_L could result in the production of a low number of large tillers (Lemaire and Chapman 1996). However, tiller appearance also depends on the propensity for tiller buds to develop into tillers. The earliest measure of tiller bud activity was site filling ratio (Davies 1974), defined as the ratio of tiller production : leaf

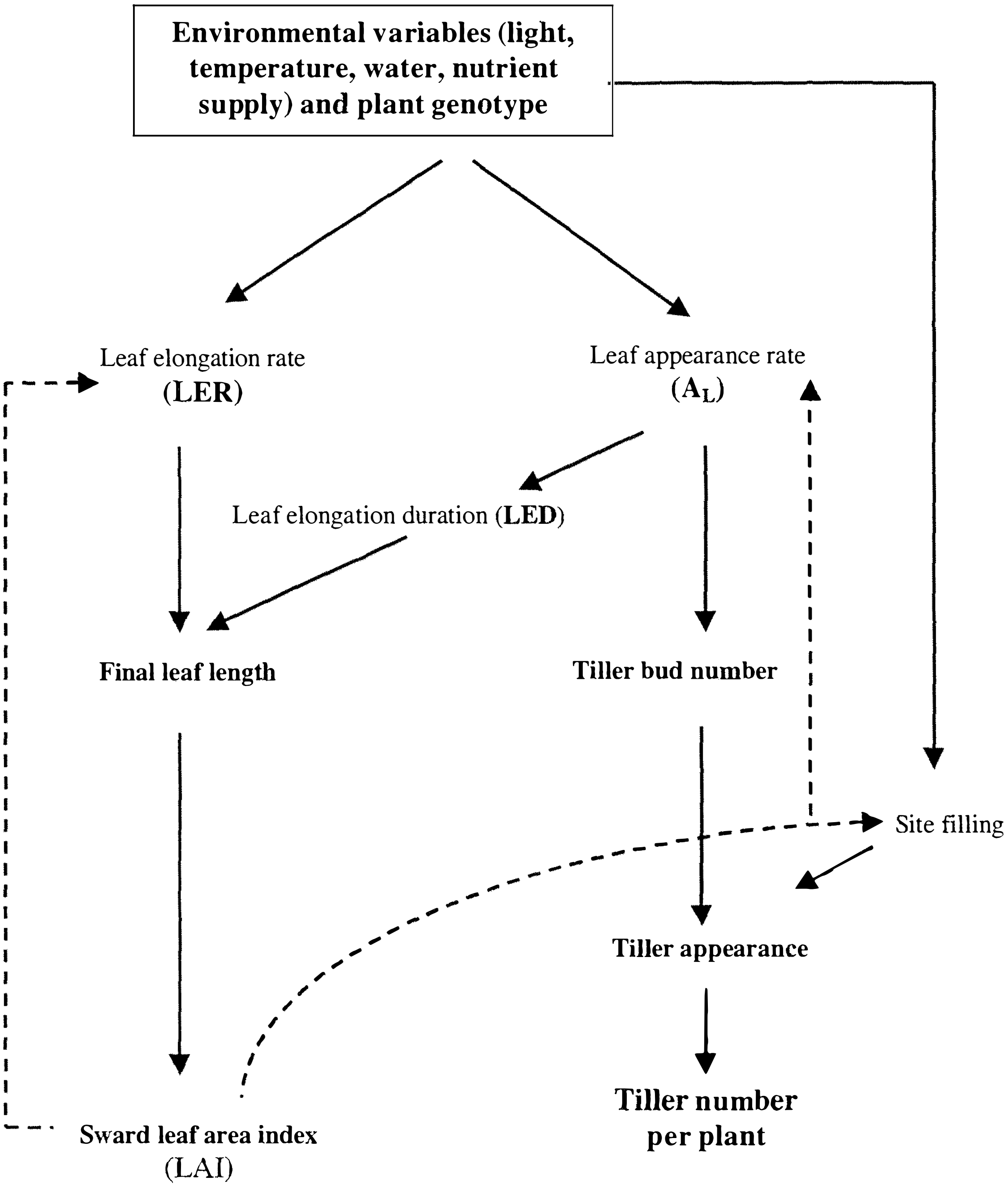


Figure 4.1. Relationships between the components of leaf growth, site filling, sward leaf area index and tillering.

production, or equivalently, the natural logarithm of the factor by which tiller number per plant increased with each leaf appearance interval. Site filling has a theoretical maximum of 0.69 (Log_e 2) denoting doubling of the tiller population with each leaf appearance interval (Neuteboom and Lantinga 1989). More recently tillering activity has been measured as site usage (Skinner and Nelson 1992), or nodal probability (Matthew et al., 1998), effectively the proportion of tiller buds that eventually form new tillers, with a theoretical maximum of 1.00. At the present time there is still rather limited understanding at the physiological level of the inter-relationships shown in Figure 4.1, and of their interaction with environmental factors such as light and temperature. Consequently there is uncertainty among plant breeders as to which characteristics to select for to optimise plant performance.

At the canopy level, a negative relationship between tiller size and tiller density, sometimes called size/density compensation, has been well described in undefoliated (Kays and Harper 1974; Lonsdale and Watkinson 1982) and in defoliated grass swards (Matthew et al., 1995). However, the underlying mechanism involved in the compensation remains unclear. This negative relationship could be driven by morphogenetic correlation between leaf size and tiller bud growth and/or by light-mediated effects on tiller bud initiation, and hence site filling.

Light environment can also modify leaf growth and tiller appearance. It has been shown that self-shading within a dense canopy at the tiller base is associated with increased leaf length and decreased tillering (Kays and Harper, 1974). Casal et al. (1985, 1987) linked these effects with low red : far red ratio associated with shading, which triggered an increase in leaf area through increased LER and LED (Allard et al., 1991), partially compensating for the lower light interception. Consequently, the effect of a high sward leaf area index (LAI) in inhibiting tillering (Simon and Lemaire 1987), is an important mechanism controlling tiller density, and leaf length is in turn a major component of sward LAI.

4.2 Objectives

This experiment aimed to characterise the morphology of 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars, in particular the relationship between leaf and tiller growth in the vegetative stage.

To be able to generalise the relationship between leaf size and tillering for 'Ellett' and 'Grasslands Ruanui', additional comparisons with short- and long-leaved ('SL' and 'LL', respectively) genotypes derived from divergent selection on their lamina length (Hazard et al., 1996) were included.

Cultivar tillering differences were related to A_L and site filling, and their differences in leaf size to LER and LED. These morphogenetic traits were studied under contrasting light environments, so as to characterise cultivar responses to different levels of light competition.

4.3 Materials and methods

4.3.1 Materials

The two commercial cultivars used were the New Zealand genotypes 'Ellett' (long leaved) and 'Grasslands Ruanui' (short leaved), both early flowering (Corkill et al., 1981). 'Grasslands Ruanui' was first released in 1936 and 'Ellett' in 1975. In a dense sward under normal farm practice, 'Ellett' had a lower tiller density and larger tiller size than did 'Grasslands Ruanui' (Easton, 1983).

Two experimental breeding lines were derived from divergent selection within a collection of French ecotypes (Hazard et al., 1996). For simplicity, when referring collectively to the two commercial cultivars or the two experimental breeding lines in the text below, the term "genetic lines" will be used. Although the experiment comprised two early and two late flowering genetic lines, all plants remained vegetative for the duration of the experiment. All plant material was endophyte-free.

4.3.2 Environmental conditions

The experiment was carried out at INRA, Lusignan, France (Latitude, 46°26'N, Longitude, 0°09'E) from February to May 1998. Seeds of the four ryegrass genotypes were germinated in Petri dishes on 2 February 1998, then transplanted (9 March 1998) into pots (170 mm diameter, one plant per pot) containing a mixture of sterilised soil, sand and peat (1:1:1). The plants remained in a glasshouse from the 9 of March to 8 of April 1998, when 80 plants of each genotype were arranged in eight trays, each with forty plants. Each tray contained 20 'Ellett' and 20 'Grasslands Ruanui' plants or 20 'LL' and 20 'SL' plants. Two trays of each combination were allocated to each light treatment. These 320 individually potted plants were the experimental units on which the statistical analysis described below were based. Trays were 0.85 m wide and 1.4 m long and were raised 0.7 m above the ground under larger filters, also raised above the ground. This construction prevented direct sunlight reaching the plants, but allowed free air circulation for temperature stabilisation.

The filter used as the control light treatment transmitted 90% of the photosynthetically active radiation (PAR), without spectral modification. The filter used to simulate a green shade (i.e. the shade treatment) transmitted 15% of PAR, but only 6% of blue and with a reduced red : far red ratio of 0.17 (Plate 4.1). When the light treatments were commenced on 8 April 1998, the main shoot had on average four fully emerged leaves. Growing degree-day (GDD) values cited in this Chapter were calculated starting from 8 April 1998 (18 GDD) and ending at 360 GDD.

The plants were watered individually every two hours with an automatic irrigation system. Air temperatures inside each canopy were continuously recorded throughout the experiment (10 second sampling interval and 5 minute recording interval) using thermocouples located 30 mm above the soil surface. Differences in daily temperature between the two light environments averaged 0.4°C. Air humidity was monitored from 12 to 17 May 1998 using a psychrometer located 150 mm above the soil surface (sampling and recording intervals as for air temperature). Differences in air humidity between the control and shade treatments were small (< 3%) and inconsistent.

Plate 4.1. The shade treatment simulated by a green filter (at the left) and the control treatment by a transparent filter (at the right).

4.3.3 Measurements

The number of mature and emerging leaves and primary tillers present on the main shoot, and the number of tillers per plant were counted 3 times a week, from 8 April to 11 May 1998. New tillers were recorded when the leaf tip appeared above the subtending leaf sheath. The length and width of each fully emerged leaf on the main shoot were measured from leaf number four to leaf eight. On 12 and 13 of May, 25 'Ellett' and 'Grasslands Ruanui' plants were randomly selected from under both light filters and the main shoot was dissected from each plant and dried in oven at 80 °C before weighing.

4.3.4 Derived data

A_L, A_T, and LER were determined for the main shoot. A_L and A_T were calculated as the slope of the regression of number of fully developed leaves or tillers on growing degree-days (calculated from 8 April, base temperature 0°C). The temperature summation in degree-days was calculated using daily mean temperature measured under each canopy, taking into account the slight differences in temperature on plants due to shading. LED was measured from main shoot leaf 5 to 8 as the number of degree-days between leaf appearance and full emergence. LER was then estimated by dividing final leaf length by LED. The average leaf length, LED and LER were calculated for each cultivar in each light environment from the mean for leaves 6 to 8 appearing during the measurement period. Site filling (Fs) was calculated as the slope of the linear regression between the logarithm of the number of tillers per plant and the number of leaves on the main shoot, since no mortality occurred during the measurement period. This relationship follows from Davies' (1974) definition of site filling mentioned above, and is illustrated graphically in Fig. 4.5a and 4.5b.

Bos and Neuteboom (1998a) found that tillers at different hierarchical positions on a plant show different rates of daughter tiller development. In the present study, the ratio $A_T : A_L$ is effectively a site usage (SU_m) statistic (Skinner and Nelson 1992) for the main shoot. Therefore, rate of tiller development for the main shoot can be compared to the average for the whole plant, either by converting the whole plant site filling statistic to the equivalent site usage statistic, or by converting the main shoot site usage, obtained from the ratio of regression slopes of A_T and A_L on growing degree-days, to the equivalent site filling value (designated here F_{Sm}). This conversion varies depending on the number of leaf appearance interval delay between leaf and tiller formation at a particular phytomer (Equation 3 of Matthew et al., 1998). Where this delay is 1 leaf appearance interval the equation simplifies to:

$$SU = \mathrm{Exp}\,(F_S) - 1 \qquad (4.1)$$

Since SU_m is equivalent to A_T/A_L, this can be rearranged to:

$$F_{Sm} = \mathrm{Ln}\,(1 + A_T/A_L) \qquad (4.2)$$

Since values for the delay between leaf and tiller appearance were close to 1.0 (see results, below), equation 4.2 was adopted.

Analyses of variance were performed using PROC GLM of SAS (SAS 1989, version 6) to study the effects of light environment, genetic lines and the interactions between genetic lines, light environment effects and GDD on tiller number per plant, tiller weight and tiller and leaf appearance rates, site filling, leaf length, leaf elongation and duration rates before and after 148 GDD. Because 'Ellett' and 'Grasslands Ruanui' plants and 'LL' and 'SL' plants were randomised in equal numbers in alternate trays, results for the respective pairs of genetic lines were analysed as separate experiments.

4.4 Results

4.4.1 Main shoot leaf length, LER and LED

No significant interaction was found between genetic line and light environment for leaf length, LER and LED for either early- or late-flowering genetic lines. The shade treatment increased overall leaf length by 55% compared to the control treatment ($P<0.001$, Table 4.1). This increase resulted from an average 35% increase in LER in all genotypes ($P<0.001$), and for 'Ellett' and 'Grasslands Ruanui' from a 30% increase in LED compared to the control treatment ($P<0.001$). The LED of the late flowering selections was unchanged by light treatments (Table 4.1).

Table 4.1. Effects of light treatment on leaf length, leaf elongation duration (LED) and leaf elongation rate (LER) of early ('Ellett' and 'Grasslands Ruanui') and late flowering genetic lines ('LL' and 'SL').

Variable	Genetic line	Control	Shade	SED[a]
Leaf length	Ellett	179 **	293 **	
	Ruanui	167	266	
				7.0
	'LL'	169 **	227 **	
	'SL'	132	208	
				4.9
LED	Ellett	135^{NS}	176^{NS}	
	Ruanui	131	170	
				4.6
	'LL'	164^{NS}	163^{NS}	
	'SL'	164	164	
				6.4
LER	Ellett	1.36^{NS}	1.69^{NS}	
	Ruanui	1.29	1.58	
				0.05
	'LL'	1.11 *	1.44 *	
	'SL'	0.87	1.38	
				0.07

Leaf length: mm; LED: degree-days; LER: mm per degree-days.
Level of significance, from ANOVAs comparing the genetic lines within the same group of flowering maturity, are: $P<0.001$ (**), $P<0.05$ (*), $P>0.05$ (NS).

[a] Standard error of difference between pairs of means for the genetic lines × light treatment interaction.

4.4.2 Main shoot leaf and tiller appearance rate

For all genetic lines, the shade treatment reduced both A_L and A_T on the main shoot, with A_T being more strongly affected (Fig. 4.2a and 4.2b). SU_m (calculated from A_T/A_L as described above) ranged from 0.87 to 0.93 depending on the genetic lines (Table 4.2), and this converted to Fs_m of 0.621 to 0.658 (Table 4.3). The delay between the leaf appearance and tiller appearance at the same node increased slightly between 18 and 360 degree-days under the control treatment. As a consequence of the greater effect of shade on A_T than A_L, the delay between appearance of a leaf and its tiller increased more rapidly under the shade treatment where Fs_m ranged from 0.482 to 0.571. No significant interaction between genetic lines and light environment was found for A_L, A_T or Fs_m for either early- or late-flowering genetic lines. 'Ellett' and 'Grasslands Ruanui' had similar A_L whereas 'LL' had a higher A_L than 'SL' ($P<0.01$) (Fig. 4.2a and 4.2b). No significant genetic lines effect was found for A_T. Therefore, 'LL' had a lower Fs_m than 'SL', while 'Ellett' and 'Grasslands Ruanui' had similar values of Fs_m (Table 4.3).

4.4.3 Main shoot weight

No significant interaction was found between cultivars and light environments for main shoot weight. Main shoot weight, regardless of cultivar, was strongly reduced under the shading compared with the control treatment (0.169 vs 0.243 g, $P<0.001$). 'Ellett' had a larger main shoot weight than did 'Grasslands Ruanui', regardless of the light treatment ($P<0.001$) (Fig. 4.3).

4.4.4 Whole plant tiller number and site filling

The shade treatment drastically reduced tiller number per plant, compared to the control treatment, for all genetic lines (Plate 4.2 and 4.3). Tiller number per plant increased exponentially with GDD under the control treatment while under the shade treatment this increase was approximately linear (Fig. 4.4a and 4.4b). There was a significant ($P<0.05$) genetic lines x light environment x growing degree-day interaction for tiller number per plant for the late flowering genetic lines (Fig. 4.4b), but not for the early flowering genetic lines (Fig. 4.4a). At the beginning of the experiment, 'LL' had 29% more tillers per plant than 'SL'. At the end of the experiment, this difference was still 22% under the shade treatment but only 9% under the control treatment. Convergence of tiller number for 'LL' and 'SL' under the control treatment is possible

Table 4.2. Tiller and leaf appearance rate ratio (A_T/A_L) on the main stem of the early ('Ellett' and 'Grasslands Ruanui') and late ('LL' and 'SL') flowering genetic lines under the control and shade treatments.

Genetic line	**Light treatment**	
	Control	**Shade**
Ellett	0.87 ^{NS}	0.64 ^{NS}
Ruanui	0.87	0.62
'LL'	0.86 *	0.67 *
'SL'	0.93	0.77

(A_T/A_L): tillers per leaf

Level of significance, from ANOVAs comparing the genetic lines within the same group of flowering maturity, are $P<0.05$ (*), $P>0.05$ (NS).

Table 4.3. Comparison of FS and FSm of the four ryegrass genetic lines under the different light environments.

	Control		**Shade**	
Genetic line	F_S	F_{Sm}	F_S	F_{Sm}
Ellett	0.599	0.626	0.196	0.495
Ruanui	0.617	0.626	0.293	0.482
'LL'	0.543	0.621	0.179	0.513
'SL'	0.618	0.658	0.209	0.571

Fs was calculated from 18 to 360 degree-days under the control treatment and from 148 degree-days under the shade treatment. At this time the average leaf number on the main shoot per plant was 5.6 for Ellett, Ruanui, and 'SL', and 6 for 'LL'.

Fs: Site filling calculated as the slope of the linear regression between the logarithm of tiller number per plant and the leaf number on the main shoot.

Fsm: Site filling calculated from observations on leaf and tiller appearance rates on the main shoot.

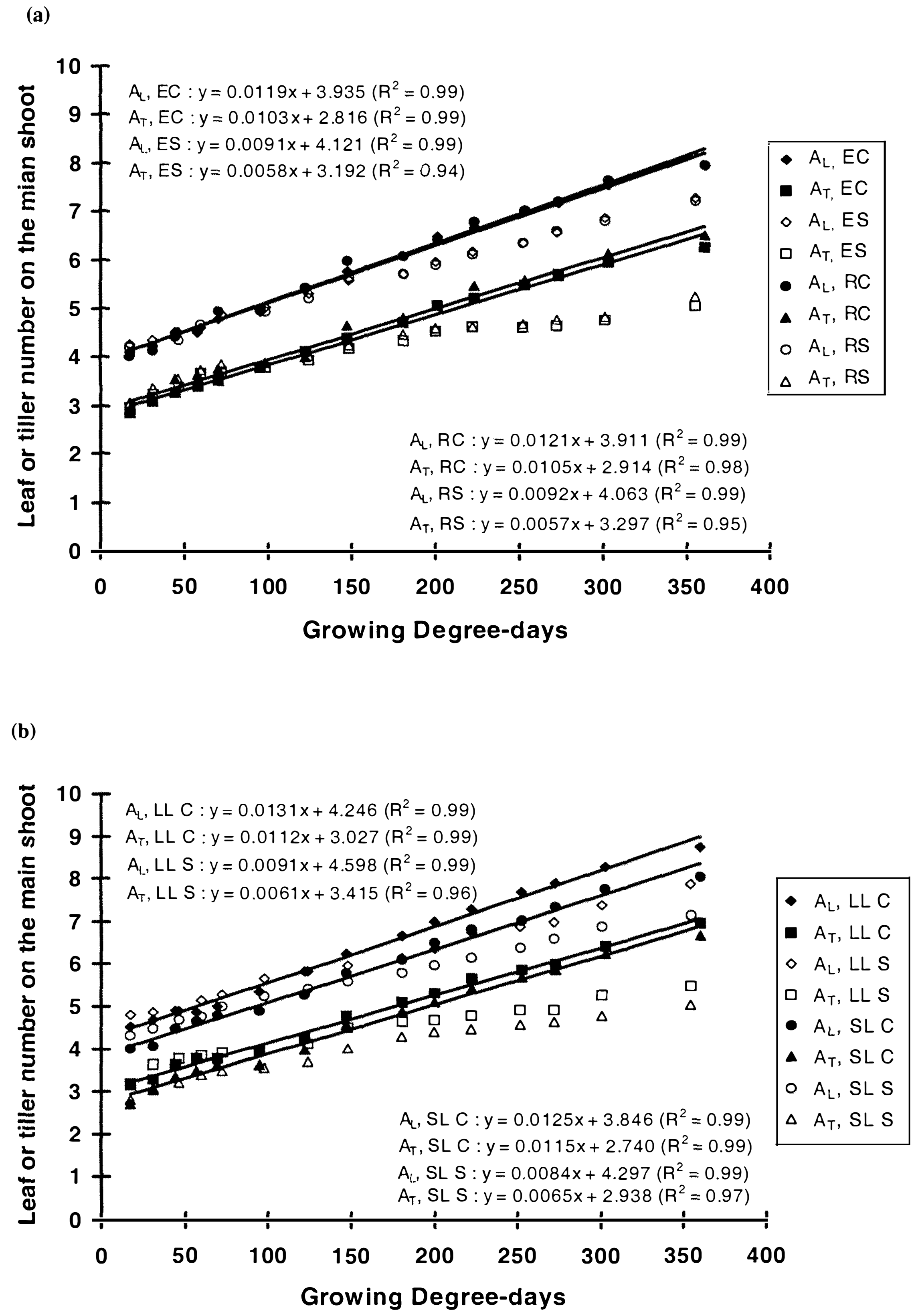
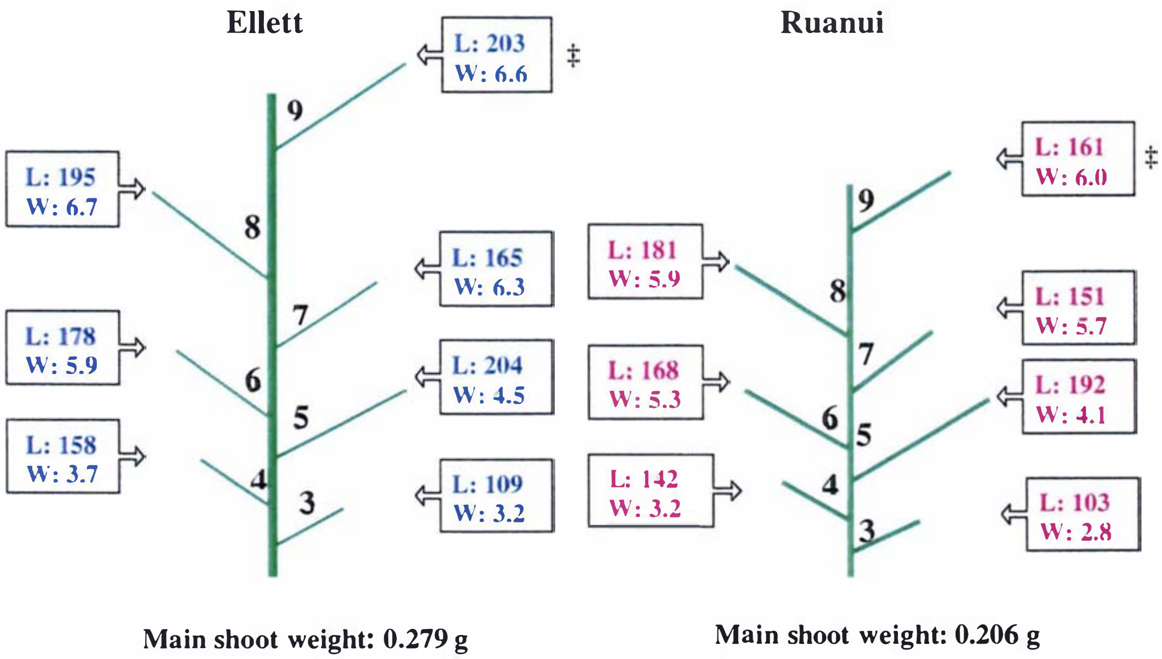


Figure 4.2. Effects of light treatments on leaf and tiller appearance rate on the main shoot of early (a) and late (b) flowering ryegrass genetic lines. EC, RC, LL C and SL C; 'Ellett', 'G. Ruanui', 'LL' and 'SL' under the control treatment. ES, RS, LL S and SL S under the shade treatment.

(a) Full light



(b) Simulated shade

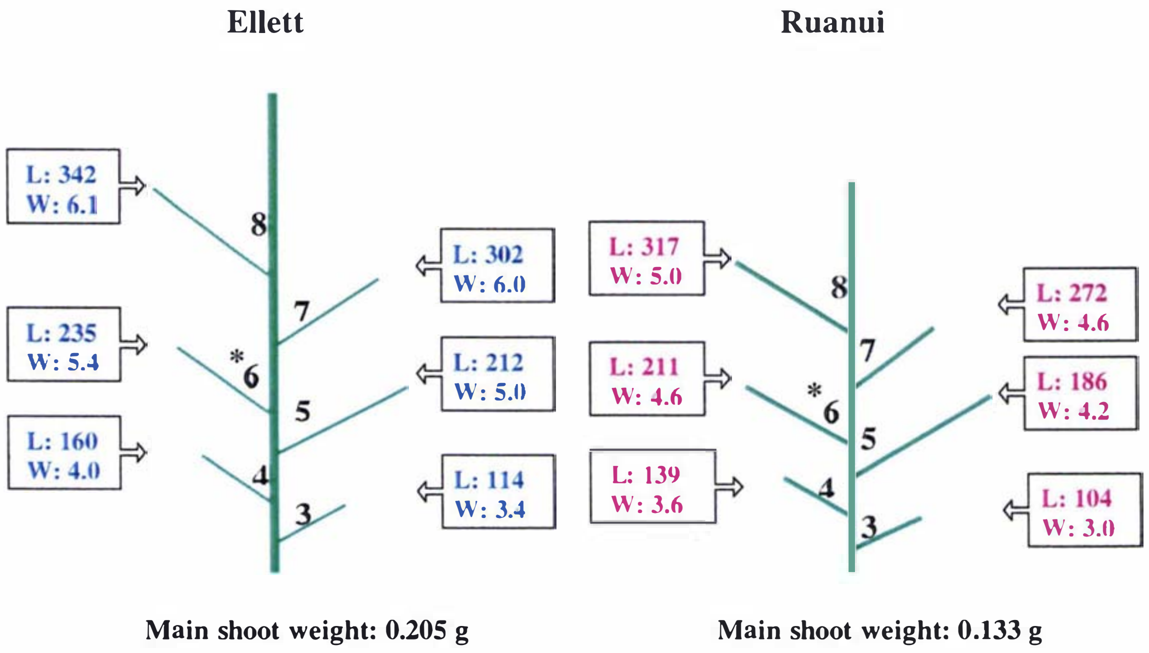
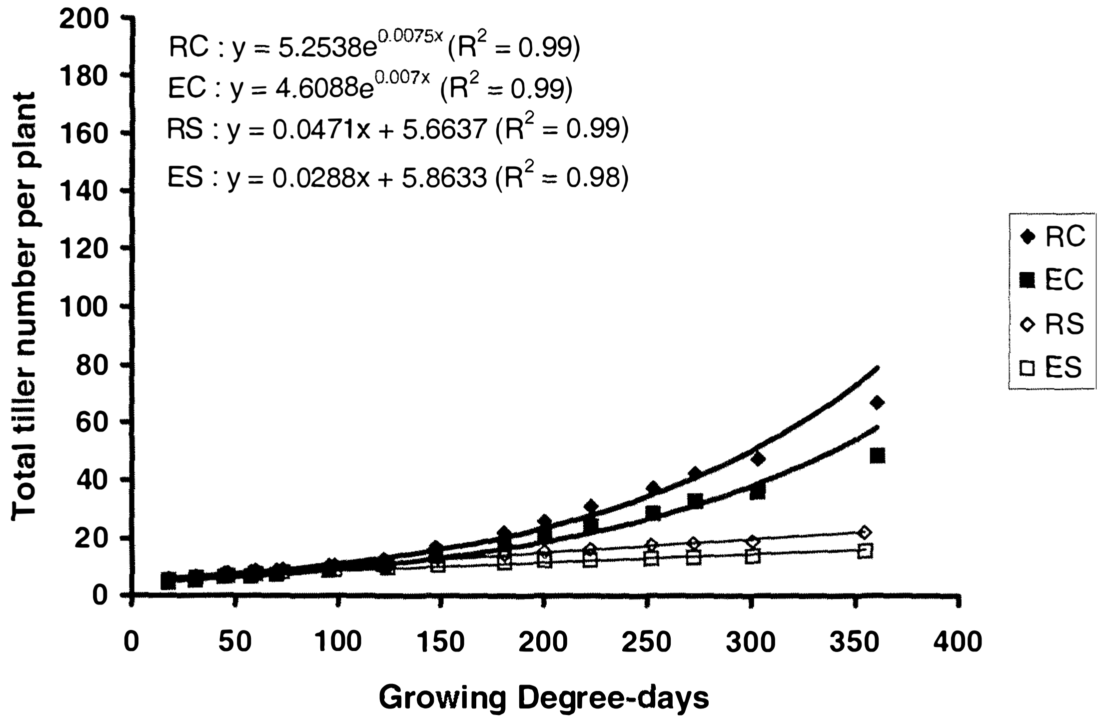


Figure 4.3. Main shoot morphology of 'Ellett' and 'Grasslands Ruanui' ryegrasses under the control and shade treatments. Differences in leaf length between the control and shade treatments appeared at leaf number 6 (*). The average length of leaf number 9 was the mean of eight 'Ellett' and five 'Grasslands Ruanui' plants (‡). L: Length; W: width.

(a)



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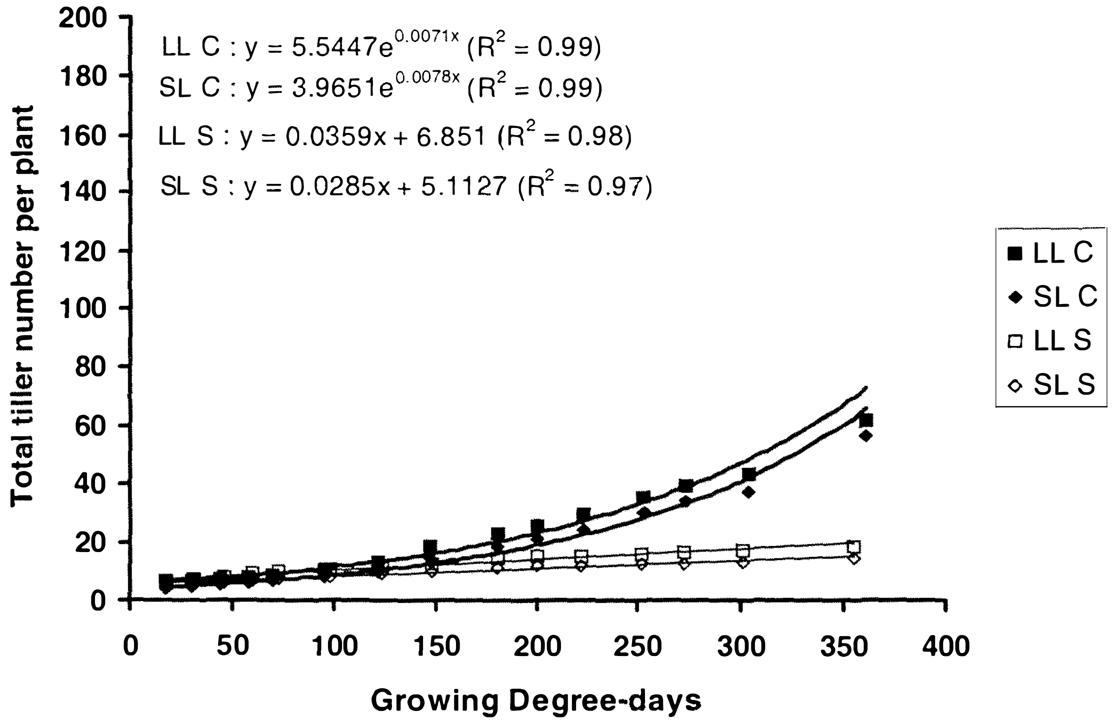
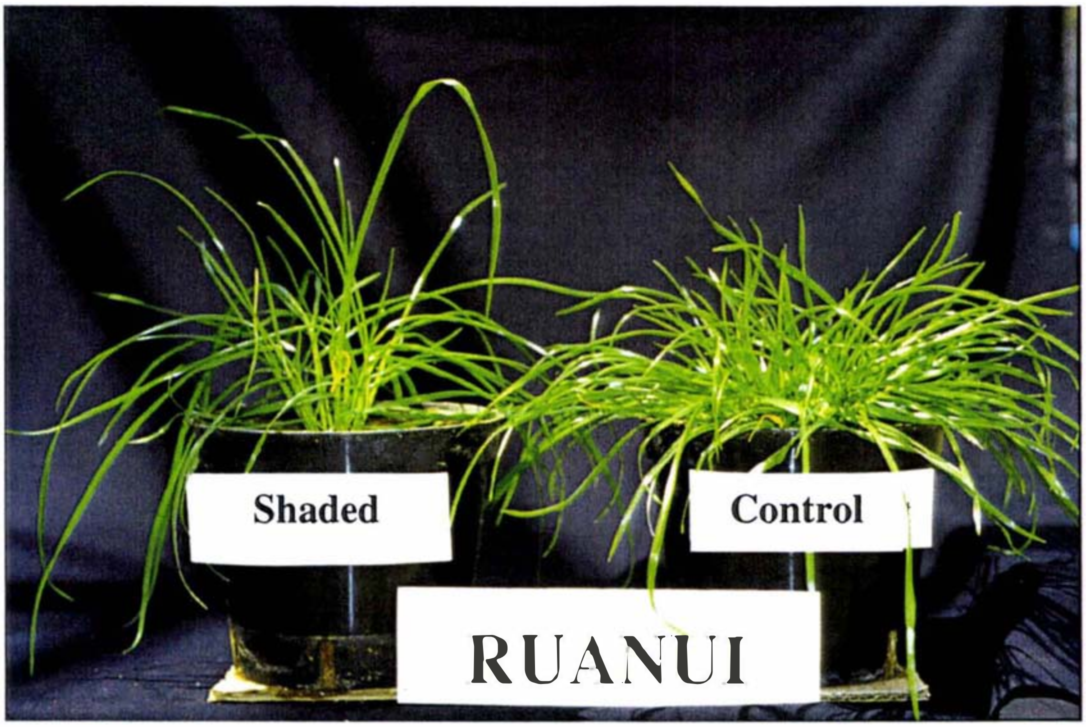


Figure 4.4. Effects of light treatments on tiller number per plant of early flowering ryegrass genetic lines, (a) 'Ellett' and 'G. Ruanui' and late flowering ryegrass genetic lines, (b) 'LL' and 'SL'. RC, EC, LL C and SL C; 'G. Ruanui', 'Ellett', 'LL' and 'SL' under the control treatment. RS, ES, LL S and SL S; 'G. Ruanui', 'Ellett', 'LL' and 'SL' under the shade treatment.

(a)



(b)

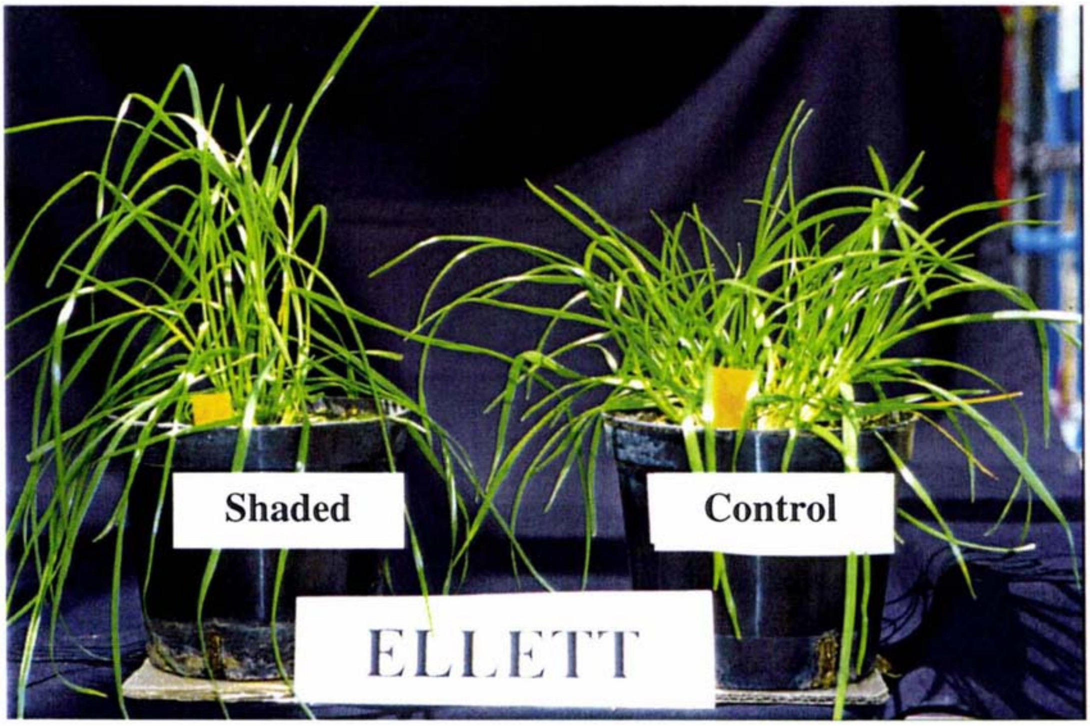


Plate 4.2. Comparison of 'Grasslands Ruanui' (a, short-leaved) and 'Ellett' (b, long-leaved) ryegrass plants after 33 days exposure to the control (at the right of each photograph) or the shade treatment (at the left of each photograph).

(a)

(b)

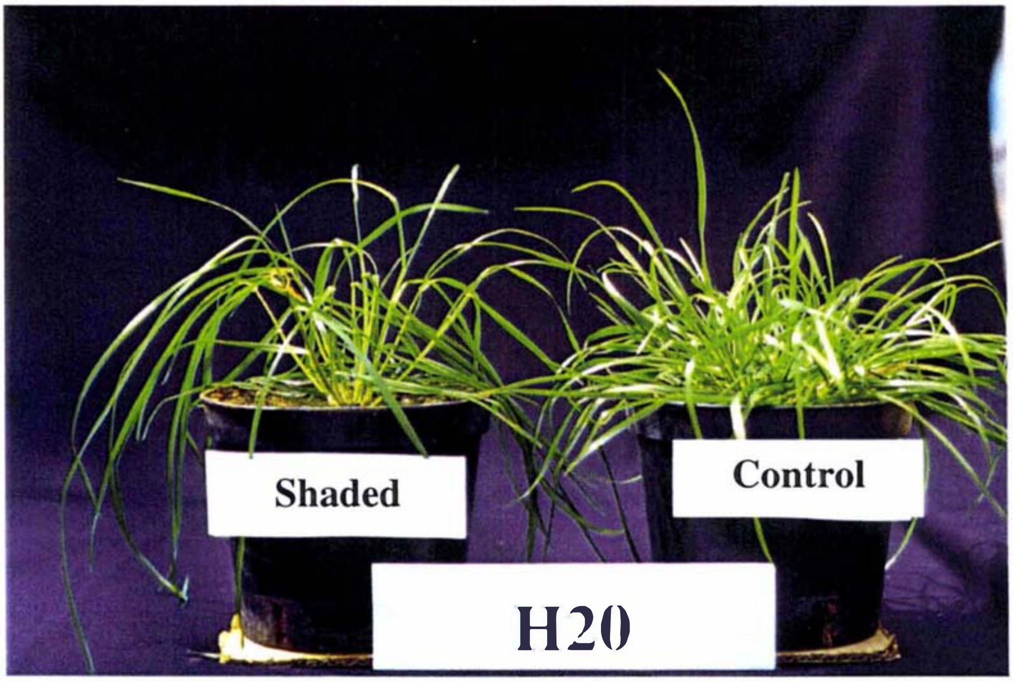


Plate 4.3. Comparison of 'B10' (a, short-leaved, 'SL') and 'H20' (b, long-leaved, 'LL') ryegrass plants after 33 days exposure to the control (at the right of each photograph) or the shade treatment (at the left of each photograph).

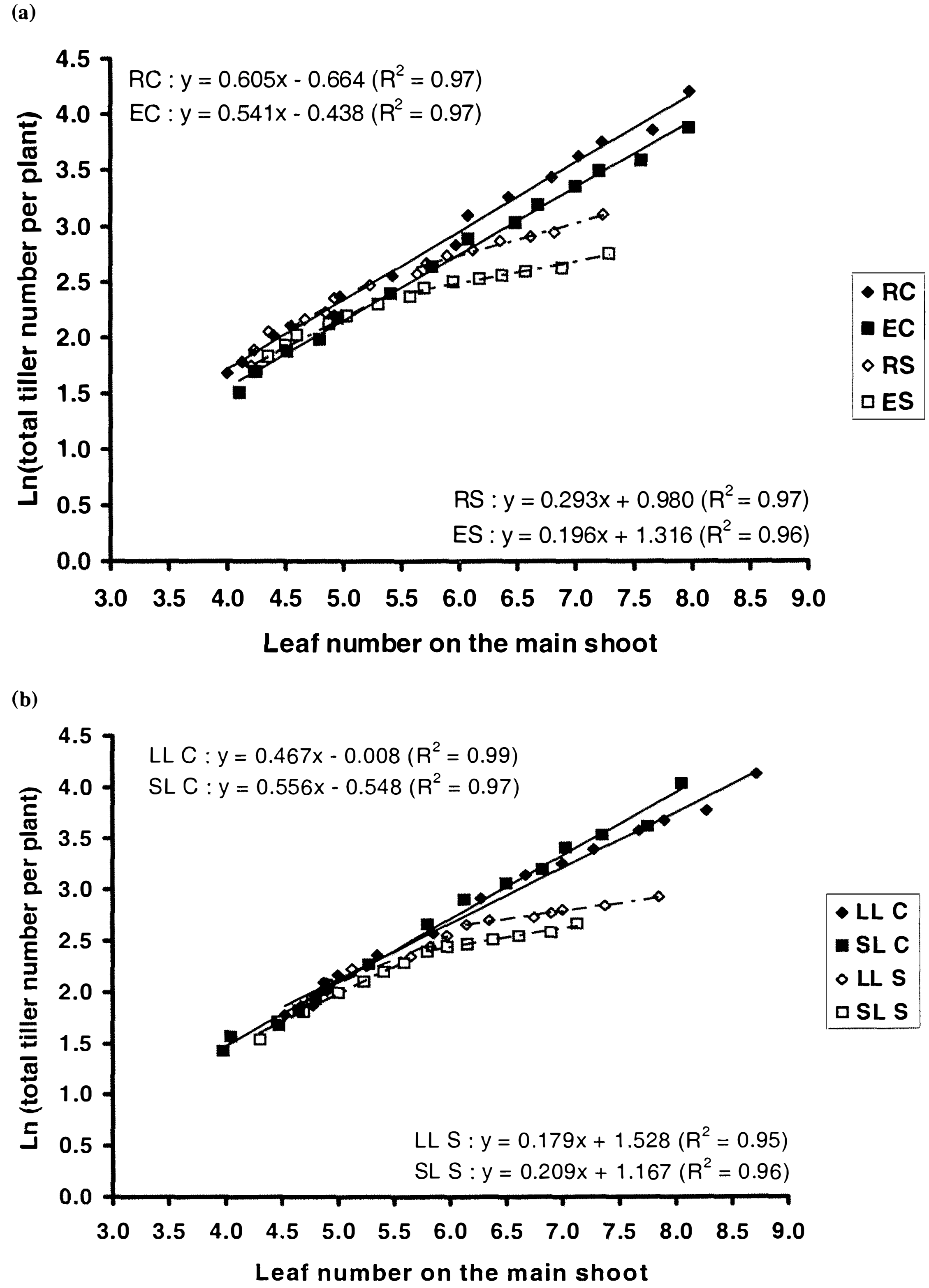


Figure 4.5. Effects of light treatments on site filling (Fs) of the early and late flowering (b) ryegrass genetic lines. Equations describing the Fs of 'Ellett', 'G. Ruanui', 'LL' and 'SL' under both light environments, from leaf number 6. EC, RC, LL C and SL C; 'Ellett', 'G. Ruanui', 'LL' and 'SL' under the control treatment. ES, RS, LL S and SL S; 'Ellett', 'G. Ruanui', 'LL' and 'SL' under the shade treatment.

(Fig. 4.4b). 'Grasslands Ruanui' and 'Ellett' both had 5 tillers per plant at the beginning of the experiment, but 'Grasslands Ruanui' produced more tillers than 'Ellett' in both light environments (Fig. 4.4a).

Plotting $\log_e$ tiller number per plant against leaf number on the main shoot to estimate whole plant site filling (Fig. 4.5a and 4.5b) showed that the shade treatment significantly reduced F_S ($P<0.001$). Under both light environments 'Grasslands Ruanui' had a higher F_S than 'Ellett' ($P<0.001$, Fig. 4.5a) and 'SL' had a higher F_S than 'LL' (see slope coefficients of equations, Fig 4.5). In the late flowering genetic lines the genetic lines x light environment x growing degree-days interaction was significant ($P<0.01$). This interaction is shown by the difference in site filling between control and simulated shade environments, which was 0.347 for the 'SL' genetic line, but only 0.288 for the 'LL' genetic line (Fig. 4.5b).

From extrapolation of the linear regression lines (Fig. 4.5a and 4.5b), the first tiller appeared when 'Grasslands Ruanui' had 1.77 leaves on the main shoot, 'Ellett' 1.84, 'LL' 1.90 and 'SL' 1.96 leaves.

4.4.5 Comparison of main tiller and whole plant site filling

Whole plant site filling, F_S, was only slightly less than main tiller site filling, F_{Sm} under the control treatment. By contrast, under the shade treatment, F_S was very much lower than F_{Sm} (Table 4.3).

4.5 Discussion

4.5.1 Experimental design

Nonreplication of the light environments raises issues in interpretation of the results. In such cases the probabilities determined statistically for class mean differences are valid, but assigning those differences to the experimental treatments may or may not be, depending on whether or not confounding with external factors, such as shadows from nearby buildings, occurred. Independently of this consideration, where light environment is modified by housing, as in this experiment, the possibility of associated temperature and/or humidity differences must be considered. The latter problem was addressed in this work by housing *both* light environments with a canopy of identical design, by designing canopies for good ambient air circulation by convection to eliminate internal heating, and by continuous automatic monitoring of both relative humidity and temperature, the latter at multiple points within each light environment. The differences in temperature and humidity were never biologically significant. On the issue of possible confounding between light environment and external factors, it would have been impractical to individually house the experimental units, single potted plants, and the regression analyses used to relate leaf and tiller appearance would not have been easily adapted to handle a split-plot design. As a more realistic alternative, extreme care was taken in the siting of the full light and simulated shade canopies close to each other but not so close that one would shade the other, raised from the ground, and distant from trees, buildings and other structures, to eliminate any such confounding. Plants of the two pairs of long- and short-leaved genetic lines were individually potted and fully randomised within canopies. There remains a very small chance that some external factor may have been overlooked and the results below are presented with that qualification. However, the overwhelming balance of probability is that the class mean differences observed were due to the differences in light environment.

4.5.2 'Ellett' and 'Grasslands Ruanui' morphology

Inherent differences in morphology were observed between 'Ellett' and 'Grasslands Ruanui' regardless of light environment (Fig. 4.3). When grown as spaced plants, 'Ellett' had longer leaves, larger main shoot weight and lower tiller number than did 'Grasslands Ruanui' which confirmed results found in grazed swards (Chapter 3). The morphological differences observed between the two ryegrass genetic lines are presumably genetically determined, since the same trends were evident under full light and shaded conditions.

4.5.3 Effect of shade on plant development

Shade consistently increased final leaf length (Table 4.1) and reduced tiller appearance rate (Fig. 4.2 and 4.4). The differences in leaf length for 'Grasslands Ruanui' and 'Ellett' and for 'LL' and 'SL' have been described previously (Easton, 1983; Hazard et al., 1996), are genetically determined, and were maintained in both light environments. Effect of shade on leaf length was mainly through increased LER, but also through increased LED in 'Ellett' and 'Grasslands Ruanui'. Effect of shade on tiller appearance rate was through decreased F_S, but not F_{Sm}. The factor increase in tiller number per plant per leaf appearance interval can be calculated as e^{F_S} (Neuteboom and Lantinga, 1989). When applying this calculation to data in Table 4.3, shade reduced main shoot tiller appearance by 11%, compared with 31% for whole plant tiller appearance. It is therefore clear that formation of primary tillers on the main shoot is much less susceptible to shading than is formation of larger order secondary and tertiary tillers. This is consistent with previous studies in wheat. For example, Casal (1988) showed that the proportion of primary to secondary and tertiary tillers was larger in far-red treated wheat plants than in untreated plants, and Bos and Neuteboom (1998b) measured SU at specific bud positions for wheat and also found differences in bud utilisation between tillers at different hierarchical positions.

Shade treatments were imposed when plants had four leaves on the mean shoot but changes in site filling were not evident for another 5 leaf appearance intervals (Fig. 4.5a and 4.5b). The extent of the delay in response to shading depends on the status of the tiller buds and the growth rate of daughter tillers within the sheath of the main tiller. Inability to record daughter tiller formation until its leaf tip appeared above the subtending leaf sheath, was another contributing factor to this delay.

4.5.4 Relationship between leaf length and tiller appearance

Long leaf length has been associated in some previous studies with increased LED and low A_L (cf. Fig. 4.1), resulting in low tiller number per plant. Such responses have been previously observed in tall fescue (Robson, 1967; Zarrough et al., 1984; Allard et al., 1991) and wheat (Bos and Neuteboom, 1998a) and were identified as a general principle by Lemaire and Chapman (1996). However, in this experiment the selection 'LL' had both high LER and high A_L, showing that these two variables need not always be negatively related. Indeed, Skinner and Simmons (1993) have already shown that supplemental far red illumination in grass seedlings increased leaf length through an increase in LER while LED was unaffected. The present result also suggests that the 'LL' selection for high LER and leaf length has a different genetic basis than that of previous selections with a similar behaviour.

Another mechanism, which can give rise to a negative association between LER and A_L is a negative relationship between LER and Fs. In this experiment, comparisons of 'Grasslands Ruanui' with 'Ellett', 'SL' with 'LL' and the control treatment with the shade treatment, all show a common response in that high site filling was associated with low LER and short leaves, and a similar observation was made by Zarrough et al. (1984) in tall fescue. Intuitively a negative association between F_S and LER might be viewed as an indication of competition between daughter tiller and adjacent leaf meristems for available carbon, but the response could equally well be morphogenetically determined. Since a plant whose tillers have high LER will accumulate sward LAI more quickly after defoliation, the same plant will experience basal shading and associated tiller bud suppression earlier in the regrowth cycle.

4.5.5 Factors affecting tiller number per plant

The delay between the appearance of a given leaf and the appearance of its axillary tiller (termed 'n' by Neuteboom and Lantinga, 1989) can be measured for the main tiller as the vertical distance between regression lines of A_T and A_L on growing degree day (Fig 4.2), since all tillers formed on the main tiller during the experiment were from the bud immediately above the previous tiller, with no buds missed. This delay was a little greater for 'LL' than 'SL', did not differ between 'Grasslands Ruanui' and 'Ellett', but did increase as plants aged (Fig. 4.2). Also of interest, is the time of appearance of the first primary tiller. Based on extrapolation of regression lines in Fig 4.5, the first tiller appeared sooner (1.77 leaves) in 'Grasslands Ruanui' than in 'Ellett' (1.84 leaves), but sooner in 'LL' (1.90 leaves) than in 'SL' (1.96 leaves). These apparent differences in timing of first primary tiller appearance may partly explain the high tiller number per plant in 'Grasslands Ruanui' compared with 'Ellett', and the initially higher tiller number per plant in 'LL', compared with 'SL'. Another factor contributing to the higher tiller number per plant in 'LL' than in 'SL' at the beginning of the experiment (18 degree-days) must have been difference in A_L because 'LL' had more leaves than 'SL' at this time. At the end of the experiment, differences in tiller number per plant had diminished because of the higher site filling of 'SL', and would be expected to eventually exceed that of 'LL' (Fig. 4.4b). Gautier et al. (1999) have also shown that a long-leaved perennial ryegrass from the same population as 'LL' had a lower tillering rate than comparable 'SL' material, because of lower site filling.

Under the shade treatment, 'LL' still produced more tiller bud sites than 'SL' but, unlike the control treatment, both genetic lines had a similar F_S. It is likely that increase in delay between leaf and tiller appearance, 'n', which includes the inhibition, or bud mortality of higher order tillers, explains lower site filling in simulated shade. However, since the observations were made only on main stem tillers, further investigations are necessary to determine accurately why the F_S is much lower than the F_{Sm} under the shade treatment.

4.6 Conclusion

Increased leaf length of 'Ellett' and 'LL' genetic lines was achieved mainly through increased LER. This has been associated with increased productivity in both cases (Hunt and Easton 1989; Hazard and Ghesquière 1997), but contrary to previous indications (Robson 1967; Zarrough et al., 1984), decreased A_L and tillering was not necessarily associated with long leaf length. This occurred with 'Ellett', but not with 'LL'. This suggests it may be possible to select for higher tillering rate at a given tiller size, although other strategies to improve persistence, such as selection for increased longevity of individual tillers, used in tetraploids by Neuteboom et al. (1992), should also be kept in mind.

4.7 Summary

4.7.1 Differences in morphology between genotypes

- 'Ellett' had longer leaves than 'Grasslands Ruanui' and 'LL' longer leaves than 'SL' in both light environments.

- Differences between genotypes in leaf length were attributable mainly to higher LER in the two long-leaved genotypes, and LED did not differ significantly between genotypes.

4.7.2 Differences in tillering between genotypes

- 'Grasslands Ruanui' had a higher tiller number per plant than 'Ellett' in both light environments, explained by higher site filling and similar leaf appearance rate.

- 'LL' had a higher tiller number per plant than 'SL', arising from a higher leaf appearance rate in 'LL', although this difference decreased during the experiment under the control treatment because 'SL' tended to have a higher site filling ratio than 'LL'.

- Under the shade treatment, differences in tiller number between 'LL' and 'SL', were more mediated by the leaf appearance rate than site filling.

4.7.3 Relationship between leaf length and tillering

- Genotypes with high LER and long lamina length, even though associated with reduced site filling in both light environments, did not necessarily result in reduced tiller number plant.

CHAPTER FIVE

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STUDY OF THE TILLER DYNAMICS OF 'ELLETT' AND 'GRASSLANDS RUANUI' RYEGRASS SWARDS UNDER TWO LEVELS OF NITROGEN AND IRRIGATION

CHAPTER 5: A STUDY OF THE TILLER DYNAMICS OF 'ELLETT' AND 'GRASSLANDS RUANUI' RYEGRASS SWARDS UNDER TWO LEVELS OF NITROGEN AND IRRIGATION

5.1 Introduction

As defined in Chapter 2, perennial ryegrass plants are a collection of tillers which appear at different times of the year. The number of tiller generations constituting the tiller population are determined by the rate of tiller appearance and tiller longevity (Briske 1991). Because the ryegrass tiller continually undergoes morphological changes, the structure of the ryegrass sward is dynamic and continuously changing. The structure of the tiller population varies with time, reflecting seasonal changes in the developmental morphology of individual tillers, resulting from both genetic and environmental factors.

Previous studies reported in Chapter 2 showed that the pattern of tiller population demography was different from one species to another, and possibly between cultivars within a species. Matthew (1996) observed in the field that 'Grasslands Ruanui' ryegrass had a seasonal low in tiller appearance and a peak tiller death rate in late spring (November) and autumn (May), respectively, whereas in early spring (late August) tiller appearance was high and tiller death low. The pattern of tiller appearance for 'Grasslands Ruanui' ryegrass was similar to that for S23 and S24 perennial ryegrass cultivars in Britain (Garwood 1969). 'Grasslands Ruanui' did not show high tillering activity in late spring/early summer in New Zealand as observed in 'Grasslands Nui' swards (Korte 1986; Hernandez-Garay et al., 1997) and also in a mixture of modern ryegrasses including 'Grasslands Nui' (L'Huillier 1987). Moreover, the annual replacement of tillers at flowering, often observed in perennial ryegrass (Colvill and Marshall 1984; Korte 1986; Hernandez-Garay et al., 1997), was almost absent in the age-cohort survival diagram for 'Grasslands Ruanui' ryegrass (Matthew 1992). Finally, observations of single marked tillers in separate experiments suggested that 'Ellett' was more dependent on new daughter tiller production from reproductive tillers (reproductive pathway), whereas 'Grasslands Ruanui' seemed more dependent on the survival of the existing secondary daughter tillers (vegetative pathway) for perennation (Matthew 1992; Matthew et al., 1993). Also, a study of 'Grasslands Nui' (Korte 1986) showed the vegetative perennation pathway predominated in the first year after sowing, and the reproductive pathway in the second.

Environmental factors and cultural practices also influenced the seasonal pattern of tiller dynamics. L'Huillier (1987) showed that rotationally grazed dairy pastures, based on 'Grasslands Nui' ryegrass, had a low tiller density due to low tiller appearance and high death rates of vegetative tillers in late summer. Several factors could have been responsible, such as dry weather, a high stocking rate, insect damage or lack of nitrogen. Hunt and Mortimer (1982) showed that high nitrogen input rapidly increased appearance of perennial ryegrass tillers and was associated with a high death rate of young tillers. As reported in Chapter 3, nitrogen and irrigation treatments consistently increased ryegrass sward tiller density in summer, suggesting both treatments may have improved the persistence of ryegrass-dominant dairy pastures.

Reasons for the differences in tiller turnover during flowering of 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars are unclear. An understanding of the tiller population demography of both ryegrass cultivars under different management conditions could be helpful in explaining why the grass swards may differ in their tillering behaviour. Thus, a trial was started (Chapter 3), to provide information on the tillering patterns of 'Ellett' and 'Grasslands Ruanui' ryegrass. This chapter reports on the tiller demography of these ryegrass cultivars under nitrogen and irrigation treatments. Further information on the flowering behaviour of 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars will be discussed in Chapter 6.

5.2 Objectives

The objectives of this Chapter were:

(i) to compare the tiller population demography patterns of 'Ellett' and 'Grasslands Ruanui ryegrass cultivars by analysing tiller birth and death rates.

(ii) to characterise the seasonal changes in tiller population dynamics in relation to the morphology of each cultivar.

(iii) to determine the effects of irrigation and nitrogen treatments on the seasonal tillering patterns of both cultivars, and on sward persistence.

5.3 Materials and methods

5.3.1 Plant material

Endophyte-free lines of 'Ellett' and Grasslands Ruanui' ryegrass cultivars were sown on April 1996. In February 1999, 2-3 tillers from each of the plastic frames (Plate 5.1) still containing plants (6 in 'Ellett' and 7 in 'Grasslands Ruanui' plots) were randomly selected and tested for endophyte presence using an immunoblot technique (Gwinn et al., 1991). Of the 20 'Grasslands Ruanui' tillers tested only 1 contained endophyte; none of the 16 'Ellett' tillers contained endophyte, suggesting that the endophyte status of the study plant population was essentially the same as the seedlines sown in April 1996.

5.3.2 Trial design and statistical analysis

Details of the trial design and management are described in Chapter 3. The statistical analysis of all parameters was performed using the split-split-plot model as described in Chapter 3 (section 3.3.4.3). A model was developed to test tiller population profiles through time using the repeat measures mixed model in SAS, specifying a compound symmetry covariance structure. The model is defined as follows:

$$Y_{ijk}=\mu+b_i+c_j+t_k+(ct)_{jk}+P_l+e_{ijk}$$

where:

y_{ijk} is the observation on the i^{th} replicate, on the j^{th} cultivar, on the k^{th} date

μ is the overall mean

b_i is the effect of the i^{th} replicate, $i=1,2,3,4$

c_j is the effect of the j^{th} cultivar, $j=1,2$

t_k is the effect of the k^{th} date, $k=1,2,\ldots,20$

$(ct)_{jk}$ is the cultivar by date interaction term

P_l is a random effect for plot with a compound symmetry covariance structure

e_{ijk} is the residual error term

No data transformations were required, except for dead tillers, which were square root transformed to stabilise the variance.

5.3.3 Tiller dynamics

Ryegrass tiller dynamics was measured using the fixed quadrat method (Korte 1986). Counts of new and surviving tillers in the fixed quadrats were made at different time intervals, varying with season, over the two year field experiment (Table 5.1). Three circular plastic frames (64 mm diameter, Plate 5.1) per sub-plot were randomly located over ryegrass drill rows on the 5 September 1996; one such frame was similarly located in each sub-sub-plot (Fig. 5.1). The frames were permanently fixed at ground level such that a continuous drill row of ryegrass plant was enclosed and passed through the centre of each frame. The ryegrass clump size was approximately the same in each frame. Total frame number was 96 until the 28 January 1997 and 64 thereafter. Measurements were discontinued on two randomly chosen frames per sub-plot, representing 8 frames per replicate. This reduction in frame number was necessary because of time constraints and physical demands on technical staff.

On 17 September 1996, all live ryegrass tillers within each frame were counted and marked with rings made from short lengths of coloured split plastic tubing (2-5 mm

Table 5.1. Dates of tiller dynamics measurements in the field.

Date	Time interval between tiller measurements in days
17-Sep-1996	First measurement
8-Oct-1996	21
29-Oct-1996	21
25-Nov-1996	27
16-Dec-1996	21
6-Jan-1997	21
28-Jan-1997	22
17-Feb-1997	20
10-Mar-1997	21
1-Apr-1997	22
21-Apr-1997	20
3-Jun-1997	43
21-Jul-1997	48
1-Sep-1997	42
21-Oct-1997	50
17-Nov-1997	27
15-Dec-1997	28
12-Jan-1998	28
25-Feb-1998	44
30-Mar-1998	32

Colour code : Spring; Summer; Autumn; Winter.

Plate 5.1. Example of the plastic frame used to enclose 'Ellett' and 'Grasslands Ruanui' ryegrass plants for the field study of tiller dynamics. The circular frame was 64 mm diameter.

Plate 5.2. Plastic tags (2-5 mm, diameter) used to identify individual tillers within each circular frame. Different coloured tags identify different age-cohorts.

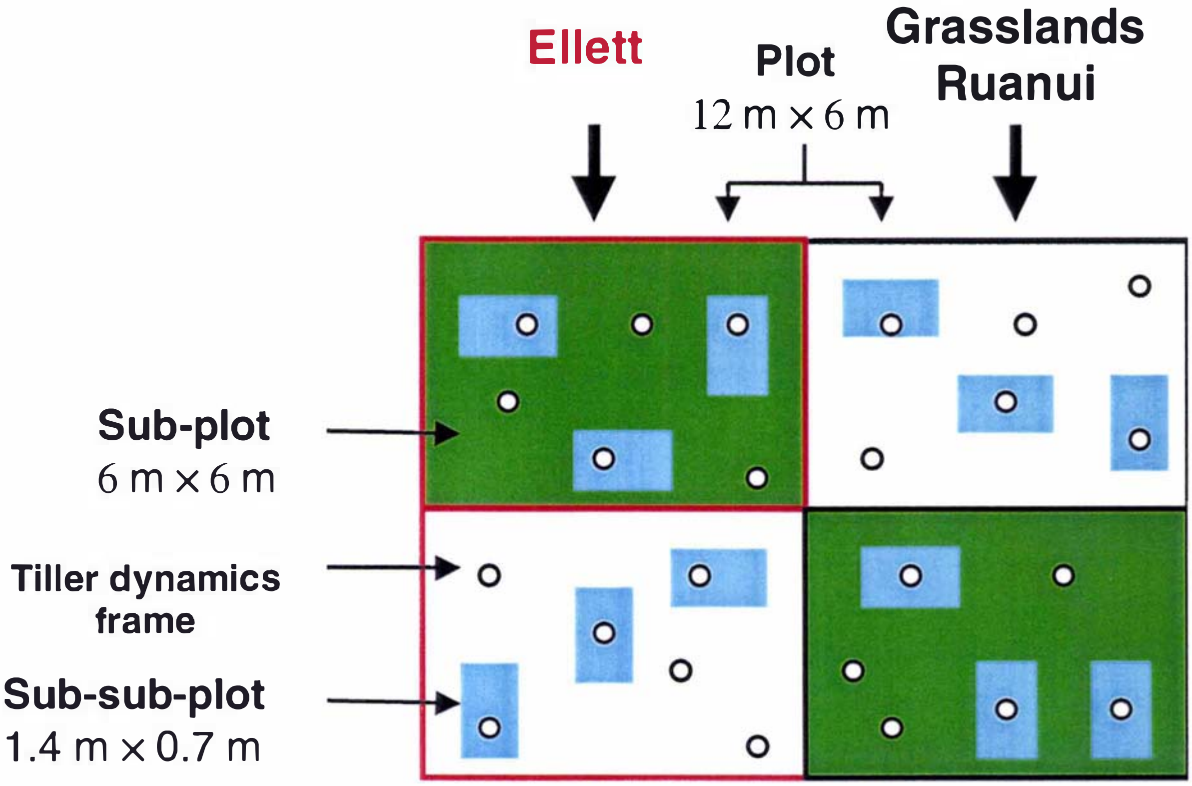


Figure 5.1. Representation of a replicate of the trial design. Nitrogen fertiliser was applied to green areas (sub-plot) and water was applied to blue areas (sub-sub-plot). White areas did not receive irrigation or nitrogen. The trial had four replicates. Circular plastic fixed quadrat frames (64 mm diameter) randomly positioned in plots, sub-plots and sub-sub-plots, were used to study the tiller dynamics of the ryegrass cultivars. There were 24 frames per replicate.

diameter, Plate 5.2). At each assessment, new tillers with at least one fully emerged leaf were counted and tagged using a different coloured tubing. Rings were removed from dead tillers and counted. Vegetative tillers were reclassified as reproductive when the first node became visible above ground level. Reproductive tillers were identified using the same procedure as for vegetative tillers. Reproductive tillers appeared from October to January. Tagged vegetative tillers, which were brown and withered or had no live leaves inside the sheath, were classified as dead. Reproductive tillers were classified as dead when the defoliated stem was brown and sapless. However, reproductive tillers with a brown defoliated stem that supported new daughter tillers were not recorded as dead.

5.3.4 Derived data

Variations within grass populations were studied based on the premise that changes in a population of individuals can be described by accounting for births and deaths occurring within the population (Harper 1980) (see Chapter 2). Tiller birth and death rates were therefore averaged over the whole tiller population representing each treatment.

5.3.4.1 Tiller birth rate

Relative tiller birth rate (B) was calculated as the number of new tillers recorded at each new date ($B_{(t+1)}$) divided by the total number of tillers at the previous date ($N_{(t)}$), (1).

$$B = B_{(t+1)} / N_{(t)} \qquad (1)$$

5.3.4.2 Tiller death rate

Relative tiller death rate (D) was calculated as the total number of dead tillers plus the number of lost or untagged tillers at each new date ($D_{(t+1)}$) divided by the total number of tillers at the previous date ($N_{(t)}$), (2).

$$D = D_{(t+1)} / N_{(t)} \qquad (2)$$

5.3.4.3 Tiller survival rate

Tiller survival rate (S) was calculated as the total number of tillers at each new date ($N_{(t+1)}$) divided by the total number of tillers at the previous date ($N_{(t)}$) (3). Tiller survival rate is also related to tiller death rate as defined below.

$$S = N_{(t+1)} / N_{(t)} = 1 - D \qquad (3)$$

Because the time between measurements differed over the seasons, ranging from 24 days in autumn to 46 days in winter, on average (Table 5.1), tiller birth, death and survival rates were expressed as tiller number per tiller over a standard interval of 30 days.

5.3.4.4 Tiller longevity

The tiller dynamics data sets are presented as diagrams showing numbers of live tillers in successive tiller age-cohorts, expressed as tiller number per unit area. Survival of tillers from each age-cohort was also examined by fitting an exponential decay curve expressed mathematically as:

$$N_{(t)} / N_{(0)} = e^{(b \times t)} \qquad (4)$$

where:

$N_{(0)}$ was the initial number of tillers at the beginning of the trial (17 September 1996), $N_{(t)}$ the number of tillers alive at each measurement date (from 8 October 1996 to 30 March 1998), and b is a constant. The parameter b was converted to a half-life ($t_{½}$), the time taken for half the tillers to die, expressed in days (5).

$$t_{½} = (\mathrm{Ln}\ 2)/\text{-}b \qquad (5)$$

The half-life of each tiller age-cohort was calculated and statistically analysed for the 59 frames for which measurements were continuous over two years.

5.3.5 Sward stability

A sward stability diagram was developed, based on the principle that for the population density of a grass sward to be maintained, there must be a balance between tiller birth and tiller survival. A relationship defining tiller population change using births and survival rates, has been developed by Matthew and Sackville Hamilton (C. Matthew and N. R. Sackville Hamilton, 1999, unpublished manuscript) from the matrix algebra equations of Leslie (1945) as follows (6):

$$P_t/P_0 = S \times (1 + B) \qquad (6)$$

where:

P_0 is the initial tiller population and P_t the total tiller population at time t. B and S are the birth and survival rates, respectively, of the total tiller population as defined above (section 5.3.4). This equation requires an assumption that tillers in field swards will not produce daughter tillers in the first month of their life. From equation (6) a sward stability diagram can be generated by plotting values for P_t/P_0 as contour lines (Fig. 5.2) indicating an increase or decrease in the tiller population. Population density is constant when P_t/P_0 equals 1. As an indication of the tiller population fluctuation, the contour lines of P_t/P_0 equal to 0.5 and 1.5 were plotted. When P_t/P_0 equals 0.5 or 1.5, the tiller population will decrease or increase by 50 %, respectively, in the time t_0 to t_1, in comparison with the contour line of Pt/P_0 equal to 1 (Fig. 5.2). Seasonal values of S and B for 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars under different nitrogen and irrigation treatments were plotted as co-ordinates to visualise the trajectory of the sward over the seasonal cycle. From equation (6), the P_t/P_0 index was calculated by using the value of B and S for each ryegrass cultivar under different nitrogen and irrigation treatments. The index P_t/P_0 was then plotted against time (month) and compared with the stable grass sward (i.e. $P_t/P_0 = 1$).

5.4 Results

Results from monitoring tillers in fixed quadrats were examined from four perspectives; the effects of tiller births and deaths on total tiller population, the longevity or survival of different tiller age-cohorts, seasonal population change (P_t/P_0, as set out in section 5.3.5), and in terms of the sward stability diagram presented previously in Fig. 5.2.

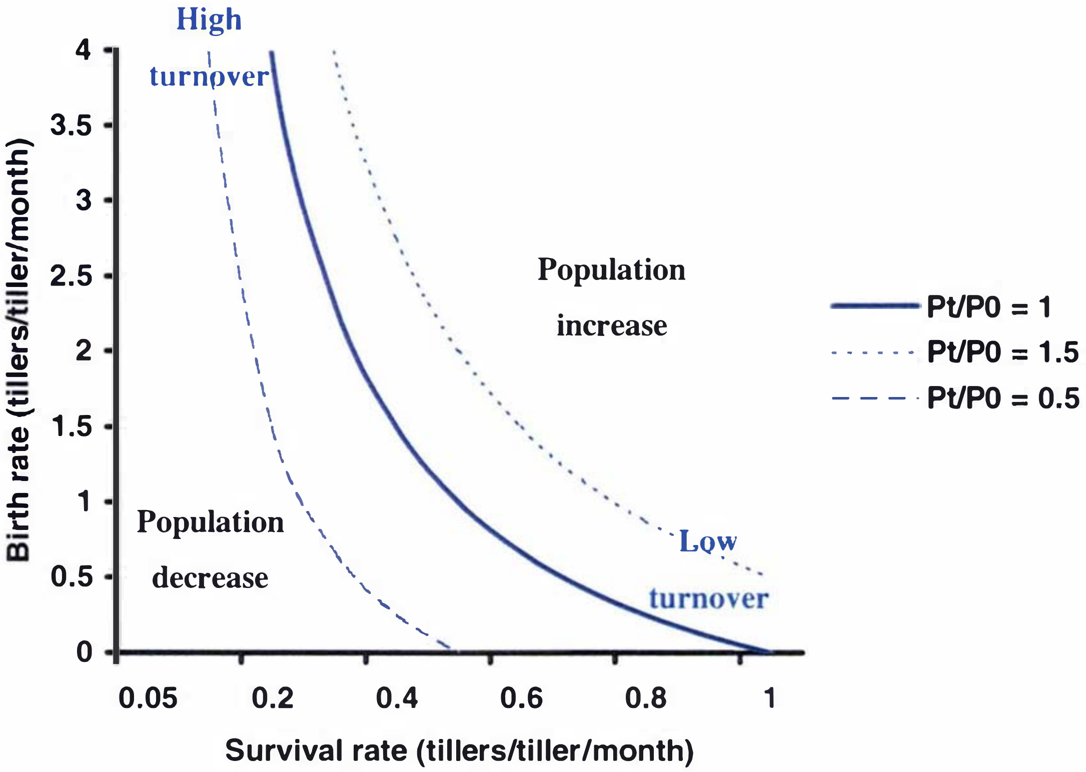


Figure 5.2. Sward stability diagram. Grass sward is stable when $P_t/P_0 = 1$. Grass sward increases or decreases its tiller population when $P_t/P_0 = 1.5$ or 0.5, respectively, in comparison with $P_t/P_0 = 1$.

5.4.1 Effects of tiller births and deaths on total tiller population

5.4.1.1 Seasonal pattern and cultivar effects on tiller dynamics

Data were first analysed by ANOVA (model as specified in section 3.3.4.3) with averages calculated for the seasonal periods outlined in Table 5.1. Then the SAS repeat measures mixed model (section 5.3.2) procedure was applied to test for differences in the way the tiller population changed over time (referred to below as the tiller population profile). The main effect of cultivar was tested for each measurement date (Appendix 5.1). 'Grasslands Ruanui' had a higher total tiller population than 'Ellett' ($P<0.1$) from the first measurement but cultivar differences were not statistically significant from April 1997 to December 1997 and again in March 1998 (Appendix 5.1). Cultivar tiller population profiles for total tiller number, averaged over nitrogen or irrigation treatments, were not significantly different.

The cultivar main effects for seasonal differences in tiller population are not shown graphically, but can be extracted from the graphs of nitrogen and irrigation effects in Fig. 5.3 to 5.6 (see below). Briefly, the highest total tiller population was observed in summer 1997 and 1998 ('Ellett' and 'Grasslands Ruanui': 33 975 and 46 793, respectively, in 1997; 29 726 and 41 864 tillers/m^2, respectively, in 1998, $P<0.05$) and the lowest in autumn 98 ('Ellett' and 'Grasslands Ruanui': 22 919 and 27 751 tillers/m^2, respectively, $P<0.01$). Tiller births in summer were high ('Ellett' and 'Grasslands Ruanui': 7658 and 9509 tillers/m^2, respectively, in 1997; 8552 and 10 313 tillers/m^2, respectively, in 1998) and deaths low ('Ellett' and 'Grasslands Ruanui': 2794 and 3893 tillers/m^2, respectively, in 1997; 6152 and 7733 tillers/m^2, respectively, in 1998) compared with autumn ($P<0.01$), when tiller births were low ('Ellett' and 'Grasslands Ruanui': 5148 and 7474 tillers/m^2, respectively, in 1997; 4321 and 3559 tillers/m^2, respectively, in 1998) and deaths high ('Ellett' and 'Grasslands Ruanui': 7173 and 11 079 tillers/m^2, respectively, in 1997; 11 780 and 15 414 tillers/m^2, respectively, in 1998). In winter 1997, tiller births ('Ellett' and 'Grasslands Ruanui': 9053 and 14 006 tillers number/m^2, respectively) were higher than tiller deaths ('Ellett' and 'Grasslands Ruanui': 8562 and 11 860 tillers number/m^2, respectively). A decline in tiller number was also observed during late spring 97 ('Ellett' and 'Grasslands Ruanui': 8868 and 10 061 tillers number/m^2, respectively) but not during the spring of the establishment year (1996).

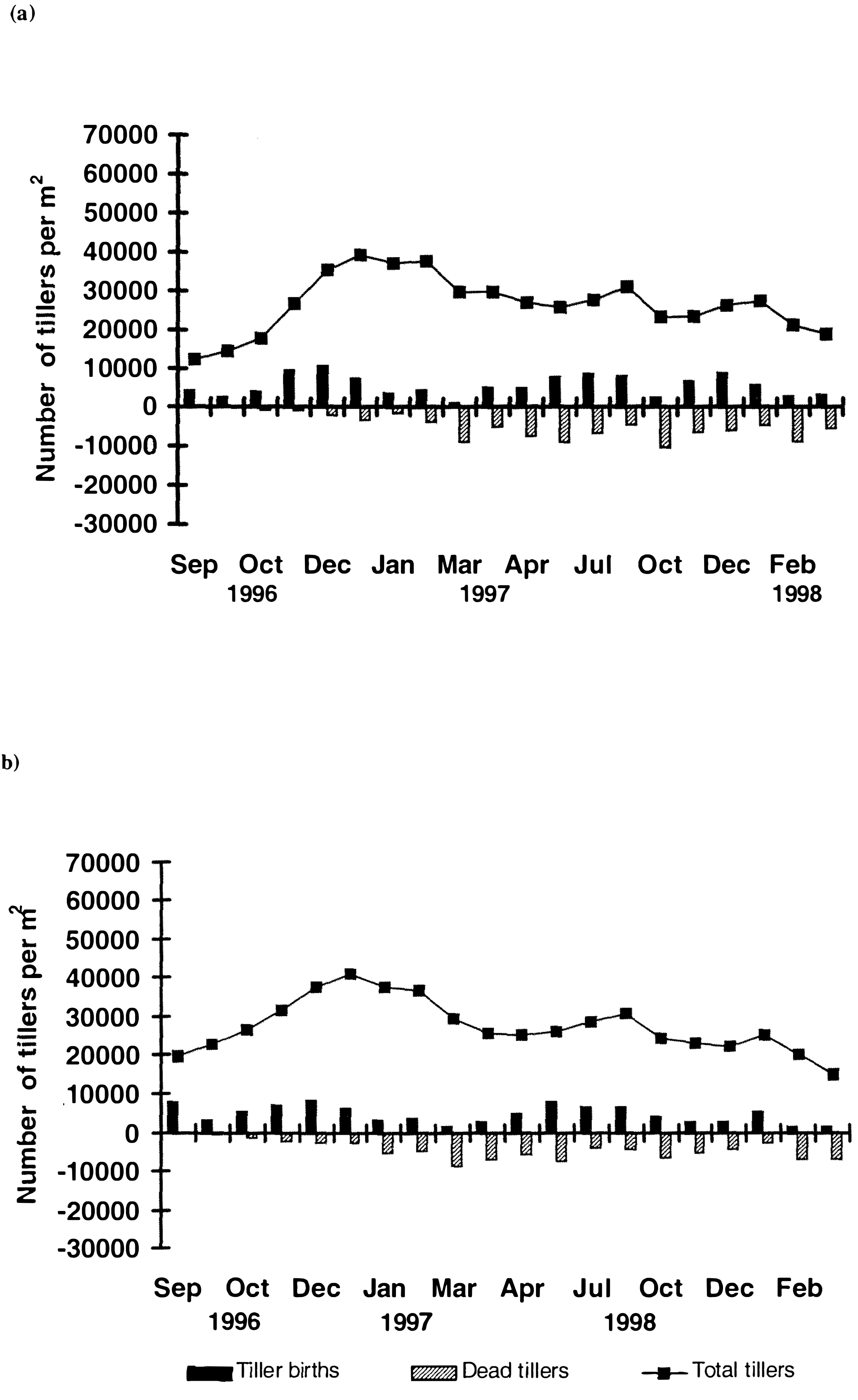


Figure 5.3. Average total tillers, and tiller births and deaths in fixed quadrats of (a) 'Ellett' and (b) 'Grasslands Ruanui' receiving no nitrogen (-N) and no irrigation (-Irr) (control treatment). See Table 5.1 for dates of successive measurements.

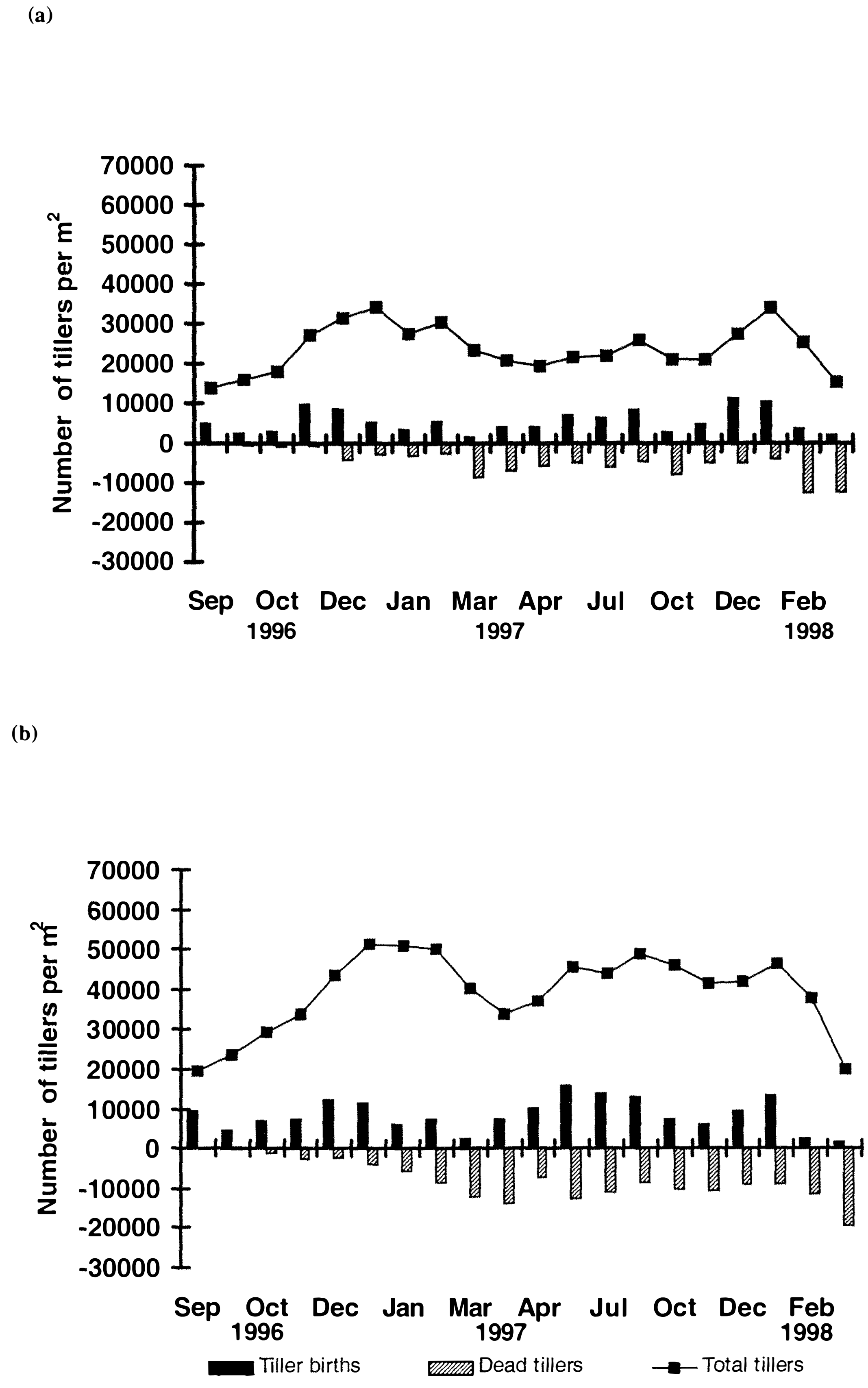


Figure 5.4. Average total tillers, and tiller births and deaths in fixed quadrats of (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses receiving irrigation (+Irr) and no nitrogen fertiliser (-N). See Table 5.1 for dates of successive measurements.

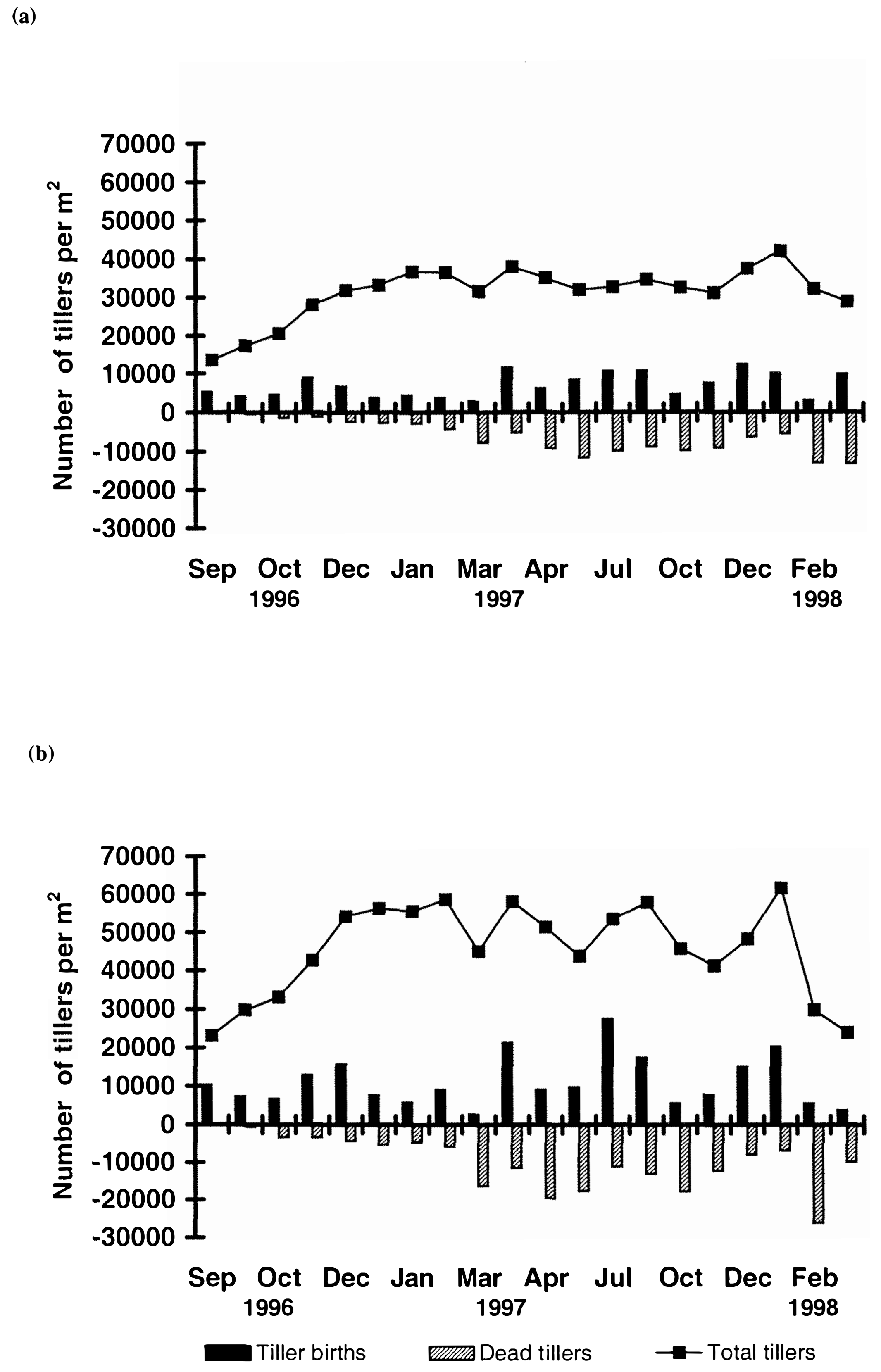


Figure 5.5. Average total tillers, and tiller births and deaths in fixed quadrats of (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses receiving nitrogen fertiliser (+N) and no irrigation (-Irr). See Table 5.1 for dates of successive measurements.

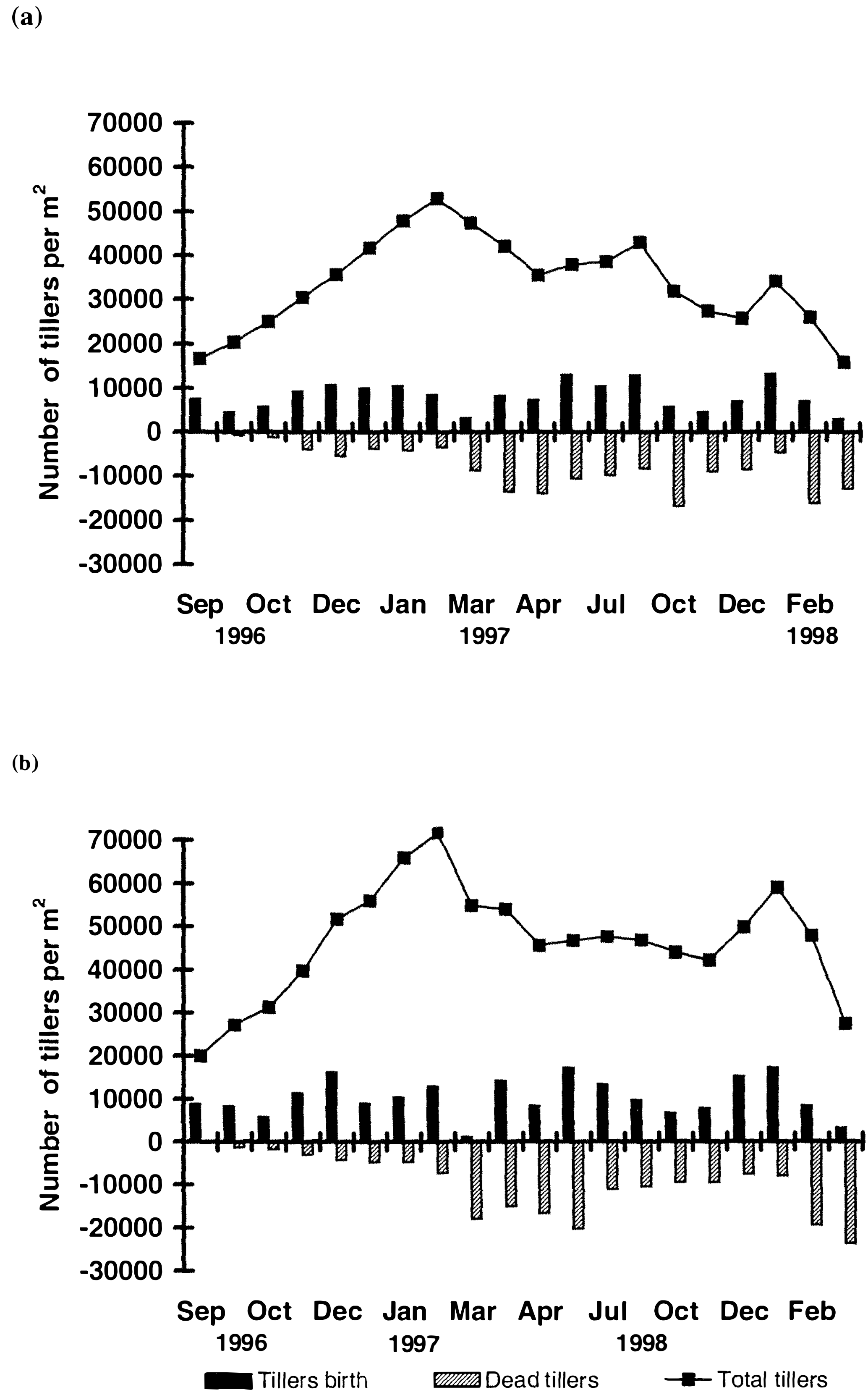


Figure 5.6. Average total tillers and tiller births and deaths in fixed quadrats of (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses receiving nitrogen fertiliser (+N) and irrigation (+Irr). See Table 5.1 for dates of successive measurements.

5.4.1.2 Effects of nitrogen and irrigation treatments on ryegrass tiller dynamics

Contribution of tiller births and deaths to change in the total tiller population of 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars from September 1996 to March 1998, and under different nitrogen and irrigation treatments is shown in Fig. 5.3 to 5.6. Nitrogen increased the total tiller population for both ryegrass cultivars from 16 December 1996 to 21 April 1997 ($P<0.05$) and from 15 December 1997 to 30 March 1998 ($P<0.05$) (Fig. 5.5 and 5.6). Tiller births increased with nitrogen on 28 January 1997 ($P<0.01$), 1 April 1997 and from 15 December 1997 to 30 March 1998 ($P<0.05$). Nitrogen also increased tiller deaths compared with the no nitrogen treatment and differences were significant on 1 September 1997, 8 October 1996 and 21 October 1997, 17 November, 21 April 1997, 5 February 1998, 10 March 1997 and 30 March 1998 ($P<0.05$).

A significant cultivar × nitrogen interaction on total tiller number was detected in December 1996 with 'Grasslands Ruanui' responding more to nitrogen than 'Ellett' ('Ellett' and 'Grasslands Ruanui' with nitrogen: 33 994 and 52 855 tillers/m^2, respectively; and without nitrogen 33 379 and 40 611 tillers/m^2, respectively, $P=0.05$).

Irrigation increased 'Grasslands Ruanui' total tiller population in both summers (from December to February/March) and did not change 'Ellett' total tiller number, but differences between the irrigated and unirrigated plots were not significant for both cultivars. Tiller births were increased by irrigation in both summers but differences were only significant on 28 January 1997, 17 February 1997 and 25 February 1998 ($P<0.05$). No significant effects of irrigation on tiller deaths were observed except on 1 April 1997 and 30 March 1998 when both ryegrass cultivars lost more tillers with irrigation compared to the unirrigated treatment ($P<0.05$). However, 'Grasslands Ruanui' lost more tillers than 'Ellett' in March 1998 giving rise to a significant cultivar × irrigation interaction ('Grasslands Ruanui' and 'Ellett' +Irr: 21 575 vs 12 552 tillers/m^2, respectively; –Irr: 8341 vs 9304 tillers/m^2, respectively, $P<0.05$).

On 1 September 1997, the two ryegrass cultivars did not respond in the same way to the nitrogen and irrigation treatments ($P<0.05$). Total tiller population of both ryegrass cultivars increased with nitrogen (Fig. 5.5 and 5.6) compared to the no nitrogen treatment (Fig. 5.3 and 5.4). 'Ellett' and 'Grasslands Ruanui' had a similar total tiller population ('Ellett' and 'Grasslands Ruanui': 31 120 and 30 759 tillers/m^2, respectively) in the control treatment (-N-Irr, Fig. 5.3), 'Ellett' decreased its tiller population with irrigation (-N+Irr, Fig. 5.4) whereas 'Grasslands Ruanui' total tiller population increased ('Ellett' and 'Grasslands Ruanui': 25 947 and 48 725 tillers/m^2, respectively) via higher tiller births ('Ellett' and 'Grasslands Ruanui': 8341 and 13 154 tillers/m^2, respectively), since tiller deaths for both ryegrass cultivars was similar ($P>0.1$). However, nitrogen and irrigation treatments (+N+Irr, Fig.5.6) increased 'Ellett' total tiller population compared to the nitrogen and unirrigated treatment (+N-Irr, Fig. 5.5) ('Ellett' with +N+Irr: 42 950 tillers/m^2; and with +N-Irr: 34 529 tillers/m^2) via higher tiller births and lower tiller deaths whereas 'Grasslands Ruanui' total tiller population decreased with nitrogen and irrigation ('Grasslands Ruanui' with +N+Irr: 46 720 tillers/m^2; and with +N-Irr: 57 908 tillers/m^2).

The repeated measures analysis of tiller population profile over time was carried out for the experimental main effects and differences between the nitrogen and no nitrogen treatments were significant ($P<0.05$), while irrigation treatments did not differ. Higher level interactions could not be tested because the SAS programme 'crashed' when this was attempted.

5.4.2 Age-cohort survival

5.4.2.1 Seasonal effects on ryegrass tiller longevity

Survival of tillers tagged at the start of the experiment, (age-cohorts '**a**' and '**b**') and those tagged monthly, are shown in Fig. 5.7 to 5.10. Tillers tagged at the start of the experiment (age-cohorts '**a**' and '**b**') survived the longest with an average half-life of 166 and 170 days, respectively, across all treatments (Table 5.2). Tillers tagged from September to December, lived longer (half-life of 137 days) than those tagged over the same period in 1997 (half-life of 99 days, Table 5.2). The age-cohort '**h**', which was tagged on 28 January 1997 had the shortest half-life (58 days on average). Tillers tagged in summer (age-cohorts from '**f**' to '**i**' and '**r**' to '**s**') and autumn (age-cohorts from '**j**' to '**l**') did not survive long with an average half-life of 58 to 96 days in summer and 78 to 89 days in autumn. Age-cohorts '**m**' and '**n**', which were tagged in winter (June and July 1997) survived longer than the previous age-cohorts (from '**g**' to '**l**') with a half-life averaging 110 days. During spring, tillers tagged in November had a shorter half-life (108 and 100 days in 1996 and 1997, respectively) than those tagged in October (134 and 119 days in 1996 and 1997, respectively) (Table 5.2).

5.4.2.2 Effects of nitrogen and irrigation on tiller longevity of 'Ellett' and 'Grasslands Ruanui' ryegrasses

Nitrogen reduced the half-life of tiller age-cohorts '**a**' and '**b**' tagged in September 1996 (+N: 151 and 143 days, respectively; -N: 181 and 197 days, respectively, $P<0.05$), '**o**' tagged in September 1997 (+N: 73 days; -N: 86 days, $P<0.05$), and '**m**' tagged in June 1997 (+N: 116 days; -N: 137 days, $P<0.05$) despite no nitrogen being applied in that month.

A significant cultivar × nitrogen × irrigation interaction was found for tiller age-cohorts '**b**' and '**q**' tagged in September 1996 and November 1997, respectively (Table 5.2). 'Grasslands Ruanui' had a longer half-life when both nitrogen and irrigation were applied compared with the nitrogen and no irrigation treatment, whereas 'Ellett' showed the opposite trends. Both ryegrass cultivars had a similar half-life for the tiller age-cohort '**q**' under the control treatment and the irrigation with no nitrogen treatment (Table 5.2). An irrigation effect was also observed for tillers of both ryegrass cultivars tagged in November 1997; they had a longer half-life with irrigation than without (+Irr: 112 days; -Irr: 88 days, $P<0.05$) (Table 5.2).

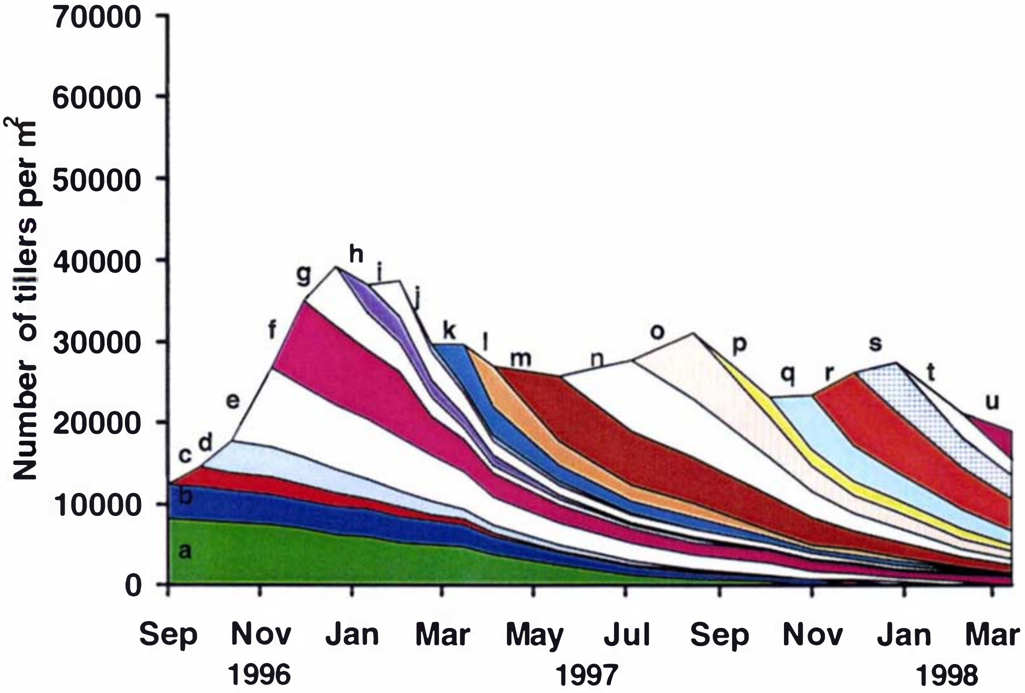
5.4.3 Seasonal tiller population change

From the sward stability equation defined in section 5.3.5, a tiller population index (P_t/P_0) was determined at monthly intervals for each cultivar under different nitrogen and irrigation treatments (Fig. 5.11 to 5.14). The tiller population of both ryegrass cultivars was plotted against a constant population density with P_t/P_0 equal to 1 from 9 October 1996 to 30 March 1998.

5.4.3.1 Season and cultivar effects

As in earlier sections in this chapter, main effects of season and cultivar are not shown in a separate figure, but can be seen in Fig. 5.11 to 5.14, for nitrogen and irrigation treatments (see below). Tiller population increased during the first spring-early summer period, fell in autumn, tended to increase in the following winter and

(a)



(b)

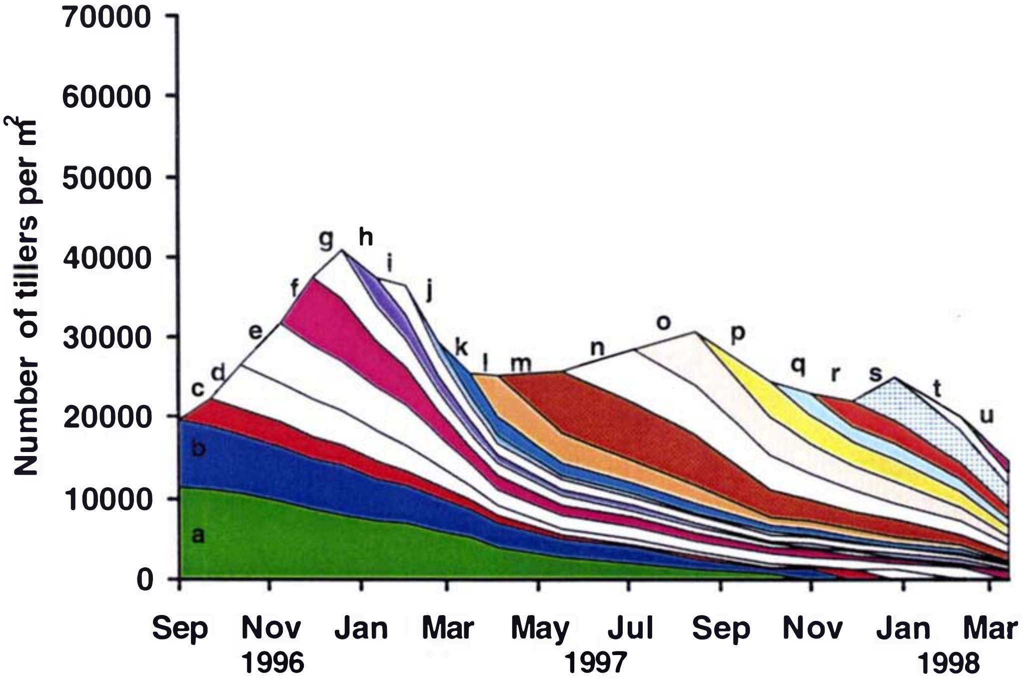
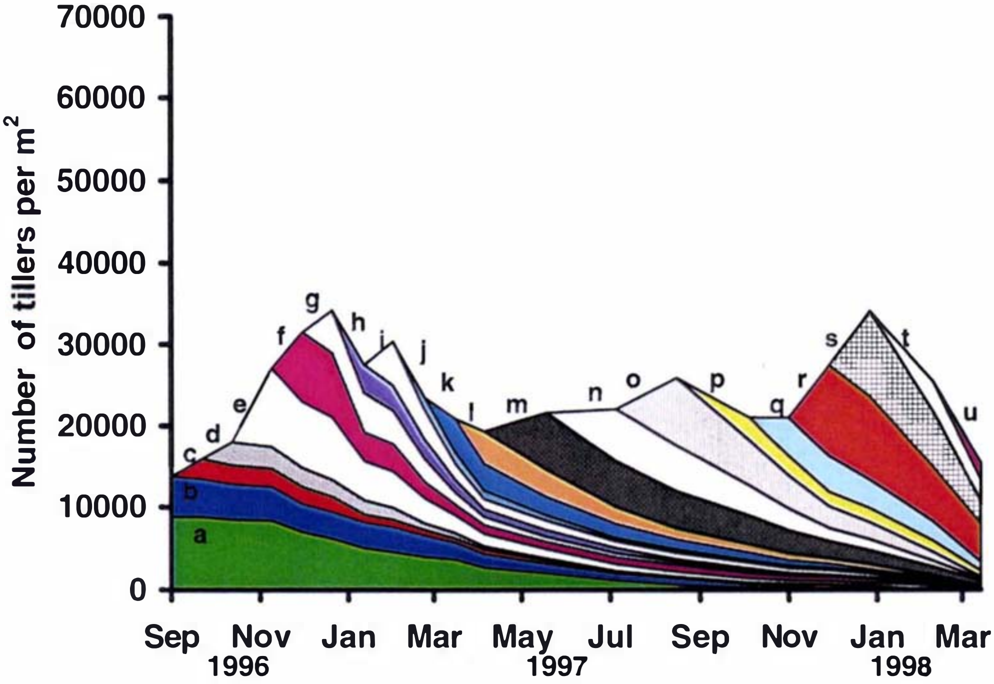


Figure 5.7. Tiller age-cohort diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with no nitrogen fertiliser (-N) and no irrigation (-Irr) (control treatment).

(a)



(b)

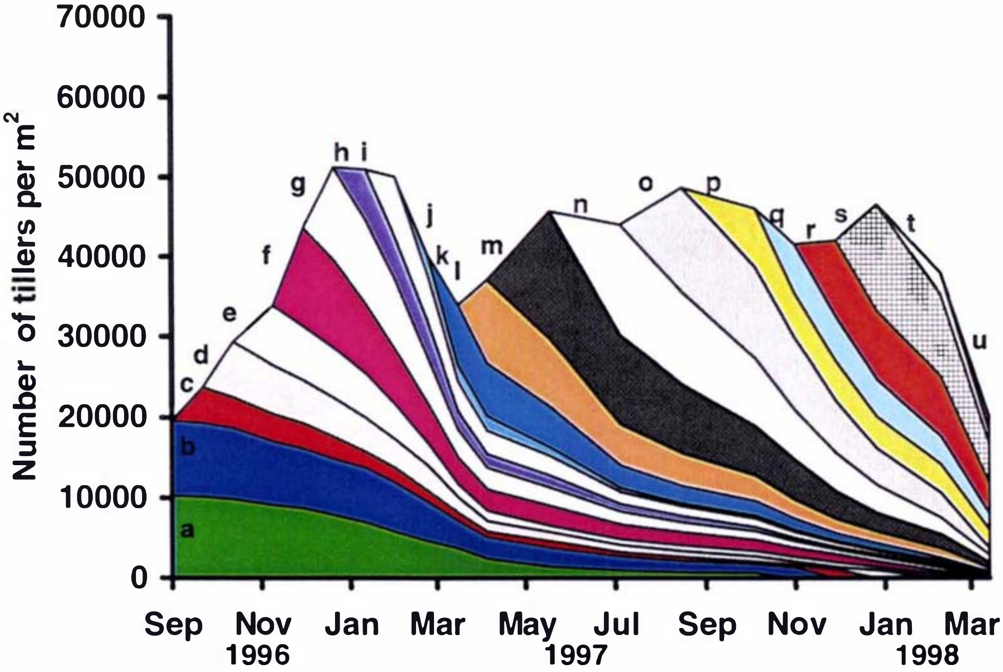
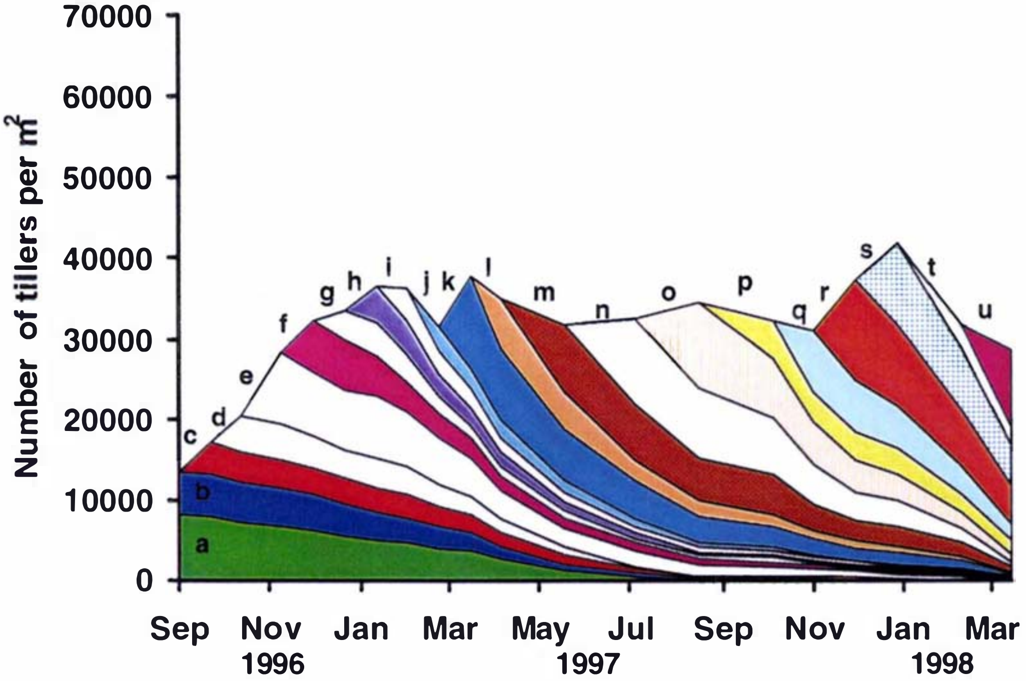


Figure 5.8. Tiller age-cohort diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with no nitrogen fertiliser (-N) and with irrigation (+Irr).

(a)



(b)

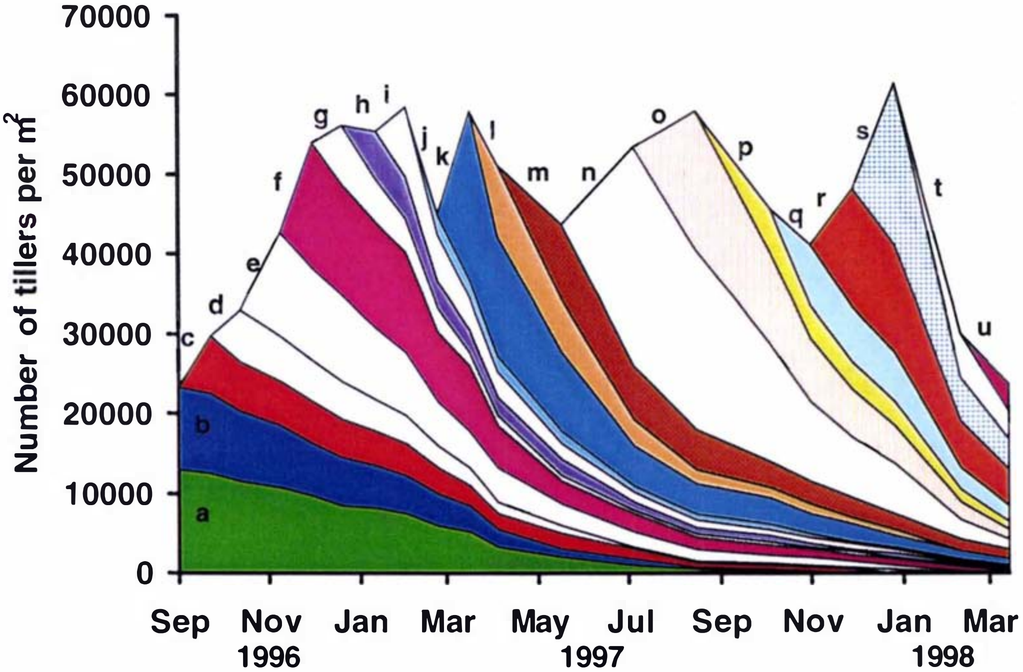
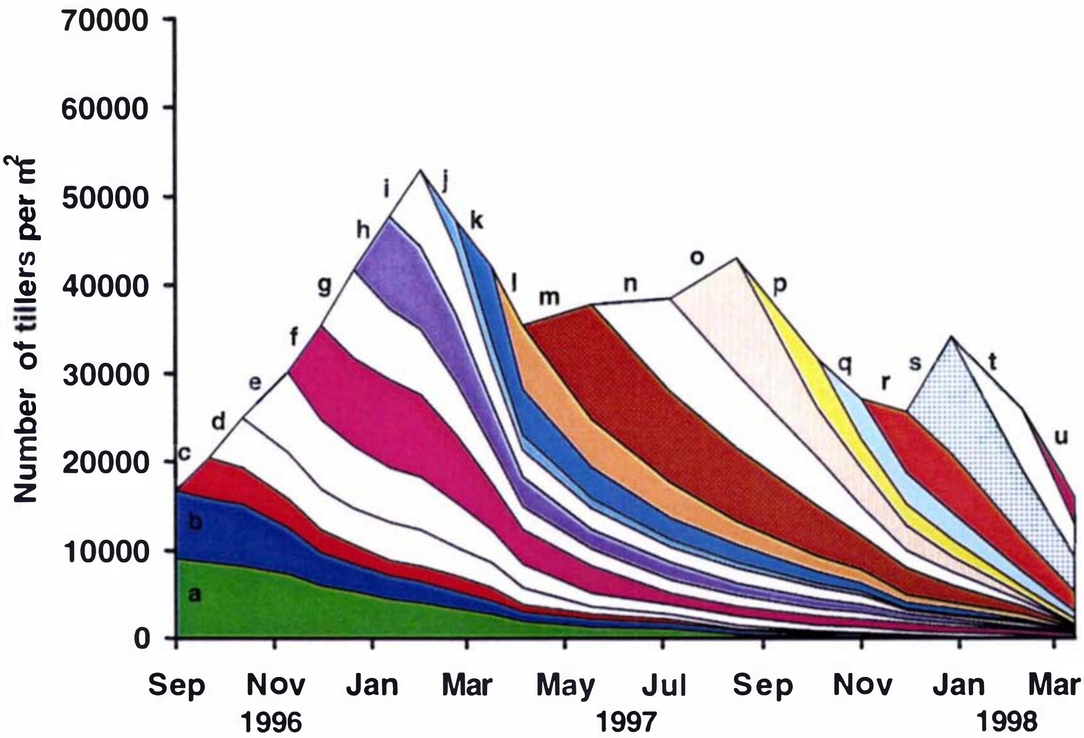


Figure 5.9. Tiller age-cohort diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with nitrogen fertiliser (+N) and no irrigation (-Irr).

(a)



(b)

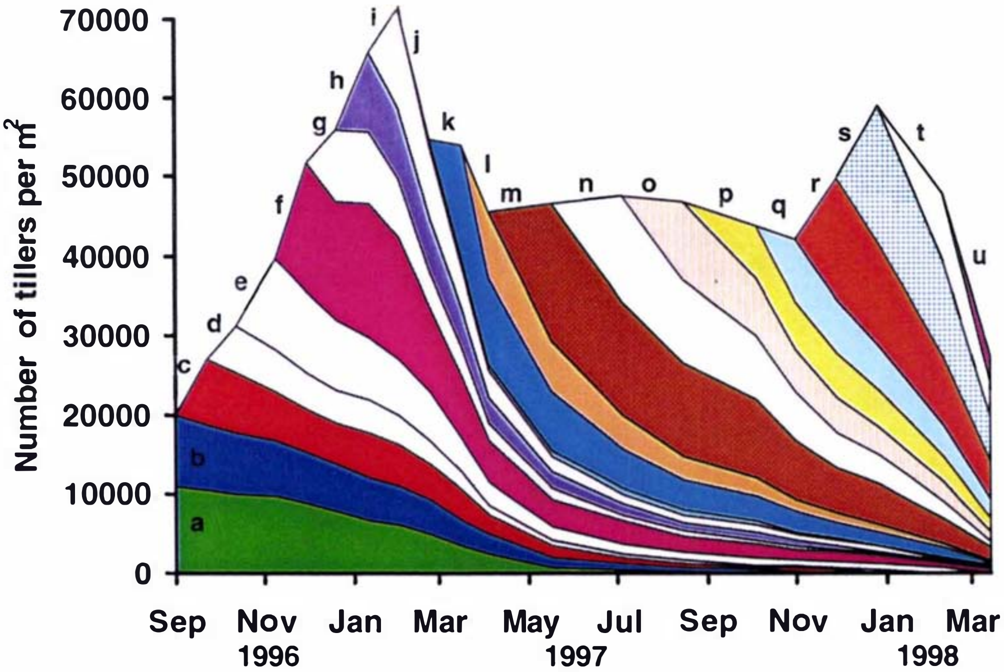


Figure 5.10. Tiller age-cohort diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with nitrogen fertiliser (+N) and irrigation (+Irr).

Table 5.2. Half-life (in days) of each tiller age-cohort for 'Ellett' (E) and 'Grasslands Ruanui' (R) ryegrasses receiving nitrogen (+N) or no nitrogen (-N) fertiliser and irrigation (+Irr) or no irrigation (-Irr) during the field experiment.

		Half-life									
		-N-Irr		**-N+Irr**		**+N-Irr**		**+N+Irr**			
Age group	Tagging date	E	R	E	R	E	R	E	R	Sig.	SED[a]
	1996										
a	**17-Sep**	196	171	190	165	166	141	143	156	NS	17.4
b	**17-Sep**	203	206	195	184	175	124	112	159	*	32.4
c	**8-Oct**	184	178	176	140	159	121	106	139	NS	46.9
d	**29-Oct**	289	119	115	110	109	102	119	110	NS	88.9
e	**25-Nov**	134	127	100	89	108	100	98	109	NS	16.3
f	**16-Dec**	91	84	94	79	98	95	98	92	NS	15.7
	1997										
g	**6-Jan**	72	55	54	67	73	66	77	65	NS	15.1
h	**28-Jan**	49	52	60	64	55	64	63	60	NS	11.4
i	**17-Feb**	90	169	46	40	60	55	72	39	NS	51.4
j	**10-Mar**	52	86	101	81	88	75	48	94	NS	30.2
k	**1-Apr**	74	102	106	105	114	66	58	83	NS	74
l	**21-Apr**	66	89	97	98	87	80	86	93	NS	14.5
m	**3-Jun**	138	150	146	112	123	120	102	118	NS	16.3
n	**21-Jul**	104	122	99	96	91	81	71	92	NS	17.6
o	**1-Sep**	74	99	72	98	78	70	57	86	NS	16.5
p	**21-Oct**	170	107	208	98	113	73	59	124	NS	74.9
q	**17-Nov**	78	87	146	116	96	91	66	118	*	37.1
r	**15-Dec**	102	114	102	97	91	70	109	87	NS	29.3
	1998										
s	**12-Jan**	82	127	55	68	75	45	48	67	NS	41.8
T	**25-Feb**										
u	**30-Mar**										

[a] Standard error of the difference between paired means

NS: Not significant; $P<0.05$ (*); **colour code**: **spring**; **summer**; **autumn**; **winter**;

Tillers tagged on 25 February and 30 March 1998 were not assessed long enough to estimate their half-life.

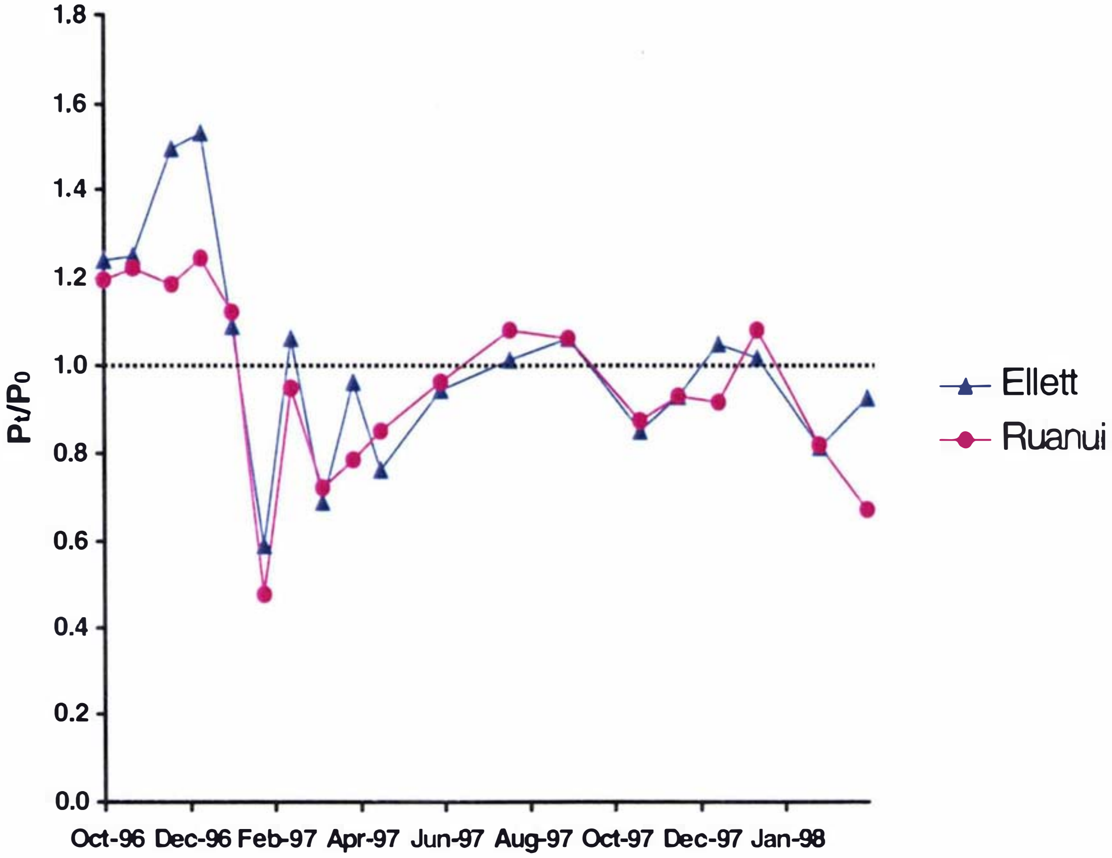


Figure 5.11. Changes in population index (P_t/P_0) over time for 'Ellett' and 'Grasslands Ruanui' cultivars with no nitrogen fertiliser and with no irrigation (control treatment, -N-Irr). See Table 5.1 for dates of successive measurements, beginning on 8 October 1996.

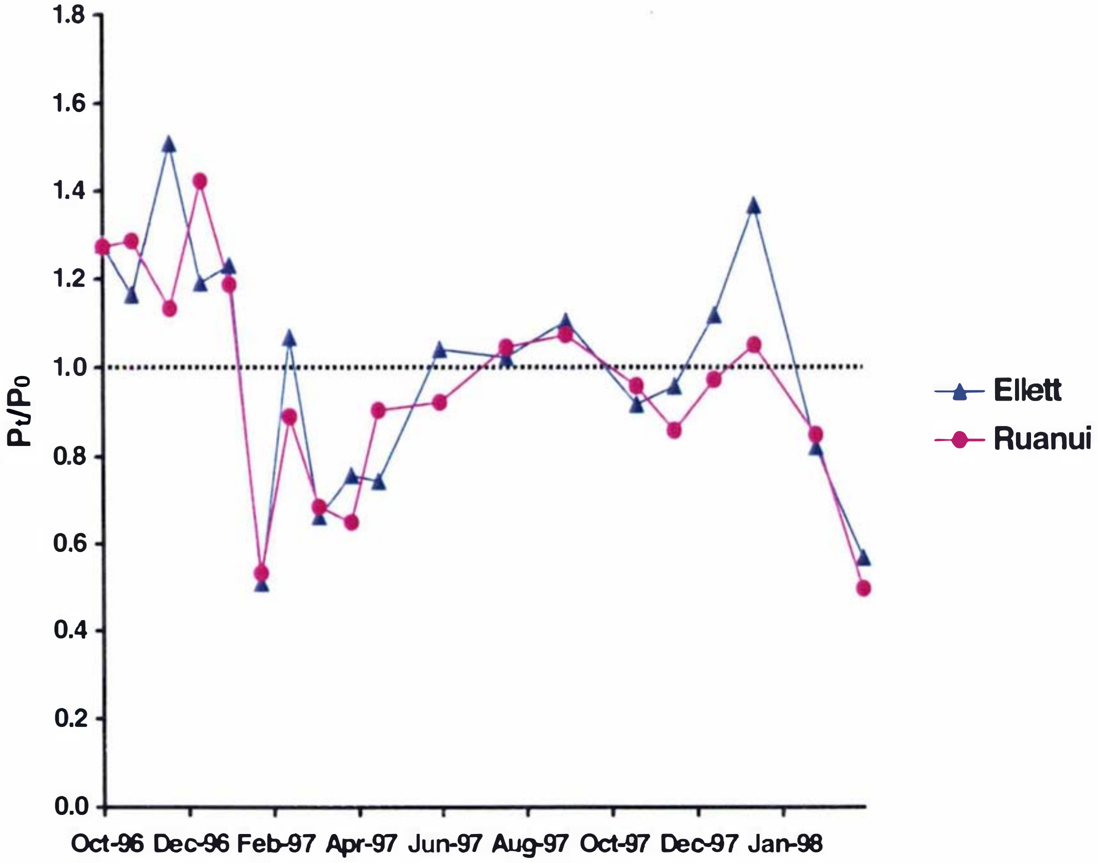


Figure 5.12. Changes in population index (P_t/P_0) over time for 'Ellett' and 'Grasslands Ruanui' cultivars with no nitrogen fertiliser and with irrigation (-N+Irr). See Table 5.1 for dates of successive measurements, beginning on 8 October 1996.

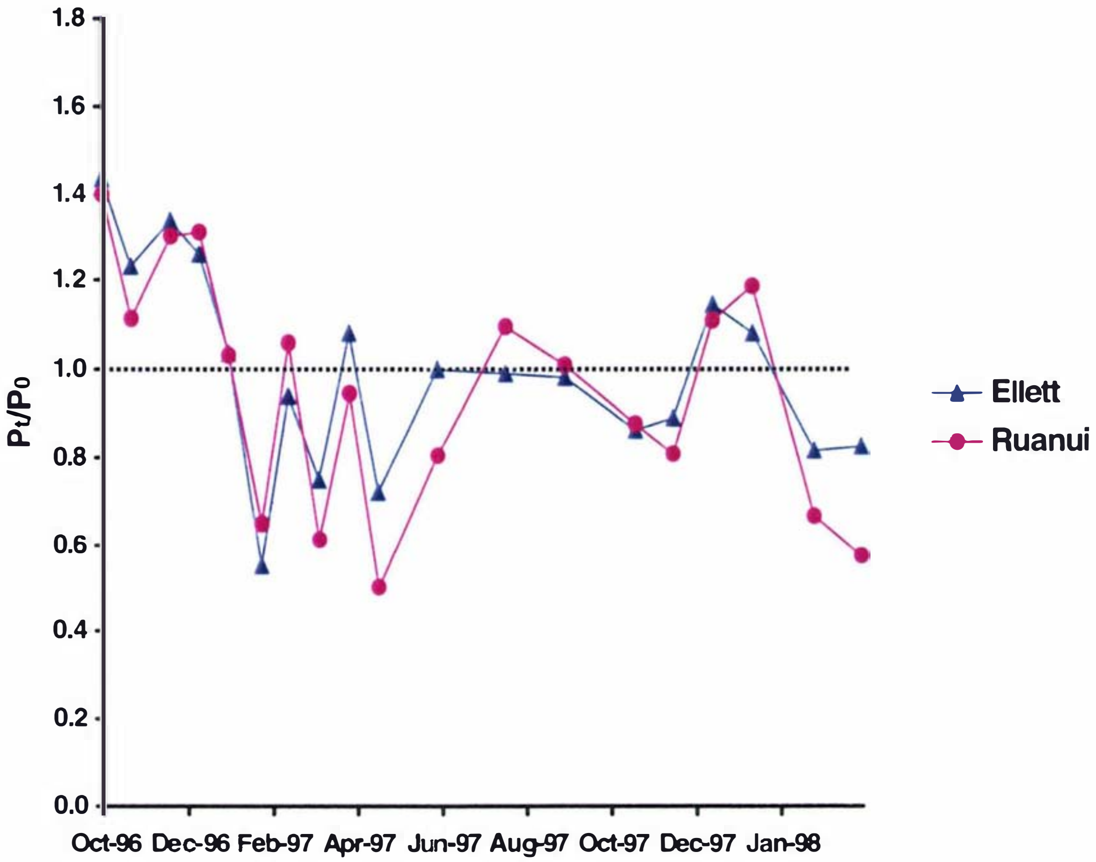


Figure 5.13. Changes in population index (P_t/P_0) over time for 'Ellett' and 'Grasslands Ruanui' cultivars with nitrogen fertiliser and with no irrigation (+N-Irr). See Table 5.1 for dates of successive measurements, beginning on 8 October 1996.

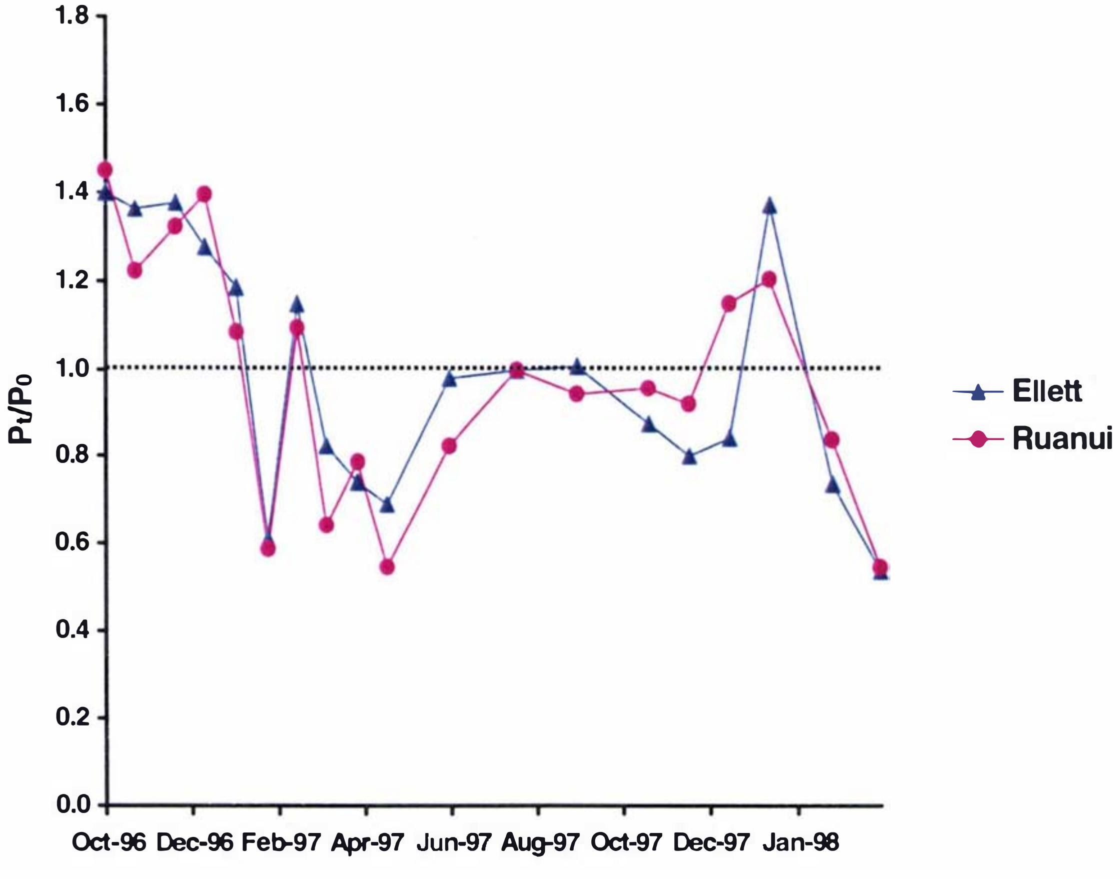


Figure 5.14. Changes in population (P_t/P_0) over time for 'Ellett' and 'Grasslands Ruanui' cultivars with nitrogen fertiliser and with irrigation (+N+Irr). See Table 5.1 for dates of successive measurements, beginning on 8 October 1996.

summer, but showed a decrease during the flowering period in the second spring. This feature of the data is dealt with more fully in section 5.4.4 below.

For the average across nitrogen and irrigation treatments, 'Ellett' had a higher P_t/P_0 than 'Grasslands Ruanui' in June 1997 (0.991 vs 0.880, $P<0.001$) but by July 1997 it had a lower P_t/P_0 than 'Grasslands Ruanui' (1.006 vs 1.055, $P<0.05$, Fig. 5.11 to 5.14).

5.4.3.2 Nitrogen and irrigation effects

Nitrogen resulted in a decreased tiller population averaged over ryegrass cultivars in September 1997 (+N: 0.986 vs –N: 1.055, $P<0.05$) and February 1998 (+N: 0.765 vs –N: 0.828, $P<0.001$) (Fig. 5.13 and 5.14). However, 'Ellett' and 'Grasslands Ruanui' did not respond in the same way to nitrogen treatment in March and December 1997 (Fig. 5.13 and 5.14) giving rise to a significant cultivar × nitrogen interaction.

In March 1997, 'Ellett' responded to nitrogen by an increase in P_t/P_0 (+N+Irr: 0.827 and +N-Irr: 0.748) (Fig. 5.13 and 5.14) via an increase of both survival and birth rates compared to the no nitrogen treatment (-N+Irr: 0.662 and –N-Irr: 0.692) (Fig. 5.11 and 5.12). In contrast with 'Ellett', 'Grasslands Ruanui' responded to nitrogen treatment by a decrease of P_t/P_0 (+N+Irr: 0.643 and +N-Irr: 0.611) (Fig. 5.13 and 5.14) via a decrease of both survival and birth rates compared to the no nitrogen treatment (-N+Irr: 0.685 and –N-Irr: 0.723) (Fig. 5.11 and 5.12).

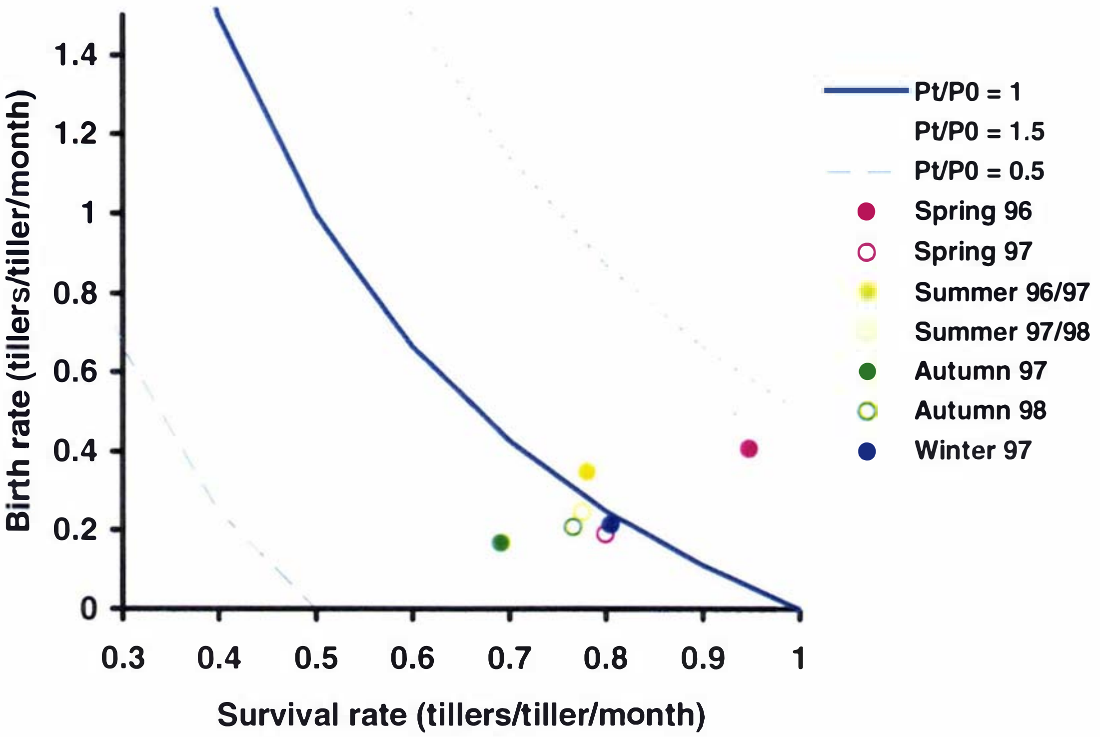
Conversely, in December 1997, nitrogen decreased P_t/P_0 for 'Ellett' (+N+Irr: 0.845 and +N-Irr: 1.148) via a decrease of birth rate but increased it for 'Grasslands Ruanui' (+N+Irr: 1.148 and +N-Irr: 1.109) (Fig. 5.13 and 5.14) via an increase of birth rate compared to the no nitrogen treatment ('Ellett' vs 'Grasslands Ruanui, -N+Irr: 1.118 vs 0.975 and –N-Irr: 1.047 vs 0.916) (Fig. 5.11 and 5.12).

No significant effects of irrigation on P_t/P_0 were observed.

5.4.4 Seasonal sward stability

Seasonal tiller population fluctuations for each cultivar and with different nitrogen and irrigation treatments are presented in Fig. 5.15 to 5.18.

(a)



(b)

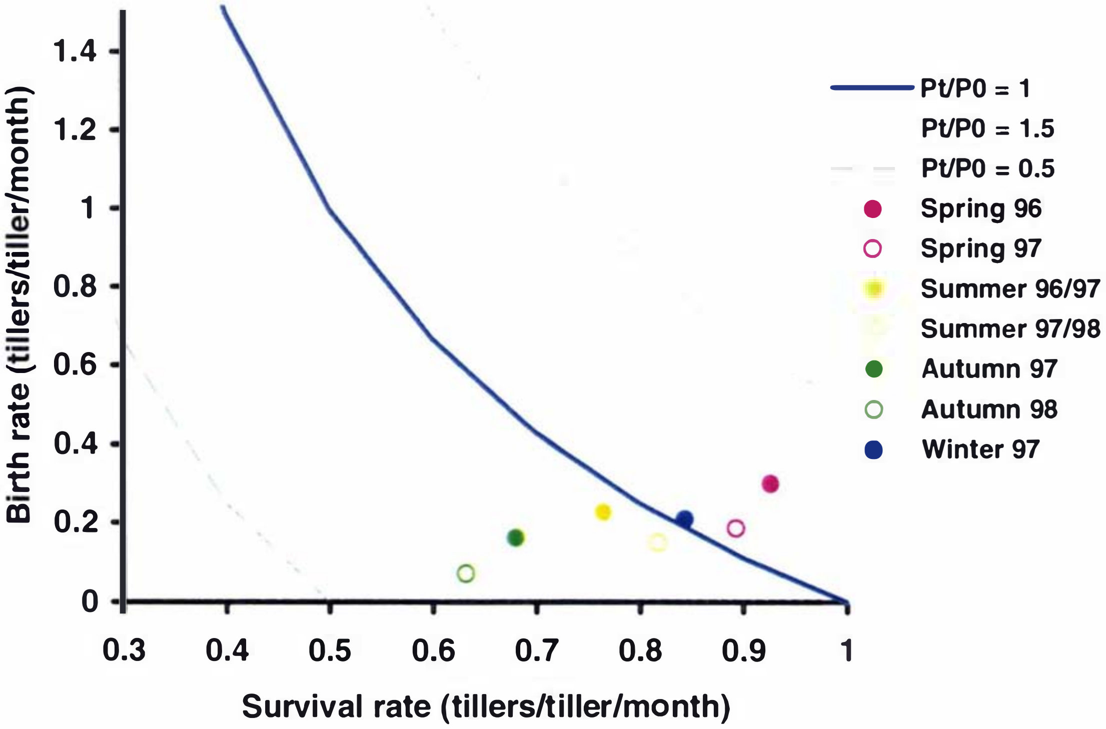
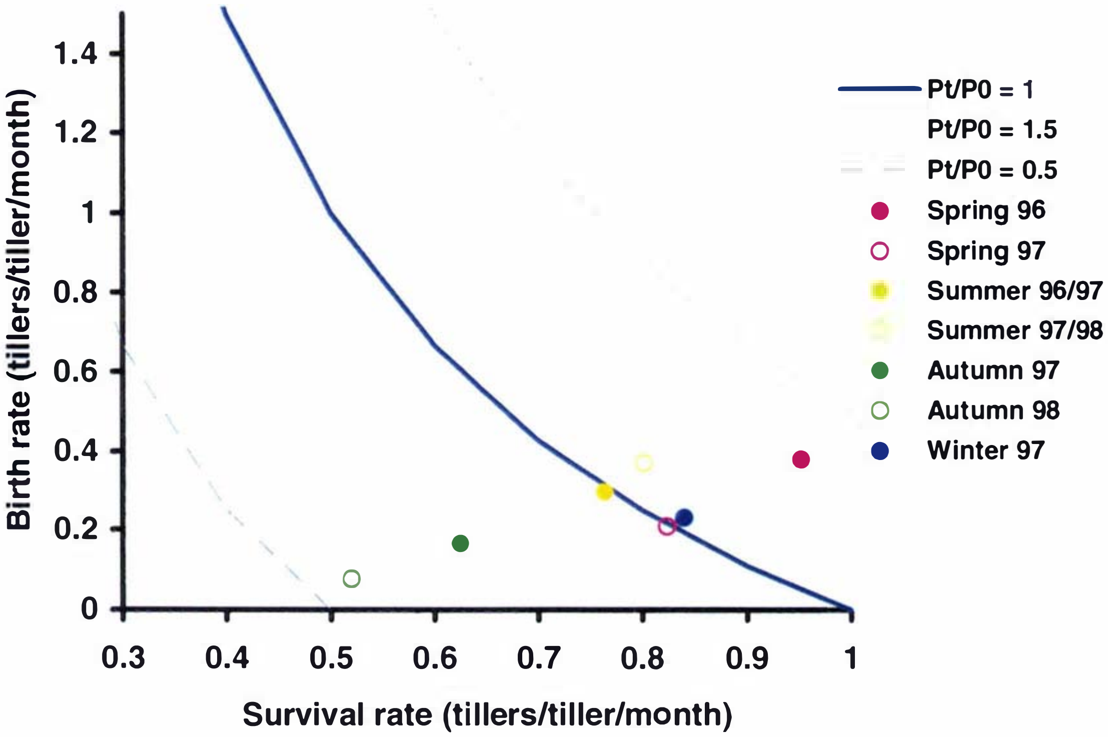


Figure 5.15. Seasonal sward stability diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with no nitrogen fertiliser and with no irrigation (control treatment, -N-Irr).

(a)



(b)

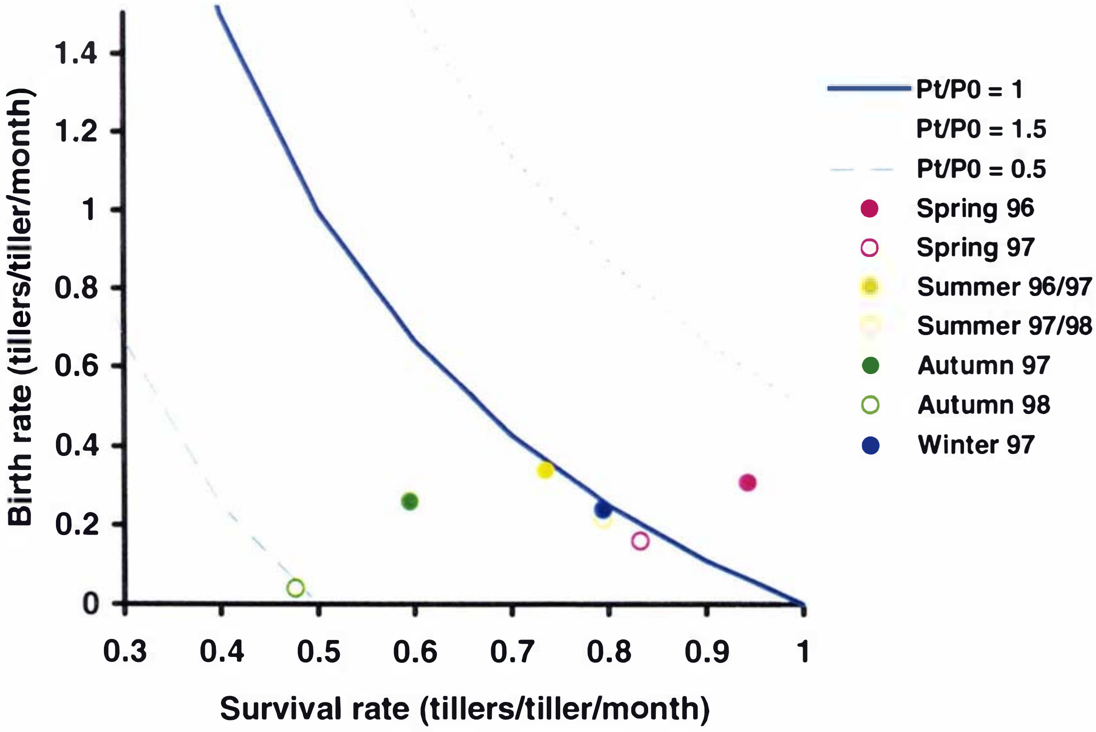
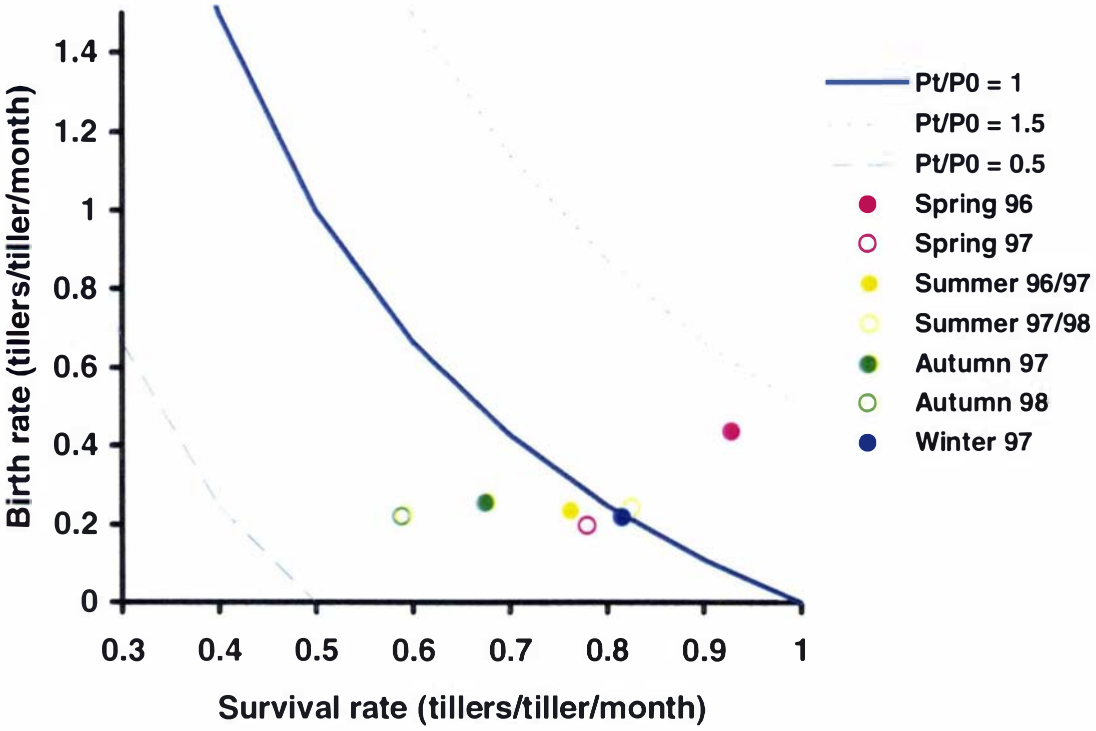


Figure 5.16. Seasonal sward stability diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with no nitrogen fertiliser and with irrigation (-N+Irr).

(a)



(b)

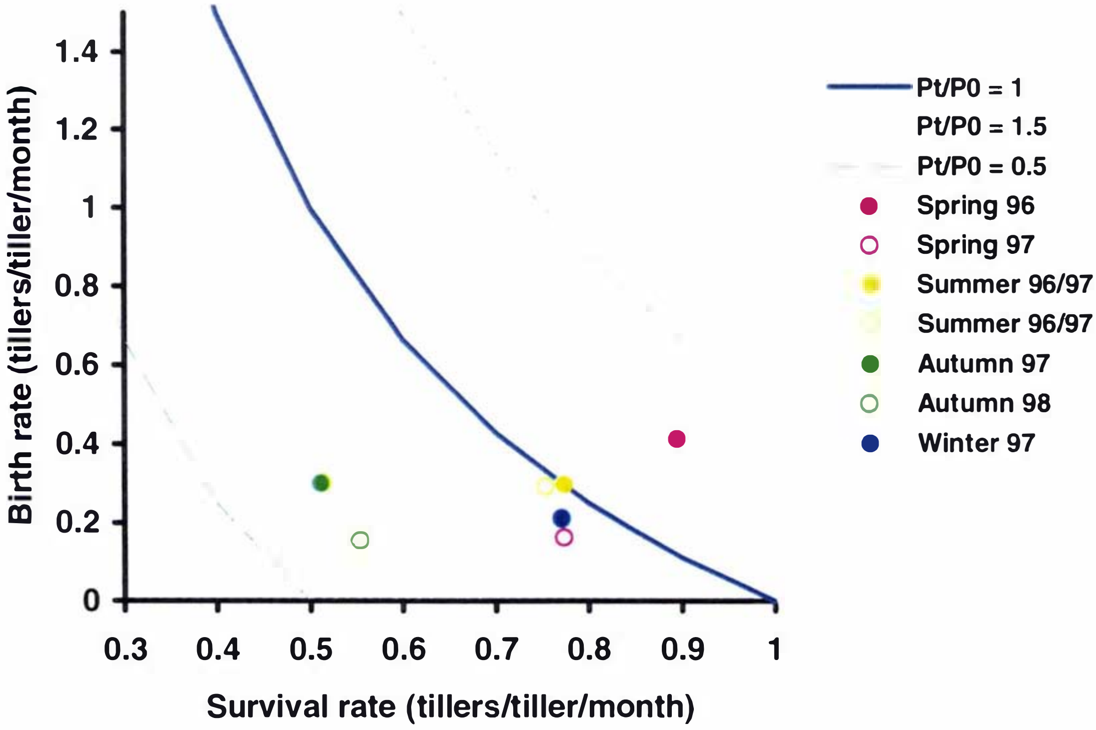
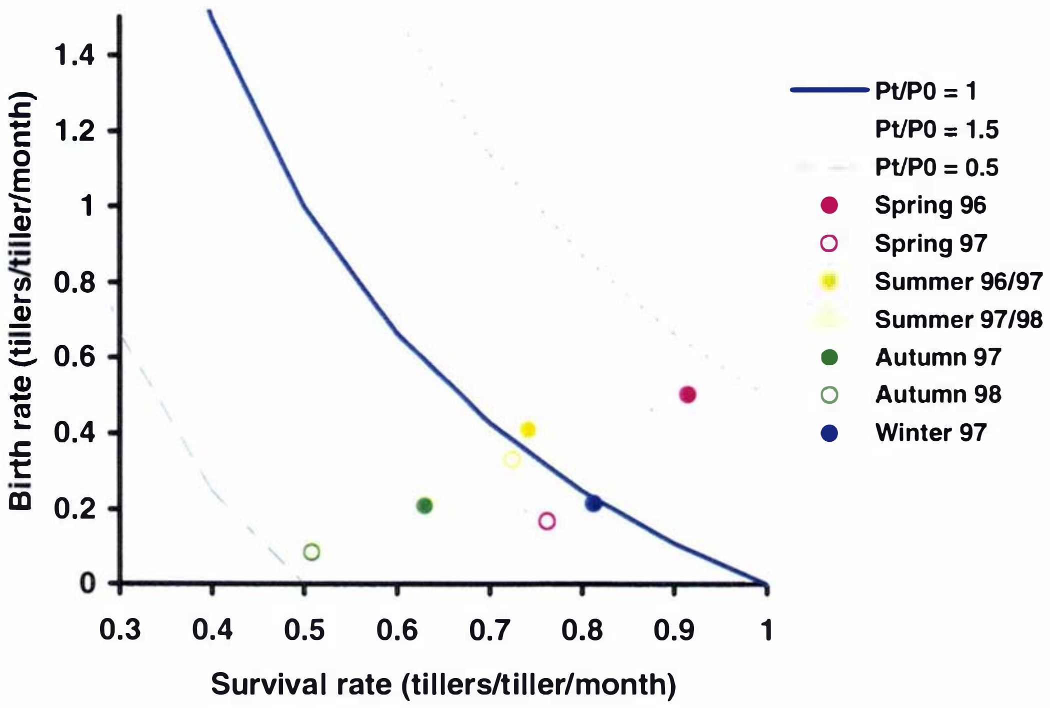


Figure 5.17. Seasonal sward stability diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with nitrogen fertiliser and no irrigation (+N-Irr).

(a)



(b)

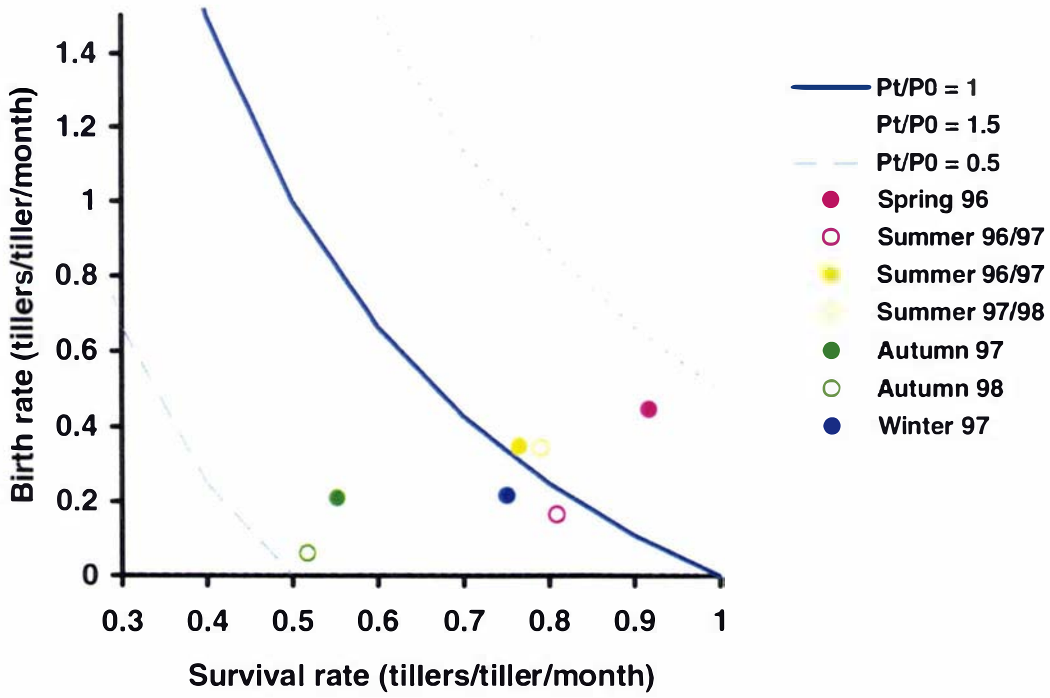


Figure 5.18. Seasonal sward stability diagram for (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses with nitrogen fertiliser and with irrigation (+N+Irr).

5.4.4.1 Effects of seasonal birth and survival rates on sward stability

The population increase in the early phase of the experiment (section 5.4.3.1) is clearly seen in the position of the sward in the stability diagrams in spring 1996, and results from high birth and survival rates (average over treatments and cultivars was 0.399 and 0.928 tillers/tiller/month, respectively). During the two summers, tiller populations were approximately stable with an average birth rate of 0.311 and 0.272 tillers/tiller/month and an average survival rate of 0.826 and 0.753 tillers/tiller/month in 1996/97 and 1997/98, respectively. Tiller birth and survival rates decreased consistently in both autumns (1997: 0.216 and 0.620; 1998: 0.114 and 0.570 tillers/tiller/month) resulting in an average P_t/P_0 of less than 1 (1997: 0.822 and 1998: 0.720). Overall, ryegrass tiller populations were more stable in winter than in other seasons with P_t/P_0 averaged across cultivar, nitrogen and irrigation treatments close to 1 (0.983). A stable tiller population in winter was attributable to a high survival rate (0.804 tillers/tiller/month) and a medium birth rate (0.220 tillers/tiller/month).

5.4.4.2 The effects of nitrogen and irrigation on seasonal ryegrass tiller populations

Nitrogen decreased the ryegrass tiller population (Fig. 5.17 and 5.18) in spring 1997 (P_t/P_0, +N: 0.986; -N: 1.076, $P<0.01$) and autumn 1998 (P_t/P_0, +N: 0.694; -N: 0.747, $P=0.06$) compared with the no nitrogen treatment (Fig. 5.15 and 5.16).

No significant effects of irrigation were observed on ryegrass tiller population changes over the seasons.

5.5 Discussion

5.5.1 Tiller dynamics

5.5.1.1 Methodology

Field studies of tiller dynamics are not as numerous as those dealing with single plants in controlled environments and, in view of the many interacting factors (for example, grazing, urine, dung and earthworm activity) which influence this process, interpretation of field experiments presents some difficulties. Cow dung and urine randomly affected the growth and survival of tillers of 'Ellett' and 'Grasslands Ruanui' in frames assessed in this study. During the experiment, some adult tillers lost their tags and consequently identity of the generation they belonged to was lost. However, this category of tillers represented on average only 4.6 % of the tiller population, and was added to the dead tiller number. Including the unidentified tillers with dead tillers did not change the treatment trends.

Tillers within the fixed circular frame were subject to regular disturbance during the counting and identification of individual tillers. Since light intensity at the base of the plant is a major determinant of tiller bud initiation (Langer 1963; Jewiss 1972; Ong 1978a, b; Ong and Marshall 1979), it might be expected that only brief exposures to light would be needed to initiate axillary bud development, and that disturbance may in itself stimulate tiller initiation. Such disturbance effects have been referred to by a number of authors (Davies 1981; Korte 1981; Arosteguy 1982; Matthew 1992; Hernandez-Garay 1995) and could have occurred in the current experiment.

In this study, tiller densities determined from tiller counts in fixed circular frames on the drill rows were consistently greater than those determined by random location of frames (compare tiller densities in Table 3.5 with those in Fig. 5.3 to 5.10), and they were also higher than those previously reported (Korte 1986; L'Huillier 1987; Matthew 1992; Hernandez-Garay 1995). Some of these differences could be due to the fact that each fixed circular frame was placed over a drill row; this study was also carried out on an establishing sward with the likelihood of a higher ryegrass tiller density (Thom et al., 1993) than was recorded for the well established swards used by other researchers (L'Huillier 1987; Matthew 1992; Hernandez-Garay 1995). High tiller population densities within fixed quadrats compared with the surrounding swards have been common features of earlier studies of this type (Matthew 1992; Hernandez-Garay 1995) and have been assumed not to affect the performance of one treatment or cultivar disproportionately compared with the others. As in the earlier studies, this assumption is also made here, in interpreting results.

5.5.2 Seasonal patterns of ryegrass tiller dynamics

During the first spring after sowing (September to November 1996), tiller production was rapid and tiller number reached a maximum in mid-summer (January) before declining over late summer and autumn (Fig. 5.3 to 5.6). This tillering pattern has often been observed in New Zealand swards under grazing (Chapman et al., 1983; Korte et al., 1984; L'Huillier 1987; Matthew et al., 1989; Matthew 1992; Da Silva et al., 1993; Da Silva 1994; Hernandez- Garay et al., 1993, 1997) and cutting (Korte 1986). Reduced tillering was associated with a high tiller death in summer and this may be due to adverse environmental factors such as high air and soil surface temperatures, lack of nitrogen and moisture stress. Other factors such as severe grazing and pulling losses (see Chapter 3) could also be important. However, nitrogen and water application did not change the pattern of a decline in tiller population over late summer/autumn (Fig. 5.4, 5.5 and 5.6), which suggests increased air (Mitchell 1953) or soil (10 cm depth) temperature (Davies and Thomas 1983) could have influenced tiller production. Temperature influenced the rate at which leaves expand (LER) and the frequency at which they appear, and since tiller production was partially controlled by the latter (Davies and Thomas 1983), temperature can influence seasonal tiller production via the rate of tiller bud development (Parsons and Robson 1980). Tiller birth rate was found to be correlated with daily average air and soil temperature (Table 5.3); tiller birth rate decreased when the daily average temperature increased over summer under limiting and non-limiting nitrogen and water conditions. Tiller birth rate was lowest when the daily average air temperature exceeded 15.4 ^{o}C, suggesting that tiller production of perennial ryegrass declined rapidly when the daily average air temperature ranged from 15.4 (December 1996) to 16.8^{o}C (January 1997). The same effect was evident in February/March 1998 when temperatures again exceeded 15.4^{o}C. Mean maximum temperatures ranged from 18 to 24^{o}C in December 1996 and from 20 to 25^{o}C in January 1997, whereas the optimum temperature for perennial ryegrass growth was suggested to be around 20^{o}C (Cooper and Tainton 1968; Silsbury 1971; Dirven and Deinum 1977; Langer 1979). Tiller birth rate may have been affected by LAI, since leaf area via LER (Lemaire and Chapman 1996) and A_L (Peacock 1975b) increased as temperature increased, shading the base of the plant, with a negative effect on tiller production.

Table 5.3. Tiller birth rate of 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars under different nitrogen and irrigation treatments, and changes in average daily air and soil temperature with season.

	Tiller birth rate (tillers/tiller/day)									
	-N-Irr		-N+Irr		+N-Irr		+N+Irr			
Date	Ellett	Ruanui	Ellett	Ruanui	Ellett	Ruanui	Ellett	Ruanui	Temp[a]	Temp[b]
Oct 96	0.011	0.010	0.010	0.011	0.015	0.013	0.016	0.015	13.1	12.4
Nov 96	0.020	0.010	0.019	0.009	0.015	0.015	0.018	0.014	13.7	13.6
Dec 96	**0.023**	**0.013**	**0.014**	**0.020**	**0.015**	**0.018**	**0.020**	**0.021**	**15.3**	**15.6**
Jan 97	**0.008**	**0.006**	**0.009**	**0.009**	**0.006**	**0.006**	**0.013**	**0.008**	**16.8**	**17.0**
Feb 97	**0.007**	**0.005**	**0.007**	**0.007**	**0.005**	**0.009**	**0.010**	**0.009**	**17.1**	**17.6**
Mar 97	0.001	0.002	0.002	0.002	0.003	0.002	0.003	0.001	19.6	19.3
Apr 97	0.008	0.007	0.007	0.012	0.011	0.014	0.009	0.010	14.4	15.4
Jun 97	0.007	0.007	0.009	0.009	0.008	0.004	0.008	0.007	12.4	12.2
Jul 97	0.007	0.007	0.007	0.008	0.007	0.009	0.006	0.007	7.7	7.9
Sep 97	0.007	0.006	0.009	0.008	0.008	0.008	0.007	0.005	8.4	7.7
Oct 97	0.002	0.003	0.003	0.003	0.002	0.002	0.004	0.004	11.8	11.7
Nov 97	0.010	0.009	0.009	0.005	0.010	0.006	0.006	0.008	13.6	14.6
Dec 97	**0.014**	**0.005**	**0.015**	**0.008**	**0.015**	**0.012**	**0.008**	**0.015**	**13.4**	**16.6**
Jan 98	**0.008**	**0.009**	**0.020**	**0.012**	**0.010**	**0.014**	**0.021**	**0.016**	**15.4**	**19.7**
Feb 98	**0.002**	**0.002**	**0.002**	**0.001**	**0.002**	**0.002**	**0.004**	**0.003**	**20.0**	**20.8**
Mar 98	0.007	0.002	0.003	0.001	0.010	0.005	0.003	0.002	18.7	18.5

[a] daily air temperature averaged across the tiller measurement period in degrees Celsius.

[b] daily soil temperature at 10 cm depth averaged across the tiller measurement period in degrees Celsius.

Colour code: **spring**; **summer**; **autumn**; **winter**.

The rapid decline in tiller number in autumn (February and March) was characterised by low tiller births (Table 5.3) and high tiller deaths (Fig. 5.3 to 5.6) and was followed by a tillering flush in autumn (April 1997). Similar results have been observed in the United Kingdom (Garwood 1969; Wade 1979; Tallowin 1981; Colvill and Marshall 1984). Korte (1986) and L'Huillier (1987) did not find such a tillering flush during autumn in New Zealand, although Korte and Chu (1983) and Hernandez-Garay et al. (1997) observed this phenomenon during recovery of tiller populations depleted by summer drought. Few reasons have been given for autumn tillering. Korte and Chu (1983) suggested prolonged drought resulted in death of ryegrass plants thereby lowering the tiller density. Autumn air and soil temperatures were still above the optimum for perennial ryegrass (Table 5.3), as light intensity was decreasing (Parsons 1988). High temperatures and reducing light would be expected to increase tiller mortality as well as reduce tiller production through increased respiration and reduced photosynthesis, respectively, and consequent reduction of carbohydrate supply. Parsons (1988) showed that the poor photosynthetic potential of the grass canopy in autumn, combined with decreasing light energy receipt resulted in a high death rate of tissues, and therefore the possibility of high tiller death.

Total tiller population in winter seemed more stable compared with the other seasons. P_t/P_0 tended to be slightly greater than 1.0 in winter 1997 (Fig. 5.11 to 5.14), attributable to a high survival probability, in particular (Fig. 5.15 to 5.18). Tiller birth per day was lower than in summer but still sufficient to replace deaths in these conditions. Hunt and Field (1979) and Korte (1986) have also reported increased tiller density in winter. During winter, low temperature (Brereton et al., 1985; Thomas and Norris 1977, 1981) and low light intensity (Lorenzetti et al., 1971) are both major limitations to perennial ryegrass growth, and a decline in tillering as observed here (Table 5.3) would be expected. However, this does not necessarily mean that the lower tiller appearance in winter would be automatically balanced by increased survival. Indeed, Chapman et al. (1983) found that in hill country mixed swards both ryegrass and browntop (*Agrostis capillaris*) tiller populations increased in winter under rotational grazing with sheep, but decreased under a continuous grazing management.

Peacock (1975a), by experimentally raising soil temperature, showed that the rates of appearance and extension of grass leaves were closely related to the soil surface temperature. Since air and soil temperatures between the observation dates were low in winter (June/July 1997) (Table 5.3), then leaf appearance rate and therefore potential tiller bud number, were probably low (Chapman et al., 1983). However, tiller birth rates (Table 5.3) from June to September 1997 seemed to be less affected by air temperatures than they were in summer. Brereton et al. (1985) have shown that tiller turnover for perennial ryegrass during winter was not affected by temperature or vernalisation, and that the ratio of tiller appearance to leaf appearance (site filling) was influenced by light intensity. Tiller initiation and appearance were also related to light intensity (Brereton et al., 1985) assuming that increased tiller production in winter was due to a lower ratio of respiration to photosynthesis than in summer. Moreover, it would be possible for tiller births to continue in winter, even with a low light intensity, because LAI would be low due to low temperature and resulting slower regrowth rate.

A trend for a decreasing tiller population in late spring (November) was noticeable in 1997 (Fig. 5.3 to 5.18) but did not appear in the first year. The reason why this effect occurred in only one of the two seasons is unclear. In the first months of the trial, tiller population steadily increased in all treatments (Fig. 5.3 to 5.18). It appears that the swards were still establishing a tiller population equilibrium over this period. Presumably the factor or factors responsible for this masked other effects. The pattern in the second year suggests reproductive development (see Chapter 6), which is usually concentrated at the end of spring and early summer (Davies 1977; Korte 1986; L'Huillier 1987; Matthew et al., 1989; Da Silva 1994; Hernandez-Garay 1995, Hernandez-Garay et al., 1997), was the main cause of this change within the tiller population. The spring tiller population was lowest in October and November 1997 (Fig. 5.3 to 5.18), at the time when the most reproductive tillers were present (Thom 1991). This was probably due to buds at the base of reproductive tillers being constrained from developing daughter tillers by hormonal influences from the elongating stem internodes or developing inflorescences (Clifford 1977), and by competition for assimilates (Colvill and Marshall 1984; Ong et al., 1978b). After grazing of reproductive tillers, tiller births had noticeably increased by December 1997 (Fig. 5.3 to 5.6) probably due to the removal of apical dominance of the daughter tiller buds located at the base of the reproductive tillers, and by further stimulation as reallocation of carbon assimilate occurred to subsidise the early growth of young tillers (Matthew et al., 1989). However, light quality has been demonstrated to influence tiller initiation in several grasses. Increased red : far red ratio within the canopy increased tiller bud initiation. Tillering was reduced by a decrease in the ratio of red: far red radiation, independent of the availability or interception of photosynthetically active radiation (Deregibus et al., 1985; Casal et al., 1987, 1990). The physiological processes associated with phytochrome-mediated reductions in tiller initiation and apical dominance are not clearly understood (Murphy and Briske 1992). High tiller deaths were also evident at this time (October1997, Fig. 5.3 to 5.6) and this was probably restricted to young secondary or tertiary vegetative tillers (age-cohort '**o**', Table 5.2, Fig. 5.7 to 5.10), as the smallest tillers were usually the first to die when the plant was stressed (Ong 1978a).

Tillers born just before the flowering period (age-cohorts '**o**') could not be relied on for perennation of the ryegrass plant since they had a short lifetime. It seems to be a consistent feature of perennial ryegrass behaviour that pre-flowering tillers are most likely to be short-lived. Colvill and Marshall (1984) and Korte (1986) have also observed the same behaviour. By contrast, pre-flowering tillers of meadow fescue appear to be the key to the perennation process (Jewiss 1966).

Tillers formed during and immediately after the flowering period (age-cohorts '**p**' and '**q**') had variable half-life (Table 5.3) and their percentage of the summer population was not as high as in the studies of Korte (1986) and Matthew (1992). This suggests that the 'late control' grazing management strategy (Matthew 1991), which aims to encourage perennation based on post-flowering tillers is more applicable to some cultivars and environmental conditions and not others. For example, for age-cohort '**p**', tillers of 'Ellett' without nitrogen fertiliser had a long half-life, especially with irrigation (Table 5.2).

Tillers born after the tillering slump in autumn (age-cohorts '**m**' and '**n**') were important since they were long-lived and represented the largest proportion of the population the following spring (Korte 1986). Overall, average ryegrass tiller longevity was somewhat less than one year (Table 5.2), which agrees with previous observations (Korte 1986; Briske 1991).

It is interesting to note that the seasonal growth trajectory of perennial ryegrass swards on the stability diagrams, regardless of cultivar and the nitrogen or irrigation treatments, followed a yearly cycle from spring to winter with the highest tiller population index in summer and the lowest in autumn (Fig. 5.15 to 5.18). The seasonal tillering pattern of these perennial ryegrass swards was consistent across cultivar and treatments and showed a tiller population decline followed by increased tillering, with the seasonal periods of low tiller survival rates followed by a compensatory period of increased tiller birth rates for the population tiller density to recover.

Overall, the seasonal tiller population decline was greater in the second year than in the first, possibly due to climatic differences between the two years (see Chapter 3) especially in summer and autumn. A detailed analysis of climatic conditions during these years (April 1996 to April 1998) (Chapter 3), showed that the second year was warmer in late summer (February) and early autumn (March) than at comparable times in the first year. Monthly air temperatures in February and March 1998 were 1.6 and 2.8 °C, respectively, higher than in February and March 1997. As mentioned above (section 5.5.2) tiller births and survival could have been limited by temperature increase promoting leaf area expansion and shading.

5.5.3 Cultivar tiller dynamics

Differences in the density of 'Ellett' and 'Grasslands Ruanui' tillers enclosed in fixed circular frames, were consistent with the comparable estimates of sward tiller density (Chapter 3, Table 3.5). 'Grasslands Ruanui' had a higher total tiller population than 'Ellett' from the beginning of the measurements (September 1996), suggesting this could be due to differences in leaf appearance rate, site filling and/or timing of the appearance of the first primary tiller. However, cultivar population differences are most likely due to different timing of the appearance of the first primary tiller and/or site filling, since both cultivars had a similar leaf appearance rate (Chapter 4).

At Hamilton, tiller birth data for 'Grasslands Ruanui' ryegrass did not show the late winter/early spring (August) peak as observed in Palmerston North by Matthew (1992 and 1996). 'Ellett' and 'Grasslands Ruanui' had a high tiller turnover in summer and autumn. The high summer tillering of 'Ellett' was also described for other 'modern' perennial ryegrasses, including 'Grasslands Nui' (Korte 1986; L'Huillier 1987).

However, the high tiller turnover, characterised by high birth and death rates for 'Grasslands Nui' during spring of the second year (Korte 1986) was not very pronounced in the tiller demography (Fig. 5.3 to 5.6) and age-cohort (Fig. 5.7 to 5.10) diagrams for 'Ellett' and 'Grasslands Ruanui' in the current work. The seasonal pattern observed in the sward stability diagrams (Fig. 5.15 to 5.18, section 5.5.2) differed from that found in a similar diagram drawn from Korte's (1986) data for 'Grasslands Nui' perennial ryegrass (L.G. Barioni, Massey University, 1997, unpublished). In Korte's data, 30-day survival probability of tillers was as low as 0.3 to 0.4 during the flowering period (early December), making the flowering period, rather than the autumn period, the time of greatest seasonal instability in population density. The fact that unrelated cultivars 'Ellett' and 'Grasslands Ruanui' showed a similar seasonal pattern in this experiment, whereas a cultivar related to 'Ellett', 'Grasslands Nui' behaved differently in Korte's (1986) experiment suggests that both environmental and cultivar effects are responsible for differences in tillering pattern. Spring tillering differences between 'Ellett' and 'Grasslands Ruanui' in relation to their flowering behaviours are discussed further in Chapter 6.

'Ellett' had a higher value of the population index (P_t/P_0), averaged across treatments (Fig. 5.11 to 5.14), than did 'Grasslands Ruanui' in June 1997 but a lower value in July (section 5.4.3.1). Tiller appearance for 'Grasslands Ruanui' was lowest in winter in Palmerston North, but highest in early spring, suggesting that it had a tendency to be dormant in winter with a sequence of recovery in spring, involving first root, then tiller and leaf production (Mathhew 1996); Ellett showed some winter activity (Matthew 1992). The results of the current study show some evidence of a similar difference between the cultivars in Hamilton.

5.5.4. Cultivar responsiveness to nitrogen and irrigation

'Grasslands Ruanui' was responsive to nitrogen increasing its tiller birth and death rates (Fig. 5.5 and 5.6), resulting in larger increases in the tiller population followed by more rapid decreases than in no nitrogen plots, especially in summer and autumn. Births and deaths were high at these times, and tiller turnover was accelerated by nitrogen, as was also found by Hunt and Mortimer (1982) and Hunt and Easton (1989). Therefore, nitrogen reduced tiller longevity. This view was supported by the observation that vegetative tillers died earlier in fertilised than unfertilised plots of perennial ryegrass as a consequence of the more rapid development of shading within the sward (Ong 1978b; Colvill and Marshall 1984). However, responses of 'Ellett' and 'Grasslands Ruanui' tiller populations to nitrogen in autumn (March 1997) and during the post-flowering period (December 1997) were different (sections 5.4.1.2 and 5.4.3.2). In autumn, 'Grasslands Ruanui' may have reached the ceiling leaf area faster than 'Ellett' causing a decline in its tiller population while 'Ellett' was still able to produce new tillers. Simon and Lemaire (1987) showed that the ceiling leaf area of intermittently defoliated swards was around 3-4, when tiller density began to decline. Therefore, autumn tiller density for 'Ellett' varied less in response to nitrogen than did the tiller density for 'Grasslands Ruanui'. However, nitrogen increased 'Grasslands Ruanui' tiller population and decreased 'Ellett' tiller population when tillers became reproductive (December 1997). Nitrogen stimulated vegetative tiller production in 'Grasslands Ruanui' through a higher birth rate, but not in 'Ellett'. 'Ellett' however, showed nitrogen-related differences in flowering behaviour (see Chapter 6).

Irrigation did not have important effects on total tiller populations except in January 1997 and February 1998 when the tiller populations were increased with water. However, irrigation decreased the tiller population (P_t/P_0) of 'Grasslands Ruanui' compared to the unirrigated treatment with 'Grasslands Ruanui' more than for 'Ellett'. Possibly, high summer temperatures could also have restricted ryegrass growth despite the water application.

5.5.5 Use of the population index and the stability diagram

The stability diagram and population index, mathematically defined by Matthew and Sackville Hamilton (C. Matthew and N. R. Sackville Hamilton, 1999, unpublished manuscript) allow tiller dynamics to be studied from a different angle. One outcome of this approach is the combination of tiller birth and survival rates into one component, the tiller population index. Secondly, compared to a constant tiller density curve ($P_t/P_0 = 1$), it is possible to visualise the amplitude of tiller population changes in relation to nitrogen and/or irrigation treatments (Fig. 5.11 to 5.14). This amplitude represents the ability of the tiller population to move above or below the constant tiller density line, which can be defined as the plant "responsiveness" to environmental factors. During this study, some time was spent trying to develop a responsiveness index from P_t/P_0. A preliminary index (7) was defined as:

$$R = 1 - P_t/P_0 \qquad (7)$$

where:

R represents the responsiveness of the population. However, a number of problems emerged which were not easily solved, and this remains a topic for possible further development in the future.

Although a responsiveness index was not developed, there was some evidence from visual inspection of Fig. 5.11 to 5.14 that the responsiveness of ryegrass to water was far less than it was to nitrogen, and that 'Grasslands Ruanui' was more responsive to nitrogen than 'Ellett', as discussed in the previous section. High responsiveness to nitrogen through tiller production and loss could constrain the long term size of the tiller population and hence the sward persistence. Therefore, to maximise persistence when nitrogen is applied, it is necessary to have a shorter period between defoliations to avoid a high herbage mass accumulation, and to efficiently use the effect of nitrogen fertiliser on ryegrass growth, dates of application of nitrogen fertiliser will have to be strategically planned in relation to the cultivar response.

In the literature, different types of response of the tiller population to environmental factors are identified. The stability diagram allows these responses to be categorised according to the balance between birth and survival (Fig. 5.2). Although the sward stability diagrams in this experiment were similar (Fig. 5.15 to 5.18, section 5.5.2) it is clear that these diagrams would be useful to distinguish different seasonal patterns of tiller birth and survival in different studies.

5.6 Conclusion

Overall, the cultivars 'Ellett' and 'Grasslands Ruanui' had similar tiller dynamics patterns regardless of the nitrogen and irrigation treatments. However, the cultivars behaved differently in December and March 1997 when nitrogen was applied giving rise to a significant cultivar × nitrogen interaction. Differences in tiller population index between cultivars in December 1997 could be explained by differences in their flowering behaviour (Chapter 6). Tiller dynamics data from the field study were analysed in a descriptive sense using mathematical tools to describe tiller population changes in different ways. Representation of tiller population changes via a population index was useful to visualise the ryegrass plant responsiveness to nitrogen and irrigation treatments. However, none of these mathematical representations of seasonal tiller dynamics aid the understanding of the effects of environment on tiller population changes. A link between the environment and tiller population dynamics needs to be made. In an attempt to help with the interpretation of tiller dynamics, a conceptual approach is presented in Chapter 7. Useful follow-up to this experiment could include development of the proposed responsiveness index, further investigation of the extent to which genetic and seasonal effects influence tiller dynamics of perennation, and experiments designed to test the effect of different perennation strategies on the fitness of a cultivar.

5.7 Summary

5.7.1 Seasonal pattern of perennial ryegrass tiller dynamics

- Seasonal patterns over two years were characterised by high tiller populations in summer and a rapid population decline in autumn followed by a gradual increase over winter and early spring.

- A reduction in tiller population during the flowering period was evident in the second year but not in the first.

5.7.2 Cultivar differences in tiller dynamics pattern and plant persistence

- 'Grasslands Ruanui' had a higher total tiller number than 'Ellett', regardless of nitrogen and irrigation treatments.

- No significant differences in the seasonal profile of tiller populations were observed between 'Grasslands Ruanui' and 'Ellett'.

- 'Ellett' had a higher population index in June 1997 than did 'Grasslands Ruanui' since 'Ellett' had a higher birth rate than 'Grasslands Ruanui'. The opposite trend occurred in July 1997.

- No clear differences in tiller turnover between 'Ellett' and 'Grasslands Ruanui' were observed before and after flowering.

5.7.3 Effects of nitrogen and irrigation on perennial ryegrass tiller dynamics

- The autumn (March 1997) tiller population of 'Grasslands Ruanui' decreased with nitrogen whereas for 'Ellett' it increased. The opposite trend was observed between nitrogen treated cultivars during the post-flowering period (December 1997) with an increase in the 'Grasslands Ruanui' tiller population and a decrease in the 'Ellett' population.

- Nitrogen reduced the half-life of ryegrass tillers.

- Irrigation increased total tiller number of both cultivars in January 1997 and February 1998 but tiller populations declined again in March 1998 with 'Grasslands Ruanui' losing more tillers than 'Ellett'.

- Plant responsiveness to nitrogen was much greater than it was to irrigation.

CHAPTER SIX

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DIFFERENCES IN THE FLOWERING BEHAVIOUR OF 'ELLETT' AND 'GRASSLANDS RUANUI' IN DIFFERENT ENVIRONMENTS

CHAPTER 6: DIFFERENCES IN THE FLOWERING BEHAVIOUR OF 'ELLETT' AND 'GRASSLANDS RUANUI' IN DIFFERENT ENVIRONMENTS

Results from the controlled environment experiment presented in this Chapter form the basis for a paper submitted to the **Grass and Forage Science** journal in May 1999.

6.1 Introduction

As reported in Chapter 1, one of the objectives of this work was to identify possible differences in perennation strategies likely to influence the persistence of 'Ellett' and 'Grasslands Ruanui' ryegrass under intensive dairy cow grazing, and to determine effects of nitrogen fertiliser and irrigation treatments on their persistence. Indeed, Matthew et al. (1993) suggested that 'Ellett' ryegrass had a different perennation strategy to 'Grasslands Ruanui', with the former more dependent on survival of daughter tillers produced at the base of flowering tillers, and the latter more dependent on surviving vegetative tillers. However, this tentative suggestion was based on data from separate experiments in different years.

In Chapter 5, it was shown that the total tiller population of 'Ellett' and 'Grasslands Ruanui' ryegrass declined over the second spring following establishment, but there were no significant cultivar differences. The lack of cultivar differences may have been partly due to the classification of defoliated reproductive tillers bearing daughter tillers as living, in contrast to Korte (1986) and Matthew (1992). However, during the post-flowering period (December to January/February) the 'Ellett' tiller population decreased when treated with nitrogen while that of 'Grasslands Ruanui' increased, because of a high appearance rate in response to nitrogen. Reasons for the different tillering responses to nitrogen during the post-flowering period needed further investigation.

The perennation of grasses is dependent on successful tiller initiation from axillary buds on older tillers. Within a dense canopy, tiller initiation has been observed to be reduced by a low (< 0.3) ratio of red to far red light (R:FR) arising from shading and, independently, by reduced availability or interception of photosynthetically active radiation (Casal et al., 1990). The consensus is that light competition is an important factor in tillering regulation through light quality modification, whereas the carbon supply is the more important factor affecting the survival of existing tillers. It is also known that defoliation of a flowering tiller may promote tillering through a hormonal mechanism often termed apical dominance (McIntyre 1977; Hillman 1984; Martin 1987; Tamas 1987; Cline 1991). Murphy and Briske (1992) noted that the physiological processes associated with a phytochrome-mediated reduction in tiller initiation and apical dominance were not well understood. Several authors including Mitchell (1953) and Gautier et al. (1999) have studied the effects of light competition on tillering of vegetative plants, but there are few data sets describing post-flowering tillering and the implications for plant persistence.

6.2 Objectives

The objectives for this chapter were initially:

(i) to compare the flowering behaviour of 'Grasslands Ruanui' and 'Ellett' ryegrass cultivars in the field study described in Chapter 5.

(ii) to test the hypothesis of Matthew et al. (1993), and to assess the effects of different nitrogen and irrigation treatments on flowering behaviour.

From the field experiment it was concluded that further research on the effects of light competition on tillering at the flowering stage is also needed for a better understanding of perennation. Therefore, a further experiment is presented to describe tillering of ryegrass plants growing in an artificial sward under contrasting light treatments, after removal of the seed-head by cutting.

The discussion is presented in two parts. In section 6.5.1, the responses of the cultivars under full light and unmodified by nitrogen and irrigation are compared in terms of the hypothesis of Matthew et al. (1993). In section 6.5.2, the responses of cultivar flowering behaviour to nitrogen, irrigation and shade treatments are considered.

6.3 Materials and methods

6.3.1. Field experiment (Experiment 1)

The plant material, design and the management of the two year field experiment carried out at DRC in Hamilton, New Zealand, were previously described in Chapter 3.

Tiller measurements from this same experiment were described in Chapter 5. The reproductive and vegetative tiller numbers for 'Ellett' and 'Grasslands Ruanui' ryegrasses were recorded during the pre- and post-flowering period (from September to January) in both years (1996/97 and 1997/98), and under different nitrogen and irrigation treatments.

6.3.2 Controlled experiment (Experiment 2)

6.3.2.1 Environmental conditions

The experiment was carried out at INRA, Lusignan, France (Latitude 46°26'N, Longitude 0°09'E) from October 1997 to July 1998. Endophyte-free seed of 'Ellett' and 'Grasslands Ruanui' perennial ryegrass cultivars were germinated on 6 October 1997 and planted in a tray (each 1.40 x 0.85 m) containing equal proportion of soil, peat and sand over a 20 cm depth without additional fertiliser. Mixtures of 'Ellett' and 'Grasslands Ruanui' plants were arranged in each tray using a 75 x 100 mm grid to form mini-swards of 11 rows of 14 plants (108 test plants, surrounded by 46 border plants). Each row contained 6 tests plants of each cultivar with a border plant at each end; the position of each test plant within the row was chosen at random. The mini-swards were located in the field on separate support stands 1.16 m above ground level, except from 8 February to 19 March 1998, when they were placed in a glasshouse (air temperature of 5 °C until the 20 February and 15 °C for the remainder; no humidity control) to avoid frost damage. Swards were returned to their field position on 20 March and were left uncovered. The herbage was cut at 50 mm above soil level on 24 March when plants were vegetative, and again on 19 May 1998 (Plate 6.1) when plants had 50% of seed-heads emerged on tagged tillers (see below). Nitrogen as ammonium nitrate (11.1 g/litre of water, 10 ml/plant) was applied on 23 February 1998 and the 4 May 1998, and after each cutting. Each application was approximately equivalent to 150 kg N/ha, ensuring a high level of nitrogen nutrition. The mini-swards were watered daily (between 8 am and 8 pm) during the experiment with an automatic irrigation system applying 0.03 to 0.06 litres of water every 2 h to reduce water stress. These quantities of water correspond to 8 to 16 mm per day, and compensated for the evaporative demand of 1 to 6 mm per day recorded at a Climatological Station, 2 km from the trial site. The seedlines used were the same as those used in the field experiment in New Zealand.

6.3.2.2 Light treatments

Immediately following the second cut on 19 May 1998, each mini-sward was covered by a tunnel-shaped altuglas (material provided by Atohaas-France SA 27660 Bernouville) light filter with different light transmission characteristics (Table 6.1). The filters were 190 cm wide and 200 cm long with a maximum height of 100 cm above the plants, forming a complete cover over the mini-swards, with the closed ends facing east and west. The filters were held in place by a light tubular framework that did not shade the plants. The filters were used to create different light environments, but with near-identical temperature and humidity. This was achieved by raising plants and filters 0.8 m above the ground to promote free air circulation around the plants (Plate 6.2). A filter transmitting more than 90% of photosynthetically active radiation (PAR) without spectral modification and with a red: far red (R: FR) ratio similar to the incident solar radiation was used as the control treatment and covered one mini-sward; the other filter simulating canopy shading (Plate 6.2) (reduced PAR with spectral modifications) (Table 6.1), covered the other mini-sward. The light level of the shade treatment was similar to that measured in a dense pasture canopy (Marriot et al., 1997). The properties of the two types of filters were established from measurements with a spectroradiometer Li-Cor 1800 (provided by EUROSEP, Instrument 95801, Cergy-Pontoise), as was the variability of the spectral composition and the level of the radiation transmitted to the plants at different times of the day. The PAR transmission varied from 92 % to 95 %

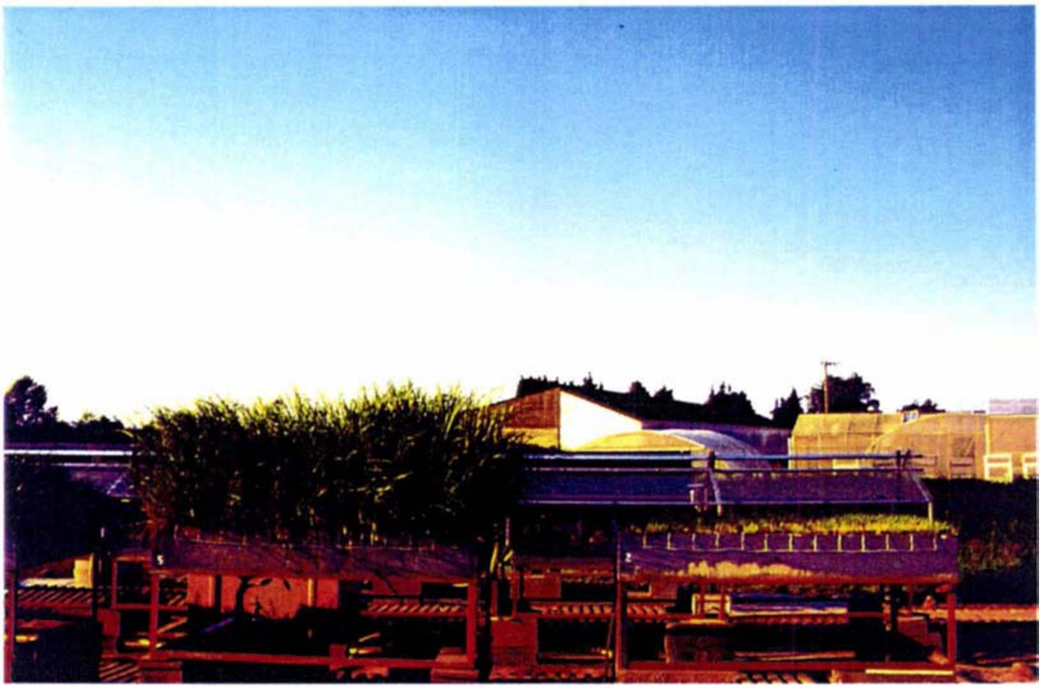

Plate 6.1. 'Ellett' and 'Grasslands Ruanui' ryegrass plants in mini-swards at 50% of seed-head emergence on tagged tillers (at the left) and when cut at 50 mm above the ground level (at the right).

Plate 6.2. The shade treatment simulated by a green filter (at the left) and the control treatment by a transparent filter (at the right).

Table 6.1. Characteristics of the light transmitted by the tunnel-shaped filters. Values are relative to incident solar radiation.

	Control	Shade
Photosynthetic photon flux (400-700 nm)	92.1	13.5
Photosynthetic efficiency[a]	90.8	14.0
Blue photon flux	81.0	6.0
Red photon flux	93.1	19.0
Far-red photon flux	93.9	87.0
Red/far-red (655-665/725-735 nm)[b]	1.10	0.17
Phytochrome photoequilibrium (φ_c)[a,b]	0.71	0.44

[a] Photosynthetic efficiency and phytochrome photoequilibrium state were calculated according to Sager et al. (1988)

[b] Absolute value

(See Table 6.1) for the control treatment and from 13.5 % to 14.5 % for the shade treatment. The spectral composition of the radiation transmitted (% of blue and R : FR) was constant.

Air temperature was monitored throughout the experiment using six thermocouple probes per canopy, located 30 mm above the soil surface. Air temperatures were sampled every 10 seconds, and recorded as the average for each 5 minute interval under both filters. Small differences between the two light environments in air temperature did occur. Such differences did not consistently favour a particular treatment and averaged 1 °C (Appendix 6.1). Given this level of temperature control in the range experienced, 11 to 27 °C, it was felt there should be little effect on treatment responses. Air humidity was also monitored, using one psychrometer (Kruszewski 1997) per filter, located 150 mm above the sward. As with temperature, humidity differences between the two light environments were small and inconsistent (< 4 %, Appendix 6.2).

6.3.2.3 Measurements

Pre-light treatment

On 19 March 1998, 30 plants of each cultivar from both mini-swards were randomly selected. Five tillers per plant were randomly selected according to a visual ranking (two large, two medium and one small) and were tagged near their bases with a different coloured plastic ring.

Post-light treatment

After 45 days of light treatment, counts of daughter tillers on tagged tillers were made. Twenty plants per cultivar and light treatment were randomly chosen from the original 30, and were destructively sampled to determine number of vegetative and reproductive tillers. Vegetative and reproductive tillers were distinguished by the appearance of a node at the base of the latter. All tillers in each category were dried in an oven at 70°C before weighing, and the average weights of vegetative and reproductive tillers were determined. Daughter tillers, which did not have one fully emerged leaf, were not counted or weighed.

6.4 Statistical analysis

6.4.1 Experiment 1

Data from the field experiment were analysed as a split-split plot design ANOVA using Genstat 5 (Rothamsted Experimental Station). The same model described in Chapter 3 was used to determine the main effects of cultivar, nitrogen, and irrigation treatments and the cultivar × nitrogen, cultivar × irrigation, cultivar × nitrogen × irrigation interactions, on reproductive and vegetative tiller number. Square root transformation was required for reproductive tiller number data of 1 September, 21 October and 17 November 1997.

6.4.2 Experiment 2

Analysis of tiller data was performed using SAS PROC Mixed (SAS 1989, version 6). Plant was specified as a random effect to determine the effects of light treatment, cultivar, tiller size, reproductive status and their interactions for number of tillers per plant, number of tillers per tagged tiller, and weight of vegetative and reproductive tillers. For comparing cultivars within light treatments plants were used as replicates.

6.5 Results and discussion

6.5.1 Reproductive development

6.5.1.1 Field experiment

From visual observations, 'Ellett' and 'Grasslands Ruanui' ryegrasses are both early flowering cultivars. They flowered at approximately at the same time, under both controlled and field conditions. The Plant Variety Rights applications for both cultivars (Lincoln University 1990/91, Appendix 6.3), and other reports (Easton 1983; Charlton and Stewart 1999), also support these observations.

In the field (Experiment 1), 'Ellett' had a higher proportion of reproductive tillers than did 'Grasslands Ruanui' (from October to January) and these differences increased during the second year when 'Grasslands Ruanui' produced fewer reproductive tillers than in the first year (Table 6.2). Also, 'Grasslands Ruanui' showed a different flowering behaviour in the two years, with a reduced proportion of flowering tillers in the second year compared with the first whereas 'Ellett' had a similar proportion of flowering tillers in both years (Table 6.2). Thus, perennation in 'Grasslands Ruanui' was more via the vegetative pathway (See Chapter 2, Section 2.3.1) than was perennation in 'Ellett' and this difference was more marked in the second year. However, these differences in flowering behaviour between 'Ellett' and 'Grasslands Ruanui' in year 2 seem to be smaller than those reported by Matthew (1992). In Matthew's (1992) studies up to 36 % of tillers in 'Ellett' swards in November were reproductive and tillers present in mid-November formed only 10 to 20 % of the autumn tiller population measured on 4 April. For 'Grasslands Ruanui' 21.8 % were reproductive in November and surviving November tillers formed 38 % of the tiller population in the following April. It is also possible that a number of factors such as frequency, timing and intensity of defoliation affect the perennation behaviour and it may well be that the more extreme results reported by Matthew (1992) reflect not only cultivar effects but also different experimental conditions.

Conversely, one factor contributing to the apparently lower turnover of the tiller population during flowering in this experiment is that defoliated reproductive tillers bearing daughter tillers were not recorded as dead. Thus, tiller death was underestimated at this time. However, this should have had only a small effect on the results and the conclusion remains in the present experiment that the tiller dynamics pattern of 'Ellett' was not significantly different to that of 'Grasslands Ruanui' (see Chapter 5, Fig.5.7 to 5.10).

6.5.1.2 Controlled environment experiment

This experiment clearly showed the expected morphological difference between the cultivars. 'Grasslands Ruanui' had a higher tiller number per plant (Table 6.3), slightly lower vegetative tiller weight, and lower reproductive tiller weight than 'Ellett' (Fig. 6.1, $P>0.05$ and $P<0.01$, respectively), under both light treatments. These results agree with field observations in Chapter 3.

As expected, vegetative tillers weighed less than reproductive tillers (Fig. 6.1, Hernandez-Garay et al., 1997). However, the ratio of reproductive tiller weight to

Table 6.2. Cultivar mean for reproductive and vegetative tillers and the proportion of total tillers in circular frames, during the flowering periods in 1996/97 and 1997/98 (Experiment 1).

	Dates									
	First year					**Second year**				
	7/10/96	**29/10/96**	**25/11/96**	**16/12/96**	**6/1/97**	**1/9/97**	**21/10/97**	**17/11/97**	**15/12/97**	**12/1/98**
Reproductive tiller number										
Ellett	12.6	40.9	58.4	74.7	82.6	3.7	34.9	42.1	40.6	37.4
Ruanui	10.1	41.1	50.9	65.8	66.8	2.9	10.0	24.0	26.7	27.7
SED[a]	3.2	3.8	5.4	5.1	10.4	**b**	**c**	**d**	9.1	5.8
Signif.	NS	NS	NS	NS	NS	NS	*	*	NS	NS
Vegetative tiller number										
Ellett	147	149.8	206	242	267	198	129	113	135	169
Ruanui	230	240	266	237	374	285	236	207	225	274
SED	15.2	17.7	43.6	51.6	54.7	46.2	29.7	28.6	21.9	24.8
Signif.	*	*	NS	NS	NS	NS	*	*	*	*
% of reproductive tiller number										
Ellett	6.9	21.4	22.3	23.7	23.0	2.1	18.2	24.8	22.2	18.1
Ruanui	3.7	14.1	15.8	16.2	15.0	1.1	4.1	10.7	12.2	11.1
SED	2.4	2.8	1.9	1.6	1.2	0.99	2.1	1.0	3.0	2.2
Signif.	NS	(†)	*	*	**	NS	**	***	*	*
% of vegetative tiller number										
Ellett	93.1	78.6	77.7	76.3	77.0	97.9	81.8	75.2	78.5	81.9
Ruanui	96.3	85.9	84.2	83.8	85.0	98.9	95.9	89.3	87.8	88.9
SED	2.4	2.8	1.9	1.6	1.2	0.99	2.1	1.0	3.4	2.2
Signif.	NS	(†)	*	*	**	NS	**	**	(†)	*

Signif.: Significance:

Colour code: spring and summer:

[a] Standard error of differences between pairs of means;

(†): P<0.1; * P<0.05; ** P<0.01; *** P<0.001; NS not significant.

b, c, d: data were transformed before statistical analysis; means on the original scale are presented for simplicity.

Table 6.3. Tiller characteristics of 'Ellett' and 'Grasslands Ruanui' after 45 days regrowth (19 March – 4 July 1998) under light treatments (control and shade) (Experiment 2).

	Control		**Shade**			
	Ellett	Ruanui	Ellett	Ruanui	SED	Signif.
Tiller number per plant	52	79	30	40	7.60	**
New tillers per large and medium sized tagged tiller	1.83	1.54	0.84	0.73	0.17	NS
New tillers per small tagged tiller	0.87	0.76	0.64	0.32	0.20	NS
Percentage of reproductive tillers (%)	34	25	27	14	2.13	**

Level of significance, from ANOVAs comparing the shade and control treatment for each cultivar was $P<0.01$ (**) and $P>0.05$ (NS) respectively. SED: Standard error of differences between pairs of means comparing 'Ellett' and 'Grasslands Ruanui' within each light treatment.

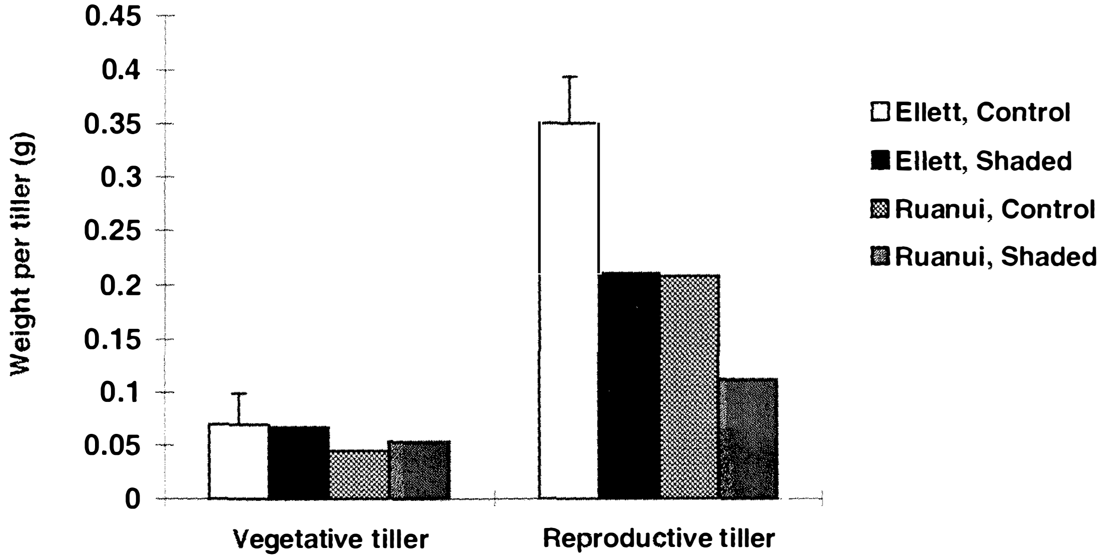

Figure 6.1. Dry weight of vegetative and reproductive tillers of 'Ellett' and 'Grasslands Ruanui' after 45 days regrowth (19 March – 14 July 1998) under different light environments (Experiment 2). Bars are $LSD_{5\%}$ for cultivar comparisons within each light treatment.

vegetative tiller weight was less for Grasslands Ruanui than for Ellett, and was reduced by shade for both cultivars (Fig. 6.1, Plate 6.3, effects on 'Ellett' tillers). These differences raise the possibility that manipulation of reproductive tiller size could be a useful way to modify plant characteristics, for example, to minimise the impact of flowering on sward quality from an animal nutrition perspective.

Prior to imposing the light treatments and cutting in Experiment 2 (19 May 1998), 95 % of the large and medium sized tagged tillers were reproductive for 'Grasslands Ruanui', and 98 % of these were reproductive for 'Ellett'. Of the small tagged tillers, 32 % of the 'Grasslands Ruanui' tillers and 47 % of the 'Ellett' tillers were reproductive. Regardless of cultivar, the large and medium sized tagged tillers were almost exclusively reproductive, and produced more new tillers than the smaller tagged tillers. Many of the smaller tagged tillers remained vegetative (Table 6.3, $P<0.001$). Although 'Ellett' produced more new tillers per tagged tiller than did 'Grasslands Ruanui', this difference was not significant (Table 6.3). The present results do show, however, that propensity to flower is strongly related to tiller size, with the smaller tillers of both cultivars being less likely to flower, and with this effect being more for 'Grasslands Ruanui', than for 'Ellett'. Further study is therefore needed to separate flowering and tiller size effects on daughter tiller production.

In the summer of the establishment year, 'Ellett' produced a higher proportion of reproductive tillers than did 'Grasslands Ruanui' (34 % vs 25 %, respectively) under the full light treatment. These differences suggest a greater turnover and replacement of the tiller population in the flowering period for 'Ellett' than for 'Grasslands Ruanui', and are consistent with the possible differences in perennation strategy for the two cultivars, as suggested by Matthew et al. (1993). However, they do not fully quantify cultivar differences because flowering and tiller size effects on daughter tiller production are linked, as mentioned above. That the greater tiller turnover at flowering occurred in 'Ellett' in the establishment year is of interest because the tiller survival diagram of Korte (1986), for 'Grasslands Nui', a cultivar bred from material from the same source as 'Ellett', shows this pattern was not strongly evident in the establishment year, and was only clearly evident in the second year.

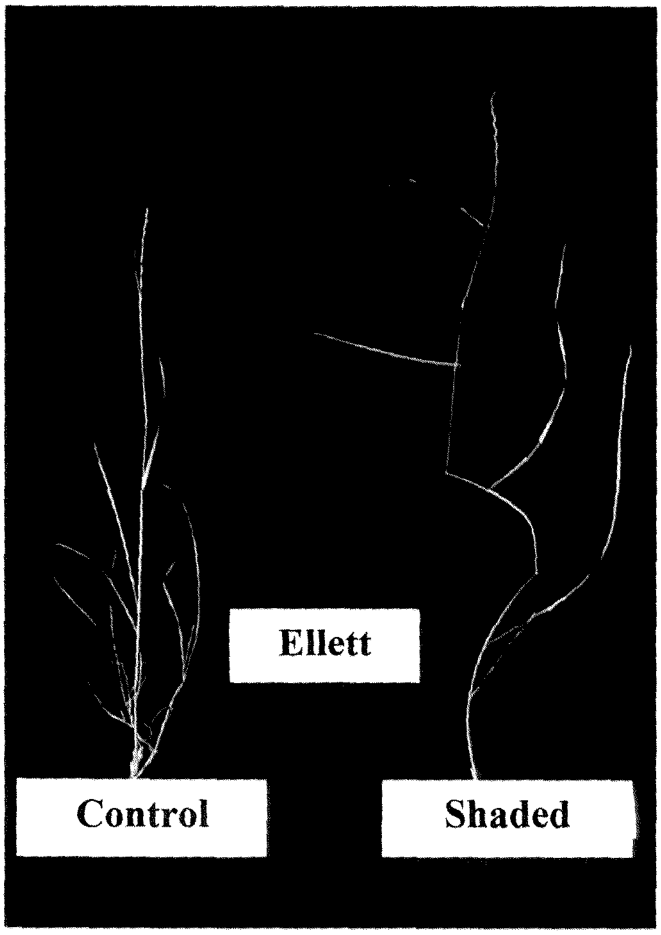

Plate 6.3. Reproductive tillers of 'Ellett' ryegrass from the control treatment (at the left) and the shade treatment (at the right).

6.5.1.3 Overview of flowering behaviour

In a more general sense, the flowering behaviour of 'perennial ryegrass' may be genetically and/or environmentally determined (Langer 1963; Jewiss 1972). Environmental factors controlling the transition from vegetative to reproductive growth in grasses are photoperiod (daylength) and temperature (vernalisation requirement). It was reported by Cooper (1960) that perennial ryegrass required a dual induction of low temperatures and short days to enable the plant to initiate the floral primordia and a secondary induction requirement for long days allowing inflorescence development. When the various studies, including the data presented here, are arranged by latitude, there is evidence of a correlation between the proportion of tillers flowering and the latitude (Table 6.4). In Hamilton, New Zealand, (37 °47' S), the proportion of reproductive tillers for 'Ellett' was about 25 % in spring (November) of the second year (Table 6.2). Thom (1991) recorded a slightly lower figure of 18 % in a mixed ('Grasslands Nui' and 'Ellett') perennial ryegrass and white clover pasture under dairy cow grazing, at the same research station. Matthew (1992) observed a range from 6 to 36 % of reproductive tillers for 'Ellett' during spring in Palmerston North (latitude 40 °23' S) under different sheep grazing managements, so for this data set it is difficult to separate management and latitude effects. However, McKenzie (1997b) reported 'Ellett' tillers were mostly vegetative during spring (< 9 % reproductive) in Natal, South Africa (latitude 30 °24' S), under sub-tropical conditions. In contrast, in Lusignan (46 °26' N), 'Ellett' under controlled environment conditions, had a higher percentage of reproductive tillers than in Hamilton (37 °47' S, Table 6.2), during the establishment (first) year.

Although Table 6.4 is organised by latitude, it is not clear to what extent this a daylength response. Since temperature also increases with decreasing latitude, vernalisation responses may also be involved in the trend for a lower percentage flowering at lower latitudes (Table 6.4).

To summarise, it is clear that flowering behaviour is controlled by grazing management regime, tiller size and a range of environmental variables including degree of vernalisation, latitude and underlying genetic differences in the way cultivars respond to environmental variables. The genetic effect is illustrated by significant differences

Table 6.4. Percentage of reproductive tillers of 'Ellett' and 'Grasslands Ruanui' ryegrasses at different latitudes for established swards. Proportion of reproductive tillers was estimated within tiller dynamics circular frames.

Latitude	Climate	Grazing management	Cultivar Grasslands Ruanui	 Ellett
South Africa, Natal, **30°24'S**	Tropical	Sheep	-	< 9 (Nov 1995)
New Zealand, Hamilton, **37°47'S**	Warm temperate	Rotational dairy cow	10.7 (Nov 1997)	24.8 (Nov 1997)
New Zealand, Palmerston North, **40°23'S**	Temperate	Sheep	21[b] to 22.5 (Nov 1989)	6.2[c] to 36.4 (Nov 1987)
France[a], Lusignan, **46°26'N**	Temperate	Cutting	25.0 (July 1998)	34.0 (July 1998)

[a] % of reproductive tillers per plant observed during the establishment year.

[b] % of reproductive tillers under medium intensity rotational grazing by sheep. Range of values based on three replicates.

[c] % of reproductive tillers under different frequency and intensity of grazing by sheep.

between the two cultivars when they were compared in the same environment at Hamilton and Lusignan.

The basis of the genetic difference between 'Ellett' and 'Grasslands Ruanui' is unclear but the above results are consistent with a difference in magnitude of a common vernalisation response. Standard plant breeding practices (Corkill 1949) were used to produce the cultivar Grasslands Ruanui'. However, 'Ellett' ryegrass was the product of natural selection on a dairy farm in South Auckland, where Italian and perennial ryegrass had been sown together from about 1950 to 1960, as a cultural practice to increase the biomass (See Chapter 2). Thus it is possible that 'Ellett' has some genes from the Italian ryegrass by introgression, increasing the propensity of 'Ellett' to produce reproductive tillers.

6.5.2 Tillering responses in different environments

6.5.2.1 Tillering responses to simulated shade (Experiment 2)

Both ryegrass cultivars had greatly reduced tiller number per plant, tiller number per tagged tiller and proportion of reproductive tillers under the shade treatment compared with the control (Table 6.3) ($P<0.01$). Differences in tiller number per plant, new tillers per tagged tiller, proportion of reproductive tillers and tiller weight between 'Grasslands Ruanui' and 'Ellett' remained the same under the shade treatment, since no significant cultivar × light environment interaction was found for any of the measurements.

Vegetative tiller weight of both cultivars was similar under both light treatments whereas reproductive tiller weight was reduced by 40 % for 'Ellett' and 43 % for 'Grasslands Ruanui' under the shade compared with the control treatment (Fig. 6.1). At anthesis, the undefoliated reproductive perennial ryegrass tiller, retained most of the carbon it has fixed, despite its vascular association with vegetative defoliated tillers (Ong et al., 1978b). However, when stressed, most plants preferentially allocated carbohydrate to seed filling, to the detriment of vegetative tillers. Indeed, Casal et al. (1985) showed for *Lolium multiflorum*, that a low R : FR advanced reproductive development and increased the number of fertile tillers per plant. The opposite response for the perennial ryegrasses 'Ellett' and 'Grasslands Ruanui' was observed in

Experiment 2. Both cultivars tended to maintain vegetative tiller weight under shade at the expense of development of reproductive tillers. This strategy may assist the persistence of a perennial ryegrass, which is more dependent on the survival of pre-flowering tillers or production of new vegetative tillers after flowering, than a grass dependent on seed set and recruitment of seedlings.

6.5.2.2 Tillering responses to nitrogen (Experiment 1)

Nitrogen treatment did not significantly affect the reproductive or vegetative tiller number and percentage of total tillers for either of the ryegrass cultivars over the first year (Table 6.5). However, 'Ellett' and 'Grasslands Ruanui' ryegrass cultivars had different responses to nitrogen during the second flowering period giving rise to a significant cultivar × nitrogen interaction (December 1997 and January 1998) on the percentage of reproductive (Fig. 6.2, Table 6.5) and vegetative tillers (Table 6.5). 'Ellett' had a tendency for increased reproductive tiller number whereas 'Grasslands Ruanui' increased vegetative tiller number in response to nitrogen. The effects of applied nitrogen fertiliser on vegetative and reproductive tiller number was dependent on cultivar, despite the fact that many authors showed that increasing levels of nitrogen resulted mainly in increased vegetative tiller production (Curll and Wilkins 1982; Thomas et al., 1990; Harris et al., 1996). McKenzie (1998) showed that 'Ellett' ryegrass reproductive development was promoted when 240 kg/ha of nitrogen fertiliser was applied in a subtropical environment, which suggests these observations could be repeatable under temperate conditions. Wilkins (1995 and 1997) also showed that the mean proportion of reproductive tillers of the perennial ryegrass cultivar 'Merlinda' increased when nitrogen fertiliser was applied at rates ranging from 100 to 400 kg nitrogen per hectare per year. However, increased nitrogen resulted in increased vegetative tillering by 'AberElan' ryegrass (Wilkins 1997), which is similar to the behaviour of 'Grasslands Ruanui'.

A decline in the 'Ellett' tiller population (P_t/P_0) in response to nitrogen in December 1997 (see Chapter 5) could be explained by the increase in the proportion of reproductive tillers following nitrogen application (Table 6.5). In December 1997, the combination of dry weather (see Chapter 3) and defoliation of reproductive tillers could have contributed to lower tiller survival and tiller birth rates for 'Ellett'. 'Grasslands Ruanui' tiller population (P_t/P_0) increased in December 1997 in response to nitrogen,

Table 6.5. The effects of nitrogen (N) fertiliser on the mean number of reproductive and vegetative tillers and the proportion of total tillers in circular frames, during the flowering periods in 1996/97 and 1997/98 (see footnotes under Table 6.2).

	Dates									
	First year					**Second year**				
	7/10/96	**29/10/96**	**25/11/96**	**16/12/96**	**6/1/97**	**1/9/97**	**21/10/97**	**17/11/97**	**15/12/97**	**12/1/98**
Reproductive tiller number										
N+/N-										
Ellett	16.0^{NS}	41.7^{NS}	57.0^{NS}	78.4^{NS}	83.2^{NS}	2.5^{NS}	49.9^{NS}	56.7^{NS}	53.9^{NS}	48.9^{NS}
	9.1	40.1	59.9	71.1	82.0	4.9	20.0	27.4	27.3	25.9
Ruanui	13.9	45.1	52.8	70.5	68.3	2.1	15.6	23.4	25.5	27.6
	6.2	37.0	49.0	61.0	65.2	3.8	4.4	24.6	27.9	27.8
SED	3.7	8.2	8.6	11.1	14.6	**b**	**c**	**d**	12.9	9.8
Vegetative tiller number										
N+/N-										
Ellett	161^{NS}	173^{NS}	219^{NS}	243^{NS}	269^{NS}	222^{NS}	138^{NS}	118^{NS}	130 †	172 †
	133	127	193	240	265	173	119	107	141	165
Ruanui	252	257	276	354	383	325	264	237	280	353
	209	224	256	319	365	245	207	177	171	195
SED	26.3	30.9	50.8	54.8	58	61	37.4	37	36.2	42.3
% of reproductive tiller number										
N+/N-										
Ellett	7.8^{NS}	19.9^{NS}	21.5^{NS}	24.2^{NS}	23.0^{NS}	1.2^{NS}	22.6^{NS}	29.4^{NS}	26.6*	21.6*
	6.0	23.0	23.1	23.2	23.1	3.0	13.8	20.2	17.8	14.6
Ruanui	4.8	14.6	15.5	16.4	15.0	0.6	5.8	9.2	8.1	7.4
	2.6	13.6	16.2	16.1	15.0	1.7	2.3	12.2	16.4	14.8
SED	2.5	3.6	2.5	2.2	1.8	1.2	3.4	3.6	3.9	3.2
% of vegetative tiller number										
N+/N-										
Ellett	92.2^{NS}	80.2^{NS}	78.5^{NS}	75.8^{NS}	77.1^{NS}	98.9^{NS}	77.4^{NS}	70.6^{NS}	73.4**	78.4*
	94.0	77.0	76.9	76.8	76.9	97.0	86.2	79.8	83.6	85.4
Ruanui	95.2	85.4	84.5	83.6	85.0	99.4	94.2	90.8	91.9	92.6
	97.5	86.4	83.8	83.9	85.0	98.3	97.7	87.8	83.6	85.2
SED	2.5	3.6	2.5	2.2	1.8	1.2	3.4	3.6	4.2	3.2

[a] SED for comparison of interaction means or pairs of means within N treatments.

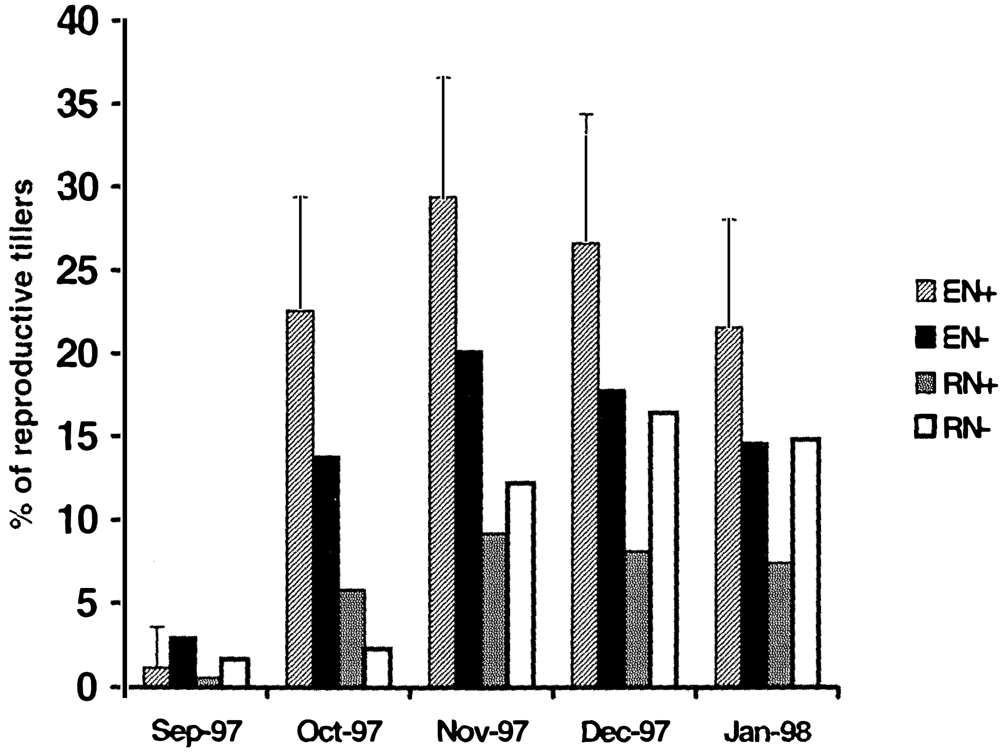

Figure 6.2. Effects of nitrogen on the percentage of reproductive tillers of 'Ellett' and 'Grasslands Ruanui' ryegrasses in circular frames under different nitrogen treatments during the second flowering period (1997/98). N+: with nitrogen and N-: no nitrogen (Experiment 1). Bars are LSD$_{5\%}$ for cultivar comparisons within each treatment.

probably because nitrogen promoted vegetative tiller production (Table 6.5) through an increase in tiller birth rate.

Differences in perennation between 'Ellett' and 'Grasslands Ruanui' ryegrass relate to differences in the number of reproductive tillers produced and the proportion of these tillers that produce reproductive daughter tillers (re-heading). Persistence and perennation of perennial ryegrass in temperate environments relies on initiation of daughter tillers from flowering tillers or the maintenance of existing vegetative tillers during the post-flowering period (Matthew et al., 1993). Since nitrogen fertiliser caused different responses for established swards, dependent on the propensity of the cultivar to produce reproductive tillers, management decisions relating to nitrogen applications should also consider ryegrass cultivar. Applying nitrogen to 'Ellett' ryegrass a few weeks before the flowering period could compromise its persistence. On the other hand, such an application to 'Grasslands Ruanui' could improve its persistence via improved vegetative tillering.

Reproductive development in ryegrass affects the nutritive quality of pasture (Browse et al., 1984; Tallowin et al., 1989) and animal performance in terms of apparent intake and feeding value, which also declined with increasing tiller maturity (Ulyatt 1973; 1981a, b). Differences in flowering behaviour between 'Ellett' and 'Grasslands Ruanui' ryegrass promoted by applications of nitrogen, could be of interest to plant breeders wishing to modify reproductive tiller number in perennial ryegrass cultivars so as to improve sward quality and possibly animal performance.

6.5.2.3 Tillering responses to irrigation (Experiment 1)

In November and December 1996 there were more reproductive tillers per frame in irrigated plots than in un-irrigated plots (Nov: +Irr: 65.3 vs –Irr: 44 rep. tillers, SED= 7.5, $P<0.05$; Dec: +Irr: 82.2 vs –Irr: 58.3 rep. tillers, SED= 10.3, $P<0.05$, Table 6.6). Water stress affected reproductive development by advancing the onset of the reproductive state (Dougherty 1973). This is seen as a survival mechanism (Boyer 1973). Water stress also increased the proportion of reproductive tillers (Dougherty 1973). The differences observed in November and December 1996 could indicate either later flowering on irrigated plots or increased reheading on these plots. However, the

Table 6.6. The effects of irrigation (I) on the mean number of reproductive and vegetative tillers and the proportion of total tillers in circular frames during the flowering periods in 1996/97 and 1997/98 (see footnotes under Table 6.2). Water was applied from November to March in both years (see Chapter 3).

	Dates									
	First year					**Second year**				
	7/10/96	29/10/96	25/11/96	16/12/96	6/1/97	1/9/97	21/10/97	17/11/97	15/12/97	12/1/98
Reproductive tiller number										
Irr+/Irr-										
Ellett	14.4^{NS}	51.0^{NS}	70.5^{NS}	87.1^{NS}	87.1^{NS}	4.1^{NS}	29.1^{NS}	37.2^{NS}	31.8^{NS}	29.9^{NS}
	10.8	30.9	46.4	62.4	78.1	3.3	40.7	46.9	49.4	44.9
Ruanui	7.4	42.2	60.1	77.4	68.3	1.9	2.2	26.0	23.8	23.3
	12.8	39.9	41.6	54.1	65.2	4.0	17.8	22.0	29.6	32.1
SED	6.7	7.5	9.2	11.5	13.9	**b**	**c**	**d**	11.5	8.5
Vegetative tiller number										
Irr+/Irr-										
Ellett	156^{NS}	152^{NS}	200^{NS}	228 †	268 †	199^{NS}	135^{NS}	109^{NS}	132^{NS}	183^{NS}
	138	148	212	255	266	196	122	116	139	155
Ruanui	230	241	283	368	420	296	278	236	262	305
	231	239	250	305	328	274	193	179	189	243
SED	24.8	26.0	49.7	56.4	59.7	53	39	38.6	34.5	41.4
% of reproductive tiller number										
Irr+/Irr-										
Ellett	7.6^{NS}	25.8*	26.3^{NS}	26.6^{NS}	23.2^{NS}	2.6^{NS}	13.8^{NS}	22.9^{NS}	19.1^{NS}	14.4^{NS}
	6.2	17.1	18.2	20.9	22.8	1.5	22.6	26.7	25.3	21.7
Ruanui	2.7	14.5	17.1	17.1	15.7	0.6	0.8	9.3	8.0	7.1
	4.7	13.7	14.6	15.4	14.4	1.7	7.3	12.0	16.5	15.1
SED	2.7	3.2	2.8	2.7	2.3	1.2	2.2	3.3	4.2	3.6
% of vegetative tiller number										
Irr+/Irr-										
Ellett	92.4^{NS}	74.2*	73.7^{NS}	73.4^{NS}	76.8^{NS}	97.4^{NS}	86.2^{NS}	77.1^{NS}	80.9^{NS}	85.6^{NS}
	93.8	82.9	81.8	79.1	77.2	98.5	77.4	73.3	76.1	78.3
Ruanui	97.4	85.5	82.9	82.9	84.3	99.5	99.2	90.7	92.0	92.9
	95.3	86.4	85.5	84.6	85.6	98.3	92.7	88.0	83.5	84.9
SED	2.7	3.2	2.8	2.7	2.3	1.2	3.6	3.3	4.6	3.6

[a] SED for comparison of interaction means or pairs of means within irrigation treatments.

opposite trend occurred in 1997, so the interpretation of the response in 1996 is very uncertain.

In December 1996 and January 1997, 'Grasslands Ruanui' showed a larger increase in vegetative tiller number in response to irrigation than did 'Ellett' (Table 6.6). These effects of irrigation on vegetative tiller number were discussed previously in Chapter 3.

No significant cultivar × irrigation interaction was found on reproductive tiller number (Table 6.6) suggesting that both ryegrass cultivars had a similar response to water application.

6.6 Conclusion

There were cultivar differences in post-flowering tiller production in the field and controlled environment, that were consistent with those reported previously for established swards (Matthew et al., 1993). 'Ellett' had a tendency to produce more reproductive tillers than did 'Grasslands Ruanui' especially during the second year, implying that the perennation of 'Ellett' was more dependent on 'reproductive pathway' than it was for 'Grasslands Ruanui'. These differences between ryegrass cultivars were emphasised with nitrogen but generally not with irrigation treatments. Moreover, there was no evidence that the ryegrass cultivars responded differently to shading. Cultivar perennation pathways were not influenced or regulated by the light environment; the mechanisms responsible for cultivar differences are unknown. Both ryegrass cultivars showed an unexpected response to shading in that reproductive tiller weight was strongly reduced whereas vegetative tiller weight was not. The different proportions of reproductive tillers at flowering for each cultivar suggests the need for specific grazing and nitrogen management strategies to optimise tiller replacement post-flowering.

6.7 Summary

6.7.1 Cultivar differences during the flowering period

- In the field experiment at Hamilton, New Zealand, and in the controlled experiment at Lusignan, France, 'Ellett' had a higher percentage of reproductive tillers than 'Grasslands Ruanui', regardless of environmental factors. These differences occurred during the establishment year and also over the next year.

- Differences in the percentage of reproductive tillers between 'Ellett' and 'Grasslands Ruanui' were stronger in the second year in the field trial.

- As found in the field (see Chapter 3) and at the vegetative stage (see Chapter 4), 'Grasslands Ruanui' had a higher tiller number per plant and a slightly lower vegetative and reproductive tiller weight than 'Ellett', in both light treatments in the controlled environment experiment.

6.7.2 Effects of the environment on reproductive development

- Shading reduced the percentage of reproductive tillers in both cultivars compared with the full light treatment.

- 'Ellett' had a tendency to produce more reproductive tillers in response to nitrogen whereas 'Grasslands Ruanui' produced more vegetative tillers, especially after the establishment year.

- Reproductive tiller number averaged across cultivars increased with irrigation in November and December 1996 but the interpretation of this response is uncertain.

- In December 1996 and January 1997 'Grasslands Ruanui' had a slightly higher vegetative tiller number in response to irrigation than did 'Ellett'.

- Vegetative tiller weight of both cultivars was similar under both light treatments whereas shading reduced reproductive tiller weight by 40 % for 'Ellett' and 43 % for 'Grasslands Ruanui' compared with full light.

CHAPTER SEVEN

⁂

TOWARDS A CONCEPTUAL APPROACH FOR UNDERSTANDING SEASONAL TILLER DYNAMICS

CHAPTER 7: TOWARDS A CONCEPTUAL APPROACH FOR UNDERSTANDING SEASONAL TILLER DYNAMICS

7.1 Introduction

Tiller dynamics data from the field study were analysed in a descriptive or mathematical sense (Chapter 5) and also from the perspective of reproductive behaviour and associated perennation strategy (Chapter 6). Another feature of tiller dynamics is the seasonal interaction of the tiller population with the environment. In the present study the seasonal pattern for perennial ryegrass was characterised (Chapter 5) by an increasing tiller population during winter and summer followed by a population decline in autumn (March/early April).

Brereton (1994) described a dynamic model of tiller appearance and death in perennial ryegrass. This model considers tiller appearance and death as a function of canopy light interception and herbage relative growth rate and requires three input parameters K', K'' and n (K' is the proportional light interception at which Fs is half of the potential maximum; K" modifies K' when light interception is incomplete; n is a constant which determines the shape of the response curve). These parameters were estimated by comparing model output with observed tiller density changes in perennial ryegrass in the field.

It would be preferable to develop a model where input parameters are derived from observations and not merely mathematical tools to fit the output to the data. Informal discussions among researchers over the last 5 years on the way to interpret and model tiller dynamics of grass swards, have produced a number of ideas which are as yet largely untested experimentally, and for the most part unpublished. This chapter examines whether or not these ideas can form a basis to explain seasonal changes in the tiller populations reported in Chapter 5.

7.2 Emerging theories on factors promoting tiller population change

7.2.1 Plant morphology and tiller population dynamics

It has been shown in Chapter 4 that leaf appearance rate (A_L), leaf elongation rate (LER), leaf elongation duration (LED), final leaf length, site filling and tiller appearance are all interdependent (Fig. 7.1). In particular, A_L controls both tiller bud number and LED. Robson (1967) found that A_L decreased as LED increased and the number of tiller buds produced decreased, since there is one tiller bud in the axil of each leaf. Consequently, a low A_L should result in the production of a low number of large tillers (Lemaire and Chapman 1996). However, this pattern cannot be generalised. 'Ellett' and 'Grasslands Ruanui' ryegrasses had similar A_L with different tiller number per plant, while in the genetic lines 'LL' and 'SL', 'SL' had the lower A_L and also the lower tiller number per plant (see Chapter 4). These different responses for the two pairs of genetic lines arise because tiller appearance depends not only on A_L but also on site filling, the propensity of tiller buds to develop into tillers (Fig. 7.1).

A second influence on tiller appearance is leaf area index (LAI). An important determinant of LAI is leaf length (Fig. 7.1). Leaf length is determined by the ratio LER : A_L (Lemaire and Chapman 1996) and an increase in LER or a decrease in A_L, as previously observed (see Chapter 4), was associated with increased leaf length. Kays and Harper (1974) showed that self-shading of tiller bases within a dense canopy was associated with increased leaf length and decreased tillering. Casal et al. (1985, 1987) linked self-thinning with a low red : far red ratio, and observed an associated increased resource of leaf area per tiller through increased leaf elongation rate (LER) and leaf elongation duration (LED) (Allard et al., 1991), partially compensating for the lower light interception. Therefore, LAI of the sward canopy interacts with LER, LED and site filling, and strongly influences tiller appearance and tiller death (Fig. 7.1). A high LAI decreased tiller appearance and increased tiller death (Simon and Lemaire 1987). LAI also determines the amount of light transmitted to the soil level and is an appropriate measure of light interception where the objective is to assess plant responses.

A third factor to be considered when predicting tiller population increase or decrease is size/density compensation, also known as the self-thinning rule. The –3/2

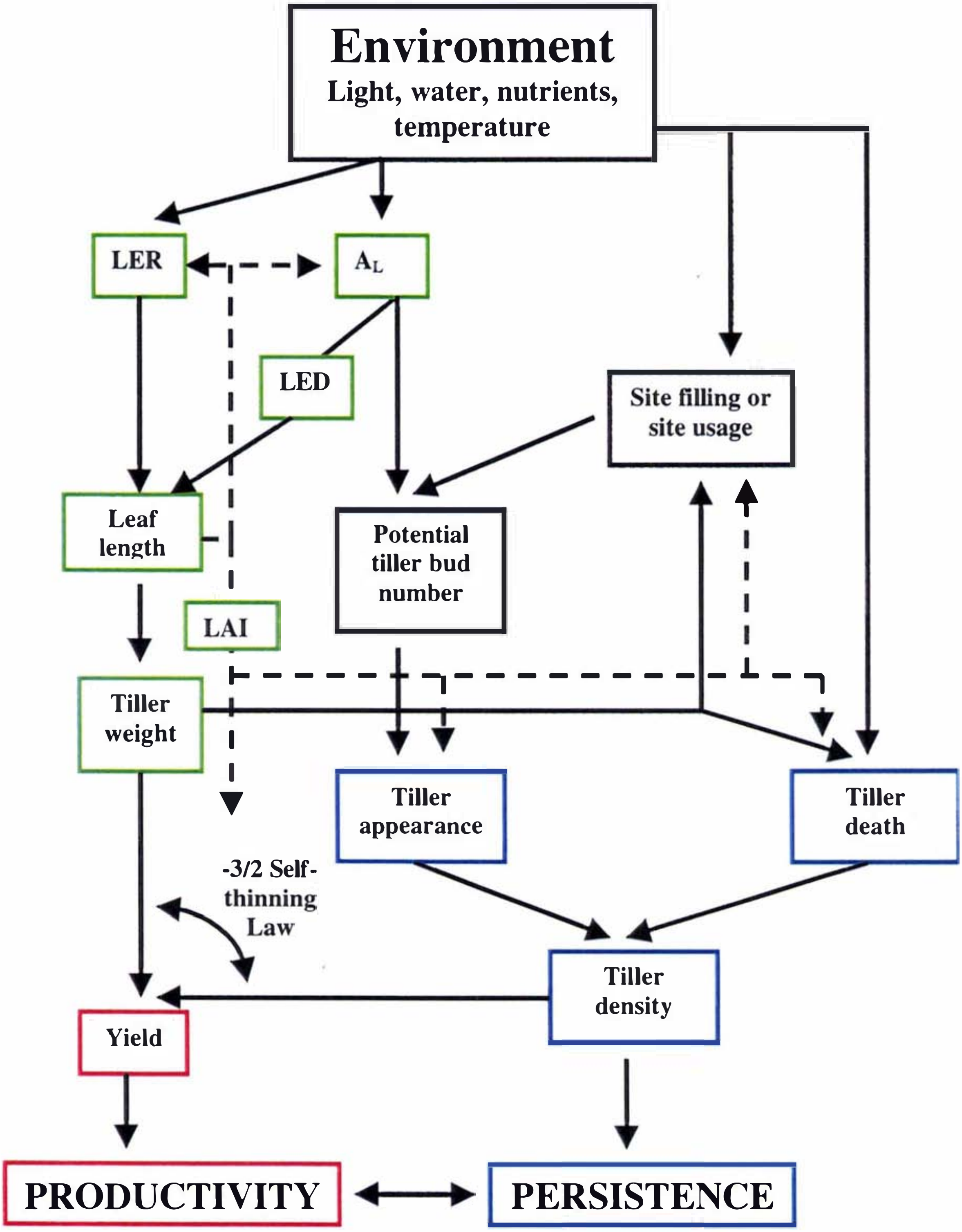

Figure 7.1. Relationships between plant morphological characteristics (green borders), persistence through tiller population demography (blue borders) and productivity (red borders).

self-thinning relationship, which is characterised by the inverse relationship between weight of individual adult tillers and the tiller density of the sward (Fig. 7.1), has been well described for undefoliated (Kays and Harper 1974; Lonsdale and Watkinson 1982) and defoliated swards (Matthew et al., 1995; Matthew et al., 1996). After a re-evaluation of this relationship, Sackville Hamilton et al. (1995) suggested that the –3/2 self-thinning line could be conceptualised as defining a line of constant leaf area index and perpendicular movement of size/density co-ordinates from the self-thinning line could be used as a productivity index (Matthew et al., 1996). In theory, grass swards with large tillers and low tiller density (for example, dairy pastures) can have the same leaf area as grass swards with small tillers and high tiller density (for example, sheep pastures). This illustrates the theory of size/density compensation but, more importantly here, movement along a –3/2 self-thinning line indicates changes in herbage mass. With larger tillers, a higher herbage mass is required than with smaller tillers, to achieve the same LAI. This leads to the recognition that tiller density will vary with herbage mass. Adjustment of tiller density data for herbage mass (represented as tiller weight in Fig. 7.1) may therefore provide a tool or model to assist in interpretation of tiller density data.

Tiller weight and leaf size are closely related (Fig. 7.1). Both were defined as genetically determined morphological characteristics (Lemaire and Chapman 1996) and tiller density is a sward characteristic often used as an indicator of persistence (Matthew et al., 1999). A high tiller weight is often associated with long leaves, rapid LER and low tiller production ('Ellett' and 'LL', see Chapter 4), while low tiller weight is more often associated with short leaves, slow LER and high tiller production ('Grasslands Ruanui' and 'SL', see Chapter 4).

Finally, sward productivity and persistence overlap or influence each other via a common component tiller density. Tiller density is determined by the equilibrium between tiller appearance and death (Fig. 7.1) and is an important mechanism for expression of changes of LAI. Because the tillering process is a consequence of leaf growth, sward productivity and persistence are both linked to LAI, and in this sense, LAI is an indicator of productivity as well as tillering responses. Therefore, canopy cover or LAI of the sward plays an important role in many plant processes and could be a useful way of describing interactions between plants and their environment.

7.2.2 Sward regrowth and tiller population density

The previous section described the interaction between plant morphology and tiller dynamics with an implied assumption that the processes discussed were static. In fact, in the majority of situations including the dairy farm swards described in Chapter 5, tiller dynamics is strongly influenced by cyclical patterns relating to defoliation and regrowth. To understand tiller dynamics it is necessary to appreciate the time course of LAI increase after defoliation, and the associated effects on tiller appearance and death.

A recently defoliated sward typically has a LAI of about 0.5 to 1.0 (Hodgson 1990). At a LAI around 3.0, sometimes called the critical LAI (Brougham 1960) 95% of incident light was intercepted by the canopy. As leaf area continues to accumulate, an 'optimum' LAI is reached. This was defined by Donald (1961) as a point where the lowest leaves in the canopy receive just enough light to make a small but positive contribution to photosynthesis, and are not below their light compensation point. Eventually, the point was reached where leaf senescence equals leaf production and a maximum or 'ceiling LAI' is reached (Davidson and Donald 1958; Donald 1961).

Ceiling LAI varies with season, plant species and sward structure (Chapman and Lemaire 1993); ceiling LAI was higher in spring and summer and lower in autumn and winter when light intensities were high and low, respectively (Brougham 1958; Black 1963). Recognising the environmental effect on ceiling LAI, Matthew et al., (1995) defined the 'environmental ceiling' LAI (ECLA) as the maximum area of green leaf a sward was able to support in a given environment. In a continuously grazed sward, the LAI representing maximum environmental ceiling leaf area (ECLA) was linked to the $-3/2$ self-thinning boundary line (Sackville Hamilton et al., 1995). It was also noted (Mohler et al., 1978) that the leaf area of canopies undergoing self-thinning was almost constant, so that the boundary line was conceptualised as a constant leaf area line.

An attempt to calculate seasonal change in ceiling LAI arising from variation in solar radiation was made by Bishop-Hurley (1999). He combined equations 1.1 and 1.2 of Lemaire and Chapman (1996), describing the light extinction profile and incident radiation, to derive an equation for the amount of light absorbed by the canopy (7.1). If the proportion of incident light absorbed by the canopy is known, then ECLA can be estimated as:

$$\mathbf{ECLA = -Ln\,(1 - (PAR_a \div (PAR_o \times k_1))) \times 1/k_2} \qquad (7.1)$$

where:

PAR_o is incident photosynthetically active radiation, PAR_a is the quantity of photosynthetically active radiation absorbed by green leaf material, k_1 is a coefficient determined by the optical properties of leaves, and k_2 is the light extinction coefficient, which depends on sward structural characteristics.

This method raises a question in that equation 1.2 of Lemaire and Chapman (1996), shows that light extinction within a canopy is exponential, and therefore very large increases of leaf area are indicated to capture small amounts of light reaching the bottom of the canopy. In this sense, the application of the model has to be undertaken with care, because the predicted ceiling LAI varies greatly depending on the value assumed for PAR_a/PAR_o.

In parallel with changes in LAI during regrowth, there is also a cycle of tiller appearance and death. During early phases of regrowth, tiller appearance greatly exceeds tiller death and consequently tiller population density increases. In latter phases of regrowth, tiller death exceeds tiller appearance and the tiller population density decreases. This presumably occurs as leaves in the lower canopy are shaded below their compensation point (Donald 1961) and small tillers start dying (Ong 1978b). Therefore co-ordinates for total tiller number plotted against tiller size follow a curved trajectory as regrowth proceeds and LAI increases following grazing (Kays and Harper 1974) perennial ryegrass; Matthew et al., 1999, tall fescue, Fig. 7.2).

The trajectory of tiller density during regrowth has in the past seldom linked to sward LAI, but to use LAI as a tool for modelling tiller density, it would be necessary to make this link.

For regrowth after defoliation, perennial ryegrass tiller density was found to peak when sward LAI was between 3 and 4, and started to decline when sward LAI exceeded these values. The limiting value of sward LAI for tillering was found to be around 3 in

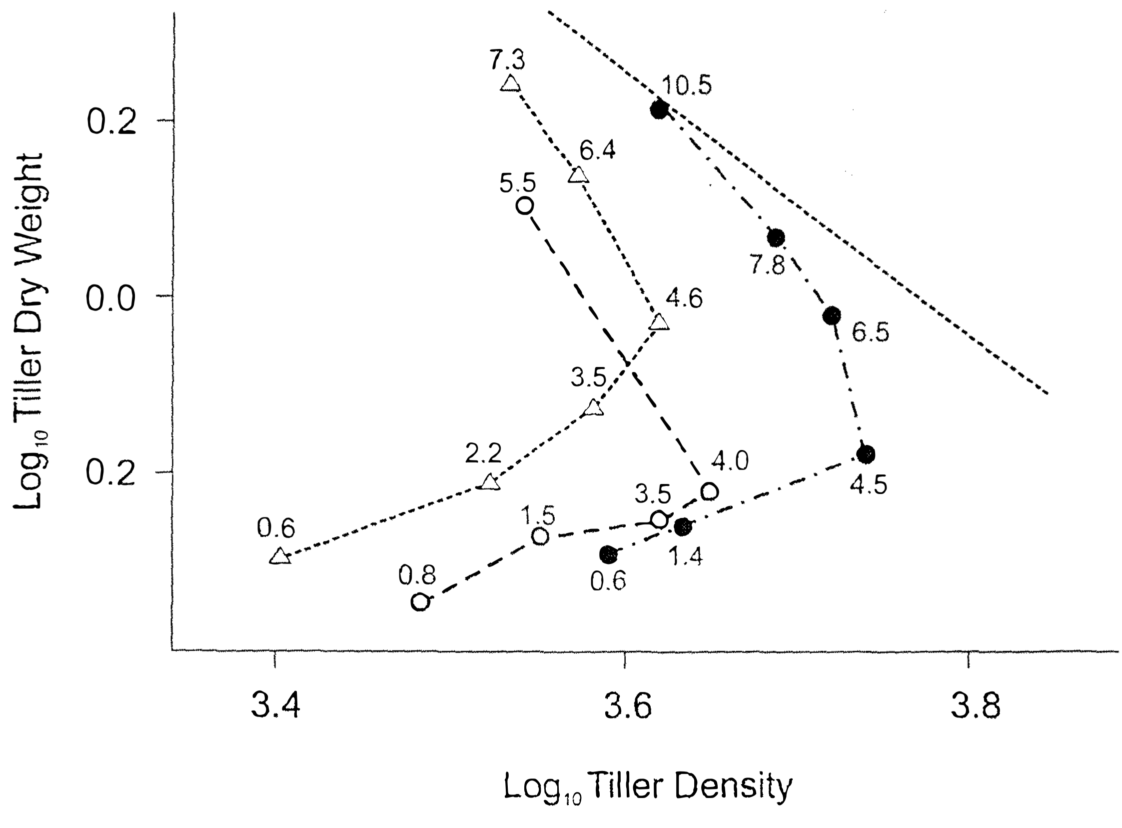

Figure 7.2. Regrowth trajectory for size/density co-ordinates of tall fescue. Distances from the arbitrarily placed –3/2 boundary line (dashed line) correlate closely with sward LAI (r = 0.94, P>0.001). (Unpublished data from experiment of Onillon et al. 1995, supplied by G. Lemaire).

different seasons for a vegetative sward, suggesting that it was not related to particular climatic events (Simon and Lemaire 1987). The LAI at which tiller density began to decline in tall fescue was slightly higher, ranging from 4 to 5 (Matthew et al., 1999).

As illustrated in Fig. 7.2, tiller population density declines as tiller death occurs, before ECLA is reached. This implies that a sward LAI of 3 to 4 is sufficient to limit tiller appearance and increase tiller death. Therefore, to model tiller population dynamics, it will be insufficient to know a value for ECLA; it will also be necessary to know what LAI can potentially accumulate during the regrowth period and whether or not this value is greater or less than the ECLA. This LAI limit, determined by the maximum leaf area developed by a population of tillers between two grazing events, could be defined as the morphogenetic ceiling leaf area (MCLA). Thus, in rotationally grazed swards, increases in tiller population would be expected following a defoliation where MCLA (i.e. LAI at the end of regrowth) is less than 3.

Mathematically, considering only adult tillers in the sward, and considering canopy leaf area rather than single tiller leaf area, the potential canopy leaf area (m^2/m^2 ground) within a regrowth interval (MCLA) can be calculated by using the following equations within a regrowth interval:

MCLA = Sward tiller density x Maximum number of leaves/tiller x Leaf size (7.2)
(tiller number/m^2) (m^2)

where:

Leaf size = LER × mean leaf width / A_L (7.3)
(m/GDD) (m) (leaf number/GDD)

Sward tiller density: the number of tillers per unit area. The methodology described to measure sward tiller density in Chapter 3 could be used.

Number of live leaves per tiller: is determined by the product of leaf life-span and A_L (Fig. 7.1) (Lemaire and Chapman 1996). Davies (1977) showed that the number of live leaves per tiller for perennial ryegrass ranged from 2.55 in January to 2.87 in May, in the Northern hemisphere (Aberystwyth). Lemaire and Chapman (1996) also reported that the maximum number of live leaves per tiller was about 3 for perennial ryegrass and appeared to be genetically determined. Leaf number per tiller varies between seasons with slightly lower values in winter than summer and the maximum number per tiller occurs when seed-heads are emerging (Davies 1977).

Leaf size: As shown in Figure 7.1, leaf size depends on LER and LED. Robson (1967) showed that the leaf elongation duration for tall fescue was proportional to the phyllochrone (the inverse of A_L). For this reason, it should be possible to relate leaf size to both leaf elongation rate (LER) and leaf appearance rate (A_L) for individual leaves (Fig. 7.1). Thus leaf size represents the ratio LER : A_L, assuming the ratio between A_L and leaf elongation duration is constant, or that new leaves do not appear simultaneously. Since LER (Watts 1972) and A_L (Durand et al., 1982) are closely related to temperature, they need to be converted to m^2 and leaf number per growing degree-day, respectively. The conversion to growing degree-day takes into account the effects of ambient temperatures on LER and A_L, and both can then be considered as constants.

The above theory primarily relates to the light environment and effects of shading at the canopy base in reducing tillering, when other environmental factors such as nitrogen and water supply are assumed to be non-limiting. Further adjustments will be required to accommodate effects of other environmental factors.

7.3 Application of ECLA and MCLA concepts to field data

7.3.1 Size/density compensation in 'Ellett' and 'Grasslands Ruanui'

Results presented in Chapter 3 showed that the cultivars studied had different sward structures. 'Ellett' ryegrass had large tillers and lower tiller density while 'Grasslands Ruanui' had small tillers and higher tiller density. One question that arises from the theory developed above is whether or not these cultivar differences could be explained by size/density compensation and productivity differences or whether they represent a more fundamental difference in growth strategy.

Since 'Ellett' and 'Grasslands Ruanui' had different sized tillers and density of tillers, they could possibly have had a similar LAI if size/density compensation had occurred.

In other words, the co-ordinates at the equilibrium for tiller size and tiller density for 'Ellett' and 'Grasslands Ruanui' could fall in different regions of a common –3/2 self-thinning line, 'Ellett' in the upper region and 'Grasslands Ruanui' in the lower part of the same line. At the end of the first summer, a tiller size/density graph was compiled to assess these questions (Fig. 7.3). Data plotted are the treatment means for cultivar tiller size and population density with and without nitrogen and irrigation treatments. For this assessment, the position of the –3/2 reference line is arbitrary and the important consideration is the distance of each point from the reference line. The distance from the line or productivity index (Matthew et al., 1996) showed a statistically significant correlation with herbage accumulation (Fig. 7.4) but the intercept on the y axis for 'Ellett' was higher than for 'Grasslands Ruanui'. That is to say, size/density compensation between treatments within a cultivar was observed but the tiller density and productivity index of 'Ellett' compared with 'Grasslands Ruanui' were lower than would be expected from consideration of size/density compensation alone.

There could be many explanations for this difference between 'Ellett' and 'Grasslands Ruanui' in productivity index (that is, difference in intercept of the self-thinning line). It was considered unproductive to pursue this line of analysis, as the field trial was not designed to determine the compensation line with different nitrogen and water managements. To investigate further the effects of the different sward structures of 'Ellett' and 'Grasslands Ruanui' on their respective yields and leaf areas, and to compare them under different managements, a new experiment would be needed to definitively answer this question.

7.3.2 Seasonal variation in tiller population density

As reported in Section 7.2.2, sward LAI controls tillering and a LAI above 3 limited tiller population increase (Simon and Lemaire 1987). Knowing that LAI is considered as a good indicator of the canopy light interception, then it is possible to assume that tiller population changes would be influenced by light intensity changes over season. To test this assumption, tiller dynamics diagrams ('Ellett' and 'Grasslands Ruanui' ryegrasses with nitrogen and previously presented in Chapter 5) were matched with the daily solar radiation curve calculated from the relationships reported by Bonhomme (1993, 1994). Visual inspection of these graphs, suggests that tiller population decline in autumn coincided with seasonal decrease in light intensity (Fig.

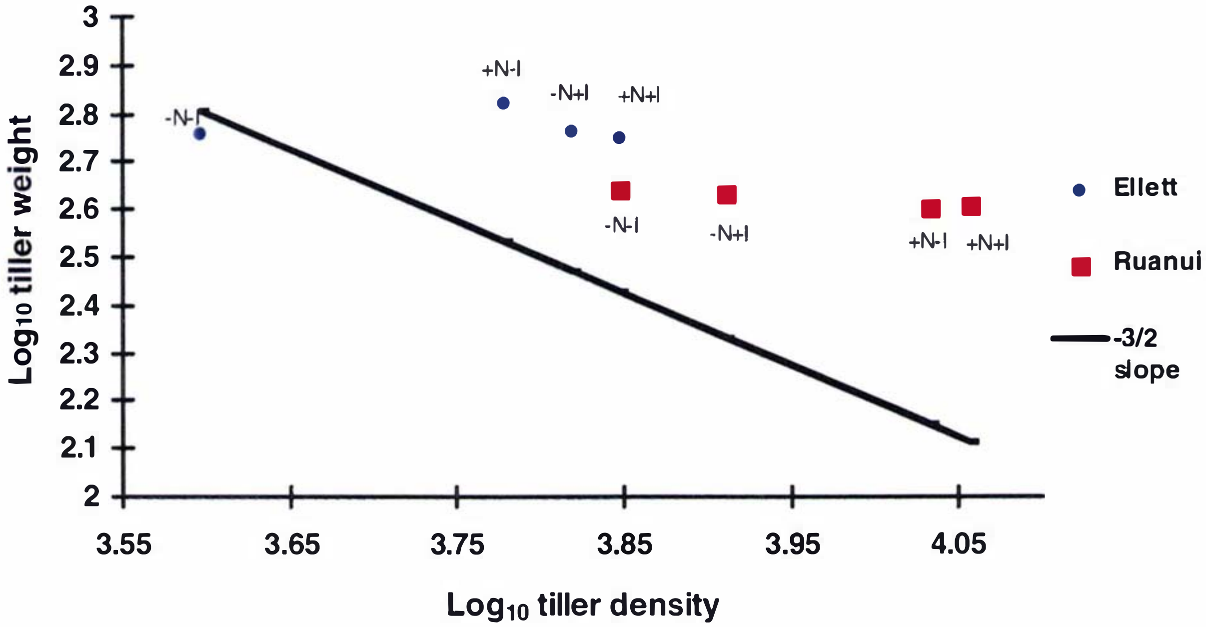

Figure 7.3. Nitrogen, irrigation and cultivar effects on tiller weight and tiller density in summer (after Bahmani et al., 1997).

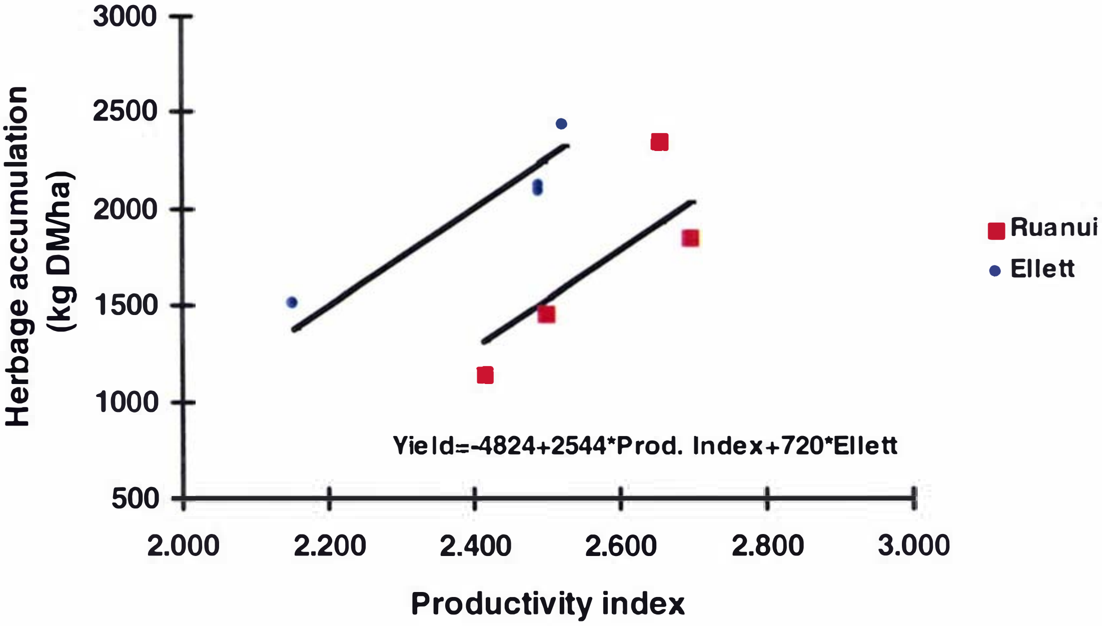

Figure 7.4. Correlation between herbage accumulation in summer and productivity index (after Bahmani et al., 1997).

7.5) suggesting that the light curve partly explained tiller population changes. However, during winter tiller population remained constant (Fig. 7.5b) or began to increase even while light intensity was still declining in May (Fig. 7.5a) implying that other factors such as herbage mass, temperature, photosynthesis and respiration rates could be responsible for controlling winter tiller population density. Similarly, when tiller dynamics diagrams for other treatments, including the control treatment, were matched with the daily solar radiation curve, there was not a close match between change in solar radiation and tiller population density in winter.

It was shown that biomass or herbage mass was inversely correlated to sward tiller density following a slope of –1/2 when both co-ordinates were plotted on a logarithmic scale (Matthew et al., 1996), suggesting that herbage mass limits sward tiller population density and could be used as an indicator of tiller population changes. An attempt to predict tiller dynamics changes with a model estimating sward tiller density from herbage mass (assuming –1/2 size/density compensation with biomass), tiller shape (assuming that, the shape parameter varied from about 40 in short swards to about 60 in long swards[1]) and the effect of PAR on LAI (ECLA), was proposed by Bishop-Hurley (1999). However, validation of the model using field data was not possible because of the small number of field tiller density counts collected (14 counts over three years), and because of concerns that counts made by different people at different stages in the experiment may not have been consistent.

Seasonal pre-grazing herbage mass and sward tiller density data for both ryegrass cultivars, averaged across nitrogen and irrigation treatments (Chapter 3), also showed a negative correlation between these two components (Table 7.1). This suggests that herbage mass strongly influenced tiller density. However, this relationship does not explain how the environment affects tiller population changes. An alternative approach eliminating the need to consider the herbage mass would be to calculate MCLA and compare MCLA with ECLA. The definition of MCLA (equation 7.2) implies that environmental factors such as temperature, light, nitrogen and water supply influence MCLA since, for example, leaf size responds directly to temperature. In theory, a tiller population increase would be expected when MCLA is lower than ECLA, and conversely a decrease in tiller population would be expected when MCLA is higher than ECLA.

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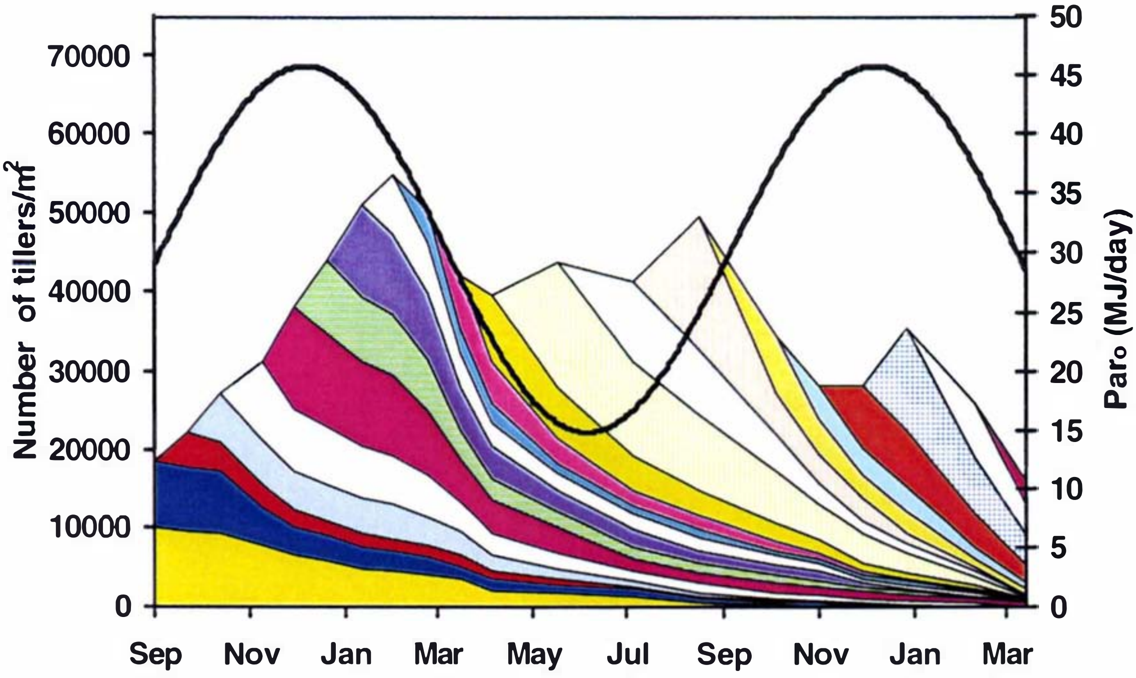
[1] A tiller shape parameter, R, was defined by Matthew et al. (1995) as (mean leaf area, m^2 per tiller)$^{3/2}$ / (mean volume, m^3 per tiller).

(a)



(b)

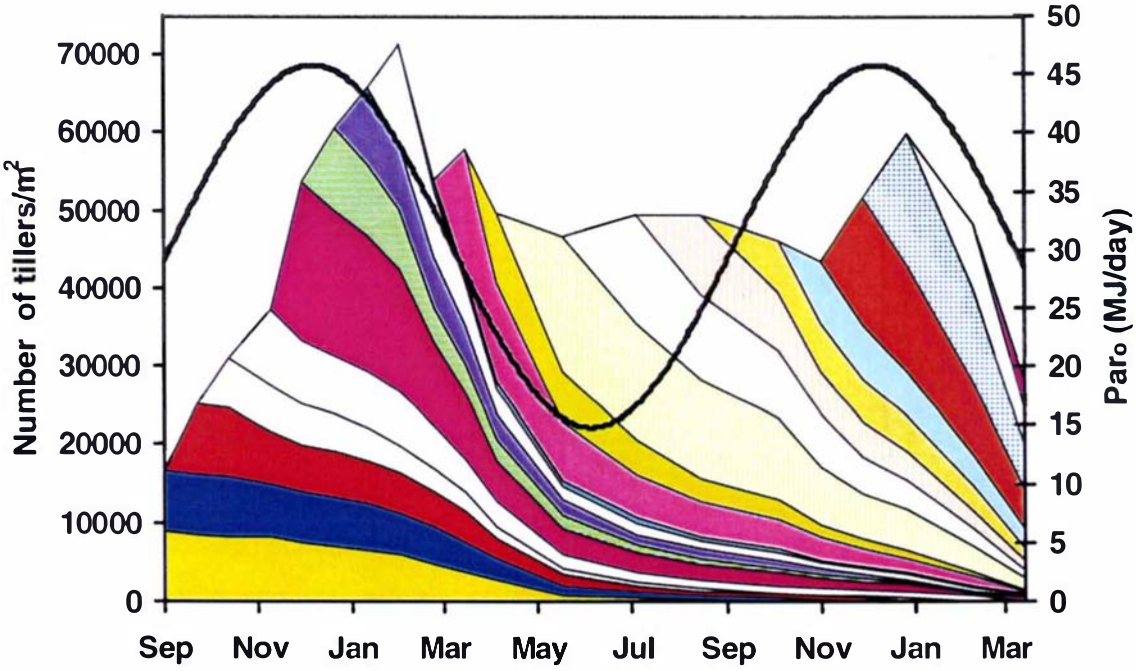


Figure 7.5. Tiller dynamics diagrams of (a) 'Ellett' and (b) 'Grasslands Ruanui' ryegrasses under nitrogen and irrigation treatments (+N+Irr) matched with the incident photosynthetically active radiation (PAR_o) over time.

Table 7.1. Seasonal pre-grazing herbage mass and tiller density for 'Ellett' and 'Grasslands Ruanui' ryegrass swards averaged across nitrogen and irrigation treatments.

	+N+Irr			
Season	**Pre-grazing herbage mass (kg DM/ha)**		**Pre-grazing tiller density (tillers/m^2)**	
	Ellett	Ruanui	Ellett	Ruanui
Spring 96	2835	2897	5863	8825
Summer 96/97	2761	2577	7037	10800
Autumn 97	2984	2682	10425	10344
Winter 97	1790	1737	12800	12475
Spring 97	3086	2669	9400	12200
Summer 97/98	2863	2792	12425	20819
Autumn 98	3017	3031	8138	14344

To test this theoretical concept, ECLA (equation 7.1) and MCLA (equation 7.2) should be estimated in relation to tiller population changes. Preliminary data were collected over 4 week periods in April/May and September/October 1998 following the field trial, but these data were considered insufficient to accurately estimate MCLA. A new experiment focused on collecting leaf growth data (LER, A_L, leaf width and live leaf number per tiller) during seasonal regrowth cycles of an established sward, is required, to validate the use of MCLA to predict seasonal tiller population changes.

CHAPTER EIGHT

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SYNTHESIS AND CONCLUSION

CHAPTER 8: SYNTHESIS AND CONCLUSION

8.1 Synthesis of results

The primary aims of this study were to identify possible differences between 'Ellett' and 'Grasslands Ruanui' ryegrasses in perennation strategy, and to assess the productivity of these cultivars under different nitrogen and irrigation treatments and under rotational grazing. Matthew (1992) observed that an established ryegrass sward of the cultivar 'Grasslands Ruanui' tended to replace tillers by the formation of daughter tillers on existing vegetative tillers. On the other hand, an established sward of the cultivar 'Ellett' replaced a large part of its tiller population by the formation of new daughter tillers on decapitated reproductive tillers in summer. Moreover, it has also been observed that 'Grasslands Nui' ryegrass, a cultivar related to 'Ellett', had a tiller dynamics pattern in the establishment year that was different from that in the second year (Korte 1986). A vegetative pathway more like that observed by Matthew for 'Grasslands Ruanui' was predominant in the first year, with the reproductive pathway, involving production of daughter tillers from flowering tillers, predominant in the second (Matthew et al., 1993). These observations lead to the hypothesis that 'Ellett' and 'Grasslands Ruanui' may have different tillering behaviours, and so a field experiment was carried out at Hamilton, New Zealand, to test this hypothesis.

In this experiment 'Ellett' outyielded 'Grasslands Ruanui' especially in spring and summer, but the two cultivars showed a similar seasonal pattern of tiller dynamics. Superior performance of 'Ellett' over 'Grasslands Ruanui' in spring-summer production contrasts with previous reports (Corkill et al., 1981; Goold 1982; Easton 1983) that the greatest production advantage was in winter. The enhanced spring-summer production of 'Ellett' was partly due the promotion of reproductive tillering by nitrogen fertiliser. Irrigation increased yield of both cultivars in summer 1996/97, 1997/98 and autumn 1998. 'Ellett' ryegrass showed strong reproductive development in the second spring. Four studies from different countries (see Table 6.4) suggested that percentage of tillers flowering in both cultivars decreased as latitude decreased, but for any one latitude, 'Ellett' had a higher percentage of tillers flowering than did 'Grasslands Ruanui'. 'Ellett' produced more reproductive tillers when treated with nitrogen in December 1997 (Fig. 6.2) and this was reflected in a lower population index than for 'Grasslands Ruanui' (section 5.4.3). Since reproductive tillers die after they are decapitated, cultivars such as 'Ellett' with a higher percentage of reproductive tillers will be vulnerable to stresses in late spring/early summer (November/December), which reduce survival of replacement tillers. Examples of such stresses include severe grazing and nitrogen deficiency.

The link between leaf morphology and tillering was investigated to assist with the interpretation of ryegrass tiller dynamics. An experiment was set up in France to provide relevant information on the morphological characteristics of both ryegrass cultivars under contrasting light environments (see Chapter 4). Results showed that 'Ellett had longer leaves and lower tiller number per plant than did 'Grasslands Ruanui', regardless of the light environment. Differences in leaf length were due to a higher LER for 'Ellett' than for 'Grasslands Ruanui' as LED for both was similar; differences in tiller number per plant were mainly due to a higher site filling for 'Grasslands Ruanui' than for 'Ellett', as their leaf appearance rates were similar. This was true for both shaded and full light environments. Leaf growth parameters were shown to be important regulators of tillering (Chapter 4) and leaf and tiller formation processes are intimately linked by reciprocal feed back mechanisms.

The results presented in Chapters 3, 4 and 5, allowed for the concept of MCLA to be introduced as a way of assessing environmental effects on tiller dynamics (Chapter 7). MCLA links leaf growth components (LER, A_L, leaf width and live leaf number per tiller) and sward tiller density to define potential pre-grazing LAI. Since it was shown that the tillering process is controlled by sward LAI, this linked the descriptive study of tiller dynamics with plant leaf morphological characteristics, which directly respond to the plant environment (see Chapter 7). A high MCLA would also indicate high productivity.

8.2 Further work

Further work is necessary to understand how the seasonal tiller dynamics pattern of perennial ryegrass changes over time in relation to environmental factors. The concept of a MCLA may provide a way of assessing environmental effects on tiller dynamics and estimates of sward MCLA (or some equivalent measurement of sward state, in respect to LAI) should accompany tiller dynamics measurements. Such a study would enable modellers to develop a predictive model of tiller population dynamics under rotational grazing that incorporated environmental effects. Such a tool would be helpful for making grazing management decisions conducive to better pasture persistence. This approach could be an alternative to and more mechanistic than the approach explored by Bishop-Hurley (1999), based on calculated tiller size/density compensation at different levels of herbage mass.

'Ellett' perennial ryegrass had a different perennation strategy from 'Grasslands Ruanui' favouring reproductive over vegetative tillering. The higher percentage of tillers flowering in 'Ellett' compared with 'Grasslands Ruanui' (Table 6.4) is suggestive of the difference between an Italian and a perennial ryegrass (Davies 1977). It is interesting to note that from 1935 to 1953, Italian ryegrass was commonly sown with perennial ryegrass to increase total feed supply (Duder 1976), on the area where the parents of 'Ellett' were later selected, so the opportunity for hybridisation existed. An investigation of the genetic background of 'Ellett' ryegrass would help explain its flowering behaviour, especially if linkage to an Italian ryegrass could be shown. The use of molecular biology techniques such as enzyme electrophoresis may be appropriate to compare the allele frequency of 'Ellett', 'Grasslands Ruanui' and an Italian ryegrass cultivar, to clarify this point.

8.3 Implications for the pastoral industry in New Zealand

8.3.1 Effects of nitrogen fertiliser

Nitrogen fertiliser applications resulted in different cultivar responses, dependent on the propensity of the cultivar to produce reproductive tillers (see Chapter 6).

Therefore, management decisions relating to nitrogen applications should also consider the ryegrass cultivar, to maintain a high productivity without compromising sward persistence. Applying nitrogen to 'Ellett' ryegrass a few weeks (from September) before the flowering period could compromise its persistence by increasing production of reproductive tillers (Table 6.5), and thereby increasing the rate of turnover of the tiller population. However, nitrogen fertiliser application during spring increased herbage accumulation (Fig. 3.7). Nitrogen fertiliser application (December to February) after the main flowering period should be beneficial, providing a stimulus for post-flowering vegetative tiller production (section 5.4.1.3), and therefore the potential for increased sward persistency.

In contrast to 'Ellett', nitrogen fertiliser application to 'Grasslands Ruanui' before flowering should improve sward persistence, since nitrogen fertiliser was shown in Chapter 6 to increase vegetative tiller production at the expense of reproductive tiller production. However, the data suggest an application of nitrogen fertiliser just before the autumn (March) tiller population decline may not be beneficial since 'Grasslands Ruanui' rapidly increases tiller birth in response to nitrogen. Tiller appearance at this time will therefore be followed by increased tiller death (see Chapter 5). Births and deaths of tillers were high in autumn; so, in these circumstances, tiller turnover was accelerated by nitrogen.

Application of nitrogen fertiliser in late autumn (April/May) may be beneficial for both ryegrass cultivars studied since winter herbage accumulation, pre-grazing herbage mass and tiller density consistently increased in nitrogen plots compared to untreated plots, after the nitrogen application had ceased (see Chapter 3). Thus, to optimise herbage production and allow the pasture to increase its tiller number over winter, a grazing in early autumn would be necessary. A low herbage mass combined with a high tillering activity over winter should enhance the productivity of that pasture in spring. Such a grazing plan will help the farmer to match more closely the pasture growth and feed requirements, especially over winter-spring when the feed demand of newly calved cows is high.

8.3.2. Possible application of results to plant improvement

Sward productivity depends on the size of individual tillers, on the number of tillers per unit area, and on plant factors such as LER (Fig. 7.1). Improved grass productivity tends to conflict with improved grass persistence. Sward tiller density is well known as an agronomic indicator of persistency. Since perennial ryegrass plants increase tiller density by producing new tillers, a high ratio of vegetative to reproductive tillers and a high rate of appearance of new tillers are necessary to improve persistency.

LER, A_L, and site filling interact with each other and are all important determinants of mean tiller size and tiller number per plant. One way to select plants for high productivity would be to select for high MCLA. This could be achieved by selection for high LER and a combination of low A_L and/or increased number of leaves per tiller, maximising leaf area per tiller.

The expression of a high MCLA can result in a low tiller density in a vegetative sward when, as seasons change MCLA exceeds ECLA. To the extent that a seasonal reduction in tiller density forced in this way implies reduced persistence, selection for persistence would require criteria of low LER to achieve low MCLA. The achievement of a low MCLA can result in a high tiller density in vegetative swards over time.

For this concept to be useful in plant breeding, a desirable tiller density and productivity for a particular situation has to be defined as an appropriate starting point.

Tiller dynamics of 'Ellett' and 'Grasslands Ruanui' were monitored for only two years in the field, which is insufficient time to draw strong conclusions about the persistence characteristics of these cultivars. Therefore, determining the consequences of the production of a higher proportion of reproductive tillers by 'Ellett' than by 'Grasslands Ruanui' remains outside the scope of this study of this experiment. However, it does seem possible that the poor persistence of the modern perennial ryegrass as identified by Thom et al. (1998a) might be related to the production of a higher proportion of reproductive tillers and consequential increased susceptibility to stress in summer, when replacement of reproductive tillers is necessary for persistence. Thus, if this explanation is correct, selection for a high LER accompanied by low production of reproductive tillers would be desirable for improved productivity and persistence. 'Ellett' currently exhibits a high MCLA due to high leaf length (high LER) and has a high proportion of tillers that become reproductive. Suggested changes for improved persistence of 'Ellett', and possibly for other cultivars developed from the Mangere ecotype, relate to reducing the propensity to produce reproductive tillers.

Breeding programs aimed at reducing reproductive development would have the added benefit of improving nutritive value of the pasture (Browse et al., 1984; Tallowin et al., 1989) and therefore animal performance.

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APPENDICES

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