Defoliation management, tiller density and productivity in perennial ryegrass swards

A thesis presented
in partial fulfilment of the
requirements for the degree of
Doctor of Philosophy (PhD) in
Plant Science
at Massey University, New Zealand

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July, 1995

ABSTRACT

Lax spring grazing management followed by hard grazing at the time of anthesis has been suggested as a means to improve herbage production of perennial ryegrass pastures during summer and autumn by enhancing tillering activity. However, there is little comparative information on the effects of variation in the duration of the period of lax grazing. Thus, the aims of this study were (i) to investigate the effects of timing and duration of lax spring grazing on tiller dynamics, rates of leaf growth, botanical composition and pasture production in perennial ryegrass swards, with and without white clover, and (ii) to determine which physiological and/or morphological factors are important in influencing regrowth after defoliation of such swards. Two field experiments and one glasshouse experiment are reported.

In the first field experiment (September 1992 to March 1993), swards of perennial ryegrass (Grasslands Nui) with and without white clover (Grasslands Tahora) were rotationally grazed by sheep every 21 days to a residual height of 70-100 mm (lax) and every 14 days to a residual height of 30-50 mm (hard). Two periods of lax grazing (short release "SR" from 26 October to 8 December and long release "LR" from 15 September to 8 December) were compared against conventional hard grazing (early control "EC"). All treatments were grazed to a residual height of 30-50 mm every 14 days from 8 December until the end of the Experiment. Treatments were arranged in a factorial design with 3 replicates. Plots without white clover received 28 kg N ha^{-1} every two weeks as urea. During spring, herbage mass increased in SR and LR as a consequence of an increase in tiller weight. Leaf growth in ryegrass and white clover and sward productivity all increased after lax spring grazing, and responses were greater following LR than SR. Evidence of effects on ryegrass tiller densities were inconclusive, although tiller production appeared to be greater in SR and LR treatments than under conventional hard grazing. White clover responses were variable.

In the second field experiment (September 1993 to April 1994) plots were subjected to similar grazing managements, the only differences being that all spring treatments were imposed at a consistent grazing interval of 21 days. There was also an increase in the number of replicates per treatment (from 3 to 4), and a reduction in N level (from 28 to 14 kg N ha^{-1} every 2 weeks). The results from this trial confirmed that SR and LR treatments, because of their greater percentage of reproductive tillers, increase ryegrass herbage production during spring by increasing tiller weight. During summer and autumn production remained high on SR and LR treatments due to enhanced tiller population density and leaf growth per tiller and/or stolon. White clover responses were variable, and in general SR and LR treatments tended to produce more leaf per locus than EC. For white clover, no statistical differences were observed in net production per unit of area (g m^{-2} day^{-1}).

Size/density compensation implies that at higher herbage mass, individual tillers are larger, but the population density is correspondingly decreased. To investigate the links between tiller dynamics and herbage production, and the relationship between sward height, tiller density and tiller size, an index of sward productivity (size/density compensation index, SDCI) was generated. Size/density compensation index was defined using the -3/2 self thinning relationship of plant ecology. Shoot density and tiller weight were plotted as X and Y coordinates, respectively and SDCI defined as the distance between the point plotted for a particular sward and a theoretical self-thinning line of slope -3/2. A plot of herbage production from January to April against SDCI showed a strong positive correlation between SDCI and productivity. The results indicate that the distance from the -3/2 self-thinning line, or size/density compensation line, can be used as a predictor of sward productivity.

In a glasshouse experiment the effect of defoliation management on tiller size/density compensation (SDC) was studied. Under controlled environmental conditions perennial ryegrass swards growing from seed were defoliated to stubble heights of 20 mm, 40 mm, 80 mm, 120 mm and 160 mm twice a week (simulating continuous stocking) over a six month period. The results demonstrated an increase in tiller weight and a decrease in tiller population density as defoliation intensity decreased. The optimum combination of tiller density and leaf growth per tiller which maximised herbage harvested per unit time was observed at a defoliation height of 120 mm.

The response of plants to defoliation was decreased total, below and above ground plant mass, gross and net photosynthesis per unit of ground area and tiller weight as the severity of cutting increased, while leaf appearance rate and gross and net photosynthesis per unit of leaf weight were increased.

The use of the -3/2 self-thinning rule to describe the relationship between tiller population density (X) and individual weight per tiller (Y) was also examined. For cutting heights between 40 mm and 120, the size/density relationship had a slope steeper than -3/2. For defoliation heights above 120 mm SDC slope was closer to 1.0. However, slope corrections for change in leaf area index (C_a) and leaf:non leaf ratio (C_r) largely explain observed deviations from the theoretical -3/2 size/density compensation line. Again, the plot of herbage harvested against SDCI showed strong positive correlation between the two.

It is concluded that lax spring grazing management of ryegrass-white clover swards (70 to 100 mm) followed by hard grazing (30-50 mm) at the time of anthesis enhances pasture production, particularly during the summer-autumn period, by increasing both tiller population density and net leaf growth per tiller and/or stolon. Effects were larger following an extended spell of lax grazing (12 weeks) than following a shorter spell of 6 weeks. Size/density compensation index was shown to be a predictor of sward productivity, sward productivity having a strong positive correlation with SDCI.

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my chief supervisor, Professor John Hodgson and to my co-supervisor Dr Cory Matthew for their patience, enthusiastic encouragement, guidance and close supervision throughout the course of this study. Special thanks are due to Professor John Hodgson who went far beyond the call of duty as a supervisor to ensure my studies were appropriately finished.

The help and support of the field and plant growth unit technicians is also acknowledged. Special thanks to Mr Terry Lynch, Mr Mark Osborne, Mr Gary Evans, Brian Sturgess, Ms Sheralin Cleland, Ms Frith Brown, Ms Cally McKenzie, Mrs Jackie Harrigan for their technical and organisational assistance. Thanks are extended to Charlie Forbes for assisting and building the chambers used to measure photosynthesis and to R. Johstone for his generous help with glasshouse facilities. The help of Kathy Hamilton is also appreciated.

Thanks are extended to Dr. Peter Kemp, Dr. Ian Valentine and Dr. David Woolly for assisting in different ways. Special thanks to Dr. David F. Chapman and Gilles Lemaire for their helpful comments.

The friendly environment provided by my fellow graduate students in the Pastoral Science group, is much appreciated, especially the friendship of Mr Fabio Montossi, Mr Gilberto Aranda, Dr. Sila Da Silva, Dr. Manzoor-ul-Haque Awan, Mr Gregory Bishop-Hurley, Mr Wagner Brod-beskow, Mr Daniel Real, Mr Mauricio Padilla, Ms Silvia Assuero, Mr Cesar Poli, Mr Fuyuan Liu, Mr Sam Oppong and Mr Guangdi Li will never be forgotten.

I would like to express my sincere thanks to the New Zealand Ministry of Foreign Affairs and Trade, the Consejo Nacional de Ciencia y Tecnologia (CONACYT, México) and the Colegio de Postgraduados (México) for provision of post-graduate stipend and financial assistance during my studies.

Special thanks to my wife Lourdes for her patience and assistance in a number of ways, but especially for being responsible for the education of our children. To my children Miguel Alejandro, Alfonso and Silvia hoping that the adventure of living in a different country help them to overcome the difficulties that they will face in México. My father Donato and brothers, the late Miguel, Rafael A., Vicente D., Leonel, Jesus A. and Severino and other family members are thanked for their considerable encouragement and assistance in a number of ways. Finally, I would like to express my deepest gratitude to my mother Vicenta for her unconditional support and encouragement during my studies.

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Chapter 1

INTRODUCTION

A major aim in pastoral agriculture is to obtain the maximum productivity per unit of area. To achieve this goal, it is important to have good management practices which maximise growth and utilization of high quality herbage for animal consumption. This requires a fuller understanding of all facets of the system including the role of the grazing animal, nutrient cycling and soil fertility, influence of environmental variables (Brougham, 1983) and especially the dynamics of plant and pasture growth (Hodgson, 1985).

In systems based on grazed herbage, where pasture growth and animal feed requirements rarely match and where animals must be maintained for a full season or year, the objective of most pasture managers is to optimise animal feed requirements rather than maximise herbage accumulation (Brock & Hay, 1993). Therefore, knowledge of the dynamics of pasture production, and its distribution throughout the year, is essential to planning an efficient plant/animal system (Judd *et al.*, 1990).

New Zealand systems of grassland management attempt to make the maximum use of grass as a low-cost feed source. Pasture growth is restricted by low temperature during winter, and frequently by drought stress in summer. It is greatest in spring, as temperatures increase and soil moisture is non-limiting. A key role of management, then, is in those critical periods of high growth, to place pastures in a position better able to cope with the oncoming adverse conditions. As a consequence, grazing management during the spring months may be a factor in overcoming the negative effects of summer decline in pasture production.

Yield component considerations indicate that increased herbage production by grasses may arise from two sources; a higher tiller density and/or a higher tiller weight. An understanding of the overall implications of physiology in herbage production depends on knowing the relative contribution of each source (Nelson & Zarrough, 1981). Also, the mechanisms which determine the structure of the sward (e.g. tiller number and size) in response to management are unclear, although the changes in sward structure that arise are well described (Parsons *et al.*, 1988). It is well known that tillers in grass swards are subject to size/density compensation (SDC). Generally, an un-defoliated sward has been observed to follow the -3/2 self-thinning rule, except at low light levels (White & Harper, 1970; Kays & Harper, 1974; Lonsdale & Watkinson, 1982). However, in the last ten years the evidence supporting this rule has come under close critical scrutiny (Zeide, 1985, 1987; Weller, 1985, 1987a, b, 1989, 1990, 1991, Lonsdale, 1990) and these authors have questioned the fundamental validity of the rule itself. Additionally, a decrease in population density of larger tillers is the result of more lenient defoliation regimes (Bircham & Hodgson, 1983; Grant *et al.*, 1983; Matthew, 1992). Therefore, increase or decrease in tiller density is not an unambiguous indicator of sward vigour and may, in some cases, merely reflect SDC in response to change in defoliation intensity (Matthew *et al.*, 1996).

Additionally, it has been widely emphasised in recent years that spring management of pasture can have an important influence on sward composition, sward quality and herbage production (Korte, 1982; Korte *et al.*, 1982, 1984, 1985; Korte, 1986; Butler, 1986; Korte & Harris, 1987; L'Huillier, 1987b, Matthew *et al.*, 1989b; Xia *et al.*, 1990, Matthew, 1992; Da Silva, *et al.*,1993; Da Silva, 1994). The spring period is critical in terms of grazing management once pasture growth rates exceed animal feed requirements. Traditionally, late spring pasture management has had the goal of maintaining sward quality. This has been achieved by intensive grazing, silage conservation and often topping. However, several studies have reported substantial increase in green herbage production in summer and autumn by allowing some reproductive development, and then controlling it at the time of anthesis, through effects on tiller numbers and individual tiller production (Korte *et al.*, 1984; Xia *et al.*, 1990;

Matthew *et al.*, 1989b; Matthew, 1992; Da Silva *et al.*, 1993, 1994; Da Silva, 1994), with flow-on effects on the performance of grazing animals (Thomson *et al.*, 1984; Bryant & L'Huillier, 1986; McCallum *et al.*, 1991; Hoogendoorn *et al.*, 1988, 1992). In general it has been assumed that enhancement of tillering would occur upon removal of seedheads (implying that seedheads limit tillering through shading and apical dominance effects). However, one detailed study (Matthew *et al.*, 1989b) suggested that substrate supply from tillers whose development has been interrupted at early flowering actually promotes tiller bud initiation at the base of those flowering tillers. These authors therefore suggested that a timely lax/hard grazing would be the ideal management to promote tillering in early summer.

Lax grazing in spring which allows early seedhead development, followed by hard grazing at anthesis, has been shown to result in advantages to tillering activity in early summer, associated with increased pasture growth rate, pasture production and pasture persistence during summer-autumn (Matthew, 1988, 1992; Matthew *et al.*, 1989b; Da Silva *et al.*, 1993, 1994; Da Silva, 1994). However, there is little information regarding the effect of timing and duration of lax spring grazing on these parameters, and also regarding the effect of different intensities of defoliation on tiller population, tiller size, photosynthesis rate, herbage production and tiller size/density compensation (SDC). With this in mind the objectives of this study were;

i) to evaluate the effect of variation in the timing and duration of lax spring grazing on tiller dynamics, rates of tissue turnover and sward structure in perennial ryegrass swards, with and without white clover.

ii) to examine the response of ryegrass-white clover swards to contrasting spring grazing management and effects on summer-autumn herbage production, tiller size and botanical composition.

iii) to determine which physiological or morphological factors are important in influencing regrowth after defoliation in perennial ryegrass.

iv) to study the effects of intensity of defoliation on tiller weight, tiller population, carbon uptake, sward structure and size/density compensation.

Chapter 2

LITERATURE REVIEW

2.1. INTRODUCTION

Low cost and high level of animal production from grazed pasture systems are best achieved by growing high quality pasture and matching pasture growth with animal requirements. Knowledge of the dynamics of pasture production throughout the year is essential to the planning of an efficient plant/animal system.

Defoliation management influences the amount of feed grown and the efficiency with which it is utilized. Thus, the essence of grassland management is to achieve an effective balance between the efficiency of the three main stages of animal production: herbage growth, herbage consumption and animal productivity (Hodgson, 1990). These stages of crop growth and utilization interact with one another in a number of ways and the interactions between them exert an important influence on the eventual output of animal products.

Herbage production of the sward can be divided into two components: the number of tillers per unit area of land and the yield per individual tiller (Volenec & Nelson, 1983). Thus, the persistence and production of the pasture depends on the balance between the production of new tillers and death of established tillers. This balance is strongly influenced by management practices, especially the frequency and intensity of defoliation.

Defoliation of forage plants results in the readjustment of plant metabolism for promotion of new leaf area expansion and re-establishment of the photosynthetic capacity of the sward (Culvenor *et al.*, 1989a). Regrowth can be influenced by residual leaf tissue, carbohydrate reserves, meristem activity, nutrient status (particularly nitrogen) and water uptake. Therefore, an understanding of the effects of frequency and severity of defoliation is an essential pre-requisite to optimising the dynamics of pasture growth.

This review deals particularly with the effect of spring grazing management on factors influencing pasture production, and opportunities for manipulating pasture to advantage. Attention will be concentrated on the effects of frequency and intensity of defoliation on pasture production, and on the components of plant dynamics which determine production responses and their sensitivity to management. Also attention will be given to tiller population density and size/density compensation, tissue turnover per tiller, physiological control of leaf and root turnover, and inter-specific competition.

2.2. SEASONAL CHANGES IN HERBAGE PRODUCTION AND SPECIES BALANCE

In New Zealand, herbage production normally exceeds animal requirements during spring (Judd *et al.*, 1990). With the onset of reproductive growth, increasing temperatures and high soil moisture availability, pasture growth rate peaks during this period. In autumn, reducing evapotranspiration demand leading to soil moisture recovery, coupled with decreased animal demand in late season, often leads to pasture surpluses in this period also. By contrast, the herbage growth rates over the summer frequently fall below stock requirements (Brougham, 1970), probably due to moisture stress (Brougham, 1956a, 1957; Brock, 1974; Judd *et al.*, 1990) and a limiting supply of a plant nutrients such as nitrogen (Brougham, 1957). As a consequence of low temperatures, growth from pasture during winter may not be sufficient for the daily feed requirements of the animals (Brougham, 1970).

In New Zealand farming systems ryegrass and white clover are the dominant components of most pastures. Both species possess quite distinct biological characteristics and, for that reason, different grazing managements are likely to generate different patterns of response in the case of each species. Grass and clover in a mixture compete for light, moisture and nutrients. Ryegrass is a more aggressive species, and any aspect of management which favours its growth usually results in some suppression of clover (Wolton *et al.*, 1970). Generally, for most of the year the clovers are shaded by the grasses resulting in a reduced growth rate of clover and in some instances a decrease in yield. However, clovers may compete to better advantage than the grasses during the summer and autumn. Brougham (1957) attributed this to better tolerance of high temperatures and lower water supply.

2.3. INFLUENCE OF DEFOLIATION MANAGEMENT ON HERBAGE PRODUCTION

Increasing output depends on increasing pasture production and/or improving the utilization of the pasture grown (Campbell, 1970). Evidence from several studies has indicated that productivity of pastures can be manipulated to advantage by grazing management. For example Brougham (1959, 1960, 1970), Jameson (1963), Davidson (1968), Tainton (1974), L'Huillier (1987b) have observed that the rate of accumulation of herbage after grazing or cutting is higher when defoliation is lenient than when it is severe, though there are examples where intense defoliation increases herbage production and subsequently animal production (Hoogendoorn *et al.*, 1988). Kerrisk & Thomson (1990) found that lax defoliation gives significantly higher growth rates than intense defoliation in spring, summer and autumn for ryegrass, tall fescue and phalaris pastures. Brougham (1960) showed that under grazing management systems involving repeated overgrazing, particularly in the summer, the amount of herbage produced is severely reduced. Hard defoliation intensity reduces herbage production by decreasing both tiller population density and tiller weight and consequently decreases pasture growth through reductions in LAI, longevity of individual leaves, and photosynthetic efficiency, and a shortage of carbohydrate reserves (Tavakoli, 1993). Also, for species of erect growth habit, net herbage accumulation decreases as frequency of defoliation increases (Brougham, 1959; Jameson, 1963; Davidson, 1968). The converse, however, occurs for species of more prostrate growth habit (Davidson, 1968).

The effects of defoliation intensity on herbage accumulation depend on the length of the regrowth period. Thus, when the spell in late autumn and winter was 18 weeks rather than 6 weeks the total herbage accumulation was approximately 70 % greater for the treatment more frequently defoliated (2120 kg DM ha^{-1} and 3620 kg DM ha^{-1} for 18 and 6 weeks of spell) (Brougham, 1970). Similarly, Brougham (1957, 1960), observed that long spelling of pastures over the late autumn, winter and early spring resulted in reduced dry matter yields and poor recovery growth in the spring. Additionally, L'Huillier (1987b) found that the rate of green herbage accumulation was greater for hard than for lax grazed swards, when the regrowth period was 70 rather than 28 days, at least during late spring and autumn. Growth rates reached maximum values approximately 4 weeks after grazing and then declined rapidly with further spelling (Tainton, 1974; L'Huillier, 1987b), because longer spelling resulted in excessive senescence losses (Hodgson, 1989; Parsons & Penning, 1988), and an increase in dead herbage accumulation (Tainton, 1974; L'Huillier, 1987b; Korte *et al.*, 1985).

Judd *et al.* (1990) observed that under a 28 days defoliation interval ryegrass produced 20% more dry matter than under a 14 days interval. Similarly, Fulkerson *et al.* (1993) in ryegrass-white clover swards, concluded that defoliation at 4 weeks or when ready (before the onset of senescence), compared to defoliation at 2 weeks, increased DM yield by 18% and 32% in year 1 and 41% and 59% in year 2 respectively. Korte *et al.* (1985) found that mowing at 95% light interception compared with mowing every 3 weeks increased herbage mass accumulation. Additionally, Hodgson & Wade (1979) observed that defoliation at intervals less than 2 weeks may reduce net herbage accumulation by up to 40%. These authors concluded that grazing every 4 weeks consistently increased production 15-17% over 2-3 weekly grazing when the height of grazing was controlled.

Bircham (1981) and Bircham & Hodgson (1983) showed that net herbage production in ryegrass-white clover swards was reduced by intensive defoliation (down to levels of herbage mass of the order of 700 kg OM ha^{-1}). However, above this level there was little difference in net production over a wide range of herbage masses (from 1000 to 2000 kg OM ha^{-1}). Several studies in the UK (Grant *et al.*, 1983; Parsons *et al.*, 1983b; Parsons & Penning, 1988) have observed similar patterns of relationship between herbage mass and net herbage mass accumulation.

The results reported above indicate clearly the variation in response of pasture to management in different seasons of the year. Also, it has been pointed out by Brougham (1970), Tainton (1974) and Sheath & Bircham (1983) that defoliation practices must be flexible according to the season of the year and the climatic conditions. For example, during dry summer periods lax infrequent grazing increased production by 20 %, while in the vegetative growth period in autumn those pastures which were alternately lax and hard grazed outyielded by 63 % those which were hard grazed (Tainton, 1974).

Matthew *et al.* (1989b) showed that a lax-hard late spring grazing management gave high summer-autumn pasture production compared with other spring grazing managements. This increase in pasture growth rates was due to an increase in both tiller population density and net pasture production (Xia *et al.*, 1990). Similarly, Da Silva *et al.* (1993, 1994) and Da Silva (1994) observed that lax grazing during late spring followed by hard grazing at anthesis (early summer) increased herbage accumulation in spring by 1000 kg DM ha^{-1} and in summer and autumn by a further 1000 kg DM ha^{-1}.

Despite the evidence that rates of net herbage production in ryegrass-based temperate pastures are relatively insensitive to substantial ranges of variation in pasture condition or grazing management (Hodgson, 1989; Bircham & Hodgson, 1983; Parsons, *et al.*, 1988; Korte *et al.*, 1987), pasture accumulation can be increased by grazing management, as has been showed by Brougham (1957, 1960, 1970), Tainton (1974), Xia *et al.* (1990), Xia (1991), Da Silva *et al.* (1993, 1994), Da Silva (1994), Matthew *et al.* (1989b), Matthew, (1992). Sheath & Bircham (1983) indicated that the extremes of over-grazing and under-grazing should be avoided because insufficient pasture cover limits new growth and insufficient utilisation means feed wasted. Fulkerson *et al.* (1994) working with two *Lolium* genotypes (*L. multiflorum* and *L. perenne*), concluded that the marked defoliation by cultivar interaction on regrowth confirms the need to consider defoliation responses in any evaluation of cultivars. They found the effect of frequent, compared to infrequent, defoliation was to suppress regrowth by 100%, 95% and 80%; stubble water soluble carbohydrate (mg plant^{-1}) by 97%, 89% and 81%; root DM (g plant^{-1}) by 76%, 60% and 6%, for a pupulation of biennial ryegrasses and two populations perennial ryegrasses, respectively. The effect of defoliation height accentuated this response, with biennials defoliated frequently at 20 mm stubble height all dying.

Local climate and soil fertility determine the botanical composition of pasture, but grazing management can further influence the balance between species (Sheath & Bircham, 1983). In areas of high soil fertility, associated pasture species occur naturally and extreme grazing management is required to change composition. However, in less fertile areas, small changes in grazing management can have a marked influence on pasture composition. Grazing management not only influences plant growth and morphology, but also the nutrient economy of the pasture through changes in the quantity and quality of soil organic matter (Brock *et al.*, 1989).

2.4. EFFECT OF DEFOLIATION ON SWARD PERSISTENCE

The frequency and intensity of defoliation may affect the persistence of the pasture. An increase in frequency of defoliation in ryegrass (Davies & Simons, 1979) and other grasses has been shown to reduce persistence and production from the surviving plants in the subsequent season (Lawrence & Ashford, 1969). Also, hard defoliation intensity reduces plant regeneration (Tavakoli, 1993) by reducing leaf area per tiller, leaf area duration and photosynthetic efficiency.

In the UK, Grant *et al.* (1983) and Bircham & Hodgson, (1983) observed that perennial ryegrass was replaced progressively by *Poa annua* under severe defoliation to below 20 mm. Repeated removal of most of the photosynthetic area would be detrimental to sustained production and persistence (Tavakoli, 1993). Matches (1966) reported that tall fescue plants cut to 25 mm every 10 days died after the fourth defoliation was imposed.

2.5. EFFECT OF DEFOLIATION ON SWARD DYNAMICS

2.5.1. Seasonal changes in tiller population

Most New Zealand studies of tillering in perennial forage grass species have shown similar seasonal patterns of tiller appearance and death (Korte, 1986; L'Huillier, 1987a; Matthew, *et al.*, 1989a, b; Da Silva *et al.*, 1993, 1994; Da Silva, 1994). According with Korte (1986) there are usually two periods of tillering activity in ryegrass swards. The first, in spring, continues until internodal elongation starts, and the second begins at anthesis and continues until winter. The highest tillering activity has been observed from November to January, especially soon after defoliation of the apices of the main group of reproductive tillers (Korte, 1986; Da Silva *et al.*, 1993, 1994).

Tillering occurs in response to changing temperatures and solar radiation levels, and is controlled by the rate of leaf appearance which is insensitive to defoliation (Hunt & Field, 1978; Davies & Thomas, 1983; Anslow, 1966; Davies, 1988). The second period of tillering in grazed pastures occurs in early summer in frequently grazed or mown swards in New Zealand, not autumn as observed in United Kingdom or where swards have been harvested for seed (Korte *et al.*, 1985). The seasonal pattern of tillering described above with its characteristic pre-and post-flowering peaks in the number of live tillers per plant is very similar to that described by Langer *et al.* (1964) with other species grown in sward conditions.

Colvill & Marshall (1984) showed that tiller production and death in the UK occurred at all times of the year but at different rates, with a great variability in the production of tillers by surviving plants. Net tiller number fluctuated with time, increasing in both years from a minimum in July to a maximum at the end of April. Periods of rapid increase were observed during March/April and after flowering in July. In contrast, tiller appearance rates were comparatively low from October to May. Garwood (1969) recorded the greatest number of tillers of perennial ryegrass in spring and early summer.

The high rate of tiller appearance prior to and during the early stages of stem elongation may be attributed to improved temperature and light conditions compared with those prevailing over winter. On the other hand the subsequent rapid decline in the appearance of new tillers to a level compared with mid-winter rates and then the rapid post-flowering increase suggest that internal factors could be involved in regulation of tiller production (Colvill & Marshall, 1984). In addition, Jewiss (1972) and Clifford (1977) reported some evidence that tiller buds may be directly inhibited by a hormonal influence from the elongating stem internodes or developing inflorescence.

The pattern of tiller death closely follows that of tiller appearance and is highest between late spring and early summer (L'Huillier, 1987a). Tiller death is normally greatest during reproductive growth, initially resulting from death of vegetative tillers, as reproductive tillers do not translocate assimilate to heavily shaded, smaller, vegetative tillers (Ong *et al.*, 1978), and later from death of defoliated reproductive tillers.

In the work of Colvill & Marshall (1984) the number of live tillers per plant declined by 50% during stem elongation and inflorescence emergence and the majority of dead tillers were young secondary (in the first year) and tertiary (in the second year) tillers with a mean age of 40 days. Competition is especially acute during stem elongation and results in the death of a high proportion of the small, non flowering tillers. Tillers which died had poor assimilatory capacity prior to the onset of death and were not supplied with assimilate from the main shoot (Colvill & Marshall, 1984).

Management practices can modify the tiller population. For example, Tallowin *et al.* (1989) studying the effects of two intensities of continuous grazing (severe to 35 mm and lenient to 75 mm) imposed during the spring (phase I), followed by a uniform continuous grazing management from mid-summer onwards (phase II) observed at the end of phase I more tillers per locus in the severe (S) treatment than in the lenient (L), mainly due to enhanced daughter tiller production in the S treatment, with 1.1 new tillers per locus produced overall compared with 0.6 new tillers per locus in the L treatment. This reduction appeared to be due to inhibition of development of tiller buds rather than to the presence of few buds (Tallowin *et al.*, 1989).

In a New Zealand experiment (L'Huillier, 1987a) the seasonal pattern of tiller density differed between stocking rates. Low stocking rate had no effect on tiller densities, but at the high stocking rate tiller density generally increased during the experiment.

2.5.2. Spring grazing management of perennial ryegrass-white clover swards

The basic unit of production of a grass sward is the tiller. Tillers are continually emerging, growing and dying at rates which differ appreciably, depending on environmental conditions and stage of development. Thus, herbage production and persistence are modified by the rates of appearance, growth and death of tillers within the sward. Several studies with *L. perenne* (Korte *et al.*, 1984, 1985; Korte, 1986; L'Huillier 1987a; Matthew *et al.*, 1989b; Da Silva *et al.*, 1993; Da Silva, 1994), *P. pratensis* and other grass swards (Langer *et al.*, 1964; Garwood, 1969; Hill & Watkin,

1975) have revealed a similar seasonal pattern of tillering. The results of these and other agronomic studies (Spiertz & Ellen, 1972; Hebblethwaite, 1977; Xia *et al.*, 1990; Xia, 1991) have emphasised the degree and the rapidity of turnover of leaves and tillers in the swards.

Ryegrass tiller density in spring pastures can be manipulated by grazing frequency (Bryant & L'Huillier, 1986) and intensity (Matthew *et al.*, 1989a, b; Xia *et al.*, 1990; Da Silva, 1994). During spring, day length, temperature and total hours of sunlight increase, stimulating pasture growth rate to the point where it exceeds animal requirements. This increase in herbage production is generally associated with an increase in leaf elongation and a decrease in the nutritive value of the sward.

Reproductive development in ryegrass reduces leaf percentage, affecting the digestibility of the pasture (Browse *et al.*, 1984; Tallowin *et al.*, 1989), and so conventional spring grazing management practices are aimed at maintaining the growth of vegetative tillers and minimising that of reproductive tillers. Matthew (1988), Matthew *et al.* (1989b), Xia *et al.* (1990), Xia (1991), Da Silva *et al.* (1993, 1994) and Da Silva (1994) all found that allowing some reproductive tiller growth in perennial ryegrass and controlling it at anthesis may be important to promote survival of daughter tillers formed following flowering. Logically, there must be implications for persistence of the ryegrass. This line of research (Matthew *et al.*, 1989b; Da Silva *et al.*, 1993, 1994; Da Silva, 1994) studying the seasonal patterns of tiller appearance and death in ryegrass swards has shown that a lax-hard pattern of late spring grazing management gave high summer-autumn pasture growth rates compared with other spring grazing managements. Detailed measurements showed that the high pasture growth on the lax-hard grazed plots had resulted from increased formation of new tillers, which occurred shortly after seedhead formation on these plots. Matthew *et al.* (1989b; Matthew, 1990) concluded that the seedheads must have stimulated daughter tiller appearance by providing photosynthetic products to subsidise or encourage the early growth of young tillers. This increase in tiller population was also accompanied by an increase in leaf elongation rate (Xia *et al.*, 1990; Xia, 1991). The new tillers produced during the reproductive phase play an important role in the biology of the grass plant as the majority survive the winter and thus ensure its perenniality; they also form the majority of the flowering tiller population in following year (Lambert & Jewiss, 1970; Colvill & Marshall, 1984).

Several authors (Korte *et al.*, 1984, 1985; Korte, 1986; L'Huillier 1987a; Matthew *et al.*, 1989b) found that reproductive development was concentrated in late October and early November. Korte (1986), L'Huillier (1987a) and Matthew (1988) showed that ryegrass tillering was most active during late spring-early summer, and this was closely followed by increased death rates of vegetative and reproductive tillers. Vegetative tillers becoming reproductive face decapitation and early death compared to those that remain vegetative (Korte *et al.*, 1984, 1985; Korte, 1986; L'Huillier, 1987a).

Swards may respond to defoliation by net gains, net losses or no overall changes in tiller population, depending on initial tiller numbers at the time of harvesting and the time of the year (Davies, 1977, 1988), as well as the frequency and intensity of defoliation. Thus, Hodgson *et al.* (1981) reported that the total population densities of tillers and stolons declined at herbage masses both above and below 700 kg OM ha^{-1}. Furthermore, Grant *et al.* (1983) reported the highest tiller population densities in swards maintained between 20 and 30 mm surface height.

2.5.3. Effects of management on leaf growth and senescence

Leaves, tillers and other plant parts grow and die or are harvested, such movements of material through the system being known as tissue fluxes. Estimates of tissue turnover are normally based either on rates of leaf appearance or leaf extension. Rates of leaf appearance give an indication of the overall scale of tissue turnover, especially in grasses where the number of leaves per tiller may remain relatively stable for long periods (Davies, 1993). Grass and clover leaves appear on average at a similar rate, but grass leaves appear less frequently in tall swards than in short ones. In clover, leaf appearance is unaffected by grazing intensity but in tall swards the leaves take longer to complete their expansion (Parsons *et al.*, 1991).

The rates of leaf growth and senescence are important because leaves are the primary photosynthetic organs and if LAI is lower than 95% an increase in LAI will generally increase light interception and sward growth rate. Hodgson *et al.* (1981) suggested that the rate at which herbage accumulates for harvesting represents the balance between the rate of growth of new plant tissue and the rate of loss of established tissue to senescence and decomposition. Initially the rates of both growth and loss are low; the rate of growth then accelerates but is ultimately balanced out by the later acceleration in the rate of loss to senescence as mature herbage accumulates (Hodgson, 1990). Furthermore, any advantages to growth from the maintenance of a relatively high leaf area are likely to be accompanied by an increase in senescence losses (Hodgson *et al.*, 1981).

Leaf elongation rates of forage grasses such as tall fescue are easily modified by management practices and/or environmental conditions (Volenec & Nelson, 1983). Thus, the response of the sward to a particular management may involve changes in population density, in tissue turnover per individual plant unit, or in some combination of the two (Bircham & Hodgson, 1983, Grant *et al.*, 1981). Bircham & Hodgson (1983) demonstrated the existence of a homeostatic mechanism in continuously and rotationally grazed swards, whereby compensatory changes in species population density and tissue turnover on individual plant units combined to maintain relatively constant net production of green herbage mass.

There is always a delay between the production of tissue and its subsequent death. Thus, changes in the rate at which old tissue is lost tend to lag behind changes in the rate at which new tissue is produced (Parsons, 1980; Parsons & Robson, 1981a). Bircham & Hodgson (1984) studying the influence of a change in herbage mass on rates of herbage growth, senescence and net production found that rates of change in tiller population were indeed slower than changes in tissue turnover per tiller, but the increase in growth rate per tiller resulting from an increase in herbage mass was accompanied by a concurrent increase in senescence rate so that the net production of green herbage remained unchanged. Leaf extension rate is positively related to the amount of green leaf remaining on a tiller after defoliation (Grant *et al.*, 1981).

Also, leaf extension is very sensitive to temperature (Williams & Biddiscombe, 1965; Grant, 1968), but the response curves differ due to seasonal effects associated with the vegetative/reproductive phases of growth (Peacock, 1976; Thomas, 1977). Grant *et al.* (1981) found that extension rate was unaffected by light level in the initial stages of regrowth, but by the fourth week of the regrowth period extension rate was significantly increased in shaded plants. Thomas & Davies (1978) observed similar results. However, Silsbury (1970) presents data which suggest that leaf growth rates in ryegrass are independent of the level of radiation.

Leaf extension and senescence vary according to species and defoliation management. In perennial ryegrass, lamina elongation rate per tiller increases linearly with an increase in sward surface height and herbage mass (Grant *et al.*, 1983; Bircham & Hodgson, 1983; Butler & Hodgson, 1993). These authors also reported that net production in ryegrass was depressed under hard grazing as a result of lower production per tiller and instability of tiller population density. The balance between leaf extension and senescence, and tiller density resulted in net extension per unit of area being generally greatest at sward heights of 55 mm in yorkshire fog and ryegrass and 100 mm in tall fescue (Butler & Hodgson, 1993).

2.5.4. Effects of defoliation management on sward structure

A grass sward has not only biomass but a highly organised structure which changes with season and management, and which can also vary according to species, variety or genotype being grown. Generally, a typical sward canopy has a high concentration of leaf sheaths and dead tissue in the lower layers, whereas, live leaf occurs principally in the upper layers.

Roggero *et al.* (1993) studying three sward surface heights of 100, 150 and 200 mm in annual ryegrass (*Lolium rigidum* Gaudin) observed that cutting when the sward reached a height of 100 mm resulted in significantly lower yields but a better canopy structure (denser sward, higher percentage of leaves in the bottom layers, higher leaf:sheath ratio) than the other swards.

Sward surface height has a major effect on the structure and characteristics of the sward. Observations by Penning *et al.* (1991), working with four sward surface heights (30, 60, 90 and 120 mm) showed that the sward surface height has a direct effect on tiller number, mass and leaf area. They found that as stem elongation occurred in late spring, there were a greater number of tillers and a lower proportion of reproductive tillers in the swards maintained at 30 mm and 60 mm than in the sward maintained at 90 and 120 mm. On the taller swards, structure was inferior, becoming sparsely tillered, open and stemmy. These results showed that the optimum sward surface height for continuously stocked swards, grazed by sheep, was between 30 mm and 60 mm.

According to Chapman & Lemaire (1993) sward structure is determined by leaf size, tiller density and number of leaves per tiller. Leaf appearance rate plays a central role because of its direct influence on each of the three key sward structural characteristics. Thus, high leaf appearance rate leads to swards with a high density of small tillers and low leaf appearance rate leads to swards with a lower density of larger tillers.

Hay *et al.* (1987) studying the seasonal variation in the vertical distribution of white clover stolons concluded that white clover growing in grazed pastures throughout New Zealand is subject to an annual cycle, consisting of burial of stolons in winter, re-emergence of growing points in spring, and surface stolon development over summer. Pinxterhuis *et al.* (1993) show that management has little effect on the seasonal variation in structure of the plants or the stolon branching of the white clover population grazed by bulls. However, sheep have a greater selectivity for white clover (Hay *et al.*, 1989a, 1989b). Selection by animals is likely to modify the relative proportions of the different plant species or components and their distribution in the canopy (Hodgson, 1986). Animals grazing a mixed sward frequently tend to graze some plant species and avoid others (Hodgson, 1990).

2.6. PHYSIOLOGICAL RESPONSES OF PLANTS TO DEFOLIATION

The physiological responses of forage plants to defoliation and the characteristics that allow them to recover rapidly have been reviewed widely. Most of the material presented in this section has been reviewed elsewhere (Richards, 1993; Chapman & Lemaire, 1993) and for this reason a detailed review of the literature will not be given here.

2.6.1. Photosynthesis and respiration

Two major determinants of high productivity in a crop are its ability to produce high levels of photosynthates over a wide range of environmental conditions and to efficiently transport and partition a high proportion of those assimilates into economically important organs. Plant primary production is ultimately dependent on photosynthetic CO_2 uptake. However, if a crop plant is not able to allocate a major portion of the fixed carbon into foliage, high photosynthetic rates would not translate into increased food production (Daie & Wyse, 1985). Photosynthate production also depends on the amount of photosynthetically active tissue constructed by the plant and on many aspects of carbon use (expenses and investments) (Körner, 1991).

Since more than 90% of the plant's dry matter accumulation is the result of photosynthesis, it seems likely that a predictable correlation should exist between net photosynthesis and dry matter content of the whole plant. Both net photosynthesis and dry matter production vary among cultivars (Evans, 1975; Ozbun, 1978). However, the relationship between photosynthesis and yield is very complex and for many crops a positive correlation is not obtained (Wottwer, 1980). The reasons for a poor correlation between leaf photosynthesis and yield are varied. Before a crop canopy achieves full interception of light, leaf area is more important than photosynthetic rate per unit leaf area in determining crop growth rate. After canopy closure, the carbon exchange rate (CER) per unit leaf area becomes the most important factor (Gifford & Jenkins, 1983).

Photorespiration occurs in C-3 plants and is considered a wasteful process. This process is pronounced at high temperature and high light intensity, high O_2 or low CO_2 concentration (Calvin, 1990). Dark respiration is a key physiological process for growth and maintenance. Robson *et al.* (1988) found that respiration provides energy for synthesis and maintenance of live tissue by using about half of the CO_2 fixed in photosynthesis. Dark respiration appears to continue in the light and it is positively related to the rate of previous photosynthesis (Ludwig *et al.*, 1965; Sale, 1974; Azcon-Bieto & Osmond, 1983; McCree & Troughton, 1966; Veen, 1981). This is presumably due to greater levels of respiratory substrate available or ADP availability.

The photosynthetic and respiration capacity of grass leaves declines with age (Woledge, 1971). Within an established crop, each tiller bears an average of three live leaves, the youngest with the highest photosynthetic potential and the oldest with the lowest. Parsons *et al.* (1983a, b) observed that growing leaves and fully expanded leaves contributed 77% of the net photosynthesis of the sward canopy, whereas, sheaths contributed less than 5%, even though the area of the sheath was almost as great as the area of the young laminae.

Culvenor *et al.* (1989a) studying the carbon economy of subterranean clover swards subjected to three defoliation treatments (removal of 30%, 70% and 80% of shoot dry weight) observed that net photosynthesis fell by up to 100% immediately after defoliation. Recovery of the net photosynthesis to rates achieved by uncut swards occurred over 4 days in the 30% cut treatment and at least 12 days in more severe treatments. Root respiration also comprised a large respiratory cost (up to 75% of net photosynthesis) during early regrowth. A rapid drop in the respiration associated with nitrogen fixation has also been observed in white clover after defoliation (Ryle *et al.*, 1985b).

The carbohydrate produced in photosynthesis is used in part for the synthesis of cell contents and structural tissue, but up to 50% of it is used as a source of energy to support the growth of new tissue in leaves, stems and roots and to maintain the life processes in established tissue (Hodgson, 1990). Parsons & Penning (1988) observed that during regrowth following a severe defoliation, rates of canopy photosynthesis, and so the rate of production of new leaves, increased rapidly but there was a delay before there was a corresponding increase in the rate of leaf death. They suggest that regrowth of at least 14 days but less than 28 days will be effective in achieving not only close to the maximum average growth rate of highly digestible material, but also in sustaining a densely tillered, leafy sward which regrows rapidly from severe defoliation and is more reliably harvested (utilized) by sheep.

The main effect of defoliation on production is to reduce photosynthesis by reducing leaf area duration (Briske, 1991). Leafe (1972) found a predominance of young leaves during the early stages of regrowth following severe cutting. The proportion of young leaves increased during the regrowth following severe rotational grazing (residual LAI < 0.5) and the photosynthetic potential of the canopy became greater than under continuous grazing (Parsons *et al.*, 1988). The total photosynthetic uptake of this system involving some 12 - 13 days regrowth and 3 days grazing exceeded that of a well utilized continuously grazed sward.

2.6.2. Residual leaf area and light interception

The growth rate of the new tissue is related to the content of reserves (Alberda, 1966) and to the photosynthetic activity of the residual leaf area (Brougham, 1956a, b, 1958; Davies, 1974). Brougham (1956a, b), Davidson & Donald (1958) and Langer (1959) concluded that regrowth after defoliation depends on the residual leaf area. The immediate effects of leaf removal, in white clover plants, was the reduction in area and weight of new leaves (Carlson, 1966).

The immediate effects of defoliation depend mainly on defoliation intensity and are best related to a direct measure of the degree of reduction of leaf area, because defoliation effects play the principal role in whole-plant photosynthesis or daily carbon gain. Leaf extension rate was positively related to the amount of green leaf remaining on tillers after defoliation (Grant *et al.*, 1981). However, the reduction in photosynthesis is often not proportional to leaf-area loss because of changes in canopy microclimate after defoliation and because of the unequal photosynthetic contribution of leaves of various age (Richards, 1993). Loss of old leaves usually has much less effect on growth rate than loss of the same amount of young leaves (Davies 1966, 1974; Gold & Caldwell, 1989a; Richards, 1993). Thus, when young leaves remain after defoliation, the reduction in photosynthesis is more directly related to leaf area loss (Ludlow & Charles-Edwards, 1980; Parsons *et al.*, 1983a; Gold & Caldwell 1989b). But, when mature and senescent leaves predominate in the sward, the low photosynthetic capacity of these tissues resulted in a greater reduction in canopy photosynthesis than expected owing to the proportional area removed (Davies *et al.*,1983; Ludlow & Charles-Edwards 1980; Gold & Caldwell, 1989b; Richards, 1993) and a sharply reduced photosynthesis/transpiration ratios (Caldwell *et al.*, 1983; Gold & Caldwell, 1989b; Richards, 1993).

At very low levels of LAI or herbage mass, canopy photosynthesis is markedly reduced because insufficient young green leaf tissue is present to intercept light, much of which may fall on bare ground (Parsons *et al.*, 1983a).

Managing pastures to maximise accumulation of herbage over time requires that all, or nearly all of the light falling on the pasture is intercepted by photosynthetically active leaf material throughout periods of active growth (Chapman & Lemaire, 1993). The efficiency with which a crop uses incoming radiation to fix carbon depends on (i) the proportion of the light intercepted by the leaf canopy, (ii) the way in which it is distributed over the leaf surface and (iii) the photosynthetic potential of the individual leaves (Robson, 1981). For example, in spring, because the level of incoming radiation rises steeply, the rate of tissue production is high and normally exceeds the rate of death. However, in autumn, once a crop is fully light-intercepting, its rate of dry matter production slows as the level of incoming radiation falls.

Woledge (1977) studying the effect of shading and cutting treatments on the photosynthesis rate of ryegrass leaves observed that the changes in photosynthetic capacity in grass swards are consequences of changes in light climate of the developing leaf rather than of changes in demand for assimilates or growth substance supply. The decline in photosynthetic capacity was contributed to by both stomatal and residual diffusion resistances.

2.6.3. Carbohydrate reserves

The rate of regrowth depends on a supply of readily available energy which can be utilized to build the new tissue; this may be current photosynthate from remaining leaves or the products of earlier photosynthetic activity. Watersoluble carbohydrates, principally fructosan, are among the most readily available substances present in the stubble of temperate grasses.

Regrowth, especially in the early stages, is initiated and developed largely at the expense of previously accumulated organic reserves (Brougham, 1957). Carbon reserves are used for maintenance, respiration and translocation of carbon skeletons to leaves (Hodgkinson, 1969). Their quantity and their availability sharply limit the amount of both top and root growth that will occur. Carbon and N reserves of roots and stubble contributed to a large extent to regeneration of new leaves after removal of shoots in different species such as *Bromus mollis, Trifolium subterraneum* (Phillips *et al.*, 1983; Culvenor *et al.*, 1989b), *Trifolium repens* (Davidson *et al.*, 1990; Gordon *et al.*, 1986), *Lolium perenne* (Gonzalez *et al.*, 1989; Ourry *et al.*, 1993), *Dactylis glomerata* (Colby *et al.*, 1966), *Medicago sativa* (Ourry *et al.*, 1993), *Festuca ovina* (Atkinson, 1986) and *Festuca arundinacea* (Volenec, 1986). When photosynthesis decreased during early regrowth, and consequently reduced availability of carbon skeletons within plant, both N uptake (*Lolium perenne*) and N_2 fixation (*Medicago sativa*) decreased (Ourry *et al.*, 1993).

In general, plants respond to defoliation with a rapid and marked reallocation of assimilate from root to leaf meristem (Ryle & Powell, 1975), reduction of the respiratory rate in remaining tissue (Davidson & Milthorpe, 1966b; Ryle *et al.*, 1985a), and the mobilization of stored carbohydrate and nitrogen compounds to sustain both growth and existing tissue (Culvenor *et al.*, 1989b). Ryle & Powell (1975) also observed that on removing all leaf tissue above the ligule of leaf 3, the rate of photosynthesis of the remaining two older leaves fell to 90-95% of that of the control leaves, but they exported more of their assimilated carbon to meristem elsewhere in the plant during the first 48 h after defoliation. However, the level of export began to decline on regrowth of new leaf tissue from the shoot apex, and fell below that of the control leaves 4 days after defoliation. In *Trifolium subterranean,* Culvenor *et al.* (1989b) concluded that the loss of carbohydrate and nitrogen from roots and branches lasted 5-9 days when 80% of shoot dry weight was removed.

Ourry *et al.* (1993) studying the time course of re-mobilization of reserves during the regrowth of *L. perenne* found that about 40% of foliar N was derived from N reserves of roots and stubble when sufficient N was available in the nutrient solution. When regrowth occurred on a N-deficient medium, N content in leaves decreased and the contribution of N reserves to foliar regrowth increased to about 68%. Therefore, during regrowth, shoots of ryegrass accumulated N from reserves to a large extent. Kinetic studies have shown that these transfers occurred mainly during early regrowth and accounted in ryegrass for nearly all N in leaves 6 days after defoliation (Ourry *et al.*, 1988, 1990). Similarly, in lucerne (Kim *et al.*, 1991) N accumulation within regenerating shoots occurs within the first 10 days of regrowth.

Gonzalez *et al.* (1989) studying the changes in stubble carbohydrate content during regrowth of ryegrass found that regrowth at non-limiting nitrogen levels involved two different physiological periods. The initial phase occurs during the first 6 days and is characterized by the mobilization of 60 to 90% of soluble carbohydrates (Davidson & Milthorpe, 1966a, b). The second phase (6-28 days) is characterized by recovery of carbohydrate levels. This suggests that the regrowth ability of ryegrass is predominantly dependent on the size of mobile reserves, both nitrogen and carbon, in the stubble (Gonzalez *et al.*, 1989; Ourry *et at.*, 1988). Additionally, Lefevre *et al.* (1991) in experiments with ^{15}N labelling clearly showed that during the first days nearly all the nitrogen in new leaves came from organic nitrogen re-mobilized from roots and stubble.

The seasonal pattern of assimilate partitioning is considered in relation to changes in the natural environment and the rate at which the crop fixed carbon in photosynthesis. Parsons & Robson (1981b) working with ryegrass observed that a decrease in the proportion of assimilates partitioned to roots during late spring was significant in increasing the production of shoots at that time, but seasonal differences in partition contributed very little to the marked differences in shoot growth between the spring and autumn crop.

Danckwerts & Gordon (1987, 1989) used ^{14}C labelling techniques to show that, although a relatively small fraction of photosynthesis was invested in long-term labile reserves in *Lolium perenne* (4%) and *Trifolium repens* (10%), this small fraction could build up to form a large pool over an extended period. In a white clover sward, reserve depletion was associated with reduced carbohydrates levels in both stolons and roots, but stolon reserves were preferentially utilized. However, in ryegrass depletion involved contribution from stem bases, not roots.

Experiments with simulated swards of perennial ryegrass grown in flowing nutrient solution with NO_3^- held at 0.1 N l^{-1} show that the rate of NO_3^- uptake was related to diurnal, day-to-day, and seasonal changes in radiation. In summer the diurnal variation in NO_3^- uptake ranged from 25 to 50 mg N m^{-2} h^{-1} and the day-to-day variation ranged from 500 to 1500 mg N m^{-2} d^{-1}. Mean daily rates of uptake over 12 d periods in summer and winter averaged 908 and 44 mg N m^{-2}, respectively (Clement *et al.*, 1978).

2.6.4. Meristematic tissue

The final size and shape of a plant is determined by the differential activity of meristem which controls where, how much and what sort of tissue is developed (Körner, 1991). Thus, growth is a consequence of the functioning of meristem. The position of meristems and their specific activity determines plant morphology and growth rate (Körner, 1991).

The location of the stem apex is important with regard to grazing management. Generally, apical meristem of vegetative, culmless grasses are positioned at, or below, the soil surface and are therefore inaccessible to grazing animals and protected from damage (Chapman & Lemaire, 1993). However, forage legume species display a greater variation in habits than forage grasses. Prostrate or decumbent legumes like white clover and subterranean clover usually have meristem positioned at, or even below the soil surface.

Because the meristematic region of individual leaves is located at the base of the leaf, the amount and type of leaf tissue removed, and when the loss occurs in relation to plant development and the prevailing environment, are the most important factors in determining the impact of defoliation on plants (Richards, 1993). Several researchers (Branson, 1953; Booysen *et al.*, 1963; Hyder, 1972; Richards & Caldwell, 1985; Briske, 1986, 1991; Bilbrough & Richards, 1993) reported that loss of meristematic tissues usually has a much greater effect than proportional loss of biomass, leaf area or plant resource such as carbon or nitrogen. This is because growth is largely governed by the rate at which cells are produced (Körner, 1991). Additionally, the rate at which new cells are produced in plant tissue depends on the number of meristematic cells and the length of the cell cycle (Dale & Milthorpe, 1983; Dale, 1988).

2.6.5. Root growth

Root systems are important in maintenance and function of plants, in terms of water and nutrient uptake and carbohydrate reserves. Possibly the most profound effect of defoliation is on root growth and activity (Milthorpe & Davidson, 1966; Ryle & Powell, 1975). Several authors (e.g. Crider, 1955; Troughton, 1957; Oswalt *et al.*, 1959; Evans, 1971, 1973) have observed cessation or marked reduction in root growth, often accompanied by decomposition, following defoliation. Oswalt *et al.* (1959) observed that root growth ceased within 24 h of defoliation and induced decomposition of the existing roots within 36 to 48 h. Crider (1955) reported that root growth stopped after removal of 40% to 50% of the foliage.

Bloom & Caldwell (1988) studying the effect of root excision found that within a few hours of excision, root respiration and mineral nitrogen absorption decreased to less than 50% and 25%, respectively, of their control levels. Culvenor *et al.* (1989a) working with subterranean clover concluded that the roots, by virtue of their relatively large weight, were the major source of mobilized nitrogen during a period when root growth had ceased. Almost complete cessation of root extension, accompanied by decreases in root respiration (to about one-third) and phosphorus uptake were observed in *Dactylis glomerata* (Davidson & Milthorpe, 1966b). Additionally, a rapid drop in respiration associated with nitrogen fixation has also been observed following defoliation in white clover (Ryle *et al.*, 1985b).

Root growth, root respiration and nutrient absorption decline after defoliation. The magnitude of reductions in root respiration and nutrient absorption are proportional to the intensity of defoliation. However, the reductions are less than for root growth (Davidson & Milthorpe, 1966b).

Observations by Matthew *et al.* (1991) show that root mass and new root production in field swards are relatively insensitive to grazing management, in contrast to earlier studies involving more physiologically severe defoliation of artificial swards. Seasonal fluctuations in new root production were large in comparison to those produced by contrasting hard and lax grazing regimens. Studies of seasonal changes in dry weight of roots in the field (Garwood, 1967; Behaeghe, 1974, 1978) have shown some increase in root weight in autumn but greater increase in early spring. Matthew *et al.* (1991) observed increased root production in spring, but also continued high rates of root formation during peak tiller appearance early in summer. Additionally, under non-limiting conditions, relative carbon partitioning to the roots was 17% and 15.8% during summer and autumn regrowth but decreased to 11.1% during spring regrowth (Belanger *et al.*, 1992). However, in the absence of N fertilization, the relative carbon partition to the roots averaged 31.3%, 26.5% and 26.7% in summer, autumn and spring regrowth, respectively (Belanger *et al.*, 1992).

2.7. GROWTH IN COMPETITION

2.7.1. Intra-specific competition

Plants do not regrow in a defoliated pasture as isolated individuals, but as members of a usually crowded population where the surrounding vegetation exerts a strong influence on inherent species characteristics through competition (Chapman & Lemaire, 1993). Competition occurs during the whole year, but it is especially acute during stem elongation (Colvill & Marshall, 1984) and results in death of a high proportion of the small, non-flowering tillers.

Generally, herbage production in a grass sward is related to the number of live tillers per unit area and their corresponding tiller weight. Observations by Hodgson *et al.* (1981) have shown that tiller population density and individual tiller weights in swards maintained at different herbage masses by continuous grazing are related to each other through the -3/2 self-thinning rule. For grasslands, this relationship holds true down to levels of herbage mass of the order of 700 kg OM ha^{-1}, the value of the exponents derived from 4 studies lying in the range from -1.2 to -1.7, but is modified as tiller population density declines at lower herbage mass (Hodgson *et al.*, 1981). Similarly, Grant *et al.* (1983) found that above 30 mm of sward surface height tiller number and weight changed in a manner consistent with the self-thinning rule. Below 20 mm height, uprooting and death depressed tiller numbers and created gaps in the canopy. Thus, the self-thinning rule does not cover circumstances in which tiller numbers are increasing or where (as in very short, hard grazed swards) there is a loss of plant cover (Davies, 1988).

In successional vegetation associations, populations move up the self-thinning line only, whereas grass dominant pastures are reversible with respect to the size/density relationship such that a single pasture may move up or down the line depending on defoliation management or in response to seasonal variation (Chapman & Lemaire, 1993). Matthew (1992) found in ryegrass swards that tiller size/density compensation slopes were more typically around -5/2 than -3/2. Also both Zeide (1985) and Weller (1985, 1987a) observed that biomass/density thinning slopes are most often steeper than -0.5[1]. Weller (1987a) concluded that the thinning slope was much more variable than previously suspected.

Kays & Harper (1974) working with a wide range of population densities of *Lolium*

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[1] Biomass:Density (B:D) slope of -0.5 therefore equivalent to a weight:density slope -3/2.

perenne found that the rate of elimination of genets from the population was related to the rate of growth of the survivors according to the -3/2 thinning rule. Under low light intensities the thinning process was radically altered in a way which suggests that the density stress within the grass population was caused by mutual self-shading.

A number of authors (e.g. Furnas, 1981; Lonsdale & Watkinson, 1982) have noted that the intercept of the thinning line is dependent upon the level of light. Increased light levels raise the intercept. Furnas (1981) and Lonsdale & Watkinson (1982) also noted a change in slope to -1 at very low light levels, a finding which Furnas (1981) explains in terms of self thinning at constant herbage mass, in this case when swards are near the compensation point. In addition, under unshaded conditions the thinning occurs along a slope of -3/2 whereas under deep shade along a slope of -1. Additionally, Chapman & Lemaire (1993) noted that in pastures the -3/2 size/density relationship holds only when the interception of light by a canopy is more-or-less complete, and when mortality due to crowding is occurring. Similarly, Grant *et al.* (1981) suggested that variation in light level and herbage mass are the regulators of major importance.

Lonsdale & Watkinson (1983) found that the slopes in the three species they studied were significantly different from -3/2. Lonsdale (1990) re-analysing the results of several researchers (Weller, 1987a; Zeide, 1987) concluded that there is no evidence to support a thinning rule at present. He found that the mean self-thinning slope for 419 data sets examined was -1.61, significantly different from -3/2. He did not reject the theoretical -3/2 value outright, but suggested that a final rejection of the hypothesis would require experiments carried out under controlled conditions, since fluctuations in resource levels might alter the intercept, and thus apparently the slope, of the thinning line as the experiment proceeds. Such experiments should attempt to assess the thinning slope in terms of both biomass and volume (Lonsdale, 1990).

2.7.2. Inter-specific competition

Grass and clover in mixed swards compete for light, moisture and nutrients. Grass is the more aggressive species and any aspect of management which favours its growth usually results in some suppression of clover (Wolton *et al.*, 1970).

Turkington & Harper (1979) studying 23 species present in a sward suggested that the structure of the vegetation at any time is determined by a regeneration cycle, which is directed by the dominant species in the community. They observed that *Lolium perenne* characteristically has two peaks of leaf growth, a March-June flush of growth and a lesser peak in August-September. In contrast, *Trifolium repens* has a single season of active growth, with its peak in June-July coinciding with the July gap of *Lolium perenne*. Thus, white clover increases when the ryegrass is suppressed by the low available supply of water (Brougham, 1955) and higher temperatures (Mitchell, 1953, 1954).

Management practices also affect plant competition. Brereton *et al.* (1985) showed that clover dominance was maintained over 3 years in swards cut at 28-day intervals during the growing season, but declined progressively in swards cut at 14-day intervals. This decline was also related to an increase in grass tiller population. Thus, the instability observed in grass-clover swards under rotational grazing was due to the sensitivity of white clover to grass tiller density within the normal range found in swards.

White clover is also affected by animal selectivity. Wolton *et al.* (1970) observed that white clover regrowth was more rapid following cutting than grazing, suggesting that nonselective defoliation by the mowing machine left clover in a stronger position for regrowth than did selective close grazing by sheep.

Küppers (1985) provided a good example of interspecific competition. He studied the carbon balance of a number of deciduous woody species in a hedgerow community. The success of the various species in that community, in terms of ultimate biomass accumulation and species persistence, was not related to their photosynthetic capacity at ambient CO_2 levels. In fact the species with the lowest photosynthetic capacity, *Fagus sativa* L. was the most competitive and became the dominant species in the end. This was attributable to its ability to position photosynthetic surfaces to capture light (e.g. superior branching angle, differential bud activity, leaf position and internode length-features) which became obvious growth determinants once plants were studied under natural competitive conditions, rather than in isolation.

Similarly, Beyschlag *et al.* (1990) compared two C-3 graminoids in competition and found that the differences between species in carbon gain were associated more with structural features than with photosynthetic characteristics.

2.8. SUMMARY AND CONCLUSION

This literature review examined the influence of defoliation management as a means of improving pasture and animal production. The experiments reviewed demonstrate the importance of spring grazing management as the most important time to increase herbage production during spring, summer and autumn. Also, they show that grazing management during late spring-early summer is the most critical factor to maintain, increase or decrease pasture density and herbage production.

The physiological responses of the plant to defoliation with particular reference to ryegrass and white clover swards, were also reviewed. Defoliation was shown to influence tillering activity, leaf appearance and leaf growth rate, photosynthesis activity, residual leaf area and light interception, carbohydrate reserves, nutrient content and root growth. The importance of intra- and inter-specific competition and their influence upon plant persistence and production were also examined.

There is considerable information to show advantages for pasture production and animal productivity during summer and autumn from lax grazing during spring in rotational systems, which allows early seedhead development. However, there is little evidence regarding the effect of timing and duration of lax spring grazing and also, there is a lack of information about inter- and intra-specific implications on plant competition. Provision of answers to these questions is an important pre-requisite for optimising harvest efficiency through appropriate defoliation management, and further research is, therefore, necessary to integrate these principles into grazing systems.

Chapter 3

THE INFLUENCE OF TIMING OF LAX SPRING GRAZING MANAGEMENT ON HERBAGE PRODUCTION AND TILLER POPULATION IN A PERENNIAL RYEGRASS/WHITE CLOVER PASTURE

3.1. INTRODUCTION

A primary objective of grassland management is to maximise production of digestible material and protein per hectare per growing season from plants which are periodically defoliated. On the other hand, the primary functions of the forage plants are to trap sunlight in the foliage to ensure a supply of energy for growth, and to absorb water and minerals from the soil via the roots (Hodgson, 1990). The form and function of the plants are adapted to these ends, but are also strongly influenced by the strategies adopted to survive the consequences of defoliation and disturbance by grazing animals.

The responses to defoliation of forage plants will depend on the interrelationships between root and shoot growth and the ratio of elongating to non-elongating tillers. The translation of these responses into systems of management depends on several components, including the species composition, the stage of growth and general economic considerations (Milthorpe & Davidson, 1966).

During the development of a grass sward, tillers are continually emerging, growing and dying at rates that differ appreciably, depending on environmental conditions and stage of development. At any one time, therefore, there is a population of tillers ranging in size from dormant buds to perhaps elongating flowering stems. The rate of growth of the sward, being the integral of the growth rates of the component tillers, is influenced by the rate of tiller production as well as the growth rates of individual tillers (Milthorpe & Davidson, 1966).

Studies of tillering with several temperate perennial forage grass species have revealed remarkably similar seasonal patterns of tiller appearance and death (Lamp, 1952; Langer *et al.*, 1964; Garwood, 1969; Colvill & Marshall, 1984). Additionally, it has been pointed out by several researchers (Brougham, 1959, 1960, 1970; Jameson, 1963; Davidson, 1968; Tainton, 1974; L'Huillier, 1987b; Matthew *et al.*, 1989a, b; Matthew, 1992; Da Silva *et al.*, 1993, 1994; Da Silva, 1994) that productivity of pastures can be manipulated to advantage by grazing management, through control of tiller population density, particularly during the flowering period (Matthew *et al.*, 1989a, b; Matthew, 1992; Da Silva *et al.*, 1993, 1994; Da Silva, 1994).

Observations by Matthew (1991, 1992), Matthew *et al.* (1989a, b), Da Silva *et al.* (1993, 1994) and Da Silva (1994), Xia *et al.* (1990), Xia (1991) have demonstrated the potential advantages to tiller population and herbage production of perennial ryegrass/white clover pastures in late summer and autumn from a spring management which allows early seedhead development followed by defoliation at or soon after anthesis. However, the evidence of Matthew *et al.* (1989a, b) is not entirely supported by the results of Da Silva *et al.* (1993, 1994), Da Silva (1994) in large scale studies.

They found that the pasture production responses were variable over the two years of study. In 1990/91 the extra growth was mainly due to ryegrass but in 1991/92 to white clover. The explanation is unclear and further studies are needed to examine the effects of different late spring grazing managements on tiller age profiles and subsequent summer and autumn pasture production. One possible reason for the difference noted above is that whereas the experiments of Matthew *et al.* (1989a, b), Matthew (1992) were performed on pure ryegrass swards, those of Da Silva *et al.* (1993, 1994) and Da Silva (1994) were performed on mixed ryegrass-white clover swards. The experiments described in the following chapters were designed to investigate these specific issues.

3.1.1. Objective

The objective of the two Experiments described in this chapter was to study tissue and tiller dynamics and production of perennial ryegrass-white clover swards and intensively fertilized simple perennial ryegrass swards following lax spring grazing periods of different duration.

3.1.2. Chapter structure

Experiments 1 and 2 were very similar, and the materials and methods were practically the same. They will therefore be described together. Minor differences between Experiments will be pointed out when necessary. Also, results will be explained sequentially, and then considered in a combined discussion.

3.2. MATERIALS AND METHODS

3.2.1. General description

3.2.1.1. Sward and site

Experiment 1 was conducted between September 1992 and March 1993 and Experiment 2 between September 1993 and May 1994 at the Pasture and Crop Research Unit, Massey University, Palmerston North on a sward containing perennial ryegrass (*Lolium perenne*, cv. 'Grasslands Nui') with or without white clover (*Trifolium repens*, cv. 'Grasslands Tahora') as sown species and some volunteer grasses, especially *Poa* species. The pasture was sown in March 1988 at rates of 25 and 2 kg ha^{-1} for ryegrass and white clover, respectively. The two Experiments were sited on different areas of the same pasture.

The soil at the site is Tokomaru silt loam (Cowie, 1972). It is classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth) (Cowie *et al.*, 1978). Mean annual rainfall is 995 mm and long term average temperature ranges from 8 °C in July to 17.6 °C in February. Monthly weather data (rainfall, soil and air temperature) collected at the meteorological station at Grasslands Division DSIR, Palmerston North, over the Experimental periods, are presented in Appendices 3.1 and 3.2.

3.2.1.2. Treatments and management

In the 1992/93 season (Experiment 1) 18 individual plots of 86.5 m^2 were grazed by sheep every 14 (hard grazing) or 21 days (lax grazing) to maintain post-grazing sward surface height at 30-50 mm (hard grazing) and 70-90 mm (lax grazing), respectively. From 8 December onwards all treatments were grazed every 14 days at 30-50 mm. Three grazing treatments, with (W) and without (N) white clover, were arranged in a factorial (3 x 2) randomized block design with three replicates (Figure 3.1).

In Experiment 2, due to the development of patchy growth on all treatments during the previous season, plot size and number of replicates per treatment were further increased to 100 m^2 and four, respectively. Swards were also rotationally grazed by sheep every 3 weeks, to maintain the same post-grazing sward surface heights as in Experiment 1. Figure 2 shows a plot diagram of the second Experiment. Differences between lax and hard grazing can be observed in Plate 3.1.

Experiment 1 comprised the following three treatments with (W) and without (N) white clover:

(i) EC (early control) - Hard grazing during the entire Experimental period (From middle September to late March) to a residual pasture cover of 900-1000 kg DM ha^{-1} (residual height of 30-50 mm);

(ii) SR (short release) - Lax grazing from 26 October to early December to a residual pasture cover of 1500-1700 kg DM ha^{-1} (residual height of 70-90 mm), switched to hard grazing (residual height of 30-50 mm) at the time of anthesis of the perennial ryegrass (8 December);

(iii) LR (long release) - Lax grazing from the middle of September to early December to a residual pasture cover of 1500-1700 kg DM ha^{-1} (residual height of 70-90 mm), switched to hard grazing (residual height of 30-50 mm) at the time of anthesis of the perennial ryegrass (8 December);

Grazing treatments for Experiment 2 were the same as for Experiment 1. The only difference between them was that the grazing treatments in Experiment 2 started and ended a week earlier (8 September to 1 December) than Experiment 1 (15 September to 8 December). Also, the second trial had the same interval between grazings (21 days) and finished 45 days later (middle of May).

									Block
LRW		SRW	LRN		ECW	ECN		SRN	C
ECN		ECW	LRW		SRN	SRW		LRN	B
SRN		LRN	ECN		SRW	LRW		ECW	A

Figure 3.1. Distribution of the experimental treatments in the field for Experiment 1.

A month before the beginning of the Experimental periods, the white clover was removed in half the plots by the use of Versatill at 1.5 litres ha^{-1} (450 g ai ha^{-1} clopyralid). To ensure that nitrogen supply was not a constraint on growth in Experiment 1, urea fertiliser was applied at 28 kg N ha^{-1} every two weeks throughout the trial on those plots without white clover. In Experiment 2 the amount of N was reduced to 14 kg N ha^{-1} per fortnight.

Block A			Block B			Block C			Block D		
EC W	SR W	EC N	LR W	EC N	LR N	SR W	EC W	LR W	EC W	SR W	SR N
LR N	LR W	SR N	SRW	EC W	SR N	EC N	LR N	SR N	LR W	LR N	EC N

Figure 3.2. Distribution of the experimental treatments in the field for Experiment 2.

Plate 3.1. An overview of the experimental area after grazing. Differences between lax and hard plots are clearly observed.

3.2.2. Sward measurements

3.2.2.1. Herbage harvested

Herbage mass in Experiment 1 was determined from three 0.1 m^2 quadrats per plot before and after each grazing. Samples were harvested at ground level using an electric shearing hand piece. Also, 20 pasture height readings were taken with a rising plate meter in each plot. Herbage was washed and dried at 80 °C for 24 hours, and weighed. Estimates of mean herbage mass per paddock were derived from the pasture height measurements, using quadrat sample data to generate separate pooled regression equations for pre- and post-grazing measurements in the periods before and after the "control" grazing on 8 December. Use of this predictive procedure helped to minimise the impact of the ground-level quadrat cuts on the plots by reducing the number of quadrats taken.

Regression equations for the pre-control period (From 15 September to 7 December) were:

Post-grazing residual herbage mass:

$$HMI\ (kg\ DM\ ha^{-1}) = 18 + (127 * RPI)$$

$$s = 186$$

where:
HMI is the initial (post-grazing) herbage mass, RPI is the initial (post-grazing) rising plate meter reading and s is the residual standard deviation (kg DM ha^{-1}).
Pre-grazing residual herbage mass:

$$HMF\ (kg\ DM\ ha^{-1}) = 145 + (128 * RPF)$$

$$s = 313$$

where:

HMF is the final (pre-grazing) herbage mass and RPF is final (pre-grazing) rising plate meter reading.

Post-control period (10 December to 29 March):

Post-grazing residual herbage mass:

$$HMI\ (kg\ DM\ ha^{-1}) = 476 + (43.3 * RPI)$$

$$s = 158$$

Pre-grazing residual herbage mass:

$$HMF\ (kg\ DM\ ha^{-1}) = 727 + (99.4 * RPF)$$

$$s = 275$$

From the above equations, herbage accumulation was calculated as follow:

$$HA\ (kg\ DM\ ha^{-1}) = \sum_{i=1}^{n} HMF - \sum_{i=1}^{n} HMI$$

where:

HA = Herbage accumulation

HMF = Herbage mass final

HMI = Herbage mass initial

i = 1...n denotes successive regrowth cycles.

In the second trial, herbage accumulation was predicted from rising plate meter measurements. Since quadrat cuts interfered with estimates of tiller population, persistence and sward structure in Experiment 1, in the second trial they were omitted from September to late November. Herbage mass was in this period monitored using only the rising plate meter technique. Before and after each harvest, in all plots 20 pasture height readings were taken. From December 1 onwards three pre- and three post-grazing quadrat cuts (0.1 m^{-2}) per plot were made, at ground level, dried at 80 °C for 24 h, and weighed. At the same time, inside these quadrats a rising plate height reading was recorded. This information (quadrat cuts and rising plate meter) was used to obtain two regression equations (pre- and post-grazing) for estimation of herbage mass. These equations are:

Post-grazing residual herbage mass:

$$HMI\ (kg\ DM\ ha^{-1}) = 547 + (82.4 * RPI)$$

$$s = 321$$

Pre-grazing herbage mass:

$$HMF\ (kg\ DM\ ha^{-1}) = 739 + (107 * RPF)$$

$$s = 280$$

Herbage accumulation was then calculated, as in Experiment 1, as the sum of the differences between herbage mass estimates at one post-grazing measurement (HMI) and the next pre-grazing measurement (HMF).

3.2.2.2. Botanical composition and tiller size

From the three ground level quadrat cuts one pooled sub-sample of herbage from each plot was used to determine pre-grazing botanical composition with the following components: ryegrass leaf and stem, white clover leaf and stolon, weeds and dead matter. These determinations were made at the beginning of both trials and, from 26 October onwards, every grazing period in Experiment 1; in Experiment 2 measurements were made before the switch from lax to hard grazing and then every second grazing.

Once the sub-sample was separated into its components, the number of tillers in the ryegrass fractions (ryegrass stem number) was counted and after drying, tiller weight was determined by dividing ryegrass fractions dry weight by tiller number. For both Experiments, before the switch from lax to hard grazing, ryegrass tillers were classified as vegetative or reproductive and the two classes counted and weighed separately. In Experiment 2 reproductive tillers were also classified into reproductive with flag leaf and reproductive with seedhead, counted and weighed.

3.2.2.3. Tiller population density

In Experiment 1 tiller population density was determined six times during the Experimental period using the technique of Mitchell & Glenday (1958) (15 September, 20 October, 2 December, 1 January, 28 January and 23 March). Except for the initial measurements on 15 September where 200 tiller cores were sampled at random over the whole trial area, at each sampling 30 cores of 53 mm diameter were taken per plot from which was recorded the number of ryegrass and other grass tillers per unit area (tillers m^{-2}). White clover stolon length (SL) and growing points (GP), and weed numbers, were also recorded. Plot mean values were used to estimate the changes in ryegrass and other grass tiller population densities as well as white clover density throughout the Experimental period. In Experiment 2 the tiller population density was studied using the same technique as in the previous year, but was determined only five times during the Experimental period (9 September, 29 November, 10 January, 22 February and 29 April).

3.2.2.4. Tiller dynamics

In the first year (Experiment 1) two circular plastic fixed quadrats (65 mm diameter) per plot were placed at ground level. All live ryegrass tillers within each fixed quadrat were tagged on 15 September 1992, after the treatments had been applied. Short lengths of coloured split plastic tube (2-5 mm diam. and 3-5 mm long) were used as tags. The fixed quadrats were placed randomly within plots. The live, new and dead tillers were recorded at two-week intervals, normally a week after each grazing. The new tillers were tagged with a new colour at each recording. As the tiller tagging usually took five days, the dates presented represent the mid-point of each period. Individual quadrat values were used for calculation which included change in tiller population density, tiller appearance and tiller death rates.

In the second trial tillering activity was studied using the same technique as in Experiment 1, but monitoring of the tillering activity was performed less often in four fixed quadrats (50 mm diameter) per plot, permanently fixed at ground level. As in the first trial, all live ryegrass tillers within each fixed quadrat were tagged between 14 September and 16 September 1993 with short lengths of coloured split plastic tubing (2-5 mm diam. and 3-5 mm long). The frames were sited randomly within plots. The live, new and dead tillers were recorded before the switch from lax to hard grazing (24 November). From then on, observations were made every two grazing periods.

Because tiller populations from fixed quadrats were always higher than random samples (tiller cores), and to obtain information on the potential for this to be caused by non-random placement of fixed quadrats, a sample of ten cores per plot were collected at the end of the second trial from visually identified "clumps" of high ryegrass tiller density. The clump tiller population density was then compared with population densities from randomly collected tiller cores and those from fixed quadrats.

3.2.2.5. Tissue turnover

Leaf elongation and senescence were measured three times in both trials using the techniques of Bircham & Hodgson (1983) for ryegrass and Williams *et. al.* (1964) for white clover. At the beginning of each Experiment, two two-metre long transects per plot were randomly placed. At each measurement, in each transect five individual ryegrass tillers and five white clover stolons were selected at random at 20 cm intervals. The selected tillers and stolons were identified by tagging with short lengths of coloured split plastic tubing (2-5 mm diam. and 3-5 mm long), a day after grazing. The marked tillers and stolons were changed each period.

3.2.2.5.1. Tissue turnover in ryegrass

For ryegrass tillers, the length of the lamina was recorded for each leaf of each tiller on three occasions over a 14 or 21 day period (Experiment 1: days 1, 7 and 13; Experiment 2: days 1, 10 and 20) using a ruler with a precision of 1 mm. The leaf lengths were measured as the distance from the point of insertion (ligule) to the lower edge of the yellow region or the tip of the leaf. Only green lamina was recorded, and if a lamina had a dead tip, the length measured was from the base of the dead tissue to the base of the lamina (ligule).

All leaves were measured individually, and according to the leaf growth stage were classified as mature or immature. Immature leaf was the youngest one and mature leaves were those which were subtended at an angle to the sheath, and the ligule was visible. In daughter tillers on tagged tillers, measurements were made of total leaf length.

Leaf extension rates were calculated by the difference between leaf length at the beginning and the end of each grazing interval divided by the number of days in the interval. The rate of leaf elongation (E) is defined as:

$$E = \frac{L_{t2} - L_{t1}}{T_2 - T_1} \quad (mm\ tiller^{-1}\ day^{-1})$$

for any leaf when $L_{t2} \geq L_{t1}$, although generally leaf elongation or leaf growth only occurs on the youngest immature leaf.

where:

L_{t2} = leaf length at time 2

L_{t1} = leaf length at time 1

$T_2 - T_1$ = number days elapsed since start of measurements.

Leaf senescence only occurs on mature leaves, and was calculated as decrease in mature length between successive measurement intervals, divided by the number of days in the interval. Rate of leaf senescence (S) is defined as:

$$S = \frac{ML_{t1} - ML_{t2}}{T_2 - T_1} \ (mm\ tiller^{-1}\ day^{-1})$$

Where T_1 and T_2 are as above and ML_{t1} and ML_{t2} are the lengths of the individual mature leaves for which $ML_{t1} \geq ML_{t2}$. Normally, each tiller had two or three mature leaves and generally the oldest leaf was senescing.

Net leaf growth per tiller (NG) is the difference between leaf elongation rate and leaf senescence rate:

$$NG\ (mm\ tiller^{-1}\ day^{-1}) = E - S$$

These procedures gave estimates of tissue turnover in linear dimension (mm tiller^{-1} day^{-1}). Estimates of leaf weight per unit length (mg mm^{-1}) then allowed calculation of tissue turnover on a dry weight basis (mg tiller^{-1} day^{-1}). To estimate the relationship between leaf length and leaf weight, before each grazing a sub-sample of ten ryegrass tillers per replicate were taken. Immature and mature leaves were separated, bulked and their total length and dry weight were recorded in mg DM mm^{-1} of leaf length.

Net herbage production (g DM m^{-2}) was also estimated using the leaf elongation and senescence data together with the tiller population data recorded at the time of each set of tissue turnover measurements. The above leaf length and weight data were then used in transformation from linear change per tiller to weight change per tiller and to weight change per unit of ground area, as follows:

$$NHP = (LW * NG) * TP$$

Where:

NHP = Net herbage production (g DM m^{-2})
LW = Leaf weight per unit length (g DM mm^{-1})
NG = Net leaf elongation per tiller (mm $tiller^{-1}$)
TP = Tiller population during the period of tissue turnover readings (tillers m^{-2}).

3.2.2.5.2. Tissue turnover in white clover

White clover petiole elongation and leaf expansion were estimated from measurements on ten stolons per plot on three occasions over a 14 or 21 day period (Experiment 1: days 1, 7 and 13; Experiment 2; days 1, 10 and 20), as in ryegrass.

Clover petiole elongation measurements were made from the stipule to the tip or the lower edge of the senescent region (as in ryegrass). Meanwhile, leaf expansion was determined by the technique of Williams *et al.* (1964). All white clover leaves were classified according to visual assessment of leaf area (cm^2), using standard scores (Williams *et al.*, 1964). Scores ranged from 6 (lowest) to 24 (highest), and these scores where later used to estimate leaf area.

Leaf expansion rates (cm^{-2} $locus^{-1}$ day^{-1}) were calculated by the difference between leaf score at the beginning and the end of each grazing interval divided by the number of days in the interval. To estimate the relationship between leaf area and leaf weight, one sub-sample per replicate of white clover leaves was taken before the harvest, leaf area measured (about 200 cm^{-2}) and then leaves were dried and weighed. These values were used to estimate leaf accumulation from leaf expansion in mg $locus^{-1}$ day^{-1}.

Tissue turnover components and net production were calculated using the formulae from section 3.2.2.6.1, except that values for white clover lamina were in area rather than in length units.

3.2.2.6. Sward canopy structure

The term canopy structure is used to encompass the distribution and arrangement of the above-ground plant parts within a community including the absolute weight and percentage contribution of the parts to the sward in addition to their spatial distribution (canopy geometry). Sward structure was determined in Experiment 1 only, using the inclined point quadrat technique (Rhodes, 1981), before the switch from lax to hard grazing on 6 December; 200 contacts per plot were taken.

3.2.3. Statistical analysis

All data were evaluated by analysis of variance using the General Linear Model (GLM) procedure of SAS (SAS Institute Inc. 1989). The two sward types with three grazing treatments were analyzed as a factorial combination with a randomised complete block (RCB) design. No transformation of data was necessary. In order to obtain an overview of the way in which variables related to each other, a multivariate analysis, Canonical Discriminant Analysis (CDA), was carried out.

3.3. EXPERIMENT 1 - RESULTS

3.3.1. Herbage accumulation

Herbage accumulation (HA) throughout the trial period is reported in Table 3.1. Total HA was 29% and 33% less ($P \leq 0.001$) for EC plots than for SR and LR, respectively. There were seasonal differences in the pattern of response across grazing treatments. In the pre-control phase, the reduction on EC plots, compared to SR and LR, respectively, was 28% and 47%. No differences were observed during the control phase. However, during summer and autumn the EC treatment produced 500 kg DM ha^{-1} less than the SR and LR treatments ($P \leq 0.001$).

Nitrogen also increased total herbage accumulation as compared to W swards (Table 3.1), with these effects being observed in pre- and post-control periods. During spring N treatments produced 61% more herbage than W treatments ($P \leq 0.001$). The corresponding difference was only 16% ($P \leq 0.01$) in summer and autumn.

A significant interaction effect between SR and LR and N/W treatments was observed only during the pre-control phase ($P \leq 0.001$), with LR being more responsive to N than SR and EC.

3.3.2. Botanical composition

At the beginning of the trial the botanical composition of the N fertiliser swards was as follows: 68% ryegrass, 19% other grasses, 1% weeds and 12% dead material; while white clover swards had 75% ryegrass, 4% white clover, 8% other grasses, 1% weeds and 8% dead material. No changes were observed in botanical composition to the middle

Table 3.1. Herbage accumulation (kg DM ha^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements (Rising plate meter determination[+]). Experiment 1.

Treatment[1]	15 Sep-7 Dec Pre-control	10 Dec-23 Dec Control	25 Dec-29 Mar Post-control	Total
ECW	3420	720	3620	7760
ECN	4880	900	4310	10090
EC	4150	810	3970	8930
SRW	4090	850	4010	8960
SRN	6560	870	4840	12270
SR	5320	860	4430	10610
LRW	4440	880	4290	9610
LRN	7790	910	4680	13388
LR	6110	900	4490	11490
W	3980	820	3980	8780
N	6410	900	4610	11910
SEM[++]	200	50	190	390
Effect of:				
Treatment	***	ns	*	***
W vs N	***	ns	**	***
Interaction[2]	**	ns	ns	ns

*:P<0.05; **:P<0.01; ***:P<0.001; ****:P<0.0001; ns:no significant differences

[+] = Quadrat cuts were used together with sward surface height to determine the regression equations used here.

[++] = Standard error of least square means.

[1] EC = Early Control, SR = Short Release, LR = Long Release, W = Ryegrass and white clover sward, N = Ryegrass sward with fertiliser nitrogen.

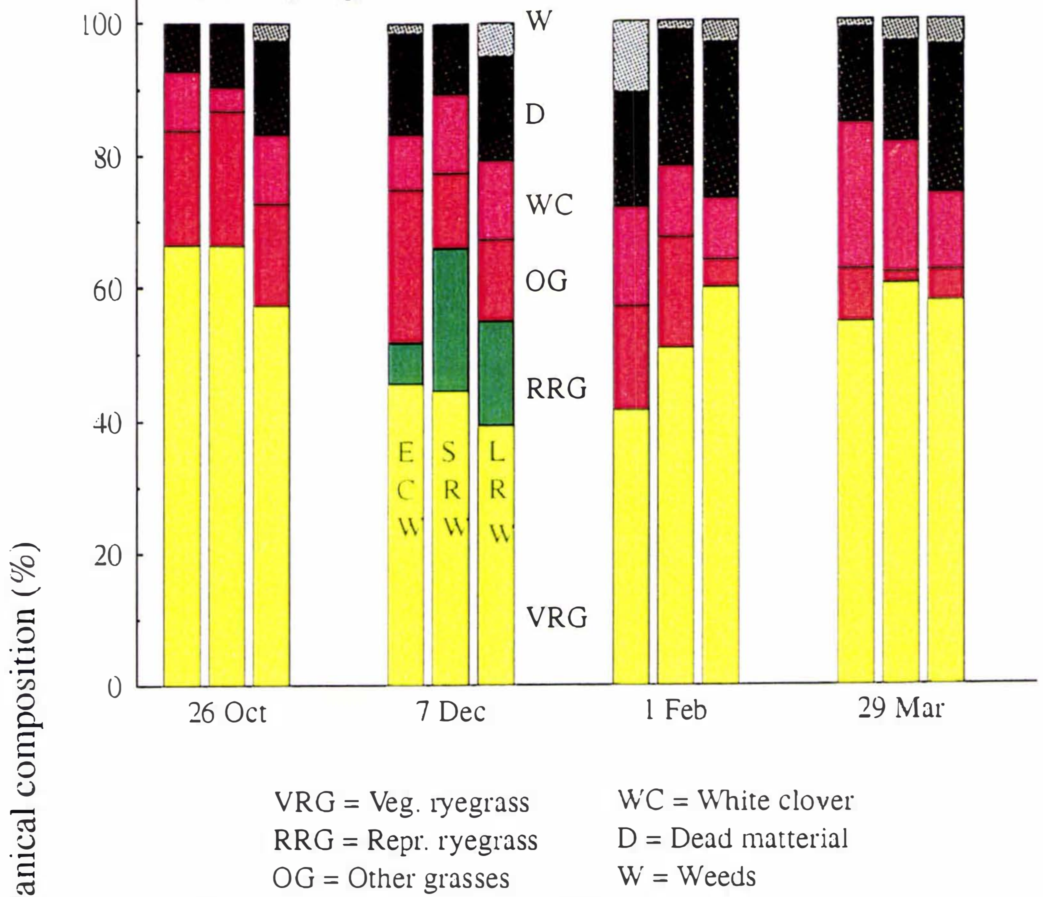
[2] = Interaction tests for differences between W and N swards in treatment responses {(EC/SR/LR) * (W/N)}.

of spring (before the second switch from hard to lax grazing, on 26 October). However, before the reverse switch from lax to hard grazing (7 December), ryegrass percentage in EC was only 54%, compared with 70% ($P \leq 0.05$) and 65% ($P = 0.14$) in SR and LR, respectively. The opposite was the case with other grasses ($P \leq 0.01$); the proportion of other grasses in EC was double that in SR and LR treatments. Also, no differences between treatments were found in the percentage of vegetative tillers, but in SR and LR treatments reproductive tillers comprised a higher proportion of total herbage mass than EC (Figure 3.3 and Appendix 3.3). EC swards had a leaf:stem ratio of 2.03 (67:33), while SR and LR swards had a ratio of 1.17 ($P \leq 0.05$) and 1.38 ($P \leq 0.05$), respectively (Table 3.2 and Appendix 3.3).

On 1 February, ryegrass, other grass and white clover percentages were not statistically different between treatments, but SR and LR treatments had less weeds and more dead material than EC ($P \leq 0.05$). Figure 3.3a also shows that the ryegrass content of the sward was 44% and 18% higher in LRW than ECW ($P \leq 0.06$) and SRW ($P = 0.32$), whereas all N treatments were similar. No differences were observed in ryegrass and other grass populations at the end of the trial, but the LR treatment had more dead material than SR and EC (Figure 3.3 and Appendix 3.4).

The white clover proportion changed with season. Thus, the lowest proportion of white clover was found in spring and the highest in the autumn. In general no big differences in white clover proportion were observed between grazing treatments. ECW had slightly less clover than SRW and LRW on 7 December (Figure 3.3a), but from 1 February onwards the opposite was the case.

(a) Ryegrass-white clover swards



(b) Ryegrass swards

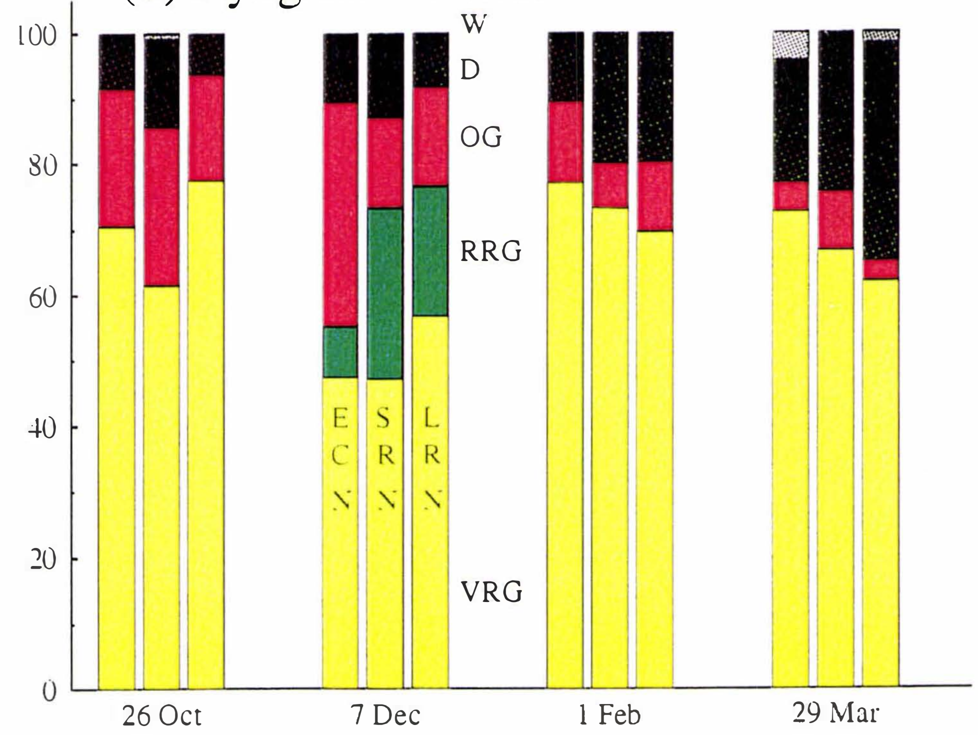


Figure 3.3. Effect of duration of lax spring grazing management on botanical composition (% dry weight) of ryegrass-white clover (a) and ryegrass (b) swards. Experiment 1.

Table 3.2. Relative proportion (%) of leaf and stem in grasses, and leaf and stolon in white clover throughout the trial period of ryegrass-white clover and ryegrass swards. Experiment 1.

Treatment	Ryegrass		Other grasses		White clover	
	Leaf	Stem	Leaf	Stem	Leaf	Stolon
			26 October			
ECW	64	36	59	41	100	0
ECN	67	33	72	28		
SRW	62	38	58	42	100	0
SRN	66	34	65	35		
LRW	62	38	65	35	98	2
LRN	60	40	61	39		
			7 December			
ECW	64	36	46	54	84	16
ECN	70	30	64	36		
SRW	53	47	38	62	68	32
SRN	55	45	43	57		
LRW	56	44	48	52	79	21
LRN	60	40	50	50		
			1 February			
ECW	71	29	65	35	63	37
ECN	72	28	60	40		
SRW	67	33	70	30	80	20
SRN	76	24	57	43		
LRW	70	30	51	49	68	32
LRN	82	18	39	61		
			29 March			
ECW	69	31	46	54	52	48
ECN	68	32	66	34		
SRW	66	34	33	65	44	56
SRN	67	33	72	27		
LRW	68	32	57	43	65	35
LRN	70	30	66	34		

3.3.3. Tiller weight

Tiller dry weight changed with season and management (Table 3.3). Ryegrass tiller weight in LR was greater than in EC and SR before the switch from hard to lax grazing on 26 October ($P \leq 0.01$). Following reproductive growth, tiller weight on 7 December was higher ($P \leq 0.001$) for SR and LR than for EC treatment. During the active tillering period (January), no differences in tiller weight were found between treatments, possibly because there was a compensation between tiller size and tiller population density (as the tiller population increased in LR and SR treatments, the tiller weight tended to decrease).

The lowest tiller weight was found in autumn (Table 3.3), and at this time treatments were statistically different ($P \leq 0.05$). Tillers on SR and LR treatments were 19% heavier than EC overall, but there was an interaction effect between treatments. No differences in tiller weight were observed in N treatments, but SRW and LRW tillers were 39% and 36% heavier than ECW tillers (Table 3.3). With the exception of 29 March, where ryegrass tiller weight in W swards was greater than in N swards ($P \leq 0.05$), tiller weights in N treatments were generally heavier than W treatments, the differences being statistically significant ($P \leq 0.05$) before the switch from lax to hard grazing early in December.

3.3.4. Tiller population density

Tiller population densities calculated from tiller core data are presented in Table 3.4, while those from fixed quadrats are presented in Figures 3.4 and 3.5. The initial tiller population densities were 78% greater in fixed quadrats than from random core samples

Table 3.3. Effect of grazing treatment on mean ryegrass tiller dry weight (mg) in ryegrass-white clover swards. Experiment 1.

Treatment	26 Oct	7 Dec	4 Jan	1 Feb	29 Mar
ECW	15.9	15.7	13.3	17.4	8.4
ECN	14.3	15.6	16.2	17.7	9.3
EC	15.1	15.7	14.8	17.5	8.7
SRW	13.1	36.5	19.0	19.9	11.4
SRN	12.3	48.1	18.0	21.0	9.2
SR	12.7	42.3	18.5	20.5	10.3
LRW	22.3	29.0	12.2	16.3	11.7
LRN	25.8	42.5	19.3	15.8	9.1
LR	24.0	35.8	17.8	16.0	10.4
W	17.1	27.1	16.2	17.9	10.5
N	17.4	34.4	17.8	18.4	9.2
SEM	2.8	4.3	2.4	2.1	0.6
Effect of:					
Treatment	**	***	ns	ns	*
W vs N	ns	*	ns	ns	*
Interaction	ns	ns	ns	ns	*

Table 3.4. Tiller population density (tillers m^{-2} from tiller cores) of perennial ryegrass and other grasses growing either with white clover or fertiliser nitrogen under contrasting spring grazing managements. Experiment 1.

Treatment	20 Oct		2 Dec		1 Jan		28 Jan		23 Mar	
	RG[1]	OG[2]	RG	OG	RG	OG	RG	OG	RG	OG
ECW	4700	2200	3830	4590	6990	6820	7760	6880	5050	3240
ECN	4540	3420	4370	7050	7000	8000	9910	6670	10500	2420
EC	4620	2780	4100	5820	7000	7410	8830	6770	7770	2830
SRW	4530	1870	3280	2650	5840	5620	8820	4740	8050	3490
SRN	5100	3810	5030	3940	10330	5950	11700	4760	9770	3320
SR	4810	2840	4150	3300	8090	5780	10260	4750	8910	3400
LRW	4770	2700	3740	1800	7070	5810	11800	5440	7210	3580
LRN	4200	3130	5100	3910	9340	5950	12120	5000	7970	2170
LR	4490	2920	4420	2860	8210	5880	11960	5220	7590	2870
W	4660	2240	3620	3010	6640	6080	9460	5690	6770	3430
N	4610	3450	4830	4970	8890	6630	11240	5480	9410	2640
SEM	310	510	490	860	1120	1020	1680	670	1090	670
Effect of:										
Treatment	ns	ns	ns	**	ns	ns	ns	*	ns	ns
W vs N	ns	*	**	*	*	ns	ns	ns	**	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

[1] RG = Ryegrass

[2] OG = Other grasses

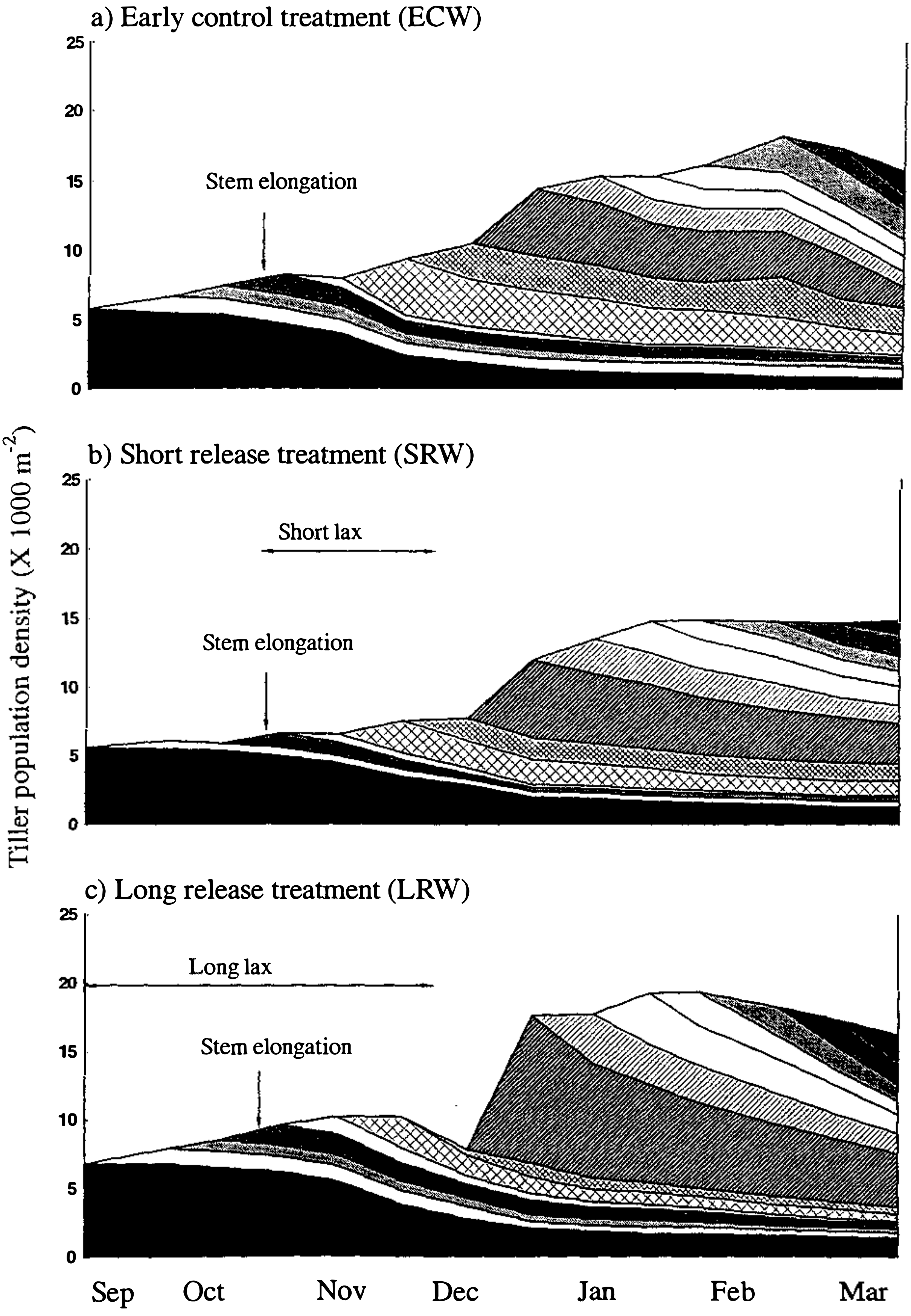


Figure 3.4. Time trends in tiller population density from fixed quadrats for ryegrass-white clover swards under contrasting spring grazing managements. Experiment 1.

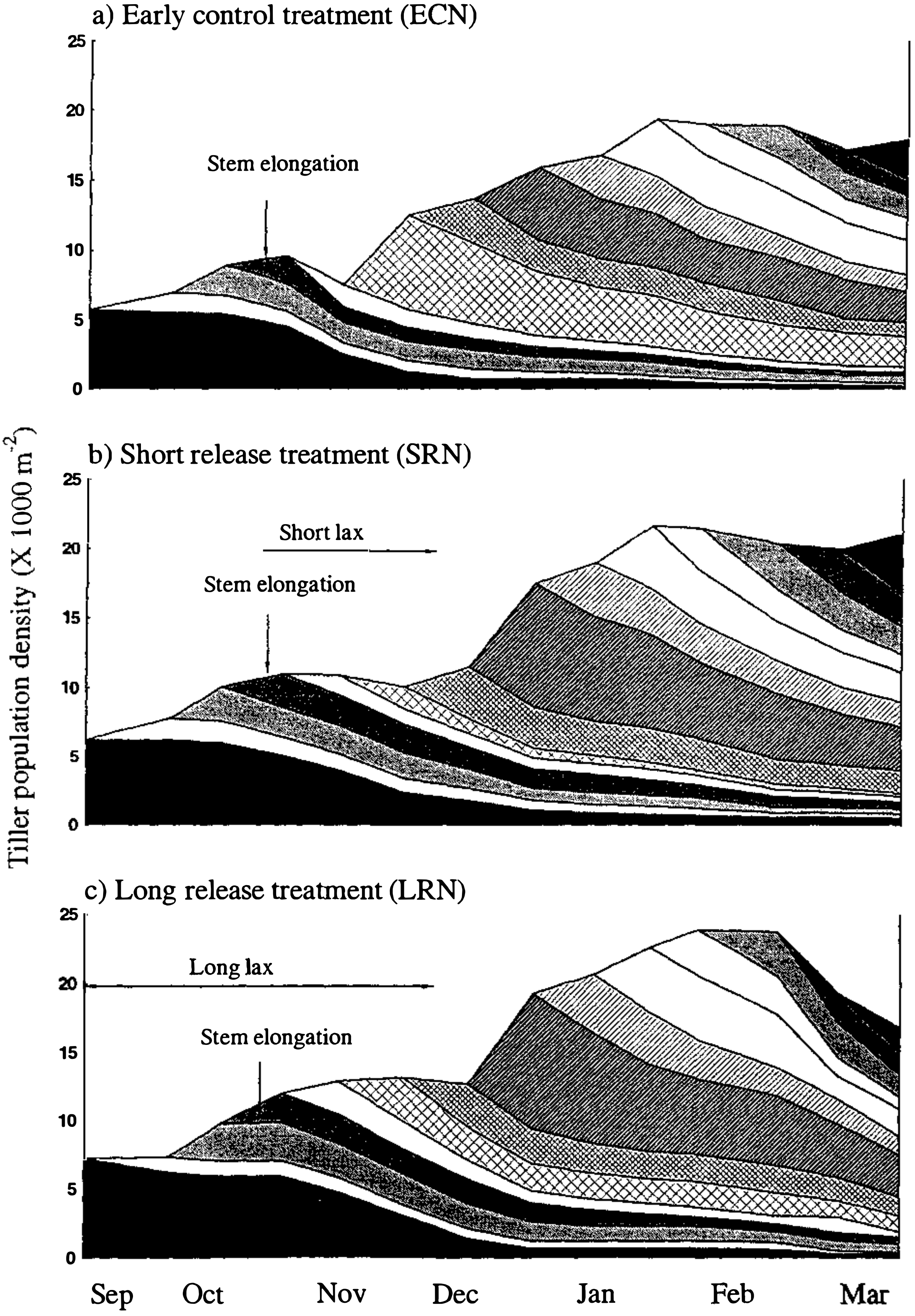


Figure 3.5. Time trends in tiller population density from fixed quadrats for ryegrass swards under contrasting spring grazing managements. Experiment 1.

(6270 and 3500 tillers m^{-2} in fixed quadrats and cores, respectively). This difference persisted throughout the Experimental period (Table 3.4 and Figures 3.4 and 3.5).

Figures 3.4 and 3.5 show an increase in tiller population density from September to February, with high rates of tillering activity late in December and during January, soon after the switch from lax to hard grazing. From 31 November to the peak of tillering activity (31 December) tiller population in fixed quadrats increased 43% in EC and 64% in SR and LR treatments. From February onwards there was a decrease in tiller population density, particularly in LR treatments (Figures 3.4 and 3.5). However, those tillers born late in December in SR and LR treatments comprised a greater proportion of the final tiller population density than the corresponding tillers from EC.

In tiller cores, from 2 December to 28 January tiller population increased 170% in LR treatment, 147% in SR and 115% in EC, respectively (Table 3.4). This increase was slightly greater in white clover swards (162% average across all treatments) than in those with nitrogen (132%). Ryegrass tiller density was generally greater in N than W plots (Figures 3.4 and 3.5 and Table 3.4). At the end of the trial N treatments had 39% more tillers than W treatments ($P \leq 0.01$).

Tiller population of other grasses made a substantial contribution to total tiller population (Table 3.4), especially from early December to the end of January. Other grass tiller densities were slightly higher in the EC than the SR and LR treatments. Moreover, other grasses reached their highest level on 1 January (Table 3.4), and this peak was 27% greater in EC than SR and LR treatments. This effect was significant in early December, but not later.

3.3.5. Tiller appearance and loss

Tiller populations decreased during December in the late reproductive phase (Table 3.4, Figures 3.4 and 3.5), just before the main period of tillering activity. Tiller appearance and loss occurred throughout the trial, but were particularly high from late spring to the middle of summer (Figures 3.4 to 3.7). Figures 3.4 and 3.5 show continuing increase in tiller density in all treatments from September to the end of January, with particularly rapid tillering activity late in December, especially in both SR and LR treatments.

Tiller natality was high in late spring and early summer (Figure 3.6). Tiller appearance rate (tillers 100 tillers^{-1} day^{-1}) in EC, late in November, was 31% and 80% greater than SR and LR ($P \leq 0.01$), respectively, but the difference was reversed ($P \leq 0.05$), in late December. No other treatment differences were significant.

In general, tiller appearance was higher in N than W treatments, but these differences were only statistically significant in the middle of October ($P \leq 0.05$) and at the end of the trial ($P \leq 0.01$).

No statistical differences between treatments were found in tiller death throughout the experiment, but there were seasonal differences common to all treatments, with higher tiller mortality during November and December (Figure 3.7). Treatment EC recorded the highest tiller loss in the middle of November, while on SR and LR swards the highest tiller loss occurred just before and soon after the switch from lax to hard grazing.

Tiller losses expressed as tillers per 100 tillers per day were generally greater in N than W plots, but the differences were only statistically significant on 31 October ($P \leq 0.05$) and 15 November ($P \leq 0.05$).

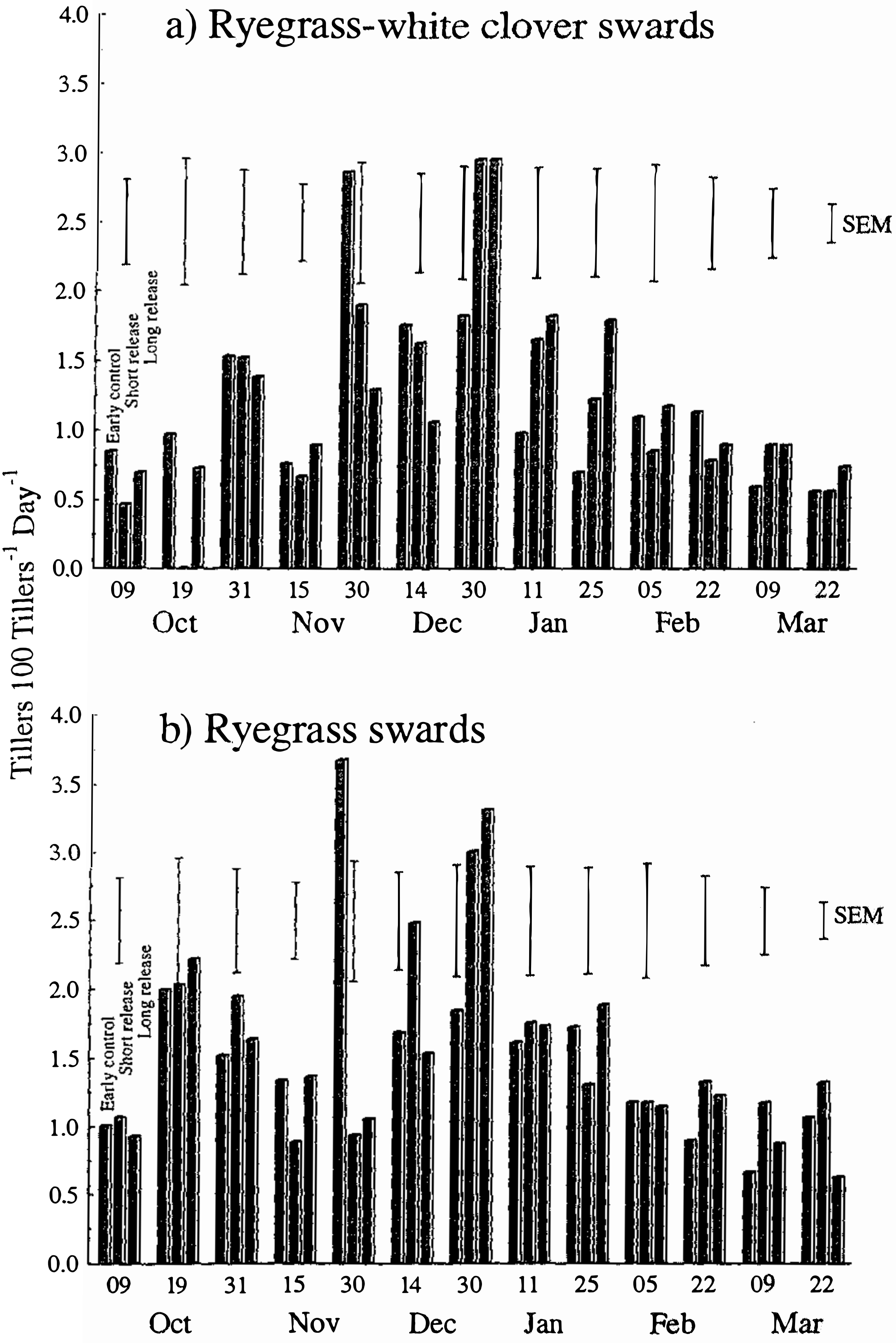


Figure 3.6. Effect of duration of lax spring grazing management on tiller natality of ryegrass-white clover (a) and ryegrass (b) swards. Experiment 1.

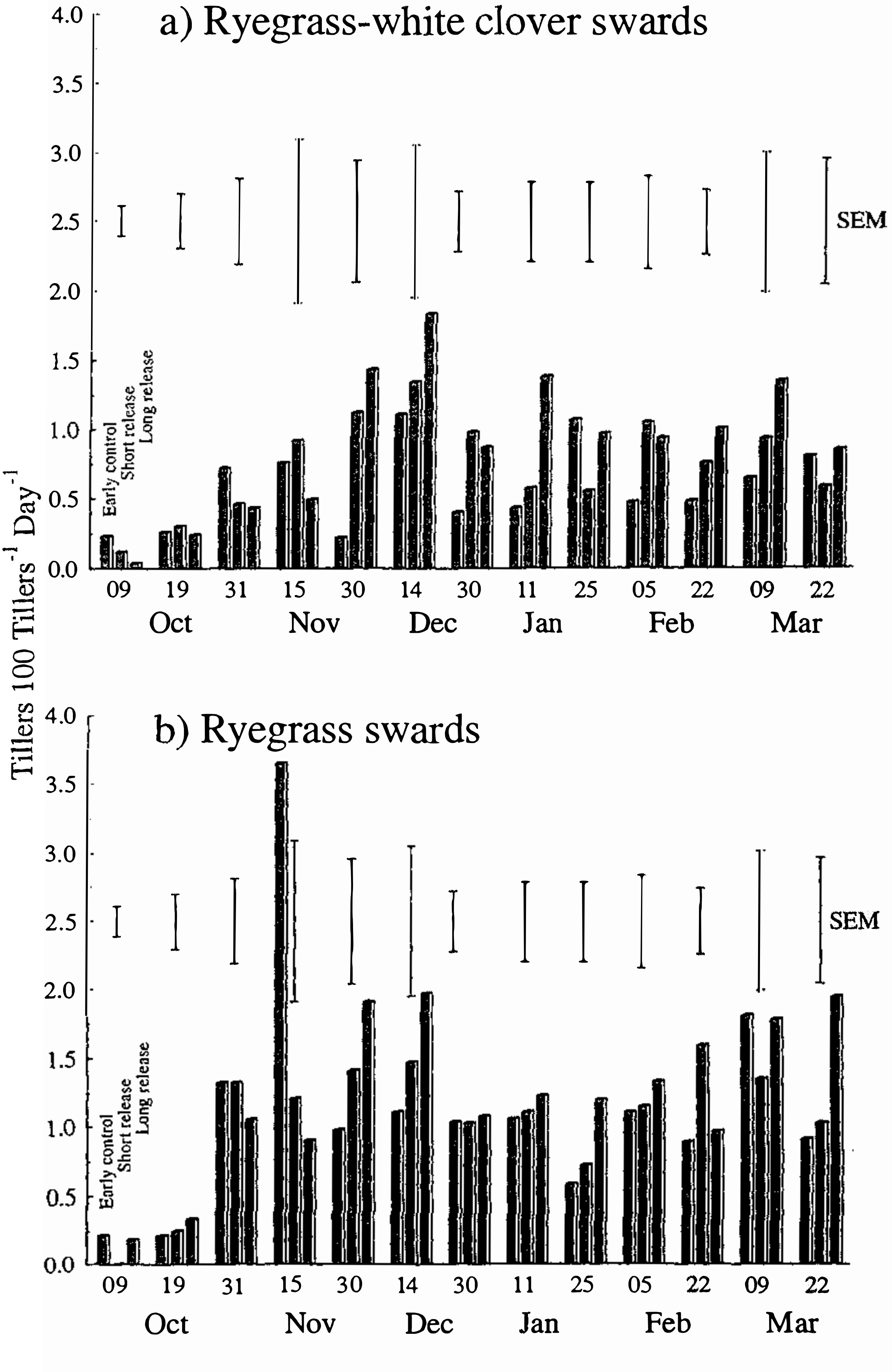


Figure 3.7. Effect of duration of lax spring grazing management on tiller mortality of ryegrass-white clover (a) and ryegrass (b) swards. Experiment 1.

3.3.6. Clover growing points and stolon length

Table 3.5 shows changes in stolon growing point densities (GP) and stolon length (SL) for Experiment 1. During the study period no statistical differences in GP density and SL were found between treatments ($P \geq 0.05$). However, ECW generally had greater GP and SL than LRW and SRW.

3.3.7. Tissue turnover

In this section tissue turnover results are presented separately for each species.

3.3.7.1. Ryegrass tissue turnover

In general, SR and LR treatments affected a number of components of tissue turnover, resulting in substantial increases in net herbage production in December (Table 3.6), January (Table 3.7) and March (Table 3.8).

Soon after decapitation of the reproductive tillers in early December, there was an increase in leaf elongation (mm tiller^{-1} day^{-1}) in all SR and LR treatments ($P \leq 0.05$). Total leaf elongation (mg tiller^{-1} day^{-1}) in SR and LR swards was 41.5 % greater than in EC. As there were no differences in senescence losses, net growth showed the same effects ($P \leq 0.001$). When the tiller population was added to this calculation (Section 3.2.2.5.1), net pasture growth (g m^{-2} day^{-1}) differences were even greater, especially for LR. Table 3.6 also shows interaction and N effects ($P \leq 0.01$) on leaf elongation (mm and mg tiller^{-1} day^{-1}), total elongation (mg tiller^{-1} day^{-1}) and net growth (mg tiller^{-1} day^{-1}), but only N effect ($P \leq 0.01$) in net pasture growth (g m^{-2} day^{-1}). In particular daughter

Table 3.5. Stolon density (growing points m^{-2}, GP) and length (m stolon m^{-2}, SL) in tiller cores from a ryegrass-white clover sward under contrasting spring grazing managements. Experiment 1.

Treatment	20 Oct		2 Dec		1 Jan		28 Jan		23 Mar	
	GP	SL	GP	SL	GP	SL	GP	SL	GP	SL
ECW	820	26.6	3520	33.8	5160	55.8	6520	75.3	6420	56.2
SRW	770	26.4	1610	21.1	3510	32.5	3580	41.2	7110	66.1
LRW	1210	42.0	1670	30.7	2790	30.2	3920	46.5	4530	39.6
SEM^{+}	140	6.7	1480	9.7	780	9.9	1610	17.5	1060	12.3

$^{+}$ = No treatment effects significant ($P > 0.05$)

Table 3.6. Rates of leaf growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 11 Dec-16 Dec-21 Dec. Experiment 1.

	Treatments									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W vs N	Int W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	6.6	10.4	9.5	9.7	9.2	11.0	0.62	*	**	*
Daugh Elon	0.75	1.75	0.27	2.60	2.30	0.00	0.61	ns	ns	**
Senescence	0.39	0.61	0.44	0.29	0.33	0.25	0.21	ns	ns	ns
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.42	0.58	0.66	0.73	0.69	0.75	0.04	***	**	ns
Daugh Elon	0.05	0.10	0.02	0.19	0.17	0.00	0.06	ns	ns	**
Total Elon	0.47	0.68	0.68	0.92	0.87	0.75	0.04	***	**	**
Senescence	0.037	0.055	0.044	0.031	0.034	0.026	0.020	ns	ns	ns
Net Growth	0.432	0.626	0.641	0.894	0.832	0.724	0.040	***	**	**
Tiller Pop^{+}	6990	7000	5840	10330	7070	9340	1120	ns	*	ns
Net Production (g m^{-2} day^{-1})										
	3.12	4.38	3.75	9.29	5.85	6.77	0.99	*	**	ns

$^{+}$ = From Table 3.4.

Table 3.7. Rates of leaf growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 20 Jan-26 Jan-1 Feb. Experiment 1.

	Treatment									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W vs N	Int W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	6.50	9.93	8.12	9.10	8.44	9.76	0.56	ns	**	ns
Daugh Elon	1.65	2.31	2.62	2.48	3.56	2.14	0.89	ns	ns	ns
Senescence	0.38	0.11	0.20	0.25	0.13	0.17	0.09	ns	ns	ns
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.41	0.56	0.57	0.68	0.64	0.67	0.04	**	**	ns
Daugh Elon	0.11	0.13	0.18	0.19	0.27	0.15	0.06	*	ns	ns
Total Elon	0.52	0.69	0.75	0.87	0.90	0.81	0.08	*	ns	ns
Senescence	0.036	0.010	0.020	0.027	0.014	0.018	0.009	ns	ns	ns
Net Growth	0.483	0.679	0.732	0.843	0.890	0.793	0.08	*	ns	ns
Tiller Pop^{+}	7760	9910	8820	11700	11800	12120	1680	ns	*	ns
Net Production (g m^{-2}day^{-1})										
	3.93	6.73	6.28	9.26	11.33	9.67	1.23	**	ns	ns

$^{+}$ = From Table 3.4.

Table 3.8. Rates of leaf growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 17 Mar-23 Mar-27 Mar. Experiment 1.

	Treatment									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W vs N	Int W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	5.28	7.66	5.57	7.21	5.03	7.97	0.50	ns	***	ns
Daugh Elon	0.48	2.44	0.83	3.85	0.34	1.14	0.80	ns	**	ns
Senescence	0.09	0.13	0.14	0.23	0.07	0.05	0.07	ns	ns	ns
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.27	0.50	0.30	0.46	0.33	0.54	0.02	*	***	ns
Daugh Elon	0.02	0.15	0.04	0.24	0.02	0.08	0.05	ns	**	ns
Total Elon	0.29	0.66	0.34	0.71	0.35	0.62	0.06	ns	***	ns
Senescence	0.007	0.011	0.011	0.019	0.006	0.005	0.005	ns	***	ns
Net Growth	0.29	0.65	0.33	0.69	0.34	0.62	0.06	*	ns	ns
Tiller Pop^{+}	5050	10500	8050	9770	7210	7970	1090	ns	**	ns
Net Production (g m^{-2}day^{-1})										
	1.42	7.00	2.58	6.79	2.41	4.89	0.92	ns	***	ns

$^{+}$ = From Table 3.4.

elongation and net growth were greater for SR on N fertiliser plots but were greater for LR on white clover plots.

Although leaf elongation was slightly greater in SR and LR swards, no treatment differences ($P \geq 0.05$) in leaf elongation and senescence (mm tiller^{-1} day^{-1}) were found at the end of January (Table 3.7). Despite differences in leaf elongation being non-significant, a tendency to higher elongation rates, higher specific leaf weight, and the higher tiller density (Table 3.7) combined to give highly significant treatment differences in net pasture growth ($P \leq 0.01$). Treatment LRW produced 80% and 180% more net pasture growth than SRW and ECW, respectively, while SRN and LRN had 38% and 44% respectively, more net pasture growth than ECN. No interaction effects were observed in any of the tissue turnover components in January (Table 3.7).

At the end of the experiment in the second half of March, N treatments produced more herbage ($P \leq 0.001$) than those with white clover (Table 3.8). No interaction effects were observed ($P \geq 0.05$), though statistical differences between SR and LR treatments ($P \leq 0.03$) for leaf elongation and net growth (mg tiller^{-1} day^{-1}) were still evident.

Losses by senescence did not differ statistically ($P \geq 0.05$) between treatments in the 3 periods of study (Tables 3.6 to 3.8). Generally senescence losses in all treatments were less than 25% of gross tissue production.

3.3.7.2. White clover tissue turnover

Overall, treatment did not affect any of the white clover tissue turnover components, resulting in little difference in net clover herbage production during summer and autumn (Tables 3.9, 3.10 and 3.11). Leaf expansion in cm^2 locus^{-1} day^{-1} was slightly higher in SR and LR treatments than ECW in all evaluation periods. This tendency remained when leaf weight was added. A similar tendency was observe with net growth.

Table 3.9. Rates of petiole elongation and leaf growth, senescence and net production of ryegrass-white clover swards under contrasting spring grazing managements: 11 Dec-16 Dec-21 Dec. Experiment 1.

	Treatment				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm $locus^{-1}$ day^{-1}) and leaf growth (cm^2 $locus^{-1}$ day^{-1})					
Petiole Elon	3.45	3.37	3.74	0.34	ns
Petiole Sen	0.34	0.24	0.28	0.15	ns
Leaf Expansion	0.30	0.33	0.39	0.04	ns
Leaf Sen	0.016	0.008	0.00	0.006	ns
White clover petiole elongation and leaf growth (mg $locus^{-1}$ day^{-1})					
Petiole Elon	0.246	0.239	0.286	0.033	ns
Petiole Sen	0.025	0.017	0.021	0.011	ns
Leaf Expansion	1.22	1.40	1.56	0.25	ns
Leaf Sen	0.065	0.029	0.000	0.022	ns
Net Growth	1.38	1.60	1.83	0.028	ns
Growing Points$^+$	5160	3510	2790	780	ns
Net Production (g m^{-2} day^{-1})$^{++}$					
	1.86	1.94	1.81	0.39	ns

$^+$ = From Table 3.5.

$^{++}$ = Adjusted using the number of growing points per locus.

Table 3.10. Rates of petiole elongation and leaf growth, senescence and net production of ryegrass-white clover swards under contrasting spring grazing managements: 20 Jan-26 Jan-1 Feb. Experiment 1.

	Treatments				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm locus^{-1} day^{-1}) and leaf growth (cm^{2} locus^{-1} day^{-1})					
Petiole Elon	3.00	3.35	3.82	0.18	ns
Petiole Sen	0.23	0.11	0.19	0.077	ns
Leaf Expansion	0.21	0.26	0.27	0.043	ns
Leaf Sen	0.001	0.000	0.010	0.003	ns
White clover petiole elongation and leaf growth (mg locus^{-1} day^{-1})					
Petiole Elon	0.098	0.125	0.126	0.006	*
Petiole Sen	0.008	0.004	0.007	0.003	ns
Leaf Expansion	1.12	1.38	1.34	0.18	ns
Leaf Sen	0.007	0.000	0.053	0.019	ns
Net Growth	1.20	1.50	1.41	0.174	ns
Growing Points^{+}	6520	3580	3920	1610	ns
Net Production (g m^{-2} day^{-1})$^{++}$	2.60	1.68	2.04	0.89	ns

$^{+}$ = From Table 3.5.

$^{++}$ = Adjusted using the number of growing points per locus.

Table 3.11. Rates of petiole elongation and leaf growth, senescence and net production of ryegrass-white clover swards under contrasting spring grazing managements: 17 Mar-22 Mar-27 Mar. Experiment 1.

	Treatments				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm $locus^{-1}$ day^{-1}) and leaf growth (cm^{-2} $locus^{-1}$ day^{-1})					
Petiole Elon	1.86	2.04	2.11	0.11	ns
Leaf Expansion	0.105	0.124	0.116	0.009	ns
Leaf Sen	0.003	0.001	0.000	0.0004	*
White clover petiole elongation and leaf growth (mg $locus^{-1}$ day^{-1})					
Petiole Elon	0.092	0.097	0.100	0.007	ns
Leaf Expansion	0.472	0.603	0.662	0.049	ns
Leaf Sen	0.015	0.005	0.000	0.002	*
Net Growth	0.550	0.695	0.762	0.052	ns
Growing Points^{+}	6420	7110	4530	1060	ns
Net Production (g m^{-2} day^{-1})$^{++}$					
	1.04	1.60	1.12	0.18	ns

$^{+}$ = From Table 3.5.
$^{++}$ = Adjusted using the number of growing points per locus.

However, due to the number of growing points m^{-2} always being greater in ECW ($P \geq 0.05$), the net production (g DM m^{-2} day^{-1}) reflected this tendency (Tables 3.9 to 3.11).

3.3.8. Sward structure

The spatial distribution of the sward components before the control grazing in December differed according to the management (Figures 3.8 and 3.9). Thus, before the switch from lax to hard grazing (late November), all components in EC swards occurred below 15 cm, with more than 80% of the total contacts within the first 5 cm layer. By comparison in the SR treatment foliage was distributed over a greater range: around 75% of the contacts were below 10 cm, but there were contacts above 30 cm. All sward components in LR occurred in a greater range than EC and SR (Figure 3.8).

Ryegrass leaf accounted for the highest number of contacts and was found predominantly from the 3 cm layer upwards in SR and LR treatments, but in EC it was present below 2 cm (0-1 cm). Early control presented more other grass leaf and stem than SR and LR treatments, especially in the lowest 4 cm.

White clover leaf and petiole were greater in SRW and LRW treatments than ECW. Petiole was found mainly in the first cm layer in ECW, while in SR and LR treatments it was found between 0 and 2 cm. LRW had a higher leaf component than ECW and SRW, and clover leaves were found in all layers between 0 and 12 cm. In SRW and ECW, however, they were recorded only below 9 cm and 6 cm, respectively. White clover stolon occurred in the 0-4 cm layer and was more frequent in EC than SR and LR treatments.

Dead material comprised 9% of the total contacts in EC and was mainly found above 2 cm from ground level, whereas SR and LR swards had 10.6% and 10.9%, respectively, distributed in the first 4 cm.

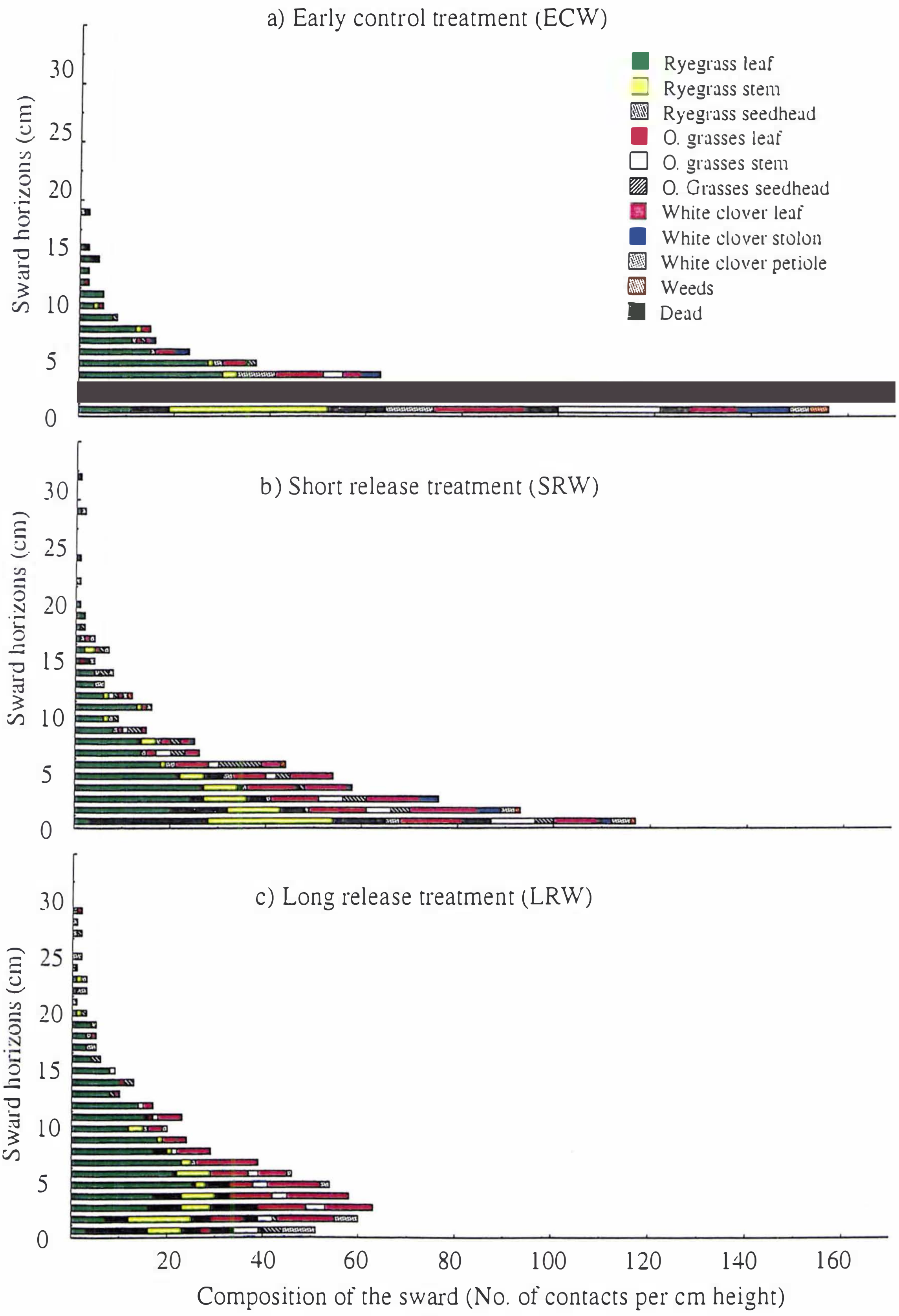


Figure 3.8. Effect of duration of lax spring grazing management on structure of ryegrass-white clover swards (Compiled from 600 contacts per treatment). Experiment 1. Dead fraction graphed separately for each sward component.

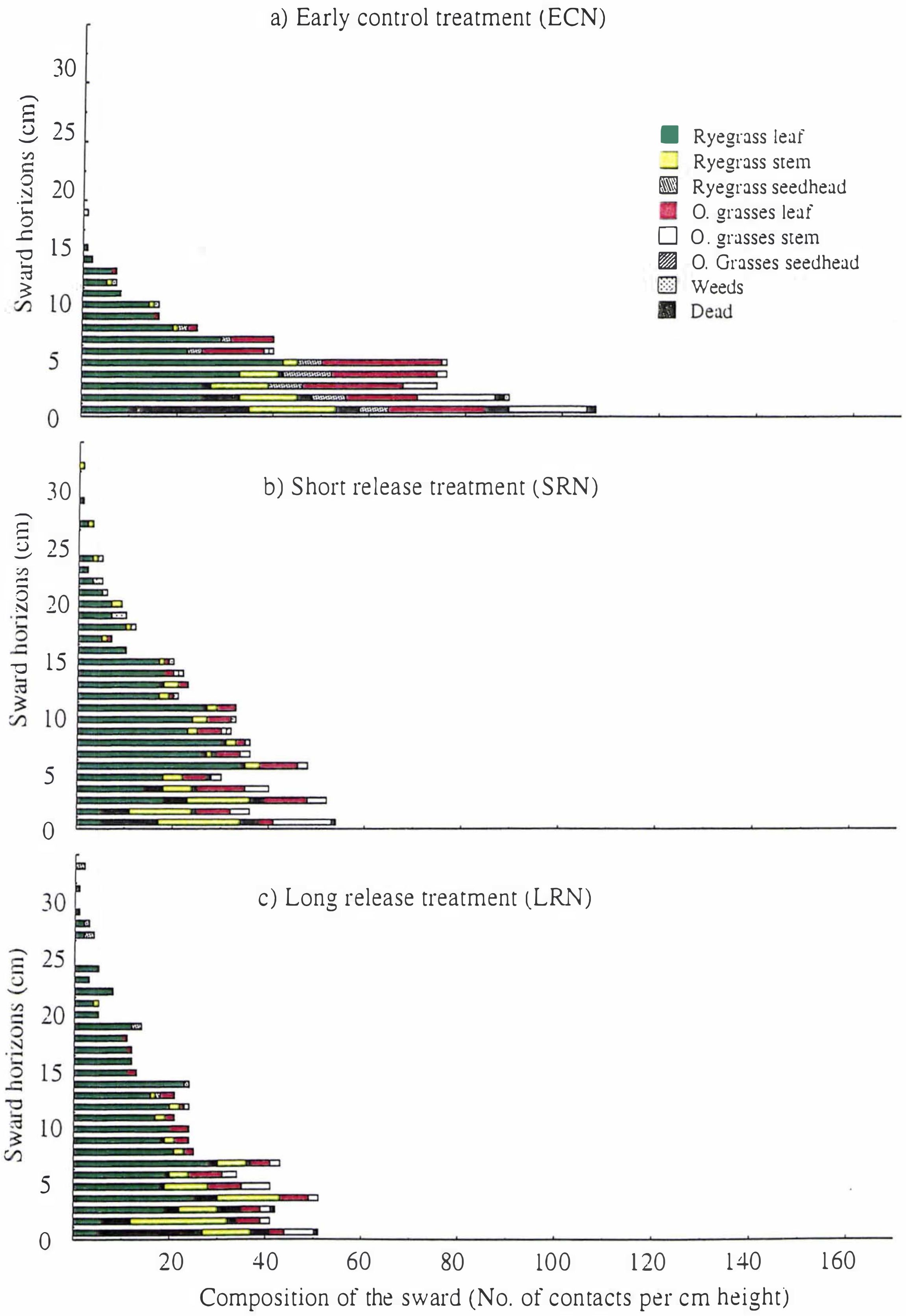


Figure 3.9. Effect of duration of lax spring grazing management on structure of rygrass swards (Compiled from 600 contacts per treatment). Experiment 1. Dead fraction graphed separately for each sward component.

3.3.9. Determination of herbage production in summer and autumn

It is of interest to have an overview of how variables related to each other. In particular it would be of interest to examine the link between tiller dynamics (patterns of tiller birth and death) and herbage production, and also to deal with the relationship between pre-grazing sward height, tiller size and tiller population density and pasture production during summer and autumn. To this end an index of sward productivity, named size/density compensation index (SDCI) was generated and, also, a canonical discriminant analysis (CDA) was carried out.

3.3.9.1. Environmental potential tiller density

It is recognised that tiller population density and tiller size should not be considered in isolation, but are interrelated. A recent theoretical treatment of tiller size/density compensation (SDC) has suggested that the -3/2 self-thinning line (Sackville Hamilton *et al.*, 1995; Matthew *et al.*, 1995) represents the environmental potential tiller density for a particular environment, and that the -3/2 self-thinning line is determined by maximum canopy leaf area sustainable in the environment. This hypothesis is highly relevant to the current experiment where it is clearly of interest to compare tiller densities for particular treatments with the environmental potential. This hypothesis was tested in both Experiments by treating $\log_{10}$ tiller density (tillers m^{-2}) and $\log_{10}$ tiller size (kg) data for individual swards as X, Y coordinates respectively, and calculating the vertical distance (in $\log_{10}$ units) of particular swards from an arbitrarily positioned self-thinning line of slope -3/2 and intercept 1.3. This distance was designated as size/density compensation index (SDCI). The rationale for the SDCI is that since the -3/2 line represents a possible combination of tiller size and density at constant environmental potential leaf area, then distance from this SDC line is a measure of the extent to which tiller density of a sward has reached (or exceeded) the potential for that environment.

The possibility that the SDCI might be useful as a measure of tiller density limitation of sward productivity is addressed in the discussion section.

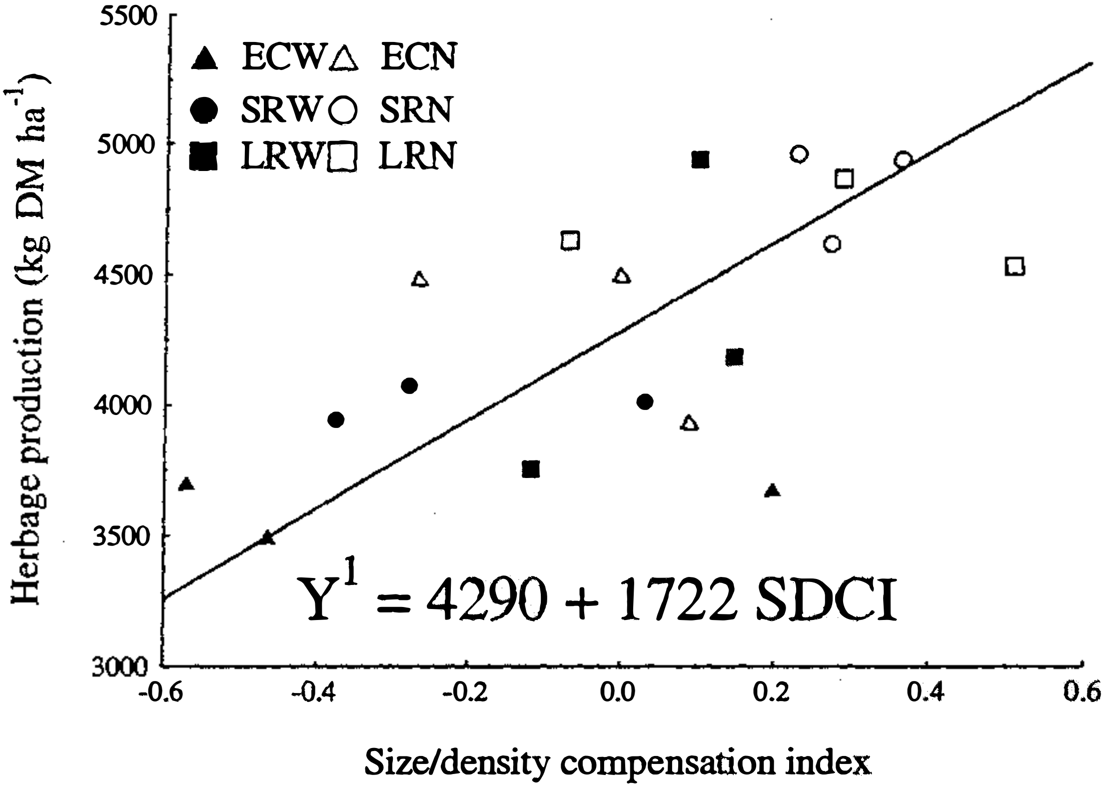
3.3.9.2. Relationship of herbage productivity and size/density compensation index (SDCI)

Size/density compensation index was estimated using $\log_{10}$ tiller density and $\log_{10}$ tiller size data averaged from January and February for individual swards as X, Y coordinates, respectively, and calculating the vertical distance (in $\log_{10}$ units) of individual plots from an arbitrarily positioned self thinning line. It is clear that tiller populations are subject to size/density compensation, and it is generally believed that size/density compensation largely negates any potential advantages from manipulating tiller density. The results indicate that manipulation of tiller SDCI, as distinct from manipulation of tiller density *per se*, affected herbage production (Figure 3.10). Whether plotted on an individual plot basis or a treatment mean basis, there was a positive correlation between SDCI and herbage production (Figures 3.10a and 3.10b). White clover treatments are closer to the origin, whereas N treatments are further from it. Also, LRW was greater than SRW and ECW ($P \leq 0.05$), and LRN was greater than SRN and ECN, respectively ($P \leq 0.05$).

3.3.9.3. Canonical discriminant analysis of herbage production

Canonical discriminant analysis is a multivariate statistical technique, used to maximise the correlation between two sets of variables, generating linear combinations that discriminate between groups of individuals. CDA is one way to explore the relationships between the several variables measured in this experiment. Variables entered into the analysis were: (i) herbage production (23 December onwards); (ii) tiller mortality (15 Nov and 15 Dec); (iii) tiller natality (30 Nov and 30 Dec) (iv) tiller population (28 Jan

a) Using all replicates individually



b) Using treatment means

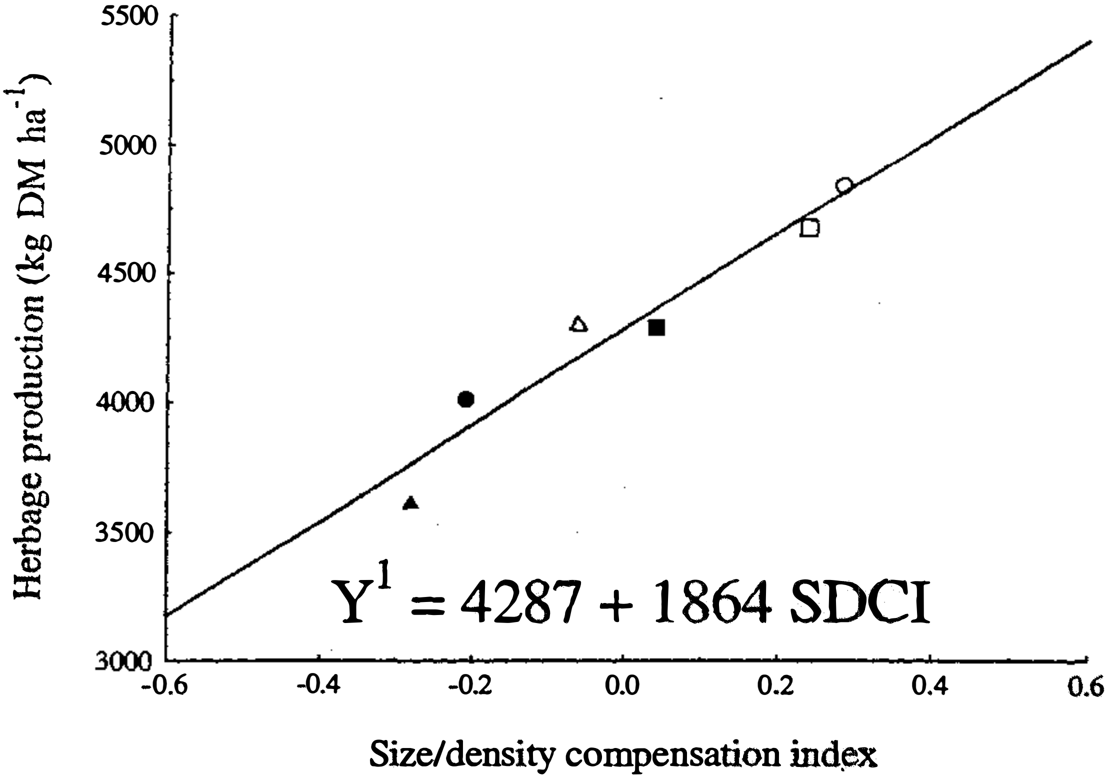


Figure 3.10. Relationship between post-control sward productio (January-March) and size/density compensation inde (SDCI). Experiment 1.

[1] Calculated by reduced main axis regression (RMA, LaBarbara, 1989

and 29 March) (Table 3.12). The canonical structure for the first discriminant function (DF) indicates that high herbage production is associated with high tiller turnover in December (high tiller natality and mortality on 30 December and on 15 December, respectively) rather than November, and with high tiller population density from January-March ($P \leq 0.02$). The first discriminant function accounted for 96% of the multivariate dispersion (Table 3.12).

Table 3.12. Canonical structure and summary statistics for first discriminant factor for multiple discriminant analysis of herbage production (23 Dec 1992 to 29 Mar 1993) and associated tiller demography measurements. Experiment 1.

Variables	Discriminant 1
Herbage Production	-0.9969
Tiller Mortality 15 Nov	0.9834
Tiller Mortality 15 Dec	-0.7385
Tiller Natality 30 Nov	0.9758
Tiller Nat 30 Dec	-0.9288
Tiller Pop 28 Jan	-0.8963
Tiller Pop 29 Mar	-0.2120
Canonical r^2	0.968
P	< 0.02
Proportion of Disc (%)	0.9598

3.4. EXPERIMENT 2 - RESULTS

3.4.1. Herbage accumulation

Details of the estimates of herbage accumulation between sample dates using the rising plate meter are shown in Table 3.13. Total herbage accumulation was 25% and 18% lower in EC than LR and SR, respectively ($P \leq 0.0001$). Grazing management produced seasonal effects on herbage production. During the pre-control period EC accumulated 28% and 24% less herbage mass than LR and SR ($P \leq 0.0001$), respectively. No differences were recorded in the control phase, but EC maintained these differences ($P \leq 0.0001$) in the post-control period (EC produced 25% and 18% less DM than LR and SR, respectively). Total herbage accumulation was higher ($P \leq 0.0001$) in N swards than W swards. This trend was found in all periods of the study ($P \leq 0.05$).

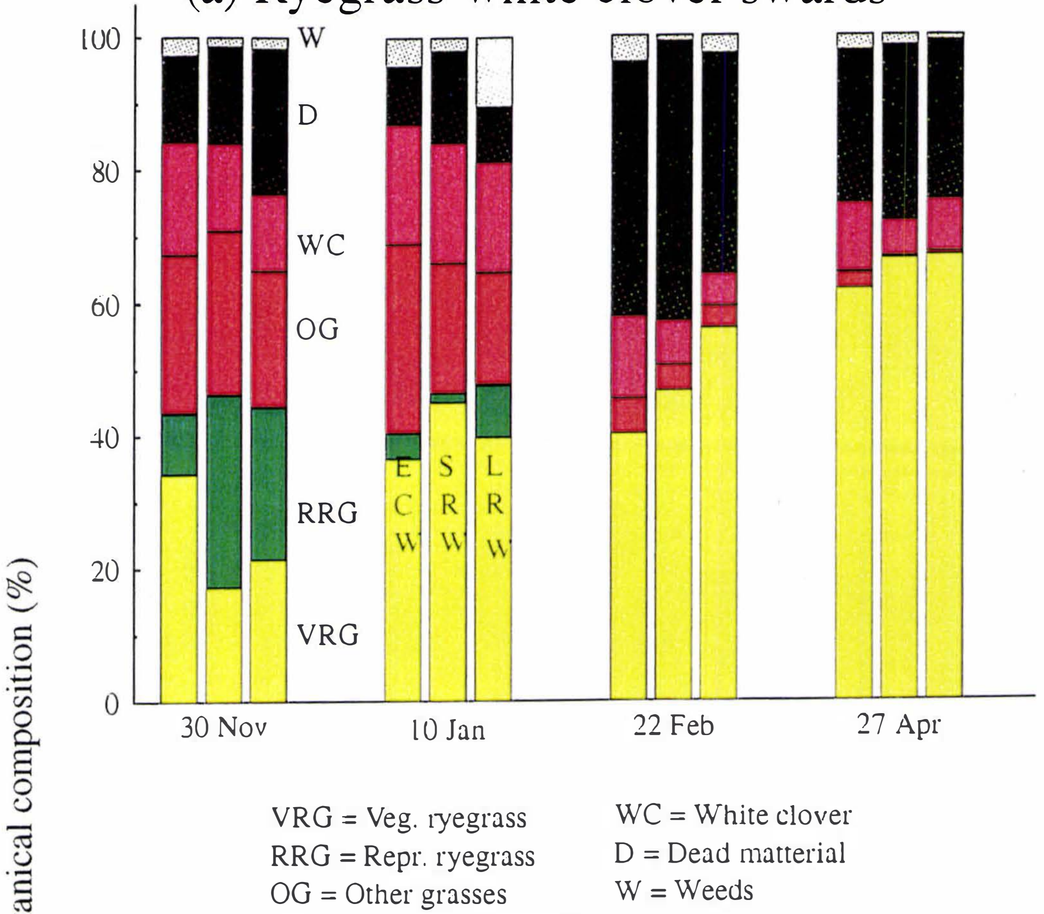
3.4.2. Botanical composition

Botanical composition was determined four times during the Experimental period. Herbage mass botanical analysis in late spring showed that around 50% of the ryegrass in SR and LR treatments came from reproductive tillers, while in ECW this proportion was less than 20% (Figure 3.11a). The ECW treatment also had slightly more white clover, weeds and other grasses than SR and LR treatments, while the LRW treatment presented the greatest amount of dead material. From January on, the ECW treatment had more other grasses and white clover, and less ryegrass, than SR and LR treatments. On 22 February ryegrass contribution to the sward was 16% and 10% higher in LRW than ECW ($P \leq 0.03$) and SRW ($P = 0.06$), respectively. The difference between SRW and ECW had almost disappeared at the end of April, but remained 5 % higher for LRW than ECW (Appendices 3.5 to 3.7).

Table 3.13. Herbage accumulation (kg DM ha^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements (Rising plate meter determinations). Experiment 2.

Treatment	8 Sep-31 Nov	3 Dec-21 Dec	23 Dec-27 Apr	Total
	Pre-control	Control	Post-control	
ECW	3060	500	3510	7070
ECN	3830	610	3820	8270
EC	3450	570	3660	7670
SRW	3680	480	4030	8190
SRN	4890	610	4440	9940
SR	4290	540	4240	9060
LRW	3850	470	4560	8870
LRN	5000	680	4670	10350
LR	4420	570	4610	9610
W	3530	480	4030	8040
N	5570	630	4310	9520
SEM	140	30	170	280
Effect of:				
Treatment	***	ns	***	***
W vs N	***	***	*	***
Interaction	ns	ns	ns	ns

(a) Ryegrass-white clover swards



(b) Ryegrass swards

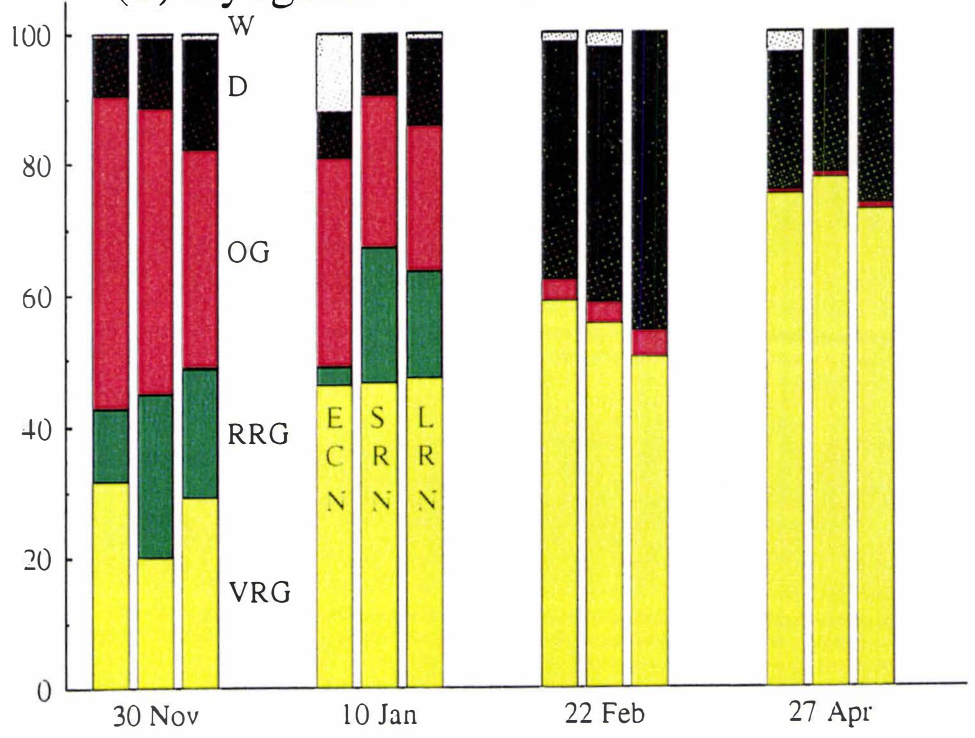


Figure 3.11. Effect of duration of lax spring grazing management on botanical composition (% dry weight) of ryegrass-white clover (a) and ryegrass (b) swards. Experiment 2.

The relative proportions of leaf and stem in ryegrass and other grasses and leaf and stolon in white clover throughout the Experimental period are shown in Table 3.14. Other grasses stem was generally greater in EC than SR and LR treatments. Also, ECW showed less leaf and more stolon than SRW and LRW treatments, especially soon after the switch from lax to hard grazing.

Herbage mass botanical composition in ryegrass swards with nitrogen is shown in Figure 3.11b. Before the switch from lax to hard grazing management in late November, the vegetative tiller component of herbage mass was higher in ECN than SRN and LRN treatments. The opposite was the case with the reproductive tiller component of herbage mass. From November to January the contribution of ryegrass to production was greater in SRN and LRN treatments than ECN, but these differences disappeared from February onwards (Figure 3.11b). During summer ECN had more other grasses, weeds and less dead material than SRN and LRN treatments, but there were no differences in botanical composition during autumn between treatments (Figure 3.11b).

3.4.3. Tiller weight

The dry weights of vegetative and reproductive tillers were recorded before the switch from lax to hard grazing in early December (Table 3.15). There were no differences between treatments in vegetative and reproductive flag leaf tiller weight ($P \geq 0.05$). However, the weights of those reproductive tillers which had already produced seedhead were higher ($P \leq 0.001$) in SR and LR treatments than in EC (Table 3.15). In ryegrass swards, although there were only statistically significant differences in tiller weight at the end of the trial ($P \leq 0.05$), SR and LR treatments tillers were always heavier than ECN (Table 3.16).

During early summer, in ryegrass-white clover swards, tiller weight was not statistically different between treatments. However in late summer-autumn, tillers in SRW and LRW

Table 3.14. Relative proportion (%) of leaf and stem in grasses, and leaf and stolon in white clover throughout the trial period of ryegrass-white clover and ryegrass swards. Experiment 2.

Treatment	Ryegrass		Other grasses		White clover	
	Leaf	Stem	Leaf	Stem	Leaf	Stolon
			1 December			
ECW	61	39	29	71	85	15
ECN	59	41	32	68		
SRW	30	70	46	54	89	11
SRN	34	66	59	41		
LRW	36	64	66	34	92	8
LRN	46	54	48	52		
			11 January			
ECW	72	28	32	68	72	28
ECN	70	30	33	67		
SRW	75	25	25	75	91	9
SRN	52	48	39	61		
LRW	65	35	33	67	93	7
LRN	61	39	27	73		
			22 February			
ECW	71	29	65	35	63	37
ECN	75	25	64	36		
SRW	72	28	52	48	75	25
SRN	73	27	59	41		
LRW	74	26	60	40	71	28
LRN	75	25	63	37		
			29 April			
ECW	72	28	49	51	48	52
ECN	74	26	57	43		
SRW	69	31	53	47	52	48
SRN	71	29	69	31		
LRW	66	34	41	59	59	41
LRN	71	29	31	69		

Table 3.15. Ryegrass vegetative and reproductive tiller dry weights (mg) before the switch from lax to hard grazing on 1 December. Experiment 2.

		Vegetative	Reproductive	
			Flag leaf	Seedhead
Treatment	ECW	17.5	35.8	24.5
	ECN	20.1	33.2	31.8
	EC	18.8	34.5	28.15
	SRW	17.9	46.5	68.2
	SRN	24.5	35.6	72.0
	SR	21.2	41.05	70.1
	LRW	17.6	34.5	55.9
	LRN	22.9	36.6	60.5
	LR	20.25	35.55	58.2
	W	17.7	38.9	49.5
	N	22.5	35.1	54.8
SEM		1.6	9.0	6.0
Effect of:	Treatment	ns	ns	***
	W vs N	*	ns	ns
	Interaction	ns	ns	ns

Table 3.16. Effect of grazing treatment on mean ryegrass tiller dry weight (mg) of ryegrass-white clover swards. Experiment 2.

		1 Dec	11 Jan	22 Feb	29 Apr
Treatment	ECW	17.5	20.8	11.1	8.7
	ECN	20.1	18.4	11.8	10.1
	EC	18.8	19.6	11.45	9.4
	SRW	17.9	18.3	11.8	10.0
	SRN	24.5	20.5	12.7	11.8
	SR	21.2	19.4	12.25	10.9
	LRW	17.6	19.7	13.8	9.8
	LRN	22.9	20.8	13.8	11.0
	LR	20.25	20.25	13.8	10.4
	W	17.7	19.6	12.2	9.5
	N	22.5	19.9	12.8	11
SEM		1.6	1.6	1.0	0.6
Effect of:	Treatment	ns	ns	*	*
	W vs N	**	ns	ns	**
	Interaction	ns	ns	ns	ns

treatments were slightly heavier than ECW (Table 3.16). Furthermore, in February LRW tillers were 17% and 25% heavier than SRW and ECW, respectively, but at the end of the trial this difference had already disappeared with SRW and it was only 13% with ECW.

3.4.4. Tiller population density

Figures 3.12 and 3.13 show fixed quadrat data while Table 3.17 shows tiller core data. The initial ryegrass tiller population density, estimated from random tiller core samples over all treatments, was around 6500 tillers m^{-2}. Tiller populations decreased during the reproductive phase (Table 3.17), and this loss was slightly greater in the SR and LR treatments to the end of November ($P \geq 0.05$). Soon after the switch from lax to hard grazing in SR and LR treatments there was a large increase in tillering activity. From 29 November to 10 January tiller population increased 97% in LR treatments, 95% in SRW and 126% in SRN, but only 25% and 48% in ECW and ECN, respectively (Table 3.17). These differences persisted until the end of the trial and were highly significant ($P \leq 0.01$).

Tiller population density in the fixed quadrats was also higher in SR and LR treatments than in EC from late December onwards, and this difference persisted throughout the trial (Figures 3.12 and 3.13). From January onwards those tillers appearing at the peak of tillering activity (late December) comprised a higher percentage of the total population in SR and LR treatments than in EC.

Figures 3.12 and 3.13 and Table 3.17 show a second peak of tiller appearance late in March, but, this peak was less pronounced than that in December. Ryegrass tiller density was generally higher in N than W treatments, though the difference was not always significant (Figures 3.12 and 3.13 and Table 3.17).

Table 3.17. Tiller population density (tillers m^{-2} from tiller cores) of perennial ryegrass and other grasses growing either with white clover or fertiliser nitrogen under contrasting spring grazing managements. Experiment 2.

Treatment	7 Sep		29 Nov		10 Jan		22 Feb		29 Apr	
	RG[1]	OG[2]	RG	OG	RG	OG	RG	OG	RG	OG
ECW	6400	5610	5430	6170	6790	5580	8660	1260	11020	1250
ECN	7240	3380	5670	10120	8406	7080	10050	1280	13490	960
EC	6820	4490	5550	8150	7600	6330	9360	1270	12250	1100
SRW	6300	5170	4990	4830	9380	4710	11120	1220	13370	680
SRN	6600	4010	4840	8870	10910	6790	11410	1080	15540	870
SR	6450	4590	4910	6850	10150	5750	11270	1150	14460	770
LRW	6650	4270	4830	4610	9500	5200	11220	1550	12470	1240
LRN	6110	4900	5190	9450	10140	6210	11570	1410	14400	1330
LR	6330	4590	5010	7030	9820	5700	11400	1480	13440	1280
W	6410	5020	5430	5200	8560	5160	10340	1340	12290	1060
N	6640	4090	5670	9480	9820	6700	11010	1260	14480	1050
SEM	950	930	370	520	660	670	600	280	590	370
Effect of:										
Treatment	ns	ns	ns	*	*	ns	**	ns	**	ns
W vs N	ns	ns	ns	***	**	**	ns	ns	***	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

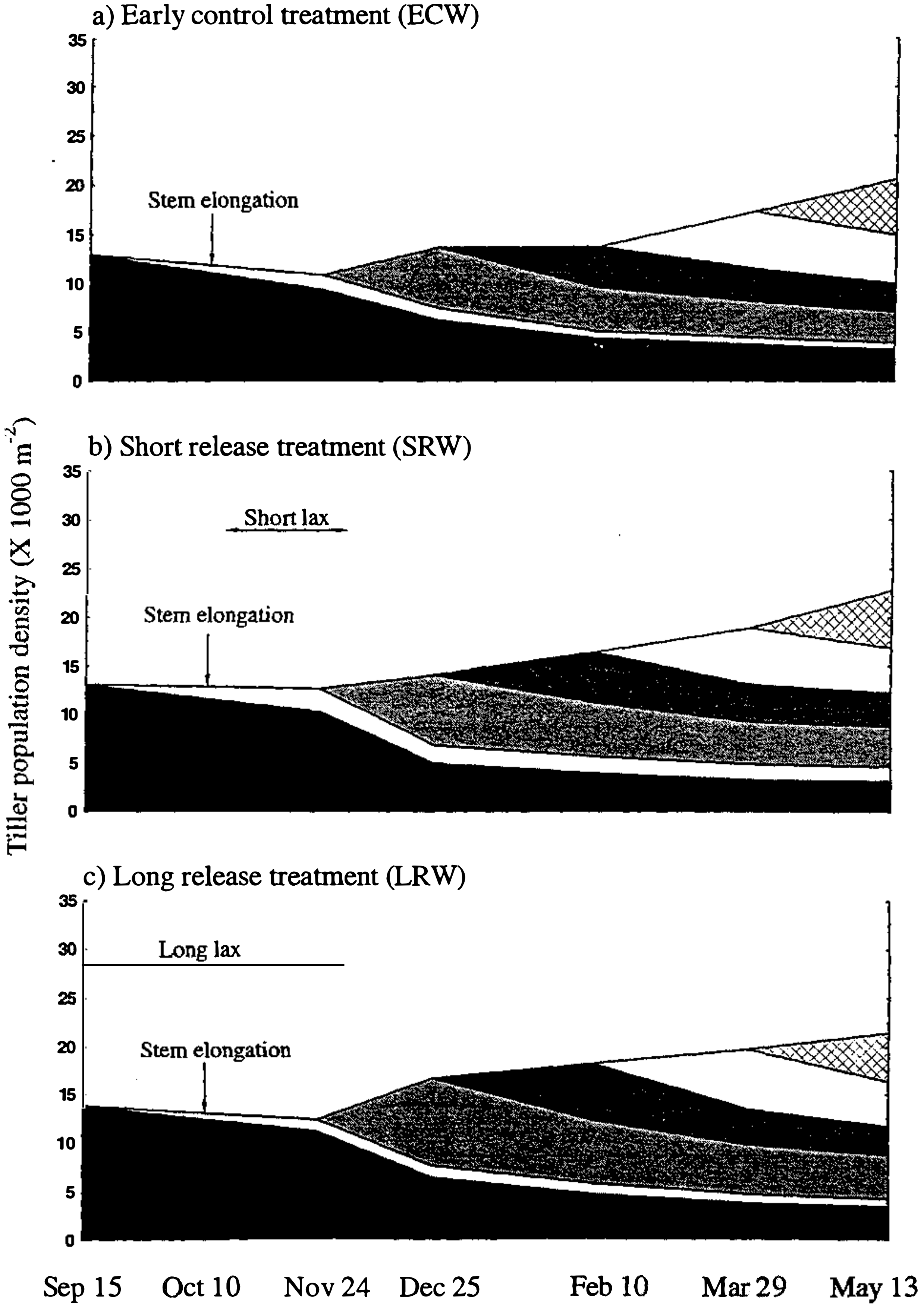
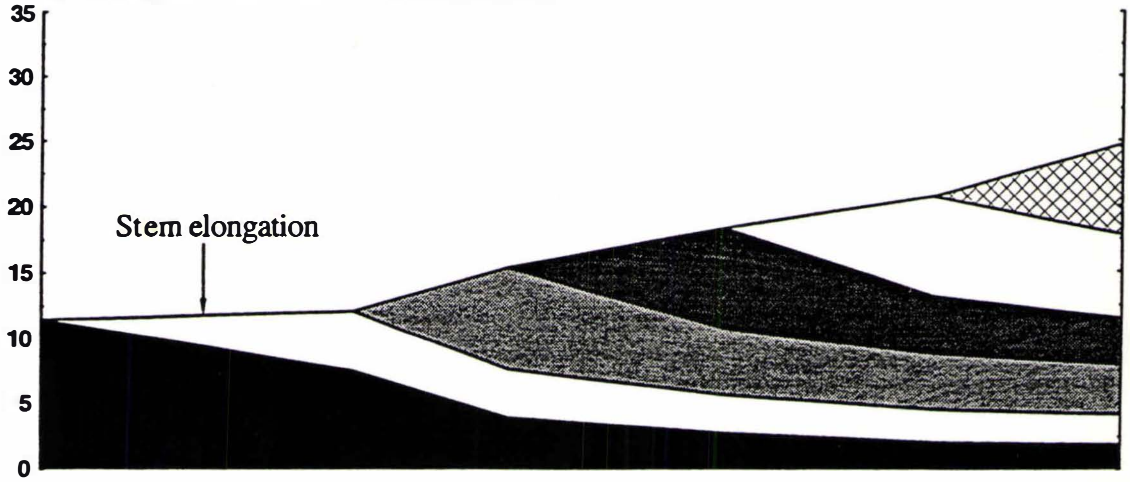
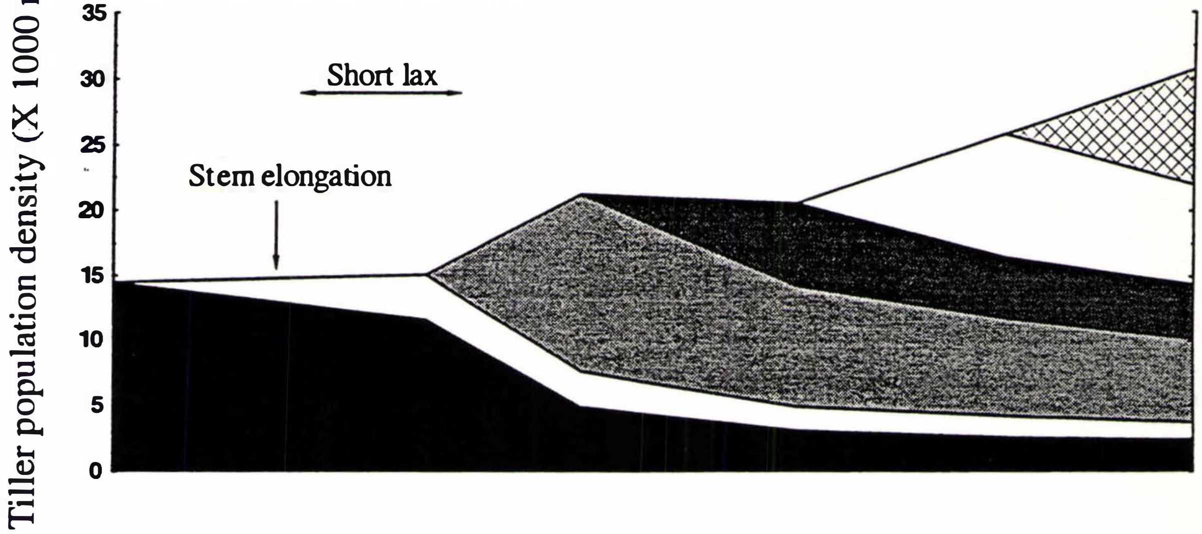


Figure 3.12. Time trends in tiller population density from fixed quadrats for ryegrass-white clover swards under contrasting spring grazing managements. Experiment 2.

a) Early control treatment (ECN)



b) Short release treatment (SRN)



c) Long release treatment (LRN)

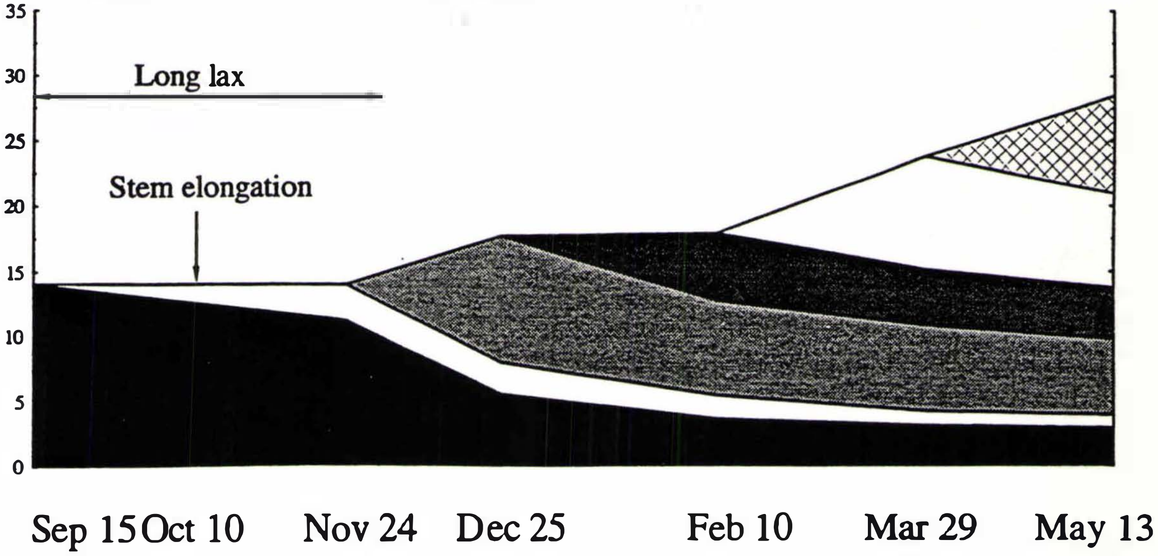


Figure 3.13. Time trends in tiller population density from fixed quadrats for ryegrass swards under contrasting spring grazing managements. Experiment 2.

From September to February tiller populations of other grasses made a substantial contribution to pasture production (Table 3.17). However, from March onwards their population was less than 10% of the total tiller population. Moreover, other grass reached their highest level before the switch from lax to hard grazing (Table 3.17). Other grasses tiller density was slightly higher in the EC than the SR and LR treatments, and was almost twice as great in ryegrass swards with nitrogen as in those with white clover ($P \leq 0.01$).

The results from Table 3.18 indicated that clump populations and plastic frame estimates exceeded the random population estimates by around 200% and 92%, respectively.

3.4.5. Tiller appearance and loss

Before the switch from lax to hard grazing (reproductive phase) tiller natality in N treatments was greater than in those with white clover ($P \leq 0.01$). No other statistical differences between N and W were observed, although tiller appearance was slightly greater in N treatments (Table 3.19).

During the reproductive phase the rate of tiller appearance was similar in all white clover treatments ($P \geq 0.05$). However, the ECN treatment presented a higher relative tiller appearance rate than LRN ($P \leq 0.03$) and SRN ($P = 0.09$), respectively (Table 3.19). The switch from lax to hard grazing in December resulted in a peak of tiller appearance, 23% greater in SR and LR treatments than EC ($P = 0.07$).

Stem elongation started in early October in all treatments (Figures 3.12 and 3.13). Tiller loss was greater in EC than SR and LR, late in November ($P \leq 0.05$), but the opposite was the case soon after decapitation of the reproductive tillers, late in December ($P \leq 0.05$). Furthermore, all treatments showed their highest tiller losses in December. No other statistical differences were observed. Although tiller mortality was slightly higher

Table 3.18. Tiller population density (tillers m^{-2}) from tiller cores, plastic frames and clumps at the end of the experimental period. Experiment 2.

Treatment	Tiller cores	Plastic frames	Clumps
ECW	11020	20560	39940
ECN	13490	24740	40150
EC	12250	22650	40040
SRW	13370	22830	46260
SRN	15540	30630	40930
SR	14460	26730	43590
LRW	12470	21560	41410
LRN	14400	28520	36210
LR	13440	25040	38810
W	12290	21650	42540
N	14480	29960	39100
SEM	370	2110	1560
Effect of:			
Treatment	**	ns	*
W vs N	***	***	*
Interaction	ns	ns	ns

Table 3.19. Tiller appearance and mortality under contrasting spring grazing managements (tillers 100 tillers^{-1} day^{-1}). Experiment 2.

Treatment	24 Nov		25 Dec		10 Feb		29 Mar		13 May	
	App	Loss	App	Loss	App	Loss	App	Loss	App	Loss
ECW	0.18	0.40	1.79	1.04	0.63	0.63	0.96	0.38	0.76	0.30
ECN	0.61	0.53	2.11	1.29	0.73	0.61	1.01	0.40	0.80	0.28
EC	0.40	0.47	1.95	1.17	0.68	0.62	0.99	0.39	0.78	0.29
SRW	0.32	0.34	1.83	1.49	0.81	0.44	0.72	0.42	0.73	0.24
SRN	0.38	0.30	2.94	1.60	0.63	0.71	0.94	0.41	0.74	0.33
SR	0.35	0.32	2.39	1.55	0.72	0.58	0.83	0.42	0.74	0.29
LRW	0.14	0.31	2.49	1.23	0.75	0.55	0.73	0.55	0.58	0.36
LRN	0.30	0.31	2.29	1.40	0.6	0.62	1.03	0.32	0.74	0.27
LR	0.22	0.31	2.39	1.32	0.68	0.59	0.88	0.44	0.66	0.32
W	0.22	0.35	2.04	1.25	0.73	0.54	0.80	0.45	0.69	0.30
N	0.43	0.38	2.45	1.43	0.65	0.65	0.99	0.38	0.76	0.29
SEM	0.94	0.06	0.26	0.12	0.09	0.07	0.14	0.07	0.09	0.07
Effect of:										
Treatment	ns	*	ns	*	ns	ns	ns	ns	ns	ns
W vs N	**	ns	ns	ns	ns	ns	ns	ns	ns	ns
Interaction	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

in N treatments, no significant differences were noted. Also, no interaction effects were observed during the whole Experimental period (Table 3.19).

3.4.6. Clover growing points and stolon length

At the beginning of the Experimental period stolon growing point densities by chance were 48% ($P = 0.11$) and 72% ($P \leq 0.05$) higher in ECW than SRW and LRW treatments, respectively (Table 3.20). Similar trends were found in stolon length, which were 47% ($P = 0.06$) and 82% ($P \leq 0.02$) higher in ECW than in SRW and LRW (Table 3.20). White clover growing points densities and stolon length increased sharply during late spring and early summer (Table 3.20), but differences between treatments became non significant by early January. The highest and lowest clover populations were found in January and late April, respectively.

3.4.7. Tissue turnover

Estimates of tissue turnover were made during the second half of summer and during autumn and the results are described separately for ryegrass and white clover.

3.4.7.1. Ryegrass

Tissue turnover in ryegrass was studied during three regrowth periods during the post-control phase. Overall, SR and LR treatments had substantially greater net herbage production in December (Table 3.21) and April (Table 3.23) than EC, though not during the dry conditions of February (Table 3.22).

Table 3.20. Stolon density and length in a ryegrass-white clover sward under contrasting spring grazing managements (growing points m^{-2} (GP) and stolon length m m^{-2} (SL) from tiller cores). Experiment 2.

Treatment	7 Sep		29 Nov		10 Jan		22 Feb		29 Apr	
	GP	SL	GP	SL	GP	SL	GP	SL	GP	SL
ECW	2070	59.0	5140	69.2	5700	75.8	3690	44.8	2600	33.7
SRW	1400	40.2	3460	61.0	4680	66.4	2390	30.6	1920	24.2
LRW	1210	32.4	4220	61.6	3940	58.5	2770	35.3	2310	33.0
SEM	260	5.7	370	56.0	750	8.7	310	4.8	230	2.5
Signif.	ns	*	*	ns	ns	ns	ns	ns	ns	ns

Table 3.21. Rates of growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 20 Dec-29 Dec-8 Jan. Experiment 2.

	Treatment									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W vs N	Int W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	9.4	11.7	11.5	12.6	10.3	12.9	0.70	*	*	ns
Daugh Elon	2.6	4.1	6.4	3.4	6.4	5.4	0.71	**	ns	*
Senescence	2.05	1.31	1.56	1.45	1.63	1.83	0.25	ns	ns	ns
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.60	0.80	0.74	0.86	0.66	0.88	0.05	ns	***	ns
Daugh Elon	0.16	0.28	0.41	0.23	0.41	0.36	0.06	**	ns	*
Total Elon	0.77	1.08	1.15	1.08	1.06	1.25	0.07	**	*	*
Senescence	0.164	0.106	0.125	0.117	0.130	0.148	0.02	ns	ns	ns
Net Growth	0.603	0.970	1.023	0.968	0.934	1.098	0.060	**	**	*
Tiller Pop^{+}	6788	8406	9380	10914	9503	10136	655	**	**	ns
Net Production (g m^{-2} day^{-1})										
	4.10	8.17	9.64	10.57	8.80	11.26	0.88	***	**	ns

$^{+}$ = From Table 3.17.

Table 3.22. Rates of growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 3 Feb-11 Feb-18 Feb. Experiment 2.

	Treatment									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W v N	Int W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	3.35	3.65	3.51	3.53	3.60	3.93	0.27	ns	ns	ns
Daugh Elon	1.49	1.83	2.66	2.07	1.44	0.66	0.93	ns	ns	ns
Senescence	0.81	0.67	0.59	0.70	0.54	0.71	0.16	ns	ns	ns
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.21	0.21	0.25	0.27	0.27	0.27	0.02	**	ns	ns
Daugh Elon	0.10	0.10	0.19	0.16	0.11	0.05	0.07	ns	ns	ns
Total Elon	0.31	0.31	0.43	0.42	0.38	0.31	0.07	ns	ns	ns
Senescence	0.077	0.062	0.059	0.076	0.056	0.073	0.020	ns	ns	ns
Net Growth	0.23	0.25	0.37	0.35	0.32	0.24	0.07	ns	ns	ns
Tiller Pop^{+}	8660	10049	11123	11411	11223	11574	597	**	**	ns
Net Production (g m^{-2} day^{-1})										
	2.04	2.51	4.23	3.98	3.56	2.73	0.85	ns	ns	ns

$^{+}$ = From Table 3.17.

Table 3.23. Rates of growth, senescence and net production per tiller (mm and mg tiller^{-1} day^{-1}) and net pasture production (g m^{-2} day^{-1}) of ryegrass-white clover and ryegrass swards under contrasting spring grazing managements: 10 Apr-18 Apr-26 Apr. Experiment 2.

	Treatment									
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	W vs N	In W*N
Leaf Turnover (mm tiller^{-1} day^{-1})										
Elongation	3.99	4.67	3.83	5.49	3.98	5.26	0.35	ns	***	ns
Daugh Elon	0.35	0.54	0.58	0.65	0.96	1.21	0.03	ns	ns	ns
Senescence	0.65	0.46	0.33	0.97	0.39	0.66	0.13	ns	*	*
Leaf Turnover (mg tiller^{-1} day^{-1})										
Elongation	0.20	0.30	0.20	0.37	0.26	0.36	0.03	ns	***	ns
Daugh Elon	0.07	0.10	0.08	0.11	0.13	0.14	0.02	*	ns	ns
Total Elon	0.27	0.40	0.29	0.48	0.39	0.51	0.04	*	***	ns
Senescence	0.047	0.040	0.025	0.079	0.032	0.056	0.010	ns	**	*
Net Growth	0.22	0.36	0.26	0.40	0.35	0.45	0.04	*	**	ns
Tiller Pop^{+}	11019	13485	13373	15542	12469	14403	592	**	***	ns
Net production (g m^{-2} day^{-1})										
	2.46	4.92	3.53	6.16	4.42	6.45	0.54	**	***	ns

$^{+}$ = From Table 3.17

Soon after the switch from lax to hard grazing (late December and early January), SR and LR treatments had a greater leaf growth than EC ($P \leq 0.05$). Net production (g m^{-2} day^{-1}) in SR and LR was 65% and 63% greater than EC ($P \leq 0.001$). Table 3.21 shows that, with the exception of daughter elongation and senescence, all the tissue dynamic components were higher in N swards than in those with white clover ($P \leq 0.05$). Also, total elongation and net growth in N swards were 16% and 15% greater in LRN than SRN and ECN, but in W plots these parameters were 8%, 49%, 10% and 70% greater in SRW than LRW and ECW, respectively, showing an interaction effect between N/W components ($P \leq 0.05$).

Senescence losses were not statistically different ($P \geq 0.05$) between treatments in the three periods of study (Tables 3.21-3.23). Generally senescence losses were less than 25% of tissue growth rate in all treatments.

With the exception of leaf elongation (mg $tiller^{-1}$ day^{-1}), no statistical differences were observed between treatments during February (Table 3.22). However, all tissue turnover components were slightly greater in SR and LR plots than EC (Table 3.22). Net production (g m^{-2} day^{-1}) was 100% and 38% higher in SR and LR swards than in EC, respectively. Although N plots grew slightly more DM than W plots, no statistical differences between treatments were observed.

Table 3.23 shows tissue dynamics during April. Leaf elongation, daughter elongation and senescence in mm $tiller^{-1}$ day^{-1} were not different between treatments ($P \geq 0.05$). But, when leaf weight and tiller population were added to these calculations, total growth, net growth (mg $tiller^{-1}$ day^{-1}) and net production (g m^{-2} day^{-1}) were greater in SR and LR than EC ($P \leq 0.01$), respectively (Table 3.23).

Nitrogen effects were large. With the exception of daughter elongation, there was a significant N effect on all the tissue turnover components (Table 3.23). White clover swards showed a 68% lower net production compared to those with N ($P \leq 0.001$).

3.4.7.2. White clover

Tissue flow in white clover was also studied during summer and autumn (Tables 3.24 to 3.26). The results show a greater increase in white clover production during December and April in SRW and LRW treatments than ECW.

Although petiole elongation was 30% higher in SRW and LRW treatments than ECW, no statistically significant differences were recorded in late December and early January ($P \geq 0.05$). Leaf expansion was 56% and 34% greater in SRW and LRW than in ECW ($P \leq 0.05$), respectively. Those differences were reflected in the net growth, where SRW and LRW showed 61% ($P \leq 0.02$) and 42% ($P = 0.08$) greater growth rate than ECW (Table 3.24), respectively. No statistical differences in net production (g DM m^{-2} day^{-1}) were found between treatments, though SRW and LRW showed 40% and 17% higher net production than ECW, respectively.

During February no significant differences in leaf expansion or petiole elongation per locus were recorded between treatments (Table 3.25). Leaf expansion was only 40%, 23% and 26% of values recorded in ECW, SRW and LRW, respectively, in late December and early January. Similar depressions were observed in petiole elongation (Tables 3.24 and 3.25). This decrease in leaf growth rate, observed in all the treatments, could have been due to the drastic drought recorded in this period (Average rainfall 24.6 mm; Appendix 3.2).

In April LRW and SRW showed 36% and 8% more petiole elongation, and 63% and 15% more leaf expansion than ECW ($P \leq 0.01$), and 59% and 13% ($P \leq 0.01$) more net growth per locus than ECW (Table 3.26), respectively. Despite this, ECW showed a net production (g m^{-2} day^{-1}) 14% greater than SRW, but 36% lower than that produced by LRW ($P \leq 0.05$).

No differences in petiole and leaf senescence were observed between treatments during

Table 3.24. Rates of petiole elongation and leaf growth, senescence and net production of ryegrass-white clover swards under contrasting spring grazing managements: 20 Dec-29 Dec-8 Jan. Experiment 2.

	Treatment				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm locus^{-1} day^{-1}) and leaf growth (cm^{2} locus^{-1} day^{-1})					
Petiole Elon	5.09	6.63	6.65	0.46	ns
Petiole Sen	2.07	1.35	1.43	0.30	ns
Leaf Expansion	0.160	0.261	0.214	0.020	*
Leaf Sen	0.006	0.019	0.005	0.007	ns
White clover petiole elongation and leaf growth (mg locus^{-1} day^{-1})					
Petiole Elon	0.290	0.378	0.379	0.026	As above[1]
Petiole Sen	0.117	0.077	0.082	0.017	
Leaf Expansion	0.746	1.218	1.000	0.093	
Leaf Sen	0.027	0.087	0.025	0.030	
Net Growth[+++]	0.891	1.433	1.272	0.128	ns
Growing Points[+]	7580	6640	5850	870	ns
Net Production (g m^{-2} day^{-1})[++]					
	1.96	2.74	2.29	0.558	ns

[1] = Since weight change = mm mm^{-1} day^{-1} or cm^{2} locus^{-1} day^{-1}, respectively, multiplied by a constant (experimental mean mg mm^{-1} day^{-1}) statistical analysis for both entities is identical.

[+] = From Table 3.20. [++] = Adjusted using the number of growing points per locus. [+++] = ($P < 0.06$)

Table 3.25. Rates of petiole elongation and leaf growth, senescence and net production of ryegrass-white clover swards under contrasting spring grazing managements: 3 Feb-11 Feb-18 Feb. Experiment 2.

	Treatments				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm locus^{-1} day^{-1}) and leaf growth (cm^2 locus^{-1} day^{-1})					
Petiole Elon	0.99	0.85	0.80	0.15	ns
Petiole Sen	0.141	0.124	0.138	0.043	ns
Leaf Expansion	0.062	0.059	0.056	0.005	ns
Leaf Sen	0.009	0.003	0.006	0.004	ns
White clover petiole elongation and leaf growth (mg locus^{-1} day^{-1})					
Petiole Elon	0.056	0.049	0.046	0.009	As above[1]
Petiole Sen	0.008	0.007	0.008	0.002	
Leaf Expansion	0.29	0.28	0.26	0.025	
Leaf Sen	0.04	0.012	0.027	0.018	
Net growth	0.297	0.305	0.272	0.042	ns
Growing Points[+]	4480	3060	3530	480	ns
Net Production (g m^{-2} day^{-1})[++]	0.415	0.297	0.341	0.058	ns

[1] = Since weight change = mm mm^{-1} day^{-1} or cm^2 locus^{-1} day^{-1}, respectively, multiplied by a constant (experimental mean mg mm^{-1} day^{-1}) statistical analysis for both entities is identical.

[+] = From Table 3.20. [++] = Adjusted using the number of growing points per locus.

Table 3.26. Rates of petiole elongation, leaf growth and net production of ryegrass-white clover swards under contrasting spring grazing managements: 10 Apr-18 Apr-26 Apr. Experiment 2.

	Treatment				
	ECW	SRW	LRW	SEM	Sign
White clover petiole elongation (mm locus^{-1} day^{-1}) and leaf growth (cm^{2} locus^{-1} day^{-1})					
Petiole Elon	1.59	1.71	2.17	0.06	**
Leaf Expansion	0.089	0.102	0.145	0.08	**
White clover petiole elongation and leaf growth (mg locus^{-1} day^{-1})					
Petiole Elon	0.076	0.082	0.104	0.003	As above[1]
Leaf Expansion	0.415	0.474	0.677	0.037	
Net growth	0.165	0.183	0.249	0.011	**
Growing Points[+]	2600	1920	2310	310	ns
Net Production (g m^{-2} day^{-1})[++]					
	0.139	0.119	0.179	0.013	ns

[1] = Since weight change = mm mm^{-1} day^{-1} or cm^{2} locus^{-1} day^{-1}, respectively, multiplied by a constant (experimental mean mg mm^{-1} day^{-1}) statistical analysis for both entities is identical.

[+] = From Table 3.20. [++] = Adjusted using the number of growing points per locus.

the three periods of study ($P \geq 0.05$). Also, senescence was negligible in April on all treatments. Leaf senescence was always less than 15% of the total leaf expansion. Petiole senescence in late December and early January was 40% and 20% of the elongation in ECW and release treatments, respectively. However, in February it was only 15% of elongation in all treatments.

3.4.8. Determination of herbage production in summer and autumn

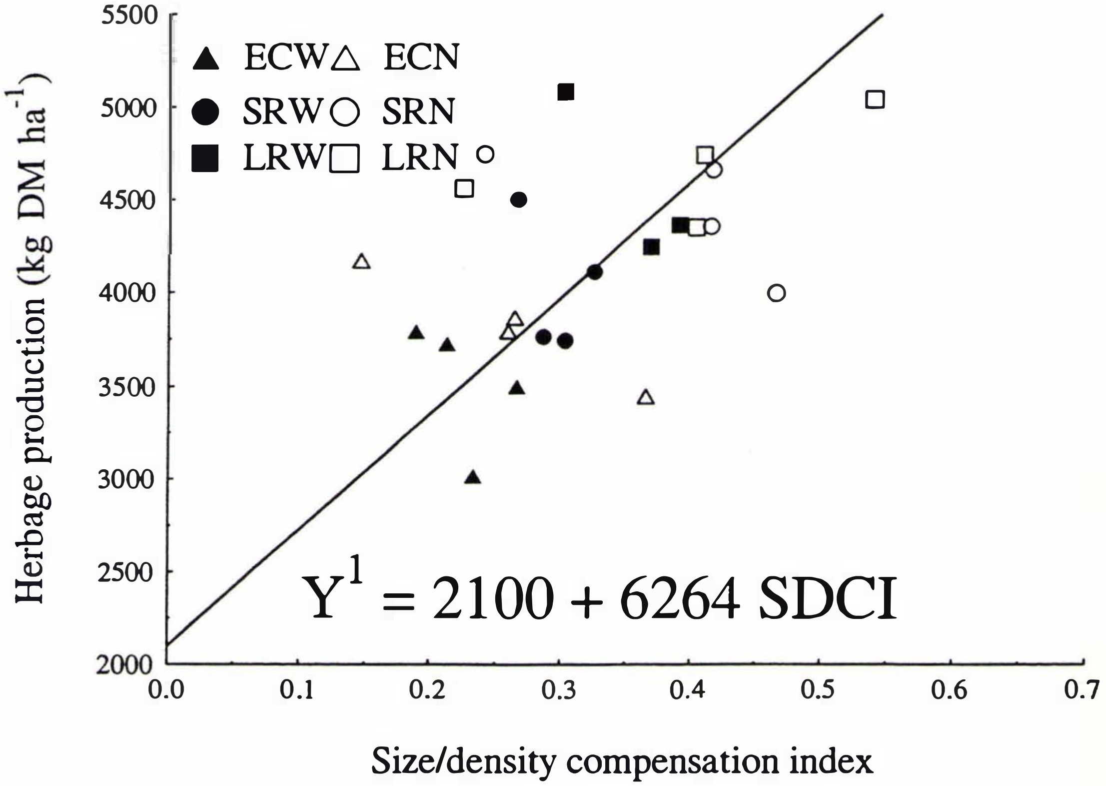
3.4.8.1. Relationship between herbage production and size/density compensation index (SDCI)

The relationship between herbage production and SDCI for the period January to April 1994 is presented in Figure 3.14. The results, again, indicate that distance from an arbitrary -3/2 self-thinning line as measured by SDCI is related to pasture production. An increase in herbage production was accompanied by an increase in SDCI. Thus, LR was greater than SR and EC. Early control treatments were located closest to the origin, whereas SR and LR treatments were further from the origin.

3.4.8.2. Canonical discriminant analysis of herbage production

Multiple discriminant analysis was used in this study to gain an overview of the effects of different grazing managements on components of herbage production during summer and autumn, and to examine if the variables taken together showed evidence of association between particular patterns of tillering and increased or decreased herbage production. Hence, the variables used were: herbage production from 1 December onwards, tiller natality and mortality during December, tissue turnover from late

a) Using all replicates individually



b) Using treatment means

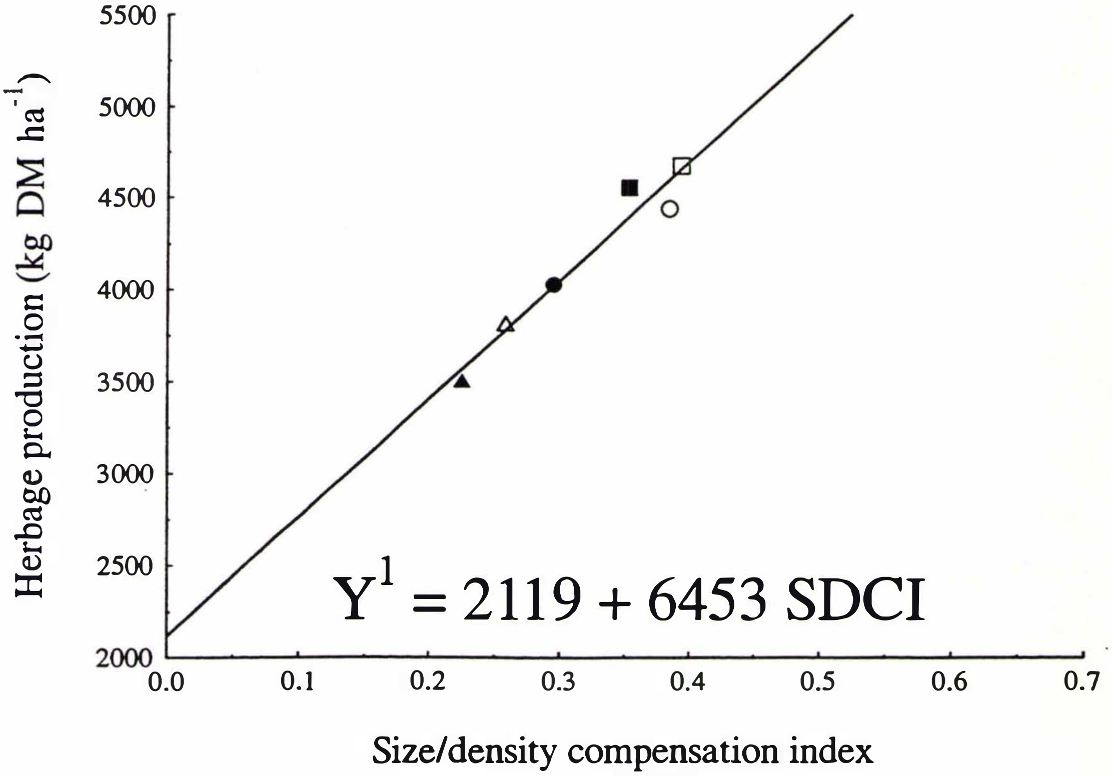


Figure 3.14. Relationship between post-control sward production (January-April) and size/density compensation index (SDCI). Experiment 2.

[1] Calculated by reduced main axis regression (RMA, LaBarbara, 1989).

December to early January and tiller population in early January and in late February (Table 3.27).

Table 3.27. Canonical structure and summary statistics for first discriminant factor for multiple discriminant analysis of herbage production (15 Dec 1993 to 29 Apr 1994) and associated tiller demography measurements. Experiment 2.

Variables	Discriminant 1
Herbage Production	0.9682
Tiller Mortality 25 Nov-26 Dec	0.6684
Tiller Natality 25 Nov-26 Dec	0.9917
Tissue Turn 20 Dec-8 Jan	0.9979
Tiller Pop 10 Jan	0.9633
Tiller Pop 22 Feb	0.9954
Canonical r^2	0.9322
P	< 0.0001
Proportion of Disc (%)	0.9574

The first discriminant function explains 96 % of the multivariate dispersion and is highly correlated with all variables. Thus, the canonical structure for the discriminant function (DF) indicates that a high herbage production was associated with high tiller natality during December, high tissue turnover late in December and early January and high tiller population in January and February ($P \leq 0.0001$). Tiller mortality contributed less strongly to the discriminant function and is therefore less strongly related to sward productivity than the other variables.

3.5. GENERAL DISCUSSION

3.5.1. Research techniques

Defoliation intensity imposed by the grazing animal is rarely uniform, and as result of selective grazing, treading and fouling, pasture consists of a mosaic of patches with variable density and defoliation intensity (Brock & Hay, 1993). In the present study, Experimental plots were relatively small and therefore likely to present problems of variation due to defoliation management and sampling techniques. In Experiment 1, a considerable variability was observed in the results from tiller cores and fixed plastic frames, mainly due to variation within plots. This effect in tiller cores was due, in part, to the fact that the Experimental plots were relatively small and the ground level quadrat cuts exerted a disproportionate effect on botanical composition, persistence and structure. Also, there were a small number of replicates per treatment and the number of sub-replicates within each plot was relatively small. These problems in Experiment 1 were reflected in the number of non-significant treatment effects. To overcome these difficulties, increases in plot size, number of sub-samples per plot and replications per treatment were made for Experiment 2. Also, the number of quadrat cuts was reduced. In the pre-control period (September to December 1) quadrat cuts were made only once just before the "control" grazing. This procedure provided less information for predicting herbage mass from sward height records, but greatly reduced the impact of bare quadrat areas on other sward observation. Overall these modifications proved to be effective in controlling both between and within plot variability. Thus, a number of non-significant trends in Experiment 1 were confirmed as significant treatment effects in Experiment 2.

The estimates of herbage production and accumulation from the sward height records (rising plate meter) were demonstrated to be reliable. In both years, the pre-grazing and post-grazing regression equations proved to have a low residual standard deviation (average for both years was s = 188 and 289 for post- and pre-grazing, respectively). However, in Experiment 2, herbage mass during the pre-control phase could have been under-estimated, particularly in short release and long release treatments, because these swards had greater proportions of reproductive tillers than early control.

The higher tiller population density observed in fixed quadrats than in surrounding swards (Figures 3.4, 3.5, 3.12 and 3.13; Tables 3.4 and 3.17) did not appear to be associated with the sward disturbance involved in tiller counting as Davies (1981) and Matthew *et al.* (1989b), suggested. Patterns of tillering activity in both years were very similar, and the absence of disturbance of the sward in Experiment 2 (from the beginning of the trial to the control phase) did not modify the patterns of tiller natality and mortality observed in the first year. Furthermore, fixed quadrats are seldom truly random samples because they tend to be placed in localised areas of higher than average ryegrass tiller density. Also, this greater tiller population density could be due to the fact that the number of fixed frames per replication was relatively small (2 and 4 for Experiment 1 and 2) in comparison with that from random samples (30 cores). No evidence of progressive change in balance between tiller cores and fixed quadrats was observed (Figures 3.4, 3.5, 3.12 and 3.13; Tables 3.4 and 3.17). This would be expected if repeated handling affecting tillering behaviour. Clump populations were substantially higher than fixed quadrat populations. It is therefore assumed that estimates of tiller dynamics are reasonable, at least on a tiller per tiller basis.

Routine sward structure measurements in Experiment 1 were laborious. They were only carried out just before the switch from lax to hard grazing, because of the importance of this stage to subsequent sward behaviour. The measurements were not repeated in Experiment 2, in order to allow more time for other measurements.

3.5.2. Botanical composition and sward structure

The botanical composition of the sward changes throughout the year according to the season and management practices. In Experiment 1 estimates of botanical composition were made before and after each grazing. These results showed that changes from grazing to grazing in spring were small, so results reported here are the sward components before the switch from hard to lax grazing on October 26, from lax to hard on December 7 and, from then onwards, before and after every grazing. Also, as the results for the pre-control phase of Experiment 1 (Figure 3.1 and Table 3.2) did not show great differences in sward components, and to reduce plot damage and change in sward composition arising from frequent cuts as in Experiment 1, measurements for Experiment 2 were only made at the control grazing (1 December) and then after alternate grazings.

At the beginning of the Experiment, in both years, all swards were of similar botanical composition (except for the second year where white clover was greater in early control). The main changes in sward components and structure were observed during the reproductive period, particularly in SR and LR plots. Overall, short release and long release treatments had more ryegrass reproductive tillers, more stem and less leaf material and other grasses than early control swards. Similar patterns have been reported by several workers (e.g. Colvill & Marshall, 1984). The contribution of the sward components to the herbage mass was affected by grazing intensity (Figures 3.3 and 3.11). The increased levels of total herbage accumulation observed during the pre-control phase in short release and long release treatments were mostly due to increased accumulation of senescent material and to the higher ryegrass individual tiller weight because of their greater proportion of ryegrass reproductive tillers.

In late spring SR and LR swards had a greater proportion of reproductive tillers than early control swards. Early control swards had higher proportions of vegetative ryegrass tillers, other grasses, white clover and weeds; they also had more other grasses and white clover during January. The proportion of other grasses was generally greater in early control treatments, and increased in the absence of clover. These results indicate that severe defoliation in spring decreases the proportion of ryegrass and increases the proportion of other grasses. This supports the finding of Grant *et al.* (1983) and Bircham & Hodgson (1983) in the UK, that perennial ryegrass was replaced progressively by *Poa* species under severe defoliation.

Figures 3.3 and 3.11 also show that the white clover contribution to herbage mass was affected by grazing management. In an earlier study Tavakoli (1993) showed than the mass of white clover in mixed swards increased as the intensity of defoliation increased. Similarly, Brock *et al.* (1989) and Davies (1993) suggest that close, frequent defoliation favours clover whereas lax infrequent defoliation increases the content of ryegrass. The results of both present trials support this finding. Short release and long release treatments generally resulted in more clover leaf and less stolon than early control (Tables 3.2 and 3.14). The greater proportion of white clover in the early control swards was mainly due to the fact that stolon comprised a greater proportion of total above ground dry matter, than did leaf. Detailed sward structure and tissue flow measurements confirm this view, and also suggest that short release and long release treatments tend to produce higher clover leaf content than early control (Figure 3.8 and Tables 3.9, 3.10, 3.11, 3.24, 3.25 and 3.26).

Soon after the switch from lax to hard grazing, the proportion of ryegrass in short and long release swards increased sharply, particularly in plots with white clover. The early control treatments tended to have a slightly lower proportion of ryegrass, less dead material and more other grasses than short and long release treatments. The greatest proportion of dead material was observed in the second Experiment, during February, across all the treatments probably as a consequence of the drought conditions prevailing at this time (Appendix 3.2).

The aim of the sward structure measurements was to quantify the effect of the spring grazing management on the spatial distribution of the sward components. The results in

Experiment 1 (Figures 3.8 and 3.9) suggest that defoliation management during the reproductive period can modify the sward structure by changing the balance between and within sward components. Thus, hard grazed swards had a more homogeneous canopy structure, with a higher percentage of contacts in the bottom layers, than lax grazed swards. Similar results have been found by Roggero *et al.* (1993) under cutting conditions.

White clover was the second most important sward component and showed a greater vertical distribution in short release and long release treatments than in early control treatment. Leaf and petiole were found in all the layers between 0 and 12 cm in short release and long release treatments, while in early control it was found between 0 and 6 cm. These results suggest that white clover growth was increased by lax grazing during late spring and this agrees with results of Da Silva (1994) and Da Silva *et al.* (1994). This may be explained in terms of clover's upright habit (Eagles & Othman, 1986) when in competition with grasses. Finally, short and long release swards had less other grasses than early control. Weeds were present in insignificant quantities in all the plots.

3.5.3. Population dynamics

Since the basic unit of growth is the tiller and/or stolon, herbage production of the sward can be expressed in terms of the number of tillers and/or stolons per unit area of land and the production per tiller and/or stolon (Volenec & Nelson, 1983; Nelson & Zarrough, 1981). In this section, ryegrass and white clover population densities will be discussed separately.

3.5.3.1. Tiller population density

Defoliation management can influence the amount of herbage growth by changing tiller population density and their individual weight. The results of both years shows that ryegrass swards are dynamic entities where tillers are appearing and dying at rates which differ according to management and season. The balance between tiller appearance and death determines the tiller population density.

Figures 3.4, 3.5, 3.12 and 3.13 indicate that tillering was most rapid between November and February, with the highest tiller appearance rate at the end of December, soon after interruption of reproductive growth, particularly in release treatments (Figures 3.6 and 3.7 and Table 3.19). A similar period of intense tillering by perennial ryegrass during late spring and early summer has been observed previously in swards under grazing (Chapman *et al.*, 1983; Korte *et al.*, 1984; L'Huillier 1987a; Matthew *et al.*, 1989b, 1991; Da Silva *et al.*, 1993, 1994; Da Silva, 1994) or cutting (Korte, 1986). These results (Figures 3.4, 3.5, 3.6, 3.7, 3.12 and 3.13 and Table 3.19) indicate that lax grazing during spring, switched to hard grazing at anthesis, increased tiller population density during summer and autumn by increasing rate of tiller production at this time.

Reproductive development started late in October in all treatments (Figures 3.4, 3.5, 3.12 and 3.13). The tendency of tillers to express reproductive growth was more accentuated in release treatments than under hard grazing. Several researchers (Korte, 1986; L'Huillier, 1987a; Matthew *et al.*, 1989a, b; Da Silva, 1994) have reported that reproductive growth is concentrated at the end of spring and during early summer. Tables 3.4 and 3.17 and Figures 3.4, 3.5, 3.12 and 3.13 also show a decrease in tiller population density just before decapitation of reproductive tillers late in November, particularly in release treatments. This was probably due to buds on the base of flowering culms being restrained from developing by hormonal influences from the elongating stem internodes or developing inflorescence (Clifford, 1977), and by competition for assimilates (Colvill & Marshall, 1984; Ong *et al.*, 1978). Defoliation of reproductive tillers removed these effects, allowing the buds to develop (Korte, 1986), and so daughter tiller appearance was stimulated by redirecting photosynthetic products to subsidise or encourage the early growth of young tillers (Matthew *et al.*, 1989a, b, 1991; Matthew, 1988, 1991, 1992). Korte (1981, 1986) found that formation of tillers from old buds, after interruption of reproductive development, was especially important, and Matthew *et al.* (1989b) described the morphology of tiller production from reproductive stubs.

A second period of tillering flush was observed in autumn, particularly in the second year (Figures 3.12 and 3.13). Similar results have been observed in the UK (Garwood, 1969; Colvill & Marshall, 1984; Tallowin, 1981). L'Huillier (1987a) and Korte (1986) did not find such a flush during autumn in New Zealand, although Korte & Chu (1983) did observe a period of rapid tillering in autumn during recovery of tiller populations depleted by summer drought (Appendix 3.2).

At the end of the second trial there was a greater tiller population in short release and long release treatments than in early control treatments. Also, in both trials, those tillers born at the peak of tillering activity, late in December, especially in short release and long release treatments, made a greater contribution to the total tiller population density. These results confirm the evidence of Matthew *et al.* (1989b), Matthew (1991, 1992), Da Silva *et al.* (1993, 1994) and Da Silva, (1994) that lax spring grazing management, switched to hard grazing at the time of anthesis, increases herbage accumulation during summer and autumn by increasing tiller population density.

Tiller appearance and death exhibited pronounced bursts of activity during the experimental period, and was most rapid between November and January. The highest tiller appearance rate recorded at the end of December, especially in short release and long release treatments (Figure 3.5 and Table 3.16), is indicative of the potential for manipulation of ryegrass tiller density during spring for advantage. However, it is also noteworthy that other studies have concluded that tillering is not influenced by grazing intensity or by cutting frequency (Tallowin, 1981; Chapman *et al.*, 1983; Korte, 1986).

It would therefore seem that the specific timing of manipulation at a period of potential response (Matthew *et al.*, 1989a, b; Da Silva *et al.*, 1993, 1994 and Da Silva, 1994) is critical in obtaining an advantage through manipulation of tiller density.

The seasonal pattern of tiller mortality closely followed that of tiller natality and was highest during November and December. Similar seasonal patterns of tiller losses have been observed in studies of swards based on 'Nui' or 'Ellett' ryegrass by L'Huillier (1987a), Thom (1991), Da Silva *et al.* (1993, 1994) and Da Silva (1994) in dairy pastures, by Korte *et al.* (1984), Matthew *et al.* (1989b) and Xia *et al.* (1990) in pastures grazed by sheep and by Korte *et al.* (1985) and Korte (1986) in cut swards. By contrast, a 'Ruanui' ryegrass sward had different seasonality of tiller natality and mortality (Matthew, 1992) as did British swards studied by Garwood (1969). The high tiller loss during stem elongation may reflect a heavily shaded environment and consequent poor assimilatory capacity for the young vegetative tillers in the sward (Ong *et al.*, 1978; Ong, 1978; Colvill & Marshall, 1984). Furthermore, Ong (1978) suggested that the main factor influencing tiller death is light level and generally the smallest or youngest tillers, irrespective of their position, tend to die first when the whole plant is stressed.

Late in December, death of defoliated reproductive tillers contributed to the greater losses in the previously lax grazed treatments. Findings by Thom (1991) also suggest that reproductive tillers have a greater overall probability ($P = 0.24$ per week) of dying than do vegetative tillers ($P = 0.09$ per week). Also, L'Huillier (1987a) indicated that death of defoliated reproductive tillers contributed to the high rate of tiller death in this period.

Ryegrass and other grass tiller population densities were always higher in nitrogen than white clover swards (Tables 3.4 and 3.17 and Figures 3.4, 3.5, 3.12 and 3.13). This could be partly due to the lack of competition with white clover and, therefore other grass tillers in nitrogen swards tended to fill in white clover gaps. Nelson & Zarrough (1981) concluded that nitrogen increased both tiller density and tiller weight compared with no nitrogen application. An initial increment in nitrogen increased tiller density, but later increments gave a preferential increase in tiller weight because tiller density was approaching maximum.

Other grass tiller population density made a substantial contribution to the total sward population density, especially during late spring and early summer (Tables 3.4 and 3.17). In both trials, other grass tiller density was greater in early control than short and long release treatments (Tables 3.4 and 3.17) before the switch from lax to hard grazing ($P \leq 0.05$). Bircham & Hodgson (1983) also reported an increase in *Poa* tiller population as a consequence of an increase in defoliation severity. After decapitation of the reproductive tillers, these differences were quickly reduced as a result of an increase in ryegrass tiller density, especially in short and long release treatments, being statistically significant only at the end of January in Experiment 1 ($P \leq 0.05$). The proportional contribution of other grasses to the herbage mass was substantially less than that to tiller population. For example, other grass tillers comprised 49% and 57% of the total tiller population in Experiments 1 and 2 respectively at the time of the switch from lax to hard grazing, but only 18% (Experiment 1) and 31% (Experiment 2) of the total herbage mass. The greater tiller population densities of other grasses observed in early control compared with short and long release treatments during December and January (Figures 3.3 and 3.11) are interpreted as evidence that reduced tiller replacement on early control plots had the effect of creating gaps in the sward which *Poa* species were able to colonise. Early development of other grass tillers in the early control treatment does not appear to have interfered with subsequent development of ryegrass tillers (Tables 3.4 and 3.17).

3.5.3.2. Stolon population density

Stolon population density was highly variable in both years (Tables 3.5 and 3.20), and the seasonal changes in growing points and stolon length in all treatments appear to follow those changes observed by Brougham (1957) in New Zealand and Turkington &

Harper (1979) in the UK. White clover stolon populations are limited during spring due to shading by companion grasses, but during summer and autumn populations increase as a consequence of ryegrass suppression by high temperatures (Mitchel, 1953, 1954) and low water supply (Brougham, 1955). Similarly, Turkington & Harper (1979) observed that *Trifolium repens* has a single season of active growth, with its peak in summer coinciding with the *Lolium perenne* gap in this period.

Tiller plug data shows that white clover stolon populations were variable and affected by grazing regimens. There were seasonal changes in both years (Tables 3.5 and 3.20), with the greatest stolon length and growing points populations in summer, particularly in Experiment 1. In this Experiment no significant differences were found between treatments, but early control generally presented slightly greater stolon length and growing point numbers than short and long release swards. In Experiment 2 stolon population by chance was greater at the beginning of the trial in early control plots, but substantial increases on short and long release treatments after the switch from lax to hard grazing early in January quickly eliminated these differences. At the end of both Experiments, early control had slightly higher growing points and stolon length than short and long release treatments. Values of white clover stolon density measured in Experiment 1 during late January and late March were almost twice as large as those measured in Experiment 2, probably a consequence of the drought period observed from January to March in year 2 (Appendix 3.2).

Growth and death processes are usually in balance, but in mid spring accelerated death of old stolon results in a higher proportion of small, less branched plants (Brock *et al.*, 1988). Several workers (Vartha & Hoglund, 1983; Brock, 1988; Brock & Moon Chul Kim, 1994) have reported the effect of drought on white clover pastures. Initially, wilting occurs, leaves die and current production is reduced (Tables 3.20 and 3.25) as the stolons adjust osmotically to survive at the expense of leaf growth (Turner, 1990, 1991). As the severity of the drought increases, stolons tend to die and plant death increases, resulting in a decline in population density (Table 3.20) and long-term losses (Brock & Moon Chul Kim, 1994). The results of the second Experiment confirm this view. During this period, leaf expansion, net growth and net production decreased substantially in comparison with December results. Values of tissue turnover components during February were about 25% of those observed in December (Tables 3.24 and 3.25). Brock & Moon Chul Kim (1994) concluded that the main factor influencing drought survival of white clover appears to be grazing management, particularly in the pre-drought period, placing pastures in a position better able to cope with the oncoming adverse condition (Brock & Hay, 1993). Lax grazing reduces the direct solar radiation to the soil surface and hence heat stress to the plants, which is thought to be the main operative feature influencing plant survival (Brock & Hay, 1993). The April results (Table 3.26) seem to confirm the positive effects of lax grazing on net production, after a long drought period.

3.5.3.3. Ryegrass:white clover population density balance

Chapman & Lemaire (1993) indicated that plants do not regrow in a sward as isolated individuals, but as a members of a usually crowded population where surrounding vegetation exerts a strong influence on inherent species characteristics through competition. Da Silva (1994) working with dairy pastures reported that in one study late control plots showed an increase in summer-autumn herbage accumulation mainly due to enhanced ryegrass accumulation, and that was associated with an increase in grass tiller and stolon density. However, in a subsequent experiment increased summer-autumn herbage accumulation was mainly due to enhanced white clover accumulation, and that was associated with bigger ryegrass tillers and greater internode length. He did not find statistical differences in either grass tiller or white clover node or stolon densities, but a clear seasonal ryegrass:white clover balance effect influencing the summer-autumn herbage accumulation of pastures was observed for all treatments. In this study the relationship between ryegrass tiller population density and white clover stolon growing points density was examined (Table 3.28). The results of a combined regression analysis for both years, demonstrated that an increase in ryegrass tiller population was associated with a decrease in white clover growing points population ($P \leq 0.02$). Early control was associated with greater population of other grasses, but with a lower ryegrass tiller population, while short release and long release treatments showed the reverse effects. This suggests that other grasses and white clover tend to fill gaps in the swards associated with low size/density compensation index.

In summary the responses of different pasture species to defoliation management, particularly ryegrass and white clover, have been attributed to their differences in growth response to temperature and seasonal factors (Barthram & Grant, 1994) and the differences in the physiological responses to stress of plants conditioned by defoliation patterns (Brock *et al.*, 1981). Because of the high temperatures during summer (Appendices 3.1 and 3.2), white clover had greater advantages than ryegrass, and in this Experiment short release and long release treatments responded with a greater increase in white clover leaf expansion and net leaf growth per locus than early control (Tables 3.9 to 3.11 and 3.24 to 3.26). However, the lower tiller population density observed in early control (Tables 3.4 and 3.17) was soon compensated for by an increase in white clover population (Tables 3.5 and 3.20), minimising the positive effects of late control on white clover growth per locus (Tables 3.9 to 3.11 and 3.24 to 3.26). It is concluded that the overall increase in summer-autumn pasture production of late control treatments is a result of enhanced ryegrass tiller population density at the expense of clover production.

Table 3.28. Ryegrass and white clover population densities at the time of peak tillering activity (28 January 1993 and 10 January 1994).

	28 January 1993		10 January 1994	
Treatments	RG[1]	WC[2]	RG[1]	WC[2]
ECW	7760^{+}	6250	6790	5700
SRW	8820	3580	9380	4680
LRW	11800	3920	9500	3940
SEM	1680	1610	660	750
Significance	ns	ns	*	ns

[1] = Ryegrass tiller population density

[2] = White clover growing point density.

$^{+}$ = Combined years regression equation of ryegrass tiller population density vs white clover growing points population densities showed a negative relationship at $P \leq 0.02$.

$Y = 12607 - 0.754GP$, $s = 2369$

3.5.4. Effect of defoliation on tissue dynamics of ryegrass

It has long been advocated that herbage production can be manipulated to advantage by grazing management (Brougham, 1955, 1959, 1960, 1970; Jameson, 1963; Davidson, 1968; Tainton, 1974; Korte *et al.*, 1985; L'Huillier, 1987a; Judd *et al.*, 1990; Fulkerson *et al.*, 1993; Da Silva *et al.*, 1993, 1994; and Da Silva, 1994). For example, Judd *et al.* (1990) observed that under a 28-day grazing interval ryegrass produced 20% more dry matter than under a 14-day interval. Similarly, Fulkerson *et al.* (1993) in ryegrass/white clover swards, concluded that grazing at 4 weeks or when ready (before onset of senescence), compared to grazing at 2 weeks, increased DM yield by 18 and 32% in year 1, and 41 and 59% in year 2, respectively. Some of these authors identify strategies for improving light interception (Korte *et al.*, 1985). Korte *et al.* (1985) found that mowing at 95% light interception compared with mowing every 3 weeks increased herbage mass accumulation. In contrast, other workers have shown that rates of net herbage production in ryegrass-based temperate pastures are relatively insensitive to substantial ranges of variation in pasture condition or grazing management (Hodgson, 1989; Bircham & Hodgson, 1983; Parsons *et al.*, 1988; Korte *et al.*, 1987), although the rate of accumulation of herbage after grazing or cutting may be higher when defoliation is lenient than when it is severe (Brougham, 1959; Jameson, 1963; Davidson, 1968; Tainton, 1974; L'Huillier, 1987a, Da Silva *et al.*, 1993, 1994; and Da Silva, 1994). In the present study an immediate effect of lax grazing in spring agrees with earlier results; the subsequent effect during the summer-autumn period was consistent with the findings of Matthew *et al.* (1989a, b), Xia *et al.* (1990), Matthew (1992), Da Silva *et al.* (1993, 1994) and Da Silva (1994) (Tables 3.1 and 3.13). The mechanisms for the increase in herbage production vary according to the season. Production was increased during spring by increasing tiller weight (Tables 3.3, 3.15 and 3.16), and during summer and autumn by encouragement of new tiller formation from the stubs of grazed reproductive tillers (Korte *et al.*, 1984, 1985).

Leaf elongation rates are dependent on leaf area per tiller and associated tiller weight (Grant *et al.*, 1981; Bircham & Hodgson, 1983; Chapman *et al.*, 1983; Volenec & Nelson, 1983). In both Experiments, lax grazing during the pre-control period (September-early December) increased tiller weight (Tables 3.3, 3.15 and 3.16). As a consequence of replacement of ryegrass reproductive tillers by small vegetative tillers, tiller weight was not statistically significant between treatments ($P \geq 0.05$) soon after the control period (January), but tillers in short release and long release treatments were always heavier than those produced in early control swards and from February onwards the differences were significant ($P \leq 0.05$). Similarly, Da Silva (1994) observed that tillers formed after the control phase on swards laxly grazed during spring were heavier than those on hard grazed swards.

Response of the sward to a particular management may involve changes in population density, in tissue turnover per individual plant unit, or in some combination of the two (Bircham & Hodgson, 1983; Grant *et al.*, 1981). The results of these Experiments indicated that tillers formed in short release and long release plots after interruption of reproductive growth had a greater leaf elongation rate and net growth over the summer and autumn than those formed in early control swards (Tables 3.6-3.8 and 3.21-3.23). Furthermore, short release and long release plots had higher net herbage production than early control plots in five out of the six tissue turnover comparisons (net growth per tiller multiplied by tiller population density) carried out in Experiments 1 and 2, with long release nitrogen plots in Experiment 1 being the only case in which that effect was not observed. The greater performance of the early control nitrogen sward at the end of March (Table 3.8) could be due to the fact that, with high applications of nitrogen, tiller density could recover faster on the early control treatment than would occur with lower nitrogen application rates. This seemed to be the case, because the results from the second Experiment did not show the same pattern of recovery with lower N rates. Also, in clover plots, the early control treatment consistently had the lowest net production rate in summer and autumn. These detailed measurements of tissue dynamics confirm findings of Xia *et al.* (1990), and Xia (1991) that the switch from lax to hard grazing late in spring increased tiller appearance, net pasture production and net leaf production over the summer (Tables 3.6, 3.7 and 3.21) compared with conventional tight grazing management.

A comparison of tiller population density, herbage production and tissue turnover in both ryegrass and white clover results reveals further important differences between short and long release treatments (Tables 3.1, 3.4. 3.6 to 3.11, 3.13, 3.17 and 3.21 to 3.26). The data suggest that the long period of lax grazing increased herbage productivity to a greater extend than did the shorter period of lax grazing.

Results from tiller population density, tiller weight, herbage production and tissue turnover measurements showed, in both Experiments, that nitrogen treatments produced overall more herbage than clover plots, though differences were not always statistically significant. These findings indicated that the N fixation and transfer by the white clover to the ryegrass was less than that provided by fertiliser applications. They support the finding of Nelson & Zarrough (1981) in comparison with field plots receiving no nitrogen, that the addition of 90 kg ha^{-1} N annually increased herbage production by increasing tiller density. At higher nitrogen rates, tiller density approached a maximum, and additional yield increases were via increased tiller weight. Furthermore, Parsons *et al.* (1991) observed that the interval between the appearance of grass leaves in an all-grass sward was less than in the grass in the grass-clover sward of the same height. In this study, tiller population responses to nitrogen fertiliser varied depending on the quantity applied. Experiment 1 showed that the early control treatment recovered tiller population density faster at high nitrogen rates than at lower rates (Experiment 2). In the first trial, the advantages of late control disappeared at the end of the experimental period because nitrogen stimulated tillering activity and net leaf growth. Tiller population density and net leaf growth were greater from December to February (Tables 3.4, 3.6 and 3.7). In the second year using 50% less nitrogen than in the first year, the late control advantages persisted during the whole period (Tables 3.17, 3.21, 3.22, and 3.23).

3.5.5. Effect of defoliation on tissue dynamics of white clover

Detailed tissue flow measurements indicated that, in general, clover plants in release plots tended to have bigger petiole and leaf size than early control plots. Although tissue turnover measurements in Experiment 1 did not differ significantly, petiole elongation, leaf expansion and net growth in release swards were generally greater than in early control. In the second Experiment, tissue flow studies show the same tendency, being statistically different in two out of three evaluation periods (late December-early January, and April). In both periods leaf expansion and net growth per locus were greater in long release and short release than the early control treatments ($P \leq 0.05$). These observations and those from sward structure measurements confirm the finding of Da Silva *et al.* (1993, 1994) and Da Silva (1994) that lax grazing management during spring is likely to lead to increased stolon growth and, probably, increase storage of more carbohydrate reserves, which may results in bigger stolons and more competitive white clover plants (Barthram & Grant, 1994). When net production was adjusted for differences in stolon growing points density per unit of area, no statistical differences were observed in five out of six study periods. Furthermore, release treatments produced less in two of those six observation periods than early control ($P \geq 0.05$). These results suggest that early control swards tended to have more bare ground than short release and long release treatments, which was occupied by many small plants of white clover, while short release and long release treatments tended to have less bare ground and fewer, larger white clover plants, compared to early control.

3.5.6. Towards a general measure of sward productivity

Given the number of variables measured in Experiments 1 and 2 and the consistent effects of release treatments on herbage accumulation (Sections 3.3.4 and 3.5.4), tiller population density (Sections 3.3.1 and 3.5.1), and tiller appearance and loss (Section 3.3.3 and 3.5.3) it was of interest to gain an overview of the interrelationships between these individual effects. Canonical discriminant analysis (CDA) is an appropriate way to gain such as overview of the relative contribution of several variables. The results of canonical discriminant analysis in both years (Sections 3.3.9.1 and 3.4.8.1) indicated that increased sward production during summer and autumn was closely associated with high tiller natality late in December, high tiller population from December to February as well as high leaf growth of the individual tillers late in December and early in January. Tiller mortality in both Experiments and tiller population at the end of Experiment 1 did not have a great effect on sward productivity. This pattern of association, especially the association between tiller population density and herbage accumulation, is consistent with the late control hypothesis that increased seedhead formation would promote early summer tillering and subsequently enhanced summer and autumn pasture growth

(Matthew *et al.*, 1989b).

Da Silva previously attempted to confirm the pasture production benefits of late control grazing (Da Silva *et al.*, 1993, 1994; Da Silva, 1994). These authors observed the expected increase in pasture production during the summer-autumn period, but their results did not conclusively show the link between increased pasture production and seasonal patterns of tillering. In fact in one of Da Silva's experiments, increased pasture production was associated with increased ryegrass tiller size, rather than increased tiller density.

In order to better understand the results of Da Silva (1994) the present results were used to explore further the more general relationship between tiller density, tiller size and herbage productivity. It is well recognised that tiller populations are subject to size/density compensation (Davies, 1988; Chapman & Lemaire, 1993). This would imply that tiller density itself would be an ambiguous measure of sward productivity without concomitant measurement of tiller size. A suitable analytical framework for carrying out such analysis has recently been proposed by Sackville Hamilton *et al.* (1995) and Matthew *et al.* (1995), Matthew *et al.* (1996). These authors propose that the classical -3/2 self-thinning line represents a constant "environmental potential" leaf area. On this basis the extent to which individual treatments or plots had achieved their environmental potential tiller density would be measured by their distance from a -3/2 self-thinning line. In calculating the distance from the common -3/2 self thinning-line, the actual position of the reference line is immaterial because the relative distance from the line for different treatments will not be affected by movement of the line itself. Accordingly, a size/density compensation index (SDCI) calculated as the vertical distance of a point defined by the tiller size/density ordinates of a particular plot and an arbitrary -3/2 self-thinning line was developed (Section 3.2.2.4). The results of Experiments 1 and 2 (Figures 3.10 and 3.14) show a consistent and statistically significant relationship between herbage production and size/density compensation index. In both cases the longer duration of lax grazing increased size/density compensation index and herbage production.

The results therefore show that the distance from the -3/2 line may be useful as a sward productivity index. This indicates a need, when evaluating agronomic effects of a particular grazing practice, to differentiate between simple size/density compensation and movement of swards closer to or away from a -3/2 reference line. The former implies no change in sward leaf area, while the latter implies increased sward leaf area. On this basis it is interesting to note that increased leaf elongation was observed on short and long release treatments as compared to early control plots. Early control management moved the sward further to the left of the self-thinning line. That is, the equilibrium tiller density was less than would have been predicted by the -3/2 rule for the reduction in tiller size compared to short release and long release treatments (Matthew *et al.*, 1995).

3.6. SUMMARY AND CONCLUSIONS

The findings of this study indicated that lax spring grazing management of perennial ryegrass swards switched to hard grazing at the time of anthesis, enhanced herbage production during spring and summer-autumn periods. The higher herbage production during spring was due to the higher tiller weight, and during summer-autumn to higher tiller population density and leaf growth per tiller.

The duration of lax grazing was important in determining pasture production. Herbage production increased as the duration of lax grazing increased. For maximum increase in herbage yield lax grazing should start early in September.

Tissue flow measurements in white clover show that lax grazing tended to increase petiole elongation, leaf expansion and net growth. However, tiller core data suggests that lax grazing tended to decrease stolon density. Although white clover responses appear to differ between years, there was some evidence that late control increased net leaf growth.

In both Experiments, an increase in tiller population density was accompanied by a decrease in tiller size. Evaluation of these effects in terms of -3/2 size/density compensation appeared to provide a reliable index for assessing implications on sward productivity.

Tissue turnover measurements indicated that an increase in the size/density compensation index was accompanied by an increase in leaf elongation and net growth per tiller. Canonical discriminant analyses demonstrated that herbage production during summer-autumn was highly associated with tiller population density from December to February and with high tiller natality late in December and ryegrass leaf growth during December and January. Tiller demography patterns were consistent with enhancement of what Matthew *et al.* (1993) called the reproductive pathway, also represented by category 7 tillers of Korte (1986).

Chapter 4

THE INFLUENCE OF DEFOLIATION MANAGEMENT ON SWARD DYNAMICS AND STRUCTURE

4.1. INTRODUCTION

In the pasture the primary growth unit is the individual shoot or tiller, and pasture can be regarded as a population of tillers. Increased herbage production of grasses may be attributed to increases in tiller density or tiller weight (Nelson & Zarrough, 1981). Experiments with plants at low density are often interpreted to suggest that tiller formation is a more important yield determinant than is tiller weight (Nelson & Zarrough, 1981). When tiller population density is high or the sward becomes reproductive, tiller weight becomes more important. However, while herbage production responses have been explained in terms of responses in tiller population density or tiller weight, it has also been recognised that tiller populations are subject to size/density compensation (Hodgson, *et al.*, 1981; Bircham & Hodgson, 1983; Davies, 1988; Chapman & Lemaire, 1993). That is to say, a tiller size increase may be observed in the case of a tiller population decrease with increasing biomass, without any change in sward productivity. It would therefore be helpful to provide a means to distinguish SDC response (either in tiller size or tiller density) from productivity responses.

Similarly a tiller population increase may be a simple reflection of reduced biomass, again without necessarily indicating a change in sward productivity. The results of the two previous grazing experiments (Chapter 3) suggest that treatment differences in dry matter production may be associated with differences in tiller population density, tiller weight, or a combination of both. They also suggest that there is a substantial degree of size/density compensation in ryegrass tillers. However, under grazing conditions factors such as competition with other species (Chapman & Lemaire, 1993), tiller uprooting, treading, return of dung and urine to the soil and animal selectivity may interact with physiological or morphological responses to defoliation (Hodgson, 1982; Watkin & Clements, 1978) to limit compensatory changes. To investigate the underlying adjustments to defoliation, the following experiment was set up under glasshouse conditions to study the responses of perennial ryegrass to a wider range of cutting heights. Management was designed to simulate continuous stocking, cutting two times a week to five different cutting heights. The response to defoliation was measured in terms of tiller dynamics, sward structure, tiller size, tiller size/density compensation, leaf appearance rate, leaf, shoot and root growth, and carbon exchange. This evidence is used to propose a theoretical base for distinguishing productivity responses independent of SDC.

4.2. MATERIALS AND METHODS

4.2.1. General description

One hundred mini-swards of *Lolium perenne* (cv. Grasslands Nui) were established from seed in plastic pots 15 cm per side and 15 cm deep on 5 May 1993, and grown in a greenhouse at the Plant Growth Unit, Massey University in Palmerston North. Plants were grown at temperatures of 20 °C during the day and 15 °C at night. Five 250 W mercury lamps were used (one per bench) for 2 h illumination in early morning and late afternoon to provide a 12 h photoperiod (from 06.00 h to 18.00 h). Pots were filled with 60:40 peat and pumice. Sowing rate was equivalent to 30 kg seed ha^{-1}, and once the seedlings were established, each pot was thinned to 25 kg seed ha^{-1}. Nutrients were supplied as 1000 g of agricultural lime, 3000 g dolomite, 600 g micromax, 2000 g osmocote (release over 8-9 months) and 1000 g osmocote (release 3-4 months) per m^3 of potting media. Each pot was watered daily and the sward was fertilized with 2.8 kg N ha^{-1} $week^{-1}$ on a weekly basis. Urea was used as the N source.

The experimental period was of six months duration (May to November). The one hundred pots were placed in five separate trays (20 per tray). Before applying the treatments, all pots were cut to 50 mm on 4 June (5 weeks after sowing). Soon after this the pots were randomly allocated to five treatments (20, 40, 80, 120 and 160 mm sward surface height) with 20 replicates. Each tray contained four replicates per treatment (Plate 4.1). All pots were cut twice weekly to the specified surface height, using a pair of scissors. Differential cutting heights were first imposed on 11 June, and recording began on 14 June. Every four weeks from 9 July to 5 November the 20 pots contained in one tray (four replicate pots per treatment) were withdraw for destructive measurements. Each mini-sward was surrounded by a polyethylene tube to the appropriate cutting height (see Plate 4.1).

4.2.2. Sward measurements

4.2.2.1. Herbage harvested

All pots were clipped to their designated height twice weekly (Monday and Friday), and the herbage collected, dried at 80 °C for 24 h and weighed.

Plate 4.1. A general view of the ryegrass experiment in the glasshouse. There were five tables with 20 pots each (four per treatment). All pots contained in each table were destroyed at the same time. In the foreground, the five cutting heights are illustrated and at the far rear are two later tables containing 20 pots each.

4.2.2.2. Tiller population density

Tiller population density was first determined as the average of 20 pots on 11 June (when differential cutting heights were first imposed) and from then onwards every four weeks during the experimental period, and the total ryegrass tiller number per pot was recorded. Results are shown as tiller population per unit area (tillers m^{-2}).

4.2.2.3. Tiller weight

At each destructive sampling a sub-sample of about 50 ryegrass tillers per pot was selected at random, separated into stem, leaf and dead material, and dried at 80 °C for 24 h and weighed.

4.2.2.4. Size/density compensation

Tiller size/density compensation (SDC) was determined using the monthly records of tiller weight and tiller population density. Also, the relationship between total herbage harvested and size/density compensation index (Section 3.2.2.4) was calculated for the last two months, when tiller population SDC appeared to have reached equilibrium at the various defoliation intensities. Also, the average of leaf mass for the last two harvests was determined and plotted against SDCI.

4.2.2.5. Total herbage mass, above ground herbage mass and root mass

Total herbage mass was determined every four weeks from destructive harvests, as the sum of the above ground herbage mass plus below ground root mass. Above ground herbage mass was calculated as the dry weight of all tillers present in each pot (sum of tillers used to determinate tiller weight plus tillers used for sward structure). The whole root mass in destructively harvested pots was washed free of soil, dried at 80 °C for 24 h and weighed.

4.2.2.6. Leaf appearance rate

Leaf appearance rate was measured monthly from August to November on 80 mm, 120 mm and 160 mm cutting heights (i.e. 4 times during the trial period). Because only sheath tubes remained after harvesting in 40 mm and 20 mm cutting heights and it was not possible to tag individual leaves, leaf appearance rate was determined only in the last three harvests and the last harvest, respectively for these two treatments. Each time, the top surface of the youngest mature leaf (leaf 2) of 5 random tillers per pot was marked with a drop of white correction fluid (twink). The leaves were tagged a day after the new recording period started. To estimate leaf appearance rate, before the next destructive harvest leaf number per tiller was counted from the tagged leaf to the youngest one, corrected for the two leaves represented at the initial tagging, and divided by the number of days elapsed between readings.

4.2.2.7. Sward structure

Sward structure was determined at each of the 5 destructive harvests. At each harvest a set of approximately 100 tillers per pot were harvested at soil level and cut into segments (Plate 4.2). Sections of 20 mm were cut for 20 mm, 40 mm and 80 mm cutting heights; 30 mm for 120 mm cutting height; and 40 mm for 160 mm cutting height. Material in each stratum was then sorted into leaf, stem and dead, dried at 80°C for 24 h and weighed.

Plate 4.2. A general view of the procedure used to determine sward structure of ryegrass mini-swards. From left to right +160 mm, 120-160 mm, 80-120 mm, 40-80 mm and 0-40 mm strata.

4.2.2.8. Gas exchange measurements

a. Description of the system

The closed system design for measuring photosynthesis, soil respiration and dark respiration is shown in Plate 4.3. The system consisted of two chambers mounted on a wooden base board. Each wooden base contained a thermocouple, a light sensor and fan. Each chamber was constructed of thin perspex and the diameter and height were 52.5 cm and 48.7 cm, respectively. The system was protected from air leaks by immersing the bottom edge of each chamber in vegetable oil (see Plate 4.3). Magnesium perchlorate was used to reduce the water vapour in the air passing into the infra-red gas analyzer (IRGA; BINOS II, Leybold-Heraeus GMBH). The air flow through the IRGA was set at 15 cm^3 s^{-1}. Artificial lighting (six 400 W mercury lamps HPI-T and two 500 mercury lamps white E-40) was used and foliage was placed at a distance of 2 m from lamps. To prevent changes in temperature a room with automatic temperature control was used. Temperature inside the room was regulated at 20 °C. Also, to prevent an increase in temperature inside the chamber during the recording periods, due to its proximity to the lamps, there was a constant flow of water over a glass plate fitted below the mercury lamps (see Plate 4.3). The temperature and light intensity were monitored inside the chamber with a thermocouple and light sensor connected to a data logger. Light intensity and temperature inside the chamber were on average 402 $\mu E\ m^{-2}\ sec^{-1}$ and 19.45 °C, respectively. The air inside each chamber was stirred using a small fan mounted on the wooden base. The air was stirred to maintain the boundary layer resistance constant throughout the measurement and to eliminate gradients of CO_2, O_2 and water vapour across the chamber (Sestak *et al.*, 1971). Measurements were performed in the two chambers alternately. A schematic representation of the layout of the closed system is shown in Figure 4.1.

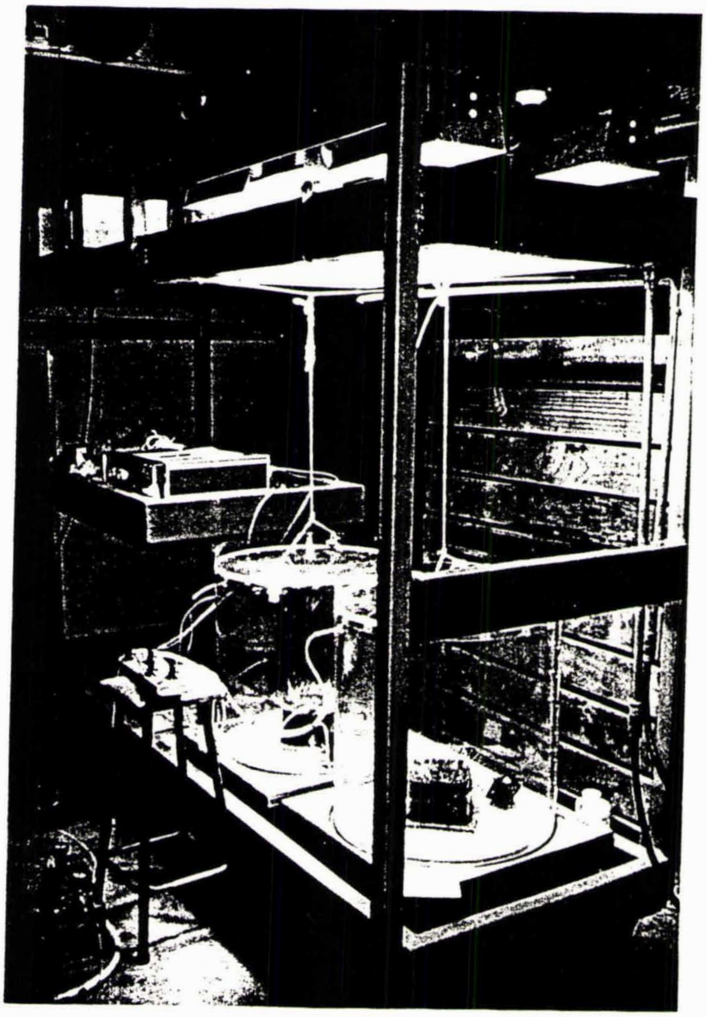


Plate 4.3. A general view of the system used for estimation of carbon exchange. The same system was used for soil respiration following removal of above ground plant material.

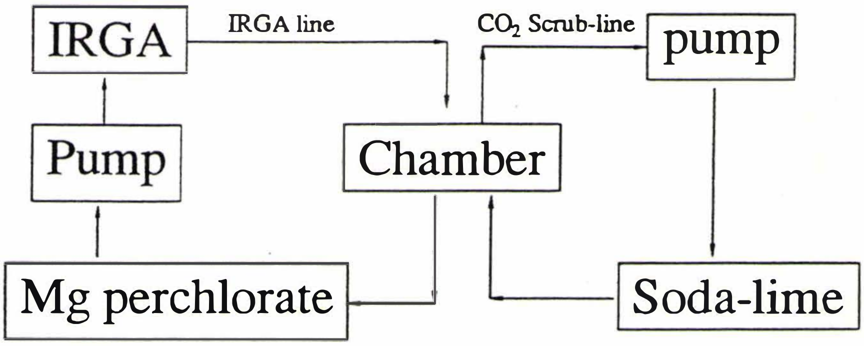


Figure 4.1. A simple schematic model of the carbon exchange system

b. Photosynthesis, soil and dark respiration

Photosynthesis was estimated by enclosing the whole pot in the chamber for 10 minutes. Air was first pumped over the soda lime scrubber until the CO_2 concentration was reduced to 340 ppm. Measurements of CO_2 concentration were then taken every minute for 6 minutes. Photosynthesis was estimated three times during the last week of the trial, and because the data obtained were very similar within and between treatments, the results presented here are the means of those measurements.

To measure dark respiration, each pot was enclosed in the chamber and when the CO_2 concentration stabilised around 340 ppm the light was turned off; 2 minutes later recordings of CO_2 were made, and continued every minute for 10 minutes. Measurements were carried out twice in the last week of the trial period and the results presented are the means of those two measurements. Soil respiration was estimated once at the end of the experimental period (5 November). All the tillers were cut off at ground level, and readings of CO_2 concentration were made every minute for 10 minutes, in the same way as those of photosynthesis (Plate 4.3).

c. Calculations

Photosynthesis and dark respiration were estimated using the equation:

$$CER = \frac{\Delta\ CO_2\ x\ V}{t\ x\ A}\ x\ 0.042$$

Where :

- CER is efflux or influx of CO_2 (µmol kg^{-1} DM s^{-1})
- Δ CO_2 is the change in CO_2 concentration (ppm)
- A is the leaf weight (kg dry weight);
- V is the volume of air enclosed in the system (m^3).
- t is the length of interval over which CO_2 concentration changes are recorded (s).

To convert CO_2 concentration in ppm (v/v) to density units (µmol m^{-3}) the molar volume of the International Civil Aviation Organization (ICAO) atmosphere was used as a conversion constant.

ICAO molar volume is 2.3645×10^{-2} m^3 / mol^{-1} = 0.0236 m^3 / mol $\therefore$ 42 mol / m^3
1 atm = 0.042 mol / litre $\therefore$ 1 ppm = 0.042 µmol / litre or 24 ppm = 1 µmol / litre

d. Estimation of chamber volume

The total volume of the system was calculated by injecting a known volume of pure CO_2 into the chamber. To do so, the CO_2 concentration present in the chamber was recorded before and after the injection of 40 ml pure CO_2, and the volume of the system was determined using the following formula:

$$\text{Volume (ml)} = A \times 10^6/B$$

Where A is the volume of pure CO_2 added (ml) and B is the increase in concentration of CO_2 (ppm) after injection. The CO_2 concentration increment was 488.3 ppm, so the total volume of the system was 81.9 litres.

4.2.3. Statistical analysis

Analyses of variance were carried out using the General Linear Model (GLM) procedure of SAS (SAS Institute Inc. 1989). The five cutting heights were analyzed as treatments in a completely random design (CRD) with four replicates and separate analyses carried out for each harvest date. To gain an overview of the interrelationship between the different variables measured a canonical discriminant analysis was performed.

4.3. RESULTS

4.3.1. Total herbage mass

At all stages above ground plant mass, root mass and total plant mass increased with increasing cutting height, though there was little difference in the values for 80 mm, 120 mm and 160 mm cutting heights (Table 4.1). With the exception of the 20 mm cutting height where above ground herbage mass and total plant mass did not change over the first three months (Table 4.1), on average above ground herbage mass and total plant mass increased about three-fold during this period. During the last two months, the 20 mm cutting height increased on average twelve-fold, while the other treatments increased about 100% (Table 4.1). Changes in root mass within treatments were relatively small over the first three months, but on average root mass increased seven-fold over the next two months.

4.3.2. Sward structure

Figures 4.2a-e show the changes in sward structure over the five destructive harvests. The spatial distribution of the sward changed over time according to the intensity of defoliation. In general, the highest amount of leaf was observed in the top stratum, and the lowest at the bottom of the sward. The opposite was the case with stem. With the exception of the 20 mm cutting height where the greatest quantity of dead material was found in the lowest strata, the greatest proportion of dead material was always found in the second stratum. Figures 4.2a-e show a continuous increase in stem, leaf and dead material from 9 July to 5 November. Also, the contribution of the different strata to herbage mass changed over time. During July and August all strata in all treatments made a similar contribution to herbage mass (Figures 4.2a and b).

Table 4.1. Effect of cutting height on root mass, herbage mass and total plant mass in ryegrass mini-swards (g DM m^{-2}).

Cutting	9 Jul			6 Aug			3 Sep			1 Oct			5 Nov		
height	RM[1]	HM[2]	TPM[3]	RM	HM	TPM	RM	HM	TPM	RM	HM	TPM	RM	HM	TPM
20	1.0	9.1	10.2	3.6	10.8	14.3	1.7	11.2	12.9	13.0	38.7	51.7	31.9	135.1	167.0
40	2.2	26.4	28.6	7.1	51.3	58.4	9.9	88.6	98.6	31.5	150.4	182.0	63.0	252.3	315.3
80	2.9	64.5	67.4	12.5	107.6	120.1	14.0	193.9	207.9	43.2	222.7	265.9	96.9	322.6	419.5
120	3.9	78.2	82.1	14.8	138.5	153.2	12.7	200.2	212.9	49.1	255.0	304.1	94.8	425.8	520.6
160	2.7	80.8	83.5	10.4	126.6	137.0	13.2	205.4	218.6	41.6	262.3	303.9	95.4	363.5	458.9
SEM[+]	0.21	3.90	3.80	0.75	8.02	8.60	0.88	11.85	12.40	3.42	13.35	16.50	12.4	27.48	38.01
Signif.	****	****	****	****	****	****	****	****	****	****	****	****	**	****	***

* = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$, **** = $P \leq 0.0001$

[1] Root mass

[2] Above ground herbage mass

[3] Total plant mass = root mass + above ground herbage mass

[+] SEM = Standard error least squares means

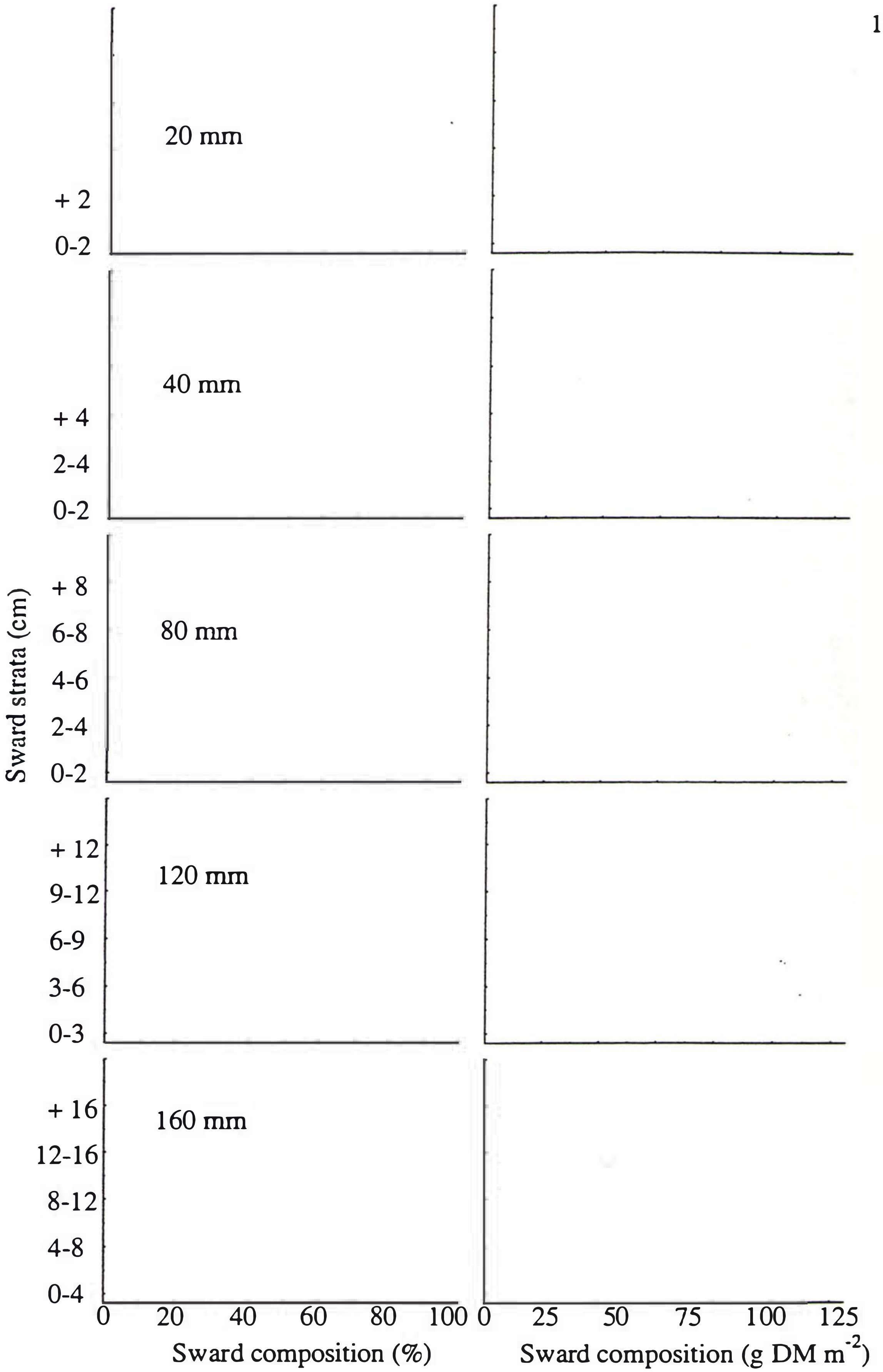


Figure 4.2. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples). Stratum increments are not the same for all treatments.

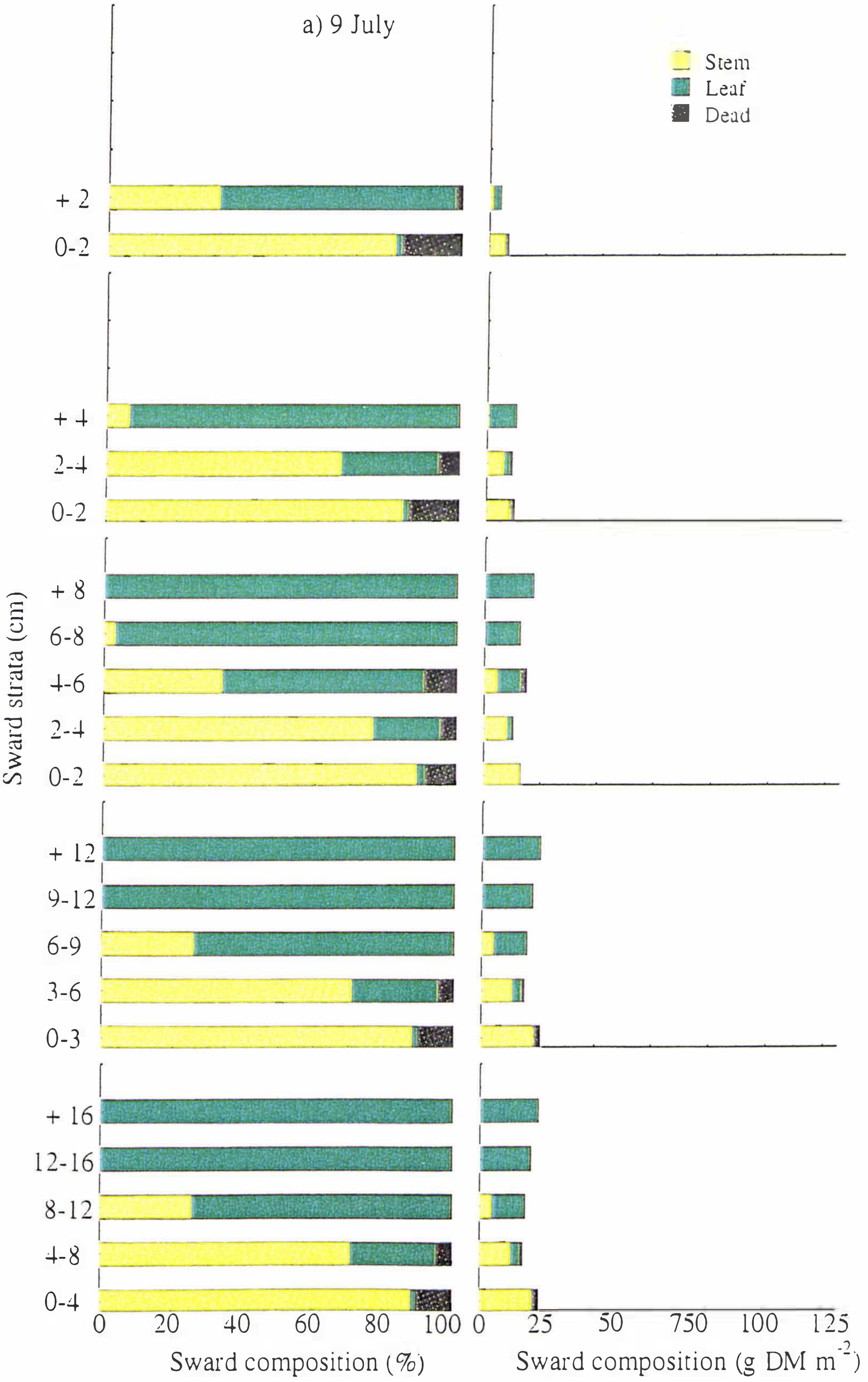


Figure 4.2a. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples).

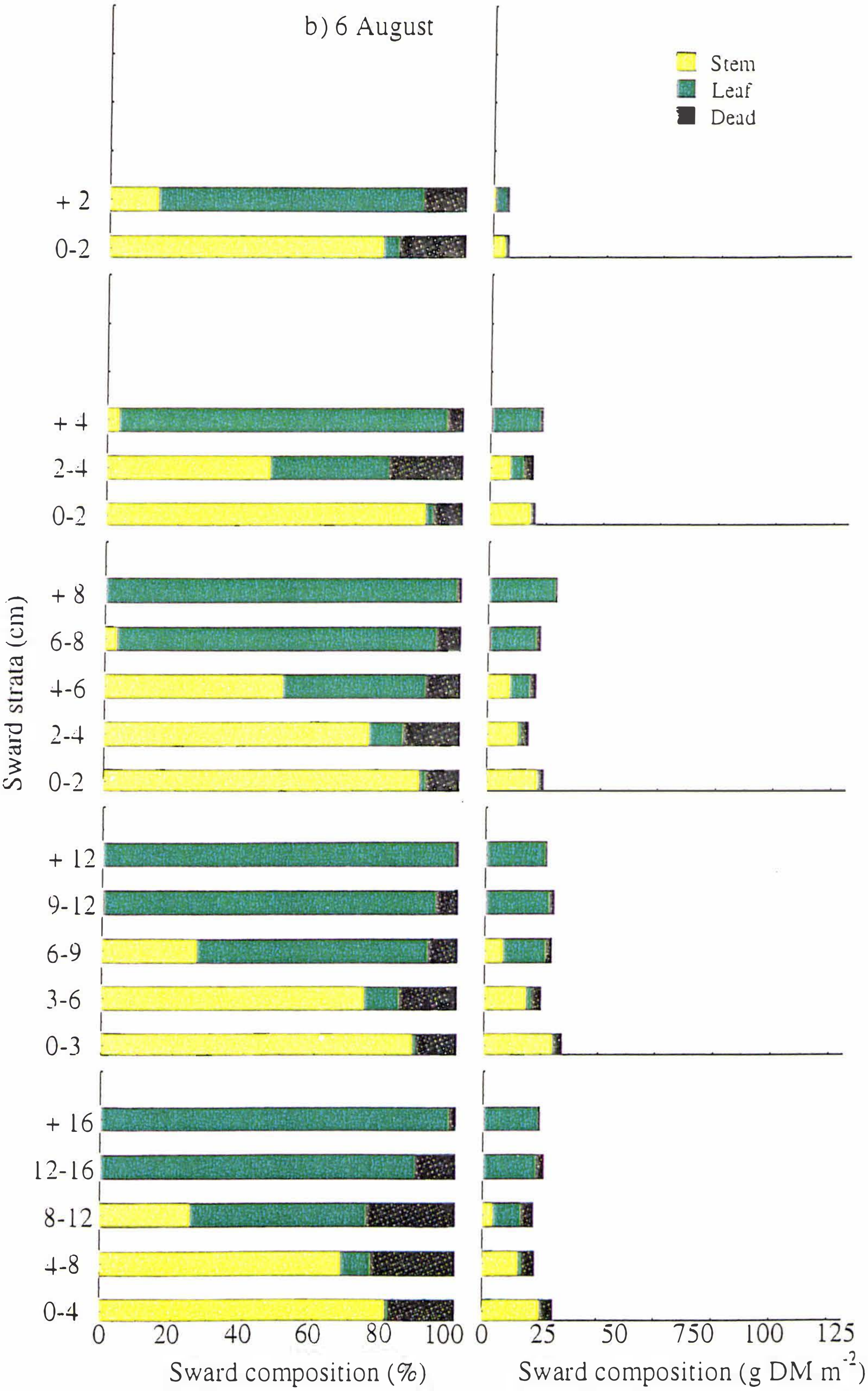


Figure 4.2b. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples).

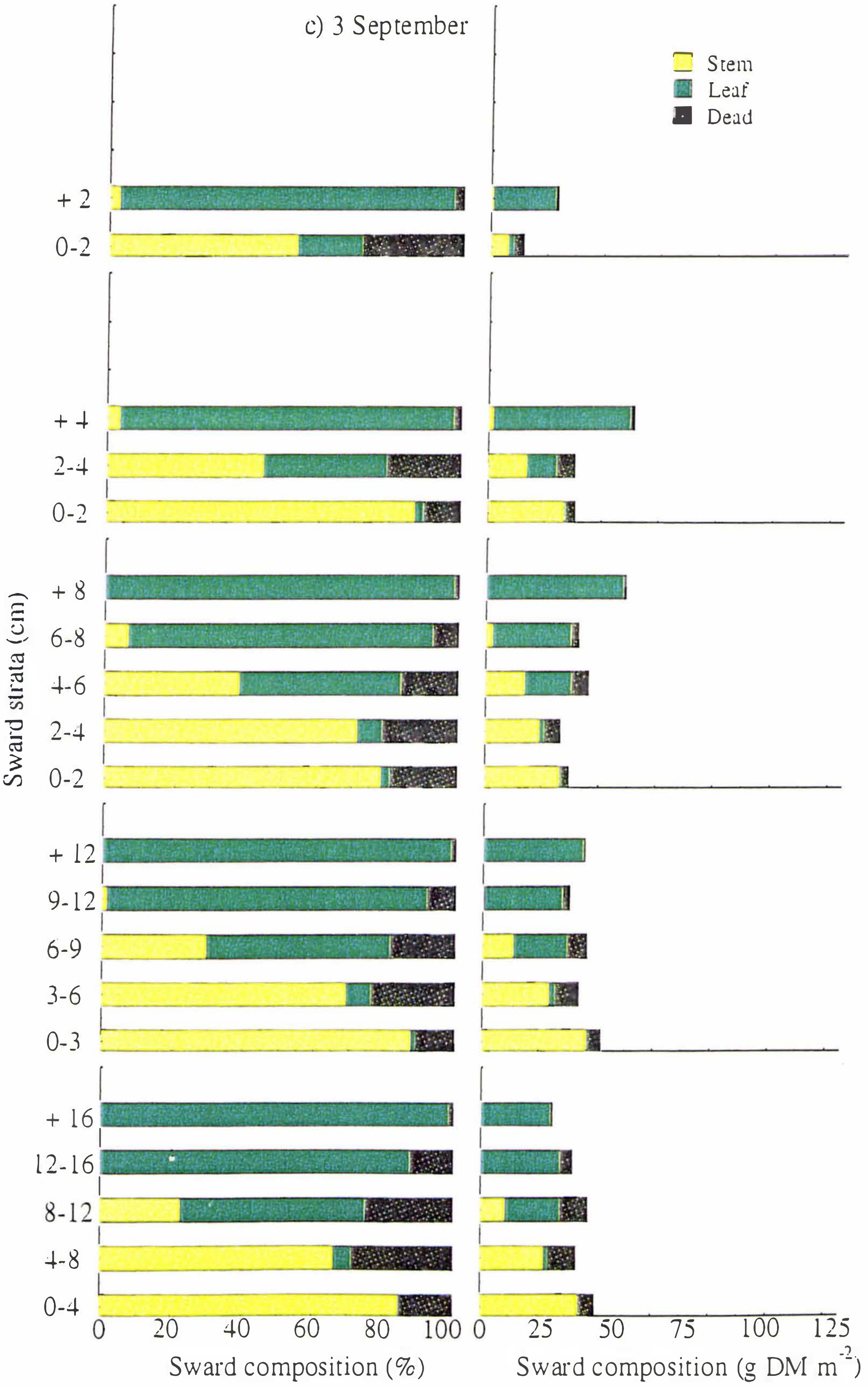


Figure 4.2c. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples).

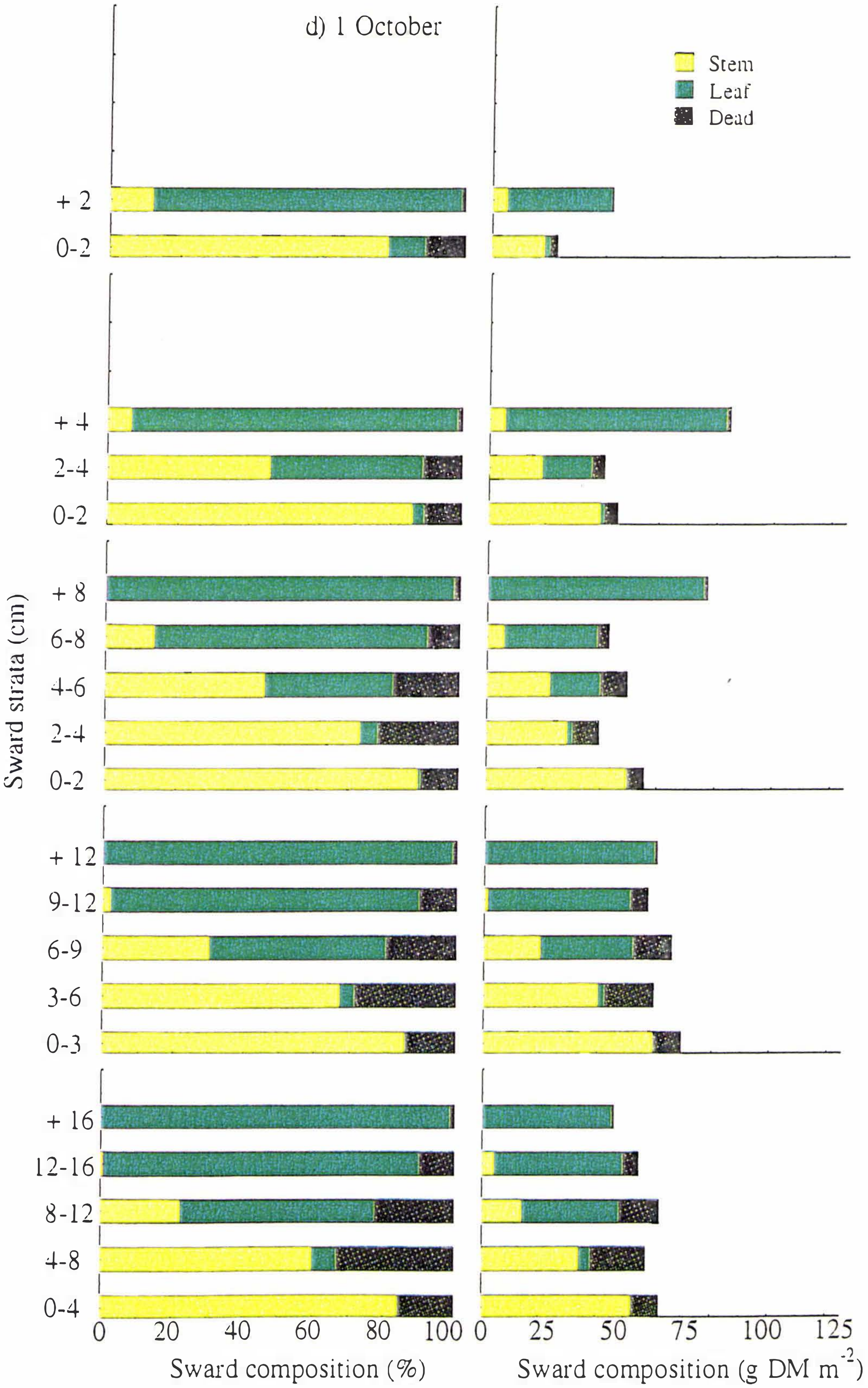


Figure 4.2d. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples).

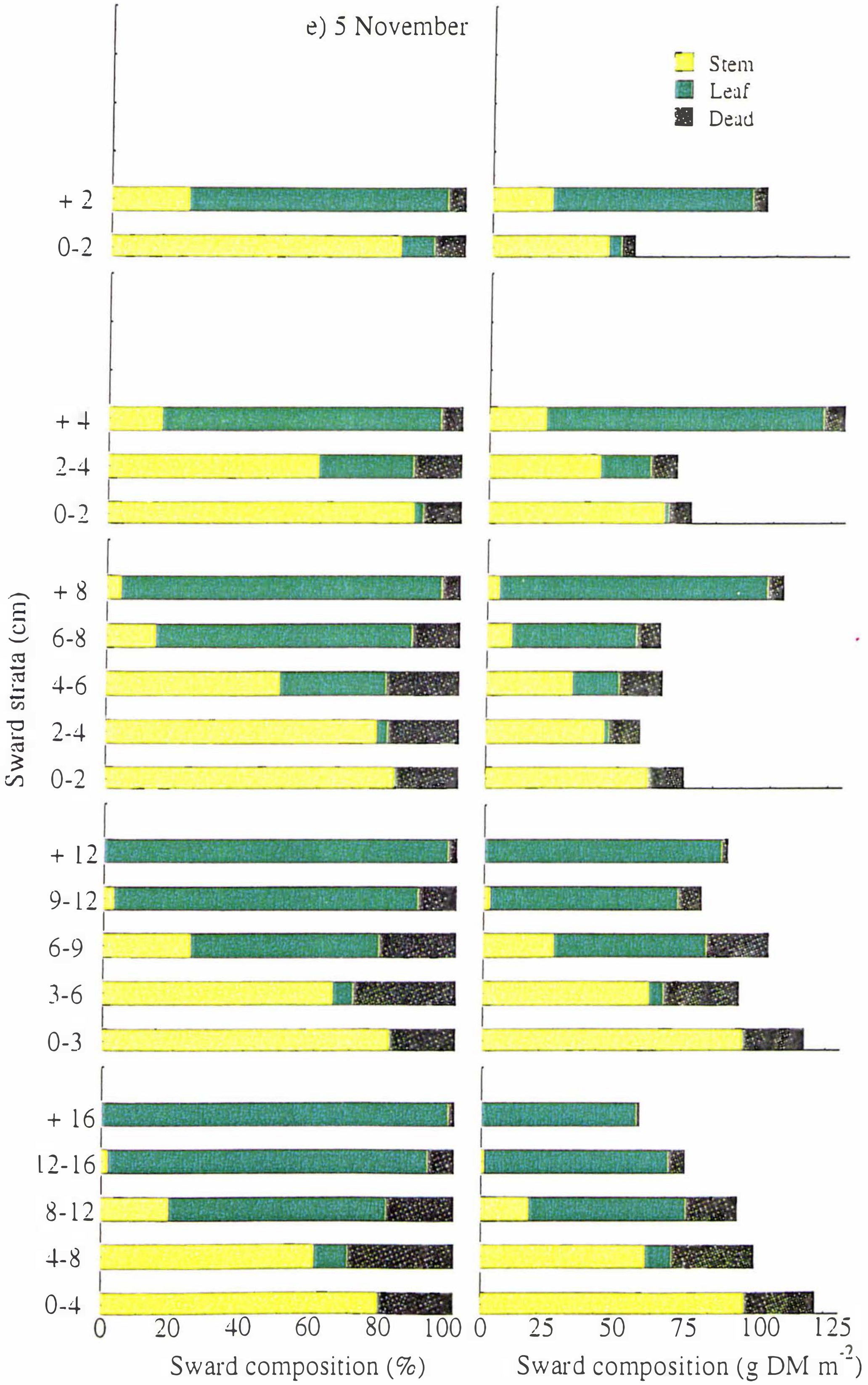


Figure 4.2e. Effect of the cutting height on structure of ryegrass mini-swards (From destructive samples).

However, from 3 September onwards the greatest contribution to herbage mass was found in the highest strata for 20 mm to 80 mm cutting heights, while for 120 mm and 160 mm cutting heights it was found in the lowest stratum (Figures 4.2c, d and e). However, this result must be interpreted with caution because it may to some extent reflect bias in the measurements introduced by the extension of vertical segments when tillers were aggregated for sectioning.

4.3.3. Herbage harvested

The cumulative mass of herbage harvested from the ryegrass swards is shown in Figure 4.3. Cumulative herbage production was lowest at 20 mm cutting height and highest at the 120 mm cutting height, with the five cutting heights ranked in the order 120>80>160>40>20 (Figure 4.3). The effect of cutting height was highly significant ($P \leq 0.001$) at all stages.

Figure 4.4 shows the changes over time in rates of herbage harvested expressed on a daily basis. Overall, the lowest herbage harvested was observed at 20 mm sward surface height and the highest between 80 and 120 mm. The daily harvest rate for 80 mm, 120 mm and 160 mm cutting heights increased steadily from the start of the experiment until early October and subsequently declined. Rates for 20 mm and 40 mm cutting were at a low level until September and late July, respectively, but then increased steadily until mid-late October. By the end of the Experiment, in early November, harvest rates for all five treatments were similar (Figure 4.4).

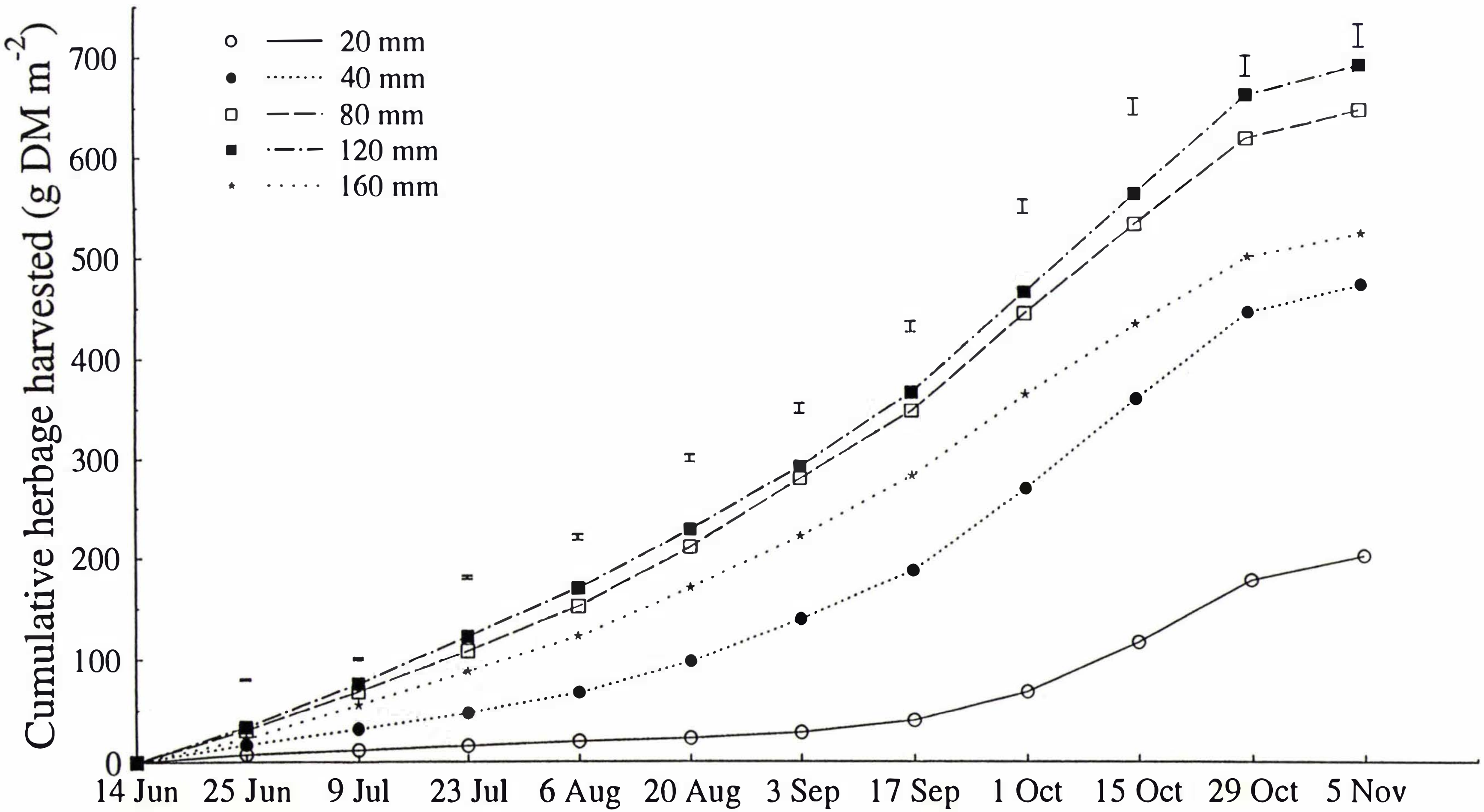


Figure 4.3. Effect of cutting height on total herbage harvested (g DM m^{-2}) for the period 14 June to 5 Noverber in ryegrass mini-swards. (Values shown are cumulative totals from twice - weekly harvests).

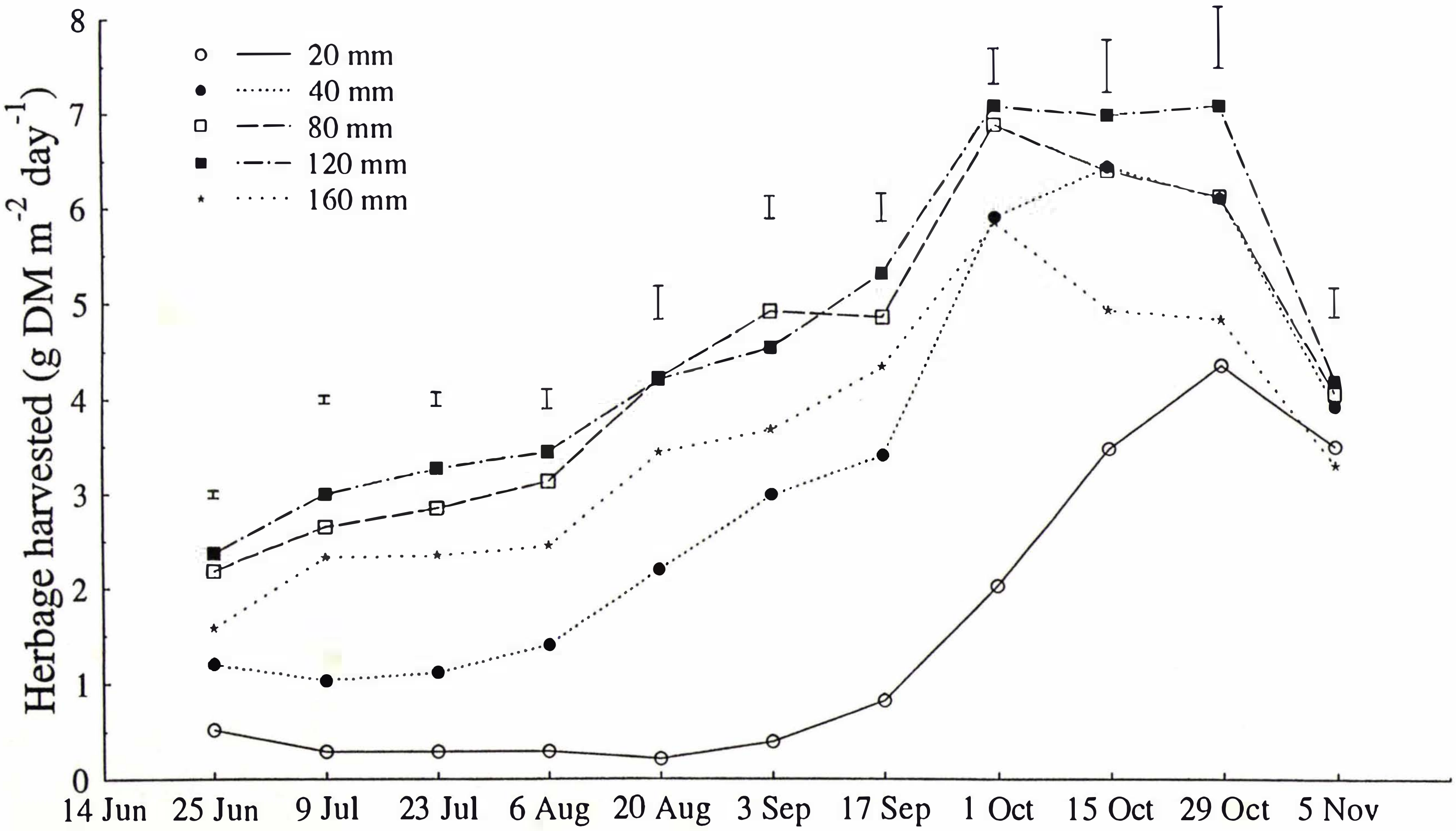


Figure 4.4. Effect of cutting height on herbage harvested (g DM m^{-2} day^{-1}) from ryegrass mini-swards.

4.3.4. Defoliation effects on rates of photosynthesis and respiration

Estimates of carbon exchange, per unit of ground area and per unit of leaf mass, are shown in Table 4.2. Since the statistical analysis of the three sets of photosynthesis data and of the two respiration measurements showed similar tendency between treatment means, rates of photosynthesis and respiration are the means of those readings. Gross and net photosynthesis per unit of ground area (μmol CO_2 m^{-2} s^{-1}) of the mini-swards harvested at cutting heights between 80 mm and 120 mm were greater than from those harvested more intensively (40 and 20 mm) and laxly (160 mm) (Table 4.2). The greatest rates of gross and net photosynthesis were observed in pots harvested at 120 mm, and the lowest in the most intensively defoliated 20 mm cutting height ($P \leq 0.01$). Conversely, rates of canopy gross and net photosynthesis per unit of leaf dry weight (μmol CO_2 kg^{-1} s^{-1}) declined as the severity of defoliation decreased from 20 mm to 160 mm (Table 4.2). Thus, the lowest gross and net photosynthesis per unit of leaf weight were observed at 160 mm and the greatest at 20 mm of cutting height ($P \leq 0.05$).

No statistical differences ($P \geq 0.05$) were observed in rates of dark respiration per unit of soil area (μmol CO_2 m^{-2} s^{-1}) or per unit leaf weight (μmol CO_2 kg^{-1} s^{-1}), or in soil respiration (μmol CO_2 m^{-2} s^{-1}), (Table 4.2). Rates of dark respiration and soil respiration were small relative to gross and net photosynthesis.

4.3.5. Leaf appearance rate

Leaf appearance rate (leaves $tiller^{-1}$ day^{-1}) was estimated four times in 80 mm, 120 mm and 160 mm cutting heights, three times in 40 mm and once in 20 mm cutting height (Table 4.3). The results showed an increase in leaf appearance rate as the severity of defoliation increased, although leaf appearance rates were similar for 120 mm and 160 mm cutting heights (Table 4.3). Hence, the order of the treatments was $20>40>80>120=160$.

Table 4.2. Effect of cutting height on net photosynthesis (NP), gross photosynthesis (GP), dark respiration (DR) and soil respiration (SR) rates of ryegrass mini-swards.

		μmol CO_2 m^{-2} soil surface area s^{-1}		
Cutting height	NP	GP	DR	SR
20	8.7	9.0	0.28	0.87
40	10.4	11.5	1.04	0.64
80	11.2	11.3	0.28	1.36
120	12.0	12.5	0.48	1.24
160	9.9	10.7	0.76	0.93
SEM	0.52	0.63	0.027	0.25
Signif.	**	*	ns	ns
		μmol CO_2 kg^{-1} leaf DM s^{-1}		
20	107.0	110.9	3.8	
40	77.1	85.0	7.8	
80	76.8	84.7	2.5	
120	72.0	74.7	2.7	
160	60.5	65.3	4.8	
SEM	10.5	11.75	2.21	
Signif.	ns[1]	ns[1]	ns	

[1] Regression analyses of NP and GP on cutting height were statistically significant for these two data sets.

NP = 178 - (1.13 x CO_2) and GP = 184 - (1.27 x CO_2). $P \leq 0.01$.

Table 4.3. Effect of cutting height on leaf appearance rates of ryegrass mini-swards (No. of leaves tiller^{-1} day^{-1}).

Cutting height	6 Aug	3 Sep	1 Oct	5 Nov
20	nd[1]	nd	nd	0.116
40	nd	0.096	0.079	0.103
80	0.085	0.088	0.068	0.096
120	0.067	0.085	0.057	0.090
160	0.063	0.087	0.056	0.087
SEM	0.0048	0.0060	0.0045	0.0042
Signif.	*	ns	**	**

[1] = Not determined

4.3.6. Tiller population density

The changes in tiller population density throughout the experimental period are shown in Table 4.4. At the beginning of the trial (11 June), the overall tiller population in all swards was around 3600 tillers m^{-2}. Four weeks after the cutting treatments were applied (July 9), tiller population density in the 20 mm cutting height had decreased by about 25% and was only 75% of values for 40 mm to 160 mm cutting heights ($P \leq 0.0001$), which maintained or increased their tiller density at this time. Tiller density in the 20 mm cutting height declined further from June to early September (Table 4.4). From then on tiller density in this treatment increased sharply. With the exception of the pots cut at 160 mm, where the tiller population density only increased 20 % over six months, there was high tillering activity on all other treatments, especially from August onwards (Table 4.4). The 40 mm defoliation intensity showed the highest tillering activity, particularly in September and October, with tiller population increasing 2 ½ times over this period. Final tiller population density, with the exception of the 20 mm defoliation intensity, was inversely related to cutting height.

Table 4.4. Effect of cutting height (mm) on tiller population densities of ryegrass mini-swards (tillers m^{-2}).

Cutting height	9 Jul	6 Aug	3 Sep	1 Oct	5 Nov
20	3078	1989	1956	3578	8667
40	3867	4678	6856	9167	9733
80	4578	4956	6500	8044	7422
120	4811	4467	4544	6644	7200
160	3778	3756	3689	4589	4833
SEM	194	255	332	497	654
Signif.	****	****	****	****	***

4.3.7. Tiller weight

In general, results of the analyses of variance over the five months of observations indicated statistical differences between treatments in leaf, stem, dead material and total weight per tiller ($P \leq 0.001$, Table 4.5). Leaf, stem, and dead material weight increased over time as defoliation intensity decreased. Thus, the greatest tiller weight was always observed at 160 mm and the lowest at 20 mm.

Table 4.5. Effect of cutting height on tiller weight (mg tiller^{-1}) in ryegrass mini-swards.

Cutting height		Leaf	Stem	Dead	Total TW
9 Jul	20	1.0	3.0	0.0	4.0
	40	2.0	4.0	1.0	7.0
	80	7.0	6.0	1.0	14.0
	120	10.0	8.0	1.0	19.0
	160	13.0	10.0	1.0	24.0
	SEM	0.06	0.03	0.01	0.07
6 Aug	20	3.5	2.3	1.5	7.3
	40	5.6	4.6	1.9	12.1
	80	11.9	8.8	2.6	23.3
	120	16.6	13.1	3.1	32.8
	160	15.8	11.7	5.4	32.9
	SEM	1.10	0.60	0.48	1.51
3 Sep	20	3.5	2.3	1.4	7.2
	40	8.3	4.7	2.2	15.2
	80	14.8	12.6	4.0	31.4
	120	21.8	18.3	6.6	46.6
	160	26.8	20.3	9.5	56.6
	SEM	0.84	1.07	0.48	1.60
1 Oct	20	7.5	4.4	0.9	12.8
	40	9.4	7.5	2.2	19.1
	80	14.1	12.6	4.3	31.0
	120	19.3	16.9	6.4	42.6
	160	25.0	25.4	11.7	62.0
	SEM	0.80	1.36	0.43	1.77
5 Nov	20	10.1	9.8	0.8	20.6
	40	14.1	13.3	4.5	31.9
	80	19.9	22.5	7.0	49.4
	120	23.5	27.1	11.6	62.2
	160	34.5	35.2	15.5	85.3
	SEM	1.30	1.07	0.53	2.30
Signif.[1]		****	****	****	****

[1] = The significance for treatment differences was common to all dates.

4.3.8. Size/density compensation and effect on herbage production

The effect of defoliation intensity on the relationship between weight per tiller (mg DM) and tiller population density (tiller m^{-2}) over time is given in Figure 4.5 using data from replicate pots within treatments. Figure 4.5 suggests that the tiller size/density relationship evolved over time, not reaching its final equilibrium until October/November. Visual inspection of the final equilibrium (Figure 4.5) also suggests a two-phase self-thinning relationship, as predicted by a recent theoretical examination of the size-density relationship (Matthew *et al.*, 1995). In order to examine this point in more detail two-phase splines were fitted to the combined data for the October and November harvests, omitting the 20 mm cutting height because of the great variation in tiller population density of this treatment (Table 4.4 and Figure 4.5). This procedure provided a significant improvement compared to fitting parallel straight lines ($F_{2,24}$ = 15.4; $P \leq 0.001$). Slopes obtained for the two phases (Matthew *et al.*, 1995) were respectively -0.17 ± 0.15 (phase-3) and -2.56 ± 0.17 (phase-2), with the break point at x = 3.79. Size/density compensation for 40 mm to 120 mm cutting heights is therefore significantly steeper than -3/2, while under lax defoliation (160 mm) there is evidence that size/density compensation may be flatter than -3/2 (Figure 4.5).

Means of combined leaf mass data from October/November harvests were used to calculate the correction factors (C_a and C_r) of Matthew *et al.* (1995). The results showed that C_a was the larger of the two correction factors (Table 4.6). An increase in defoliation intensity (from 120 to 20 mm) resulted in a reduction in C_a. C_r was similar at cutting heights 40 mm, 80 mm and 160 mm, but C (C_a + C_r) and SDCI decreased as the cutting height decreased from 120 mm to 20 mm (Table 4.6).

Size/density compensation index (SDCI) was defined in section 3.3.9.1 as the distance from an arbitrary -3/2 compensation line of a point defined by tiller population and tiller size (as x and y coordinates, respectively). Based on the theoretical derivation of the SDC line as a constant leaf area condition (Matthew *et al.*, 1995), SDCI is likely to be

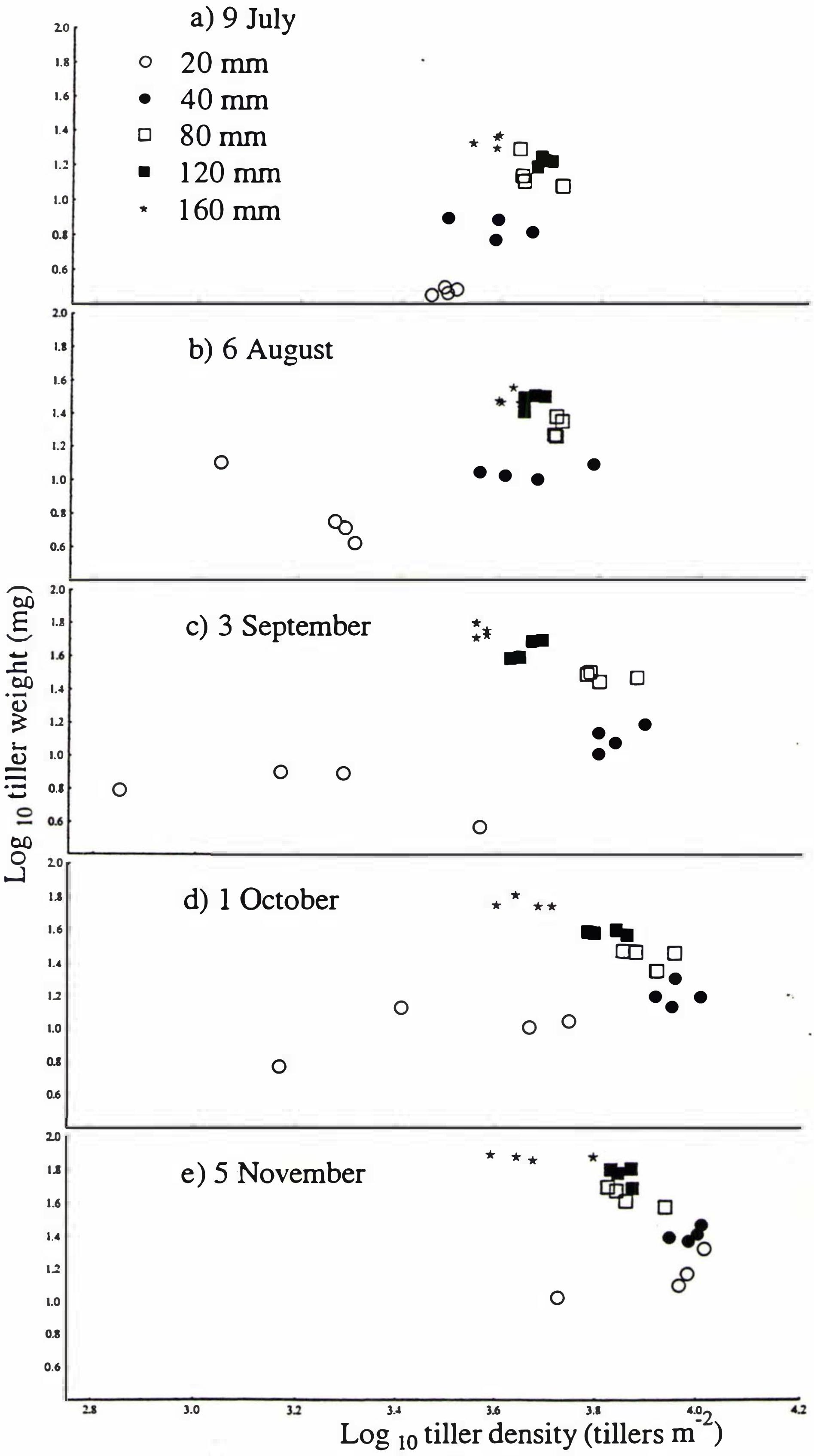


Figure 4.5. Tiller size/density compensation (SDC) in response to variation of cutting height in ryegrass mini-swards.

Table 4.6. Theoretical effect on SDCI of change in leaf area per pot (ΔC_a) and leaf:non leaf ratio (ΔC_r) with cutting height. Observed variation in SDCI compared to 120 mm cutting height shown for comparison.

Cutting height	ΔC_a[1]	ΔC_r	$\Delta C_a + \Delta C_r$	ΔSDCI
20	-0.74	-0.15	-0.59	-0.79
40	-0.26	-0.03	-0.23	-0.16
80	-0.12	-0.03	-0.09	-0.07
120	0	0	0	0
160	-0.06	-0.03	-0.03	-0.11

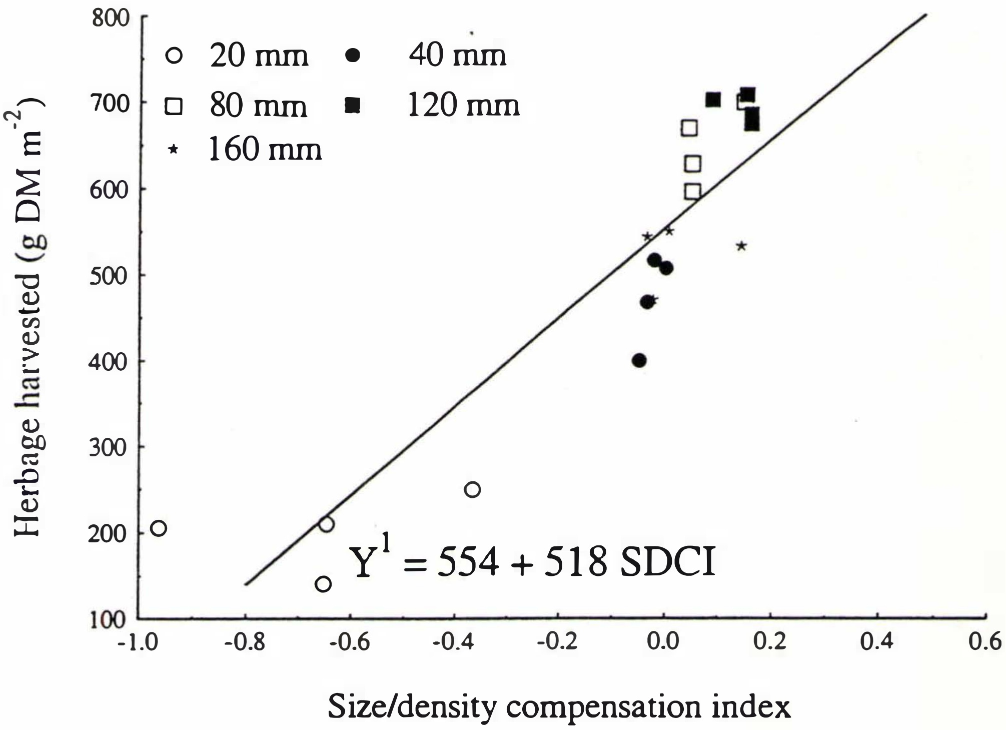
[1] = Calculations of ΔC_a and ΔC_r are based on leaf data in Table 4.5, and Equation 5 of Matthew *et al.* (1995). Differences are expressed relative to cutting height 120 mm which had the highest SDCI. (An example of the calculation is shown in Appendix 4.1).

related to defoliation intensity. The influence of defoliation intensity on sward productivity is shown in Figure 4.6.

Defoliation intensity is important in improving pasture productivity, with more productive treatments located further from the origin, and less productive treatments closer to the origin. Moreover, ranking of treatment productivity was the same as the ranking for SDCI (120>80>160>40>20).

Average of total leaf mass for the last two harvests was also plotted against SDCI (Figure 4.7). Figure 4.7 showed that treatments with lower leaf mass were closer to the origin and those with more leaf mass were further away. These relationships are all severely skewed by the 20 mm cutting height treatment. Omitting this would result in a much steeper response line.

a) Using all replicates individually



b) Using treatment means

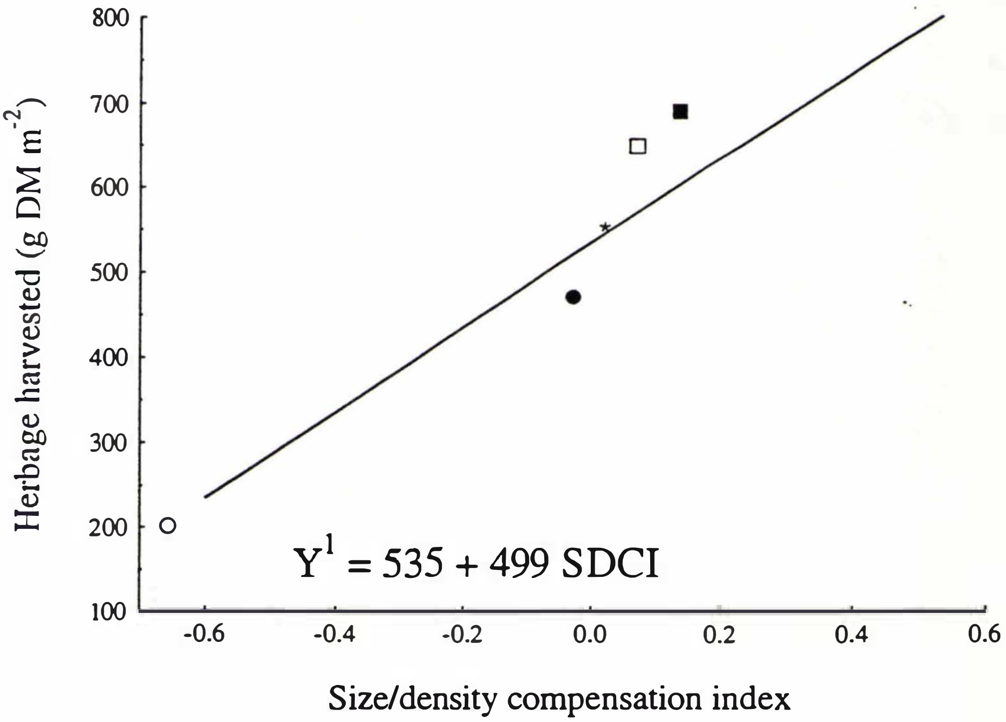
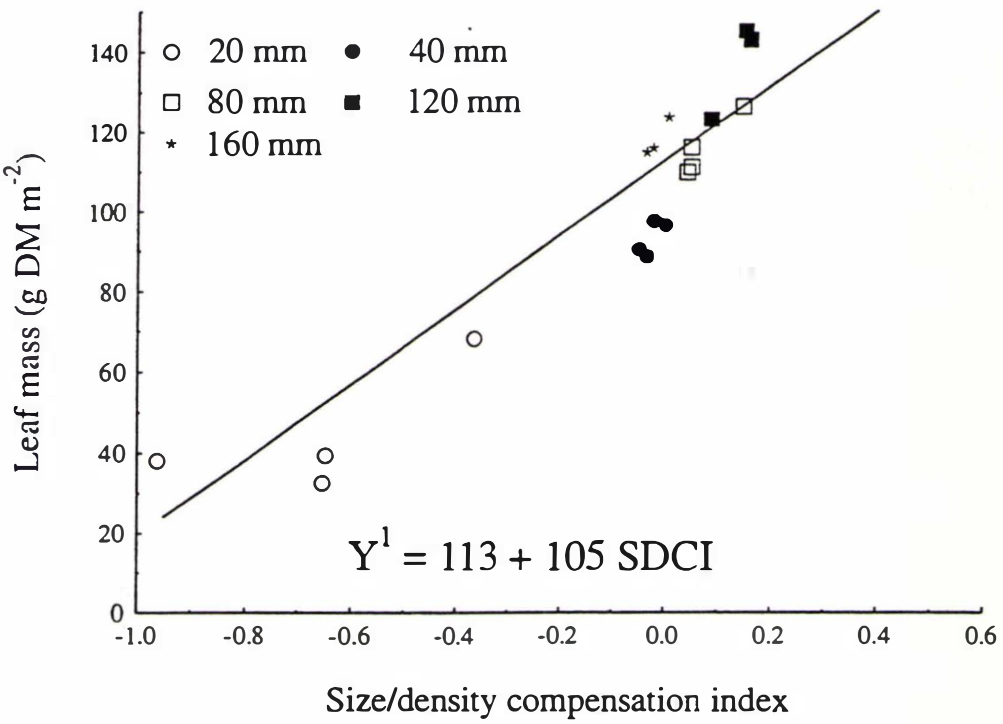


Figure 4.6. Relationship between herbage harvested (June 11-November 5) and size/density compensation index (SDCI).(SDCI was calculated using the average of the last two sets of data).

[1] Calculated by reduced main axis regression (RMA, LaBarbara, 1989).

a) Using all replicates individually



b) Using treatment means

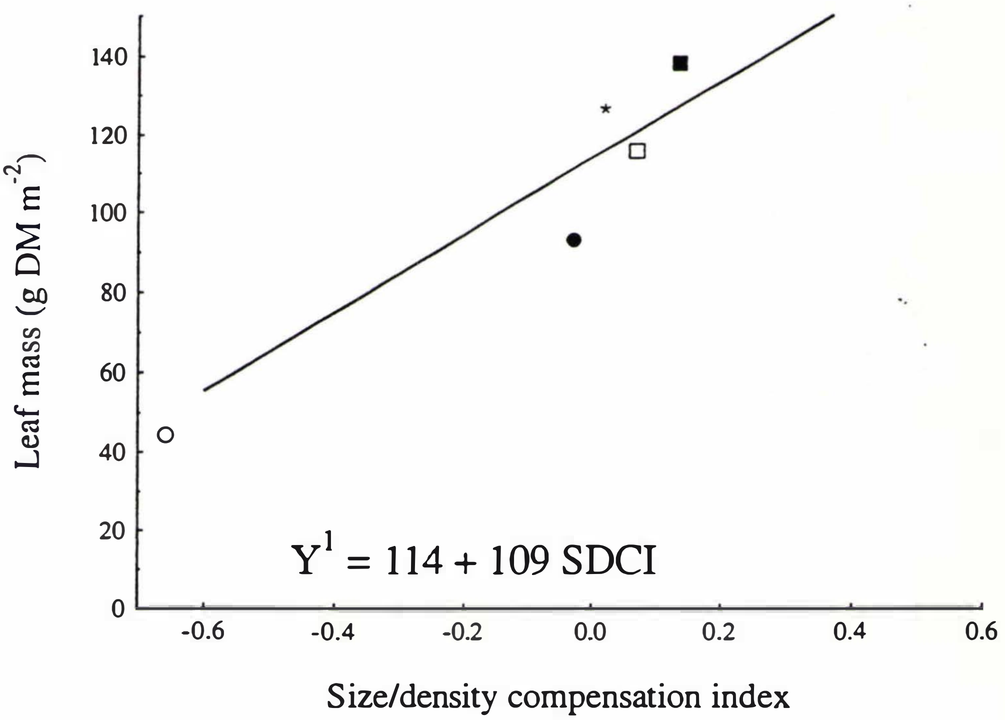


Figure 4.7. Relationship between total leaf mass (TLM) and size/density compensation index (SDCI). (SDCI and TLM were calculated using the average of the last two sets of data).

[1] Calculated by reduced main axis regression (RMA, LaBarbara, 1989).

4.3.9. Multiple discriminant analysis of herbage production

A canonical discriminant analysis (CDA) was used to understand the relationships between several variables measured in this experiment (Table 4.7). Variables for the last harvest entered into the analysis were: (i) tiller population density; (ii) tiller weight; (iii) root mass; (iv) leaf appearance rate; (v) above ground plant mass; (vi) total plant mass (root mass + above ground plant mass); (vii) leaf weight; (viii) net photosynthesis per unit of leaf weight (μmol CO_2 kg^{-1} s^{-1}); (ix) net photosynthesis per unit of ground area (μmol CO_2 m^{-2} s^{-1}) and (x) total herbage harvested. The first, second and third discriminant functions were statistically significant and accounted for 82.7%, 12.5% and 4.5% of the dispersion respectively (Table 4.7).

The canonical structure for the first discriminant function (DF) indicates that scores for this function were highly associated with total herbage harvested, tiller weight, root mass, above ground herbage mass, total plant mass, leaf weight and net photosynthesis per unit of ground (Table 4.7). Evaluation of cutting treatment means (Table 4.8) showed that the first discriminant score increased as the defoliation intensity decreased from 20 to 120 mm (Table 4.8), but was lower for the 160 mm cutting height than for the 120 mm cutting height. Treatment means scores for the first discriminant function (Table 4.8) follow the same tendency as C_a, C (C_a + C_r) and SDCI (Table 4.6).

The canonical structure for the second discriminant function indicates an association of high above ground plant mass, tiller weight and leaf weight with low root mass, with a contrast between 80 mm and 120 mm cutting height (Table 4.8). The second discriminant score was lowest for the 80 mm and highest for the 120 mm defoliation treatments (Table 4.8). The third discriminant function shows an association of high tiller population density and net photosynthesis per unit of ground with low tiller weight (Table 4.7), and appears to pick out the 160 mm cutting height as different from the other treatments (Table 4.8).

Table 4.7. Canonical structure and summary statistics for the first three discriminant factors for multiple discriminant analysis of herbage production.

Variables	Discr. 1	Discr. 2	Discr. 3
Tiller population[1]	-0.7226	-0.0360	-0.5412
Tiller weight[1]	0.9090	0.1328	0.3876
Root mass[1]	0.9833	-0.1611	-0.0123
Leaf app. rate[1]	-0.9635	-0.0343	-0.2305
Above ground hm[1]	0.9699	0.1878	-0.0482
Total plant mass[1]	0.9829	0.1171	-0.0416
Net photosynthesis/lw[2]	-0.8637	0.0685	-0.3260
Net photosynthesis/ga[3]	0.7712	0.0599	-0.5611
Total herbage harv.[4]	0.9145	-0.0761	-0.3142
Leaf weight[1]	0.9659	0.1501	0.0072
Canonical r^2	0.999	0.994	0.985
P	0.0001	0.0001	0.003
Prop. dispersion	82.7	12.5	4.5
Cumulative dispersion	82.7	95.2	99.7

[1] = Fifth destructive harvest (5 November).

[2] = Net photosynthesis per unit of leaf weight (μmol CO_2 kg^{-1} s^{-1}).

[3] = Net photosynthesis per unit of ground area (μmol CO_2 m^{-2} s^{-1}).

[4] = Total herbage harvested during the whole trial (pots were harvested twice a week).

Table 4.8. Scores for treatment means of the three discriminant scores described in Table 4.7.

Cutting height	Can 1	Can 2	Can 3
20	52.47	119.51	34.46
40	69.07	114.93	34.53
80	93.69	104.85	30.52
120	100.86	127.47	30.36
160	97.68	116.4	42.41

4.4. DISCUSSION

4.4.1. Techniques

The aim of sowing ryegrass as a pure species, rather than collecting samples from the field, was to avoid alterations in sward behaviour due to competition with other species. Also, the use of destructive sampling and the consequent high number of replicates per treatment had the objective of avoiding alterations in tillering activity due to disturbance during sward measurements (Davies, 1981; Matthew, 1989b). Such effects were noted previously under field conditions (Experiment 1, Section 3.3.1 and Experiment 2 Section 3.4.1).

Measurements of leaf appearance rates were not made for all treatments during the first month of the study because the youngest leaf initially selected for tagging was defoliated during the following harvests. To solve this problem, the second mature leaf was used for marking in the following periods. Leaf appearance rate for the 40 mm cutting height was recorded for only three periods; for the 20 mm cutting height only one reading was possible in the fifth period, because up to that time few leaves remained after cutting. In addition, in very short swards (20 mm) the leaves were very small, and it was very difficult to mark the youngest mature leaf without disturbing the sward. Also, it was not possible to determine site filling, because it was not possible to record the number of tillers which died between harvests.

The poor tillering observed during the first three months in the 20 mm cutting height may be associated with low leaf area per tiller, leaf area duration and photosynthetic efficiency (Tavakoli, 1993), because after cutting only sheath tubes remained (Plate 4.1). At this time tillers were erect and once all leaves were removed by cutting they died in a week or so. The great increase in tiller population density observed from September onwards may be associated with an increase in light intensity, as well as the plasticity of rapid adjustment of tiller population density to management. Tillers responded to defoliation intensity by adjusting from an erect to a prostrate growth habit.

4.4.2. Sward characteristics and photosynthetic efficiency

With the exception of the last harvest, the ratio of above ground herbage mass to below ground root mass increased as the cutting height increased from 20 mm to 160 mm (Table 4.1). Shoot:root ratio decreased over time from about 18.6 on July 9 to 4.0 on November 5. Also, in the last harvest, the ratio between above ground plant mass and below ground root mass was different between treatments, with 80 mm and 120 mm cutting heights having the lowest (3.3) and highest (4.5) ratio, respectively. The second discriminant function picked up these differences (Table 4.7), the scores being lowest for the 80 mm and highest for the 120 mm defoliation treatments (Table 4.8). Total, below ground and above ground plant mass increased over time. The 20 mm cutting height had the lowest total, below and above ground plant mass and 120 mm and 160 mm sward heights had the highest. Butler & Hodgson (1993) observed that net production in ryegrass swards was depressed under hard grazing as a result of lower production per tiller and instability of tiller population density. A reduction in herbage yield in response to increasing severity of defoliation may reflect a lower tiller number (Davies, 1971), a lower tiller weight (Table 4.5) or both. In the present Experiment, reduction in total and above ground plant mass were due to both reduction in tiller number (from July to October) and tiller weight (during the whole trial) (Tables 4.4 and 4.5).

Reduction in plant root growth, root respiration and nutrient absorption as the severity of defoliation increased has been reported by several researchers (e.g. Milthorpe & Davidson, 1966; Ryle & Powell, 1975). Reduction in supply of assimilate to the roots because of reduced photosynthesis, and also greater allocation to shoot meristem and leaf growth regions after defoliation, results in a reduction in root growth under more intense defoliation (Richards, 1993). The reduction in root mass observed in those swards defoliated more intensively (20 mm and 40 mm, Table 4.1) agreed with previous findings (e.g Richards 1993; Milthorpe & Davidson, 1966; Ryle & Powell, 1975).

Sward structure is determined by leaf size, tiller density and number of leaves per tiller (Chapman & Lemaire, 1993). Leaf appearance rate plays a central role because of its direct influence on each of the three key sward structural characteristics. Thus, assuming constant site filling and tiller longevity, high leaf appearance rate leads to swards with a high density of small tillers and low leaf appearance rate leads to swards with a lower density of larger tillers. The present results suggest that, in fact, leaf appearance rate might be the mechanism producing differences in tiller population density (Davies, 1974; Davies & Thomas, 1983), and the low leaf appearance rate observed at 160 mm cutting height could be one of the possible causes of the lowest tiller population density. In swards defoliated very laxly the sheath tube might remain intact and the emerging leaves may be relatively longer than those from swards defoliated more severely, and may appear more slowly (Davies, 1974, 1988).

Leaf appearance rate values were highest in early November and lowest in early October

(Table 4.3). Rates of leaf appearance give an indication of the overall scale of tissue turnover, especially in grasses where the number of leaves per tiller may remain relatively stable for long periods (Davies, 1993). The present results suggest that ryegrass plants responded to hard defoliation by increasing gross and net photosynthesis per unit of leaf weight (Table 4.2) and leaf appearance rate (Table 4.3), and reducing leaf weight (Table 4.5). Reductions in leaf weight, leaf width, length and area as a consequence of severe defoliation have been reported by Tavakoli (1993) for perennial ryegrass and tall fescue under controlled conditions. Several authors have reported similar tendencies (e.g. Davies, 1974; Bircham & Hodgson, 1983; Chapman & Robson, 1988) in perennial ryegrass and white clover swards, but Parsons *et al.* (1983) and Tallowin *et al.* (1989) observed similar leaf appearance rates for perennial ryegrass under different grazing intensities.

Defoliation height has a major effect on the structure and characteristics of ryegrass swards, because it has a direct effect on tiller number, mass and leaf area (Penning *et al.*, 1991). Roggero *et al.* (1993) observed in annual ryegrass (*Lolium rigidum* Gaudin) that cutting when the sward reached 100 mm rather than at 150 mm or 200 mm resulted in significantly lower yields but a better canopy structure (denser sward, higher percentage of leaves in the bottom layers and higher leaf:sheath ratio). The present results confirm this view. In short swards (20 mm and 40 mm) leaf mass was concentrated in the upper strata and it accounted for about 50% of the total plant mass present in all the swards layers (Figure 4.1). As the sward cutting height decreased (from 160 mm to 20 mm) the dead material decreased, especially in the lower layers. An increase in dead matter as defoliation intensity decreases has been observed previously (Grant *et al.*, 1981; Bircham & Hodgson, 1984).

Making due allowance for the poor tillering activity of the 20 mm cutting height in the early stages, by the end of the trial a notable feature of the structure of the intensively harvested swards (20 mm and 40 mm) was their larger tiller population (Table 4.4) and leaf appearance rate (Table 4.3) and their lower lamina area (leaf weight) per tiller (Table 4.5) than the taller swards. These results correspond with the findings of other researchers (e.g. Davies, 1974; Bircham & Hodgson, 1983; Brock & Fletcher, 1993; Chapman & Robson, 1988).

One major effect of increased defoliation intensity on sward productivity is to reduce photosynthesis by reducing leaf area duration (Parsons *et al.*, 1988). In this Experiment, despite the high photosynthetic efficiency per unit leaf area in the most intensively defoliated swards, canopy photosynthesis per unit ground area in these swards was less than in those defoliated more laxly (Table 4.2). Swards defoliated more leniently than 120 mm tended to decrease both gross and net canopy photosynthesis (Table 4.2). Thus, although the structure of severely defoliated swards increases the proportion of young leaves (Parsons *et al.*, 1988) and does give rise to a high photosynthetic efficiency in individual leaves, this compensates little for the small leaf area index which results from the high rate of removal of leaf material. In this experiment rates of gross and net photosynthesis per unit leaf weight decreased progressively with decreasing severity of defoliation. The decline in photosynthetic and respiration efficiency of grass leaves with age has also been observed previously by other workers (Woledge, 1971; Chapman & Robson, 1988). Parsons *et al.* (1983a, b) found that growing leaves together with the youngest fully expanded leaves, contributed 77% of the net photosynthesis of the sward canopy.

In an established crop each tiller bears an average of three live leaves, the youngest with the highest photosynthetic potential and the oldest with the lowest. On the other hand, it is well established that leaves which emerge and develop in low light have a reduced potential for photosynthesis (Woledge, 1971, 1973; Parsons & Robson, 1981). Thus, the decline in leaf efficiency as the sward height increased may have been an effect of a reduction in the intensity of light penetrating to the base of the sward (Woledge, 1978). Woledge (1977, 1978) suggested that the changes in photosynthetic capacity in grass swards are the result of changes in light intensity after defoliation rather than changes in demand for assimilates or growth substance supply. Furthermore, Tavakoli (1993) found that the photosynthetic rate of leaves per unit leaf weight of defoliated and un-defoliated swards, growing under similar light intensity, was initially similar, but repeated defoliation of plants decreased specific leaf weight and resulted in an increase in photosynthetic rate per unit leaf weight of defoliated plants relative to un-defoliated plants. The results of this study support Tavakoli's (1993) findings (Tables 4.2 and 4.6).

4.4.3. Tiller population density and sward productivity

The response of the ryegrass sward to different intensities of defoliation may involve changes in tiller population density, in individual tiller growth, or in a combination of both (Bircham & Hodgson, 1983). In this experiment, the greater quantity of herbage harvested at 120 mm compared with 40 mm and 80 mm defoliation heights was due primarily to the higher production per tiller rather than to any marked difference in tiller population (Figures 4.2 and 4.3 and Tables 4.4 and 4.5). However, when the 120 mm and 160 mm sward defoliation heights were compared, the greater total herbage harvested at 120 mm was due mainly to higher tiller population. Furthermore, the increase in herbage harvested observed from October 1 onwards in the 20 mm and 40 mm cutting heights (Figure 4.3) was largely associated with their much higher tiller population density at that time (Table 4.4). On the other hand, the differences in total herbage accumulation between 160 mm, 20 mm, and 40 mm cutting heights were due to the greater tiller weight observed at cutting height 160 mm rather than to differences in tiller population density (Figure 4.2 and Tables 4.4 and 4.5). From June to September tiller population density in the 40 mm cutting height was not enough to compensate for the higher tiller weight of the 160 mm sward, but once the 40 mm mini-sward reached its highest tiller population density (twice that of the 160 mm cutting height), in October, the contrast in daily herbage harvested was reversed. A similar tendency was observed in the 20 mm cutting height at the end of the trial (Figure 4.3). Despite the slightly greater herbage harvested observed particularly in the 40 mm cutting height, from October onwards, it was not enough to compensate for the greater daily herbage harvested recorded in the 160 mm cutting height from June to September (Figures 4.2 and 4.3).

It seems that, at the end of the trial, the highest cumulative herbage harvested observed in the 120 mm cutting height in comparison with the other treatments (Figure 4.2) was due to an optimum combination of both tiller population and tiller weight (Bircham & Hodgson, 1983). This treatment did not have the greatest tiller weight nor the highest tiller population density, but it had the greatest daily and total herbage harvested. Also, this mini-sward (120 mm cutting height) observed the highest total and above ground plant mass as well as the greatest gross and net photosynthesis per unit of ground area.

Swards may respond to defoliation by net gains, net losses or no overall change in tiller population, depending on initial tiller number at the time of cutting and the time of the year (Davies, 1988). In this experiment tiller population density changed with defoliation intensity. From June to August, for example, in swards harvested heavily (20 mm) some tillers died, but in those swards kept between 80 mm and 120 mm there was a slight net gain in tiller density. Tiller number in those pots kept at 40 mm and 160 mm did not change. From September onwards, however, the overall tendency was to net gain, particularly in those treatments defoliated more severely (Table 4.4). Similarly, tiller weight changed with defoliation intensity. Weight per tiller increased as the defoliation intensity decreased from 20 mm to 160 mm. Clearly these observations indicate that tillers in the mini-swards were subject to size/density compensation (SDC) which is well known from previous work (Bircham & Hodgson, 1983; Davies, 1988; Chapman & Lemaire, 1993; Sackville Hamilton *et al.*, 1995; Matthew *et al.*, 1995). Findings by Hodgson *et al.* (1981), Davies (1988) and Chapman & Lemaire (1993) have shown that tiller population and tiller weight in swards maintained at different herbage masses by continuous harvest are related to each other through the -3/2 self-thinning rule established by Yoda *et al.* (1963). Recent findings (Sackville Hamilton *et al.*, 1995; Matthew *et al.*, 1995) suggest that mortality due to overcrowding ensues when a small, suppressed plant no longer holds its leaves high enough in the canopy to maintain a positive carbon balance. It follows that LAI should remain constant during thinning, and that power law theory should be developed in terms of maximum leaf area index and the biomass required to support it.

In the present Experiment, using a wider range of cutting heights (20 mm to 160 mm) than previous field studies reported in Chapter 3, the compensation slope reflecting the relationship between weight per tiller and the surviving tiller density was studied. Since the 20 mm cutting height had reduced tiller population density compared to the 40 mm cutting height, indicating it fell below the limit of plasticity for ryegrass, data for this treatment were omitted from the regression analysis used to derive the size/density compensation slope. Slopes estimated for phase 2 and 3 (Matthew *et al.*, 1995) size/density compensation suggested lines significantly different from -3/2 ($P \leq 0.001$). The slope estimate for phase 2 size/density compensation suggests that the more intensively defoliated plants exhibit size/density compensation at slopes more negative than -1.5 (slope -2.56 ± 0.17 for 40 mm to 120 mm cutting heights) and as the defoliation intensity decreased to 160 mm, the slope changed to a less negative value of -0.17 (Figure 4.5). Matthew (1992) and Matthew *et al.* (1995) observed tiller size/density compensation slopes steeper than -3/2 in grazed ryegrass swards as well as in cut *M. sativa* swards. Additionally, Bircham & Hodgson (1983) found, in ryegrass-white clover swards, that the self-thinning law does not cover circumstances where herbage mass is lower than 700 kg OM ha^{-1} or where sward surface height is between 20-25 mm. Possible reasons for this behaviour could be that defoliation intensity tends to decrease levels of LAI or herbage mass, and so canopy photosynthesis per unit of ground area may be markedly reduced because insufficient young green leaf tissue is present to intercept light, much of which may fall on bare ground (Parsons *et al.*, 1983a).

A slope of -1.0 would be consistent with herbage mass remaining constant once the sward has reached its ceiling LAI (Matthew *et al.*, 1995). Lonsdale (1990) observed that populations thinning along lines of slope -3/2 should eventually reach a carrying capacity or maximal yield, so that the thinning line shifts to -1.0. Furnas (1981) and Lonsdale & Watkinson (1982) also noted a change in slope to -1.0 at very low light levels, a finding which Furnas (1981) explains in terms of self-thinning at constant herbage mass, in the case when swards are near the compensation line. The lower slope of -0.17 for the upper part of the curve in this study suggests that 160 mm swards may have begun to fall away from optimum LAI. In view of this it is interesting that discriminant function 3 picks out the 160 mm cutting height as being different from the other treatments (Table 4.8).

In summary, net production of ryegrass is depressed under hard grazing as a result of lower production per tiller and instability of tiller population density (Grant *et al.*, 1983; Bircham & Hodgson, 1983; Butler & Hodgson, 1993). The optimum balance between leaf weight (Table 4.5) and tiller density (Table 4.4) resulted in net herbage production per unit of area being generally greatest at sward height of 120 mm and declining at higher or lower cutting heights. The lower optimum sward surface height of 60 mm observed by Bircham & Hodgson (1983) and Grant *et al.* (1983) for perennial ryegrass swards under continuous stocking management may be explained in terms of a higher tillering activity than under controlled environmental conditions as a consequence of animal treading, as well as a better balance between net growth per tiller (leaf extension - senescence) and tiller density (Butler & Hodgson, 1993). On the other hand, at the end of the trial herbage harvested expressed on a daily basis were similar between pots harvested at 40 mm, 80 mm and 120 mm, suggesting that swards had reached an optimum balance between tiller density and net leaf growth per tiller, though swards defoliated more intensively took longer to attain this optimum.

4.4.4. Parameters used to predict herbage productivity

4.4.4.1. Size/density compensation index and herbage productivity

Other parameters which may be used to predict the productivity of any sward are the relationship between herbage harvested and size/density compensation index (Figure 4.5), and the relationship between total green leaf mass and size/density compensation index (Figure 4.6). Figures 4.5 and 4.6 showed that, as the cutting heights moved furthest from the origin on the size/density compensation axis, herbage productivity increased. The 120 mm cutting height produced the highest herbage harvested (Figure 4.2) and also was furthest away from the origin of both lines (Figures 4.6 and 4.7). These findings, together with results from the field trials (Sections 3.3.9.2 and 3.4.8.2), suggest that size/density compensation index may be used as an indicator of herbage productivity.

Since size/density compensation index represents the vertical distance between a point and an arbitrary -3/2 self-thinning line (environmental boundary line), leaf mass data was used to calculated the shift in intercept theoretically expected (C_a) due to changes in defoliation intensity (Matthew *et al.*, 1995). Table 4.6 shows size/density compensation index differences between treatments and the correction factors for changes in leaf area (C_a) and leaf:non leaf ratio (C_r) per treatment. These differences were expressed relative to the 120 mm cutting height treatment because it had the highest size/density compensation index. C_a, and C ($C_a + C_r$) followed the same tendency to that of the size/density compensation index, but C_r was only different in the sward most severely harvested. These results also show that C_a was much larger than C_r, as in the data of Matthew *et al.* (1995). The relationship between C_a and size/density compensation index suggests that in fact C_a does explain most of the deviation observed from the -3/2 self-thinning line slope, and that the size/density compensation index as calculated here essentially reflects difference in sward LAI as does C_a of Matthew *et al.* (1995). Both entities are an index of herbage productivity.

4.4.4.2. General overview of the interrelationship between individual effects

Multiple discriminant analysis is a form of multivariate analysis, and as such, allows several variables to be analyzed simultaneously for common treatment effects (Matthew, 1992). This analysis was used because it is an appropriate tool to gain an overview of the interrelationships between individual effects. Increase in the first discriminant score as the cutting height increased from 20 mm to 120 mm shows that the primary effect of reducing defoliation intensity is to increase plant mass, with associated changes in tiller weight, leaf weight and net photosynthesis per unit of ground area (Table 4.8). Scores for the first discriminant function were highly correlated with total herbage harvested, tiller weight, root mass, above ground herbage mass, total plant mass, leaf weight and net photosynthesis per unit of ground area. These results are largely consistent with the findings of Bircham & Hodgson (1983) that herbage mass is the result of tiller population and tiller weight.

Also, the first discriminant score showed clear relationships between tiller population density, leaf appearance rate and net photosynthesis per unit of leaf weight. These findings support previous evidence that tillering is primarily dependent on leaf appearance rate (Davies, 1974; Davies & Thomas, 1983; Tavakoli, 1993).

Scores for the second discriminant factor appear to reflect the pattern of root:shoot ratios across defoliation intensities, and differences between leaf and tiller weight with tiller population density between treatments. The fact that the third discriminant score picked out 160 mm cutting height as being different from the others (Table 4.8, Section 4.3.9) suggests that at extremely lax defoliation levels, grass swards attain a supra-optimal condition. This condition was not detected in the study of Bircham & Hodgson (1983), but may parallel 1:1 size/density compensation at high herbage masses mentioned by Lonsdale (1990).

4.5. SUMMARY AND CONCLUSIONS

The response of the ryegrass swards to different intensities of defoliation involved a decrease in tiller population density and an increase in tiller weight as defoliation intensity decreased. A notable feature of the intensively harvested swards was their larger tiller population and their lower lamina area and leaf weight per tiller than the other swards.

The optimum combination of tiller population density and leaf production per tiller. which increased the weight of herbage harvested per unit time, was observed at 120 mm cutting height.

The relationship between tiller population density (x) and individual weight per tiller (y) changed according to the defoliation intensity and with the time of the year. Under severe and very-lax defoliation the thinning process was radically altered in a way which suggests that swards harvested between 40 mm and 120 mm had slopes steeper than -3/2 and swards defoliated at 160 mm had slopes close to -1.

Quite detailed explanations of these effects have been given by Matthew ***et al.*** (1995). The use of the self-thinning rule in defoliated swards showed that the slope adjustments C_a and C_r made on a treatment mean basis explained the observed deviation from the -3/2 size/density compensation slope.

Sward structure was determined by stem and leaf size, tiller density and number of leaves per tiller. Severe defoliation tended to decrease levels of LAI or herbage mass, and so canopy photosynthesis per unit of ground was markedly reduced because insufficient young green leaf tissue was present to intercept incident light effectively. On the other hand, the high percentage of oldest leaf tissue present in swards harvested at 160 mm of surface height would certainly have reduced photosynthetic efficiency and may have been senescing and dying.

The physiological response of perennial ryegrass to defoliation was to decrea e root mass as the severity of cutting increased, but leaf appearance rate and photosynthesis rate per unit of leaf area were stimulated.

The results of this study demonstrated that the young expanding leaves in swards defoliated more severely have a high photosynthetic efficiency. Also, that photosynthesis per unit ground area and herbage production increased as cutting severity was decreased from 20 mm to 120 mm. Further increase in cutting height decreased photosynthesis rate and therefore herbage production.

Canonical discriminant analysis was used to derive mathematical descriptions of the salient features of the different variables measured. The canonical structure for the first discriminant function indicated that the main feature of this data was a high association between total herbage harvested, tiller weight, root mass, above ground plant mass, total plant mass, leaf weight and net photosynthesis per unit of ground area.

The present results indicate that the distance from the size/density compensation line can be used as a predictor of sward productivity. They show that sward productivity increases as the treatments move to the right of an arbitrary -3/2 compensation line.

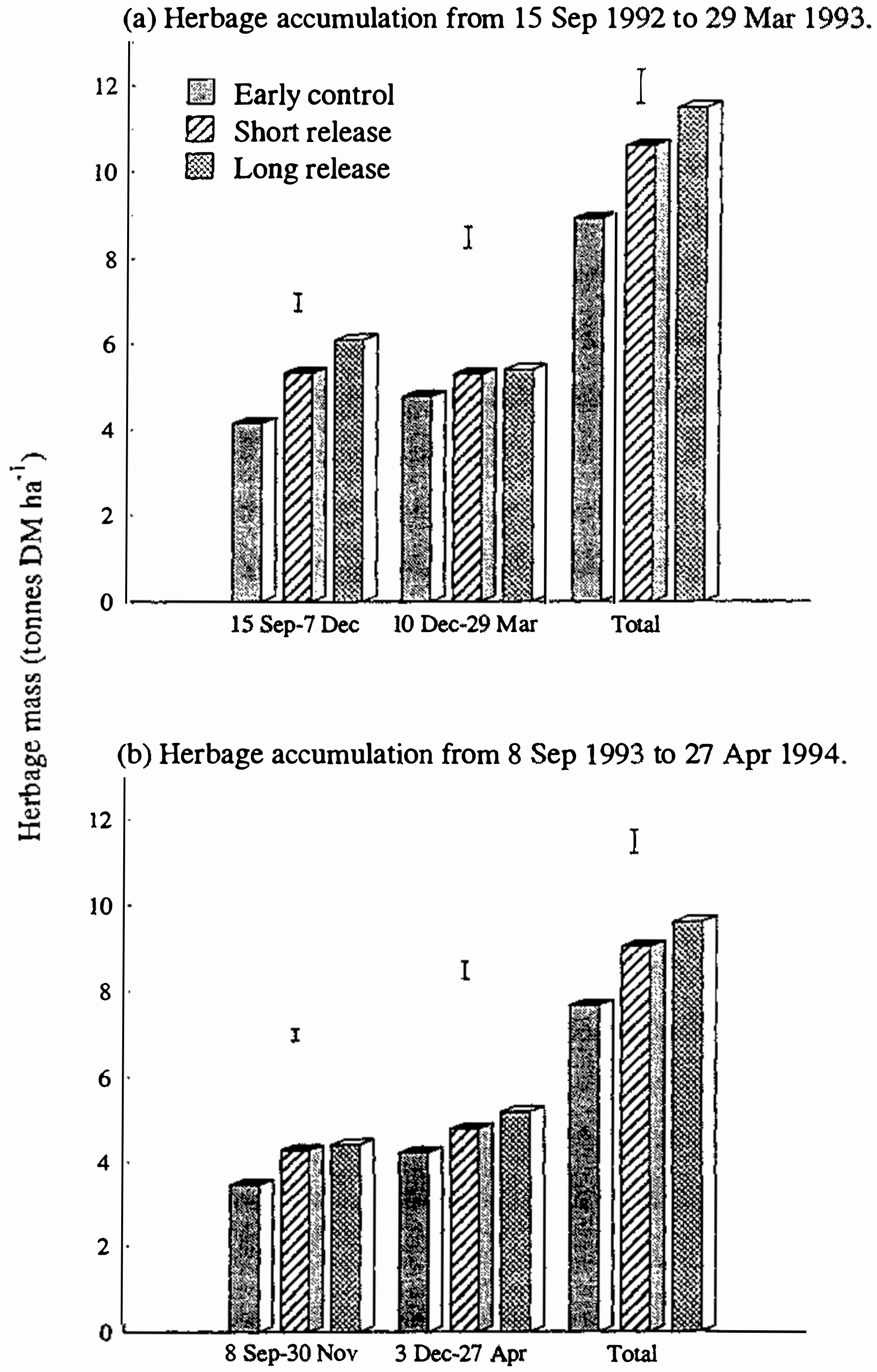
Chapter 5

GENERAL DISCUSSION AND CONCLUSIONS

Defoliation management for maximum production of quality herbage has been evolving since farming began, particularly in areas of intensive grassland farming. Pasture is the primary source of nutrients consumed by New Zealand grazing livestock (Korte *et al.*, 1987) and so management practices to improve its production, persistence and nutritive value have been the aim of all researchers. The objective of the present study was to provide further information on the response of ryegrass to defoliation management in terms of regrowth and competition with white clover, as well as to study the physiological and morphological effects of defoliation intensity on the growth and development of the basic growth unit, the tiller. To meet these aims, the responses of ryegrass alone and in association with white clover under intermittent defoliation were examined in the field (Chapter 3) and of ryegrass alone under controlled environmental conditions (Chapter 4). In this Chapter, the results are considered in a integrated general discussion. Firstly, the effect of grazing management on sward productivity will be highlighted. Secondly, the effect of grazing management on tiller demography and sward productivity will be discussed. Finally, the differences between cutting heights are discussed in terms of tillering activity, tiller weight, total herbage mass and photosynthetic rate.

5.1. SWARD PRODUCTIVITY IN FIELD EXPERIMENTS

The results from both field trials showed that lax spring grazing management increases herbage production during both the spring and the summer-autumn periods. They also demonstrated that sward productivity was further increased with longer lax spelling (Figure 5.1). The greater herbage accumulation obtained from January onwards in short and long release treatments support the results of Matthew *et al.* (1989b), Matthew (1992), Da Silva *et al.* (1993), Da Silva *et al.* (1994) and Da Silva (1994) who found that late control spring grazing management of perennial ryegrass-white clover pastures can be used as an option to enhance herbage production, particularly during the summer-autumn period. In both trials, lax defoliation in spring increased herbage production as a consequence of the greater degree of reproductive development. Several authors (Korte, 1982; Korte *et al.*, 1982, 1984, 1985; Korte, 1986; Korte & Harris, 1987; L'Huillier, 1987b) have discussed herbage production in terms of the ensuing trade off between quantity and quality. Further evaluation (Da Silva, 1994) revealed a 3% decrease (from 78% to 75%) in digestibility of the forage consumed by dairy cows grazing late control swards. Despite this, no significant reduction in herbage intake was detected in comparison with animals grazing leafy and vegetative swards. During spring, the greater herbage production observed in lax treatments appears to be the result of a greater individual tiller weight (Tables 3.5, 3.19 and 3.20), as a consequence of the higher percentage of reproductive tillers in these swards (Figures 3.7 and 3.14), rather than the result of a higher tiller population. In contrast, the greater herbage accumulation rate observed in short and long release treatments uring the summer-autumn period arose from both greater tiller population density (Tables 3.4 and 3.17) and higher net growth per tiller (Tables 3.6 to 3.8 and 3.21 to 3.23). Five out of six tissue turnover measurements carried out from late December to late April (Figure 5.2), in both years, confirm this assumption ($P \leq 0.05$). Differences were not seen during very dry conditions (Table 3.22). Also, four out of six measurements of net production ($g\ m^{-2}$ day^{-1}) verify these results (Figure 5.3).



(a) Herbage accumulation from 15 Sep 1992 to 29 Mar 1993.

(b) Herbage accumulation from 8 Sep 1993 to 27 Apr 1994.

Figure 5.1. Effect of spring grazing management on pre-control, post-control and total herbage accumulation (tonnes DM ha^{-1}) of ryegrass-white clover swards (from rising plate meter determination).

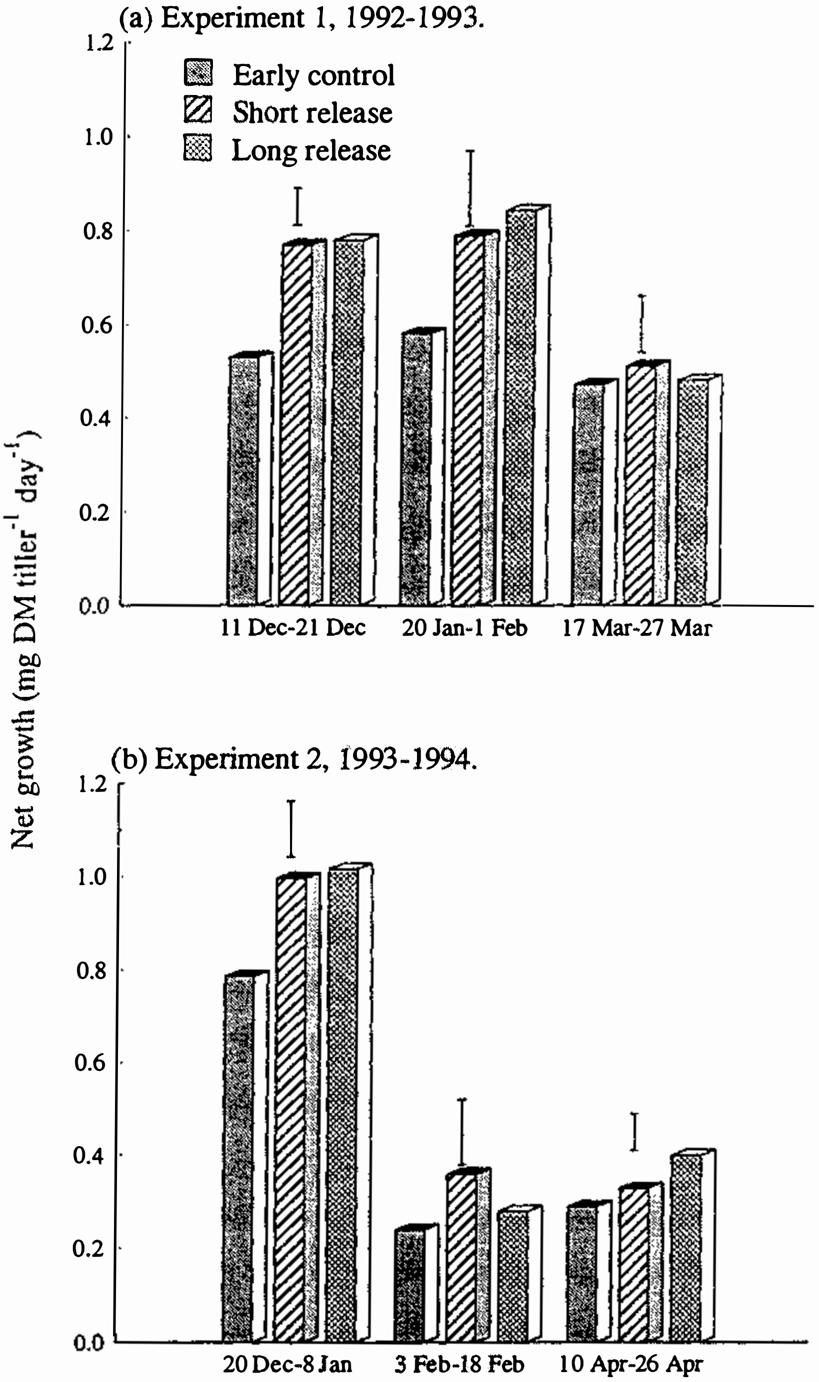
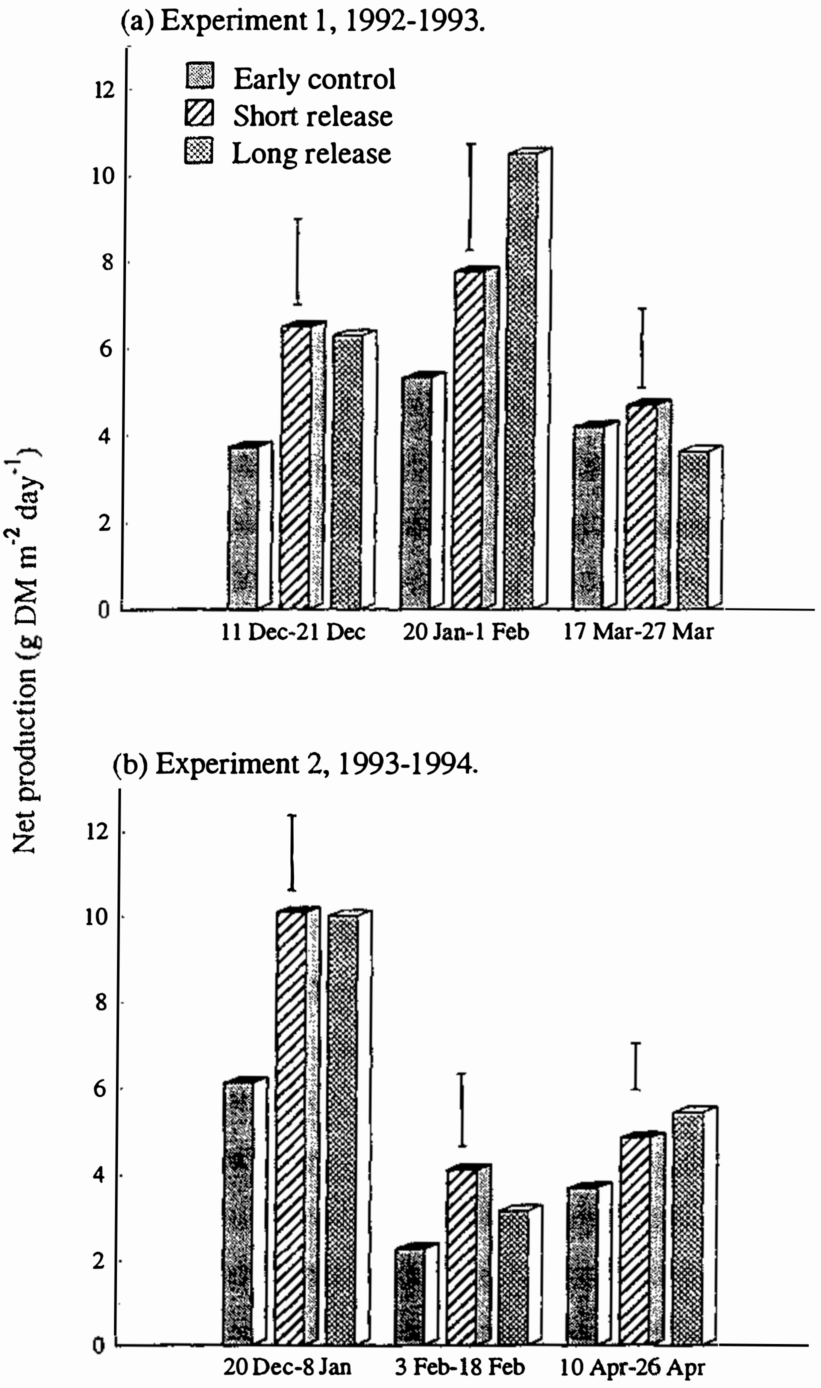


Figure 5.2. Effect of spring grazing management on net growth (mg DM tiller^{-1} day^{-1}) per tiller of ryegrass-white clover swards during the post-control phase.



(a) Experiment 1, 1992-1993.

(b) Experiment 2, 1993-1994.

Figure 5.3. Effect of spring grazing management on net production (g DM m^{-2} day^{-1}) of ryegrass-white clover swards during the post-control phase.

Based on these findings, the mechanism whereby more severe defoliation reduces herbage accumulation in the reproductive period is through decreasing tiller weight (Tables 3.3, 3.19 and 3.20), and during summer-autumn by reducing both tiller population density (Tables 3.4 and 3.17) and the rate of leaf extension (Figure 5.2). The results also suggest that the higher herbage accumulation observed in short and long release treatments in the post-control phase is basically due to a carry over effect and an increase in sward vigour, as a result of the previous management. The results from a multiple discriminant analysis carried out in both years demonstrated that tiller natality, tiller population density in January and February and growth rate per tiller during December and January are highly correlated with herbage accumulation during summer and autumn (Tables 3.12 and 3.27).

5.2. TILLER POPULATION DENSITY AND HERBAGE PRODUCTIVITY

Management effects on herbage accumulation may operate through changes in tiller density (Arosteguy, 1982; cited by L'Huillier, 1987; L'Huillier, 1987a; Bircham & Hodgson, 1983), tiller weight (Nelson & Zarrough, 1981; Bircham & Hodgson, 1983) or by a combination of both (Bircham & Hodgson, 1983). The determination of tiller population density under field conditions showed that tillering was most rapid between November and February, with the highest tiller appearance rate at the end of December, soon after decapitation of reproductive tillers, particularly in short and long release swards. A similar period of rapid tillering by perennial ryegrass during late spring and early summer has been observed previously under grazing (Garwood, 1969; Colvill & Marshall, 1984; L'Huillier, 1987a; Matthew *et al.*, 1989b; Da Silva *et al.*, 1993, 1994 and Da Silva, 1994) and cutting (Korte, 1986) conditions.

Multivariate analysis gives clear evidence of the relationship between tiller natality in late December and tiller population density in January and February with herbage productivity during summer and autumn (Table 3.12 and 3.27). Matthew *et al.* (1993)

found that the reproductive pathway is the dominant mode of perennation in the ryegrass swards, and laxer grazing pressure favoured it. Also, Matthew (1992) indicated that lax grazing during spring switched to hard grazing at the time of anthesis increases tillering activity by translocation of substrate from parent flowering to young daughter tillers. Davies (1977, 1988) added that re-mobilisation from dying tissue of cut tillers may provide substrate to promote daughter tiller formation. The increase in tillering was associated with a decrease in weight per tiller, soon after the control grazing, suggesting a size/density compensation effect. However, as all treatments received the same grazing management from December onwards, it was not possible to confirm this assumption, using the -3/2 self-thinning rule.

Several researchers have tried to explain the consequences of management on pasture productivity through effects on tiller size/density compensation (e.g. Bircham & Hodgson, 1983; Davies, 1988; Chapman & Lemaire, 1993). In the current studies an index which may be used as a general indicator of herbage productivity was calculated. Figures 3.10 and 3.15 indicate that the distance from an arbitrary -3/2 self-thinning line as measured by a size/density compensation index was clearly related to pasture productivity, and in both years an increase in herbage accumulation was accompanied by an increase in size/density compensation index. The less productive treatments were located close to the origin and sward productivity was increased as treatments moved further away from the origin. The results from both field trials suggest that short and long release treatments could produce more dry matter by increasing plant vigour and, as a consequence, both tiller population density and net growth per tiller were increased. Also, the results indicate that size/density compensation index is a measure of the degree of efficiency with which defoliation management may increase or decrease herbage production.

Additionally, the present results showed that the increase in herbage productivity in short and long release plots may reflect a carry over effect due to the previous management, or may indicate that tiller size (X) and tiller density (Y) together have reached their environmental boundary line (Matthew *et al*., 1995). The latter seems to be the case, because all treatments were located close to the environmental boundary line and, as they were moving further away from it, size/density compensation index exhibited lower values. This indicates that in fact long release treatments resulted in greater herbage accumulation by optimizing size/density compensation index and by setting the boundary line further out.

5.3. TILLER SIZE/DENSITY COMPENSATION THEORY

Size density compensation in un-defoliated (Kays & Harper, 1974; Lonsdale & Watkinson, 1982) and defoliated grass swards (Bircham & Hodgson, 1983; Davies, 1988; Chapman & Lemaire, 1993) has been observed to follow the -3/2 self-thinning rule, except at low light levels and under hard grazing, as a result of lower production per tiller and instability of tiller population density (Grant *et al.*, 1983; Bircham & Hodgson, 1983). However, under grazing conditions Matthew (1992) observed a tiller size/density compensation slope steeper than -3/2. In earlier papers (Sackville Hamilton *et al.*, 1995; Matthew *et al.*, 1995) the self-thinning rule was examined in detail, and it was shown that a self-thinning slope is a theoretical expectation where canopy leaf area index (LAI_c), and a measure of plant leaf area:plant size ratio (R) remain constant. Matthew *et al.* (1995) demonstrated that defoliation related to variation in leaf area and associated physiogenetic changes in plant structure necessitate slope corrections, designated C_a and C_r, respectively.

The glasshouse trial was established to investigate in more detail the implication of size/density compensation index on herbage productivity, using a wider range of defoliation intensities (from 20 to 160 mm sward height) and avoiding sward manipulation. In this case, too, an increase in both total herbage production and in leaf production were accompanied by an increase in size/density compensation index. Additionally, when slopes from regression equations of size/density compensation index obtained from both field Experiments were compared against that obtained in the glasshouse trial, the results suggest that the effects seen in the field were much larger than under controlled environment. The slope of the size/density compensation index in the glasshouse trial was three (1992-1993) and twelve (1993-1994) times smaller than those slopes from the field studies. This means that the production response per unit of size/density compensation index was substantially greater in the field than under controlled environmental conditions.

Tiller density is frequently used as an indicator of sward status, but often without taking account of size/density compensation effects. The glasshouse trial, with a wide range of defoliation heights, made it possible to develop a more complete test of size/density compensation theory than previous studies. Observations from this Experiment showed that the relationship between weight per tiller and tiller population density evolved over time and that an increase in tiller weight was associated with a decrease in tiller population and vice-versa, particularly at the end of the trial. Despite this tendency, total herbage harvested, total plant mass and above ground herbage mass increased as sward cutting height increased from 20 mm to 120 mm. Further reduction in defoliation intensity associated with an increase in defoliation height tended to reduce herbage harvested, total plant mass and above ground herbage mass. These results suggest that given a reduction in defoliation height, the resulting reduction in leaf weight (LAI_c) reduces the intercept of the -3/2 self-thinning line. This downward movement of the self-thinning line results in the new equilibrium tiller density failing to reach as high a value as would have been predicted by the -3/2 rule for the reduction in tiller size also associated with the reduction in defoliation height (Matthew *et al.*, 1995). The present results agree with previous observations at intermediate sward heights (Davies, 1988; Chapman & Lemaire, 1993), but more lenient (160 mm) and more severe (20 mm) defoliation intensities gave flatter and steeper slopes, respectively, than -3/2.

Recent findings by Sackville Hamilton *et al.* (1995) and Matthew *et al.* (1995) have suggested that since leaf area changes during regrowth, or in response to defoliation intensity, a multi-phased size density compensation line is expected. Figure 5.4 shows clearly the four phases of this response. At 20 mm defoliation intensity tiller population

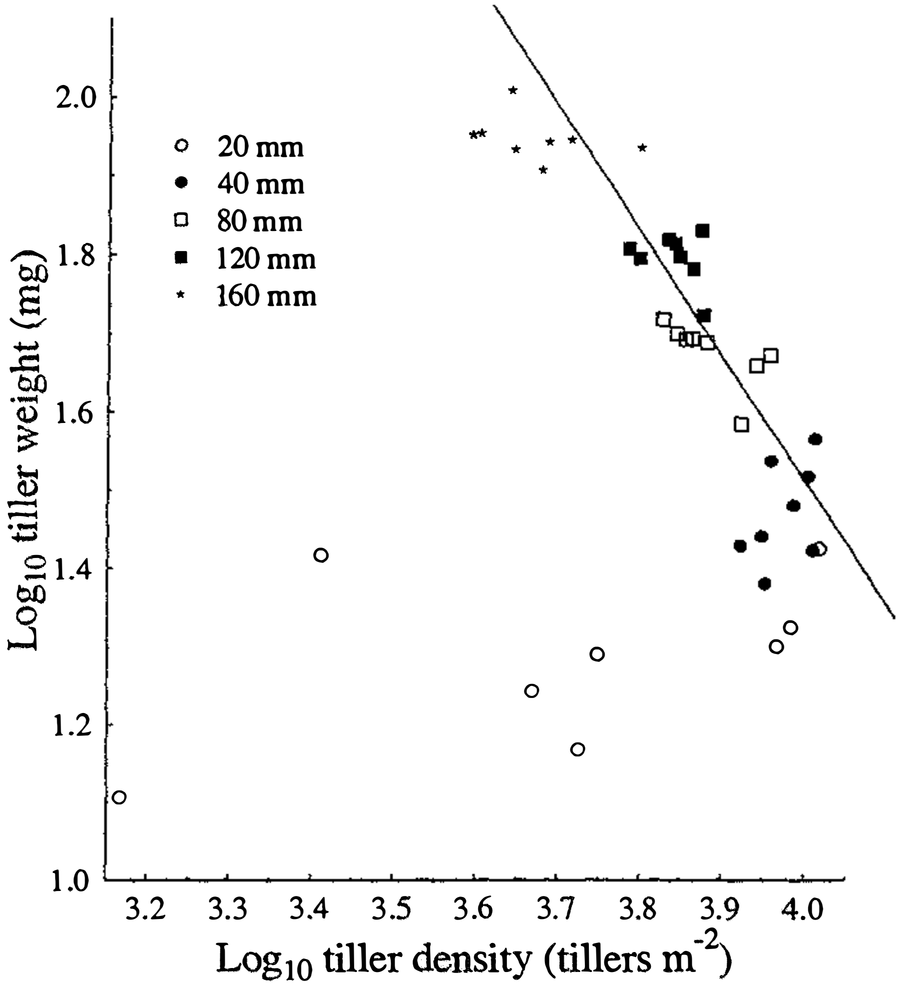


Figure 5.4. Tiller size/density compensation (SDC) in response to variation in cutting height in ryegrass mini-swards. Data from the last two harvests (1 October and 5 November, Chapter 4). Note that laxly defoliated (160 mm) and heavily defoliated (20 mm and 40 mm) swards begin to fall away from the theoretical -3/2 SDC line.

density was variable, but even the rapid increase in the later stages of the study was not enough to compensate for low tiller weight and so the sward failed to reach the common size/density compensation line (phase 1, Matthew *et al.*, 1995). A reduction in tiller numbers at grazing intensities lower than 20 mm was observed by Bircham & Hodgson (1983) and Grant *el al.* (1983). The increase in leaf weight as the defoliation intensity decreased (from 20 mm to 80 mm) suggests that leaf area increase was moving towards a ceiling value, therefore the self-thinning slope should be steeper than -3/2 (phase 2). The fact that the highest leaf weight was observed at 120 mm suggests that the sward had reached its maximum leaf area index (LAI$_c$) and so the self-thinning slope should be close to -3/2 (phase 3). The decrease in leaf weight at 160 mm compared to 120 mm sward height, accompanied by a reduction in tiller population density (phase 4), is consistent with the size/density compensation slope of -0.17 in this region, being flatter than -1.0 slope postulated for phase 4 by Matthew el al. (1995). However, the reason for the loss of leaf area and accompanying flatter than expected size/density compensation slope is unclear.

Additionally, slope corrections C_a and C_r were calculated from means the of combined leaf mass data from October/November and compared with the size/density compensation index. The results (Table 4.6) showed that C_a follows the same tendency as the size/density compensation index. The relationship between C_a and size/density compensation index suggests that in fact C_a does explain most of the deviation observed from the -3/2 self-thinning line, and it can therefore be used as a slope correction. Also, the size/density compensation index does explain the degree of efficiency with which plants respond to management practices and so it may be useful as a sward productivity index.

5.4. EFFECT OF DEFOLIATION MANAGEMENT ON HERBAGE GROWTH DYNAMICS

Defoliation management to maximise accumulation of herbage over time requires that all, or nearly all, of the light falling on the pasture is intercepted by photosynthetically active leaf material throughout periods of active growth (Chapman & Lemaire, 1993). Defoliation of forage plants results in readjustment of plant metabolism for promotion of new leaf area expansion and re-establishment of the photosynthetic capacity of the pasture (Culvenor *et al.*, 1989a, b). The results of both field trials showed that leaf growth rate in ryegrass and white clover (Tables 3.6 to 3.11 and 3.21 to 3.26) and tiller population density (Tables 3.4 and 3.17) in the former were highly associated with herbage accumulation in the post-control phase. In both species, increased leaf growth rate during the summer-autumn was observed in short and long release swards (Figure 5.2). The combination of greater tiller population density and higher leaf growth per tiller in short and long release treatments than early control treatments indicated that the former had more young growing leaves able to intercept more light and so able to recover net photosynthesis faster than swards with lower leaf area index, and therefore able to produce more dry matter because of their greater photosynthetic rate per unit of ground area.

Data from the glasshouse trial shows that gross and net photosynthesis per unit of leaf area and leaf appearance rate were greater in swards defoliated more intensively, but gross and net photosynthesis and herbage harvested per unit of ground area were greater in those swards which had more leaf mass per unit of soil area (Table 4.5). In this Experiment, canonical discriminant analysis demonstrated the effects of defoliation height on the interrelationship between the different variables measured. Results from the second discriminant function indicate an association of high above ground plant mass, total plant mass, tiller weight and leaf weight with low root mass. A possible explanation might be that plants tend to build up firstly their photosynthetically active tissue to ensure their survival and secondly their root mass. The third discriminant function highlighted an association of high tiller population density, net photosynthesis rate per unit of ground area, leaf weight and total herbage harvested with low tiller weight (Table 4.7). These relationships are partly explained by changes in the balance between leaf area index and tiller population density. Penning *et al.* (1991) observed that defoliation height has a major effect on tiller number, mass and leaf area. The fact that the 120 mm cutting height did not have the greatest tiller population density or leaf weight per tiller, but did have the greatest herbage harvested, support this assumption.

In summary, the consequence of lax spring grazing management was to increase herbage productivity by optimizing the size density/compensation index of the sward. The results show that sward productivity increases as the short and long release treatments move to the right of an arbitrary -3/2 compensation line. In the glasshouse, the decline in cumulative herbage harvested, total, above and below ground plant mass, and net photosynthesis per unit of ground area as defoliation intensity increased from 120 mm to 20 mm confirm that sward productivity depends on an op imum balance between tiller population density and weight per tiller, and that grazing management must be dedicated to achieve an optimum balance between them.

5.5. FURTHER STUDIES

Management practices have the aim of improving herbage production and animal performance per unit of area. Bearing this in mind, and in accord with the results, further research is needed to investigate ways of utilising the extra feed produced from pastures subjected to late control management during spring. To prove the effectiveness of "late control" as an alternative grazing procedure, an evaluation including animal performance is necessary under both the late control and the conventional spring grazing management.

It has been demonstrated that tiller size/density compensation follows the -3/2 self-thinning rule at intermediate defoliation intensities, and is different at very lax and/or very hard defoliation intensities. These studies provided evidence indicating that the distance from the size/density compensation line (size/density compensation index) has value as a predictor of sward productivity. Further research is required with other pasture species, and using a wider range of defoliation intensities, to validate these observations.

5.6. CONCLUSIONS

The results of the field studies show that allowing some early seedhead development followed by hard grazing at the time of anthesis increased herbage production during the summer-autumn season due to an enhancement in the tillering activity and net leaf growth per tiller. Effects were greater following an extended period of lax grazing.

Effects on tiller population density, tiller weight and tissue turnover persisted throughout the summer and autumn. Enhanced tillering was accompanied by increased elongation in ryegrass and area expansion in white clover leaves.

Tiller size/density compensation index has been shown to be a predictor of sward productivity. An increase in herbage productivity is accompanied by an increased size/density compensation index. The size/density compensation index was substantially larger in field conditions than in the controlled glasshouse study.

The results of the glasshouse Experiment demonstrated that the self-thinning rule could be used effectively to describe size/density compensation in defoliated swards when slope corrections, designated C_a and C_r were also used. Under severe and very-lax defoliation the thinning process was radically altered in a way which suggests that swards harvested between 20 mm and 120 mm had slopes steeper than -3/2, and swards defoliated at 160 mm had a slope close to -1.0.

The results of this study demonstrated that canopy photosynthesis and leaf appearance interval decrease as the defoliation intensity decreases. Also, that photosynthesis per unit ground area, herbage harvested, above ground plant mass and total plant mass increased as cutting height was increased from 20 mm to 120 mm. Further increasing in cutting height decreased photosynthetic rate.

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APPENDICES

Appendix 3.1. Summary of climate conditions from September 1992 to March 1993, at AgResearch climate station which was 1 km from the trial site ($40^0$23'S $175^0$37'E,34m asl).

92-93	Rainfall	Temperature Av.		Sunshine (h)	Relative Humidity	Evaporation
		Air	Soil			
Sep	87.7	9.8	9.4	3.5	80	1.5
Oct	85.7	11.8	11.5	3.4	77	2.5
Nov	60.8	14.7	15.3	4.4	82	3.2
Dec	167.3	15.1	15.9	5.4	82	3.2
Jan	53.9	15.7	16.5	2.8	79	4.6
Feb	43.7	16.3	16.3	3.0	84	4.4
Mar	79.8	14.5	14.6	2.3	84	2.9
Apr	53.7	12.6	12.1	2.0	85	1.7
May	78.0	11.4	11.4	1.6	86	1.0

Appendix 3.2. Summary of climate conditions from September 1993 to May 1994, at AgResearch climate station which was 1 km from the trial site (40^{0}23'S 175^{0}37'E,34m asl).

93-94	Rainfall	Temperature Av.		Sunshine (h)	Relative Humidity	Evapo-ration
		Air	Soil			
Sep	60.3	9.5	9.3	1.5	79	1.9
Oct	60.0	12.9	12.4	2.4	79	3.3
Nov	138.2	12.3	13.7	2.6	85	3.5
Dec	81.3	15.3	16.2	2.1	76	4.0
Jan	33.3	18.1	18.6	2.8	76	5.2
Feb	24.6	19.1	19.0	3.9	80	5.3
Mar	58.3	14.9	15.2	2.6	87	3.0
Apr	53.1	13.8	13.1	2.5	86	2.3
May	121.9	12.2	11.1	1.5	84	1.3

Appendix 3.3a. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards during the pre-control period (relative proportion, %). Experiment 1.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
				26 October						
RG[3]	66.4	70.6	66.3	61.5	57.3	77.5	6.6	ns	ns	ns
RGL	63.8	66.7	61.5	65.7	62.4	60.2	3.3	ns	ns	ns
OG	17.4	21.0	20.4	24.1	15.4	16.2	4.4	ns	ns	ns
OGL	59.1	72.0	58.2	65.4	64.8	61.0	4.9	ns	ns	ns
WC	9.0	na[4]	3.8	na	10.6	na	5.3	ns		
WCL	99.0	na	99.1	na	98.0	na	1.2	ns		
D	7.2	7.9	9.5	13.7	14.2	6.3	4.0	ns	ns	ns
W	0.0	0.5	0.0	0.8	2.4	0.0	1.1	ns	ns	ns

[1] = ECW, ECN, SRW, SRN, LRW, LRN, treatments as determinate in Table 3.1, pp 51.

[2] Tre = Treatments, N = Ryegrass sward with fertiliser nitrogen, NW = Interaction tests for differences between W and N swards in treatment responses {(EC/SR/LR) * (W/N)}.

[3] RG = Ryegrass, RGL = Ryegrass leaf, OR = Other grasses, OGL = Other grasses leaf WC = White clover, WCL = White clover leaf, D = dead material W = Weeds.

[4] = Not applicable - white clover not present in these swards.

Appendix 3.3b. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards during the pre-control period (relative proportion, %). Experiment 1.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
				7 December						
RG[3]	51.8	55.3	66.0	73.4	53.6	76.6	7.2	ns	ns	ns
RGL	63.9	70.1	52.9	55.1	56.0	60.4	3.6	**	ns	ns
OG	23.1	34.2	11.4	13.7	12.2	15.2	4.4	**	ns	ns
OGL	46.4	64.3	38.2	42.5	47.7	49.8	6.3	ns	ns	ns
WC	8.4	na[4]	12.0	na	12.0	na	2.4	ns		
WCL	83.7	na	68.3	na	79.1	na	12.2	ns		
D	15.2	10.3	10.4	13.1	15.8	9.6	2.6	ns	ns	ns
W	1.5	0.2	0.1	0.0	5.0	0.0	2.0	ns	ns	ns

[1], [2], [3], [4] = Abbreviations as for Appendix 3.3. pp 221.

Appendix 3.4. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards during the post-control period (relative proportion, %). Experiment 1.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
					1 February					
RG[3]	41.6	77.0	50.8	73.2	58.8	69.7	6.1	ns	***	ns
RGL	71.1	71.8	67.1	76.0	70.0	82.3	4.6	ns	ns	ns
OG	15.4	12.5	16.6	6.8	4.1	10.5	3.5	ns	ns	ns
OGL	64.6	59.9	69.9	57.4	51.0	37.0	6.7	*	ns	ns
WC	15.0	na[4]	10.8	na	9.4	na	3.0	ns		
WCL	62.7	na	80.2	na	68.1	na	11.1	ns		
D	17.3	10.2	20.4	20.0	23.4	19.7	3.1	ns	ns	ns
W	10.7	0.3	1.4	0.0	3.2	0.1	2.2	ns	*	ns
					29 March					
RG	54.6	72.7	60.3	66.8	57.7	62.0	5.2	ns	*	ns
RGL	68.8	68.0	65.9	67.3	67.6	69.8	1.8	ns	ns	ns
OG	7.6	4.3	1.6	8.8	4.5	3.1	3.2	ns	ns	ns
OGL	46.4	66.0	35.2	72.6	57.2	65.9	6.2	ns	**	ns
WC	22.2	na	19.9	na	11.6	na	4.3	ns		
WCL	52.5	na	43.6	na	64.8	na	11.7	ns		
D	14.3	18.7	15.0	24.0	22.5	33.3	4.2	ns	*	ns
W	1.2	4.4	3.2	0.4	3.7	1.6	1.7	ns	ns	ns

[1], [2], [3], [4] = Abbreviations as for Appendix 3.3. pp 221.

Appendix 3.5. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards before the control period (relative proportion, %). Experiment 2.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
					1 December					
RG[3]	44.2	46.1	46.4	43.8	44.5	49.8	4.3	ns	ns	ns
RGR	9.0	10.4	29.0	22.9	23.0	20.1	2.3	***	ns	ns
RGV	35.1	35.0	17.2	19.2	21.4	29.2	3.2	***	ns	ns
RGL	62.4	59.5	28.4	33.3	36.6	46.4	2.9	***	ns	ns
OG	23.7	44.2	24.6	43.9	20.4	32.4	2.1	**	***	ns
OGL	28.9	31.7	46.2	58.6	66.3	48.3	6.2	***	ns	ns
WC	16.6	na[4]	13.2	na	11.6	na	4.2	ns		
WCL	85.2	na	89.1	na	92.3	na	2.33	ns		
D	12.9	8.5	14.5	10.0	21.9	17.0	2.0	***	**	ns
W	2.6	1.1	1.4	0.8	1.6	0.8	0.82	ns	ns	ns

[1], [2], [3], [4] = Abbreviations as for Appendix 3.3. pp 221.

Appendix 3.6. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards during the post-control period (relative proportion, %). Experiment 2.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
					11 January					
RG[3]	40.5	48.9	46.6	67.3	44.6	63.7	5.3	ns	**	ns
RGR	4.6	6.0	1.9	23.4	8.1	18.0	7.7	ns	ns	ns
RGV	35.9	42.9	44.7	43.9	36.5	45.7	3.2	ns	ns	ns
RGL	71.9	70.3	75.8	52.3	66.7	61.0	8.4	ns	ns	ns
OG	28.4	31.9	19.5	23.1	19.9	21.8	4.3	ns	ns	ns
OGL	38.4	33.0	24.8	39.1	33.4	26.8	6.4	ns	ns	ns
WC	18.1	na[4]	18.1	na	16.7	na	3.2	ns		
WCL	72.1	na	90.9	na	93.4	na	14.6	ns		
D	8.7	7.1	13.9	9.1	8.8	13.6	2.8	ns	ns	ns
W	4.3	12.1	2.0	0.4	10.0	0.9	5.4	ns	ns	ns

[1], [2], [3], [4] = Abbreviations as for Appendix 3.3. pp 221.

Appendix 3.7. Effect of duration of lax spring grazing management on the botanical composition of ryegrass-white clover swards during the post-control period (relative proportions, %). Experiment 2.

	Treatment[1]							Significance[2]		
	ECW	ECN	SRW	SRN	LRW	LRN	SEM	Tre	N	NW
					22 February					
RG[3]	40.3	58.9	46.8	55.4	56.1	50.1	3.2	ns	*	**
RGL	71.9	70.3	75.8	52.3	66.7	61.0	8.4	ns	ns	ns
OG	5.3	3.4	3.8	3.3	3.3	4.2	4.3	ns	ns	ns
OGL	38.4	33.0	24.8	39.1	33.4	26.8	6.4	ns	ns	ns
WC	12.3	na[4]	6.6	na	4.9	na	4.2	ns		
WCL	62.6	na	74.5	na	71.2	na	4.4	ns		
D	38.2	36.4	41.9	39.0	33.1	45.7	2.8	ns	ns	*
W	4.3	12.1	2.0	0.4	10.0	0.9	5.4	ns	ns	ns
					29 April					
RG	61.9	75.1	66.5	77.5	67.0	72.6	2.5	ns	***	ns
RGL	71.9	73.7	68.7	70.6	65.8	70.7	1.8	ns+	ns+	ns
OG	2.5	0.5	0.3	0.8	0.5	1.0	0.74	ns	ns	ns
OGL	48.6	56.5	54.8	69.1	41.3	31.1	6.2	**	ns	ns
WC	8.4	na	5.4	na	7.8	na	4.7	ns		
WCL	48.9	na	52.5	na	58.7	na	6.5	ns		
D	24.9	21.2	26.2	21.5	23.9	26.2	3.2	ns	ns	ns
W	2.3	3.2	1.7	0.2	0.8	0.2	1.2	ns	ns	ns

[1], [2], [3], [4] = Abbreviations as for Appendix 3.3. pp 221.

+ = $P \leq 0.07$

Appendix 4.1. Method of calculating theoretical effect of change in leaf area with cutting height on C_a.

i) Equation 5 of Sackville Hamilton *et al.* (1995);

$$\mathbf{I = 3/2 \log (LAI_c) + \log (k'') - \log (R)}$$

ii) Assuming LAI + K leaf weight, then Log (LAI) = log k + (log leaf weight)
Since log k is constant log leaf weight may be used to calculated effect on C_a.

iii) Comparing treatments.

Cutting height	Leaf weight (lw)	3/2 log lw	C_a[1]	SDCI[2]
20	44.4	2.47	0.74	0.79
40	93.1	2.95	0.26	0.16
80	115.6	3.09	0.12	0.07
120	138.2	3.21	0	0
160	126.5	3.15	0.06	0.11

[1] = Correction relative to 120 mm defoliation height.

[2] = Distance from an arbitrary -3/2 line on a tiller size/density plot.

iv) Similarly calculation for theoretical correction of change in leaf : non-leaf ratio with cutting height (leaf weight raised to the 3/2 power).

Cutting height	3/2 log lw	log HM[1]	Diff.[2]	C_r[3]	C_a+C_r
20	2.47	1.94	0.53	0.15	0.59
40	2.95	2.3	0.65	0.03	0.23
80	3.09	2.44	0.65	0.03	0.09
120	3.21	2.53	0.68	0	0
160	3.15	2.5	0.65	0.03	0.03

[1] = Above ground herbage mass.

[2] = Difference 3/2 log lw - log HM.

[3] = Change in C_r relative to 120 mm defoliation height.