THE EFFECTS OF DEFOLIATION ON TISSUE TURNOVER AND PASTURE PRODUCTION IN PERENNIAL RYEGRASS, PRAIRIE GRASS AND SMOOTH BROMEGRASS PASTURE.

A THESIS PRESENTED IN PARTIAL FULFILMENT OF THE REQURIEMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY AT MASSEY UNIVERSITY.

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ABSTRACT

This thesis reports the results of three experiments, one with perennial ryegrass (Lolium perenne L.) cv. Ellett under rotational sheep grazing, one with prairie grass (Bromus willdenowii Kunth.) cv. Grasslands Matua under rotional dairy cow grazing, and one with smooth bromegrass (Bromus inermis Leyss) under cutting management. The first two experiments were carried out at Massey University, New Zealand, the third at Beijing Agicultural University, China. Each experiment involved management variations set within a range considered to be appropriate to the species under examination, and was complete in itself. The objective of the study reported here was to examine the sensitivity to defoliation of the three grass species, sensitivity being defined principally in terms of adjustment in tiller population density and tissue turnover to variations in defoliation treatment. The results are reported separately, but are drawn together for comparative purposes in an integrating discussion.

Flexibility in response to defoliation, measured in terms of the number of live leaves per tiller, the rate of leaf appearance, dry weight per tiller, and tiller population density, differed substantially in perennial ryegrass, prairie grass, and smooth bromegrass, and had a major influence on the sensitivity of the species to contrasting managements.

Net herbage production was relatively insensitive to hard (2.5cm, post grazing 1000kgDM/ha) and lax grazing (15cm, post grazing 2000kgDM/ha) in perennial ryegrass pasture because of rapid adaptive change in tiller population density, which was usually greater under hard grazing than under lax grazing, and compensating changes in rates of herbage growth and senescence.

Net herbage production of prairie grass was greater under lax (12cm, post grazing

2500-3500kgDM/ha) than under hard (6cm, post grazing 1500-2000kgDM/ha) grazing, associated with reduction in tiller population density under the latter treatment, and a greater reduction in herbage growth than in senescence per tiller.

In smooth bromegrass, tiller populations were greater under lax (30 cm) than under hard (10 cm) cutting, though the closer cutting treatment resulted in greater green herbage accumulation, because of a greater reduction in the rate of herbage senescence than in the rate of herbage production.

In general terms, perennial ryegrass demonstrated substantial genotypic plasticity in the adaptive changes in the balance between tiller population density and tiller size, reflecting the high tillering potential in this species. Rates of leaf production on main and daughter tillers consistently made the major contribution to tissue turnover in this. In contrast, prairie grass showed little adaptive response in tiller population density when tiller size was reduced, and the main component of tissue turnover was generaley stem material. Though tiller size was similar in smooth brome and prairie grass, adaptive changes in the balance between tiller size and population were more complete in the former species and leaf tissue made a greater contribution than stem to tissue turnover.

The effect of seasonal change in the enviroment on the growth of grass swards is complicated by progression from vegetative to reproductive development. In ryegrass pasture, there were advantages to spring and summer pasture production from a management which allowed seed head development to anthesis in spring, followed by hard grazing to enhance the subsequent development of new vegetative tillers. For smooth brome grass initial cutting at anthesis resulted in a greater rate of green herbage accumulation subsequently than did cutting one month later. In prairie grass the limited development of replacement daughter tillers contributed to the relatively poor performance of this species under hard grazing. The relationship between the timing and severity of defoliation and the physiological status of the plant was therefore critical in determining subsequent herbage growth in all three species, though there were clearly specific differences in effects on the balance between stem and new tiller production and the expansion of daughter tillers.

This study suggested that a better understanding of the limits of adaptive response in the different species, particularly in tiller population structure and tissue turnover, will provide an objective basis for planning pasture management. Studies of this kind, preferably made under strictly controlled comparative conditions, would be a particularly important component of evaluation programs for new plant genotypes.

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CHAPTER 1. INTRODUCTION

Much research work based on the dynamics of plant tissue turnover in grazed swards has been carried out under continuous stocking managements in which swards have been maintained in approximately steady state with reference to herbage mass, canopy height or leaf area index. There is a marked degree of insensitivity in net herbage production over a range of steady-state conditions (Hodgson, 1985). This is a consequence of compensating changes in tiller populations and production per tiller, of associated changes in sward structure and in the photosynthetic efficiency of leaf populations, and of the close links between rates of herbage growth and senescence (Hodgson et al., 1981). All of these effects reflect the influence of patterns of defoliation by grazing animals (Watkin and Clements, 1978; Bircham and Hodgson ,1983) on tiller morphology and on tiller and leaf turnover.

The accumulated evidence from field studies (Arosteguy et al., 1983; Bircham and Hodgson. 1983; Grant et al., 1983; Parsons et al., 1983a) displays a very encouraging degree of agreement across locations, years, seasons and measurement techniques, but the information comes mainly from relatively short duration grazing experiments on perennial ryegrass or ryegrass/white clover swards in the UK. In order to understand the compensating responses to defoliation in sward structure and function and so provide greater objectivity in advice on pasture mangement, there is a need for more information on seasonal variations in sward dynamics of ryegrass pasture, and on sward dynamics of other grass species which differ from ryegrass in plant morphology.

The objective of the study reported here was to examine the sensitivity to defoliation of three forage grass species, sensitivity being defined principally in terms of adjustment in tiller population density and tissue turnover following variations in defoliation treatment. Three experiments are reported, one with perennial ryegrass (Lolium perenne L.) cv. Ellectt under sheep grazing, one with prairie grass (Bromus willdenowii Kunth) cv. Grasslands Matua under dairy cow grazing, and one with smooth bromegrass (Bromus inermis leyss) under cutting management. The first two experiments were carried out at Massey University, New Zealand, the third at Beijing Agricultural University, China. Each experiment involved management variations set within a range considered to be appropriate to the species under examination, and was complete in itself. The results of the three experiments are reported separately, but are drawn together for comparative purposes in an integrating discussion in chapter six.

CHAPTER 2 LITERATURE REVIEW.

2.1. Introduction

One of the essential features of a pasture plant is that it should be capable of regrowth if successive defoliations are imposed. Both initial growth following dormancy and regrowth following winter show the sigmoid growth pattern common to many biological organisms. A period of very slow initial growth is followed by a period of rapid increase, eventually reaching a plateau. The beginning of the plateau is the time when growth becomes limited by the light falling on the pasture. At that time, the pasture canopy will intercept 95% of the incident light. The leaf area which will prevent all but 5% of the light from reaching the soil surface is called the critical leaf area and is usually defined by a critical leaf area index. The leaf area index (LAI) is the number of units of leaf per unit area of soil surface and the critical leaf area is different for different species (Walton, 1983).

As grasses age and mature, the critical leaf area index will increase. The leaves of a young grass plant are held in a compact rosette. As the plant matures, the internodes elongate, the leaf arrangement becomes more open, and an increased leaf area is required to intercept 95% of the light falling on the canopy. The light reaching the soil surface decreases as the LAI is increased (Walton, 1983).

The exceedingly important feature of the regrowth pattern of plants is the inverse relationship between their mass following defoliation and the length of time which passes before growth becomes exponential (Walton, 1983). Severe defoliation of the grasses will remove not only a substantial amount of dry matter, but also much of the carbohydrate reserve material stored in the stem base. Where carbohydrate reserves are low, initial growth will be slow, and the total productivity of the stand will very likely be reduced. The species respond differently to defoliation also (Walton, 1983).

Many studies have focussed on the effect of defoliation on pasture production. In this chapter the effect of defoliation on plants, the influence of defoliation on sward characteristics, the effects of defoliation on pasture production, and the characteristics of selected species, will be reviewed. Attention will be concentrated mainly on perennial ryegrass (Lolium perenne. L), the most widely sown forage grass species in temperate countries. In a final section comparative assessments are made of perennial ryegrass and two other widely grown forage grasses, prairie grass (Bromus willdenowii Kunth.) and smooth bromegrass (Bromus inermis Leyss.), which were investigated on this project.

2.2.. The effects of defoliation on herbage production

2.2.1. Effects of defoliation on plant regrowth

2.2.1.1. The effect of removal of leaf

The effect of leaf removal on the growth of a plant is dependent on whether the whole or only part of the leaf is removed, the stage of development of the leaf which is removed and the extent to which the leaf area of the plant as a whole is reduced (Tainton, 1981). In the sward the importance of maintaining leaf area sufficient to intercept most of the incident light for photosynthesis and the rapid recovery of this leaf area after defoliation was illustrated by the classic studies of Brougham (1956), in which regrowth increased as the residual LAI increased. The increase in Crop Growth Rate (CGR) was observed to continue up to the point at which virtually all of the incoming light was being intercepted and the sward formed a closed canopy (Brougham, 1956).

The penetration of light into the sward is determined by the size, shape, and angle of the leaves. The effect of defoliation height will depend on growth conditions immediately prior to defoliation (Walton, 1983). Generally the effects of removing older leaves are less than the effects of removing younger leaves in perennial ryegrass, but this may depend on nutrient status (Davies, 1988). Removal of the emerging leaf reduced extension more than the removal of the fully emerged leaves at high nutrient level, but the reverse was the case at low nutrient level with cockfoot grass (Davidson and Milthorpe, 1966).

In swards maintained at low LAI, young leaves are expanded in high light, free from shade by old leaves, and so develop a high capacity for photosynthesis (Woledge, 1973, 1977, 1978). However, at the high stocking rates required to maintain a low LAI many leaves are defoliated while they are young (Morris, 1969, McIvor and Watkin, 1973). Thus, it is a proportion of the most photosynthetically efficient tissue that is removed. Nevertheless, the growing leaf (L1) and the remainder of the youngest fully expanded leaves (L2) contribute substantially to the total photosynthesis of the canopy. In a study in a sward maintained at LAI 1.0 by continuous grazing , the growing leaves and the youngest fully expended leaves together contributed some 75% to the total photosynthesis of the canopy (Parsons et al., 1983a).

A general description of the effect of defoliation on plant regrowth was given by Walton (1983). The reduction in photosynthetic capacity of the plant will invariably affect plant vigour and in particular the growth rates of the roots and lateral daughter shoots, both of which are much more sensitive to a deficiency of energy than is the main stem. Frequent leaf removal will therefore reduce the capacity of plants to produce tillers and will reduce the size and depth of penetration of the root systems. However, the increased light penetration to the base of the sward resulting from leaf removal may stimulate the development of daughter tillers from the basal nodes in many species, or alternatively stimulate the growth of young tillers which have already begun development and which may not have survived in the dense canopy (Tainton, 1981).

2.2.1.2. The effect of removing the stem apex

Since the inflorescence of the grass plant develops directly from the apex of the stem, the most obvious effect of removing the apex is that of terminating stem growth and preventing flowering and seed production (Tainton, 1981). An important secondary effect of the removal of the stem apex results from the associated removal of the inhibiting effect of this apex on the development of lateral tillers lower down on the stem, an inhibition which results from the secretion of growth regulators by the apex (Tainton, 1981). The removal of the apex leads to growth in previously dormant tiller initials at the basal nodes of the stem, and this results in an increased tiller density (Tainton, 1981).

In addition to the above effects, the removal of the stem apex in certain species in which it is elevated above grazing or cutting height while it is still in the vegetative growth stage and therefore still producing leaves reduces the eventual number of leaves which will be formed (Tainton, 1981).

The importance of the location of the apex in relation to defoliation has been recognized. During the annual cycle of development some tillers become reproductive and basal internodes begin to elongate, carrying the developing inflorescence upwards and exposing it to decapitation. Once the apex has been removed the tiller dies, so regrowth in reproductive swards depends partly on the number and developmental status of any accompanying undecapitated tillers. The timing of cuts during the reproductive phase is thus critical in relation to the quantity and character of the regrowth (Davies, 1988). Matthew (1990) suggested that reproductive tillers supply substrate to daughter tillers and assist the initial establishment of the daughter tillers, and he (Matthew, 1990) found that the translocation to daughter tillers was greater where the parent tiller seed head had been removed than where the parent tiller seed head remained intact.

As decapitated tillers cannot continue growth, immediate regrowth depends on the tillers which have escaped decapitation and can continue to form new leaves and/or stem material. New tillers are, however, developed on the cut stubs of the decapitated tillers, which may accumulate large amounts of reserve carbohydrate. Ample evidence exists to show that when these stubs are cut short fewer new tillers are formed and regrowth is reduced (Davies, et al.,1981). Each reproductive tiller stub in perennial ryegrass seems to be capable of producing two to three new tillers (Davies et al., 1981) and under favorable conditions the number of living tillers may double in 2 weeks (Davies, 1988). On the other hand observations have shown that in dry conditions many vegetative tillers in a reproductive sward of perennial ryegrass die before or as a consequence of defoliation (Davies, 1988).

2.2.1.3. The carbon reserves

A plant which has insufficient assimilatory surface to supply its current respiratory needs for maintenance and growth must make use of available carbon resources, the most important of which are the non-structural water-soluble carbohydrates (Davies, 1988). Fructosan levels in stubble and roots of perennial ryegrass and cocksfoot plants fall rapidly after defoliation (Sullivan, et al, 1943; Sprague, et al.1950). This fall is presumably arrested when sufficient current photosynthate is produced to meet demands. The return to the original level is normally complete within 4-5 weeks, though it may be slower at low temperature (Davies, 1965). Frequent defoliation can lead to low stubble carbohydrates, poor regrowth and even tiller death (McIlvanie, 1942).

Evidence that carbohydrate levels may directly influence regrowth was provided by Alberda (1966a,b), who held perennial ryegrass plants in the dark for 3.5 days to reduce the level of carbohydrate in the stubble before defoliation. Regrowth in these plants was substantially less than in control plants receiving continuous light. In the high-carbohydrate plants the new leaf appeared to be formed almost entirely at the expense of stubble carbohydrates.

The contribution of exposed green leaf sheaths to the net carbon balance after cutting is not well documented (Davies, 1988). Regrowth of perennial ryegrass plants with most of the leaf laminae removed was reduced by 20-30% when the sheath and pseudostem was shaded (Davies et al, 1983). In a continuously grazed sward the contribution of sheath to canopy photosynthesis was found to be less than 5% (Parsons et al, 1983a).

The regrowth ability of ryegrass is predominatly dependent on the size of mobile reserves, both nitrogen and carbon (Gonzalez, et al., 1989). Gonzalez, et al., (1989) studied the changes in stubble carbohydrate content during the regrowth of ryegrass grown under hydroponic conditions at two nitrogen levels. The result showed that regrowth at a non-limiting nitrogen level (1.0 mol m-3 NH_4NO_3) involved two different physiological periods. The first occurred during the first 6 days and was characterized by the mobilization of 60% to 90% of the soluble carbohydrates. During the second period (6-28 days of regrowth) carbohydrate contents rose to the values observed prior to cutting (20% of dry matter at the 28th day of regrowth). The effect of low nitrogen conditions (0.2 mol M^{-3} NH_4NO_3) was observed only during the second phase. Plants regrown in a nitrogen-starved medium accumulated 2.3-fold more poly-fructans than plants regrown in a non-limiting nitrogen medium.

2.2.1.4. Roots

The effect of defoliation is to reduce root growth (Crider, 1955), and depress mineral uptake (Oswalt et al, 1959), effects associated with a decline in root respiration. Tracer studies using ^{14}C (Clifford and Langer, 1975; Ryle and Powell, 1975) show a reduction in photosynthetic carbon transported to roots of defoliated plants of Italian reygrass and uniculm barley immediately after defoliation. Evans (1971) found that defoliation of ryegrass plants to 75 mm reduced root growth in the following week by approximately 40% while defoliation to 25 mm reduced root growth by almost 90%. Troughton (1957) reviewed a number of experiments reporting similar reduction of root growth after defoliation. Matthew, et al. (1988) reported root mass and new root production to be relatively insensitive to grazing management; seasonal fluctuations in new root production were large in comparison to those produced by contrasting hard and lax grazing regimes.

2.2.2. Effect of defoliation on sward characterstics

2.2.2.1. Plant size

As herbage accumulates during regrowth the number of intact new leaves on each tiller increases. In vegetative swards of perennial ryegrass the mean number of living leaves per tiller rarely exceeds three (Hunt, 1965; Alberda and Sibma, 1968), and the production of a fourth leaf tends to be counterbalanced by the loss of the first one (Davies and Calder, 1969; Davies, 1971). Unless the most recently-formed leaf is appreciably larger and heavier than the one that it replaces (or stem development occurs) the net gain in weight of living leaf will be small. In many instances, and especially in the second half of the year or in the winter, any net gain of this kind is counterbalanced by the loss of whole tillers, so net herbage growth rate becomes zero and a ceiling yield is reached. Assuming that no intact leaves remain after defoliation, the ceiling yield can be expected to be attained after three leaf-appearance intervals (Davies,1977). Ceiling yields in a vegetative sward thus depend on seasonal variations in leaf lengh (Davis, 1977) and tiller numbers. The length of new leaves (and their rate of appearance) is influenced to a large extent by the length of the sheath tube though which the leaves emerge (Grant, et al, 1981a). If the sheath tube is left intact (Younger, 1972; Davies,1974) the emerging leaves will be relatively long and may appear more slowly than in comparable undefoliated material. If on the other hand the cut removes the upper part of the sheath the new leaves will be shorter and may appear as quickly as in undefoliated plants. Jackson (1976) found that the heights of insertion of the lowest green leaf blades on tillers of S.23 perennial ryegrass at constant cutting heights of 3,6,9, and 12 cm, were 2.6, 4.3, 6.6 and 9.2 cm respectively. Weights of green leaf blades were very similar for all cutting heights.

The tillers produced from reproductive stubs frequently emerge from old buds exposed by the decay of their subtending sheaths, or break through the old sheaths (extra vaginal tillers). They are considerably smaller than the old vegetative tillers (Davies et al., 1981). Regrowth may then consist of a dense mat of small tillers with exposed green sheaths which can, in turn, provide a highly efficient basis for the next regrowth cycle (Davies and Evans, 1982).

2.2.2.2. Seed head production

Responses to defoliation in the reproductive phase are related both to the duration of the phase and to the percentage of tillers which become reproductive. In swards well supplied with water and nitrogen the loss of old tillers by decapitation is quickly made up for by development of new tillers, though heavy fertilization of a reproductive crop can both increase deaths of non-flowering tillers after defoliation and reduce formation of new tillers (Dawson, et al., 1983). Each reproductive stub in perennial ryegrass seems to be capable of producing two to three new tillers (Davies et al., 1982) and under favorable conditions the number of living tillers may double in 2 weeks. In this way the sward rapidly increases its tiller population towards the maximum characteristic for the time of year.

Autumn and early spring defoliations appear to have little influence on the number of seed heads formed (Roberts, 1965), though they may influence the number of vegetative tillers and therefore the percentage of tillers which flower (Davies and Simons, 1979). Comparisons of data from different experiments, harvest years and cutting treatments for S.24 perennial ryegrass confirm that the total number of tillers which become reproductive remains similar over a wide range of circumstances (Davies, 1988). Very frequent close defoliation, however, substantially reduces the total number of reproductive tillers in a way that cannot be accounted for by tiller deaths. Box-grown swards of S.23 perennial ryegrass cut every 10 days at average heights of 3 cm and 2 cm contained only 13% and 8% of the total number of decapitated tillers observed when the swards were cut at mean ear emergence. Similarly low totals have been recorded in continuously grazed swards (Davies, 1988).

2.2.2.3. Tiller population density

Tiller development is stimulated by defoliation, though the number of new tillers initiated, and the rate at which they develop, is likely to be strongly affected by sward conditions both before and after defoliation (Jewiss, 1972). The main factor influcencing the initiation of tillering seems to be the attenuation of the incident light through the canopy, via changes in the proportions of red/far-red light and involving the phytochrome system (Deregibus et al., 1983).

The loss of tillers is increased by both severe shading (Kays and Harper, 1974) and by severe defoliation (Brougham, 1959; Smith, et al, 1971). Changes in tiller density can be extremely rapid over short periods of time (Brougham, 1960; Garwood, 1969), though it may be easier to depress than to increase populations in the short term.

Tiller populations tend to increase as the frequency of defoliation increases, and are maintained at a higher level under continuous stocking management than under rotational grazing at comparable stocking rates (Hodgson and Wade, 1978). The influence of severity of defoliation is more complex, populations tending to be greatest at intermediate levels of defoliation, but the pattern of response is sensitive to both sward and climatic conditions at time of defoliation (Brougham, 1960; Jewiss, 1972; Grant et al., 1981a.b). Hodgson et al (1981) have shown that tiller numbers and tiller weights in swards maintained at different herbage mass by continuous grazing are related to each other through the minus 3/2 law (Fig 2.1) established by Yoda et al (1963). This law, initially applied to plant numbers and plant weights during a period of self-thinning, has been shown by Kays and Harper (1974) to apply equally well to tiller numbers and tiller weights in perennial ryegrass. The self-thinning law 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).

Swards may respond to defoliation by net gains, net losses or no overall changes in tiller populations, depending on initial tiller numbers at the time of cutting and the time of year. During the spring the tendency will be to net gains, but during autumn the opposite will be the case. In the later part of the summer a sward defoliated intermittently (say every 4 weeks) may develop a stand of tillers sufficiently dense to permit rapid canopy development and suppress further tillering (Davies, 1977).

Tillers may be suppressed to the point at which they will die when the sward is cut (Alberda, 1966a). Wade (1979) observed that tiller losses in swards were high in the first week after defoliation and that subsequent tiller production was inversely proportional to LAI. When tillers cease to develop leaf sheaths accumulate, and these may die and persist after the sward has been defoliated. With continued lax defoliation tubes of dead sheaths may accumulate (Jackson, 1974) and suppress further tiller development (Davies et al., 1983).

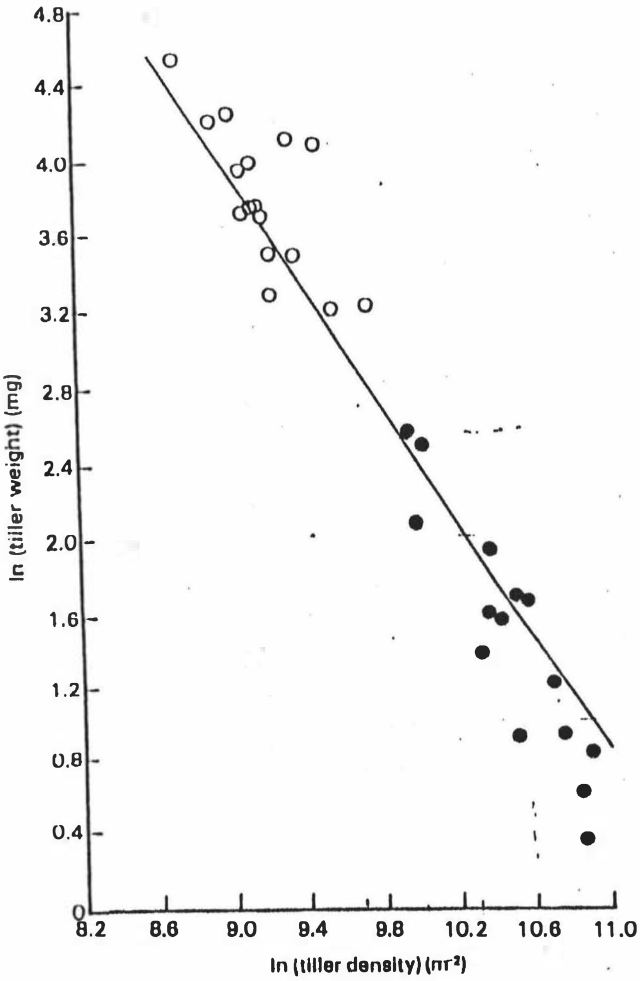

Figure 2.1 Relationship between ln (tiller weight) and ln (tiller density) in perennial ryegrass/perennial ryegrass dominant swards. O, Cut swards, 30 June–17 November. (After Davies, unpublished). ●, Grazed swards, 15 July–4 September. (After Grant *et al.* 1986). Slope of line = $-{}^3/_2$. (from Davies, 1988)

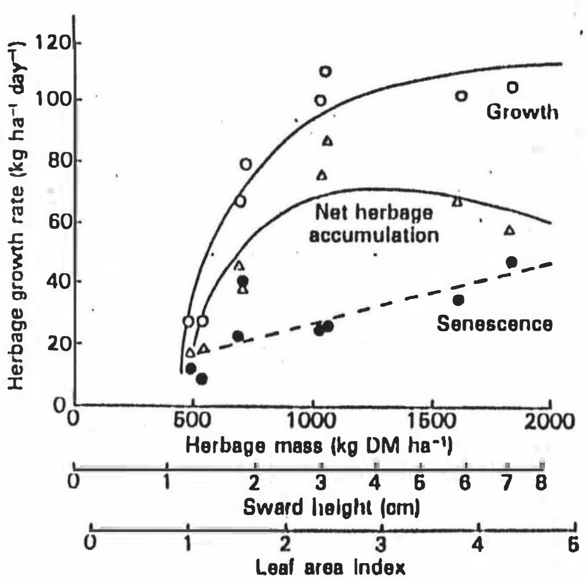

Figure 2.2 Relationships between biomass (kg ha^{-1} organic matter) sward height (cm) and LAI and rates of herbage growth, senescence and net herbage accumulation (all kg ha^{-1} DM) in swards continuously stocked by sheep. (After Bircham and Hodgson, 1983.)

2.2.3. The effects of defoliation on pasture production

2.2.3.1. The principal effects of management on tissue turnover in the grass crop

There are two characteristics of the grass crop which are central to understanding the effects of management on production. First, because the grass sward displays a rapid turnover of tissues, any material that remains unharvested is soon lost to death. This turnover is clearly the origin of a considerable potential loss to production. With a mean leaf appearance interval of 11 days, an amount equivalent to the entire standing live weight of the crop may die each month. So, in contrast with cereals, and the many crops which are harvested once at the end of a single period of growth, the grass crop must be harvested repeatedly (Parsons, 1988).

Second, it is the photosynthetic tissue, the leaves, that are predominantly harvested. Over the season the repeated defoliation that is essential to harvest a proportion of the grass crop, inevitably reduces the leaf area and light interception of the canopy, interrupts canopy photosynthesis and so reduces the capacity for the production of new leaves. Clearly, then, the way the sward is harvested on any one occasion has a profound effect on the amount grown, as well as on the degree to which the tissue produced is harvested. The objective of grassland management must be to strike a compromise between the conflicting demands of the grass plant, which needs to retain leaf area for photosynthesis, and the essential need to remove leaf tissue for harvest. This conflict leads to a dilemma that is central to grassland management (Parsons, 1988).

There has long been interest in the degree to which control of sward conditions can be used to influence herbage production and utilization. Hodgson and Wade (1978), however, concluded that Net Herbage Accumulation (NHA) was relatively insensitive to variations in grazing management or to variations in stocking rate over the range of practical interest. The absence of substantial differences in animal production between intermittent and continuous grazing managements (Arnold, 1969, Marsh, 1976) supports this view.

The development of concepts of tissue turnover or tissue flows in grazed swards provided a basis for explanation of this relative insensitivity to variations in grazing management. Hodgson et al (1981), and Bircham and Hodgson (1983) described the tissue turnover relationship. The use of Net Herbage Accumulation (NHA) as the index of comparison in both cutting and grazing experiments introduces a major difficulty in the interpretation of treatment differences. In the absence of grazing animals, NHA is the resultant of the processes of growth (G) and decay (D) but, when the grazing animal is present, NHA represents the balance between G, D, and herbage consumption (C), all expressed as rates per unit of ground area thus:

NHA = G - (D + C) (1)

In these circumstances differences in NHA between experimental treatments could be due to differences in G, D or C or to combinations of changes in two or more variables. Herbage tissue which is not harvested must eventually senescence and die (Vickery, 1981); therefore the efficiency of harvesting of the tissue grown is a determinant of NHA.

When NHA is zero, as it may be under continuous stocking management, equation (1) can be transformed to equation (2):

NP = G - S = C green (2)

here NP is the net production of green herbage and senescence (S), the rate at which live tissue becomes dead tissue, is substituted as an alternative to the parameter D which is difficult to measure. Maintenance of a sward in a steady state (i.e.NHA = 0) makes it possible to relate the many factors of the sward/animal interface to common parameters like herbage mass, sward surface height or leaf area index (LAI) (Bircham and Hodgson, 1983).

The balance between photosynthesis, gross tissue production, herbage intake and death that may be achieved in swards maintained at a range of sward states has been derived from studies of both the carbon balance of the grazed crop (Parsons et al, 1983) and from studies of the rates of tissue growth and senescence on individual tillers (Bircham and Hodgson, 1983; Grant et al., 1983). Despite the use of contrasting techniques, there is close agreement between these observations when the swards are compared on the basis of Leaf Area Index (LAI) i.e. the area of leaves per unit area of ground, or sward surface height (Hodgson, et al. 1978).

These studies have shown how rates of photosynthesis and gross tissue production are close to a maximum in swards maintained at a high LAI, but in order to sustain this level of green production, a large proportion of the leaves produced must remain in the sward to contribute to photosynthesis. As a result, this same tissue inevitably gives rise to a high rate of loss of matter to death and decomposition, and the amount harvested is small. In swards maintained at a lower LAI, a greater proportion of leaf tissue is removed and photosynthesis and gross tissue production are substantially reduced. However, the increase in the efficiency of utilization of plant tissue offsets the decrease in the amount grown, and the amount harvested is actually increased (Parsons, et al. 1983a).

Clearly then, maximum harvested herbage yield per hectare is not achieved in swards maintained at a high LAI so as to intercept a large proportion of the incident light, as was originally suggested (Donald and Black, 1958), but at a lower, intermediate LAI, as this provides the best compromise between gross tissue production on the one hand and losses to decomposition and death on the other. Bircham and Hodgson (1983) demonstrated the existence of a 'homeostatic' mechanism in continuously grazed swards, whereby compensatory changes in species population density and tissue turnover on individual plant units combine to maintain relatively constant net production of green herbage over a range of herbage mass and LAI. Leaf area index cannot readily be measured on a farm, but studies have shown that, in practice, maximum yield per hectare under continuous stocking is achieved in a sward maintained at a sward surface height of 4 to 6 cm (Bircham and Hodgson, 1983).

2.2.3.2. Continuously stocked swards

In its simplest form continuous grazing describes a situation where animals maintain access to a single, often extensive area for a large proportion of the grazing season. Although the defoliation of the sward is not uniform (Harris, 1978), animals are continuously present and so have a continuous effect on the uptake and loss of matter. Changes in leaf area index and in the rates of photosynthesis, tissue production, herbage intake and death are characteristically gradual (Parsons, 1988).

The structure of the grass sward varies considerably in response to management. Swards maintained by continuous stocking at low LAI, or low sward height, are characterized by a large number (40-60,000/sq-m) of small tillers. By contrast, swards maintained by continuous defoliation at a greater LAI, or greater sward height, are characterized by smaller numbers (10-15,000/sq-m) of large tillers (Parsons, 1988). These morphological adaptations have important consequences to the pattern and severity of defoliation experienced by individual plants in the sward. When a sward of a high LAI, and a small number of large tillers, is defoliated to a height of 3 cm, this results in the loss of a substantial proportion of the leaf tissue and the expansion and restoration of leaf area depends on reserves (Davies, 1965; Davidson and Milthorpe, 1966).

The effects of defoliation height on regrowth are particularly well illustrated by grazing studies (Bircham and Hodgson, 1983; Grant. et al., 1983), in which stocking rates were varied to maintain different fixed sward heights. Results from these studies showed that shorter swards have more smaller tillers and a slower rate of growth per tiller than longer swards but that, provided the chosen sward height allows the maintenance of a fairly complete canopy, the rate of growth per unit area remains much the same. These relationships are well illustrated in Fig 2.2 (Bircham and Hodgson, 1983). Increasingly inefficient harvesting of this growth by the animals at greater sward height leads, however, to the loss of a greater percentage of the herbage grown to senescence. This results in a reduction in the rate of net herbage accumulation, which in this instance equals herbage consumption by the animal since there is no change in the height or weight of standing green herbage. Between the limits set, on the one hand, by lack of sufficient ground cover to intercept light and, on the other hand, by inefficient harvesting, differences in maintained sward height or weight do not greatly influence herbage consumption per unit area. The range of sward conditions over which this holds true appears to include levels of standing green herbage from 700 to 1400 kg/ha (Bircham and Hodgson, 1983), and sward heights from 2 to 6 cm (Grant,et al., 1983). Further adaptation to very close grazing may be possible where tiller populations are built up gradually over a period of some years (Parsons, et al., 1983).

Efficiency of harvesting by animals seems to vary also from experiment to experiment. The proportion of herbage grown which is lost to senescence has varied from 20% to 25% (Grant, et al., 1983a; grazing by mature wethers), to 50% (Bircham and Hodgson, 1983; grazing by lambs), and 50% to 60% (Parsons, et al.,1983; grazing by yearling wethers). The subject is one which needs further investigation.

Additionally, a number of factors modify the general pattern of response to the intensity of defoliation. First, the pattern of uptake and loss of tissue in relation to LAI is greatly influenced by season (Brougham, 1958). Second, production per hectare also decreases in swards maintained by lenient grazing, as the distribution of LAI in the swards becomes less uniform as the season progresses (France et al., 1981). Third, the amount harvested by animals from a continuously grazed sward depends heavily on the behavioral response of animals to the morphological characteristics of the crop (Arnold, 1964; Williams et al., 1976), a response which varies with the physiological status of the animals involved (Arnold and Dudzinski, 1967; Arnold, 1975).

2.2.3.3. The effect of changing sward conditions

The effect of changes in herbage mass on subsequent rates of net herbage accumulation is of particular interest. Bircham and Hodgson (1984) investigated rates of growth and senescence in high and low mass swards which were respectively either grazed down to low mass (HL) or allowed to grow until a high mass had accumulated (LH). The period of adjustment allowed before measurements commenced was 3.5 weeks. Net herbage accumulation was similar from both steady-state treatments and the LH treatment, but was greatly reduced in treatment HL in which there were fewer tillers and growth per tiller was at the reduced level characteristic of a low-mass sward. Other evidence (Grant at al., 1983b) showed that the short, densely tillered LH swards may, in the short term, combine high rates of growth per tiller with high tiller populations before tillers die in response to increasing herbage mass. Successful exploitation of this temporary advantage may underlie reports of increased production from variable cutting height systems (Smith, 1968; Ollerenshaw and Hodgson, 1977).

Pasture density can be modified in spring by grazing management. For example, the results of L'Huillier (1987c), working with dairy cows on perennial ryegrass and white clover pasture, showed that frequently grazed swards (12-day rotation and set stocked treatments) had higher sward density and proportion of white clover and lower proportion of dead herbage at the end of the treatment period than swards grazed at a 30 day interval. Net herbage accumulation of set stocked and 12-day rotation swards was lower than 30-day rotation swards (L'Hullier, 1987c). This reflected a greater degree of "control" of reproductive tiller development and thus lower net herbage accumulation of this component and pseudostem (L'Hullier, 1987c).

2.2.3.4. Intermittent defoliation

In contrast with continuous grazing, in which LAI and the components of the uptake and loss of matter change only gradually with time, intermittent defoliation is characterized by marked fluctuations in LAI and in the rate processes involved in the uptake and loss of matter during each cycle of regrowth and defoliation. Moreover, not only does the rate of uptake and loss change during each cycle, but there are also marked changes in the relationship between these processes as the cycle proceeds (Parsons, 1988).

The principal effect of variations in the severity of defoliation is on the degree to which successive harvests interrupt light interception and photosynthesis, and so limit the supply of assimilates for growth. Brougham's experiments (1956, 1957) described the principal effect of variations in the severity of defoliation on the restoration of leaf area and light interception. In Brougham's experiments a sward grown to a height of 22 cm was subdivided and defoliated to three different heights: 12.5, 7.5, and 2.5 cm. The results showed that an increase in the severity of defoliation not only leads to a greater reduction in light interception immediately following defoliation, but also extends the time taken by the sward to regain full light interception. The swards defoliated to 12.5 cm took only 4 days to regain full light interception, whereas those defoliated to 7.5 and 2.5 cm took 16 and 24 days, respectively. This phenomenon is illustrated in Fig 2.3a (Johnson, et al. 1983; Johnson and Parsons, 1985), using a mechanistic model of grass production and senescence. It is clear that the effects of the severity of defoliation on photosynthesis and gross tissue production follow broadly the same patterns as those observed by Brougham for light interception (Parsons, 1988).

The rate of loss of tissue by death depends on the size and the rate of turnover of the oldest category of tissue in the sward (Morris, 1970). An increase in the rate of loss by death has been observed during periods of regrowth in the field (Hunt, 1970; Grant et al., 1981a) and under controlled environment conditions where earthworms and fauna are absent (Robson, 1973 a,b). This increase in the rate of death is predominantly the result of an increase in the size of leaves involved in the turnover of tissue (Hunt, 1965; Robson, 1973b). However, prolonged periods at a high LAI towards the end of a period of regrowth may lead to losses of tissue over and above those which result from the inevitable turnover of leaves and tillers. In dense swards the mutual shading of tillers may lead to an accelerated senescence of small tillers, or whole plants, as natural thinning occurs (Kays and Harper, 1974; Ong, 1978).

The principal effects of the severity of intermittent defoliation on the rate of loss of tissue by death is also illustrated in Fig 2.3b (Johnson and Thornley, 1983; Johnson and Parsons, 1985 a), using the same mechanistic model of grass production and senescence. The model demonstrates how an increase in the severity of defoliation leads to a decrease in the rate of death immediately following defoliation and also extends the time taken for the sward to regain maximum death rates (that is, the time when death rate equals the gross rate of production of tissue and a ceiling yield is achieved).

The broad similarity between the pattern of loss of tissue to death and the pattern of gross tissue production is more than coincidental. Regardless of the severity of defoliation, the rates of photosynthesis and death immediately following defoliation are both a reflection of the size of leaves remaining in the stubble, albeit in the case of photosynthesis and shoot growth it is the size of the youngest category of leaves that is most significant, whereas in the case of death it is the size of the oldest category of leaves that is important. Also, regardless of the severity of defoliation, a sward which takes a long time to regain full light interception and maximum rate of gross tissue production will take a long time to regain maximum death rates. This is because changes in the rate of death must lag behind changes in the rate of gross tissue production (Parsons, 1988)

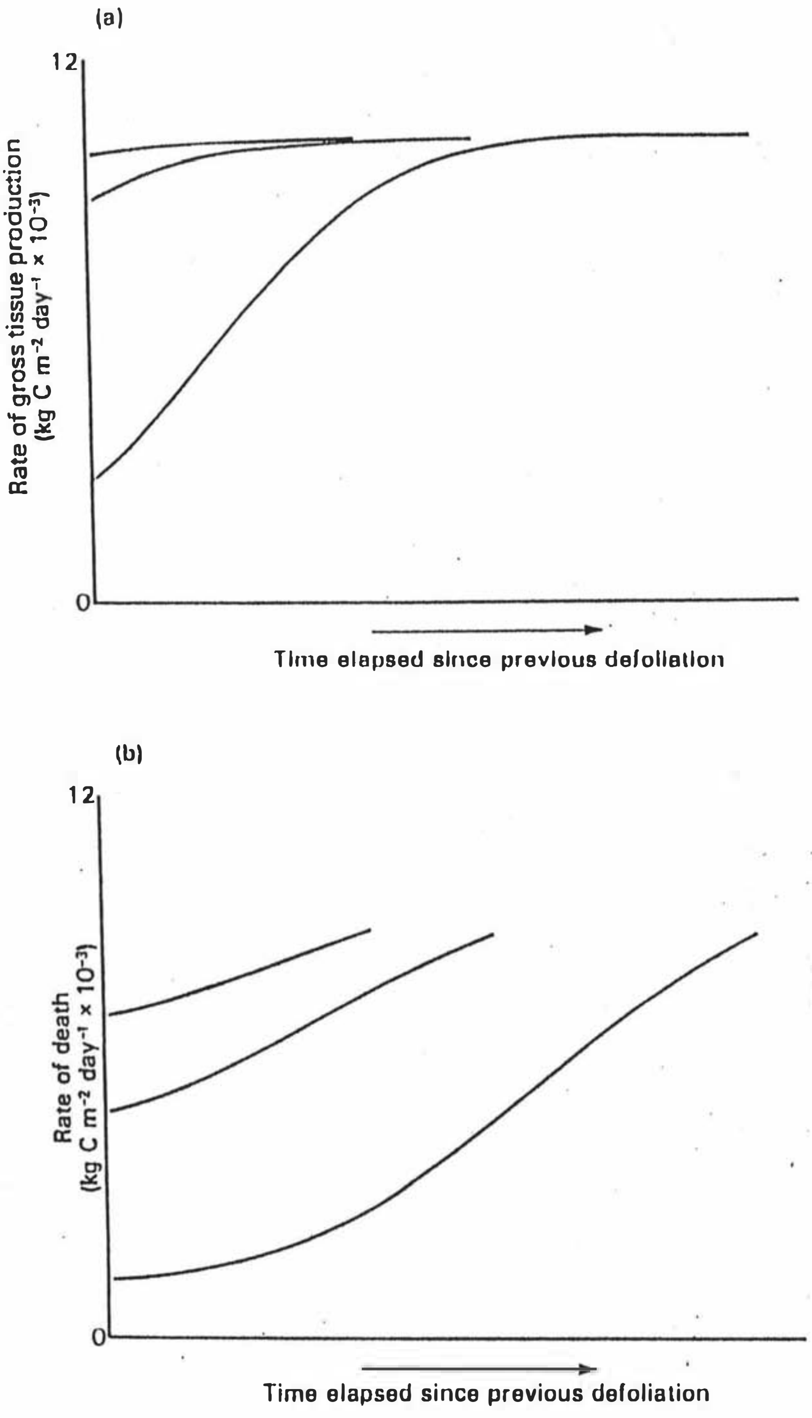

Figure 2.3 The effects of three severities of intermittent defoliation on (a) the rate of gross tissue production and (b) the rate of loss of tissue to death, as illustrated using a mechanistic model of grass production and senescence. The illustrations cover the period until the sward has reached 95% of its ceiling weight.

2.2.3.5. The duration of regrowth in an intermittently grazed sward

Parsons,et al. (1988) studied the effect of the duration of regrowth on photosynthesis, leaf death and the average rate of growth in rotationally grazed swards. They reported that the average growth rate (based on change in the weight of lamina alone) increased as the duration of regrowth was extended from 12-13 to 19-23 days, but changed little as the duration of regrowth was extended from 19-22 days to 30-34 days. In spring and summer, elongation of reproductive stems increased the average growth rate (of lamina plus stem) up to 30-40 days but the accumulated stem material could not reliably be harvested by sheep. L'Huillier (1987c) reported that net herbage accumulation of set stocked and 12-day rotation swards was lower than 30-day rotation swards. Parsons, et al (1988) suggested 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 by sheep.

In practice, conscious rationing of pasture to animals (restricting their intake) means pasture can be accumulated, transferred and used at a later date. This management strategy is most often used in New Zealand during winter when long rotations (60-100 days) are adopted to 'spin-out' autumn pasture and build up pasture mass for lambing and calving. Rationing also helps to buffer summer feed deficits, and enables transfer of pasture to nutritionally important periods such as early lactation and pre-mating (Sheath, et al., 1987).

In New Zealand cold winter environments such as in Otago and Southland where winter pasture growth rates are very low, rotation lengths of 80-100 days are required. In warmer winter enviroments where pasture growth rates are relatively high (10-15 kg DM/ha/d), current growth can be sufficient to allow for a 50-80 day rotation (Sheath, et al., 1987). Successful transfer and allocation of pasture is more difficut during late spring, summer and autumn, particularly in dry conditions. Long rotations leading into and during dry summer periods can help reduce the impact of summer deficits by transferring surplus, late spring pasture. However, prior to dry conditions there is a danger of accumulating excess pasture to the subsequent detriment of pasture density and species composition. Furthermore, decline in pasture quality will occur under dry conditions, so there is the dilemma of whether to feed stock well while high pasture quality exists or to save pasture for subsequent maintenance feeding (Sheath, et al., 1987).

2.2.3.6. Regrowth in relation to time of defoliation

The importance of the timing of spring cuts in relation to stage of development was clearly shown by Davies (1965) in his comparison of regrowth in an early- and a later-flowering timothy. Only the actual reproductive tiller elevate theirs apices in perennial ryegrass, and the situation is very similar in timothy. Regrowth after a cut on 19 May which removed 4% of the tiller apices was 4240 kg DM/ha, whereas a cut on 8 June, which removed 32% of the tiller apies (and probably destroyed virtually all of the seasons reproductive tillers) produced only 1930kg DM/ha of regrowth (Davies, 1973). Behaeghe (1974) showed clear evidence of a lag phase after mature reproductive swards were cut in early June. Comparable swards subjected to several earlier cuts were almost completely vegetative in character and regrew immediately. There was little difference in regrowth between these swards at a later cut, and it seems possible that once swards have recovered from a cut during the main reproductive phase, then further total growth may be relatively independent of the earlier cutting regime (Davies, 1969; Binnie, et al., 1980).

2.2.4. Summary

In this section the influence of changes in plant morphology, sward structure, and pasture production after cutting or grazing have been considered. Some indication has been given of how regrowth depends on the initial resources of leaf area and, when demands cannot be met by rates of current photosynthesis, on carbon compounds present in the stubble. An account has been given of how and when the accumulation of dry matter in new leaves is offset by losses of older leaves present in the stubble or accumulating during regrowth. Evidence has been presented showing how tiller populations are related to the level of herbage mass which is allowed to accumulate. However, the changing morphology of the plant strongly influences its response to defoliation in both the shorter and longer term. The structure of the grass sward varies considerably in response to defoliation; and the sward is capable of a high degree of adaptation to management (Davies, 1988).

In view of the complexity and plasticity of the response of the grass crop to defoliation, no single recipe for production can hold true under any but the most limited circumstance. In practice the need to sustain fluctuating livestock numbers against a background of seasonal variation in production requires a more flexible approach. An understanding of the physiological principles of the effects of defoliation on the uptake and loss of matter in the grass crop, supported by an appreciation of the importance of avoiding a marked deterioration in sward structure, will enable farmers to make their own management decisions as best suit their objectives and the changing conditions they experience. Such an understanding should increase the reliability and efficiency of production of the grass crop, and so increase confidence in the use of grass as an inexpensive feed stuff for ruminant production (Parsons, 1988).

2.3. Characteristics of selected species and comparison between them.

Much of the evidence which has been presented was derived from perennial ryegrass, information on other temperate grasses being much less complete. Less still is known about tropical grasses, though it is clearly evident that their response in the reproductive phase of development can vary widely (Davies, 1988). In the following sections a more detailed appraisal is given of the morphology and growth characteristics of perennial ryegrass, prairie grass and smooth bromegrass, the three grass species used in field studies in this thesis, togather with a comparison of their response to defoliation.

2.3.1. Perennial ryegrass (Lolium perenne. L)

Perennial ryegrass (Lolium perenne. L) is a long-lived perennial capable of producing very many tillers. The plant is nutritious and palatable and stands up to hard grazing. It will not do well under poor conditions, where fertility or rainfall is low. It requires an annual rainfall of between 850 and 1030 mm (34 and 41 in) and a mild climate during the growing season. Ryegrass/white clover pastures grow extensively throughout New Zealand (Korte, et al., 1987). In vegetative swards, the mean number of living leaves per tiller rarely exceeds three (Hunt, 1965; Alberda and Sibma, 1968) and the production of a fourth leaf tends to be counterbalanced by the loss of the first one (Davies and Calder, 1969; Davies, 1971). Vegetative stems are almost erect at first but become decumbent as the primary axes grow. Each stem has an apical region about 1 cm long producing leaves at successive nodes and tiller buds in each leaf axis. Internodes just below this apical region elongate, separating the bases of individual tillers by up to 2 cm (Spedding, et al. 1972). Ryle (1964) recorded that perennial ryegrass leaves were relatively narrow (4mm) and up to about 180 mm long, increasing steadily in size from the first to the 7th leaf of a tiller; each tiller, however, had no more then three leaves at any one time. Anslow (quoted in Spedding, et al.1972) showed tiller weights of 2.0 - 2.9 g/1000 tillers for S24 and 1.0 - 3.0g/1000 tillers for S23 at population densities of 77-103 and 77-223 tillers/sq-dm, respectively, under conditions of irrigation and high N input over the whole year.

The cultivar Ellett was used in this experiment. Ellett was developed from a naturally ocurring selection (ecotype) at Mangere, South Auckland New Zealand. It was first evaluted as a regional ecotype by the Ministry of Agriculture. Yates Research Division extended the Trial network to include the main climatic regions of New Zealand. Ellet was placed on the Acceptable Herbage Cultivar list in 1980 (Duder, 1986). Ellect is a semi-erect, multi-tillered, broad leaved, perennial plant with dark green glossy leaves. It is early flowering, with a high seed yield potential (Duder, 1986).

The literature review of effects of defoliation on pasture production in this chapter refers mainly to ryegrass pastures (section 2.2). In summary, a 'homeostatic' mechanism exists in continuously grazed swards, whereby compensatory changes in population density and tissue turnover on individual plant units combine to maintain relatively constant net production of green herbage over a range of herbage mass and LAI (Bircham, and Hodgson 1983).

2.3.2. Prairie grass(Bromus willdenowii Kunth.)

Prairie grass is a true perennial originating in the pampas of South America, and now has a very wide geographical distribution (Hafliger, et al, 1981). "Grasslands Matua" Prairie grass was placed on the New Zealand list of Acceptable Herbage Cultivars on 1 January 1973. It was bred by Grasslands Division, DSIR, New Zealand. Matua prairie grass is taller, more erect and more densely tillered than other genotypes of prairie grass. It has light green foliage, tends to head about two weeks earlier than other prairie grasses and produce more heads per plant (Technical information series No.1 Grasslands Division DSIR, 1982).

Compared to ryegrass, prairie grass has high leaf appearance rate but low site filling, which results in low tiller numbers. Mature plants in a mixed pasture may have fewer than 10 tillers at a given time although some of these tillers may be over 1 cm thick (Rumball, 1974). It has large tillers with long wide leaves, resulting in high herbage production. High reproductive development occurs, which has large effects on yields, herbage quality and tillering activity. Vegetative and reproductive plants perform best under infrequent defoliation regimes (Hume, 1990).

Prairie grass has found favor on many dairy farms in New Zealand as a winter-active and palatable species (Rumball, 1974). Early recommendations for the grazing of Matua stated that hard grazing was acceptable, as long as the spelling interval was adequate (Technical information series No.1 Grasslands Division, DSIR, 1982, Lancashire & Brock, 1983). Matua's persistence through dry summers was found to be maintained if not severely grazed (Technical information series No.1 Grassland Divition, DSIR, N.Z.1982). Its cool-season growth is better than other perennial grasses (Fraser, 1982) and has compared well with annual and biennial ryegrass (Wilson, 1977).

Sellars (1988) noted that Matua prairie grass persisted better on sandy soils than on finer-textured soils. Matua prairie grass is more sensitive to waterlogging than ryegrass. Mwebaze (1986) found that high soil moisture levels reduced soil oxygen levels and Matua root and tiller production. Eccles et al. (1990), reported that during waterlogging, the rate of leaf extension of Matua prairie grass plants decreased, senescence rate increased, and shoot:root ratio increased. The uprooting of tillers by animals in dairy cow pasture was an important factor in the decline of a Matua prairie grass population (Pineiro and Harries,1978). Dodd, et al., (1990) investigated the possibility of reversing the process of deterioration in a run down prairie grass pasture by aerating soil with a seed drill coulter, or improving soil fertility through nitrogen application. They reported that the technique of soil aeration failed to reverse the process of pasture deterioration, because of uncertain adverse side effects. The winter application of N fertiliser is effective in reversing deteriortion, at least in its early stages, by improving plant vigour (Dodd, et al., 1990).

Black and Chu (1989) reported that lax grazing allowed Matua prairie grass to persist in the sward but resulted in only 56% pasture utilization. Hard grazing at 75% pasture utilization, resulted in less total herbage harvested, owing primarily to sward decline. The hard grazing improved pasture utilization without affecting sward persistence if grazing was delayed until new replacement tillers appeared. "Grasslands Matua" prairie grass and "Grasslands Nui" ryegrass both sown with "Grasslands Huia", White clover were compared under sheep grazing on two soil types (Stevens and Hickey, 1989). Production from high-endophyte "Nui" swards was significantly better than from " Matua" in autumn and winter but annual production was not significantly different. White clover was greater with Matua prairie grass than with Nui ryegrass in the second year, but not in the first or third years (Stevens and Hickey, 1989).

2.3.3. Smooth bromegrass (Bromus inermis Leyss.)

Smooth bromegrass(Bromus inermis Leyss) is a native of Europe and Asia, and is adapted to most temperate climates. It is a cool-season tall grass, and is widely grown in Canada, China, USA, and USSR. In North America the region of major adaptation is centered in the corn belt and adjacent areas northward and westward into Canada. In China, its range of distribution and use extends throughout the Northeast, North and Northwest (Newell,1983; Walton,1980; Chia,1988). It is a leafy sod-forming perennial which spreads vegetatively by underground rhizomes, and is also readily propagated by seed. Inflorescences are initiated in cool short days (Newell,1951). The plant is 50-130 cm high with 5-6 live leaves per tiller (Chia, 1986). From plant breeding studies, it has been reported that the leaf number per reproductive tiller is on average 5.3 (Wai-Koon, 1977). Pan (1986) classed the vegetative tillers into long and short vegetative tillers (Vegetative tillers more than half the height of reproductive tillers were defined as long tillers.), and reported the numbers of live leaves in long vegetative tillers ranged from 5.0 to 8.2, leaf length probably being related to the leaf number.

Smooth bromegrass is resistant to drought and to extremes of temperature, being capable of withstanding both hot, dry summers and long, cold winters (Walton, 1980), and so is better adapted to climate extremes than either perennial ryegrass or prairie grass. It can be grown on a range of soil types, but grows best on deep fertile soils of well-drained silt loam or clay loam. It is deep rooted and fills the surface soil with many roots and rhizomes (Newell,1983). The species is grown both alone and in mixtures with other grasses and legumes and is used for pasture and hay. It is also used for erosion control. The forage quality of smooth bromegrass ranks well among the cool-season grasses, and it is more palatable than most species in the vegetative stage. The large amounts of green forage produced early and late in the season provide grazing through a longer period than many other grasses (Newell, 1983). The crude protein level is high, ranging from 12% to over 20%, during the time of rapid growth at the beginning of the season (Walton,1983).

Smooth bromegrass is sensitive to defoliation. In common with other cool-season grasses, it has a critical growth stage at which carbohydrate reserves are low and tillers are few (Jung,1974; Walton,1980.). This coincides with the time when elongation of the apical meristem has just occurred. Intense defoliation at this time can easily lead to a reduction of the plant population. The early period of stem elongation is a critical time to cut because stubble carbohydrate reserves may be at a low level and basal axillary buds are not yet developed to initiate rapid regrowth (Paulsen,1969, and Reynolds,1962). Cutting during an early leafy stage or after anthesis causes less damage than cutting during the period of stem elongation (Knievel,1971). Eastin, et al. (1964) demonstrated that bromegrass is most easily damaged by intensive defoliation after the apical meristem has elongated. This growth stage was characterized by a low carbohydrate reserve level and an absence of new tillers.

The timing of the first spring cutting can thus affect the persistence and productivity of smooth bromegrass. There has been some controversy on this subject. Knievel (1971) found that the highest seasonal herbage yields and best stands of smooth bromegrass in Wisconsin were obtained when the crop was first cut at early anthesis. On the other hand, Kunelius (1974) reported that the stage of development of smooth bromegrass at initial harvest had only a limited influence on stand persistence in Canada. Harvesting prior to heading reduced the forage yield and crude protein production. In China, Chia Shen-siu (1986) and Su Chiakai (1988) suggested that the best time to cut for higher seasonal herbage yield and stand persistence is at heading or anthesis. Pan (1986) on QingHei Plateau (Chian) reported that harvest (one harvest per annum) at anthesis resulted in highest leaf mass and crude protein production. Raese (1963) indicated that smooth bromegrass vigor and stand density were enhanced by cutting at the post bloom stage. But from the point of view of forage nutritive value and animal performance, Calder (1977) indicated that the largest economic return, but not the highest yield of dry matter, would be obtained when the material was cut at the vegetative stage.

There is some information on the influence of stubble height on regrowth after cutting under field conditions. Smith (1973) reported that smooth Bromegrass persisted better when cut at 10cm then when cut at 4cm either two or four times per year. There is no information on cutting height above 10 cm.

For smooth bromegrass pasture management schedules, Walton (1983) indicated that where the material is intended for hay two cuts give optimum productivity and a satisfactory balance between production and forage quality. In China, two or three cuts per annum provided an optimum regime (Chia,1986; Su,1983). Frequent cutting usually favors the grass component of bromegrass-legume mixtures as compared with infrequent cutting. Paulsen and Smith (1968) showed that smooth bromegrass grown with alfalfa produced higher yields with frequent (five) cuts than with infrequent (three) cuts. Conversely like many other tall grasses, the yield of bromegrass decreases with frequent cutting. Maximum yields of bromegrass grown in pure stand are obtained under infrequent cutting regimes (Walton, 1980). The response to these management treatments indicates the importance of maintaining fertility levels when pastures are cut frequently.

CHAPTER 3 GRAZING MANAGEMENT, TILLER POPULATION AND TISSUE TURNOVER IN PERENNIAL RYEGRASS (Lolium perenne. L) PASTURE.

3.1 Introduction

Bircham and Hodgson (1983) and Grant, et al (1983) found that the rate of net production (NP) of green herbage (growth minus senescence) was relatively constant over a wide range of herbage mass and leaf area index (LAI) in swards of perennial ryegrass or ryegrass/white clover under continuous stocking management. The same authors (Bircham and Hodgson,1984) also suggested that under continuous grazing management it was not possible to increase NP by manipulation of herbage mass but that NP can be reduced in the short term if a sward of high herbage mass and low population density is grazed hard. These results suggest that there is limited scope within practicable managements, for influencing rates of NP in such swards.

In perennial ryegrass (Lolium perenne. L) swards large numbers of new tillers are produced shortly after flowering. This high tiller appearance rate may be balanced by a high death rate of tillers produced in early spring, so that relatively little change in sward tiller numbers occurs (Colvill and Marshall,1984; Korte,1986). Tallowin (1982) showed, however, that differences in grazing management can affect the percentage of early spring tillers surviving, and so result in different tiller age profiles in the following summer. Grazing management in spring but not autumn-winter can have a large effect on pasture composition, density and performance (L'Huillier, 1987c).

It is assumed that similar principles would apply in New Zealand (Bircham and Korte,1984), though long-term effects may be masked by seasonal changes in management (Korte et al.1984; Sheath & Boom, 1985).

The objective of the experiment reported here was to define the effects of season and grazing management on tiller population and tissue turnover in a perennial ryegrass pasture, specifically to examine the influence of management flexibility during the reproductive season on subsequent pasture performance.

3.2. Materials and methods

3.2.1. Site

The experiment was carried out between October 1986 and August 1988 at the Pasture and Crop Research Unit, Massey University, Palmerston North, New Zealand, on a sward of perennial ryegrass (Lolium perenne. L) (cv.Ellett) from which the clover had been removed by the use of picloram and 2,4-D. The soil is derived from greywacke loess, and classified under the Soil Taxonomy system as a Typic fragiaqualf. Mean annual rainfall is 995 mm and long term average temperature ranges from 8.0°C (July) to 17.6°C (February). The rainfall and temperature of this area during the experiment are shown in Appendices 3.1a and 3.1b. This pasture was sown in March 1983, after two years in crop. The sward was predominantly ryegrass but contained approximately 500 to 1000 tillers m^2 Poa trivialis L. After removal of clover, nitrogen was applied as urea at approximately 15kgN/ha every three weeks. The area was irrigated, using an overhead sprinkler system, in late spring and summer when the pasture was in dry condition.

3.2.2. Design

Sixteen 100 m^2 plots (4 replicates of 4 treatments) were fenced in a randomised complete block design. The grazing management schedule is shown in Fig 3.1. Grazing was with 15-20 sheep per 100 m^2 plot approximately every 3 weeks, but less frequently in winter, and sometimes less frequently on lax grazed plots.

Initially (October 1986 to 6 December 1987) two treatments were imposed.

Hard grazing: Target post-grazing herbage mass was approximately 1000 kgDM/ha. The swards were grazed by sheep, when the herbage mass reached approximately 1500 kgDM/ha, and were grazed down in two days to approximately 1000 kgDM/ha and sward surface height 2.5 cm.

Lax grazing: Target post-grazing herbage mass was approximately 2000 kgDM/ha. The swards were grazed by sheep when the herbage mass reached approximately 3000-4000 kgDM/ha, and were grazed down to approximately 2000 kgDM/ha, with the sward surface height at 15 cm.

These grazing regimes were intended to contrast the extremes of management to which pasture might be subjected in normal farm practice and were also expected to have contrasting tiller densities. These two grazing managements were imposed from October 1986 until December 1987.

From 9 December 1987 crossover treatments were instituted, and half the hard grazed plots were switched to lax grazing management and vice versa, giving 4 final treatment combinations: sustained hard (HH), hard to lax (HL), sustained lax (LL), lax to hard (LH), which were continued until August 1988. The crossover date was chosen to coincide with the time of maximum appearance rates of post flowering tillers. Other aspects of this trial, are reported by Matthew, et al (1988,1989) and Xia, et al (1989)(Appendix 3.2).

FIG 3.1 THE GRAZING MANAGEMENT SCHEDULE FOR RYEGRASS EXPERIMENT (1987-1988)

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PERIOD    8/9-27/9  2/10-20/10 23/11-6/12    9/12-27/12 30/12-8/1-14/1 23/5-11/6  15/6-5/7 7/7-1/8

  HARD    *-------|  *-------|  *--------| HH *--------| *------------| *--------|  *------| *-----|

  HARD    *------|  *-------|  *--------| HL *--------------- |*---- | *---------------- | *-----|


  LAX     *------|  *-------|  *--------| LH *--------| *---- |*-----| *--------|  *--------------|

  LAX     *------|  *-------|  *--------| LL *--------| *------------| *-------------------------|
```

HH : Sustained hard grazing. LL: Sustained lax grazing.

HL : Hard to Lax grazing. LH: Lax to hard grazing.

*-- : Regrowth. |: Grazing.

3.2.3. Pasture measurements

Detailed measurements started on 8 September 1987 and continuoued nutil 4 August 1988, except for the period 14 January 23 May 1988.

3.2.3.1. Sward measurements

The tiller densities were estimated at mouthly intervals from thirty 53 mm diameter plugs per plot (Mitchell and Glenday, 1958), and separated out for ryegrass, other grasses and weeds. Herbage samples were cut to ground level using electric shears from three 0.1 m^2 quadrats randomly chosen from each plot after and before grazing. The herbage was mixed and dried in a forced-draught oven for 24 hours at a temperature of 70-80° C. Sub-samples were dissected into reproductive stem (seed head), vegetative stem (pseudostem), mature leaf, immature leaf, daughter tillers, dead material and weeds. The rates of herbage accumulation during regrowth were estimated from the post and pre-grazing herbage masses. The dry weight per unit length (mg/mm) of each morphological component was determined from measurements of total length and weight of all the units in each of the above sub-samples made at the beginning and end of each period of regrowth.

3.2.3.2. Individual plant unit measurement

Tissue turnover was measured on individual tillers by using the technique of Bircham and Hodgson (1983). In each plot two 2 m transects were randomly chosen. In each transect six tillers were selected at random at 30 cm intervals, each marked with a plastic ring. Marked tillers were measured before and after grazing, and at 7-10 day intervals until the next grazing. The marked tillers were changed after each grazing period. The measurements were made by recording the plant status (grazed or ungrazed), the lengths of all laminae, the length of the pseudostem of vegetative tillers, or the stem and seed head of reproductive tillers. The leaf lengths were measured from point of insertion (or ligule) to tip, pseudostem/stem from ground level to uppermost (youngest) ligule, seed head from point of uppermost ligule to tip. Only green laminae were measured, and if a lamina had a dead tip, the length measured was from the base of the lamina (ligule) to the base of the dead tissue. For daughter tillers measurements were made of total leaf and pseudostem length. Leaves were measured individually, and the leaf growth stages were categorised into mature and immature leaves. A leaf was defined as mature when the lamina was subtended at an angle to the sheath, and the ligule was apparent.

3.2.4. Tissue turnover

The tissue turnover was estimated from the sequential measurements made on leaves, pseudostem, seed head and daughter tillers on the populations of marked tillers, and tiller population density.

The procedure involved transformation from linear change per tiller to weight change per tiller then to weight change per unit area.

3.2.4.1. linear change per tiller

Under normal conditions leaf elongation only occurs on the immature leaf. The rate of leaf growth (elongation) (RLG) is defined as :

$$RLG = \frac{\sum(IL2-IL1)}{T2-T1} \text{ (mm/tiller/day)}$$

T1 and T2 are the times at which the measurements are made, and IL1, IL2 are the lengths of the individual immature leaves at T1 and T2. Under normal conditions ryegrass only has one or two immature extending leaves. IL1 and IL2 are the lengths of the same immature leaf at successive measurements.

Also under normal conditions leaf senescence only occurs on the mature leaf. The rate of leaf senescence (RLS) is defined as:

$$RLS = \frac{\sum(ML1-ML2)}{T2-T1} \text{ (mm/tiller/day)}$$

T1 and T2 are the times at which the measurements are made, and ML1, ML2 are the length of the individual mature leaves at T1 and T2. Usually each ryegrass tiller has 2-3 mature leaves.

The net production (NP) :

NP = G - S (Bircham and Hodgson, 1983)

here G is the herbage growth and S is the herbage senescence.

According to the same principle, the other parameters can be defined such as:

RDG: Rate of daughter tiller elongation, including the leaves and pseudostem.

RDS: Rate of daughter tiller senescence, including the leaves and pseudostem.

RPG: Rate of pseudostem growth (elongation).

RPS: Rate of pseudostem senescence.

RHG: Rate of seed head growth (elongation).

RHS: Rate of seed head senescence.

Net change per tiller is then the balance between the rates of growth (elongation) and senescence of leaves, pseudostem, seed head and daughter tillers on that tiller. Normally, there is little senescence on daughter tillers.

3.2.4.2. The dry weight per individual tiller and the rate of change

The dry weight per individual tiller was estimated from the linear measurements of leaf, pseudostem and daughter tillers multiplied by the dry weight per unit length of the morphological components. The weight change per tiller was estimated from change of linear dimensions multiplied by the weight per unit length. The ratios of weight to length of the immature leaves, mature leaves, pseudostems, seed heads and daughter tillers were estimated from the sub-samples and they were defined as Wil, Wml, Wp, Wh and Wd respectively. The rate of gross growth (RG) and senescence (RS) are the rates at which new material is produced and at which material is lost due to senescence and decay.

Thus:

RG = (RLG x Wil)+(RPG x Wp)+(RHG x Wh)+(RDG x Wd)

RS = (RLS x Wml)+(RPS x Wp)+(RHS x Wh)+(RDS x Wd)

The rate of increase in dry weight is defined as rate of net production (RNP), and is estimated from the equation:

RNP = RG - RS

3.2.4.3. Weight change per unit area

In order to calculate tissue turnover rates on a per unit area basis mean plot values per tiller were multiplied by plot mean tiller population densities determined as above.

3.2.5. Tiller appearance rate

Tiller appearance rate (TAR) (Thomas, 1980) is defined as the rate at which tillers become apparent to the eye without dissection of the plant. TAR can be represented in a number of ways. In this experiment, absolute TAR is given by:

$$TAR = \frac{N2 - N1}{T2 - T1} \text{ (Daughter tillers/100 tillers/day)}$$

T1 and T2 are the time at which counts are made, and N1 is the number of live daughter tillers (per one hundred marked tillers) at time T1, T2 is the number of live daughter tillers at T2. The expression gives the net TAR.

In order to express the tillering ability of parent tillers, the parent tiller activity rate (PTAR) (per one hundred tillers) was also defined as:

$$PTAR = \frac{NP2 - NP1}{T2 - T1} \text{ (Tillering tillers/100 tillers/day)}$$

$$\text{Where: } NP = \frac{\text{number of original tillers with daughter tillers}}{\text{number of original tillers (100 tillers)}}$$

and ,NP1 is the NP at the time T1, NP2 is the NP at T2. Those calculations were based on observation made on the population of tillers marked for estimates of tissue turnover.

3.2.6. Leaf Growth Efficiency Index

Leaf Growth Efficiency Index (LGEI) was used to express the relative magnitude of the rates of growth and senescence. It was defined as:

$$LGEI = \frac{\text{rate of growth}}{\text{rate of senescence}}$$

The index can be expressed both per individual tiller and per unit area.

3.2.7. Statistical analysis

The data were examined by analysis of variance using the general linear model (GLM) procedure of SAS (SAS Institute Inc.1985). Analyses of variance for each of the components of tissue turnover were based on plot means of 12 individual tillers with 4 replicate plots per treatment. Four treatment combinations: sustained hard (HH), hard to lax (HL), sustained lax (LL) and lax to hard (LH) were used in the analysis. Contrast comparisons were used to test the effects of hard and lax grazing in the two stages of the experiment, and the interaction between them. The analysis of net leaf production in December 1987 is shown in appendix 3.3 as a sample of ANOVA procedure in the current experiment .

3.3. Results

3.3.1. Tiller population density

The tiller population density under hard grazing was constantly greater than under lax grazing (Table 3.1 and Fig 3.2). This effect was statisticaly significant when comparing continued hard grazing (HH) and continued lax grazing (LL) on all occasions, except 5 July. Following the grazing management crossover on 9 December, the tiller population densities changed; tiller density in treatment HL decreased, and that in LH increased, and attained similar values to those in treatment LL and HH respectively by 23 May after 5 months.

The seasonal changes in tiller population density were similar in all four treatments, populations being highest in December and January and lowest in August. The maximal difference between treatments occurred in the late spring on 23 November 1987 when the ratio of HH to LL was 1.85, and the minimal difference was in the winter when the ratio was 1.02 on 5 July 1988. In the winter period, the hard grazing treatment and lax grazing treatments showed no significant difference in tiller density.

The interactions between treatments (HH&LL vs LH&HL) were not significant at any stage (Table. 3.1).

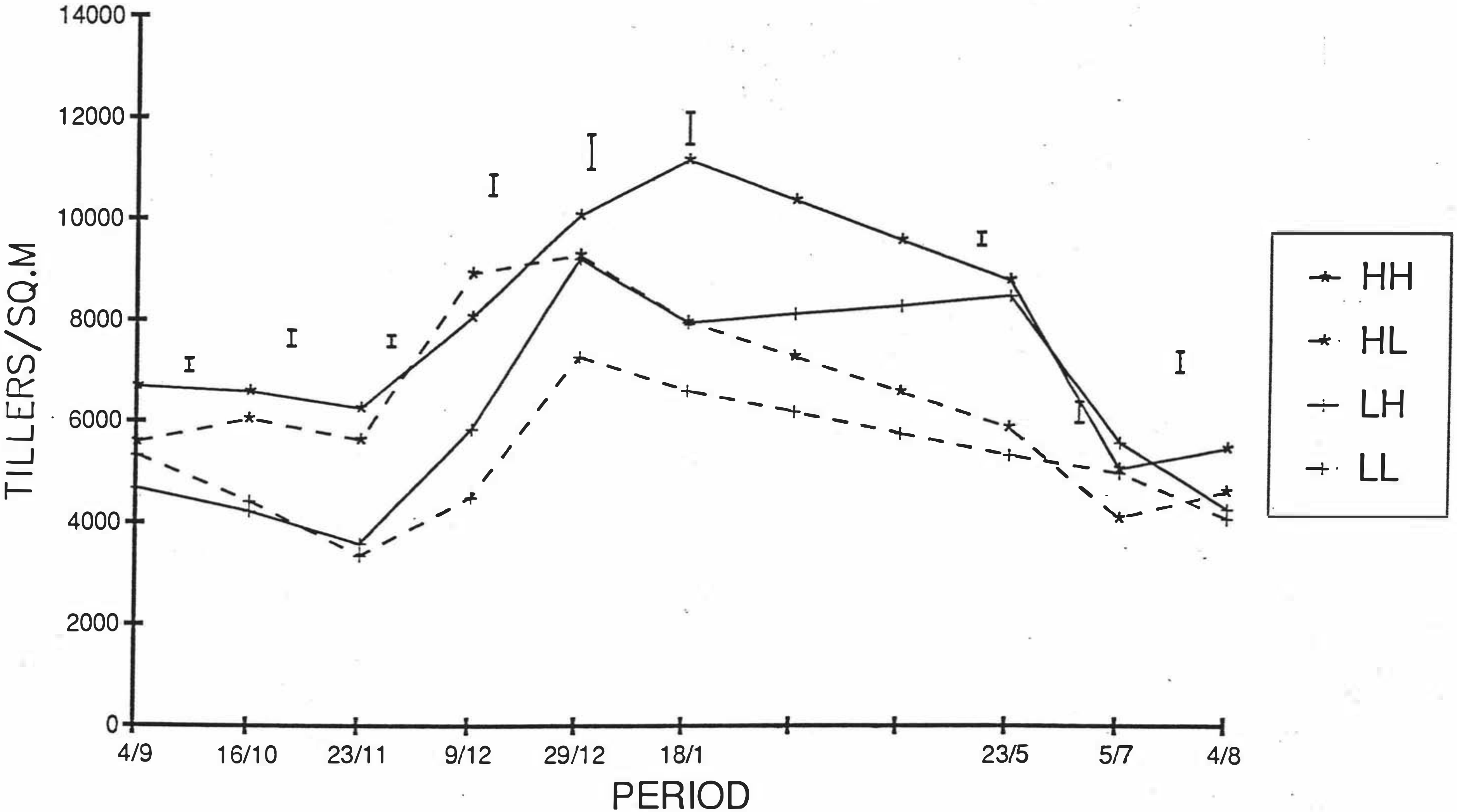
TABLE 3.1. EFFECT OF GRAZING MANAGEMENT ON PERENNIAL RYEGRASS TILLER POPULATION DENSITY (tillers/m^2)

	TREATMENT					F				
	HH	HL	LH	LL	SE of mean	HHHL vs LHLL	HHLH vs HLLL	HHLL vs HLLH	HH vs LL	HL vs LH
Tiller population density(tillers/m^2)										
4 Sep 1987	6710	5620	4710	5360	60	**	-	-	**	*
16 Oct 1987	6610	6070	4250	4450	320	***	-	-	***	**
23 Nov 1987	6280	5660	3610	3380	230	***	-	-	***	***
9 Dec! 1987	8090	8950	5880	4530	410	***	-	-	***	***
29 Dce 1987	10090	9310	9240	7290	690	NS	NS	NS	*	NS
18 Jan 1988	11180	7990	7980	6630	620	**	**	NS	***	NS
23 May 1988	8810	5900	8510	5350	260	NS	***	NS	***	***
5 July 1988	5080	4110	5610	5000	420	NS	NS	NS	NS	*
4 Aug 1988	5500	4640	4300	4110	410	NS	NS	NS	*	NS

! : treatment crossover.

* : $P<0.05$; ** : $p<0.01$; *** : $p<0.001$; NS : No significant difference.

FIG 3.2 TILLER DENSITY (Tillers/SQ-M) (Ryegrass)



3.3.2. Tiller size

Estimates of tissue weight per unit lenghth for individual components were compared across treatments and periods of regrowth in preliminary analysis of variance. Appendix 3.4 showes mean values used in caculations over main periods within which sub-period values did not differ significantlly. Periods in which treatment difference were significant are indicated; in these cases specific treatment mean values were used.

Estimates of dry weight per tiller and components (leaf, stem and daughter tillers) and the number of live leaves per tiller are shown for sample dates in Tables 3.2a, 3.2b, 3.2c, 3.2d, and 3.2e. The dates shown (27 Sep, 7 Dec, 29 Dec and 11 June) related to measurements made immediately before grazing, following periods of regrowth from the previous grazings (8 Sep - 27 Sep, 23 Nov - 7 Dec, 9 Dec - 29 Dec, 23 May - 11 June) respectively.

3.3.2.1. Leaf number

The effects of grazing management on numbers of green leaves per individual tiller pre-grazing were significant ($P<0.05$) only on 29 DEC (Table 3.2a). The number of green leaves was greater in previous hard grazing treatment (HH&HL) than in previous lax grazing treatment (LL&LH) ($p<0.01$), and the effect of crossover from lax grazing to hard grazing on number of green leaves was significant (LL vs LH,$p<0.05$). The average number of live leaves per tiller was approximately 3, ranging from 1.8 to 3.9.

3.3.2.2. Individual tiller dry weight

The total dry weights of individual tillers under lax grazing were significantly greater than under hard grazing except in winter on 11 June and the difference was mainly attributable to differences in stem and daughter tiller components (Tables 3.2b, 3.2c, 3.2d, 3.2e and Fig 3.3). The only significant difference for leaf dry weight occurred on 27 SEP (HH&HL vs LH&LL, $P<0.001$) and on 29 Dec (HH vs HL, $p<0.05$).

The effect of grazing crossover on dry weight of individual tillers was significant and immediate. There were no significant differences between treatments HH and HL, or between treatments LH and LL before the treatment switch (27 SEP, 7 DEC). After the treatment crossover the dry weight of tillers on treatment HL was significantly greater than that of treatment HH for leaf ($P<0.05$), stem ($P<0.05$), daughter tillers ($P<0.05$) and total tiller weight ($P<0.01$) at 29 DEC. In contrast, the dry weight of tillers on treatment LH was significantly lower than that on treatment LL for stem ($P<0.01$), daughter tiller ($P<0.05$) and total weight ($P<0.05$).

The dry weight of individual ryegrass tillers ranged from 16 to 55 mg approximately, the lightest under the HH treatment and the heaviest under the LL treatment on 7 December.

TABLE 3.2a THE NUMBER OF GREEN LEAVES PER TILLER
(PRE-GRAZING, LEAVES/TILLER)

	27 SEP	7 DEC	29 DEC	11 JUNE
HH	3.1	3.1	3.9	3.2
HL	3.1	2.8	3.9	2.8
LH	3.4	1.8	3.5	2.9
LL	3.1	2.8	2.9	2.4
S.E	0.3	0.4	0.3	0.2
F	NS	NS	**	NS
HHvsHL	NS	NS	NS	NS
LLvsLH	NS	NS	*	NS
HH&HLvsLH&LL	NS	NS	**	NS
HH&LHvsHL&LL	NS	NS	NS	NS
HH&LLvsHL&LH	NS	NS	NS	NS

TABLE 3.2b THE DRY WEIGHT OF LEAF PER TILLER
(PRE-GRAZING, mgDM/TILLER)

	27 SEP	7 DEC	29 DEC	11 JUNE
HH	13.8	7.9	13.8	11.3
HL	16.1	8.9	25.4	14.2
LH	28.9	10.2	16.1	12.6
LL	25.6	15.2	17.7	11.8
S.E	2.9	1.9	1.8	1.5
F	**	NS	NS	NS
HH vs HL	NS	NS	*	NS
LL vs LH	NS	NS	NS	NS
HH&HL vs LH&LL	***	NS	NS	NS
HH&LH vs HL&LL	NS	NS	NS	NS
HH&LL vs HL&LH	NS	NS	NS	NS

TABLE 3.2c THE DRY WEIGHT OF STEM PER TILLER (PRE-GRAZING, mgDM/TILLER)

	27 SEP	7 DEC	29 DEC	11 JUNE
HH	8.5	4.7	5.1	6.1
HL	11.0	6.8	7.4	8.0
LH	20.0	30.7	7.0	6.9
LL	20.0	25.4	11.7	8.6
S.E	1.5	4.2	1.3	0.6
F	**	***	***	*
HH vs HL	NS	NS	*	*
LL vs LH	NS	NS	**	*
HH&HL vs LH&LL	***	***	**	NS
HH&LH vs HL&LL	NS	NS	***	**
HH&LL vs HL&LH	NS	NS	NS	NS

TABLE 3.2d THE DRY WEIGHT OF DAUGHTER TILLERS PER TILLER (PRE-GRAZING, mgDM/TILLER)

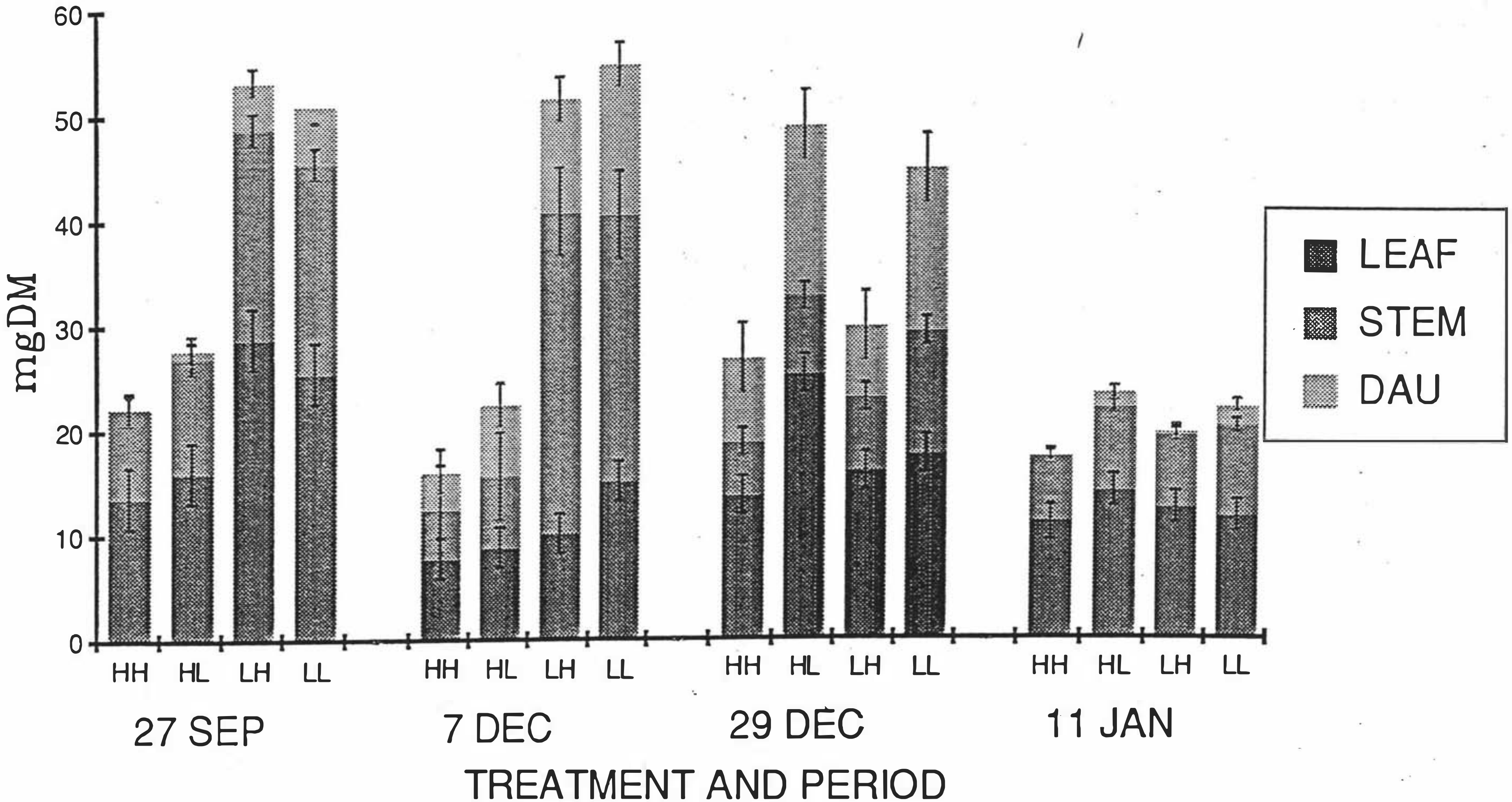
	27 SEP	7 DEC	29 DEC	11 JUNE
HH	0	3.5	8.0	0.2
HL	0.8	6.8	16.3	1.3
LH	4.4	10.8	6.8	0.3
LL	5.5	14.3	15.5	1.8
S.E	1.3	2.1	3.3	0.6
F	NS	NS	*	NS
HH vs HL	NS	NS	*	NS
LL vs LH	NS	NS	*	NS
HH&HL vs LH&LL	*	*	NS	NS
HH&LH vs HL&LL	NS	NS	**	NS
HH&LL vs HL&LH	NS	NS	NS	NS

TABLE 3.2e THE TOTAL DRY WEIGHT PER TILLER (PRE-GRAZING, mgDM/TILLER)

	27 SEP	7 DEC	29 DEC	11 JUNE
HH	22.2	16.2	26.9	17.5
HL	27.9	22.5	49.1	23.5
LH	53.4	51.6	29.9	19.8
LL	51.1	54.9	44.9	22.3
S.E	4.6	4.3	4.4	2.0
F	**	***	*	NS
HH vs HL	NS	NS	**	NS
LL vs LH	NS	NS	*	NS
HH&HL vs LH&LL	***	***	NS	NS
HH&LH vs HL&LL	NS	NS	**	NS
HH&LL vs HL&LH	NS	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.

FIG 3.3 INDIVIDUAL RYEGRASS TILLER DRY WEIGHT (mgDM/Tiller)



3.3.3. The standing herbage mass and the rate of herbage accumulation

The standing herbage mass was greater under lax than under hard grazing both before and after grazing (Appendix 3.5a, 3.5b and 3.5c). The rate of herbage accumulation was not significantly different between treatments in most of the seasons and components, except in periods 8 September to 20 October and 7 December to 28 December for stem production (Table 3.3). During 7 December to 28 December, the total herbage production was higher in HL treatment than other treatments ($P<0.05$).

TABLE 3.3. THE RATE OF HERBAGE ACCUMULATION ESTIMATED BY CUT QUADRATS (gDM/m^2/Day).

TRT	8SEP-20OCT				9DEC-27DEC				29DEC-18JAN				23MAY-1AUG			
	Leaf	Stem	Dau	Total	Leaf	Stem	Dau	Total	Leaf	Stem	Dau	Total	Leaf	Stem	Dau	Total
HH	4.0	1.1	0.0	5.1	2.5	-0.6	0.1	2.0	6.8	0.9	0.5	8.1	1.8	0.3	0.2	2.4
HL	----	----	0.0	----	7.7	5.1	0.3	13.1	7.9	1.8	0.7	10.3	2.4	-0.4	0.3	2.3
LH	----	----	0.0	----	3.4	-12.6	0.7	-8.5	10.7	1.1	1.8	13.6	1.7	0.4	0.4	2.5
LL	3.0	0.5	0.0	3.5	2.5	-5.3	-1.9	-4.7	11.5	3.0	0.7	15.2	3.1	-0.2	0.3	3.2
S.E	0.6	0.1	0.0	0.6	0.2	1.5	0.5	4.4	1.8	2.2	0.4	3.8	0.4	0.2	0.1	0.5
F	NS	*	NS	NS	NS	***	NS	*	NS	NS	NS	NS	NS	NS	NS	NS

* : p<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

3.3.4. Tissue turnover

3.3.4.1 Individual tiller

The rates of tissue turnover calculated as growth (G), senescence (S) and net production (NP) both for green leaf and for total herbage mass per tiller are shown in Table 3.4 and Fig 3.4. The seasonal pattern of tissue turnover rate was broadly similar for all treatments. Higher growth rates per tiller under lax grazing were usually balanced by higher senescence rates, so that the total net production rates showed no significant differences between treatments either before or after crossover under lax and hard grazing (Table 3.4). In spring the net leaf production of hard grazing treatments was greater than that of lax grazing treatments over period 8 SEP to 6 DEC (HH&HL vs LH&LL, $P<0.05$).

The grazing switch temporarily increased the rate of total net production in individual tillers. After the treatment crossover in period 9 DEC to 27 DEC, although the results were not significant, the total net production rate on both crossover treatments appeared to be greater than on constant treatments (HH&LL vs HL&LH, 0.69&0.71 vs 1.05&1.22 ±0.25 NS). Additionally net production was significantly greater under crossover treatment than under constant treatment between 30 DEC 1987 and 14 JAN 1988 (HH&LL vs HL&LH, 0.35&0.37 vs 0.52&0.64 ±0.08, $P<0.05$). After the crossover it was significantly greater following previous lax grazing than after previous hard grazing (period 30 DEC to 14 JAN,HH&HL vs LH&LL, $P<0.05$) in leaf net production. Grazing treatment LH resulted in the highest net production rate of the four treatments in the two months following the crossover, and it had the higher leaf component in herbage production.

In winter, the differences between treatments were not significant for either total or leaf net production (Table 3.4).

Table 3.4. RATES OF HERBAGEGROWTH (RG), SENESCENCE (RS) AND NET PRODUCTION (RNP),AND OF NET LEAF PRODUCTION (RNPL) (mgDM/tiller/day).

	Treatment					F		
	HH	HL	LH	LL	SE of mean	HHHL vs LHLL	HHLH vs HLLL	HHLL vs HLLH
8 Sep - 6 Dec 1987								
Growth	0.69	0.93	1.42	1.74	0.11	***	--	--
Senescence	0.22	0.20	0.82	0.96	0.12	***	--	--
Net production	0.47	0.73	0.60	0.78	0.11	NS	--	--
Leaf net	0.35	0.42	0.34	0.23	0.03	*	--	--
9 Dec - 27 Dec 1987!								
Growth	0.90	1.42	1.71	1.76	0.22	*	NS	NS
Senescence	0.20	0.37	0.49	1.05	0.17	*	NS	NS
Net production	0.69	1.05	1.22	0.71	0.25	NS	NS	NS
Leaf net	0.29	0.33	0.49	0.34	0.07	NS	NS	NS
30 Dec 1987 - 14 Jan 1988								
Growth	0.49	1.11	0.89	0.85	0.07	NS	**	**
Senescence	0.14	0.59	0.25	0.47	0.09	NS	**	NS
Net production	0.35	0.52	0.64	0.37	0.08	NS	NS	*
Leaf net	0.29	0.24	0.57	0.44	0.08	*	NS	NS
23 May - 5 July 1988								
Growth	0.42	0.52	0.48	0.54	0.03	*	NS	NS
Senescence	0.16	0.29	0.21	0.33	0.03	**	NS	NS
Net production	0.26	0.23	0.28	0.21	0.02	NS	NS	NS
Leaf net	0.25	0.25	0.27	0.23	0.03	NS	NS	NS

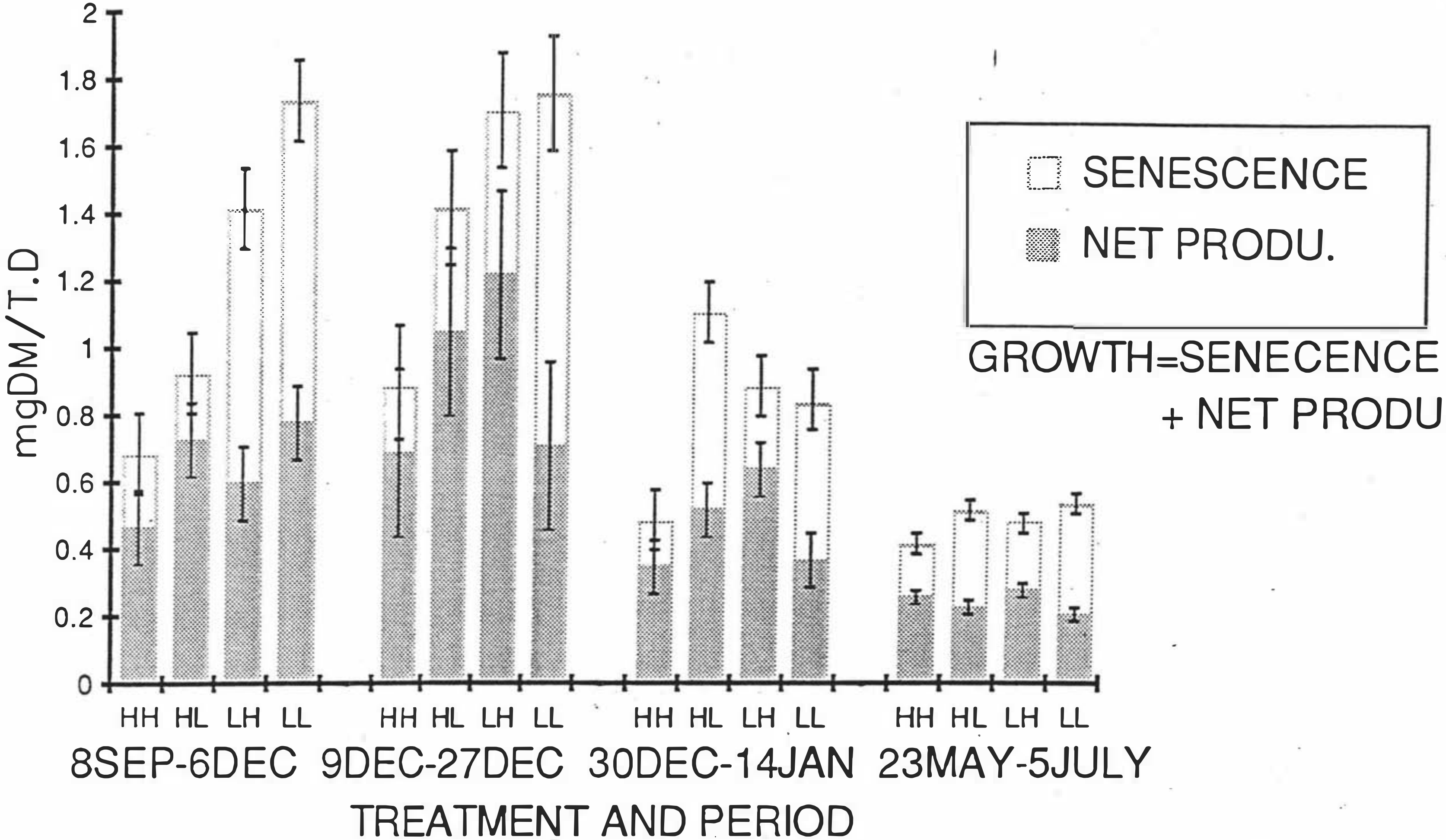
* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

! :grazing crossover.

HH: hard grazing; HL:hard to lax grazing.

LL: lax grazing; LH:lax to hard grazing.

FIG 3.4 THE RATES OF HERBAGE GROWTH SENESCENCE AND NET PRODUCTION PER INDIVIDUAL RYEGRASS TILLER(mgDM/TIL/DAY)



3.3.4.2 Herbage production per unit area

The rate of herbage growth, senescence and net production both for green leaf and total herbage mass per unit area (gDM/m^2/day) are shown in Table 3.5, and Fig 3.5. Before the treatment crossover (8 SEP to 6 DEC) the total net pasture production per unit area was not significantly different between treatments under hard and lax grazing, although the rate of growth was significantly greater under lax grazing than that under hard grazing (P<0.01), but it was balanced by a higher rate of senescence (P<0.01). The rate of net leaf production was significantly greater under hard grazing than under lax grazing in this period (P<0.001).

In the period 9 Dec to 27 Dec immediately after the treatment crossover occurred, the net leaf production was significantly greater under crossover treatments than under constant treatments (P<0.05). Additionally, the difference in the rate of total net production approached significance (HH&LL vs HL&LH, P<0.06) in this period. The rates of total net production were significantly greater under crossover treatments than under constant treatments in the period 30 Dec to 14 Jan (P<0.05).

In winter (23 MAY to 5 JULY), the rates of net production were greater under hard grazing than that under lax grazing both for leaf (HH&LH vs HL&LL, P<0.05) and total herbage production (HH&LH vs HL&LL, P<0.05), though difference were relatively small in absolute terms.

TABLE 3.5. RATES OF HERBAGE GROWTH(RG), SENESCENCE(RS), AND NET PRODUCTION(RNP), AND OF NET LEAF PRODUCTION(RNPL) ($gDM/m^2/day$).

	Treatment					F		
	HH	HL	LH	LL	SE of mean	HHHL vs LHLL	HHLH vs HLLL	HHLL vs HLLL
8 Sep - 6 Dec 1987								
Growth	4.1	5.1	5.7	7.6	0.52	**	--	--
Senescence	1.4	1.2	3.5	4.3	0.55	**	--	--
Net production	2.7	3.9	2.2	3.3	0.50	NS	--	--
Leaf net	2.3	2.5	1.5	1.1	0.18	***	--	--
9 Dec - 27 Dec 1987!								
Growth	8.0	12.9	11.8	9.3	1.79	NS	NS	NS
Senescence	1.8	3.3	3.3	5.6	1.00	NS	NS	NS
Net production	6.2	9.6	8.4	3.8	1.91	NS	NS	0.06
Leaf net	2.5	3.0	3.3	1.8	0.53	NS	NS	*
30 Dec 1987 - 14 Jan 1988								
Growth	5.1	11.0	7.2	6.3	0.64	NS	**	***
Senescence	1.5	5.8	2.1	3.6	0.81	NS	**	NS
Net production	3.6	5.2	5.1	2.7	0.76	NS	NS	*
Leaf net	3.0	2.5	4.6	3.2	0.44	NS	NS	NS
23 May - 5 July 1988								
Growth	2.9	2.7	3.3	2.8	0.30	NS	NS	NS
Senescence	1.1	1.5	1.4	1.7	0.25	NS	NS	NS
Net production	1.8	1.2	1.9	1.1	0.23	NS	*	NS
Leaf net	1.8	1.3	1.8	1.2	0.21	NS	*	NS

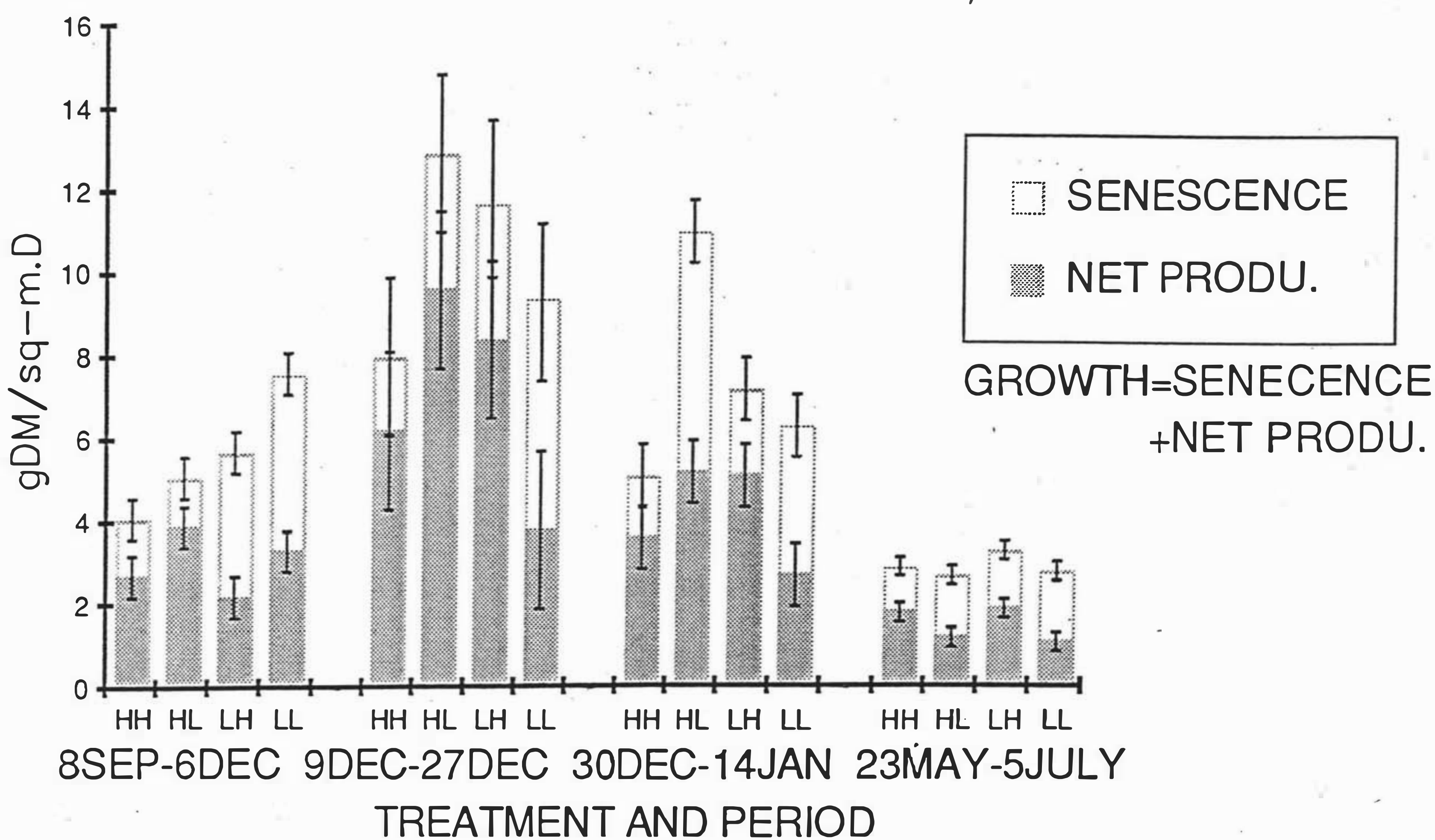
* : $P<0.05$; ** : $p<0.01$; *** : $p<0.001$; NS : No significant difference.

! :grazing crossover.

HH: hard grazing; HL:hard to lax grazing.

LL: lax grazing; LH:lax to hard grazing.

FIG 3.5 THE RATES OF HERBAGE GROWTH SENESCENCE AND NET PRODUCTION PER UNIT AREA RYEGRASS PASTURE (gDM/SQ-M/DAY)



3.3.4.3. Components and seasonal pasture production

Grazing treatment crossover affected the balance between the components of net production (Table 3.6 and Fig.3.6). Before the change (from 8 SEP to 6 DEC) the contribution of leaf to net production was greater on the hard than on the lax grazing. After the change of treatment, LH had the highest net leaf growth rate of all treatments, but this effect was temporary. The contribution of leaves on main tillers and leaves plus pseudostem on daughter tillers made a large contribution to net herbage production in all seasons and treatments (Fig. 3.6). The net contribution from main tiller stem and pseudostem was substantial only for treatment HH and HL in December, and in most other treatments and seasons there was a net loss of stem material to senescence over regrowth periods. During winter the leaf component made the greatest contribution to net herbage accumulation (Fig.3.6).

The results showed that the highest seasonal pasture net production rate was achieved in late spring (9 - 27 DEC), and this was mainly contributed by the higher growth of stem and daughter tillers. Leaf growth was the main component of net production in other seasons (Fig.3.6).

3.3.4.4. Leaf Growth Efficiency Index (LGEI)

The Leaf Growth Efficiency Indexes (LGEI)(Table 3.7) were significantly higher under hard than under lax grazing in periods 8 September to 6 December (HH&HL VS LH&LL, $p<0.001$) and 30 December to 14 Janary (HH&LH VS HL&LL, $p<0.05$). The differences between treatments HH&LL and HL&LH were not significant overall (Table 3.7), showing that the grazing crossover did not significantly affect LGEI. Overall, the LGEI was greater in HH>LH>HL>LL. The rate of growth of new leaf tissue was on average over 3 times the rate of loss of mature leaf tissue to senescence.

Table 3.6 THE RATE OF NET PRODUCTION PER UNIT AREA BY COMPONENTS (gDM/m^2/Day)

TRT	8Sep--6Dec			9Dec--27Dec			30Dec--14Jan			23May--5July		
	Leaf	Stem	Dau	Leaf	Stem	Dau	Leaf	Stem	Dau	Leaf	Stem	Dau
HH	2.30	0.10	0.69	2.53	1.22	2.42	2.98	-.33	0.66	1.76	-.28	0.35
HL	2.51	0.07	1.76	2.99	2.33	4.28	2.51	0.68	1.75	1.27	-.42	0.34
LH	1.52	-.82	1.94	3.29	-0.53	5.66	4.57	-.25	1.33	1.91	-.30	0.31
LL	1.13	-.08	2.59	1.76	-3.13	5.16	3.24	-.65	1.38	1.21	-.61	0.48
S.E	0.15	0.40	0.25	0.40	0.99	0.77	0.44	0.32	0.44	0.21	0.06	0.11
HHHLvsLHLL	***	NS	***	NS	***	**	**	*	***	NS	NS	NS
HHLHvsHLLL	NS	NS	***	NS	NS	NS	*	NS	*	*	**	NS
HHLLvsHLLH	NS	NS	NS	*	NS	NS	NS	*	***	NS	NS	NS

* : $P<0.05$; ** : $p<0.01$; *** : $p<0.001$; NS : No significant difference.

HH: hard grazing; HL:hard to lax grazing.

LL: lax grazing; LH:lax to hard grazing.

FIG 3.6 THE RATES OF HERBAGE NET PRODUCTION BY COMPONENTS IN RYEGRASS PASTURE (gDM/SQ-M/DAY)

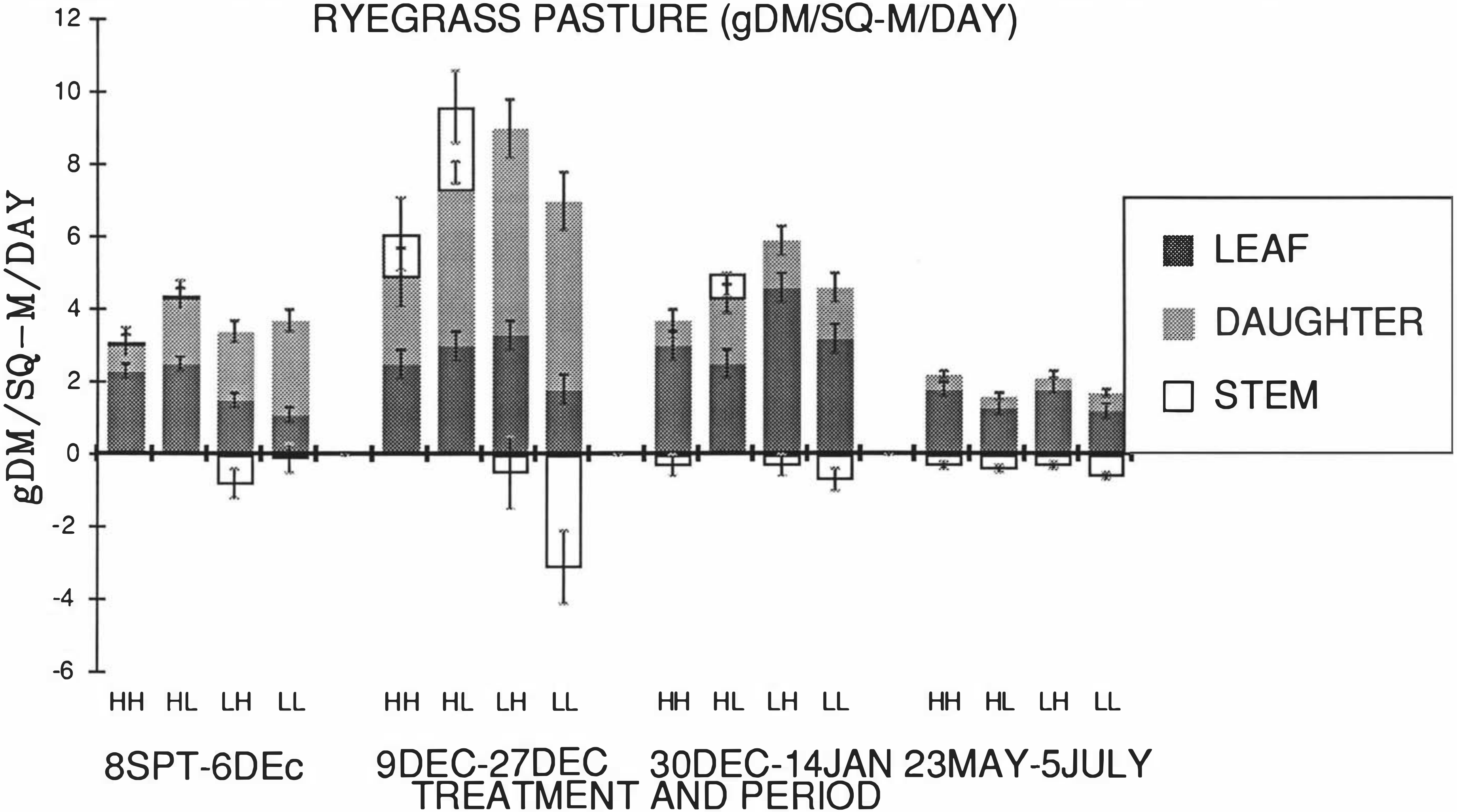


TABLE 3.7 THE LEAF GROWTH EFFICIENCY INDEX

TRT	8 Sep- 6 Dec 87	9 Dec- 27 Dec 87	30 Dec- 14 Jan 88	23 May- 5 Jul 88	AVERAGE
HH	4.66	3.60	6.00	3.84	4.52
HL	5.71	2.12	1.82	2.38	3.01
LH	2.20	2.96	4.91	3.22	3.82
LL	1.81	2.02	2.56	2.17	2.14
S.E	0.38	0.59	0.74	0.36	
F	***	NS	*	NS	
HHHLvsLHLL	***	NS	NS	NS	
HHLHvsHLLL	NS	NS	**	NS	
HHLLvsHLLH	NS	NS	NS	NS	

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.
HH: hard grazing; HL:hard to lax grazing.
LL: lax grazing; LH:lax to hard grazing.

3.3.5. **Tiller Appearance Rate (TAR)**

The absolute tiller appearance rate (TAR) and parent tiller activity rate (PTAR) for the periods from 27 Sep to 18 Dec 1987 are shown in Tables 3.8 and 3.9 respectively. The comparision was made between sustained hard and lax grazing treatments and during spring and summer only. The TAR and PTAR were higher in lax grazing treatments than in hard grazing treatments but the effects were not significant except for PTAR in September. TAR and PTAR were greater in summer (November and December) than in spring (September and October).

Table 3.8.THE ABSOLUTE RATE OF TILLER APPEARANCE (TAR) (Daughter tillers/100tiller/Day)

Month	Sep	Oct	Nov	Dec
Regrowth perid (Days)				
	27	18	14	18
H	2.20	2.37	9.74	7.17
L	3.75	3.64	14.36	8.79
S.E	0.71	0.81	1.59	1.07
F	NS	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.
H:hard grazing (HH&HL).
L:lax grazing (LL&LH).

Table 3.9. THE PARENT TILLER ACTIVITY RATE (PTAR). (Tillering tillers/100tiller/day)

	Sep(27)	Oct(18)	Nov(14)	Dec(18)
H	1.15	0.86	4.46	3.35
L	2.08	0.92	3.64	2.42
SE	0.26	0.31	0.40	0.33
F	*	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.
(27):Regrowth days.
H:hard grazing (HH&HL).
L:lax grazing (LL&LH).

3.4. Discussion

3.4.1. Techniques

The procedures outlined by Bircham and Hodgson (1983) were used to transform field recordings of leaf and stem dimensions into estimates of change in dry weight, and rates of growth, senescence and net production of green herbage per tiller. Estimates of tissue turnover per unit area were determined by multiplying individual plant unit values by the population densities of primary units.

The leaf is the main part of grass growth and senescence, and the measurement procedures gave accurate estimates of leaf elongation and senescence, but there was some limitation to the procedures for estimating pseudostem linear and weight changes. Changes in pseudostem weight are strictly net values as new sheath/leaf forms at the center and sheaths senecence and fall off from the outside; thus changes in weight per unit length may occur with little change in pseudostem length. Also minor changes in ground level as a result of worm activity or rainfall may affect the consistency of stem length measurement. New leaf growth may occasionally break through the sheath, and this will also effect the accuracy of pseudostem measurement. The coefficients of variation of individual tiller values within plots are shown in Table 3.10 (results from spring and summer as examples). The C.V of stem length was the largest overall, and the C.V of leaf was smaller than other components. Stem and pseudostem values may have higher C.V also because of big variation between tillers because of different stages of growth. Procedures to improve the accuracy of definition of stem and pseudostem changes need further study. Because the C.V per tiller was large it was necessary to sample 12 tillers per plot for adequate treatment standard errors. The statistical analyses used plot means.

The weight of stem tissue did increase particularly during the longest duration of regrowth in spring and summer, but in general, stems contributed far less to the net change in weight during grazing than did laminae. This was particularly the case when the grazing treatment was successful in removing a large proportion of the accumulated herbage (Parsons and Penning,1988). Therefore for pasture management, the leaf accumulation and total herbage mass production are the most important tissue turnover parameters in perennial ryegrass pasture.

There was poorer correlation in this study between estimates of net green herbage accumulation dervied from quadrat cuts (Table 3.3) and estimats of net herbage production derived from tissue turnover measurements (Table3.5 and 3.6). However, the estimates from quadrat cuts had high standard errors and were considered to be unreliable.

TABLE 3.10. THE COEFFICIENT OF VARIATION(%) FOR THE RATE OF HERBAGE PRODUCTION PER TILLER

	Spring (Sep - Dec)			Summer (Jan)		
	Growth	Sence	Net	Growth	Senec	Net
Leaf	32.5	80.1	60.0	42.2	93.0	87.8
Stem	176.0	179.3	1242.5	232.3	145.3	1295.5
Dau	95.5	433.3	99.8	137.5	542.7	153.1
Total	49.7	109.4	98.6	58.8	83.3	117.6

The observation that TAR and PTAR were higher under lax than under hard grazing (Table 3.8 and 3.9) was unexpected, since tiller populations were consistently greater under hard than under lax grazing (Table 3.1), though the differences were not significant. However, the effect may have been a consequence of limitations in the measurement technique, reflecting particularly the difficulty of identifying all daughter tillers produced from marked tillers on the hard grazing treatment. Rates of tiller loss were not estimated in this trial. Because of the uncertain variability of TAR and PTAR value, estimates were not made beyond mid December.

3.4.2. Pasture management

3.4.2.1. Effects of sustained hard and lax grazings

Tiller population densities were substantially higher under hard than lax grazing, and the individual tiller sizes were greater under lax grazing than under hard grazing (Tables 3.2a and 3.2b).

Hard grazing usually resulted in higher rates of net herbage production per unit area than lax grazing, and particularly of net leaf production, though not all the differences were significant. This was because lower rates of growth were more than balanced by substantially lower senescence losses (Tables 3.4 and 3.5). This result confirms the evidence from other, shorter-term studies (Bircham and Hodgson,1983;Grant et al,1983;Parsons et al 1983), and demonstrates the importance of losses to senescence and decomposition in the pasture economy. The lax grazing management involved higher levels of pasture cover before and after grazing than would often occur in sheep systems, but was nevertheless within the limits of comparable studies (Korte et al.1984; Sheath & Boom, 1985). In the studies of Tainton (1974) differences in severity of grazing resulted in similar rates of net green pasture accumulation in spring , but not in summer. However, grazing intervals were very long in Tainton's studies, except in spring (Tainton, 1974).

Senescence losses were consistently 20-25% of tissue growth rates in treatment HH, but were substantially higher (65% to 45% of growth) in treatment LL (Table 3.5). The Leaf Growth Efficiency Index (LGEI) was greater in hard grazing than in lax grazing treatment (Table 3.7). Bircham and Hodgson (1983) found that senescence losses did not fall below 20% of tissue growth rates, even in circumstances where grazing pressures were high enough to substantially depress pasture growth rates. Over the period of study from spring through winter the net rate of leaf production only varied by a factor of two. However, high rates of stem production in the spring, even on the hard grazed treatments, contributed to a substantially greater seasonal variation in net pasture production.

The TAR (absolute tiller appearance rate) and PTAR (parent tiller activity rate) were greater in summer (November and December) than in spring (September and October) and the highest TAR was recorded in November (Tables 3.8 and 3.9), in accord with previous study (Korte, 1986). In Korte's experiment tillering was more rapid in the second than the first year, but there were similarities in seasonal changes in both years. The highest TAR were recorded in November, in the regrowth immediately after defoliation of apices of the main group of reproductive tillers (Korte, 1986).

3.3.2.2. The effects of switch grazing in late spring

The switch from hard to lax grazing in late spring gave a temporary increase in net herbage production (Table 3.5). There were marked changes in the structure and physiology of the hard grazed sward switching to lax grazing. After several successive hard grazings the sward comprised a large population of small tillers. The switch reflected primarily enhanced production of stem and seed head, and the initial growth advantage was soon offset by increasing senescence losses and a fall in tiller density (Tables 3.1 and 3.5). The advantage in net leaf production was particularly short-lived, though tiller density on the switched treatments took almost 4 months to converge with that on the equivalent continued treatments (Table 3.1). This result is consistent with the observations of Bircham & Hodgson (1984), Grant et al (1988), and Sheath & Boom (1985).

The switch from lax to hard grazing in December, which coincided approximately with the timing of anthesis in flowering tillers, increased tiller population density (Table 3.1) by encouraging new tiller development from the stubs of grazed reproductive tillers (Korte et al, 1984; 1985). The effect was to increase both net pasture production and net leaf production in comparison with treatments HH and LL (Table 3.7), and these effects were sustained for a substantially longer period on treatment LH than on treatment HL (Tables 3.4 and 3.5)

3.4.2.3. Management implications

The utilization of herbage was better under hard grazing than under lax grazing. The swards under hard grazing had smaller tillers (Tables 3.2a and 3.2b) and a slower rate of growth per tiller than under lax grazing, but the effect was balanced by the slower rate of senescence, so that net production per tiller did not differ significantly. However, the tiller population density was greater under hard grazing than under lax grazing, so hard grazing usually resulted in greater net pasture production per unit area than lax grazing, especially for net leaf production (Table 3.5).

Under lax grazing the increasingly inefficient harvesting of growth by the animals at greater mean sward height leads to the loss to senescence of a greater percentage of the herbage grown. This results in a reduction in the rate of net herbage accumulation (Davies, 1988). In practice, maximum yield per ha under continuous stocking is achieved in a ryegrass dominant sward maintained at a sward surface height of 4 to 6 cm, and a standing green herbage mass ranging from 700 to 1700 kgDM/ha (Arosteguy et al., 1983; Bircham and Hodgson, 1983). Provided that residual pasture mass remains above the critical level (900-1200kgDM/ha) below which rates of new herbage growth are substantially reduced, net herbage production and herbage consumption will increase with increases in grazing pressure (Bircham,et al,1984). In this experiment the target of post-grazing herbage mass under hard grazing was approximately 1000 kgDM/ha, above the recommended critical level, and the pre-grazing herbage mass was approximately 1500 - 2000 kgDM/ha, so that the pasture utilization was always efficient.

Several studies demonstrate the influence of hard spring grazing in enhancing tiller population density and summer pasture production (L'Huillier 1987 a,b; Sheath & Boom, 1985). However, the results of this study confirm the evidence of Korte et al.(1984) and Matthew et al.(1989) that summer and early autumn production can be further increased if careful management of reproductive tillers is used to encourage the rapid development of new vegetative tillers. This can be achieved most easily in systems involving early conservation, or in mixed grazing and conservation systems, and some topping managements may achieve the same result (Korte etal. 1984).

In practical terms, the equivalent of treatment LH involves the following stages of management: First, a period of relatively lax grazing over the early phase of seed head development which allows increase in leaf area and in pasture growth rate. Second, a switch from lax to hard grazing at the time of anthesis to encourage tiller development and to prevent excessive loss of leaves to senescence. Third, to continue efficient grazing through summer and autumn in order to maintain high tiller population density and high production potential.

The stimulation of new tiller development in late spring may increase the risk of drought damage, a risk masked in this study by the limited use of irrigation, and confirmatory studies are required. However, in drought conditions there would be little direct benefit from the retention of a population of aged reproductive tillers. Barker and Chu (1985) reported that the effect of water stress was to reduce herbage yield to only 8% of that of irrigated treatments, this was attributed to reductions in tiller density and rates of leaf extension and appearance. Moreover, there is evidence (C. Matthew, unpublished data) that, provided daughter tillers are formed before drought stress occurs, they may simply delay development of secondary and tertiary tillers until conditions became more favorable for growth.

In general, these results showed further evidence of the self-compensating changes in perennial ryegrass swards which serve to maintain similar levels of net herbage production over a range of management conditions. The importance of tiller population density in allowing flexible sward responses to management changes is emphasized.

3.5. Conclusions

Tiller population density was usually greater under hard grazing than under lax grazing, whereas the dry weight of individual tillers was usually greater under lax grazing than under hard grazing.

Rates of net herbage and leaf production were usually greater under hard than under lax grazing, because greater pasture growth under lax grazing was more than offset by higher rates of loss to senescence. In general terms these results provide further evidence that rates of net pasture production are relatively insensitive to sustained differences in grazing management.

There were advantages to summer pasture production from a management which allowed seed head development to anthesis under lax grazing in spring, followed by hard grazing to enhance the subsequent development of new vegetative tillers. This pattern of lax followed by hard grazing is unusual in grazing systems, but can be achieved by judicious timing of conservation or pasture topping.

CHAPTER 4. THE EFFECTS OF SEVERITY OF GRAZING ON TISSUE TURNOVER IN PRAIRIE GRASS (Bromus willdenowii Kunth) DAIRY PASTURE

4.1. Introduction

Prairie Grass cv. "Grasslands Matua" was placed on the New Zealand list of Acceptable Herbage Cultivars on 1 January 1973 (Rumball, 1974), and it was released in New Zealand as a high yielding, cool and summer season active, high nutritive value pasture cultivar most suited to lax infrequent grazing (Rumball, 1974). More recent work with sheep (Frazer, 1985; Alexander, 1985), dairy cows (Brookes and Holmes, 1986) and with bull beef (Cosgrove and Brougham, 1988) has raised questions on Matua's feeding value, and on levels of pasture utilization when grazed to ensure persistence. The recommended practice has been to graze intensively with long rest periods (Alexander, 1985; Matthews, 1986) or to graze intensively only after replacement tillers have emerged at the base of the sward (Black and Chu, 1989).

The species offers marked contrast in morphology and growth characteristics to perennial ryegrass. Briefly, prairie grass is an erect, tall, broad leaved perennial with low tiller density and light green foliage; peak heading time is in spring, but seed heads are produced throughout the year (Rumball, 1974). Mature plants in a mixed pasture may have fewer than 10 tillers at a given time (Rumball, 1974).

Black and Chu (1989) have provided some information on tiller population changes in prairie grass under sheep grazing, but there is no information on tissue turnover for this species. This study was designed to measure the productivity and persistence of Matua prairie grass under two dairy cow grazing managements, using a tissue turnover technique. Measurements were made within a large-scale dairy cattle production study (Rugambwa, et al, 1990).

4.2. Materials and methods

4.2.1. Experimental design and field management

Three short term grazing trials were conducted at Massey University's Dairy Cattle Research Unit between September 1988 and February 1989 with spring calving cows within a large-scale dairy cattle production study (V.K.Rugambwa, 1990). The experiments were sited on a well established, one year old Matua prairie grass/white clover pasture on a well drained Tokomaru silt loam soil, and grass was 60-70% of the pasture (appendix 4.4). Each of four Matua paddocks (0.8 ha each) was divided into two parts in late August 1987. Differential grazing was imposed in early September in order to create and maintain either hard grazing (H, 6cm, 1.5-2.5 t DM/ha residual herbage mass), or lax grazing (L, 12cm, 2.5-3.5 t DM/ha) swards under rotational grazing management. Target pre-grazing herbage masses for H and L were 3.0-4.5 and 4.5-6.0 tDM/ha respectively. When necessary, H paddocks were either regrazed, topped or both to leave approximately 1.5 tDM/ha residual within 24 h after experimental grazing. One dressing of 15% potassic super phosphate (375 kg/ha) and two of urea (25 kgN/ha) were applied in autumn 1988 and early spring 1989, respectively.

The four paddocks were grazed in sequence over periods of 2-3 weeks (4-6 days per paddock) during spring to summer in period 1 (September to November), period 2 (November to December) and period 3 (January to February), by two groups of 8 lactating dairy cows, the half paddocks being grazed simultaneously. Paddocks were divided into daily strips by electric fence and the measurement areas were sited in adjacent areas of half paddocks to keep synchronization between treatments for grazing and measurement. The periods of regrowth over which measurement were made are shown in Table 4.1.

Table 4.1 Period of pasture regrowth and measurement

Block and treatment		Period 1	Period 2	Period 3
Block 1	Hard grazing	26Sep - 3Nov	11Nov - 9Dec	18Jan - 12Feb
	Lax grazing	26Sep - 3Nov	11Nov - 9Dec	18Jan - 12Feb
Block 2	Hard grazing	4 Oct - 3Nov	15Nov - 18Dec	25Jan - 22Feb
	Lax grazing	4 Oct - 3Nov	15Nov - 18Dec	25Jan - 22Feb
Block 3	Hard grazing	29Sep - 5Nov	16Nov - 11Dec	23Jan - 19Feb
	Lax grazing	29Sep - 5Nov	16Nov - 11Dec	23Jan - 19Feb
Block 4	Hard grazing	4 Oct - 7Nov	13Nov - 12Dec	29Jan - 27Feb
	Lax grazing	4 Oct - 7Nov	13Nov - 12Dec	29Jan - 27Feb

The cows were selected at the beginning of the trial and grazed as a group on ryegrass/clover pasture for a two-week covariance period; they were thereafter randomly allocated to the treatments.

4.2.2. Measurements

4.2.2.1. Sward

Sward measurements were confined to an area of pasture corresponding to a single day's allocation close to the center of each paddock. One 10 m transect was randomly chosen for each treatment in each plot for tissue turnover measurements (see 4.2.2.2.). Two permanent 0.5 sq-m quadrats were sited at random beside each transect. The tiller population and the number of plants along each transect and in each quadrat were counted at the beginning and end of each regrowth period. In addition, counts were made of plants in different size (ie. tiller number) categories within 10 randomly chosen 0.5 sq-m quadrats at the same times. The plant size categories were defined as :

Class 1 : > 65 tillers.
Class 2 : 46 - 65 tillers.
Class 3 : 26 - 45 tillers.
Class 4 : 6 - 25 tillers.
Class 5 : < 6 tillers.

Two additional 0.5 m^2 quadrats were randomly chosen from each plot for every treatment, and cut to ground level using hand shears, after and before grazing. Sub-samples were separated into seed head, stem, mature leaf, immature leaf, daughter tillers, and dead material, then dried in a forced-draught oven for 24 hours at a temperature of 70-80° C. The rates of herbage accumulation during regrowth were estimated from the post and pre-grazing herbage masses. The dry weight per unit length (mg/mm) of each morphological component was determined from measurement of total length and weight of all the units in each of the above sub-samples.

4.2.2.2. Individual tillers

The individual tiller tissue turnover was measured by using a modification of the technique of Bircham and Hodgson (1983) to allow for differences in the characteristics of ryegrass and prairie grass swards. One 10 m transect was randomly chosen for each treatment in each plot. Ten plants were selected at random at 1 m intervals approximately along each transect, omitting only plants in class 5 (< 6 tillers/plant) above, and each was marked with a 7 cm diameter plastic collar. In the marked plant one tiller was marked at random with a plastic wire in period 1. From period 2 one tiller was marked at the center of each plant and one at the periphery, in order to test the difference between tillers which were at different positions within plants. Thus forty tillers were marked and measured for each treatment in period 1 (10 plants x 1 tiller x 4 replicates) and 80 tillers in periods 2 and 3 (10 plants x 2 tillers x 4 replicates).

The leaf, stem, seed head and daughters of each marked tiller were measured as described in section 3.2.3.2 at 7 to 10 day intervals from the end of one grazing to the start of the next. The tiller population on each marked plant also was counted at the beginning and end of each regrowth period.

The dry weights per individual tiller were estimated from the summations of the length of each component multiplied by the equivalent weight per unit length.

4.2.2.3. Tissue turnover

Estimates of tissue turnover on individual tillers were derived from the sequential measurements made on leaves, stem, seed head and daughter tillers in the population of marked tillers. The procedure was as described in section 3.2.4. The procedure involved conversion from linear change per tiller to weight change per tiller then to weight change per unit area. The rates of herbage growth (RG), senescence (RS) and net production (RNP) were estimated as shown in section 3.2.4.

In order to calculate tissue turnover rates on a per unit area basis, the tiller population density (D) was estimated as in equation 4.1, and plot mean estimates of tissue turnover per tiller were multiplied by plot mean tiller population densities.

Equation 4.1: The estimate of average tiller population density per period(D) was :

$$D = DB + \frac{RT \times Days \times 0.01}{2}$$

DB : The basic tiller population density per sq-m which was measured immediately after grazing (tillers/sq-m).

RT : The rate of tiller accumulation over the regrowth period which was estimated on the marked plants in each treatment. It was defined as tillers/100 tillers/day.

Days: The days of regrowth period.

4.2.3. Statistical analysis

The data were examined by analysis of variance using the general linear model (GLM) procedure of SAS (SAS Institute Inc. 1985). Analyses of variance for each of the components of tissue turnover were based on plot means using the combined data for three periods of measurement. The effects of treatment and period and the interaction between them were tested under a split-plot design with periods as main plots and treatments and replication as sub-plots. The analysis of leaf growth rate per unit area is shown in appendix 4.1 as a sample of the ANOVA procedure in the current experiment.

4.3. Results

4.3.1. Herbage mass and morphological composition

The mean values of post-grazing and pre-grazing herbage masses and morphological composition from L (Lax grazing) and H (hard grazing) are shown in Appendix 4.2a and 4.2b (V.K.Rugambwa, 1990) for reference. The actual post-grazing herbage mass was 2.5 to 4.0 tDM/ha and 1.3 to 3.1 tDM/ha, and the pre-grazing herbage mass was 4.0 to 6.0 tDM/ha and 2.3 to 4.8 tDM/ha in L and H treatment respectively (Appendix 4.2a). The proportion of green leaf, and green stem were significantly higher in H than in L treatments ($P<0.05$, Appendix 4.2b), but the dead material was greater in L than in H treatment ($P<0.05$, Appendix 4.2b).

4.3.2. Tiller size

4.3.2.1. Number of live leaves

The numbers of live leaves per pre-grazing tiller in the lax grazing (L) treatments were greater than in the hard grazing (H) treatments over periods (Table 4.2a, $P<0.05$), the average numbers of live leaves being approximately 2.4 and 2.0 in L and H treatments respectively. The difference between periods was significant ($P<0.5$), the tillers carrying less leaves in period 2 than in periods 1 and 3. The total number of leaves was significantly greater in L than in H treatment at the beginning of regrowth (post grazing) ($p<0.001$), but not at the end (pre-grazing)(Table 4.2b). The leaf appearance interval was greater in L than in H treatment (Table 4.2b, $p<0.01$).

TABLE 4.2a THE NUMBER OF LIVE LEAVES PER TILLER BEFORE GRAZING IN HARD(H) AND LAX(L) GRAZED PRAIRIE GRASS PASTURE

Period	TRT	Leaves/Tiller
1 (Sep - Nov)	L	2.7
	H	2.5
2 (Nov - Dec)	L	1.8
	H	1.2
3 (Jan - Feb)	L	2.4
	H	2.2
S.E		0.28
TRT		*
Period		*
TRT*Period		NS

TABLE 4.2b THE TOTAL NUMBER OF LEAVES AND THE RATE OF LEAF APPEARANCE IN HARD(H) AND LAX(L) GRAZED PASTURE (SEP TO NOV, 1988, PRAIRIE GRASS)

TRT	No.Of Total leaves		Leaf appearance interval (days)
	Beginning	End	
L	2.6±0.2	4.6±0.2	18.5±1.1
H	1.3±0.2	4.3±0.2	12.1±1.1
F	***	NS	**

* : p<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.

4.3.2.2 The individual tiller dry weight

The total dry weights of individual pre-grazing tillers (Table 4.3a and Fig 4.1) under lax grazing treatments were significantly greater than those under hard grazing treatments during period 1 at 28 Oct ($P<0.5$) and period 2 at 4 Dec ($P<0.01$). The differences were mainly attributable to differences in leaf ($P<0.01$), and stem ($P<0.05$) weights at 28 Oct, and in stem ($P<0.05$), and daughter tiller weights ($P<0.05$) at 4 Dec. During period 3 at 12 Feb, there were no significant differences except in daughter tiller weight ($P<0.5$).

There was a substantial decline in dry weight per tiller over time in both treatments, much of this decline being due to a decline in the stem weight. The ratios of stem to total tiller dry weight were higher in period 1 than in period 2 and 3, but were similar between L and H treatments (Table 4.3b and Fig 4.1).

TABLE 4.3a. THE INDIVIDUAL TILLER DRY WEIGHT IN HARD(H) AND LAX(L) GRAZED PRAIRIE GRASS PASTURE
(Per-grazing, mgDM/Tiller)

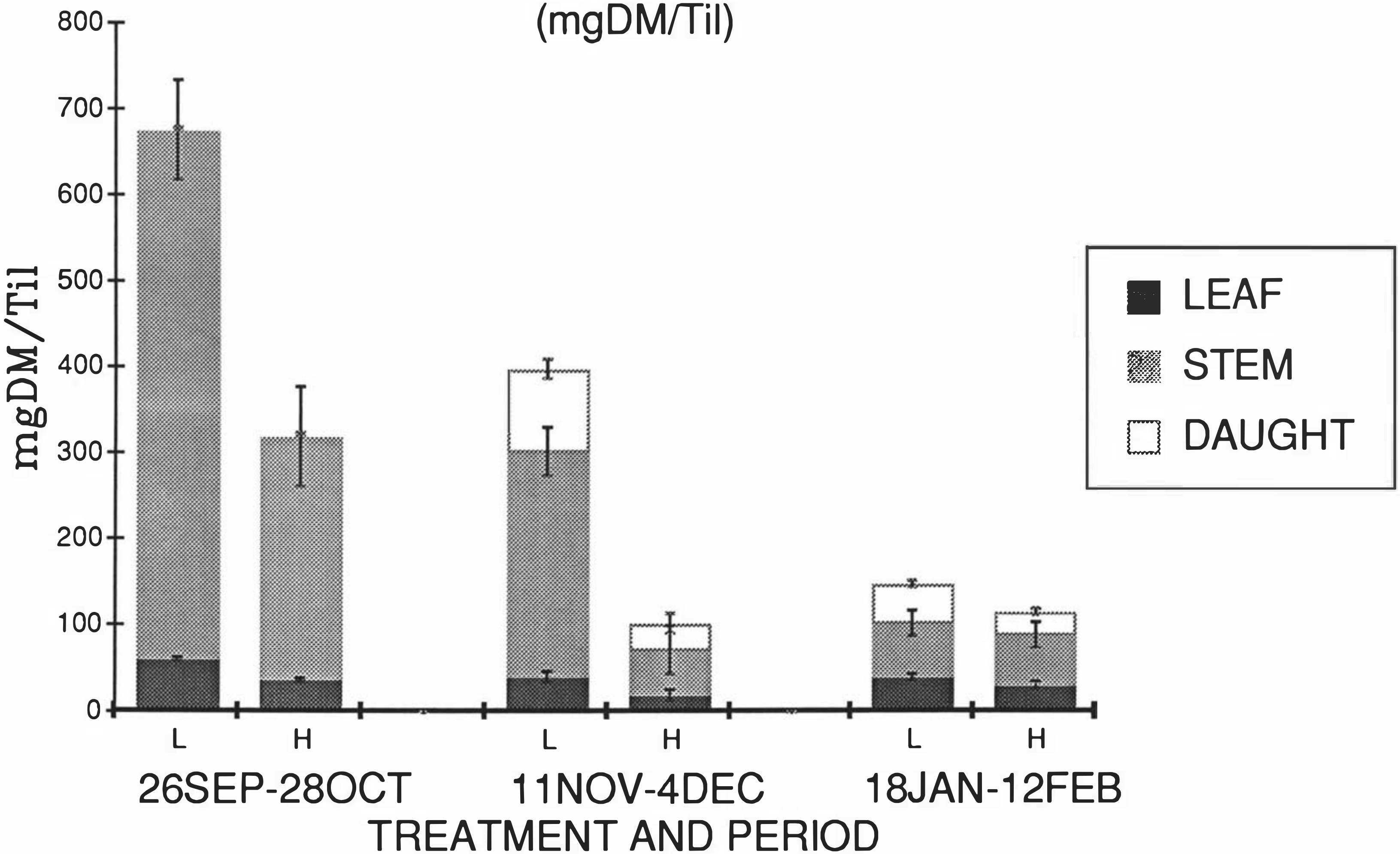
	28 Oct(26Sep-28Oct)				4 DEC(11Nov-4Dec)				12 FEB(18Jan-12Feb)			
TRT	Leaf	Stem	Dau	Tot	Leaf	Stem	Dau	Tot	Leaf	Stem	Dau	Tot
L	60.8	615.3	2.1	678.2	40.9	261.0	96.2	398.3	39.8	62.5	45.4	147.7
H	37.0	282.1	3.0	322.2	19.3	52.0	31.1	102.7	30.9	57.9	27.0	115.9
S.E	2.3	58.5	1.6	58.2	6.4	28.	11.5	17.3	4.0	15.3	3.7	16.4
F	**	*	NS	*	NS	*	*	**	NS	NS	*	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.
Note: Estimates of stem weight include seed head.

TABLE 4.3b THE RATIO OF STEM TO TOTAL TILLER DRY WEIGHT IN HARD(H) AND LAX(L) GRAZED PRAIRIE GRASS PASTURE

	28 OCT(SEP-OCT)	4 DEC (NOV-DEC)	12 FEB(JAN-FEB)	MEAN
L	0.91	0.66	0.42	0.66
H	0.88	0.51	0.50	0.63

FIG 4.1 THE INDIVIDUAL TILLER DRY WEIGHT OF MATUA PRAIRIE GRASS (mgDM/Til)



4.3.3. Population density

4.3.3.1. Tiller population density

The initial tiller population density and the net rate of change for each regrowth interval are shown in Table 4.4. The post-grazing initial tiller population density differed significantly between periods (P<0.05), and the L treatment had a higher tiller population density than H treatment (P<0.06). The rate of net tiller increase was higher in L than H (P<0.05), and differed significantly between periods (P<0.001). Tiller numbers per plant were significantly higher in period 3 than in periods 1 and 2 (P<0.05), and they were greater in L than H at P<0.08. The treatment x period interactions were not significant. The tiller population density per m^2 and the number of tillers per plant increased over time in L plots but not in the H plots (Table 4.4).

TABLE 4.4. The tiller population density on permanently marker plants in hard (H) and lax (L) grazed prairie grass pasture

TRT	Period	Tillers per sq-m	Tillers per plant	Changes per 100Tillers per day
L	1 (Sep - Nov)	457	33.3	0.018
L	2 (Nov - Dec)	496	33.6	3.630
L	3 (Jan - Feb)	647	44.9	1.601
H	1 (Sep - Nov)	447	24.4	-0.221
H	2 (Nov - Dec)	394	19.8	1.986
H	3 (Jan - Feb)	408	26.2	1.776
S.E		65	2.3	0.43
TRT		0.06	0.08	*
Period		*	*	***
TRT*Period		NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

4.3.3.2. The distribution of plant size

The distribution of plants in different size classes and plant population density were analysed both with period as the main plot and treatment as the sub-plot, and with regrowth period (post vs pre-grazing) as the main plot and treatment as the sub-plot under a split-plot design. The plants of class 4 (6-25 tillers/plant) and class 3 (26-45 tillers/plant) accounted for approximately 50% and 23% of total plants over treatments and periods respectively. The effects of treatment on the distribution of plant size were significant (Table 4.5a and 4.5b). The proportions of plants in class 1 (> 66 tillers/plant), class 2 (65-46 tillers/plant) and class 3 (45-26 tillers/plant) were greater under lax grazing treatment than under hard grazing treatment, but they were greater in class 4 (25-6 tillers/plant) and class 5 (< 6 tillers/plant) under hard grazing treatment than under lax grazing treatment (Fig 4.2a). The distribution of plants in class 1, class 3, and class 4 did not differ significantly between periods, but the proportions of class 5 plants was significantly greater in period 1 than other periods ($P<0.001$), and the proportion of class 2 plants was greater in period 2 than in period 1 and period 3 ($P<0.05$) (Fig 4.2b and Table 4.5a). The effects of interaction between treatment and period were only significant in class 5 plants ($P<0.05$).

The distribution of plant size changed over periods of regrowth (Table 4.5b). The proportions of class 1, class 2, and class 5 plants were greater in post-grazing swards than in pre-grazing swards, but for class 3 and class 4, they were greater in pre-grazing swards than in post-grazing swards (Fig 4.2c).

Plant population densities were greater in the hard grazing than in the lax grazing treatment ($P<0.05$), greater post-grazing than pre-grazing ($p<0.05$), decreased from period 1 to periods 2 and 3 $P<0.001$), and the declines were steeper in H than in L (Tables 4.5a and 4.5b). The effect of the treatment and regrowth period interaction was not significant for c1, c2, c3 and c4 plants but was significant for c5 plants (Table 4.5a). The interaction between treatment and period significantly affected plant population density ($P<0.01$,Table 4.5a). Over all the number of plants per sq-m averaged 16.

TABLE 4.5a. THE EFFECTS OF TREATMENT AND PERIOD ON DISTRIBUTION PLANT SIZE AND PLANT POPULATION DENSITY IN HARD(H) AND LAX (L) GRAZED PRAIRIE GRASS PASTURE

		Propotion of plants in category					
TRT	Period	>65	46-65	26-45	6-25	<6	Plants/m^2
L	1	0.025	0.097	0.308	0.441	0.129	16
L	2	0.094	0.197	0.277	0.411	0.021	12
L	3	0.044	0.119	0.313	0.429	0.095	12
H	1	0.005	0.015	0.116	0.563	0.300	25
H	2	0.021	0.052	0.163	0.570	0.195	14
H	3	0.012	0.033	0.221	0.590	0.145	14
S.E		0.018	0.027	0.030	0.048	0.022	1
TRT		NS	*	**	*	*	*
Period		NS	*	NS	NS	***	***
TRT*Period		NS	NS	NS	NS	*	**

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

TABLE 4.5b. THE DISTRIBUTION OF PLANT SIZE AND PLANT POPULATIO DENSITY DURING REGROWTH UNDER HARH(H) AND LAX(L) GRAZED PRAIRE GRASS PASTURE

TRT	Grazing	Propotion of plants in category					
		>65	46-65	26-45	6-25	<6	Plant/m^2
L	Post-	0.079	0.160	0.252	0.393	0.116	15
L	Pre-	0.030	0.116	0.347	0.460	0.047	12
H	Post-	0.022	0.054	0.164	0.528	0.231	19
H	Pre-	0.002	0.012	0.169	0.621	0.195	17
S.E		0.015	0.023	0.024	0.036	0.024	1
TRT		NS	*	**	*	*	*
Graz		*	NS	*	*	*	*
TRT*Graz		NS	NS	NS	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

FIG 4.2a THE DISTRIBUTION OF PLANT SIZE UNDER HARD AND LAX GRAZING

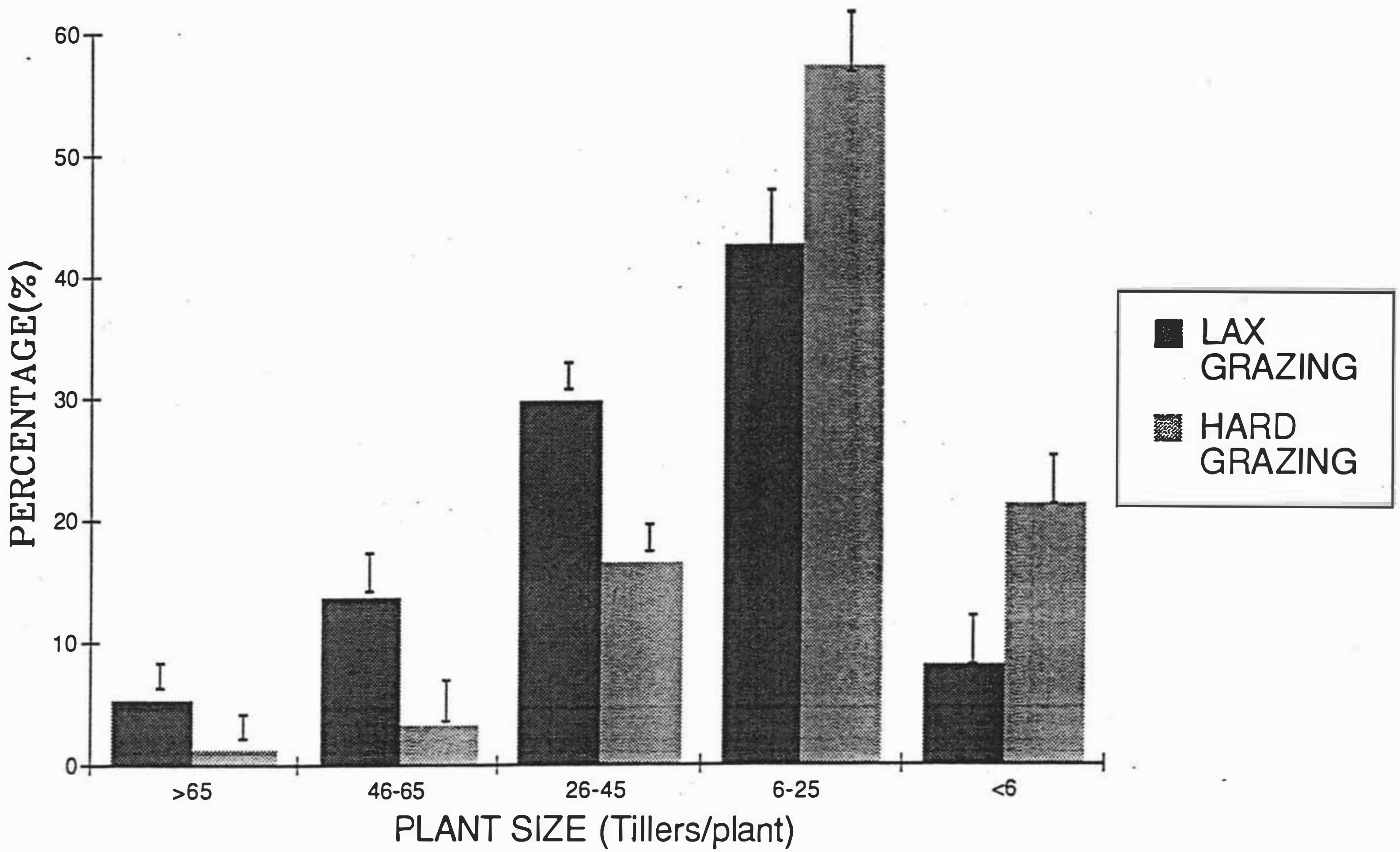


FIG 4.2B THE DISTRIBUTION OF PLANT SIZE IN DIFFERENT PERIODS

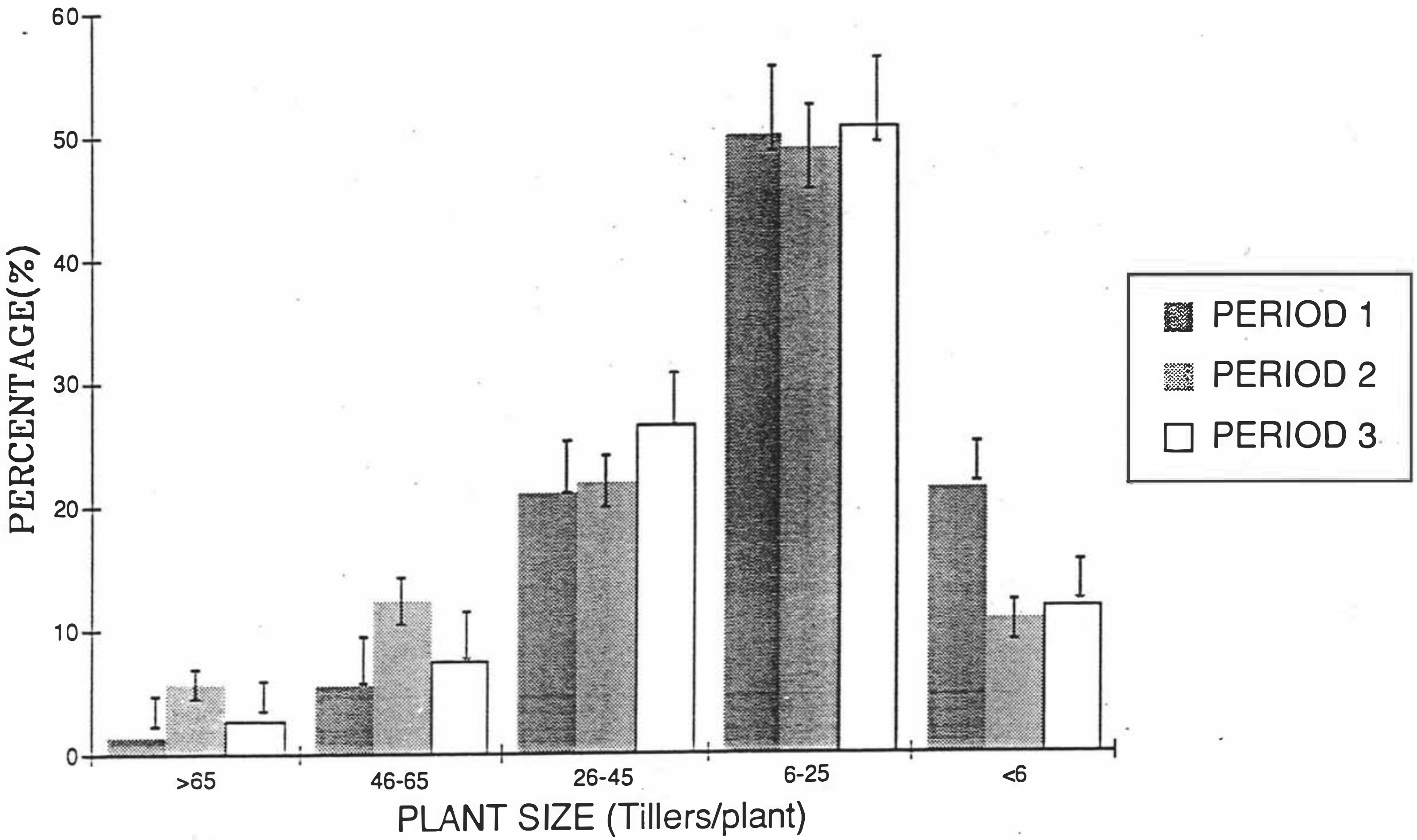
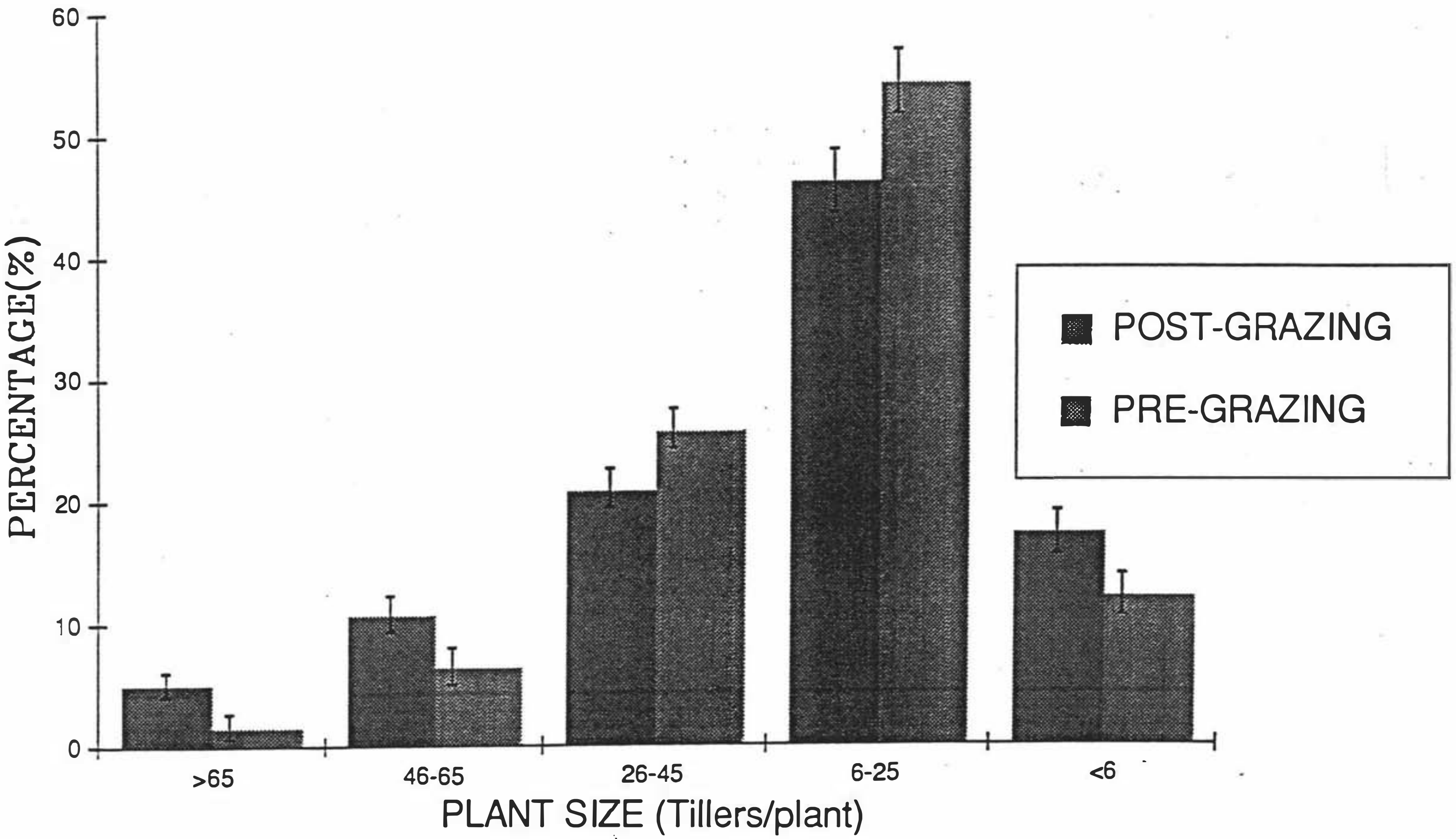


FIG 4.2C THE DISTRIBUTION OF PLANT SIZE BEFORE AND AFTER GRAZING



4.3.4. The herbage accumulation

The rates of green and total herbage accumulation between grazings and the herbage mass post grazing and pre-grazing estimated from quadrats cut to ground level are shown in Table 4.6. The rate of herbage accumulation was significantly different between periods both for green and total herbage, being highest in period 1 and lowest in period 2 for both L and H treatments (Table 4.6). The differences between treatments were significant over all periods for total herbage accumulation ($p<0.001$), and for green herbage accumulation ($P<0.05$). The interaction between treatment and period did not significantly affect the rate of total herbage accumulation, but did affect green herbage accumulation ($p<0.01$).

TABLE 4.6.THE PRE AND POST-GRAZING STANDING HERBAGE MASS (gDM/m^2) AND THE RATE OF GREEN (G) AND TOTAL (T) HERBAGE ACCUMULATION ($gDM/m^2/DAY$) ESTIMATED BY CUT QUADRATS

		Standing herbage mass				Rate of accumulation	
Period	TRT	Post(G)	Pre (G)	Post(T)	Pre(T)	Green	Total
1(Sep-Nov)	L	84.4	262.1	157.9	344.5	4.43	4.61
	H	30.0	133.3	50.8	155.2	2.56	2.58
2(Nov-Dec)	L	170.9	181.3	260.8	267.7	0.59	0.89
	H	38.8	46.4	69.6	65.9	0.22	-0.07
3(Jan-Feb)	L	37.2	123.4	132.1	199.2	3.05	2.33
	H	10.1	65.3	32.6	87.1	2.01	2.00
S.E		0.50	0.87	6.6	18.8	0.10	0.34
TRT		*	NS	**	**	*	***
Period		***	*	***	***	***	*
TRT*Period		NS	NS	***	NS	**	NS

* : $p<0.05$; ** : $p<0.01$; *** : $p<0.001$; NS : No significant difference.

4.3.5. The tissue turnover

4.3.5.1. Turnover of tissue on individual tillers

Statistical analyses were carried out on the plot mean values. The coefficients of variation of estimates of tissue turnover for the individual tillers within plot were high, in line with results from studies on ryegrass (Bircham and Hodgson, 1983). The examples shown in Table 4.7 are for estimates of herbage growth in period 2.

TABLE 4.7. THE COEFFICIENT OF VARIATION OF ESTIMATES OF HERBAGE GROWTH ON SAMPLE TILLERS IN PERIOD 2.

	Coefficient of variation			
Block	Leaf	Steam	Dau	Total
1	150.1%	133.9%	101.8%	51.3%
2	101.6%	109.4%	112.2%	110.2%
3	135.4%	148.5%	123.0%	74.7%
4	218.6%	120.0%	118.0%	71.4%

A. The effect of tiller position

The comparison of the effect of tiller position on the plant on the rates of herbage growth, senescence and net production per tiller in periods 2 and 3 are shown in Tables 4.8a, 4.8b, and 4.8c. Tiller position did not significantly affect the rates of growth, senescence or net production on any components. The results for central and peripheral tillers were therefore combined for the analyses of tissue turnover over periods which followed.

TABLE 4.8a THE EFFECT OF TILLER POSITION IN THE PRAIRIE GRASS PLANT ON RATE OF HERBAGE GROWTH PER TILLER (mgDM/TILLER/DAY)

TRT	Posetion	Leaf	Stem	Dau	Total
L	Centre	0.897	2.355	3.152	6.406
L	Peripheral	1.500	2.579	2.472	6.553
H	Centre	0.967	1.325	1.301	3.594
H	Peripheral	1.071	1.516	1.017	3.605
S.E		0.110	0.631	0.247	0.619
Position		NS	NS	NS	NS
TRT		NS	NS	*	NS

* : P<0.05; NS : No significant difference.

TABLE 4.8b THE EFFECT OF TILLER POSITION IN THE PRAIRIE GRASS PLA[N]
ON RATE OF HERBAGE SENESCENCE PER TILLER (mgDM/TILLER/DAY)

TRT	Position	Leaf	Stem	Dau	Total
L	Centre	1.799	2.044	0.057	3.900
L	Peripheral	2.089	1.665	0.021	3.776
H	Centre	0.813	1.359	0.011	2.183
H	Peripheral	0.870	1.466	0.022	2.359
S.E		0.210	0.186	0.020	0.181
Position		NS	NS	NS	NS
TRT		NS	NS	NS	NS

NS : No significant difference.

TABLE 4.8c THE EFFECT OF TILLER POSITION IN THE PRAIRIE GRASS PLANT
HERBAGE NET PRODUCTION PER TILLER(mgDM/TILLER/DAY)

TRT	Position	Leaf	Stem	Dau	Total
L	Centre	-0.902	0.312	3.095	2.505
L	Peripheral	-0.589	0.914	2.451	2.776
H	Centre	0.155	-0.034	1.289	1.411
H	Peripheral	0.201	0.049	0.994	1.245
S.E		0.105	0.806	0.234	0.702
Position		NS	NS	NS	NS
TRT		*	NS	*	NS

* : $P<0.05$; NS : No significant difference.

B. Growth

The rate of herbage growth per tiller was significantly different over treatments and periods, and the treatment x period interaction was also significant on all components except leaf (Table 4.9a). Treatment L had higher growth rates than treatment H for the leaf, stem, daughter tiller, and total herbage (Table 4.9a). The rate of growth was significantly different over periods for all components and the total herbage growth decreased from period 1 to period 3, with a small increase from period 2 to period 3 in treatment H (Table 4.9a).

TABLE 4.9a.THE RATE OF HERBAGE GROWTH PER TILLER OVER DIFFERENT TREATMENT PERIODS AS ESTIMATED BY INDIVIDUAL TILLER TISSUE TURNOVER (mgDM/TILLER/DAY)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	1.81	9.56	2.52	13.88
L	2(Nov-Dec)	1.07	3.37	4.01	8.45
L	3(Jan-Feb)	1.32	1.55	1.63	4.51
H	1(Sep-Nov)	1.24	4.20	1.45	6.91
H	2(Nov-Dec)	0.87	1.20	1.30	3.37
H	3(Jan-Feb)	1.18	1.66	1.00	3.84
S.E		0.20	0.66	0.27	0.84
TRT		*	*	*	*
Period		*	***	**	***
TRT*Period		NS	**	**	**

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

C. Senescence

The interaction of treatment with period was significant for leaf and total herbage senescence, but the L treatment had a higher overall senescence rate than H treatment for leaf and total herbage (Fig 4.3, Table 4.9b). Period differences in total herbage senescence were also significant and were mainly attributable to the leaf and stem differences (Table 4.9b). The rates of total herbage senescence in period 2 were approximately double those in periods 1 and 3 (Table 4.9b).

TABLE 4.9b.THE RATE OF HERBAGE SENESCENCE PER TILLER OVER DIFFERENT TREATMENT PERIODS AS ESTIMATED BY INDIVIDUAL TILLER TISSUE TURNOVER (mgDM/Tiller/Day)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	1.43	0.15	0.00	1.58
L	2(Nov-Dec)	2.89	2.67	0.06	5.63
L	3(Jan-Feb)	0.98	1.03	0.01	2.04
H	1(Sep-Nov)	0.87	0.68	0.00	1.56
H	2(Nov-Dec)	1.07	1.88	0.01	2.97
H	3(Jan-Feb)	0.59	0.93	0.02	1.56
S.E		0.27	0.27	0.02	0.42
TRT		*	NS	NS	*
Period		**	***	NS	***
TRT*Period		*	NS	NS	**

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

D. Net herbage production

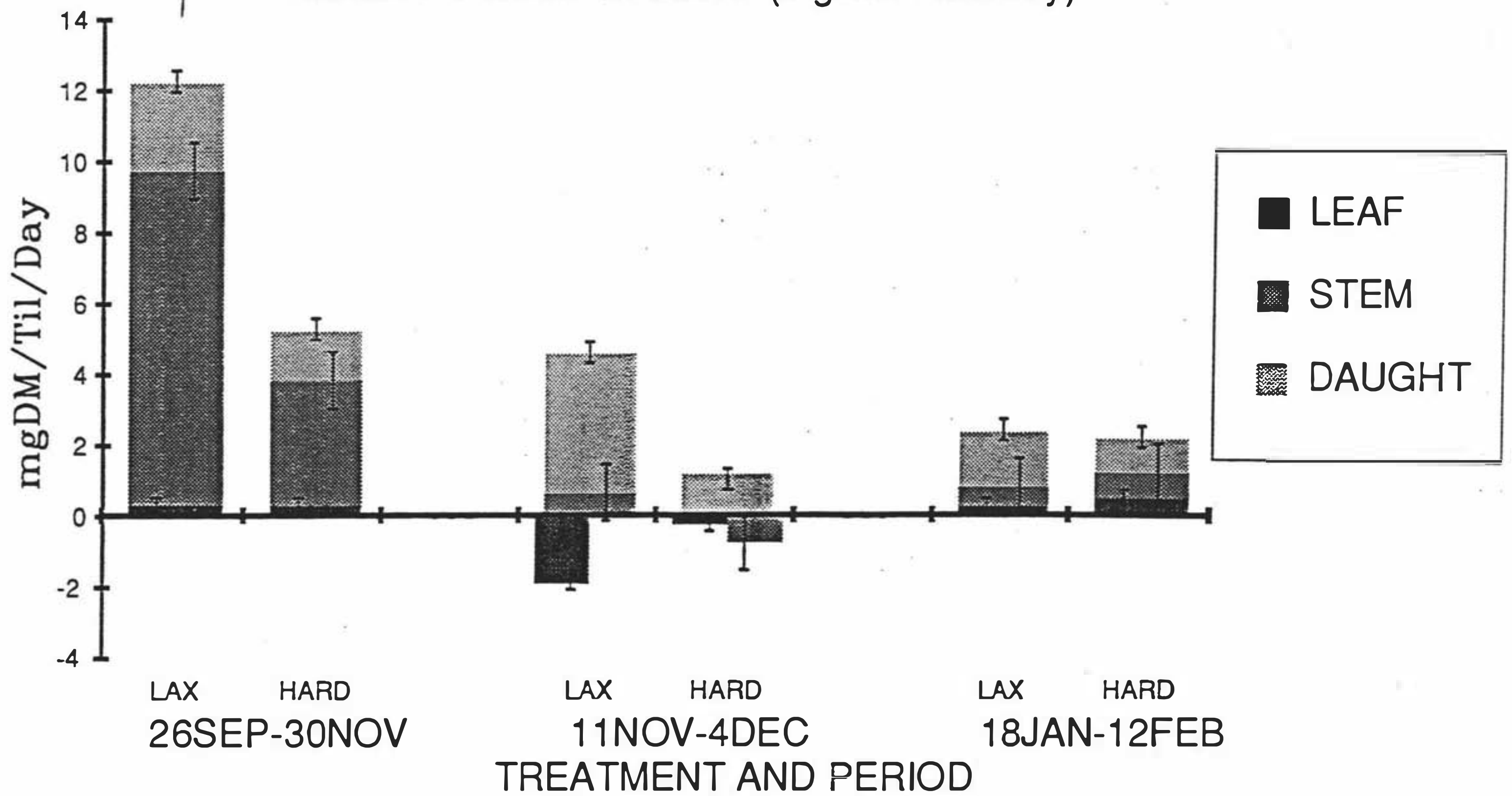
The main effects of treatment and period, and the interaction between them, were significant for all components of net herbage production rate (Table 4.9c). The L treatment gave a higher rate than the H treatment for net total herbage production over periods (Fig 4.3). This difference was due to higher net production rates in the stem and daughter tillers, despite a lower rate of net leaf production. The period differences in net herbage production were mainly accounted for by differences in daughter tillers in period 2 and period 3 (Table 4.9c). The difference between treatments was greater in period 1 than in period 2 and period 3 (Fig 4.3), the ratio of L to H net herbage production being 2.3 and 1.1 in period 1 and period 3 respectively. The net production rate for all components was higher in period 1 than in periods 2 and 3 (Fig 4.3).

TABLE 4.9c.THE RATE OF HERBAGE NET PRODUCTION PER TILLER OVER DIFFERENT TREATMENT PERIODS AS ESTIMATED BY INDIVIDUAL TILLER TISSUE TURNOVER (mgDM/Tiller/Day)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	0.38	9.40	2.52	12.29
L	2(Nov-Dec)	-1.83	0.70	3.95	2.82
L	3(Jan-Feb)	0.33	0.52	1.61	2.46
H	1(Sep-Nov)	0.36	3.51	1.45	5.35
H	2(Nov-Dec)	-0.19	-0.68	1.28	0.40
H	3(Jan-Feb)	0.57	0.72	0.98	2.28
S.E		0.18	0.80	0.27	0.95
TRT		*	*	*	*
Period		***	***	**	***
TRT*Period		***	**	**	*

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

FIG 4.3 THE RATE OF NET HERBAGE PRODUCTION PER PRAIRIE GRASS TILLER BY COMPONENTS (mgDM/Tiller/Day)



4.3.5.2. Herbage production per unit area

The rate of herbage growth, senescence and net production per unit area are shown in Tables 4.10a,4.10b,4.10c and Fig 4.4.

A. Growth

The L treatment had significantly higher rates of growth than the H treatment for all components (Table 4.10a). The stem and seed head accounted for 50% and 49% of the total herbage growth on L and H treatment respectively; the equivalent values for leaf were 16% and 24%, and for daughter tillers were 33% and 27% respectively. There were significant differences between periods for all components (Table 4.10a). Total herbage growth decreased progressively from period 1 to period 3 (Table 4.10a). The interaction between treatment and period was significant for stem and daughter tillers.

TABLE 4.10a THE RATE OF HERBAGE GROWTH PER UNIT AREA AS ESTIMATED FROM INDIVIDUAL TILLER TISSUE TURNOVER AND TILLER POPULATION DENSITY (mgDM/m^2/Day)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	0.83	4.37	1.15	6.34
L	2(Nov-Dec)	0.53	1.67	1.99	4.19
L	3(Jan-Feb)	0.85	1.00	1.05	2.92
H	1(Sep-Nov)	0.55	1.88	0.65	3.09
H	2(Nov-Dec)	0.34	0.47	0.51	1.33
H	3(Jan-Feb)	0.48	0.68	0.41	1.57
S.E		0.09	0.34	0.13	0.43
TRT		**	*	*	*
Period		*	***	**	***
TRT*Period		NS	*	**	NS

* : p<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

B. Senescence

The rate of herbage senescence per unit area differed significantly over treatments and periods, and the treatment x period interaction was also significant on all components except the daughter tillers (Table 4.10b). The rate of herbage senescence was significantly higher in L treatment than in H treatment for leaf and total herbage (Table 4.10b). The stem and seed head accounted for 44% and 57% of total senescence for L and H treatments respectively. Leaf accounted for 55% and 41% and the daughter tillers for 0.8% and 0.4% of senescence respectively. The rate of herbage senescence was significantly different over periods for leaf, stem and seed head and total herbage (Table 4.10b). For total herbage the highest senescence rate was in period 2 both in L and H treatments (Table 4.10b).

TABLE 4.10b THE RATE OF HERBAGE SENESCENCE PER UNIT AREA AS ESTIMATED FROM INDIVIDUAL TILLER TISSUE TURNOVER AND TILLER POPULATION DENSITY ($mgDM/m^2/Day$)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	0.65	0.07	0.00	0.72
L	2(Nov-Dec)	1.44	1.32	0.02	2.79
L	3(Jan-Feb)	0.63	0.67	0.01	1.32
H	1(Sep-Nov)	0.39	0.31	0.00	0.70
H	2(Nov-Dec)	0.42	0.74	0.00	1.17
H	3(Jan-Feb)	0.24	0.38	0.01	0.63
S.E		0.13	0.13	0.01	0.19
TRT		*	NS	NS	*
Period		**	***	NS	***
TRT*Period		*	*	NS	**

* : p<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.

C. Net herbage production

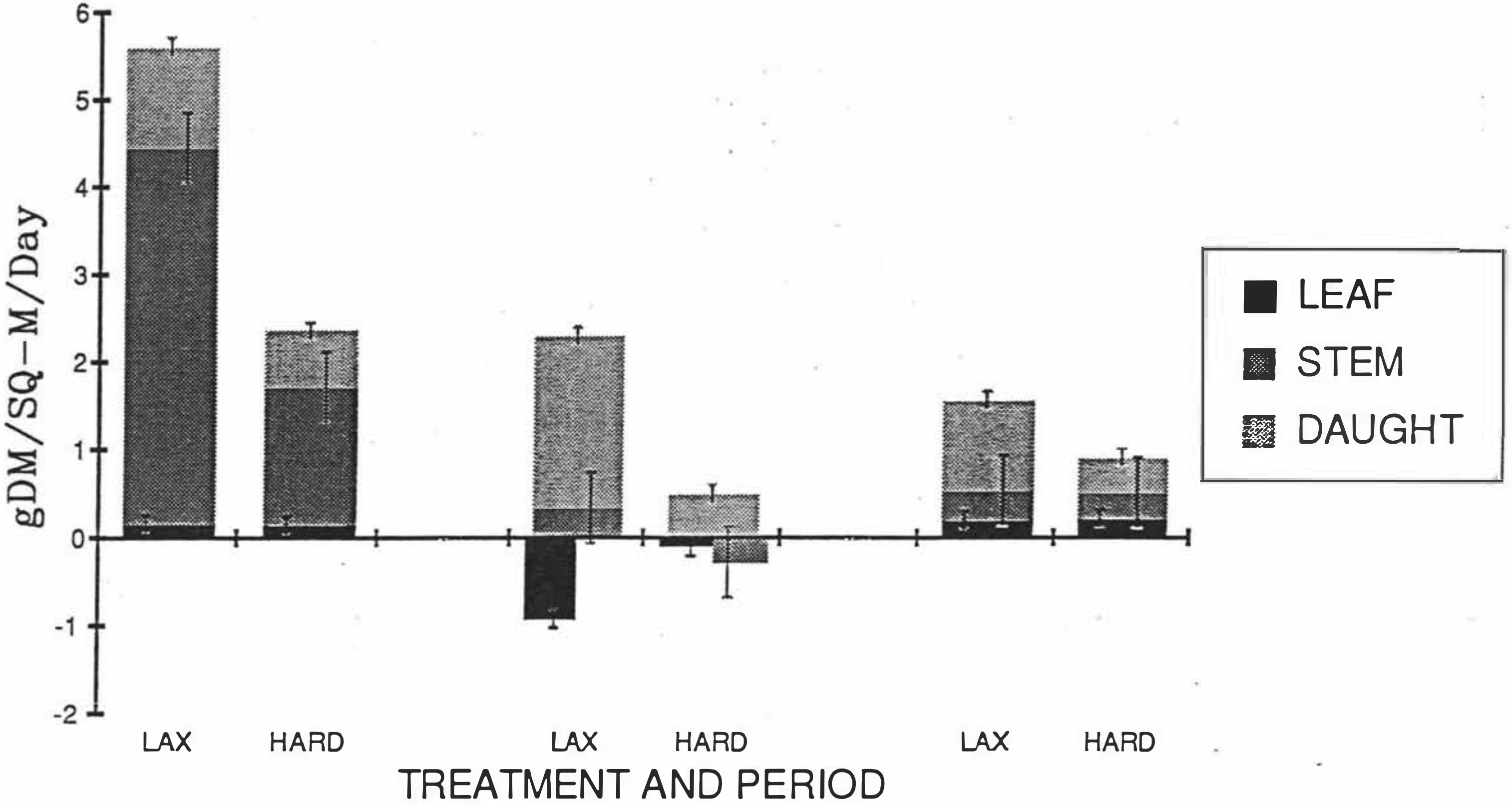
The rate of net herbage production was significantly different over treatments and periods for all components except leaf (Table 4.10c). The L treatment had higher net production rate than H treatment for total herbage, stem and seed head, and daughter tillers, but a lower rate for leaf (Fig 4.4). The leaf, stem and daughter tillers accounted for -9%, 54%, 55% and 9%, 43%, 48% of the total herbage net production on L and H treatment over periods respectively, and in periods 2 and 3 the net herbage production mainly came from daughter tillers (Table 4.10c). The highest net production for total herbage for both treatments was in period 1 (Fig 4.4). The rate of net production was lowest in period 2 for leaf, stem and seed head and total herbage, but higher for the net rate of daughter tiller production. The rates for leaf and stem and seed head under H treatment and for leaf under L treatment were negative in period 2, at which time net herbage production was largely dependent upon daughter tiller production. The interaction of treatment and period was significant for leaf, stem and daughter tillers (Table 4.10c).

TABLE 4.10c THE RATE OF HERBAGE NET PRODUCTION PER UNIT AREA AS ESTIMATED FROM INDIVIDUAL TILLER TISSUE TURNOVER AND TILLER POPULATION DENSITY (mgDM/m^2/Day)

TRT	Period	Leaf	Stem	Dau	Total
L	1(Sep-Nov)	0.17	4.30	1.15	5.62
L	2(Nov-Dec)	-0.91	0.35	1.96	1.39
L	3(Jan-Feb)	0.21	0.33	1.04	1.59
H	1(Sep-Nov)	0.16	1.57	0.65	2.39
H	2(Nov-Dec)	-0.08	-0.27	0.51	0.16
H	3(Jan-Feb)	0.23	0.29	0.40	0.93
S.E		0.09	0.40	0.13	0.49
TRT		NS	*	*	*
Period		***	***	**	***
TRT*Period		***	*	**	NS

* : p<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

FIG 4.4 THE RATE OF PRAIRIE GRASS PASTURE NET PRODUCTION BY COMPONENTS (gDM/SQ-M/DAY)



4.4. Discussion

4.4.1. Sward measurement technique

Prairie grass plants are taller and larger than ryegrass plants and have a more variable ground distribution. There were on average 30 tillers/plant and 16 plants/m^2, and the tiller population density was of the order of 400 - 600 tillers/m^2, compared with estimate of 4000 - 11000 tillers/m^2 in ryegrass swards (chapter 3). Because of the size of individual plants and tiller population density, estimates of plant and tiller density were made using 0.5 m^2 quadrats. Hume (1990b), working on Matua prairie grass plots with 1000 -1600 tillers/m^2 and approximate 100 plants/m^2 in the Netherlands, used a sample area of 0.25 m^2.

The rate of tissue turnover on a per unit area basis was estimated by multiplying individual tiller values by tiller population density estimates. There was a close correlation (r=0.86) between these estimates and values for green herbage accumulation from ground level cut quadrats, and the same trends were apparent across treatments and periods (Table 4.4 and 4.10c, Fig 4.5).

The regression equation of the two groups of values is:

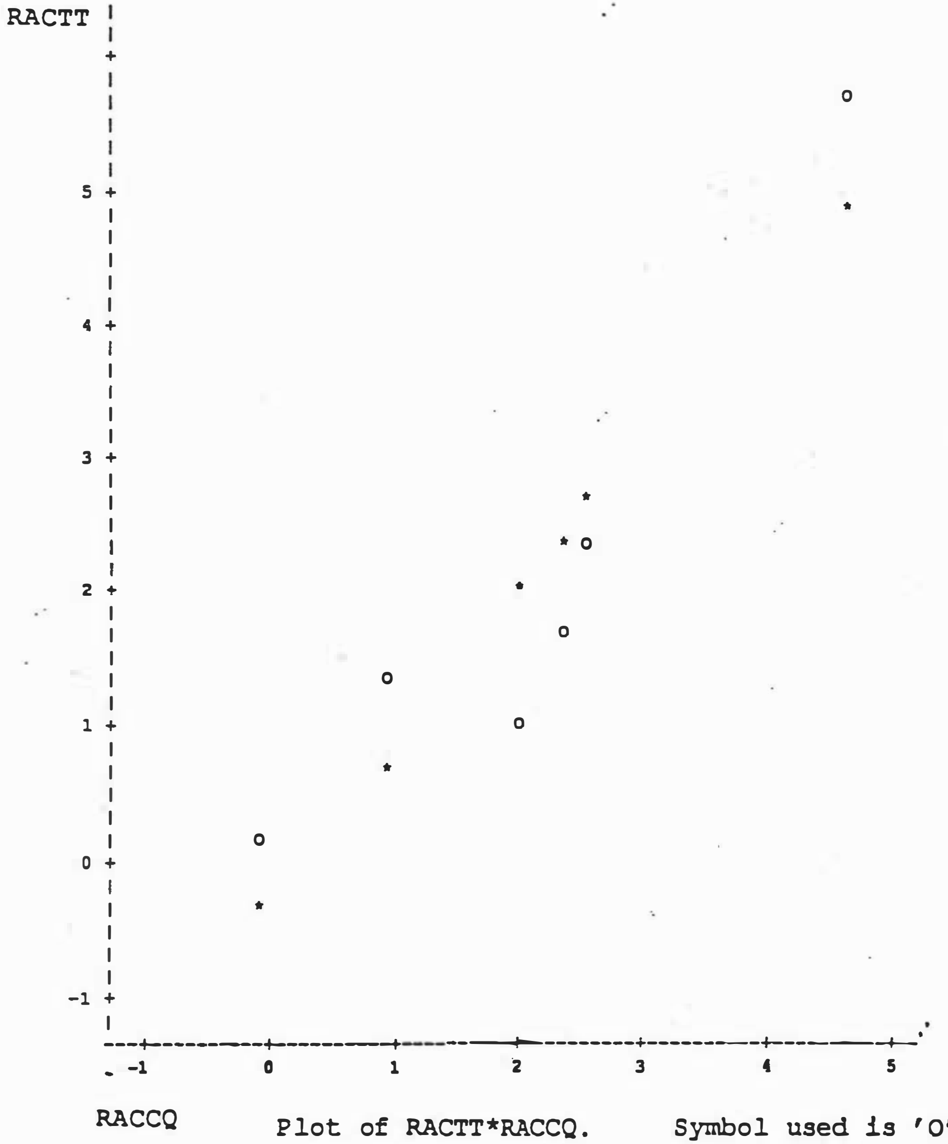
$$RACTT = -0.387(\pm 0.85) + 1.09(\pm 0.33)RACCQ \quad R\text{-sq}:0.73 \quad N=6.$$

RACTT: Rate of net herbage accumulation estimated by the tissue turnover technique.

RACCQ: Rate of green herbage accumulation estimated from cut quadrats.

In the equation, the intercept value was not significantly different from 0, and the regression constant was not significantly different from 1. The results were therefore quantitatively similar. However the values from the tissue turnover technique were considered to be more reliable than those from cut quadrats. Also, the results which were obtained from the tissue turnover technique provide more detailed information on plant responses to management and seasonal variations, such as the relationship between leaf gross growth, leaf senescence and net production.

FIG 4.5 THE REGRESSION BETWEEN ESTIMATES ACCUMULATION FROM CUT QUADRATS AND TISSUE TURNOVER PROCEDURES



Plot of RACTT*RACCQ. Symbol used is 'O'.
Plot of PREDICT1*RACCQ. Symbol used is '*'.

4.4.2. The distribution of plant size

Compensation in prairie grass swards can occur by increased plant size(tillers per plant) and tiller size(weight per tiller) (Falloon and Hume, 1988) and natural reseeding (Hume, 1990a). This experiment indicated that the distribution of plant size is dynamic under different treatments in Matua prairie grass swards (Fig 4.2a). Chu (quoted in Dodd, 1988; Appendix 4.3) showed that the deterioration of prairie grass swards under hard grazing treatment was characterized not only by fewer tiller/m^2, but also by a shift in the pattern of plant size distribution. During regrowth between grazings the proportion of plants in classes 3 and 4 (6-45 tillers/plant) increased (Fig 4.2c) and the proportion in classes 1 ,2 and 5 decreased. This was mainly because of the loss of tillers in large sized plants and the increase in tiller numbers in small plants during periods of regrowth.

The process of pasture deterioration is considered to begin with a decrease in plant size (initially tiller size then tiller numbers/plant) followed by a decrease in plant population (Dodd,et al, 1990). However, in the current experiment the distribution of plant size was relatively constant across both treatments and periods, despite marked changes in plant population density and dry weight per tiller.

Dodd (1988), working with a deteriorated prairie grass pasture, divided prairie grass plants into 10 classes at intervals of 5 tillers per plant over the range 0 - 50 tillers. Table 4.11 illustrates the relationship between the plant size categories used by Dodd (1988), and those for the current study. The proportion of small plants (< 6 tillers/plant) was greater in Dodd's experimental sward, and the proportion of large plants (>46 tillers/plant) was a little lower, but the distribution of plants which carried 6 - 45 tillers was 73% and 72% in the current study and in Dodd's experiment respectively. The difference between the two results was thus relatively small, although the present experiment was carried out in spring and Dodd's in winter. These results may indicate a characteristic distribution of plant size in Matua prairie grass swards. However, more study is needed to confirm this, and to define the relationship between the dynamics of plant size and pasture production .

TABLE 4.11 PLANT SIZE DISTRIBUTION ON PRAIRIE GRASS PASTURE
(Current study and Dodd, 1988)

Current study			Dodd (1988)			
Class	Til/plant	proportion	Score	Til/plant	Proportion	
1	< 6	0.147	1	0 - 5		0.215
2	6 - 25	0.501	2	6 - 10	0.185	0.614
			3	11 - 15	0.199	
			4	16 - 20	0.155	
			5	21 - 25	0.075	
3	26 - 45	0.233	6	26 - 30	0.018	0.110
			7	31 - 35	0.024	
			8	36 - 40	0.043	
			9	41 - 45	0.025	
4	46 - 65	0.086	10	46 - 50+		0.063
5	> 65	0.033				

4.4.3. Seasonal effects

In this experiment the seasonal effects on herbage production were significant, the rate of net production per unit area decreasing substantially from period 1 to period 3 (Fig 4.4). The tiller population densities increased over the period, but this effect was more than offset by the decrease of individual tiller net production rates. The highest rate of tiller population increase occurred in period 2 (Table 4.4), but this coincided with the lowest rate of individual tiller net production and lowest rate of net production per unit area (Table 4.9c and 4.10c). Also, the rates of herbage senescence were greater in period 2 and 3 than in period 1 (Tables 4.9b and 4.10b).

The seasonal effects on herbage production are the results of variation in climate and plant physiology. The rate of net herbage production was highest in period 1 (Sep - Nov) both for individual tillers and per unit area. The stem and seed head accounted for 73% of net production per unit area at this time. Matua prairie grass may produce reproductive heads in all seasons, but the main heading period begins in October (Rumball, 1974). The highest rate of tiller population density increase occurred in period 2 (Nov - Dec). The net rate of main tiller leaf production was negative in this period, and daughter tillers made a greater contribution to total herbage production. After grazing, the loss of reproductive tillers to death or defoliation could release buds which were previously inhibited by apical dominance (Davlin, 1975; Tainton, 1981). Hume (1990a) reported there was a rapid development of previously inhibited tillers buds after cutting, quickly compensating for the large losses of reproductive tillers that occurred at cutting in prairie grass swards. The tillers developed from these buds contributed to further production. Black and Chu (1989) recommended a management regime allowing replacement tillers to appear before grazing to the height of these new tillers.

The results of this experiment, in agreement with the results of Black and Chu (1989), showed the importance of daughter tillers in prairie grass pasture management, and also indicated the importance of stem and seed head in production. The stem accounted for 50% of the total net herbage production approximately (Table 4.10c), and the ratios of stem to total tiller dry weight were above 0.6 over treatments and periods (Table 4.3b). Hume (1990) reported a rapid increase in dry matter accumulation associated with reproductive growth, also, reduction in reproductive development may reduce natural reseeding in prairie grass and so reduce sward persistence.

The decline in net production per tiller from period 1 to period 3 may have resulted from the excessively wet soil conditions experienced in the spring of 1988, when the rainfall was substantially higher than the 60-year average, and the succeeding dry summer (Appendix 3.1a). Sellars (1988) noted that Matua prairie grass persisted better on sandy soils than on finer-textured soils. Excessive moisture limits pasture production especially during winter, when damage occurs to soil structure which may take much time to recover (Harris, et al. 1985). High soil moisture levels have been shown to reduce soil oxygen levels and Matua root and tiller production (Mwebaze,1986). Eccles et al.(1990) showed that during waterlogging, the rate of leaf extension of Matua prairie grass plants decreased, senescence rate increased and percentage of total plant weight as dead material increased.

On the other hand, rainfall was 20% and 40% below average values in November and December respectively, and the air temperatures were higher than the average values at this time (Appendix 3.1b). It is likely that pasture production was limited by soil moisture stress over this period. The difference in production between irrigated and non-irrigated pasture in the Manawatu has been estimated to be over 35%.(Harris, et al.1985).

4.4.4. The effect of treatment

The rates of herbage growth, senescence and net production were all significantly greater in L than in H treatment (Tables 4.9a, 4.9b and 4.9c). The L treatment had a significantly higher rates of net herbage production per unit area (Table 4.10c), but a lower ratio of leaf to stem (section 4.3.2.2) than the hard grazing treatment. This was the result of both a higher rate of a net production per tiller and a higher tiller population density (Table 4.4). Hume (1990) working with "Matua" swards under cutting management in the first three years after establishment on a sandy soil in the Netherlands, observed no consistant effect of cutting frequency on tiller or plant populations, though both were substantially higher than in the current study. Black and Chu (1989) reported that lax grazing permitted sward persistence and higher tiller population density but resulted in only 56% pasture utilisation, hard grazing at 75% pasture utilisation resulted in less total herbage harvested and lower tiller population density, owing primarily to sward decline. In the current study the difference between treatments for total herbage production mainly came from stem and daughter tillers, and net leaf production was not significantly different between treatments. Compared to ryegrass, leaf on main tillers made a very small contribution to herbage production in prairie grass pasture (Tables 3.5, 4.9).

The L treatment had lower values for OM digestibility ($P<0.01$) and lower concentrations of N and poorer animal performance than H treatment (Appendix 4.3 and 4.4) (Rugambwa, et.al, 1990), reflecting the higher proportion of stem in the herbage on this treatment. Additionally, the records of botanical and morphological components show that herbage on the L treatment had a greater proportion of dead material, less green leaf and less clover than did that on the H treatment (Appendix

4.4) (V.K.Rugambwa, 1990). Thus the advantage in higher herbage production would not necessarily be associated with increased animal output. From a digestibility and animal performance point of view, the largest economic return may not equate with the highest yield of dry matter. The performance of Matua prairie grass was poorer than that of ryegrass under similar management in this experiment (Rugambwa, et al. 1990). Moreover, in both treatments the dry weight of individual tillers, rates of net herbage production per tiller, and net pasture production per unit area decreased substantially over time (Tables 4.2, 4.9c, and 4.10c).

4.5. Conclusion

Grazing treatment significantly affected the morphology of prairie grass plants. The number of live leaves per tiller, and the dry weight per tiller were greater in L than in H treatment. The individual tiller dry weight ratio of stem to total dry weight was 0.66 and 0.63 under L and H treatments respectively.

The distribution of different sized plants was dynamic under grazing treatment. During regrowth the proportions of small (< 5 tillers/plant) and big (>45 tillers/plant) plants decreased, and that of medium (5-45 tillers/plant) plants increased. Over different treatments and periods in the current prairie grass swards the proportion of plants which carried 6 to 45 tillers was approximately 70% .

The L treatment had significantly higher rates of net herbage production both for individual tillers and per unit area, and the difference was mainly attributable to greater production from stem and daughter tillers. The net leaf production was not different between treatments.

The seasonal effects on pasture production are the results of variation in climate and plant physiology. There were strong seasonal effects in the current experiment, the rate of net pasture production decreasing both for individual tillers and per unit area from period 1 to period 3.

CHAPTER 5 THE INFLUENCE OF CUTTING MANAGEMENT ON HERBAGE PRODUCTION IN SMOOTH BROMEGRASS (Bromus inermis Leyss).

5.1 Introduction

Smooth bromegrass (Bromus inermis Leyss) is a native of Europe and Asia, and is adapted to most temperate climates (see section 2.3.3). It is a leafy sod-forming perennial which spreads vegetatively by underground rhizomes, and is also readily propagated by seed. Inflorescences are initiated in cool short days (Newell,1951). It is resistant to drought and to extremes of temperature, being capable of withstanding both hot, dry summers and long, cold winters (Walton,1980). Smooth bromegrass can be grown on a range of soil types, but grows best on deep fertile soils of well-drained silt loam or clay loam. It is deep rooted and fills the surface soil with many roots and rhizomes (Newell,1983).

Smooth bromegrass is sensitive to defoliation (section 2.3.3). In common with other cool-season grasses, it has a critical growth stage at which carbohydrate reserves are low and tillers are few (Jung,1974; Walton,1980.). The harvest time (Reynolds,1962; Teel,1956; Eastin,1964; Knievel,1971; Kunelius,1974), cutting height (Smith,1973) and defoliation interval all influence herbage production (Paulsen, and Smith, 1968). Results from China and elsewhere indicate the sensitivity of smooth bromegrass to defoliation, particularly in the reproductive phase of growth (Raese,1963; Knievel,1971; Kunelius,1974; Su,1983; and Chia,1986;).

However, there is still conflicting evidence about the influence of cutting management on herbage production and the mass of green herbage harvested.

The objective of this study was to determine the effects of cutting height, cutting interval and timing on herbage accumulation, yield and tiller population density, in order to develop appropriate cutting schedules for smooth bromegrass in Northern China. Information on leaf turnover, growth characteristics and underground biomass was collected to support the observations on herbage production.

5.2. Materials and methods

5.2.1. Experimental field and general management

The experiment was conducted at Beijing Agricultural University Chenpang Research Station (located at 39°58' North Latitude, 162°26' East Longitude), Beijing, China. The soil on the experimental field is a fine sandy loam. The yearly mean annual rainfall at the site is 600 mm, of which 74% falls in June, July and August; the annual mean temperature range is from -4°C (January) to 25.7°C (July). The mean annual total heat units above 10°C are 3500 to 4000 for the year. The frost-free season is from early April to mid October and is approximately 160-180 days.

In September 1988 (Northern hemisphere autumn), smooth bromegrass (Bromus inermis Leyss) seeds were drilled at a depth of 3 cm in bands 10 cm wide at 40 cm centers. The seed rate was 40 kg/ha. The area was fertilized with 20,000 kg/ha barnyard manure before cultivation, following a crop of maize. The area was flood irrigated from a main irrigation channel beside the experimental field, using subsidiary channels at 20 m intervals.

The smooth bromegrass commenced spring growth at the begining of April 1989, following a period of winter dormancy. At this time the area was irrigated and top dressed with urea at 40kgN/ha. Seed heads first appeared at the end of May and the experiment started on 30 May, at which time seed heads had appeared on most mature tillers. After first cutting on 5 June, the treatment plots were irrigated, and thereafter natural precipitation was supplemented with flood irrigation to keep soil moisture at an adequate level. On 10 August the field was top dressed with urea at 20kgN/ha again. According to the experimental cutting schedule (see next section) the treatment plots were cut by hand sickle to 10cm or 30cm (Table 5.1). On 2 October all plots were harvested to 10cm.

5.2.2. Experimental design

The experiment was designed as a randomized complete block with four replicates of six treatments on 24 8x10 m^2 plots. Six cutting treatments were imposed in order to compare the effects of different cutting frequencies, cutting heights and times on herbage production over the season from June to October.

Three main comparisons were made within a set of six treatments (Table 5.1).

A. Effect of cutting time. Treatments 2 and 3 had the same cutting residual (10cm) and same number of cuttings (3), but in different phases of the grass phenology. Treatment 3 was first cut on June 5 at anthesis, whereas cutting in treatment 2 was delayed until July 5, by which time flowering was completed.

B. Combined effects of cutting frequency and severity. Treatments 3, 4, 5 and 6 provided a 2x2 factorial comparison of cutting frequency (one month:F1 vs two months:F2 intervals) and cutting height (10cm:H1 vs 30cm:H2).

C. Effect of number of cuts. Treatments 1, 3 and 4 had the same cutting height, but one, three and five cuts per annum. Treatment 1 was left uncut until the end of the study in order to provide estimates of undisturbed grass growth and tissue turnover.

TABLE 5.1. THE EXPERIMENTAL DESIGN

TRT	Inital cut	Height of cutting	Number of cuts	Dates of cutting 5June	5July	1 Aug	2 Sep	5 Oct
1		10cm	1					cut
2	July	10cm	3		cut		cut	cut
3	June	10cm	3	cut		cut		cut
4	June	10cm	5	cut	cut	cut	cut	cut
5	June	30cm	3	cut		cut		cut
6	June	30cm	5	cut	cut	cut	cut	cut

5.2.3. Measurements

5.2.3.1. Herbage harvested

Two 20x40 cm^2 quadrats per plot were randomly placed across the rows, and were cut to the specified harvesting height before each harvest using hand clippers. Each sample was separated into green leaf lamina, green stem and dead material. Sub-samples were dried in a forced-draught oven at 70-80°C for 24 hours, then weighed to estimate component mass and total mass per unit area (gDM/m^2). There were only traces of plant species other than Bromus inermis in all swards.

5.2.3.2. Standing mass and herbage accumulation

Every month at each harvest date, two 20x40 cm^2 quadrat samples were cut at random along the rows to ground level in each plot using hand clippers. These samples were separated and dried as described in section 5.2.3.1. to provide estimates of total herbage and components standing mass (gDM/m^2), and herbage accumulation.

The herbage accumulation was estimated as:

Accumulation 1,2 = Standing2 - (Standing1 - Harvest1)

where:

Accumulation 1,2 : Herbage accumulation from time 1 to time 2.
Standing 2 : Standing mass at time 2.
Standing 1 : Standing mass at time 1.
Harvest 1 : Harvested mass at time 1.

Consequently, estimates of herbage accumulation follow from harvest 1; they do not include the initial period of spring production for which yield estimates were obtained at harvest 1.

5.2.3.3. Tiller population density and tiller weight

In each plot two fixed 20x40 cm^2 quadrats along the rows were chosen at random and identified by fixed iron wire quadrats to measure the tiller population density. The total numbers of vegetative tillers, reproductive tillers and dead tillers in each quadrat were counted monthly.

On 5 October, two 20x40 cm^2 quadrats per treatment were chosen at random to measure the final tiller density. Tillers in these samples were classed into groups as follows:

Class1. > 9 leaves per tiller;
Class2. 4-9 leaves per tiller;
Class3. < 4 leaves per tiller;
Class4. Buds.

The dry weights per tiller were estimated by dividing harvested mass by tiller population density at each harvest.

5.2.3.4. Leaves per tiller

On 5 July and 22 September, 10 individual tillers were cut at random to ground level from each plot and the numbers of green and senescent leaves per tiller were recorded.

5.2.3.5. Underground biomass

On 22 October one 20x40 cm quadrat per plot was chosen at random and dug out to a depth of 40 cm. The above ground material was cut off, then all the soil was removed by washing and the remaining plant material was separated into rhizomes, nodal roots and adventitious roots. The components were dried in a forced-draught oven at 70-80°C for 24 hours before weighing.

5.2.3.6. Subsequent spring regrowth

On April 17, 1990 two 20x40 cm^2 quadrats per plot were chosen at random on each treatment to examine the following spring regrowth. The tiller population density, standing herbage mass and the weight per tiller were measured.

5.2.3.7. Statistical analysis

The data were examined by analysis of variance using the general linear model (GLM) procedure of SAS (SAS Institute Inc., 1985). Analyses of variance for each of the components of tissue turnover were based on plot means of 2 quadrats on the data for 4 replications. Contrast analysis was used to test the effects of treatments and the interactions. Combining effects of cutting frequency and severity, a two by two factorial comparison was used between treatments 3, 4, 5 and 6 (Examples of ANOVA and CONTRAST analyses are shown in Appendix 5.1).

5.3. Results

5.3.1. Tiller size

5.3.1.1.Leaf number

The differences between treatments were significant in July and September for all leaf components (Tables 5.2a and 5.2b).

TABLE. 5.2a NUMBER OF GREEN(G),SENESCENT(S),TOTAL(T) LEAVES PER VEGETATIVE TILLER (Leaves/tiller) (Measured at 5 July).

Treatment	G	S	T	Period of Growth
1	7.9	2.9	10.8	1April-5July
2	7.3	3.2	10.5	1April-5July
3	4.6	1.3	5.9	5June -5July
4	4.7	1.4	6.1	5June -5July
5	5.8	1.9	7.7	5June -5July
6	5.7	1.2	6.9	5June -5July
S.E	0.5	0.4	0.5	
F	***	*	***	
3&4vs5&6	**	NS	*	
3&5vs4&6	NS	NS	NS	
3&6vs4&5	NS	NS	NS	

* : P<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference; 0.08 : P=0.08.

TABLE. 5.2b NUMBER OF GREEN(G),SENESCENT(S) AND TOTAL(T) LEAVES PER VEGETATIVE TILLER (leaves/Tiller)
(Measured at 22 September).

Treatment	G	S	T	Period of Growth
1	8.6	4.5	13.1	1Apri-22SEP
2	3.8	0.1	3.9	2 Sep-22SEP
3	6.4	2.4	8.8	3 Aug-22SEP
4	3.6	0.1	3.7	2 Sep-22SEP
5	7.4	3.3	10.7	3 Aug-22SEP
6	3.5	1.0	4.6	2 Sep-22SEP
S.E	0.2	0.2	0.3	
F	***	***	***	
3&4vs5&6	*	***	***	
3&5vs4&6	--	--	--	
3&6vs4&5	--	--	--	

* : P<0.05; ** : p<0.01; *** : p<0.001 ;
NS : No significant difference.

On 5 July the tillers of uncut treatments (treatment 1&2) carried more green leaves, senescent leaves and total leaves than did those on the cut treatments (treatment 3; 4; 5; 6) (Table 5.2a). The tillers on the lax (higher stubble) cutting treatments (treatment 5&6) carried more green leaves and total leaves than did tillers on hard (lower stubble) cutting treatments (treatment 3&4) ($P<0.01$ and $P<0.05$ respectively, Table 5.2a).

On 22 September the tillers in the lax (higher stubble) cutting treatments (treatment 5&6) again carried significantly more green ($p<0.05$), dead ($P<0.001$) and total ($P<0.001$) leaves than those in the hard (lower stubble) cutting treatments (treatment 3&4), but the other comparisons were complicated by different regrowth periods.

During the reproductive growth stage on 22 June the total number of leaves per tiller on reproductive, vegetative and young tillers in the uncut treatment averaged 5.2±0.92, 10.25±1.09 and 3.63±0.47, with the percentage of total tillers in each category being respectively 8.0±4.9%, 52.4±12.4% and 39.4±10.0%.

On the uncut sward (treatment 1) the number of live leaves was more constant than the number of dead leaves. Vegetative tillers carried 7.9±0.5 and 8.6±0.2 live leaves at 5 July and 22 September respectively, but the number of dead leaves increased from 2.9±0.4 at 5 July to 4.5±0.2 at 22 September. The maximum total number of leaves per tiller was 13 which was measured at 22 September in treatment 1 (Table 5.2b).

5.3.1.2. The dry weight of individual tillers

The dry weights of individual tillers measured over seasons within treatments and over treatment within seasons are shown in Table 5.3a and 5.3b respectively. The interaction of treatment and season was not estimated because of the unbalanced pattern of defoliation over time. Cutting at two-month intervals (treatment 3&5) resulted in greater dry weight per tiller than cutting at one-month intervals (treatment 4&6) ($P<0.01$) but no other contrasts were significant. The dry weight per tiller did not differ significantly between treatments in the following spring, but the values were smaller than the weights for the first year (Table 5.3a). The differences between months were significant ($P<0.01$), the tillers being lighter in August and October than in other months (Table 5.3b).

TABLE 5.3a. INFLUENCE OF TREATMENT ON THE DRY WEIGHT OF INDIVIDUAL TILLERS (mg/Tiller)

TRT	First year	Following Spring(April)
1	398	107
2	358	103
3	395	105
4	299	104
5	450	94
6	330	93
S.E	38	6
F	NS	NS
3&4vs5&6	NS	NS
3&5vs4&6	**	NS
3&6vs4&5	NS	NS

** : p<0.01; NS : No significant difference.

Table 5.3b Influence of season on the dry weight of individua tillers

Month	mg/Tiller
June	447
July	417
Aug	252
Sep	445
Oct	299
S.E	35
F	**

** : P<0.01.

5.3.2. Tiller population density

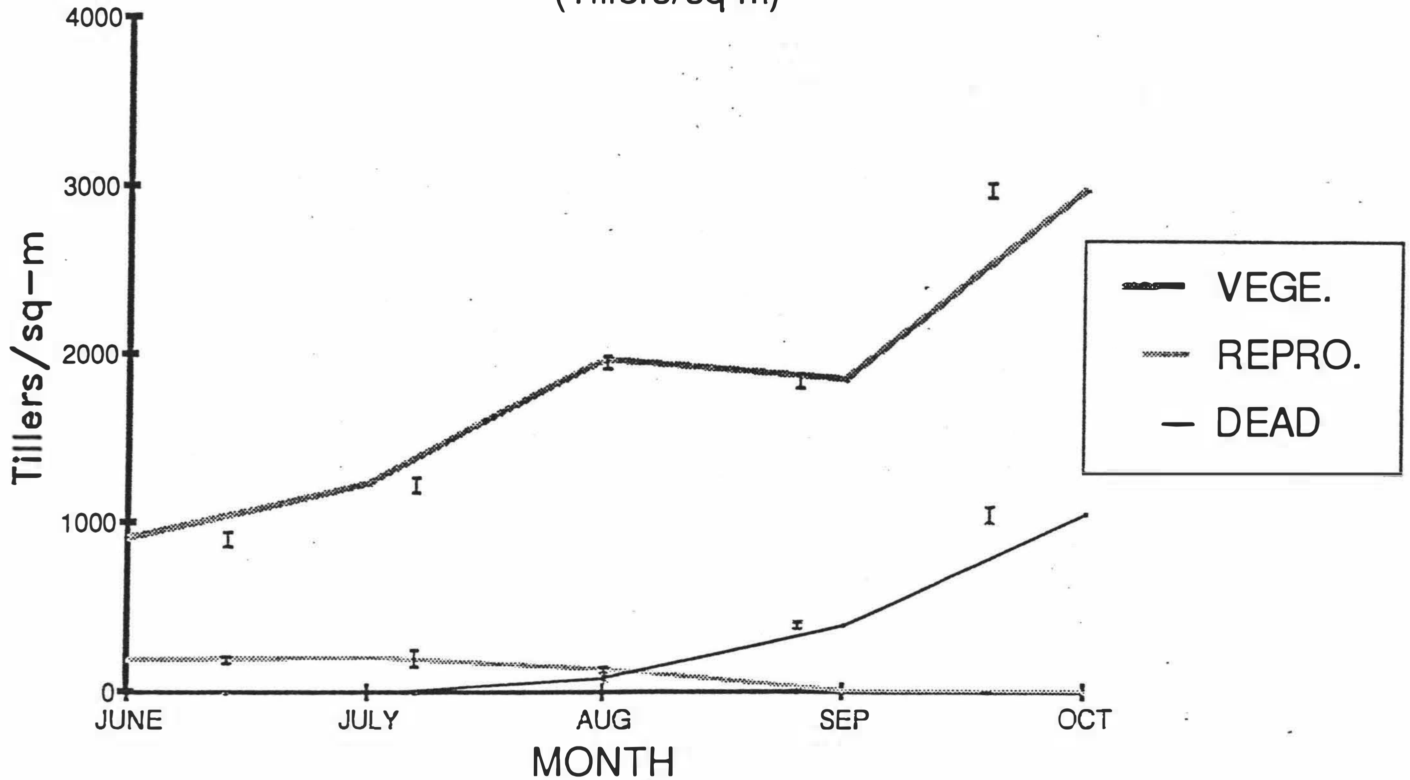
The vegetative, reproductive and total tiller population densities which were measured every month in permanent quadrats are shown in Table 5.4a. Treatment 1 had significantly higher population density than all other treatments at all times after the initial sampling on 30 May and the density increased over the season especially after September (Table 5.4a and Fig 5.1). The results show that cutting decreased total tiller population density and sharply reduced development of reproductive tillers. Reproductive tillers were found until September on the uncut treatments (treatment 1) but no reproductive tillers were seen after July on the cutting treatments. Delaying first cutting by one month (Treatment 2 vs 3), resulted in more reproductive tillers ($P<0.05$) and vegetative tillers ($p<0.01$) . Treatment 4 (cutting every month to 10cm) resulted in a relatively constant and low tiller population density over the year at approximately 1000 Tillers/m^2, and the difference between treatment 4 and other cutting treatments were significant in 5 July, 1 August and 30 September (Table 5.4a).

Table 5.4a. Smooth bromegrass(Bromus inermis Leyss) vegetative(V), reproductive(R) and total(T) tiller population density(Tillers/m^2)

	30 May			5 July			1 Aug			2 Sep			30 Sep		
TRT	V	R	T	V	R	T	V	R	T	V	R	T	V	R	T
1	909	196	1105	1232	206	1438	1967	137	2104	1848	4	1852	2979	0	2979
2	954	170	1124	1226	170	1396	1362	0	1362	0962	0	0962	1065	0	1065
3	871	170	1041	0757	007	0757	1400	0	1400	0965	0	0965	1281	0	1281
4	895	178	1072	0915	000	0915	1087	0	1087	0982	0	0982	0968	0	0968
5	910	157	1067	1039	139	1178	1345	0	1345	1142	0	1142	1356	0	1356
6	912	203	1115	1275	000	1275	1625	0	1625	1326	0	1326	1467	0	1467
S.E	43	21	32	89	48	99	112	16	110	112	1	112	254	0	254
F	NS	NS	NS	*	**	***	*	***	***	*	NS	*	***	NS	***
1 vs Rest	NS	NS	NS	NS	**	**	***	***	***	***	*	***	***	NS	***
2 vs 3	NS	NS	NS	**	*	***	NS	NS	NS	NS	NS	NS	NS	NS	NS
4vs2&3&5&6	NS	NS	NS	NS	NS	*	*	NS	*	NS	NS	NS	**	NS	**
3&4vs5&6	NS	NS	NS	**	NS	***	NS	NS	NS	NS	NS	NS	**	NS	**
3&5vs4&6	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
3&6vs4&5	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS	*

*: P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

FIG 5.1 THE TILLER DENSITY ON UNCUT SMOOTH BROMEGRASS SWARDS
(Tillers/sq-m)



The cutting height significantly affected the tiller density. On 5 July the tiller population density was greater for vegetative ($P<0.01$) and total ($P<0.001$) tillers in treatments 5&6 (30 cm) than in treatments 3&4 (10 cm). On 30 SEP, treatments 5&6 had greater vegetative ($P<0.01$) and total ($P<0.01$) tiller population densities than treatments 3&4. The effect of cutting frequency (treatment 3&5 vs 4&6) was not significant at any date. The interaction between cutting height and cutting frequency was not significant except on 30 Sep ($P<0.01$), when the tiller population density of treatment 6 was higher than in other treatments. The tiller population density on treatment 4 was significantly lower than that on all other cut treatments (treatment 2&3&5&6) in July, August and October (Table 5.4a).

The densities of various tiller classes which were measured on 5 October are shown in Table 5.4b. The tiller population densities are substantially higher than those measured on the permanent quadrats (Table 5.4a) because the former records included dead tiller stubs in class 1 (> 9 leaves per tiller). Also, measurements were taken one week later on the permanent quadrats, and there was a substantial development of new (class 3) tillers in the intervening period.

The differences between treatments in terms of tillers per plant were not significant overall but plants carried more buds in treatment 1 than in other treatments (Table 5.4b). Treatment 1 had significantly more tillers per unit area (overall and within most categories) and more buds per unit area than other treatments (Table 5.4b). The frequent close cutting treatment (treatment 4) had the lowest total tiller population per unit area, and the class 2 tillers (4-9 leaves/tiller) were significantly fewer in treatment 4 than other cutting treatments ($p<0.05$). Treatment 3 had more buds per unit area than treatment 2 ($p<0.05$). The effects of cutting height, cutting interval and the interaction between them were not significant (Table 5.4b).

Table 5.4b. Density of various class tilers,and the numbers of tillers and buds per plant in October (C1,>9 leaves/tiller; C2,4-9 leaves/tiller;C3,<3leaves/tiller)(Tillers/m^2)

TRT	Total	>9	4-9	<3	Buds/m^2	Til/p	Buds/p
1	4630	830	1560	2220	2030	5.2	2.5
2	2330	580	760	990	160	4.7	0.3
3	2840	640	930	1270	1060	4.8	1.8
4	1820	330	260	1230	450	3.7	0.6
5	4110	1950	890	1270	1090	4.5	1.3
6	2810	1330	780	770	400	3.8	0.6
S.E	510	590	180	340	220	0.3	0.5
F	NS	NS	*	NS	*	NS	NS
1 vs rest	*	NS	**	*	**	NS	*
2 vs 3	NS	NS	NS	NS	*	NS	NS
4vs2&3&5&6	NS	NS	*	NS	NS	NS	NS
3&4vs5&6	NS	NS	NS	NS	NS	NS	NS
3&5vs4&6	NS	NS	NS	NS	NS	NS	NS
3&6vs4&5	NS	NS	NS	NS	NS	NS	NS

* : $P<0.05$; ** : $p<0.01$; *** : $p<0.001$; NS : No significant difference.

5.3.3. Herbage mass and herbage accumulation

For convenience, the effects of cutting management on herbage yield and accumulation are examined separately for time of first cut (5.3.3.1), cutting height and frequency (5.3.3.2) and number of cuts (5.3.3.3).

5.3.3.1. Effect of timing of first cut

The components (green, dead and total) of harvested herbage and herbage accumulation above ground level estimated from samples cut to ground-level summed over summer (June to August), autumn (September to October) and over the full growth season for treatment 2 and 3 are shown in Tables 5.5a and 5.5b. There was a substantial effect of initial cutting time on both herbage accumulation and herbage harvested. The harvested herbage mass of treatment 3 was greater than that of treatment 2, and the difference was significant in summer for green, dead, and total herbage and overall for green and total herbage. These difference were mainly attributable to differences in harvested green material (Table 5.5a). The difference between treatment 3 and treatment 2 was also significant for accumulation of total herbage and green material overall (Table 5.5b). Treatment 2 had a lower total harvested mass and herbage accumulation in all cases, primarily as a consequence of lower green material accumulation.

Table 5.5a The effect of initial cutting time on harvested green(G), dead(D) and total(T) herbage harvested in summer, autumn and overall (gDM/m^2)

	Summer(June-Aug)			Autumn (Sep-Oct)			Total(All seasons)		
Treatment	G	D	T	G	D	T	G	D	T
2(cut July)	493	52	545	283	102	386	0777	155	0933
3(cut June)	737	90	828	349	086	435	1087	176	1263
S.E	24	4	26	12	9	16	32	9	33
F	***	*	***	NS	NS	NS	***	NS	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

Table 5.5b The effect of initial cutting time(June and July) on green(G), dead(D) and total(T) herbage mass accumulation in summer autumn and overall.(gDM/m^2)

	Summer(June-Aug)			Autumn (Sep-Oct)			Total(All seasons)		
Treatment	G	D	T	G	D	T	G	D	T
2(JULY)	251	68	303	159	83	242	411	150	545
3(JUNE)	324	112	436	417	49	466	741	161	903
S.E	34	18	42	55	37	81	57	37	85
F	NS	NS	*	***	NS	NS	***	NS	**

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

5.3.3.2. Effect of cutting height and frequency

The effect of cutting height (H) and frequency (F) on herbage mass harvested and accumulation are shown in Tables 5.6a and 5.6b as a two by two factorial comparision. Cutting to 10 cm (H1:Treatment 3&4) resulted in greater yields of harvested herbage than cutting to 30 cm (H2:Treatment 5&6), with the effects being significant for green ($p<0.001$), and total herbage yield ($p<0.001$) overall. These differences were greater early rather than later in the season (Table 6a). The effect of cutting frequency (Treatment 3&5(F1) vs 4&6(F2)) on the other hand was greater in the second half of the season (autumn), and resulted in significantly greater overall yield of green ($p<0.001$), dead ($p<0.001$) and total ($p<0.001$) herbage for the less frequently cut treatments. The interaction of cutting height with cutting frequency was significant in the autumn and overall for all components (Table 5.6a).

Cutting to 10cm (H1:treatment 3&4) consistently resulted in greater green herbage accumulation above ground level than cutting to 30cm (H2:treatment 5&6), the difference being significant in summer and overall (Table 5.6b), and this difference resulted in greater total herbage accumulation over the complete season ($p<0.05$). The green material accumulation on treatments cut at one-monthly intervals (F1:treatment 4&6) was lower than that on treatments cut at two-monthly intervals (F2:treatment 3&5) in autumn ($p<0.05$), and overall ($p<0.01$). This difference was reflected in estimates of total herbage accumulation throughout the year ($P<0.05$). The cutting height*frequency interaction was not significant for any components or any growth seasons (Table 5.6b).

The effects of cutting height and cutting frequency were similar for total herbage harvested and herbage accumulation, but they were greater in the former than in the latter case (Table 5.6a and 5.6b) (Fig.5.2).

Table 5.6a. The effect of cutting height(Treatment 3&4 vs 5&6), cutting frequency (Treatment 3&5 vs 4&6), and cutting height*frequency interaction (Treatment 3&6 vs 4&5) on hervested green(G), dead(D) and total(T) herbage harvested in summer, autumn and overall (gDM/m^2)

	Summer(June-Aug)			Autumn(Sep-Oct)			Total		
Treatment	G	D	T	G	D	T	G	D	T
3 (H1F1)	737	90	828	349	86	435	1087	176	1263
4 (H1F2)	764	66	830	230	52	282	994	118	1112
5 (H2F1)	417	85	502	616	182	698	933	267	1200
6 (H2F2)	387	78	466	234	24	259	621	103	725
S.E	24	4	26	12	9	16	32	9	33
3&4vs5&6(H)	***	NS	***	**	NS	**	***	NS	***
3&5vs4&6(F)	NS	NS	NS	***	***	***	***	***	***
3&6vs4&5(F*H)	NS	NS	NS	*	**	***	***	*	***

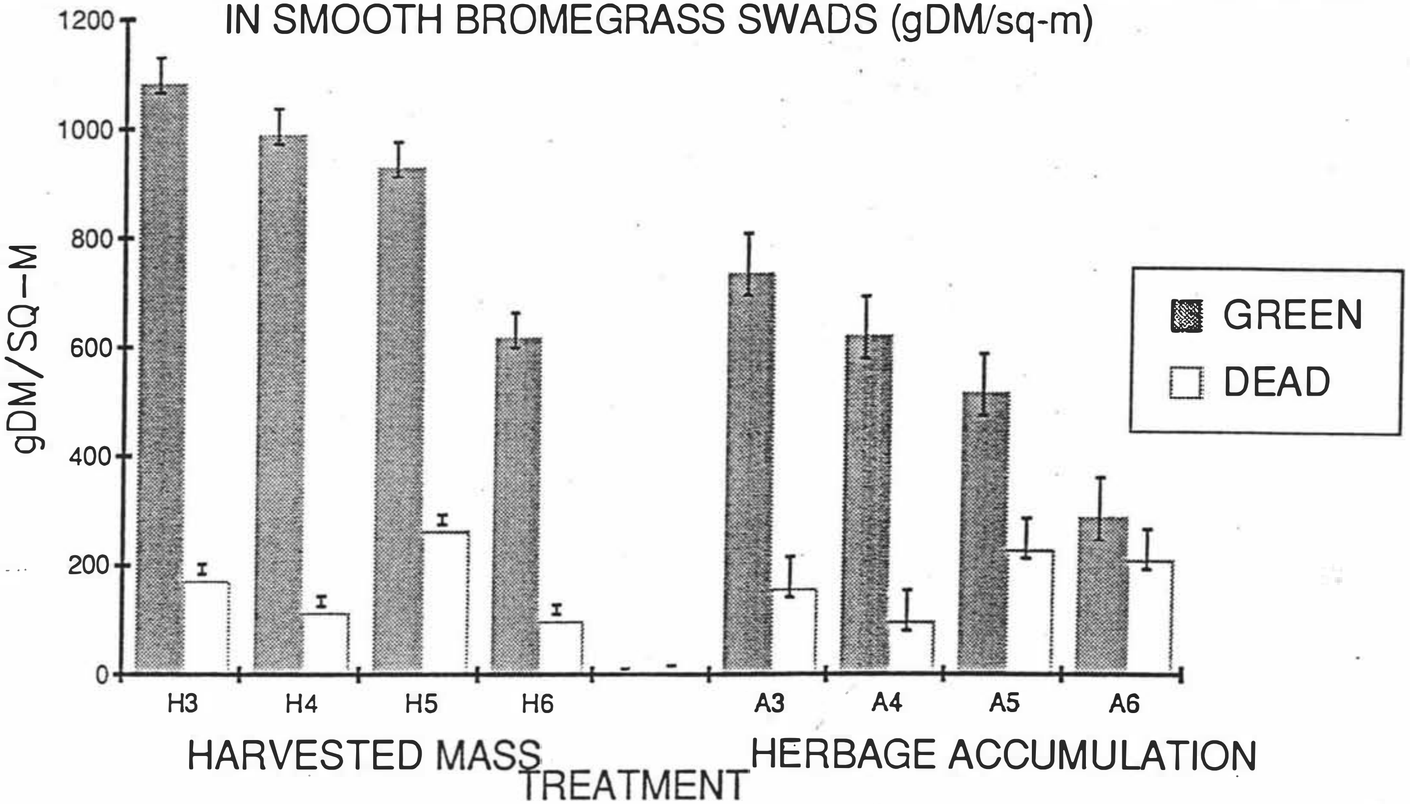
* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

Table 5.6b. The effect of cutting height(Treatment 3&4 vs 5&6), cutting frequency (Treatment 3&5 vs 4&6), and cutting height*frequency interaction (Treatment 3&6 vs 4&5) on green(G), dead(D) and total(T) herbage accunulation in summer, autumn and overall (gDM/m^2)

	Summer(June-Aug)			Autumn(Sep-Oct)			Total		
Treatment	G	D	T	G	D	T	G	D	T
3 (H1F1)	324	112	436	417	49	466	741	161	903
4 (H1F2)	329	70	399	294	30	324	625	100	723
5 (H2F1)	132	113	246	388	118	506	520	232	752
6 (H2F2)	47	143	190	246	70	316	293	213	506
S.E	34	18	42	55	37	81	57	37	85
3&4vs5&6(H)	***	NS	***	NS	NS	NS	***	*	*
3&5vs4&6(F)	NS	NS	NS	*	NS	NS	**	NS	*
3&6vs4&5(H*F)	NS	NS	NS	NS	NS	NS	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

FIG 5.2 THE HARVESTED HERBAGE MASS AND HERBAGE ACCUMULATION IN SMOOTH BROMEGRASS SWADS (gDM/sq-m)



5.3.3.3. Effect of number of cuts

The comparisons of the effects of the number of harvests per annum on herbage mass harvested and accumulation are shown in Table 5.7. Treatments 1,3 and 4 had the same cutting height (10cm), but one, three and five harvests per year. All comparisons between treatments showed significant differences except the overall herbage accumulation. The overall green and total herbage harvested and accumulated were lower for the single harvest (treatment 1) than for other treatments, but the reverse was the case for dead material harvested and accumulation (Table 5.7). The results showed that the herbage yield and accumulation for all growth seasons was greater for treatment 3 (three harvests) and treatment 4 (five harvests) than treatment 1 (one harvest) (Table 5.7).

In general, differences in total herbage accumulation were attributable mainly to differences in green herbage accumulation. The green material accumulation was greater in treatment 3 than in all other treatments.

Table 5.7. The effects of number of harvests on yield and accumulation of green(G), dead(D), and total(T) herbage over the full growth period (gDM/m^2)

	Harvested mass			Herbage accumuolatiuon		
Treatment	G	D	T	G	D	T
1(HARV 1)	529	461	990	113	400	513
3(HARV 3)	1087	176	1263	741	161	902
4(HARV 5)	994	118	1112	623	100	723
S.E	18	7	16	66	35	96
F	***	***	*	**	**	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

5.3.4. Underground biomass

Estimates of underground biomass in two categories (rhizomes plus nodal roots, and adventitious roots) and in total made in late October are shown in Table 5.8. The total underground biomass and the mass of adventitious roots were greater for treatment 1 than for all other treatments. The total underground biomass in treatment 3 was greater than in treatment 2 ($p<0.001$), coinciding with the difference in above-ground herbage mass accumulation. Cutting height (treatment 3&4 vs 5&6) did not significantly affect the underground biomass, but the higher cutting frequency sharply decreased the underground biomass both for rhizomes and nodal roots ($p<0.05$) and adventitious roots ($p<0.001$). The cutting height*cutting frequency interaction was not significant for any underground component (Table 5.8).

Table 5.8 The effect of cuttting treatment on underground biomass (Sampling on 22 Oct)(gDM/m^2,to 40cm depth).

Treatment	Rhizomes and Nodal roots	adventitous roots	Total
1	87	215	302
2	52	54	106
3	79	130	209
4	49	53	102
5	74	114	188
6	62	63	125
S.E	7	13	19
F	*	***	***
1 vs rest	*	***	***
2 vs 3	*	***	***
3&4 vs 5&6	NS	NS	NS
3&5 vs 4&6	*	***	***
3&6 vs 4&5	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

5.3.5. New season regrowth

The regrowth parameters (tiller population density, standing herbage mass and the weight per tiller) which were measured on 17 April 1990 are shown in Table 5.9. None of these parameters were significantly affected by treatment in the previous year.

Table 5.9 The effect of cutting treatment on tiller population density, standing herbage mass per unit area and weight per tiller.

Treatment	Tillers/m^2	gDM/m^2	g/Tiller
1	1480	157	0.107
2	1180	118	0.103
3	1310	138	0.105
4	1440	149	0.104
5	1380	129	0.094
6	1370	124	0.093
S.E	90	12	0.006
F	NS	NS	NS

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

5.4. Discussion

5.4.1. Technique

The estimates of herbage harvested were greater than those of herbage accumulation in summer and overall (Tables 5.5a, 5.5b, 5.6a, 5.6b, and 5.7). This was because the harvested herbage mass included the herbage accumulation before the first harvest on 5 June, whereas estimates of herbage accumulation followed from this date. Over the full growth season there were close relationships across treatments between herbage harvested and herbage accumulation :

Green herbage accumulation = - 309 + 0.937±0.09 Green herbage harvested

R-sq = 97.2% N=5;

Total herbage accumulation = - 45 + 0.698±0.14 Total herbage harvested

R-sq = 88.6% N=5;

The regression coefficent for green herbage was close to 1.0. The fact that the coefficent for total herbage was substantlly less than 1.0 is explained by the loss of senescent tissue in the pasture to decompsation. Standed errors of estimates of herbage accumulation were greater than those of herbage harvested (Tables 5.5a, 5.5b, 5.6a, 5.6b and 5.7), because estimates of accumulation were derived from the differences between measurements of herbage harvested and residual herbage mass(section 5.2.3.3).

5.4.2 Tiller characteristics

Cutting at one-month intervals resulted in lower dry weight per tiller than cutting at two-month intervals (Table 5.3a). This result showed that frequent cutting depressed the tiller size for smooth bromegrass. Eastin, et al., (1964) reported that tiller weights increased significantly between successive growth stages of the initial spring growth, and with each successive initial harvest; also the weights of tillers were significantly different between varieties. In the current study, seasonal fluctuations in tiller dry weight were large in comparison to those produced by contrasting cutting treatments (Tables 5.3a and 5.3b). The tiller dry weights were less in August and October than in other months because the weather was very dry in August and the temperature was lower in October, resulting in lower herbage accumulation.

More leaves were observed on smooth bromegrass than any other grass species for which information is avaliable. Datailed comparisons with other species are made in chapter 6. Here attention is concentrated only on the effects of treatment on tiller dry weight and leaf number.

There were marked differences between first year and second spring average values for dry weight per individual tiller (Table 5.3a). This was because the sampling date was earlier in the second year than in the first, and the tillers were morphologically younger.

From plant breeding studies, it has been reported that the leaf number per reproductive tiller is on average 5.3 (Wai-Koon, 1977). This was similar to observation in the current experiment (5.2±0.92), but Wai-Koon (1977) did not report any values for vegetative tillers, which are more important for pasture production. Pan (1986) classed the vegetative tillers into long and short vegetative tillers (Vegetative tillers more than half the height of reproductive tillers were defined as long tillers.), With this classification, the number of tillers in each category was affected by the environment. In the current study tillers were classed into young shoots and vegetative tillers by leaf number. This classification is more reliable. Pan (1986) reported the numbers of live leaves in long vegetative tillers ranged from 5.0 to 8.2, leaf length probably being related to the leaf number.

Although the comparisons of number of leaves per tiller between treatments were complicated, as the tillers of different treatments were grown in different periods, the results of this experiment have shown: First, the tillers of treatment 1 (no cutting) carried more total leaves (13) than those of any cutting treatments, and the ratio of green to total leaves was higher in all cutting treatments than in no cutting treatment; Second, the tillers in the lax (higher stubble) cutting treatments carried more leaves than did those in hard (lower stubble) cutting treatments (Table 5.7a and 5.7b). These results indicate that cutting reduces the number of leaves per tiller, but increases the ratio of green to total leaves.

These results show that the numbers of green leaves have a relatively constant relationship with the growth periods. At 5 July, treatment 1 with treatment 2, treatment 3 with treatment 4, and treatment 5 with treatment 6 had the same growth periods and cutting heights, and their numbers of green leaves were similar (Table 5.2a). At 22 September, the same situation occurred within treatments 2, 4, and 6, and within treatments 3 and 5 (Table 5.2b). As the growth period increased the number of green leaves increased, but within limits. In this experiment under continuous growth conditions (treatment 1) the average numbers of green leaves was 7.9 per tiller at 5 July and only 8.6 leaves at 22 September (section 5.3.1.1). The influence of management on green leaf number per tiller in this species deserves further study.

5.4.3. The effects of cutting treatment on pasture production

5.4.3.1. Timeing of first cut

Optimum harvest date for smooth bromegrass has been the subject of much research. Two factors are affected by date of harvest. The first is dry matter production, which increases towards the end of the growth period. The second is the quality of the herbage production, which declines with increasing maturity (Walton, 1980). In this experiment, treatment 3 and treatment 2 had the same number (3) of harvests and same cutting height (10cm), but the first cutting of treatment 3 was at anthesis, whereas treatment 2 was first cut one month later. Treatment 3 resulted in higher herbage mass harvested and herbage accumulation above ground level than treatment 2 over the spring/summer period, and throughout the year (Table 5.5a and 5.5b).

This result is evidence that delaying cutting until flowering was completed resulted in a subsequent depression in herbage yield and herbage accumulation, confirming the results of previous studies. Knievel, et al., (1971) reported highest seasonal herbage yields and stand persistence of smooth bromegrass when the first cut was at early anthesis. In China, Pan (1986) on Qinghei Plateau reported that harvest (one harvest per annum) at anthesis resulted in highest leaf mass and crude protein production. Chia(1986) and Su(1988) indicated that two cuts per annum and initial cutting at heading stage gave optimum productivity in north China. Results from this experiment suggest that three cuts per annum with the first cutting at anthesis stage give optimum productivity and a satisfactory balance between production and forage quality. Treatment 3 also had more tillers, buds and underground biomass production per unit area in October than treatment 2 (Table 5.4b).

Forage quality decreases as plants mature. Bhat and Christie (1975) reported that in vitro digestibility values declined at the rate of about 1% per day between the time of head emergence and full head extension. In the period between the beginning of the fully extended head stage and anthesis, in vitro digestibility values declined more slowly (0.1% per day). Thus, although no chemical analysis were made in this experiment, treatment 3 would be expected to result in greater production at higher nutritive value than treatment 2. The herbage accumulation ratios of green material to total mass were 0.75 and 0.82 overall in treatment 2 and treatment 3 respectively (Table 5.5b).

5.4.3.2. The cutting height and cutting intervals

The effects of cutting height, cutting interval and interactions between them had an important influence on forage production in this study. The harvested mass and herbage accumulation of frequent cutting treatments (treatment 4&6, cutting every month) was significantly lower than that of infrequent cutting treatments (treatment 3&5, cutting every two months) (Table 5.3a and 5.3b), and the tiller population density of treatment 4 was the lowest in all treatments (Table 5.4a). This result confirmed the evidence of previous studies (Smith, et al., 1973). Frequent defoliation can lead to low stubble carbohydrates, poor regrowth and even death (McIlvanne, 1942). Smith (1973) found that in close cut (4cm) smooth bromegrass harvested four times per annum only 36% of the original tiller population persisted, whereas persistence was 99% for a sward cut two times per annum (Marten, et al 1980).

In the current study the effect of cutting interval on herbage accumulation was cumulative over time, being greater in the second half of the season than in the first (Table 5.6a and 5.6b). Marten (1980) reported that smooth bromegrass persistence was poorer on an annual four cutting schedule, and recovered substantially after a change to three harvests in the second year. Frequent cutting decreased slightly the percentage of total available carbohydrates (TAC) accumulated between cuttings in the stem bases of bromegrass (Gary, 1968). It has been generally accepted that net herbage accumulation decreases as the frequency of defoliation increases, for species of erect growth habit (Brougham, 1959). In this experiment the underground biomass (rhizomes, nodal and adventitious roots) measured at 22 October was significantly lower on monthly cut than on two-monthly cut treatments (Table.5.8). This result showed that frequent cutting adversely affected both underground storage organs and the root system.

Height of cutting determines the amount of stubble left for reserve food storage, and the amount of leaf area left for photosynthesis. Smith (1973) reported that smooth bromegrass was almost eliminated within 3 years when cut three times annually at 4cm, but persisted better when cut at 10cm either cut two or four times per year. In this experiment cutting heights of 10cm (vs 30cm) significantly increased harvested mass and herbage accumulation.Green herbage accumulation and yield were substantially higher on the shorter (10cm) cut treatments, but the reverse was the case for dead material (Table 5.6a and 5.6b), and the tiller population density was higher in the higher (30cm) cut treatment than in the shorter cut (10cm) treatment (Table 5.4a). Although the total stubble would be expected to carry greater carbohydrate reserves, the shading effect due to accumulation of old leaves under lax defoliation would affect photosynthesis and new tiller development, also the leaf senescence would accelerate (Kays and Harper, 1974).

In this study the underground biomass did not differ significantly between cutting heights of 10cm and 30cm, and the main effects of cutting height and interval on herbage accumulation and underground biomass were independent of each other.

5.4.3.3. The number of cuts

Treatment 1, 3 and 4 had the same cutting height, but one, three, or five harvests per year. Although the tiller population density of treatment 1 was higher than that of the other treatments, the overall green and total herbage harvested and accumulated was lower for the single harvest (treatment 1) than for other treatments. The reverse was the case for dead material harvested and accumulation (Table 5.7), and the total herbage mass accumulation did not differ significantly between treatments (Table 5.7). This result showed that cutting did not so much affect total accumulation (which would have reflected environmental conditions) but acted instead to alter the balance between green material harvested and losses as dead material. Cutting resulted in higher green material accumulation and lower dead material accumulation in all seasons.

The tiller population density of treatment 1 (no cut) was higher than that of any cutting treatment, and the close frequent cutting treatment (treatment 4) had the lowest tiller population density (Table 5.4a). In other words, cutting decreased tiller population density, in agreement with published results for this species. Frequent defoliation can lead to low stubble carbohydrates, poor regrowth and even death (McIlvanne, 1942). The tiller density of the no cutting treatment increased to August, with a minor decrease from August to September (Fig 5.2). This was probably because reproductive tillers died in summer and tillering was not resumed until autumn. Spring growth of smooth bromegrass dies by late September; new shoots may be produced in mid October, but their growth is small (Jonu,1967). Also temperature influences herbage production. For smooth bromegrass the optimum daytime temperature for top growth is between 18.3°C and 24.8°C, and a temperature of 34.8°C gives decreased yield (Baker,1968). The optimum soil temperature for smooth bromegrass above ground dry matter production is 18.3°C (Morrow, and Power 1979). This experiment was carried out in the Beijing area, where in August the daytime temperature averages 26°C. Also, this summer was very dry and it is possible that the irrigation procedure was not adequate to keep pace with a developing moisture deficit.

Compared over all cutting treatments, treatment 3 (cut three times at 10cm, first cut at anthesis) resulted in the best herbage accumulation, herbage mass harvested and underground biomass. This is therefore the pasture management schedule recommended for smooth bromegrass in the North of China. The poorest plant performance was recorded for treatment 6 (cut every month at 30cm).

5.4.4. The effect of treatment on regrowth in following spring

There were no significant differences between treatments in tiller population density, standing herbage mass or the weight per tiller in the spring following the different defoliation managements, despite the fact that management significantly affected underground biomass in autumn. The underground biomass would be expected to affect both the population of tiller buds and the quantity of energy reserves, and therefore to have an important effect on spring growth potential. The absence of any such effect may reflect the fact that following the final cut in October, the grass would still have had a further month of growth in the Beijing area. During this period, it is possible that remaining tillers on all treatments were able to accumulate sufficient reserves to pass the winter and support regrowth in the following spring. In addition, in measuring the underground biomass in October it was not possible to separate live and dead material, and it is possible that some of the treatment variation in the weight of root and rhizomes might have reflected differences in dead rather than live material.

5.5. Conclusion

From this experiment the recommended cutting regime for smooth bromegrass in North China is for an initial cut at anthesis, at a cutting height of 10cm, and subsequent defoliation at this height at two-month intervals.

Frequent cutting (one-month interval) decreased tiller population density, herbage accumulation and underground biomass for pure smooth bromegrass pasture. The results showed that frequent cutting adversely affected both underground storage organs and the root system. The height of cutting significantly affected the herbage accumulation, Combining the results of this and other experiments, cutting to 4 cm appears to be too severe, cutting to 30 cm is too lax, and a cutting height of 10 cm probably provides optimum conditions. Cutting did not so much affect total accumulation (which would have reflected environmental conditions) but acted instead to alter the balance between green material harvested and losses as dead material. Cutting resulted in higher green material accumulation and lower dead material accumulation in all seasons.

Regrowth in the following spring was not significantly affected by the cutting time, cutting height, or cutting frequency. However, in this study the last cut was taken by the middle of October, and the evidence is based on observation following only one year of treatment.

CHAPTER 6 GENERAL DISCUSSION

6.1 Introduction

The principal morphological changes occurring as a sward accumulates herbage mass after defoliation are the effects on extension growth, on the extent of tissue losses and on tiller numbers (Davies, 1988). Three experiments were reported in chapters 3, 4, and 5 separately. In this chapter the focus is on the general results and the differences between grass species which were used in the studies. Although the experiments were carried out in different locations and different times, and the treatments were not strictly comparable, the results refer to similar seasons of management in the South and North hemisphere, and managements considered to be within the range appropriate to each species. The topics considered are: sward structure changes after defoliation; the relationship between tiller weight and tiller population density; the effects of defoliation on pasture production; and the relationship between seasons and pasture management.

6.2. Sward structure changes in response to defoliation in ryegrass, prairie grass, and smooth bromegrass pasture

Combining the results of the three experiments, the numbers of leaves per tiller, dry weight per tiller, tiller population density and the rates of leaf appearance and the proportion of reproductive tillers in the swards are shown in Tables 6.1a, 6.1b and 6.1c. The values shown in Table 6.1a were derived from samples taken immediately before cutting or grazing at a series of defoliations over the main period of reproductive development for each species. The information shown in Table 6.1b relates to a single period of regrowth at each location, and includes the number of leaves appearing and the leaf appearance interval over each period. The data shown in Table 6.1c were derived from the marked individual tiller samples in each regrowth period in ryegrass and prairie grass swards, and the value for smooth bromegrass came from the uncut treatment sward.

TABLE 6.1a THE RESPONSES OF TILLER CHARACTERISTICS TO DEFOLIATION IN RYEGRASS, PRAIRIE GRASS AND SMOOTH BROMEGRASS PASTURE (AT REPRODUCTIVE PHASE)

	RYEGRASS (9Sep-7Dec, N.Z)			PRAIRIE GRASS (26Sep-12Feb, N.Z)			SMOOTH BROMEGRASS (May-July, CHINA)		
	Hard	Lax	F	Hard	Lax	F	Hard	Lax	F
Number of leaves (Leaves/Tiller)									
	3.1±0.2	3.1±0.2	NS	1.8±0.2	2.3±0.2	*	4.6±0.3	5.8±0.3.	**
Dry weight per tiller (mg/tiller)									
Leaf	15±2.1	27±2.1	***	37±2.3	61±2.3	**	----	----	--
Total	25±3.3	52±3.3	***	322-58.2	678±58.2	*	347±22	390±20	NS
Tiller population density (Tillers/m^2)									
	6160±40	5030±40	***	420±50	530± 50	*	840±60	1230±60	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

TABLE 6.1b THE RATE OF LEAF APPEARANCE AND THE NUMBER OF LEAVES AT THE BEGINNING (POST GRAZING) AND THE END (PRE-GRAZING) OF REGROWTH IN PERENNIAL RYEGRASS, PAIRIE GRASS AND SMOOTH BROMEGRASS.

	RYEGRASS (4 - 23 Sep, 1987)			PRAIRIE GRASS (26 Sep - 3 Nov, 1988)			SMOOTH BROMEGRASS (5 Jun - 5 July, 1989)		
	Hard	Lax	F	Hard	Lax	F	Hard	Lax	F
Beiginning (Leaves/Tiller)(Initial green leaves)									
	2.3±0.1	2.7±0.1	**	1.3±0.2	2.6±0.2	***	0.6±0.3	2.7±0.3	*
End (Leaves/Tiller)(Initial green leaves plus any new leaves appearing in the recording period)									
	4.3±0.1	4.3±0.1	NS	4.3±0.2	4.6±0.2	NS	6.0±0.3	7.3±0.3	*
Leaf appearance interval (Days/Leaf)									
	11.7±0.5	12.8±0.5	NS	12.1±1.1	18.5±1.1	***	5.7±0.3	7.3±0.3	*

1

TABLE 6.1c THE PROPORTION OF REPRODUCTIVE TILLERS IN RYEGRASS, PRAIRIE GRASS AND SMOOTH BROMEGRASS SWARD

	Reygrass			Prairie grass			Smooth bromegrass
	SEP.	OCT.	NOV.	OCT.	NOV.	JAN.	JUNE.
Hard	0.00	0.27	0.02	0.83	0.25	0.24	0.08&
Lax	0.00	0.48	0.50	1.00	0.55	0.19	

& : The average value of uncut treatment swards.

6.2.1. Leaves per tiller

As herbage accumulates during regrowth the number of intact new leaves on each tiller increases (Davies, 1988). On the ryegrass sward, before grazing the number of green leaves per tiller was approximately three under both hard and lax grazing, although the swards were in the reproductive phase in October and November (Tables 6.1a, and 6.1c). Hunt (1965), Alberta and Sibma (1968) reported that in vegetative perennial ryegrass swards the mean number of living leaves per tiller rarely exceeds three, and the production of the fourth leaf tends to be counterbalanced by the loss of the first one (Davies, 1971).

In the prairie grass pasture, however, the number of green leaves per tiller was consistently less than 3.0 and was less under the hard grazing (H) than under the lax grazing (L) treatment (Tables 6.1a and 4.1). Similarly, the number of green leaves was less under the hard defoliation (low stubble cutting) treatment than under the lax defoliation (high stubble cutting) treatment in the smooth bromegrass pasture, through substantially greater than 3.0 in both cases (Tables 6.1a and 5.2). Leaf appearance was continuous in all three species, but the evidence clearly indicates the greater sensitivity of leaf production to defoliation in the tall, erect species than in the relatively prostrate perennial ryegrass, probably because the greater population of reproductive tillers in the former swards limited the development of new leaves (Table 6.1c). The limited number of green leaves on prairie grass tillers appears to reflect the high proportion of flowering tiller in this species (Table 6.1c). New leaf production on reproductive tillers ceases once the flag leaf appears (Robson, et al. 1988).

In the smooth bromegrass sward, there were on average 8 green leaves per tiller in uncut treatments in July and September (Table 5.2), and 5 green leaves in cut treatments in the same month (Tables 6.1b and 5.2). Assuming that no intact leaves remain after defoliation, the ceiling yield can be expected to be attained after three leaf-appearance intervals in perennial ryegrass (Davies, 1971). However, the results from the smooth bromegrass study suggest a very different pattern of leaf survival and hence of leaf accumulation to ceiling yield after defoliation. More work is needed on this subject in prairie grass and smooth bromegrass.

The proportions of reproductive tillers were greater under lax grazing than under hard grazing, and greatest in October across treatments both in ryegrass and prairie grass swards (Table 6.1c). This result indicated that hard grazing depresses the development of reproductive tillers both in ryegrass and prairie grass swards. Compared to ryegrass, prairie grass had a higher proportion of reproductive tillers at a similar stage of growth (Table 6.1c). The proportion was lower in smooth bromegrass than in other grasses, but this may be because the grass was not at the peak reproductive phase when the records were taken.

6.2.2. The rate of leaf appearance

The number of leaves per tiller at the beginning (post grazing) and the end (pre-grazing) of regrowth, and the leaf appearance interval in perennial ryegrass, prairie grass and smooth bromegrass are shown in Table 6.1b. The leaf appearance interval was estimated from the ratio of the regrowth days to the number of total leaves appearing during regrowth. These results related to periods of regrowth following defoliation of three weeks, five weeks and four weeks for ryegrass, prairie grass and smooth bromegrass respectively.

The numbers of leaves were significantly less under hard defoliation than under lax defoliation in all three grass species at the beginning of regrowth (Table 6.1b). However this difference disappeared through the regrowth period in ryegrass and prairie grass but not in smooth bromegrass ($P<0.05$).

The leaf appearance interval was significantly less under hard defoliation treatments than under lax defoliation treatments in prairie grass ($p<0.001$) and smooth bromegrass ($P<0.05$), but the difference between hard grazing and lax grazing was not significant in ryegrass (Table 6.1b). The average leaf appearance interval was 14 days approximately in uncut swards of smooth bromegrass throughout the growth season from 5 April to 22 September, in contrast to the estimates of 5.7 and 7.5 days shown for low and high stubble swards respectively in June (Table 6.1b). This result suggests that cutting accelerated leaf appearance, but may also be explained largely by seasonal variation in the rate of appearance which are related to the the progression from vegetative to reproductive development (Robson, et al. 1988; Table 6.3c).

Increased light penetration to the base of the sward resulting from defoliation may stimulate the development of new leaves. The rate of leaf appearance depended upon the severity of grazing in the present study, hard grazing accelerating the rate of leaf appearance in prairie grass and smooth bromegrass (Table 6.1b). In swards maintained at low LAI, young leaves are expanded in high light, free from shade by old leaves, and so develop a high capacity for photosynthesis (Woledge, 1973, 1977, 1978). However, this effect may simply reflect the shorter sheaths through which leaves developed in the hard grazed pastures. The rate of leaf appearance was relatively insensitive to severity of defoliation in ryegrss, being approximately 12 days on both hard and lax grazed treatments (Table 6.1b).

Comparing the three grasses, both the rate of leaf appearance and the number of live leaves per tiller were greater in smooth bromegrass than in ryegrass and prairie grass (Table 6.1b). The response of leaf appearance rate to management in different grass species may be related to the grass morphology and physiology. For example, the fact that smooth bromegrass carried more live leaves than ryegrass and prairie grass may have enhanced light interception and carbohydrate accumulation, this higher energy assimilation resulting in turn in a high rate of leaf appearance. Evidence on the potential benefit of a high rate of leaf appearance and the retention of a large number of live leaves per tiller on the carbon economy of smooth bromegrass must await more detailed study.

6.2.3. Dry weight per tiller

The leaf and total herbage dry weights of individual tillers were greater under lax grazing than under hard grazing in ryegrass and prairie grass swards (Tables 6.1a, 3.2 and 4.2). The effect was mainly due to differences in stem weight in prairie grass where the weight ratio of stem to total herbage averaged 0.9 (Table 4.2). However in the ryegrass sward, the weight ratio of stem to total herbage was only 0.4 and the relative weight of leaf and stem was insensitive to defoliation treatment (Table 3.2).

On average, dry weight per tiller in the smooth bromegrass was not affected by cutting treatment (Tables 6.1a and 5.3a), but there were significant differences over the seasons (Table 5.3a and 5.3b). Eastin, et al., (1964) reported that tiller weights in smooth bromegrass increased significantly between successive growth stages of the initial spring growth, and with each successive initial harvest; also the weights per tiller was significantly different between varieties. For smooth bromegrass the effects of season were stronger than those of treatment (Table 5.3b).

6.2.4. Tiller population density

The responses in tiller population density to defoliation were different in different grass species. The tiller population density was substantially greater under hard grazing than under lax grazing in ryegrass pasture, but was greater under lax grazing than under hard grazing in prairie grass and smooth bromegrass pasture (Tables 6.1a, 3.1, 4.3, and 5.4).

These results support and extend other published evidence. In ryegrass, lax defoliation has been shown to reduce tiller population density (Appadurai and Holmes, 1964; Hodgson and Wade, 1978; Bircham and Hodgson, 1981), but the reverse occurred in prairie grass (Black and Chu, 1989) and smooth bromegrass (Smith, 1973). The results showed that the resistance to defoliation was poorer in prairie grass than ryegrass; more parent tillers were dead after defoliation, and regrowth was more dependent on daughter tillers in the prairie grass sward. For smooth bromegrass, the low tiller population in hard defoliation treatments may have been caused by the death of reproductive tillers. In lax defoliation treatments it is probable that some original tillers survived, and the cutting released apical dominance (Davlin, 1975), thus encouraging bud development (Table 5.4a). The species differences in response to defoliation clearly highlight the limitation of prairie grass as a species for grazed pasture.

6.3. The relationship between individual tiller weight and tiller population density

Yoda et al (1963), working with a variety of dicotyledonous species, showed that there was a formal mathematical relationship between the mean size of the surviving plants and the residual density at various stages in the development of a population. The number of surviving individuals is related to their mean weight as $W = CP^{-3/2}$, where W is the mean dry weight per plant, P is the density of plants remaining in the community and C is a constant which varies with the species. This law, initially applied to plant numbers and plant weights during a period of self-thinning, has been shown by Kays and Harper (1974) to apply equally well to tiller numbers and tiller weights in perennial ryegrass.

Following this self-thinning law, the relationship between ln (tiller weight) and ln (tiller density) in ryegrass, prairie grass, and smooth bromegrass dominated swards from the present study are shown in Figs 6.1a, 6.1b, 6.2a, 6.2b, 6.3a, 6.3b and 6.4. The results were derived from all treatments and throughout all experimental periods. Tiller weights are quoted as the total dry weight per tiller measured immediately before defoliation, and tiller population densities were measured at the same times. The -3/2 slope lines shown in those Figures are not fitted lines; they are simply included as a basis for comparison, super-imposed on each figure and keyed to the overall mean tiller weight and population density in each case.

The results for perennial ryegrass swards (Figs 6.1a and 6.1b) are in agreement with those of Kays and Harper (1974) and Hodgson et al.(1981) for undefoliated and continuously stocked swards respectively, and show new information in different conditions also. The data in Fig. 6.1a are clustered into winter (June), late spring (September and November) and summer (December) with the hard and lax grazing treatments shown in each case. The figure demonstrates distinct seasonal relationships between tiller weight and population density, reflecting changing environmental conditions, such as day length and light intensity for photosynthesis. The tiller population density was greater in December than in September and November, or June, and tiller weights were also lower in winter than in spring or summer.

Rotational grazing is characterized by marked fluctuations in LAI and in the rate processes involved in the uptake and loss of matter during each cycle of regrowth and defoliation (Parson, 1988). Within seasons, the slope of the weight/population relationship in perennial ryegrass across treatments was greater than the -3/2 slope line (Figs 6.1a and 6.1b), possibly indicating that the sward under hard grazing was not fully adjusted at the end of a regrowth period. Brougham (1956 and 1957) showed that perennial ryegrass swards defoliated to 12.5 cm took only 4 days to regain 95% light interception, whereas those defoliated to 7.5 and 2.5 cm took 16 and 24 days, respectively. Table 6.1b illustrates the distribution of tiller weight/density relationship within treatments (grazing severity) across seasons.

FIG 6.1A THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN RYGRASS SWARDS (MONTH)

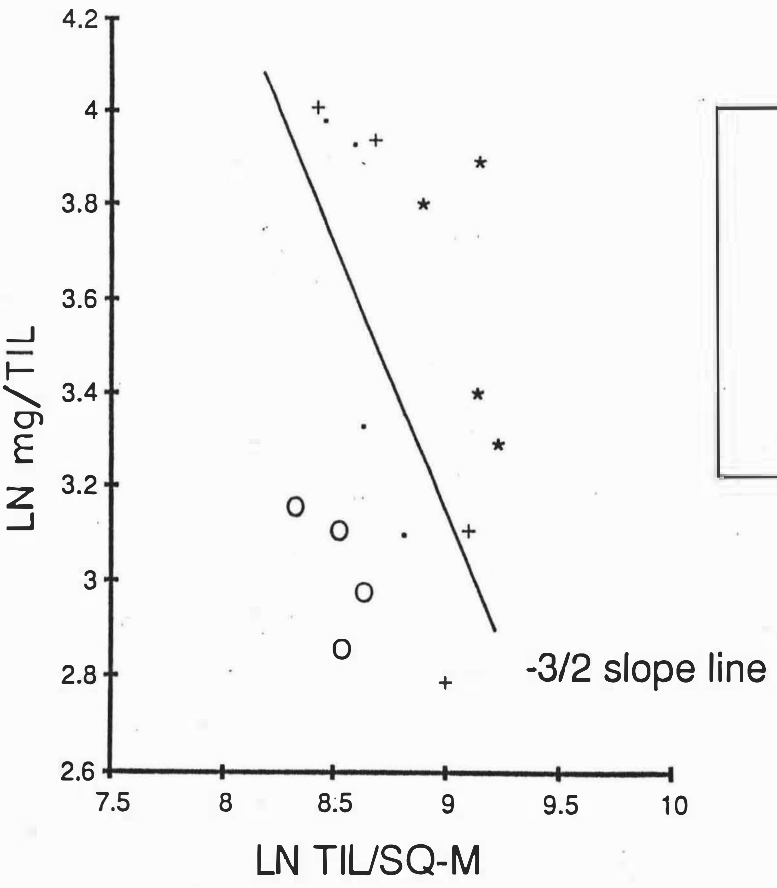
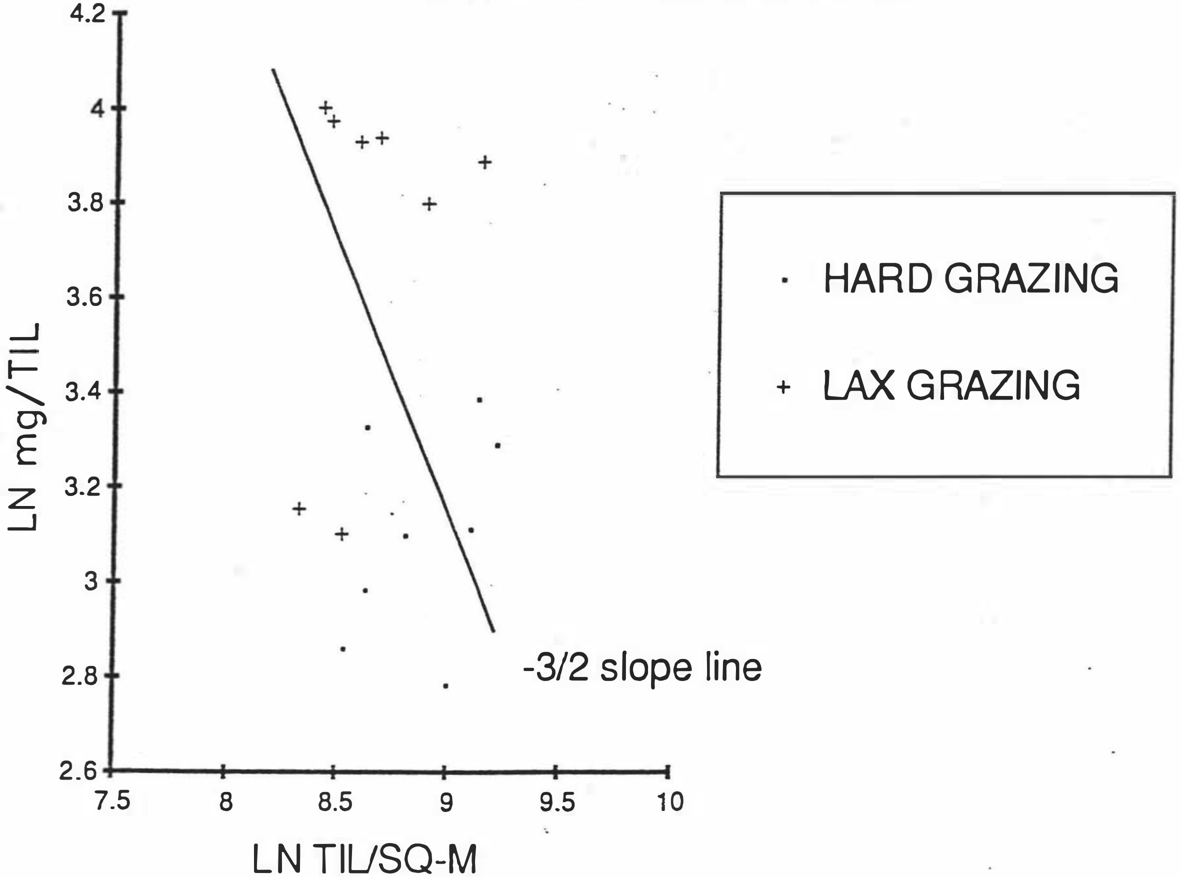


FIG 6.1B THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN RYEGRASS SWARDS UNDER HARD AND LAX GRAZING



The results for the prairie grass swards (Fig 6.2a) also indicated that the values for seasons were clustered separately, though the data is more limited. There is no indication of compensating changes between tiller weight and population density in any season. In each case the more severe grazing resulting in a reduction in both tiller weight and density, and the effect increased progressively with time.

The poor relationship between tiller size and population density for prairie grass may be explained by the poor survival rate of this species. The self-thinning law 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). The paddock was waterlogged in the winter and was very dry in spring and summer (section 4.5.3). Prairie grass has a poor persistence in waterlogged conditions (Eccles et al.,1990) and also decreases production in dry weather (Harris, et al., 1985). In this case, the competitive capacity of prairie grass in the mixed sward was poor. During the experiment the proportion of prairie grass (dry weight basis) decreased from 63% to 32% and from 83% to 58% under hard and lax grazing treatments respectively (Rugambwa, unpublish data, 1989), the balance of the sward being occupied by white clover and other grasses. When the population density was corrected by the proportion of prairie grass in the sward, the relationship between tiller weight and density fitted much more closely to the -3/2 slope line (Fig 6.2b). However, this correction takes no account of species differences in tiller weight.

The results for smooth bromegrass are shown in Figs 6.3a and 6.3b. Plots of tiller weight and tiller population density showed that treatment 1 (no cutting) values lay parallel to the -3/2 slope line and clustered separately from all other treatments (Fig 6.3a and Table 5.4a).

There was no clear distinction between cutting treatments, though treatment 4 and 6 generally had lower tiller weight than treatment 3 and 5. This result again indicates that all cutting treatments interfered with tillering in smooth bromegrass.

The graph of treatment means within periods (Fig. 6.3b) showed compensating changes between tiller population and weight, the two periods (Aug. and Oct.) with low tiller weights having relatively higher tiller populations. This result reflected the periods of active tillering. There was no clear relationship between tiller population and weight across treatments within periods, probably because cutting treatments were not synchronized.

FIG 6.2A THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN PRAIRIE GRASS SWARDS

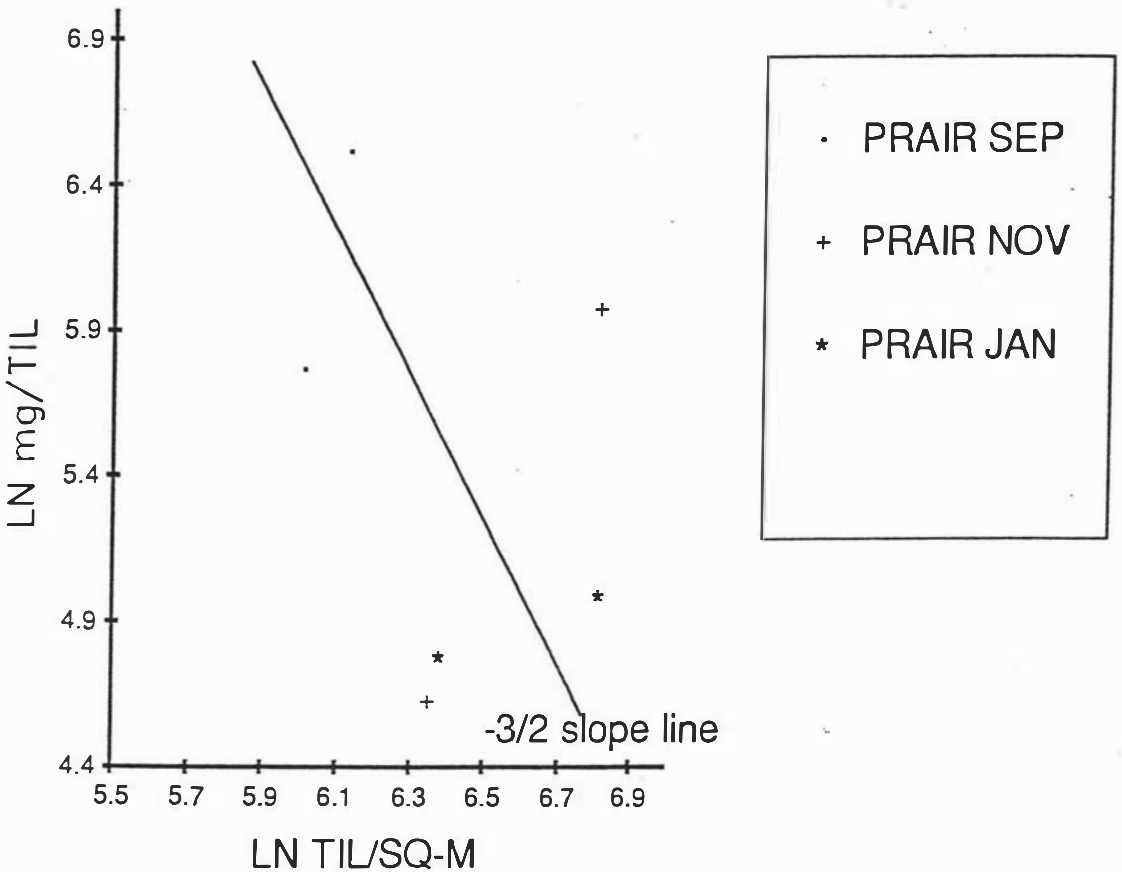


FIG 6.2b THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN PRAIRIE GRASS SWARDS (corrected)

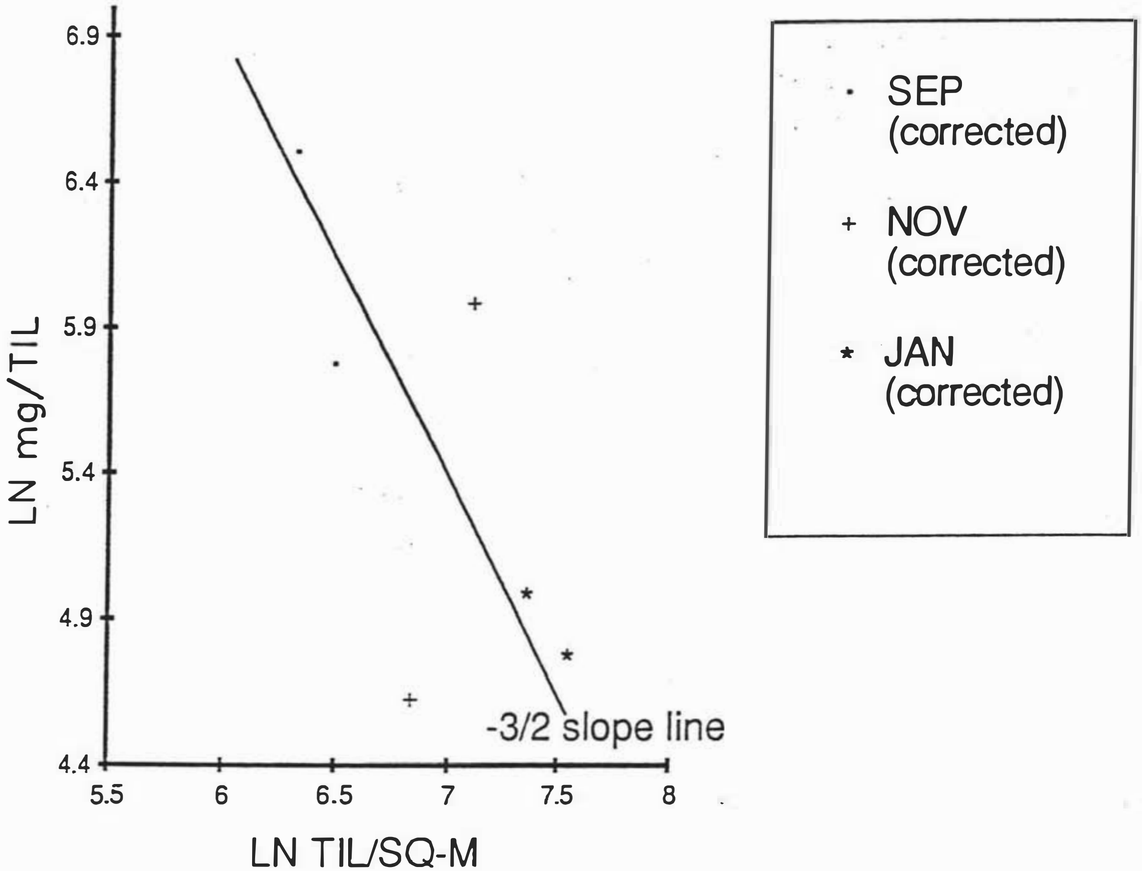


FIG 6.3a THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN SMOOTH BROMEGRASS

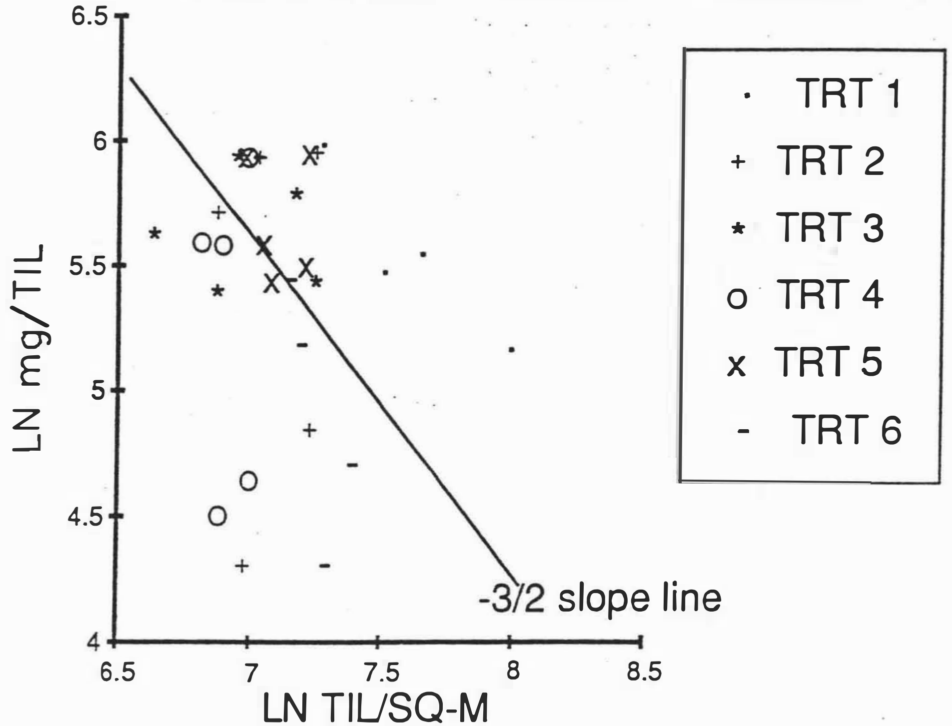


FIG 6.3b THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN SMOOTH BROMEGRASS

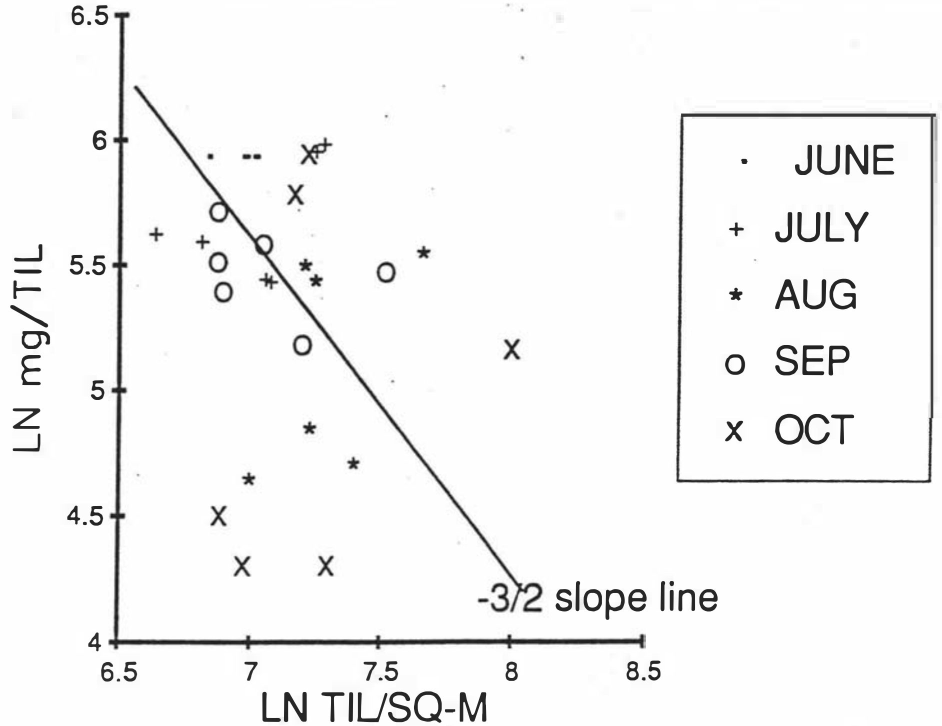
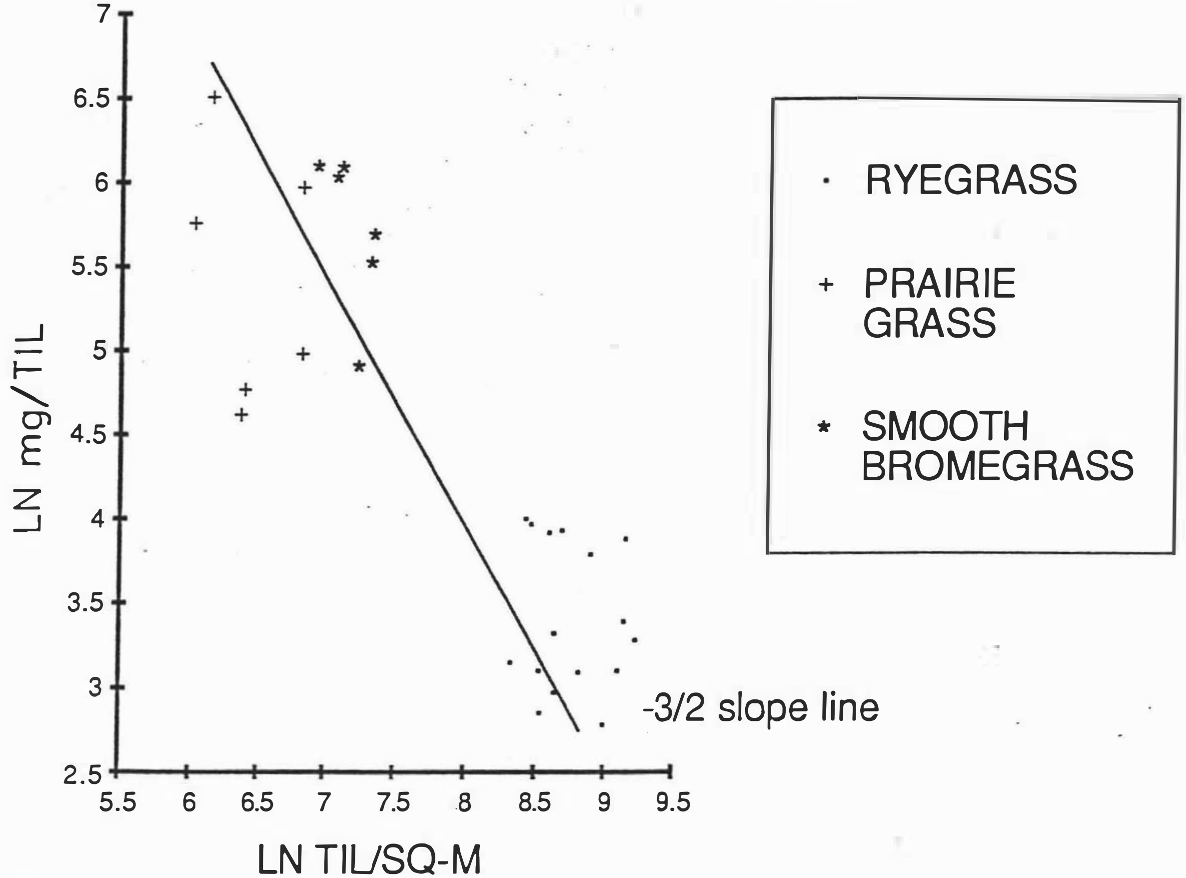


FIG 6.4 THE RELATIONSHIP BETWEEN TILLER DENSITY AND WEIGHT IN RYEGRASS PRAIRIE GRASS AND SMOOTH BROMEGRASS SWARDS



When the results for all these grass species are plotted together (Fig 6.4), the relationship between tiller population density (X) and individual tiller weight (Y) approximates to the -3/2 slope line both within smooth bromegrass and ryegrass swards, and between the two species. However, there was no functional relationship between tiller population and weight in the uncorrected prairie grass sward, tiller population density varying little despite substantial (two levels of magnitude) variation in tiller weights (Fig 6.4).

Comparing the three grass species, superficially it appears that smooth bromegrass and ryegrass occupy the same general weight and population relationship, though in clearly distinct sections, smooth bromegrass having greater tiller weight and lower tiller density than ryegrass. The responses to defoliation were similar, despite the very different morphology and development in the two species.

6.4. The effects of defoliation treatment on pasture production in swards of different species

Species may differ in relation to a number of factors which can influence regrowth after defoliation. In summary, the rates of growth, senescence and net production both for individual tillers and per unit area in ryegrass, prairie grass and smooth bromegrass pasture in similar seasons are shown in Table 6.2.

Table 6.2. THE RATES OF HERBAGE GROWTH, SENESCENCE, AND NET PRODUCTION PER TILLER(mgDM/Tiller/day) AND PER UNIT AREA(gDM/sq-m/day) IN RYEGRASS, PRAIRIE GRASS, AND SMOOTH BROMEGRASS SWARDS.

	Ryegrass (Sep - Dec, N.Z)			Prairie grass (Sep - Nov, N.Z)			Smooth bromegrass (Jun - Aug, China)		
	Hard graz	Lax graz	F	Hard graz	Lax graz	F	Hard Defo	Lax Defo	F
Individual tiller (mgDM/Tiller/Day)									
Total									
Growth	0.81±0.08	1.58±0.08	***	4.70±0.59	8.94±0.59	*	---	---	---
Senes	0.21±0.09	0.89±0.09	***	2.03±0.29	3.08±0.29	*	---	---	---
Net	0.60±0.08	0.69±0.08	NS	2.67±0.67	5.85±0.67	*	---	---	---
Leaf(Net)	0.39±0.02	0.29±0.02	*	0.24±0.13	-.37±0.13	*	---	---	---
Per unit area (gDM/sq-m/Day)									
Total									
Growth	4.6±0.37	6.7±0.37	**	1.99±0.30	4.48±0.30	*	---	---	---
Senes	1.3±0.39	3.9±0.39	**	0.83±0.13	1.61±0.13	*	---	---	---
Net	3.3±0.35	2.8±0.35	NS	1.16±0.35	2.86±0.35	*	13.18±2.25	7.05±2.25	***
Leaf(Net)	2.4±0.13	1.3±0.13	***	0.10±0.06	-.17±0.06	NS	-------	---------	---

* : p<0.05; ** : p<0.01; *** : p<0.001 ; NS : No significant difference.

In the perennial ryegrass sward, although the growth rate was greater under lax than under hard grazing, the effect was balanced by the greater senescence, so net production did not differ significantly between hard and lax grazing treatments, either per individual tiller or per unit area (Tables 6.2, 3.5, 3.6). However, net leaf production was significantly greater under hard than under lax grazing (Table 6.2). This result confirms, over a relatively long-term study, the results from earlier short-term observations (Bircham and Hodgson, 1983; Grant,et al., 1983). The rate of net herbage production is remarkably stable across a range of maintained sward conditions in this species, although the adaptive changes in tiller population, sward structure and the photosynthetic efficiency of leaf tissue and their contribution to stability may have differed in different circumstances (Hodgson, et al., 1981).

In contrast, the rate of net production per tiller was greater under lax grazing (L) than hard grazing (H) in prairie grass pasture (Tables 6.2, 4.7), because hard grazing severely depressed herbage growth rate but had little effect on rate of senescence. This result provided further explanation for poor persistence of prairie grass under hard grazing, and confirmed the results of previous studies (Baars, et al, 1978; Pineiro, et al, 1978; Black, et al, 1989). Rates of herbage growth from prairie grass were twice as great, both per tiller and per unit area, under lax as under hard grazing. The results shown in Table 6.2 again emphasis the dominant influence of the stem on tissue production in this species.

For smooth bromegrass, green herbage accumulation was greater in the hard defoliation than in the lax defoliation treatment (Tables 6.2, and 5.6). Rates of tissue turnover were not investigated, but inference from ryegrass results suggests that senescence would be high at 30 cm cutting height. Results from other published studies (Smith, 1973) suggested that cutting lower than 10 cm will depress growth rate severely enough to reduce green accumulation too, but there is a need to examine compensation in more detail in this species.

These differences between the grass species in response in pasture production to defoliation may be explained by differences in plant morphology and physiology. Compared with ryegrass, the stem was a much more important component of tissue accumulation than leaf in both prairie grass and smooth bromegrass, and tillering responses to head defoliation were substantially smaller. The characteristics of tissue turnover in prairie grass and smooth bromegrass need more study in the future.

6.5 The relationship between season and pasture management

A knowledge of the seasonal pattern of production of grass is of considerable practical value in agriculture. The effect of seasonal changes in the environment on the growth of grass swards is complicated by the progression from vegetative to reproductive development. Many grasses of importance to temperate agriculture show a marked seasonal pattern of production, even when provided with ample nutrients and irrigated to maintain the soil close to field capacity. However, both the seasonal pattern of production and the total amount harvested can be greatly modified by the defoliation management applied.

Although the net herbage production in perennial ryegrass was in general insensitive to treatment, the patterns of production reported in chapter 3 showed greater sensitivity and activity in spring and summer than in winter, and the main responses to grazing treatment also occurred in spring and summer. L'Hullier (1987c) reported that grazing management in spring but not autumn-winter can have large effects on pasture composition, density and performance on rotational dairy cow pasture.

Some workers have studied the effects of a crossover grazing regime on herbage production in ryegrass pasture (Bircham, 1981; Bircham and Hodgson, 1984; Grant, et al., 1983). Bircham and Hodgson (1984) investigated rates of growth and senescence in high and low mass swards which were respectively either grazed down to low mass (HL) or allowed to grow until a high mass had accumulated (LH). It was not possible to increase net production by manipulation of herbage mass under continuous stocking management, but net production can be reduced in the short term if a sward of high herbage mass and low population density is grazed hard (Bircham and Hodgson, 1984). In the present study, the change from hard to lax grazing in late spring gave a temporary increase in net herbage production, and a timely hard grazing of reproductive tillers following earlier lax grazing increased the rate of herbage production throughout the summer and autumn (Tables 3.5 and 3.6).

The switch grazing in late spring changed the structure and the physiology of the swards (Xia, et al., 1989). There was a temporary increase in tiller population density and a decrease in rate of senescence in the sward changed from lax to hard grazing, and a increase in rate of growth in the sward changing from hard to lax grazing (Table 3.6). Each reproductive stub in perennial ryegrass seems to be capable of producing two to three new tillers (Davies et al., 1981) and under favorable conditions the number of living tillers may double in 2 weeks. Present evidence (Matthew, 1990) demonstrates that a change from lax to hard grazing at the stage of reproductive development corresponding to anthesis enhances daughter tiller development and subsequent production potential. Rather than inhibiting the development of the secondary tillers, reproductive tillers may actually supply substrate and assist daughter tillers development provided that parent tillers are defoliated before seed filling commences.

L'Hullier (1987c) reported that on dairy cow pasture the herbage accumulation during September to December was lower for a 12-day rotation than the 30-day rotation.

These effects on herbage accumulation reflect the influence of grazing interval on the reproductive tillers. The 12-day rotation resulted in more frequent grazing of individual tillers and thus generally defoliation at an early stage of development which would limit the development of reproductive tillers. In contrast, rotational intervals (128 vs 96 vs 48 days) had no significant effect on herbage accumulation in autumn or winter (April to July) (L'Hullier, 1987c). Studies of this kind could usefully be extended to other grass species.

In the smooth bromegrass sward the timing of the first spring cutting affected persistence and production. Herbage accumulation and tiller population density were greater following an initial cut at anthesis (June) than after a cut when flowering was completed (July) (Table 5.5). Davies (1956) in his comparison of regrowth in an early and a late-flowering timothy showed the importance of the time of spring cutting in relation to stage of development. In China, Jia (1986) and Su (1988) suggested that the best time to cut for higher seasonal herbage yield and stand persistence is at heading or anthesis. Raese (1963) indicated that smooth bromegrass vigor and stand density were enhanced by cutting at the post bloom stage. Those experiments suggested that management at the reproductive stage of development was very important in smooth bromegrass pasture.

"Matua" prairie grass produces flowering heads in all seasons (Rumball, 1974). Black and Chu (1989) suggested that allowing replacement tillers to appear and then grazing to the height of these new tillers will improve persistence. This experiment showed that daughter tillers and stem play a important role in production of prairie grass (Table 4.8). Encouraging daughter tiller development and stem production should be a basic tactics of prairie grass pasture managements, however this experiment showed that the replacement of daughter tillers was not easy.

6.6. Conclusions

6.6.1

The three studies reported in this theesis, which were complete in themselves, demonstrate the potential importance of genotypic differences in phsiological and morphological responses to defoliation management in influencing the suitability of graminaceous plants for grazing systems. The evidence on adaptability in tiller population density, morphology and tissue turnover was derived from managements which were considered, superficially, to be appropriate for the three species involved, but they demonstrate clear differences in response patterns between species.

6.6.2

Rates of net herbage production in perennial ryegrass were relatively insensitive to hard grazing because of adaptive increases in tiller population density and compensating changes in rates of herbage growth and senescence. In prairie grass, tiller population density were reduced by hard grazing, and the concomitant depression in the rate of herbage growth per tiller was not offset by a reduction in the rate of senescence of mature tissue. Hard defoliation also depressed tiller population in smooth brome; however, green herbage accumulation was greater under hard than under lax defoliation because the rate of senescence of mature tissue was depressed to a greater extent than the rate of growth of new tissue under the latter treatment. For all sward types the impact of defoliation management on herbage senescence rate was a key determinant of net herbage production.

6.6.3

In general terms, perennial ryegrass demonstrated substantial genotypic plasticity in the adaptive changes in the balance between tiller population density and tiller size, reflecting the high tillering potential in this species. Rates of leaf production on main and daughter tillers consistently made the major contribution to tissue turnover. In contrast, prairie grass showed little adaptive response in tiller population density when tiller size was reduced, and the main component of tissue turnover was generaly stem material. Though tiller size was similar in smooth brome and prairie grass, adaptive changes in the balance between tiller size and population were more complete in the former species and leaf tissue made a greater contribution than stem to tissue turnover.

6.6.4

The effect of seasonal change in the enviroment on the growth of grass swards is complicated by progression from vegetative to reproductive development. In ryegrass pasture, there were advantages to spring and summer pasture production from a management which allowed seed head development to anthesis in spring, followed by hard grazing to enhance the subsequent development of new vegetative tillers. For smooth brome grass initial cutting at anthesis resulted in a greater rate of green herbage accumulation subsequently than did cutting one month later. In prairie grass the limited development of replacement daughter tillers contributed to the relatively poor performance of this species under hard grazing. The relationship between the timing and severity of defoliation and the physiological status of the plant was therefore critical in determining subsequent herbage growth in all three species, though there were clearly specific differences in effects on the balance between stem and new tiller production and the expansion of daughter tillers.

6.6.5

In view of the above differences between species in response to defoliation, no single recipe for management can be expected to hold true under any but the most limited circumstances. However, understanding of the limits of adaptive responses in the different species, particularly in tiller population structure and tissue turnover, provide an objective basis for planning pasture management. It is suggested that studies of the kind described in this thesis, preferably made under more controlled comparative conditions, would be an important component of evalution programmes for new plant genotypes.

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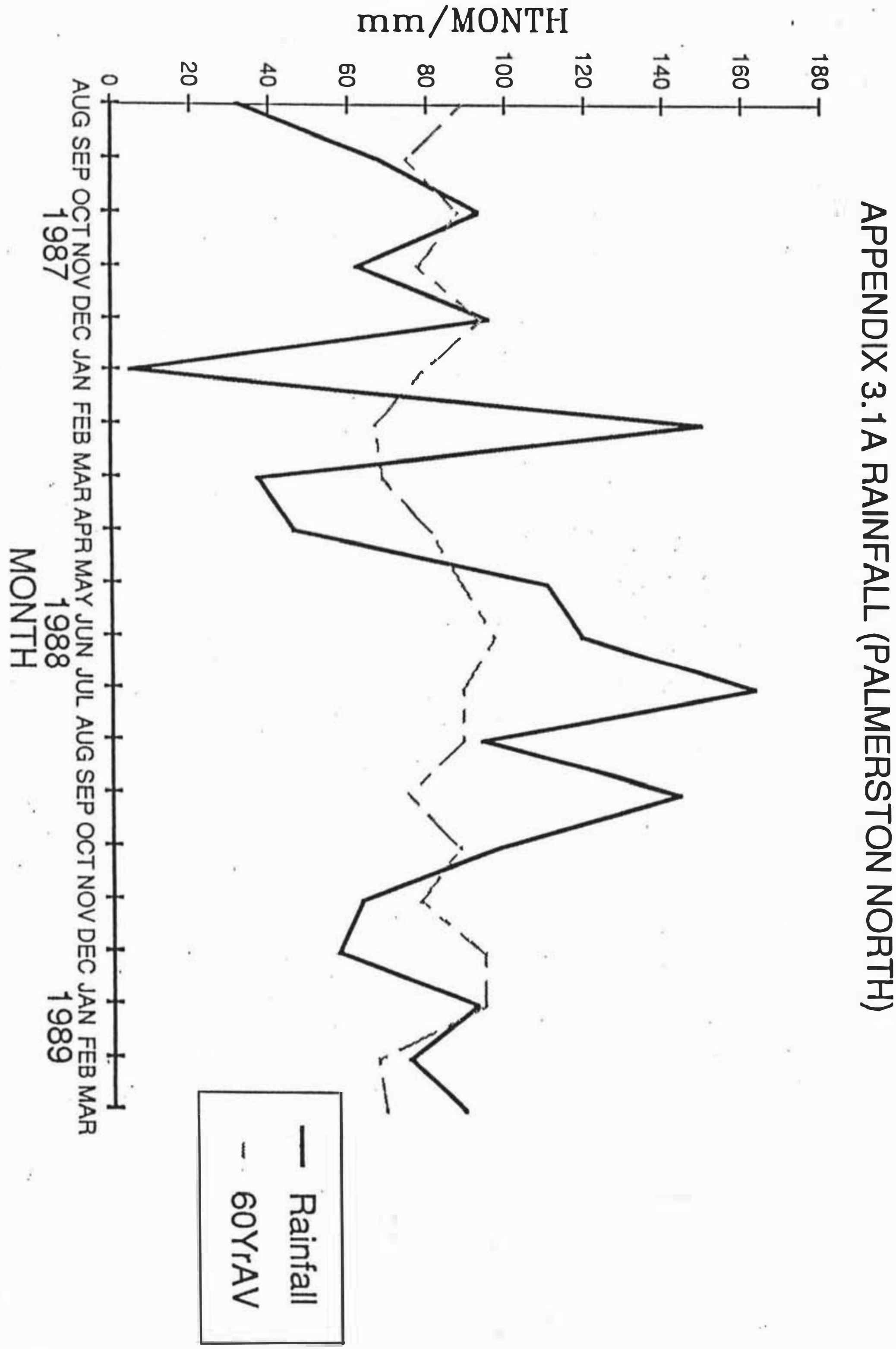
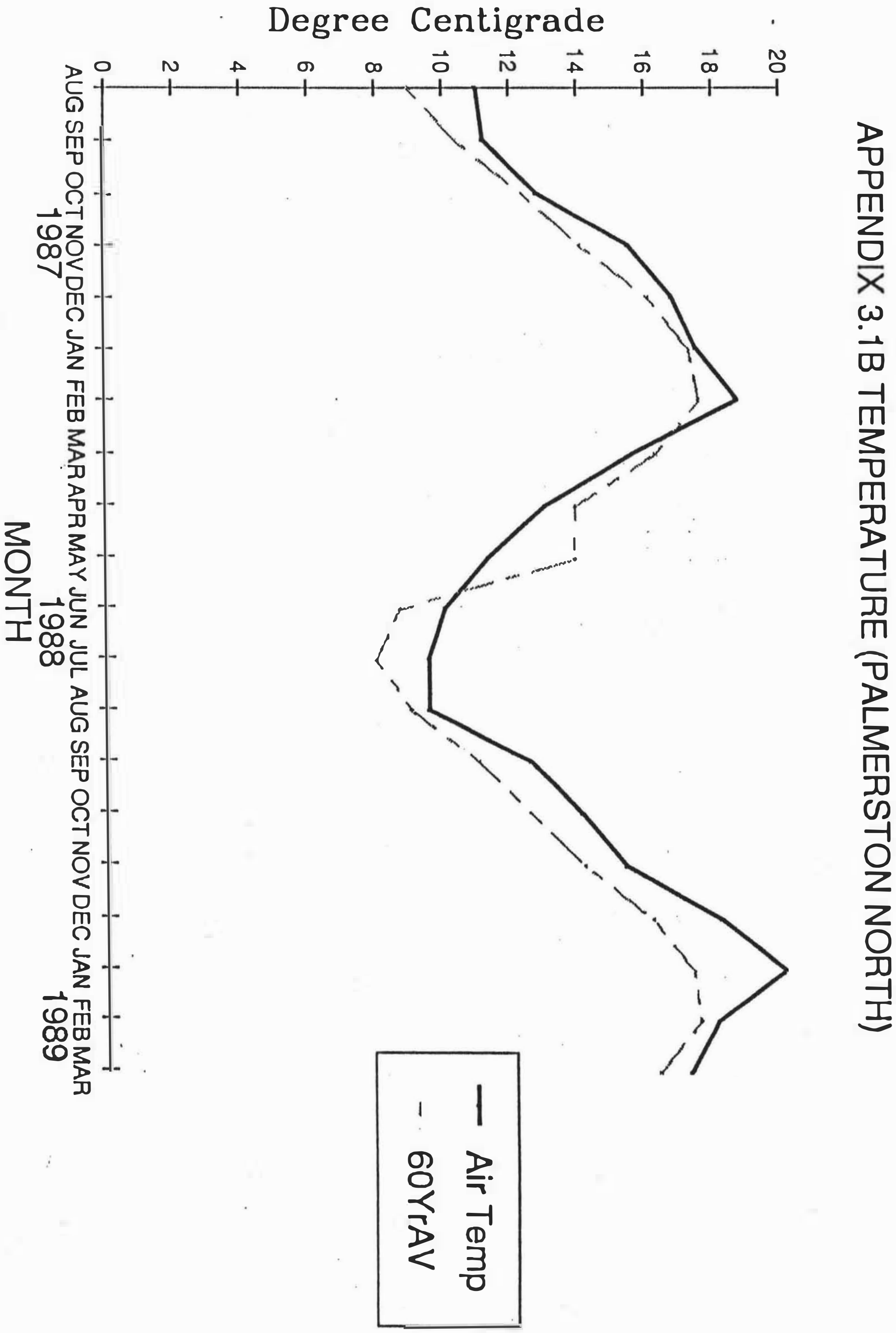
APPENDIX

Appendix 3.1a The rainfall per month from August 1987 to March 1989 (Palmerston North)



Appendix 3.2b The aveage air temperature from August 1987 to March 1989 (Palmerston North)



Appendix 3.2

Proceedings of the New Zealand Grassland Association 51: 119-122 (1990)

Tiller population and tissue turnover in a perennial ryegrass pasture under hard and lax spring and summer grazing

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ABSTRACT Plots of perennial ryegrass were grazed by sheep at 3 to 4-week intervals under hard (post-grazing herbage mass 1000 kg DM/ha) and lax (2000 kg DM/ha) management from October 1986 to August 1988. In early December 1987 treatments on half the plots were switched, giving 4 combinations of hard and lax grazing with 4 replicates. Tiller populations were consistently higher under hard than lax grazing. Net pasture and leaf production rates were also generally higher under hard grazing, because higher senescence losses compensated for higher rates of pasture growth under lax grazing. The switch from hard to lax grazing in late spring gave a transient increase in net pasture production, but the switch from lax to hard grazing at the same time resulted in a high tiller appearance and enhanced net leaf production over the summer. Management strategies to take advantage of this latter effect in pasture systems are discussed briefly.

Keywords Tiller population, tissue turnover, grazing management, perennial ryegrass

INTRODUCTION

Recent studies in the UK (Bircham & Hodgson 1983; Grant *et al.* 1983, 1988; Parsons *et al.* 1983; Parsons & Penning 1988) have shown that the rate of net herbage production (growth of new plant tissue minus senescence of mature tissue) in grazed ryegrass or ryegrass/white clover pastures is relatively constant across a range of pasture conditions and grazing managements. Similar principles appear to apply under New Zealand conditions (Bircham & Korte 1984), though long-term effects may be masked by seasonal changes in management (e.g. Korte *et al.* 1984; Sheath & Boom 1985).

The experiment described was carried out to study the influence of management and season on rates of tissue turnover in perennial ryegrass swards, and also provided the opportunity to investigate further the influence of spring management on subsequent pasture production. Evidence on the influence of tiller populations on pasture production is increasing (Sheath & Boom 1985). Korte *et al.* (1984) and Matthew *et al.* (1989) have recently provided evidence for the effect of pasture management during the reproductive phase on subsequent tillering activity and production potential.

METHODS

The experiment was carried out between October 1986 and August 1988 on a sward of perennial ryegrass (cv. Ellett) from which the clover had been removed by the use of picloram and 2,4-D. Individual plots 10 m x 10 m were grazed by sheep at 3-to 4-week intervals throughout under hard (H, post-grazing herbage mass 1000 kg DM/ha) and lax (L, post-grazing herbage mass 2000 kg DM/ha) managements. Grazing was normally completed within 2 days. On 9 December 1987 treatments on half the plots were switched, giving 4 combinations of hard and lax grazing with 4 replicates. Urea was applied at 15 kg N/ha every 3 weeks throughout the trial. Water was applied by sprinkler irrigation between November 1987 and January 1988 in limited quantities to maintain tiller viability. Over the 3 months rainfall was 159 mm, pan evaporation 469 mm, and water applied 100 mm.

Herbage mass was measured before and after each grazing from ground-level quadrat samples, and tiller population density at approximately monthly intervals throughout the trial from 30 cores per plot. Tissue turnover was measured at intervals from September 1987 to August 1988 (see Table 2), encompassing periods of spring, summer and winter growth on all pastures. Tissue turnover was estimated by the procedure of Bircham & Hodgson (1983) with 12 marked tillers per plot in 2 transects of 6, and tillers marked at 30 cm intervals. Results are based on randomised complete block analyses of variance on plot means.

RESULTS AND DISCUSSION

Effects of sustained hard and lax grazing

Tiller population densities were substantially higher under hard than lax grazing except during the final phase of the trial (HH vs LL, Table 1). Hard grazing usually resulted in higher rates of net pasture production than lax grazing, and particularly of net leaf production, because lower rates of growth were more than balanced by substantially lower senescence losses (Table 2). This result confirms the evidence from other, usually shorter-term studies under both rotational grazing and continuous stocking and from both ryegrass and ryegrass/white clover pastures (Bircham & Hodgson 1983; Grant *et al.* 1983; Parsons *et al.* 1983; Korte *et al.* 1984; L'Huillier 1987 a, b), and demonstrates the importance of losses to senescence and decomposition in the pasture economy. The lax grazing management involved higher levels of pasture cover before and after grazing than would often occur in sheep systems, but was nevertheless within the limits of comparable studies (Korte *et al.* 1984; Sheath & Boom, 1985). In the studies of Tainton (1974) differences in severity of grazing resulted in similar rates of green pasture accumulation in spring, but not in summer. However, grazing intervals were very long in Tainton's studies, except in the spring (Tainton 1974).

Table 1 Effect of grazing management on perennial ryegrass tiller population density (tillers/m²).

	Treatment				
	HH	HL	LH	LL	SE of mean
9 Dec 1987	8090	8940	5880	4520	410
18 Jan 1988	11180	7990	7980	6630	620
23 May 1988	8940	6160	8390	5090	260
4 Aug 1988	5130	4910	4670	3840	410

Senescence losses were consistently 20-25% of tissue growth rates in treatment HH, but declined from 65% to 45% of growth in treatment LL (Table 2). Bircham & Hodgson (1983) found that senescence losses did not fall below 20% of tissue growth rates, even in circumstances where grazing pressures were high enough to substantially depress pasture growth rates. Over the period of study from spring through winter the net rate of leaf production varied by a factor of only two. However, high rates of stem production in the spring, even on the hard grazed treatments, contributed to a substantially greater seasonal variation in net pasture production.

Effects of management changes in late spring

The switch from hard to lax grazing in late spring temporarily increased net herbage production (HL vs HH, Table 2). This effect reflected primarily enhanced production of stem and seed head (J.X. Xia, unpublished data), and was soon offset by increasing senescence losses and a fall in tiller density (Tables 1 and 2). The advantage in net leaf production was particularly short-lived, though tiller population densities on the switched treatments took almost 6 months to converge with those on the equivalent continued treatments (Table 1). This result is consistent with the observations of Bircham & Hodgson, Grant *et al.* (1988) and Sheath & Boom (1984).

The switch from lax to hard grazing in December (LH vs. LL) increased tiller population density (Table 1) by encouraging new tiller development from the stubs of grazed reproductive tillers (Korte *et al.* 1984; 1985). The effect was to increase both net pasture production and net leaf production in comparison with treatments HH and LL (Table 2), and these effects were sustained for a substantially longer time on treatment LH than on treatment HL (Table 2).

Table 2 Rates of pasture growth, senescence and net production, and of net leaf production (g DM/m²/day)

	Treatment				
	HH	HL	LH	LL	SE of mean
8 September - 6 December 1987					
Pasture growth §	4.6	5.1	5.7	7.5	0.42
Pasture senescence §	1.4	1.2	3.5	4.1	0.40
Pasture net production §	3.1	3.9	2.3	3.3	0.45
Leaf net production	2.3	2.5	1.5	1.1	0.15
9-27 December 1987					
Pasture growth	8.0	12.9	13.7	9.4	1.10
Pasture senescence	1.8	3.4	3.5	5.6	0.98
Pasture net production	6.2	9.6	10.2	3.8	1.32
Leaf net production	2.5	3.0	3.1	1.8	0.40
30 December 1987 - 14 January 1988					
Pasture growth	5.1	11.0	11.5	6.3	0.66
Pasture senescence	1.5	5.8	2.2	3.6	0.40
Pasture net production	3.6	5.2	9.3	2.7	0.69
Leaf net production	3.0	2.5	4.6	3.2	0.44
23 May - 5 July 1988					
Pasture growth	2.9	2.7	3.3	2.8	0.30
Pasture senescence	1.1	1.5	1.4	1.7	0.25
Pasture net production	1.8	1.2	1.9	1.1	0.23
Leaf net production	1.8	1.3	1.9	1.2	0.21

§ Failure to sum due to rounding errors

Management implications

Several studies demonstrate the influence of hard spring grazing in enhancing tiller population density and summer pasture production (L'Huillier 1987 a,b; Sheath & Boom 1985). However, the results of this study confirm the evidence of Korte *et al.* (1984) and Matthew *et* al. (1989) that summer and early autumn production can be further increased if reproductive tillers are allowed to develop to about anthesis by lax spring grazing, and are then removed by a switch to hard grazing to encourage the rapid development of new vegetative tillers.

This management is the opposite of that normally observed in grazing systems, where grazing can become increasingly lax through spring and early summer. It can be achieved most easily in systems involving early conservation, or in mixed grazing and conservation systems, and some topping managements may achieve the same result (Korte *et al.* 1984).

The stimulation of new tiller development in late spring may increase the risk of drought damage, a risk masked in this study by the limited use of irrigation, and confirmatory studies are required. However, in drought conditions there would be little direct benefit from the retention of a population of aged reproductive tillers. Moreover, there is evidence (C. Matthew, unpublished data) that, provided daughter tillers are formed before drought stress occurs, they may simply delay development of secondary and tertiary tillers until condtions become more favourable for growth.

CONCLUSIONS

Rates of net pasture and leaf production were usually greater under hard than under lax grazing, because greater pasture production under lax grazing was more than offset by higher rates of loss to senescence. However, in general terms these results provide further evidence that rates of net pasture production are relatively insensitive to sustained differences in grazing management.

There were advantages to summer pasture production from a management which allowed seedhead development to anthesis under lax grazing in spring, followed by hard grazing to enhance the subsequent development of new vegetative tillers. This pattern of lax followed by hard grazing is unusual in grazing systems, but can be achieved by judicious timing of conservation or pasture topping.

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Appendix 3.3

The ANOVA analysis of net leaf production($gDM/m^2/day$) in December 1987

General Linear Models Procedure

Class Level Information

Class	Levels	Values
TRT	4	11 12 21 22
BLOCK	4	1 2 3 4

Number of observations in data set = 16

General Linear Models Procedure

Dependent Variable: LNMD

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	6	8.6409	1.4401	1.25	0.3647
Error	9	10.3367	1.1485		
Corrected Total	15	18.9776			

R-Square	C.V.	Root MSE	LN Mean
0.455321	40.58487	1.071694	2.64062500

Source	DF	Type I SS	Mean Square	F Value	Pr > F
TRT	3	5.37281875	1.79093958	1.56	0.2658
BLOCK	3	3.26811875	1.08937292	0.95	0.4574

Source	DF	Type III SS	Mean Square	F Value	Pr > F
TRT	3	5.37281875	1.79093958	1.56	0.2658
BLOCK	3	3.26811875	1.08937292	0.95	0.4574

Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
11&12 VS 21&22	1	0.22325625	0.22325625	0.19	0.6697
12&22 VS 11&21	1	1.13955625	1.13955625	0.99	0.3452
12&21 VS 11&22	1	4.01000625	4.01000625	3.49	0.0945

General Linear Models Procedure

Least Squares Means

TRT	LNMD LSMEAN	Std Err LSMEAN	Pr > |T| H0:LSMEAN=0	LSMEAN Number
11	2.52500000	0.53584710	0.0011	1
12	2.99250000	0.53584710	0.0003	2
21	3.29000000	0.53584710	0.0002	3
22	1.75500000	0.53584710	0.0096	4

Appendix 3.4

Tissue dry weight per unit length (mg/mm)

Period	Reprod. stem	Vegetative stem	Mature leaf	Inmature leaf	Daughter tillers
25 Sep.- 23 Nov.88	---	0.2596	0.0777	0.0564	0.0473
7 Dec.- 29 Dec.88	0.3718#	0.1846	0.0717	0.0508	0.0473#
6 Jan.- 18 Jan.89	0.3718#	0.2263	0.0717	0.0508	0.0473#

Treatment differences significant (P<0.01)

Appendix 3.5a

THE STANDING HERBAGE MASS ESTIMATED

BY CUT QUADRATS IN SPRING (g/m^2)

TRT	9 SEP POST	28 SEP PRE	2 OCT POST	20 OCT PRE
HH	91.3	180.1	66.1	183.6
HL	---	---	---	---
LH	---	---	---	---
LL	242.3	277.2	188.2	308.1
S.E	6.1	22.0	18.9	12.1
F	**	*	*	**

* : P<0.05; ** : p<0.01; *** : p<0.001 ;

NS : No significant difference.

Appendix 3.5b

THE STANDING HERBAGE MASS ESTIMATED BY CUT QUADRATS IN SUMMER (g/m^2)

TRT	7 DEC POST	28 DEC PRE	29 DEC POST	6 JAN PRE	7 JAN POST	18 JAN PRE
HH	216.2	183.8	81.3	--	--	170.6
HL	118.9	--	--	229.9	373.4	312.6
LH	464.8	337.2	299.8	317.9	391.4	380.5
LL	441.9	394.3	275.1	--	--	548.2
S.E	42.3	21.7	19.3	41.0	48.8	34.6
F	***	**	**	NS	NS	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ;

NS : No significant difference.

Appendix 3.5c

THE STANDING HERBAGE MASS ESTIMATED BY CUT QUADRATS IN WINTER (g/m^2)

TRT	23MAY - 11JUN		15JUN - 5JULY		7JULY - 1 AUG	
	POST	PRE	POST	PRE	POST	PRE
HH	96.1	125.7	68.8	123.8	63.0	160.3
HL	240.9	233.3	233.3	266.8	189.0	266.6
LH	114.7	128.8	83.3	147.0	76.0	184.8
LL	292.9	262.9	262.9	309.2	233.9	293.1
S.E	26.1	28.6	29.1	19.8	24.6	15.8
F	***	*	**	***	NS	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ;

NS : No significant difference.

APPENDIX 4.1

THE ANOVA ANALYSIS OF LEAF GROWTH RATE PER UNIT AREA

General Linear Models Procedure

Class Level Information

Class	Levels	Values
BLOCK	4	4 5 9 10
TRT	2	1 2
PERIOD	3	1 2 3

Number of observations in data set = 24

General Linear Models Procedure

Dependent Variable: L

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	11	1.1174	0.1015	2.73	0.0494
Error(1)	12	0.4468	0.0372		
Corrected Total	23	1.56435673			

R-Square	C.V.	Root MSE	L Mean
0.714343	32.31796	0.192974	0.59711167

Source	DF	Type II SS	Mean Square	F Value	Pr > F
BLOCK	3	0.25931754	0.08643918	2.32	0.1269
TRT	1	0.46963311	0.46963311	12.61	0.0040
BLOCK*TRT(2)	3	0.03838697	0.01279566	0.34	0.7944
PERIOD	2	0.31584781	0.15792390	4.24	0.0404
TRT*PERIOD	2	0.03430222	0.01715111	0.46	0.6416

Tests of Hypotheses using the Type II MS for BLOCK*TRT as an error term

Source	DF	Type II SS	Mean Square	F Value	Pr > F
TRT	1	0.46963311	0.46963311	36.70	0.0090

(1) Error term for testing period effects and interaction.

(2) Error term for testing treatment effects.

Appendix 4.2a :

MEAN VALUES OF POST AND PRE-GRAZING HERBAGE MASS (kgDM/ha)

(From Rugambwa, et al 1990)

	LAX GRAZING(L)		HARD GRAZING(H)	
PERIOD	POST	PRE	POST	PRE
EARLY SPRING	2552(±200)	3829(±293)	1293(±466)	2256(±639)
LATE SPRING	3952(±671)	6074(±426)	3120(±345)	4814(±704)
SUMMER	3142(±404)	5163(±512)	2279(±276)	3883(±250)

Appendix 4.2b

MEAN VALUES FOR MORPHOLOGICAL COMPOSITION(% DRY WEIGHT) AND LEAF:STEM RATIO IN THE POST-GRAZING HERBAGE FROM LAX GRAZED(L) AND HARD GRAZED(H) PRAIRIE GRASS SWARDS, AVERAGED ACROSS ALL SEASON (From Rugambwa, et al 1990)

HEGBAGE COMPONENT	lax grazing(L)	hard grazing(H)	S.E	F
GREEN LEAF	17.4	24.9	0.93	***
GREEN STEM	32.1	35.8	0.66	**
DEAD MATERIAL	50.5	39.4	1.38	***
INFLORESCENCE	2.6	2.5	0.23	***
LEAF:STEM RATIO	0.7	0.8	0.04	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ;

NS : No significant difference.

Appendix 4.3

MEAN CHEMICAL COMPOSITION OF HERBAGE ON OFFER AND ANIMAL PRODUCTION IN HARD GRAZED (H) AND LAX GRAZED (L) PRAIRIE GRASS PASTURE (Rugambwa,et al 1990)

	H	L	S.E	F
DM digestibility (%)	67.3	64.3	0.17	***
OM digestibility (%)	73.1	70.7	0.18	***
Nitrogen (% of OM)	2.6	2.3	0.04	***
ME (MJ/kg DM)	10.4	10.0	0.03	***
Milk Yield (L/cow/d)	17.2	15.7	0.12	***
Liveweight change(kg/cow	+0.2	+0.2	1.04	NS
Condition score change	0.0	-0.1	0.04	*
Feed intake (kgDM/cow/d)	18.8	17.6	0.75	NS

Appendix 4.4

MEAN BOTANICAL COMPOSITION AND MORPHOLOGICAL COMPONENTS OF PASTURE ON OFFER (% of DM) IN HARD GRAZED(H) AND LAX GRAZED(L) PRAIRIE GRASS PASTURE (Rugambwa,1989)

	H	L	S.E	F
BOTANICAL COMPOSITION				
GRASS	61.0	71.9	1.80	**
WHITE CLOVER	16.5	12.2	0.94	*
OTHER SPECIES	22.6	15.9	1.86	*
MORPHOLOGICAL COMPONENTS				
LIVE LEAF	38.7	32.5	1.13	***
LIVE STEM	33.4	32.1	0.48	***
INFLORESCENCE	6.9	6.7	0.43	***
DEAD MATERIAL	28.0	36.4	1.19	***
LEAF:STEM	1.5	1.2	0.03	***

* : P<0.05; ** : p<0.01; *** : p<0.001 ;

NS : No significant difference.

Note: the green stem includes inflorescence.

Appendix 4.5.

PLANT POPULATION OF MATUA UNDER LAX AND HARD GRAZING (PLANTS/m^2)

(CHU, UNPUL.DATA)

PLANT SIZE	LAX	HARD
LARGE (50 TILLERS/PLANT)	6.0	3.8
MEDIUM(20-50 TILLERS/PLANT)	13.8	8.0
SMALL (20 TILLERS/PLANT)	9.8	11.3
TOTAL	29.5	23.0

Appendix 5.1

THE GREEN HERBAGE ACCUMULATION IN SUMMER (JUN-AUG) --- AN EXAMPLE OF ANOVA AND CONTRAST STATISTICAL ANALYSIS

General Linear Models Procedure

Class Level Information

Class	Levels	Values
TRT	6	1 2 3 4 5 6
BLOCK	4	1 2 3 4

Number of observations in data set = 24

Dependent Variable: G78 (GREEN HERBAGE ACCUMULATION IN JUN AND AUG)

Source	DF	Sum of Squares	Mean Square	F Value	Pr > F
Model	8	291311.3267	36413.9158	7.71	0.0004
Error	15	70871.1929	4724.7462		
Corrected Tota	23	362182.5196			

R-Square	C.V.	Root MSE	G78 Mean
0.804322	34.16695	68.73679	201.179167

Source	DF	Type III SS	Mean Square	F Value	Pr > F
TRT	5	275006.8021	55001.3604	11.64	0.0001
BLOCK	3	16304.5246	5434.8415	1.15	0.3611
Contrast	DF	Contrast SS	Mean Square	F Value	Pr > F
contrl vs rest	1	29243.7741	29243.7741	6.19	0.0251
2 vs 3	1	10679.9112	10679.9112	2.26	0.1535
4 vs 2&3&5&6	1	63320.6311	63320.6311	13.40	0.0023
3&4 vs 5&6	1	225102.8025	225102.8025	47.64	0.0001
3&5 vs 4&6	1	6504.4225	6504.4225	1.38	0.2590
3&6 vs 4&5	1	8235.5625	8235.5625	1.74	0.2065