STUDIES OF LATE SPRING GRAZING
MANAGEMENT IN PERENNIAL RYEGRASS
DOMINANT PASTURE

A thesis presented in partial

fulfilment of the requirements for the

degree of PhD in Agronomy at

Massey University

Christopher John Korte

1981

ABSTRACT

Two grazing experiments and a mowing experiment were conducted
to obtain information on the patterns of herbage accumulation and the
tiller dynamics of "Grasslands Nui" perennial ryegrass (*Lolium perenne*)
dominant pasture under a range of defoliation regimes during late spring/
early summer.   Defoliation intensity and defoliation interval were
defined in terms of plant physiological criteria, that is, light
interception and stage of reproductive growth.

The effect of four late spring/early summer grazing intensity
treatments, based on residual leaf area index (LAI), and two grazing
interval treatments, based on light interception, were compared in
the first grazing experiment.   Net herbage accumulation was greatest
when grazing was hard (LAI = 0.1-0.6) and least when grazing was lax
(LAI = 1.5-2.5) in late spring (16.5 and 13.6 t DM/ha respectively).
Grazing at 95% light interception reduced green herbage accumulation
compared with grazing two weeks after 95% light interception (14.0 and
15.8 t DM/ha respectively).   With lax grazing stemmy rank herbage
developed, whereas with hard grazing dense leafy pasture with a higher
ryegrass tiller density developed.   The grazing interval treatments
did not significantly affect ryegrass tiller density.

The second grazing experiment compared the effects of the timing
and intensity of spring grazings on herbage accumulation and ryegrass
tiller dynamics.   Interrupting reproductive growth of ryegrass at the
head emergence stage, compared with at the start of culm elongation,
did not increase herbage accumulation significantly although it resulted
in a higher proportion of stem and a lower proportion of lamina
accumulating.   As in the first experiment, hard grazing in late
spring increased herbage accumulation compared with lax grazing.
Hard grazing appeared to increase herbage accumulation by reducing
herbage death and decay, not by increasing herbage growth.

Ryegrass tiller density was greater in hard grazed swards than lax
grazed swards in summer.   This difference was mainly due to a higher
tiller appearance rate in hard grazed swards.   The difference was
still apparent in winter although all treatments were grazed similarly
during late summer and autumn.   Herbage accumulation was greater in

autumn where grazing had been hard the previous spring/summer, partly due to the higher tiller density.

Interrupting reproductive growth at the head emergence stage markedly reduced the density of vegetative tillers compared to interrupting reproductive growth at the start of culm elongation. Due to rapid tillering after interruption of reproductive growth this difference quickly disappeared.

The effects of the time of cutting to control reproductive development and the subsequent cutting interval on herbage accumulation and tiller dynamics of ryegrass pasture were examined in the mowing experiment. Herbage accumulation was reduced by more frequent mowing and where reproductive growth was prevented. Tillers present at the start of each rest period contributed most herbage because new tillers were relatively small. After the first mowing, new tillers were generally of similar weight to older tillers at the end of rest periods. It appeared that during summer, under conditions of adequate moisture and nutrients, the tiller dynamics of perennial ryegrass swards were little influenced by mowing frequency.

It was concluded that the objective for late spring grazing management should be to encourage leafy vegetative pastures and to prevent rank stemmy pasture developing. Dead culms in rank pasture reduced the digestibility of herbage and shaded photosynthetic tissue. Leafy swards had higher accumulation rates and a higher tiller density than stemmy swards. Methods of achieving leafy pasture on farms by combinations of hard grazing, forage conservation and mechanical topping are discussed.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

CHAPTER 6

LIST OF FIGURES

LIST OF PLATES

LIST OF APPENDICES

CHAPTER 1   INTRODUCTION

The New Zealand pastoral industry is based on approximately
9 million ha of sown grassland and approximately 5 million ha of
native and tussock grasslands (Harris, 1979).   Ryegrass (*Lolium sp*)
and white clover (*Trifolium repens L.*) have generally formed the base
for seed mixtures on these sown grasslands (Harris, 1968; Levy, 1970),
although in lower fertility hill country areas they may not always be
the most appropriate species (Saxby, 1948).   Rotational grazing, which
involves shifting stock from one farm paddock to another at varying
time intervals, is the accepted method of pasture management on the
dairy farm, and is receiving increasing acceptance on sheep and beef
farms (Smith and Dawson, 1976).

With rotational grazing, pastures are allowed to grow and develop
uninterrupted between grazings, whereas with set stocking, pasture is
continually accessable to grazing animals.   Compared with set stocking,
rotational grazing incorporates major and sudden "shocks" to the pasture
at each grazing which involve large and rapid changes in pasture structure
and composition.   There is a need to examine and assess the impact of
these "shocks" in terms of pasture parameters.

Although the advantages of rotational grazing in terms of pasture
production are difficult to demonstrate (Wheeler, 1962), the wide
adoption of this practice makes it important to determine optimum
rotations.   Based on his grazing studies (Brougham, 1959b, 1960a),
Brougham (1970) proposed the optimum seasonal grazing regime for
ryegrass/clover pasture at Palmerston North.   The question is whether
this proposal can be improved, and an attempt was made in this thesis
to define the optimum grazing regime in terms of plant physiological
criteria.

Responses to grazing regime may be explained in terms of changes in
botanical composition (Brougham, 1960a), or in terms of a plant
physiological parameter, such as light interception (Campbell, 1969).
By using plant physiological parameters to define grazing, instead of
pasture height or herbage mass, the influence of the physiological
parameter on herbage production can be determined directly.

Considerable research, reviewed by Brown and Blaser (1968), has highlighted the close relationship between leaf area, light interception, and pasture growth. As a result, pasture management systems have been proposed with the objective of maximizing light interception in order to obtain high annual yields of pasture (Donald, 1956; Brougham, 1956). On the basis of this previous work it was decided to critically test light interception as a criteria for grazing management.

Milthorpe and Davidson (1966) pointed out that it could be an over-simplification to base management systems only on leaf area and light interception. The growth rate of the sward, being the integral of the growth rates of the component shoots, is influenced by the rate of shoot production (tillering in grasses) as well as the growth rate of individual shoots. Reproductive development can greatly influence the growth rate of individual shoots, particularly in grasses (Lazenby and Rogers, 1962). Other plant physiological factors besides leaf area, in particular tillering and reproductive development of reygrass, were therefore reviewed (Chapter 2) and considered when designing experiments.

It was decided to concentrate research in the spring period when reproductive development of ryegrass influences herbage growth. Previous grazing studies have generally avoided considering reproductive development of ryegrass although various authors (Saxby, 1948; Hall, 1973) have stressed its importance.

Almost invariably seed stalk and roughage develop in pasture during the early summer. Saxby (1948) commented that an abundance of seed heads, combined with rank leaf growth and dry weather during the summer and autumn, was usually associated with relatively low rates of leaf production. If, however, pastures were prevented from flowering and setting seed, then the period of summer and autumn growth was apparently prolonged.

In the first experiment (Chapter 4) various grazing regimes were compared to test the importance of light interception as a criteria for grazing perennial ryegrass/white clover pasture during the period of reproductive growth. As the grazing practice in one season can affect herbage production in subsequent seasons (Brougham, 1960a)

this experiment was continued through the following autumn and
winter under a common grazing regime to determine residual effects.

As a consequence of the first years results, which showed that
reproductive development considerably influenced pasture growth,
reproductive development and light interception were used together
as criteria for defoliation by grazing in the second experiment
(Chapter 5).

In the final experiment (Chapter 6), where defoliation was by
mowing, the influence of tiller dynamics and tiller age on herbage
accumulation was examined.   The results of these experiments,
together with information reviewed on plant physiological factors
and pasture growth, are discussed in the final chapter (Chapter 7).
Some objectives for rotational grazing of perennial ryegrass/white
clover pasture in late spring are suggested.

CHAPTER 2   REVIEW OF LITERATURE

2.1   INTRODUCTION

The response of pasture to defoliation has been the subject of
considerable research and of several reviews (Donald, 1941; Jameson,
1963; Alcock, 1964; Davidson, 1968; Youngner, 1972; Harris, 1978).

The responses will be briefly reviewed with particular reference
to ryegrass/white clover pastures (*Lolium perenne/Trifolium repens*)
and then the physiological factors considered important in causing
these responses will be discussed.

2.2   RESPONSE OF PASTURE TO DEFOLIATION

Defoliation is normally defined in terms of frequency (the time
interval between successive defoliations), intensity (the degree of
defoliation or the proportion of herbage removed by each defoliation),
and timing, with particular reference to the season and the stage of
growth (Donald, 1941; Alcock, 1964; Harris, 1978). Usually herbage
dry matter production of both temperate and tropical pasture species
in many environments is reduced by more frequent and more intensive
defoliation but this is not always the case. Alcock (1964) observed
that while these responses occurred over a wide range of circumstances
there have been a number of conflicting observations, particularly with
regard to defoliation intensity. Also, because a greater proportion of
foliage escapes defoliation in prostrate species, erect growing species
suffer a greater reduction in yield from more intense defoliation than
prostrate species. The adverse effects of intense defoliation can be
reduced by decreasing the frequency of defoliation. The effect of
defoliation is greater at certain times of the year and it is possible
to control the botanical composition of pasture according to the timing
of frequent intensive defoliations (Jones, 1933).

2.2.1   Defoliation intensity

There are several reports where more intensive defoliation has
given higher hergage production than has less intensive defoliation for
ryegrass dominant swards (Reid, 1959, 1962; Appadurai and Holmes, 1964;

Frame and Hunt, 1971; Binnie and Harrington, 1972; Boswell, 1977;
Ollerenshaw and Hodgson, 1977) and for other species (Mortimer and
Ahlgren, 1936; Tesar and Ahlgren, 1950; Robinson *et al*, 1952;
Wilson and McGuire, 1961; Burger *et al*, 1962).   In contrast, Brougham
(1956) clearly demonstrated that more intensive defoliation reduced
herbage growth in a ryegrass/clover pasture, a result similar to the
general conclusion in reviews (Donald, 1941; Jameson, 1963; Alcock,
1964; Davidson, 1969; Younger, 1972; Harris, 1978).   Tayler and
Rudman (1966) concluded that greater utilization of herbage from the
base of the sward, rather than higher crop growth rates with closer
defoliation, appeared to be the main reason why the production of grass
increases so markedly when a sward is repeatedly harvested by defoliating
at a low level (down to about 3 cm from ground level) rather than at
a higher level.   It would therefore appear that it is necessary to
evaluate both herbage growth and herbage removal (by grazing or mech-
anical means) before the response to defoliation intensity can be
predicted.

2.2.2 Defoliation frequency

Although less frequent defoliation generally increases herbage
production from ryegrass/clover pasture (Brougham, 1959b; Reid, 1959;
Appadurai and Holmes, 1964; Agyare and Watkin, 1967; Boswell, 1977),
very infrequent defoliation of ryegrass swards has been reported to
reduce production (Collins and McCarrick, 1969; Le Clerc, 1976;
Bartholomew and Chestnutt, 1977; Kunelius and Calder, 1978).   Reasons
for this reduction will be discussed later (2.3.1.1.3).   For a given
defoliation intensity, the optimum defoliation frequency depends on
soil fertility (especially nitrogen status) and time of year.   At higher
fertility levels, more frequent defoliation is required to obtain the
maximum herbage production.   Bartholomew and Chestnutt (1977), for
example, found that when more than 600 kg N/ha was applied to a perennial
ryegrass pasture, less herbage was harvested annually when defoliation
was every 112 days than when defoliation was every 75 days.   At lower
levels of nitrogen fertilization, defoliating every 112 days produced
the greater yield.   Several experiments in the U.K. (Wilman *et al*, 1976
a, c; Bartholomew and Chestnutt, 1977; Chestnutt, *et al*, 1977) have
shown that cutting frequency has a less marked effect on herbage prod-
uction when the sward is vegetative than when the sward is reproductive.

The response of grass swards to less frequent cutting may not represent higher growth rates but rather greater efficiency of the harvesting process - the proportion of growth removed and measured as production. Anslow (1967) found that with a mower height of 4 cm above ground level, cutting every 3 weeks removed 50% of the crop while cutting every 6 weeks removed 65% of the crop. Even if the same rate of growth occurred in both swards, so that the crop after 6 weeks was twice as great as that after 3 weeks, 30% more herbage would have been harvested from plots cut every 6 weeks than from those cut every 3 weeks. To define the optimum defoliation frequency under grazing it is therefore necessary to measure growth from ground level (where regrowth largely originates).

2.2.3 Botanical composition

Harris (1978) reviewed the effect of defoliation on botanical composition of New Zealand pastures growing on high fertility soils and seeded with ryegrass/white clover. Infrequent and close defoliation generally results in a simple mixture dominated by ryegrass and white clover, while infrequent but less intensive defoliation allows the ingress of taller growing species such as Cocksfoot (*Dactylis glomerata*), Yorkshire fog (*Holcus lanatus*) and Praire grass (*Bromus catharticus*). Jones (1933) and Brougham (1960a) demonstrated that the timing of frequent and intensive grazings markedly influence the growth and survival of pasture species, changing the botanical composition and ultimately the herbage production of pasture. At Palmerston North, frequent hard grazings during the summer caused death of ryegrass, and led to white clover dominance (Brougham, 1960a). Subsequent yields obtained from the clover dominant pasture were severely reduced. It is therefore recommended (Brougham, 1970) that grazing be infrequent (every 3 to 8 weeks depending on season) and close (to leave a residual of at least 3 cm), except in summer when less intensive grazing is required. In this review further discussion of the effects of grazing on botanical composition is limited to where large changes in the balance between ryegrass and white clover occur.

2.2.4 Grazing experiments

In New Zealand pasture is usually utilized by grazing but because

of the high requirements of land, labour and finance associated with grazing experiments, much of the research into the response of pasture to defoliation, both in New Zealand and overseas, has been with mowing or cutting experiments. Besides defoliating pasture, grazing animals selectively graze, trample pastures, deposit dung and urine, and disperse seeds (Watkin and Clements, 1978). Mowing instantly and uniformly removes all herbage above cutting height. Both the botanical composition (Watkin and Clements, 1978) and the herbage production (Jones, 1959; Frame, 1966; Frame and Hunt, 1971) of grazed pasture is often significantly different to that of a mown sward.

Sears (1951) concluded that if reliable yields and botanical compositions were required, then pasture measurement was best carried out in actual grazing paddocks, or with a plot technique which incorporated the grazing animal or its effects to the full. Brougham (1959b, 1960a) used small paddocks ($200m^2$ and $270m^2$), fenced so that each could be grazed separately, to measure the effects of different grazing managements. Replicate paddocks were grazed at the same time and attempts were made to avoid fertility transference on or off the experimental area.

The difficulty of extrapolating from cutting experiments to grazing systems has been illustrated many times (Jones, 1959; Jackson and Williams, 1979). However, Frame (1976) suggested that it should be possible to establish suitable relationships within selected classes of sward, fertilization or grazing management to assist in predicting the yield response under grazing from the results of cutting trials. The results from mowing experiments can more readily be extrapolated in Europe where silage production and feeding are significant in farming, with up to four cuts per year being obtained from pastures (Brougham, 1977). Extrapolation of information from mowing experiments can also be useful in helping to explain responses obtained under grazing.

2.3 PHYSIOLOGICAL FACTORS INFLUENCING RESPONSES TO DEFOLIATION

Net pasture dry matter production is the result of a balance between two processes; growth of new herbage following defoliation and the death and decay of old herbage (Hodgson, 1979). Each of the factors influencing herbage growth and herbage losses will be considered separately and their relationship to the response of pasture to defoli-

ation (as described in 2.2) discussed.

2.3.1 Growth of herbage

The pattern of herbage regrowth after defoliation was shown by
Brougham (1955), and many other studies since (Brougham, 1959a;
Alberda and Sibma, 1968; Hunt, 1970a; Green *et al*, 1971; Leafe *et al*,
1974; Wilman *et al*, 1976d), to be sigmoid with respect to time. Three
phases are recognised (Brougham, 1955; Edelsten and Corrall, 1979):
an initial period when the growth rate increases exponentially with
time (the exponential phase); followed by a second period in which the
growth rate is constant at a maximum level (the linear phase), and
finally a third period in which the growth rate declines exponentially
until the ceiling herbage mass is reached (the asymptotic phase).
Brougham (1959a) presented a series of regrowth curves covering the
whole year for an irrigated ryegrass/white clover pasture at Palmerston
North. In the linear phase, the growth rate ranged from 10 kg DM/ha/
day in July to 135 kg DM/ha/day in late December, being highly correlated
with the seasonal fluctuation in solar radiation (r = 0.979). The
ceiling herbage mass (excluding herbage in the bottom 2.5 cm of the
canopy) was 1100 kg DM/ha in winter and 9100 kg DM/ha in December.

Pasture growth rate decreases in the asymptotic phase, despite
full light interception, until at the ceiling herbage mass photosynthetic
gains are equalled by respiratory and death losses. Hunt (1970a) showed
that the initial reductions in the rate of green herbage accumulation
that mark the beginning of the asymptotic phase were accounted for by
leaf death. Tainton (1974a) also showed that leaf accumulation became
negligible soon after full light interception was reached. Robson
(1973) has described how respiration increases during regrowth, there
being two components, maintenance and growth. The maintenance component
is proportional to plant biomass and therefore increases during regrowth.
The growth component is proportional to the rate of photosynthesis and
remains fairly constant after full light interception. Thus, the
asymptotic phase is caused by both leaf death and respiration increasing
in magnitude until they equal photosynthesis.

The physiological factors affecting pasture growth are considered
to be residual photosynthetic tissue, carbohydrate and other reserves,

recovery of root growth (and the associated effects on nutrient and water uptake), the number of residual shoots (tillers) and reproductive growth (Milthorpe and Davidson, 1966; Harris, 1978). Each of these factors will be reviewed separately with reference to ryegrass/white clover pasture where possible.

2.3.1.1 Residual photosynthetic tissue

Watson (1947) introduced the concept of leaf area index (LAI), defined as the ratio of leaf area to the area of ground it occupies. Brougham (1956) demonstrated that the growth rate of ryegrass/clover pasture was related to LAI. Brown and Blaser (1968) reviewed a wide range of experiments to examine the LAI concept, and concluded that in general increased LAI, or residual photosynthetic tissue, provided greater light interception and hence accelerated growth rate, other environmental factors being favourable. Once all photosynthetically active radiation is intercepted there is no further increase in growth rate with increased LAI, and eventually the growth rate declines in the asymptotic phase.

Brougham (1960b) examined a range of crops and found that daily growth rates at full light interception were more closely related to the amount of chlorophyll (from leaf and non-leaf) per unit area of land (r = 0.912) than with the LAI (r = 0.815). Although stems, petioles, leaf sheaths and inflorescences intercept light and participate to various degrees in photosynthesis, their surface area has generally been ignored when calculating LAI. For leaf sheath this is reasonable since Leafe *et al* (1979) showed that in a grazed ryegrass sward, where sheath contributed 38% of the leaf and sheath area, sheath only fixed 5% of the carbon. The grass inflorescence however, is very active photosynthetically (Ong and Marshall, 1975; Ong *et al*, 1978a) but its contribution to herbage production in grazed swards is not known. A further problem with the LAI concept is that younger emerging leaves are generally more photosynthetically efficient than older expanded leaves (Jewiss and Woledge, 1967; Woledge and Jewiss, 1969; Leafe *et al*, 1979). For example, Leafe *et al* (1979) showed that expanding leaves fixed twice as much CO_2 per hour as fully expanded leaves when compared on a leaf area basis. Despite these problems many workers have obtained a good relationship between LAI and pasture growth rate.

2.3.1.1.1 "Critical" LAI

Brougham (1958a) used the term "critical LAI" to describe the LAI required to intercept 95% of the incident light at noon, the LAI where maximum growth rate was also reached (Brougham, 1956).   A different term, "optimum LAI", was used by Australian workers (Davidson and Donald, 1958; Stern and Donald, 1961, 1962; Black, 1963) to describe the LAI where maximum growth rate was reached, further increases in LAI resulting in reduced growth rate.   McCree and Troughton (1966) investigated the growth of white clover in controlled environment cabinets and found that if only live material was considered an optimum LAI of 3 was apparent.   However, when dead material was included, no optimum was apparent and the maximum photosynthetic rate was sustained from the critical LAI (3) to the ceiling LAI (10).   They concluded that the declining growth rate above the optimum LAI observed in field experiments was partly attributable to the failure to include material which dies between harvests.   It remains debatable whether there is a clearly defined optimum LAI in some field crops (Milthorpe and Davidson, 1966; Harris, 1978), but in ryegrass dominant pasture, there is a clearly defined linear phase of growth (Brougham, 1955, 1959a) although during vegetative growth it may be very short (Alberda and Sibma, 1968; Leafe *et al*, 1974).

The LAI required for maximum pasture growth rate, the critical LAI, depends mainly on leaf angle, latitude, and time of year. Grasses generally have more erect leaves than clovers and require a greater LAI to intercept a given amount of light (Brown and Blaser, 1968). For example, Brougham (1958a) found that in mid-summer at Palmerston North the critical LAI for a white clover pasture and a perennial ryegrass pasture was 3.5 and 7.1 respectively, illustrating the effect of leaf angle.   A mixed ryegrass/clover pasture (approximately 50% grass and 50% clover) had a critical LAI of 4.5.   In winter, both the solar elevation and the light flux decline (Barry and Chorley, 1971), the decline being greater at higher latitudes.   As a result a smaller LAI is required to intercept noon sunlight in winter (Brougham, 1958a; Stern and Donald, 1962).   For example, Brougham (1962) found that the critical LAI of a white clover sward was 0.7 in winter and 3.25 in late spring at Palmerston North.

The relationship between LAI and pasture growth rate explains the general responses of pasture to defoliation. The reduction in herbage accumulation with more intensive defoliation (Donald, 1941; Alcock, 1964; Harris, 1978) reflects the lower residual LAI and the associated depressed growth rate. Similarly, more frequent defoliation can increase the proportion of time pasture remains below the critical LAI, and thereby the growth rate. Also, the observation that less frequent defoliation will reduce the adverse effects of intensive defoliation can be explained in terms of LAI. Brougham (1955) suggested that the maximum production of herbage could be obtained if pasture was kept in the linear phase of growth, for example in spring, by defoliating when 30-40 cm high to leave a stubble of 12 cm. However, continually defoliating at a low intensity reduces tillering and stubble quality.

2.3.1.1.2 Stubble quality and LAI

Hunt and Brougham (1967) cut a perennial ryegrass sward weekly, leaving sufficient residual herbage (16 cm) to intercept 90-95% of incident light at noon. The proportion of leaf lamina in the stubble declined at each cut (from 32% to 10% of residual herbage after 7 weeks) and the proportion of senescent and dead material in the stubble increased (from 51% to 72% of residual herbage). Tiller density initially increased to $12000/m^2$ in the first week but subsequently declined to $6400/m^2$ after 7 weeks. Both Jackson (1974) and Ollernshaw and Hodgson (1977) also observed considerable accumulation of dead and senescing plant material in the stubble of ryegrass swards leniently defoliated. The effect of cutting perennial ryegrass at a constant height was to raise the level of the lowest green leaf blade towards the cutting height (Jackson, 1974) so that with lenient defoliation, most of the stubble was of low photosynthetic efficiency. Cutting higher also induced basal internodes to elongate, so that the apices were above ground level, and aerial tillering occurred. Where similar residues accumulated in grazed pastures, a poor stubble quality also occurred. To obtain the advantages of higher growth rates associated with higher residual photosynthetic tissue, and also maintain stubble quality, both Jackson (1974) and Ollernshaw and Hodgson (1977) suggested periodic close defoliation of leniently defoliated pasture. A minimum frequency of 9 weeks for such close defoliations was indicated by Jackson's work. Tainton (1974b) actually found that in autumn alternate lax and hard grazing out-

yielded hard grazed pasture by 63%.

2.3.1.1.3 Defoliation interval and LAI

LAI has been used as the criteria for defining defoliation
interval in several studies.   Sheard and Winch (1966) found that if
bromegrass (*Bromus inermis*) or cocksfoot (*Dactylis glomerata*) swards were
defoliated at the critical LAI they gave a higher annual yield than more
frequent defoliation (at 70% light interception).   Wilson and McGuire
(1961) obtained a similar result from three different pasture mixtures.
Tainton (1974b) compared two defoliation intervals; grazing at the
critical LAI and grazing two weeks after the critical LAI was reached.
The average daily growth rate was reduced by delaying defoliation
beyond the critical LAI.   In contrast, Mitamura (1972) and Terai (1977)
found that delaying defoliation of cocksfoot swards beyond the critical
LAI increased herbage production.   Maximum yield was obtained by
defoliating each time the ceiling LAI was reached, and both more frequent
defoliation (each time the critical LAI was reached) and less frequent
defoliation (each time the ceiling herbage mass was reached) reduced
production.   Very infrequent defoliation reduces production because
the sward enters the asymptotic phase and actually makes no net growth
after the ceiling herbage mass is reached.   The optimum stage for
defoliation is not apparent from these studies, being either at the
critical LAI (Tainton, 1974b) or at the ceiling LAI (Terai, 1977).

2.3.1.2 Reserves for growth

Carbohydrate and other reserves have been considered to have an
important role in influencing pasture growth.   Graber *et al*, (1927)
advanced the hypothesis "that new top growths, especially in the early
stages, are initiated and developed largely at the expense of previously
accumulated organic reserves".   A similar view was expressed by Weinmann
(1948) in his review of the role of reserves in grasses, but May (1960)
pointed out that, a reduction in the amount of carboyhdrate present in
roots and stubble after defoliation might be largely caused by
continued respiration, without there being any causal role of the
reserves in initiating regrowth.   From subsequent work (Davidson and
Milthorpe, 1966a, 1966b; Booysen and Nelson, 1975) it is apparent that
both photosynthesis by residual leaf and reserve carbohydrate contribute

energy to regrowth in grasses, and that more severe defoliation
increases the dependence of regrowth on stored energy.   Although
reserves may influence regrowth of grasses for 2-7 days after defoliation,
in New Zealand, their role is not generally considered to be significant
for ryegrass/white clover pasture (Harris, 1978).

2.3.1.3 Water and nutrient uptake

Besides reducing herbage production, more intensive and more
frequent defoliation generally reduces the root growth of pasture plants
(Weinmann, 1948; Davidson, 1978) and this is true of both ryegrass
(Evans, 1971) and white clover (Butler *et al*, 1959; Chu and Robertson,
1974).   As a result of defoliation (and a less extensive root system)
nutrient uptake (O'Brien *et al*, 1967) and water uptake (Evans, 1977)
is reduced.   In situations where there is moisture or nutrient stress,
reduction in the size of the root system is likely to reduce herbage
production and to increase plant susceptibility to drought and root
eating insect pests (Davidson, 1978).   A further effect of defoliation
on white clover is reduced nitrogen fixation and a loss of root nodules
(Moustafa *et al*, 1969; Chu and Robertson, 1974).

The production and botanical composition of ryegrass/clover pasture
can be markedly influenced by grazing intensity during summer.
Brougham (1960a) grazed a "Grasslands Manawa" ryegrass/cocksfoot/red
clover/white clover pasture either closely (from 7.5 cm to 2.5 cm) or
laxly (from 18 cm to 7.5 cm) during summer (December, January, February).
Close grazing reduced pasture production both during summer (2.5 t DM/ha
compared with 4.4 t DM/ha), and in the subsequent nine months (6.3 t DM/
ha compared with 9.1 t DM/ha).   Similarly, Tainton (1974a) found that
a perennial ryegrass-white clover pasture grazed laxly and infrequently
during a dry summer produced 20% more herbage than a more closely
grazed treatment.   The need to avoid very intensive defoliation in
summer (Brougham, 1970) also depends on moisture regime.   Appadurai
and Holmes (1964) found that cutting a perennial ryegrass-white clover
pasture at 2.5 cm produced 20-41% more herbage than cutting at 7 cm when
the soil was maintained at or near field capacity.   Under a dryer
moisture regime there was no significant difference between cutting
heights and a consistent tendency for close cutting to give a lower
yield than more lenient cutting.   In the experiment of Brougham (1960a),

frequent hard grazings in summer resulted in widespread death of all
sown species except white clover, and since white clover grows more
slowly than ryegrass at lower temperatures (Mitchell, 1956), this
largely explained the reduction in herbage production during the
subsequent cooler nine months. The clover content of the sward,
measured as percentage ground cover and herbage harvested, was little
influenced by cutting height in the experiment of Appadurai and Holmes
(1964). "Grasslands Manawa", the ryegrass used by Brougham (1960a) is
less drought tolerant than "Grasslands Ruanui" (Harris and Thomas, 1970),
and death of more drought tolerant ryegrass cultivars, such as "Grass-
lands Nui" (Sheath *et al*, 1976), is less likely.

2.3.1.4 Reproductive growth

The rate of herbage growth in perennial ryegrass swards, liberally
supplied with mineral nutrients and water, is most rapid during the
period of reproductive growth in late spring (Anslow, 1965; Anslow and
Green, 1967; Alberda and Sibma, 1968; Leafe *et al*, 1974; Behaeghe,
1978). Even when ryegrass swards are harvested frequently, and the
development of inflorescences is largely intercepted, the rate of
herbage production still shows a marked peak in late spring (Anslow
and Green, 1967). In ryegrass/white clover swards, the decline in
ryegrass production during summer is compensated to some extent by an
increase in clover production (Brougham, 1959a; Rickard and Radcliffe,
1976). Depending on the degree of ryegrass dominance the period of
most rapid growth of irrigated ryegrass/clover swards can vary from
late October, for ryegrass dominant swards, to late December, for clover
dominant swards (Rickard and Radcliffe, 1976).

In the following sections the requirements for reproductive growth,
the pattern of reproductive growth and the physiological reasons for
higher growth rates during reproductive growth of ryegrass will be
examined. The effects of defoliation on reproductive growth, in
relation to yield, will then be examined.

2.3.1.4.1 Requirements for reproductive growth

The change from vegetative growth to reproductive growth is
determined by local conditions of temperature and light; the requirements,
which vary greatly with species and variety, being closely related to

the climatic or agronomic origin of the plant material (Cooper, 1960).
Three stages in the reproductive development of perennial ryegrass are
recognised: floral induction, during which apical meristems become
capable of responding to the photoperiodic stimulus; floral initiation,
in response to an appropriate photoperiod; and inflorescence development.
Exposure to winter conditions of short days and cold is obligatory for
floral induction in perennial ryegrass (Cooper, 1960; Aitken, 1966) and
each tiller must be induced independently, since there is no translocation
of the induced state to later formed tillers (Calder, 1966). The
transition from vegetative to reproductive growth, inflorescence
initiation, is broadly controlled by day length (Evans, 1964), and is
first evident from morphological changes in the growing point of the
tiller (Cooper, 1951; Barnard, 1964). First the growing point elongates,
and then spikelets begin to develop in the axils of the leaf initials.
Soon after initiation, stem elongation begins, and head emergence normally
occurs about 6 weeks after initiation (Cooper, 1952; Aitken, 1966).

The rate of development of initiated inflorescences is mainly
controlled by temperature, light intensity, and nutritional status
(Evans, 1964). The considerable range in heading date between ryegrass
cultivars depends mainly on the length of the obligatory exposure to
winter conditions (Cooper, 1952; Aitken, 1966) but inflorescence
development may be hastened in later heading cultivars by the higher
temperatures in later spring. Keatinge *et al* (1979) have suggested
that early and late cultivars have a similar accumulated temperature
(Degree days) between initiation and heading. Few tillers appearing
after early September become reproductive in "Grasslands Ruanui" perennial
ryegrass at Palmerston North (Wilson, 1959; Hill and Watkin, 1975).
Floral initiation of "Ruanui" occurs in late August and September, and
head emergence begins between late October and early November (Wilson,
1959; Brougham, 1961; Hill, 1971).

2.3.1.4.2 Physiological differences between vegetative and reproductive swards

Several reports (Alberda and Sibma, 1968; Leafe *et al*, 1974;
Behaeghe, 1974, 1978; Deinum, 1976; Woledge and Leafe, 1976;
Alberda, 1977; Sibma and Louwerse, 1977) have suggested reasons for
the higher growth rates of irrigated and well fertilized ryegrass swards

in spri..g compared with summer.   If nearly all tillers are reproductive
at the time of defoliation, regeneration is only possible by growth of
axillary tillers on the bases of flowering tillers (Williams, 1970;
Behaeghe, 1974, 1978).   Depending on species, cultivar, management
and fertilization there is a lag while regeneration of tillers occurs
reducing production.   This only occurs for the one regrowth period
after defoliation of reproductive tillers however, and dense leafy swards
at later defoliations produce less than spring swards growing under
similar environmental conditions.

Alberda and Sibma (1968) suggested that the difference between
reproductive and dense vegetative swards was caused either by a change
in photosynthetic performance or by a change in dry matter distribution
above and below the cutting level.   Leafe *et al* (1974) believed that
assimilate distribution was important since Ryle (1970) has shown that
flowering ryegrass partitions 8% and 92% of assimilate to root and
shoot respectively, while vegetative plants partition 17% and 83% resp-
ectively.   Consequently, a greater proportion of assimilate is
accessible for harvest from reproductive spring swards.

Behaeghe (1978) also suggested that because summer swards had one
fourth the active (haired) root mass of spring swards, summer root
growth was also important.   However, Troughton (1978) has shown that
summer herbage production is not significantly reduced by lack of roots
in perennial ryegrass.

Leafe *et al* (1974), Woledge and Leafe (1976), and Alberda (1977)
have shown that dense vegetative swards in summer and autumn have a lower
photosynthetic efficiency than reproductive swards in spring.   The
explanation for the different photosynthetic efficiency of flowering
and vegetative swards has been shown to be related to their structure and
to the efficiency of their leaves.   Leafe *et al* (1974), Alberda (1977)
and Sibma and Louwerse (1977) have all shown that artificially altering
leaf angle of summer swards can alter photosynthesis. Changing leaf
position from erectophile to planophile decreased the carbohydrate
production by 30% (Sibma and Louwerse, 1977).   However, Behaeghe(1978)
found that although differences in leaf angle exist between flowering
and vegetative crops, they are unlikely to cause large differences in
yield because the differences in leaf angle change during regrowth and are

non-systematic.

Woledge and Leafe (1976) explain the differences in canopy photosynthesis by changes in the efficiency of the individual leaves. Woledge (1977) suggest that differences in photosynthetic efficiency of individual leaves are a consequence of differences in the light climate of the developing leaves; leaves on elongating reproductive stems develop in high light intensities at the top of the sward, and leaves in vegetative swards develop in the shade of older leaves. Leaves developing in lower light intensities have a lower photosynthetic efficiency (Woledge, 1977).

Silsbury (1965) and Deinum (1976) suggested that high photosynthesis in a reproductive sward is caused by a high demand for assimilates from elongating stem and growing inflorescence; vegetative tillers have no such demand.

It is not clear whether demand for assimilate (Silsbury, 1965; Deinum, 1976) or greater photosynthetic efficiency of sun leaves (Woledge and Leafe, 1976) explain the greater photosynthetic efficiency of reproductive swards. Additional demand for assimilate (stem growth) results in leaves developing at the top of the canopy, and reduced demand for assimilates (no internode elongation) results in leaves developing in shade. Woledge (1979) has recently presented evidence that assimilate demand is less important than the light environment of developing leaves in determining the photosynthetic efficiency of individual leaves. Neither hypothesis can be used to explain why frequently harvested ryegrass with little internode development grows faster in spring than autumn (Anslow and Green, 1967). Behaeghe (1978) suggested that hormonal differences, not related to reproductive growth, were involved and he termed these an 'hibernation effect'.

The difference in growth rate between spring and summer grass swards is caused by differences in both assimilate partitioning and photosynthetic performance. The reasons for differences in photosynthetic performance still requires further research.

2.3.1.4.3 Pattern of reproductive growth

Herbage dry matter accumulation during uninterrupted reproductive growth of perennial ryegrass dominant swards is sigmoid (Alberda and Sibma, 1968; Leafe *et al*, 1974) with, under well fertilized conditions, a ceiling herbage mass (excluding herbage below mowing height) of 10-12 t DM/ha (Green *et al*, 1971; Corrall *et al*, 1979). Leafe (1971) reported a very high ceiling herbage mass of 16 t DM/ha above ground-level, measured from relatively small quadrats (two 30 x 30 cm quadrats per plot) and perhaps included material from outside the quadrats.

Unlike vegetative regrowth, which consists almost entirely of leaf lamina and sheath, in reproductive growth most of the herbage accumulation after the start of stem elongation is due to increased mass of stem (Wilman *et al*, 1976d). In the study of Wilman *et al*, the proportion of green leaf blade in the sward declined from 80% to 5% of the herbage mass during stem elongation. The amount of green leaf blade declined after head emergence, about mid-way through the linear phase (Leafe *et al*, 1974) and there was a steady increase in the amount of dead leaf.

Besides the change from a leafy to a stemmy sward there is a marked decline in the nutritive value of grass swards during the period of stem growth (Raymond, 1970). The maturation of the stem after head emergence, that is lignification (Raymond, 1970), is mainly responsible for the decline in digestibility of the herbage as a whole (Pritchard *et al*, 1963; Terry and Tilley, 1964), but also the decline in the proportion of green leaf has some effect (Wilman *et al*, 1976d). Thus the longer a reproductive sward grows without interruption, the greater the herbage yield, but the lower the nutritive value in terms of digestibility and protein content. In grass swards the relationship between stage of growth, yield and nutritive value depends on species and cultivar (Green *et al*, 1971) and nitrogen supply (Wilman *et al*, 1976d).

2.3.1.4.4 Effects of defoliation on reproductive growth

Brougham (1961) showed that grazing influenced the timing of reproductive growth in perennial ryegrass swards. Stem elongation occurred approximately one month later in a continuously grazed treatment

(herbage height maintained at 7-15 cm) than in a rotationally grazed treatment (grazed to 9 cm each time herbage reached 30 cm). Brown (1980) found that "Grasslands Nui" perennial ryegrass swards grazed twice in winter flowered later than swards ungrazed in winter.

Defoliation during reproductive development affects the number of both vegetative and reproductive tillers. If defoliation removes the meristem of a reproductive tiller the remaining stub cannot grow and will ultimately lose weight and die (Davies, 1977). Defoliated reproductive tillers with intact meristems can continue to develop, although if the apex was close to the cutting level, the tiller may develop in a virtually leafless condition (Davies, 1976). Regrowths in early summer contain varying proportions of fertile tillers, depending on cultivar and on the stage at which reproductive development is interrupted by defoliation (Corrall, 1974). At a given stage of development, closer defoliation will remove more meristems and reduce the proportion of fertile tillers in regrowth (Davies *et al*, 1971).

In grass swards, annual herbage production is generally reduced 20-30% (depending on subsequent management) when reproductive development is interrupted by defoliation at an early stage (when the sward is leafy) compared with interruption at anthesis (Austenson, 1963; Gillet, 1973; Corrall, 1974; Mislevy *et al*. 1977). Where little aftermath growth occurs because of summer drought or short growing season, the advantage of cutting at anthesis may be considerably greater (Bird, 1943; Bonin and Tomlin 1968a, 1968b). Interrupting growth after anthesis (at the dough stage for example) does not increase the annual yield further (Brid, 1943; Austenson, 1963; Bonin and Tomlin, 1968a, 1968b; Gervais and St Pierre, 1979). If herbage quality (DOM, TDN, protein) is considered, the advantage of delaying defoliation until anthesis is smaller and not always significant. Corrall (1974), for example, obtained from ryegrass swards annual yield of 14 t DM/ha when reproductive growth was interrupted at a leafy stage, compared with 17 t DM/ha when growth was interrupted post-anthesis. The annual DOM production was 9 t/ha and 10 t/ha respectively.

The number of reproductive tillers and the period of regrowth both influence the yield and quality of perennial ryegrass at any particular defoliation through the season (Corrall, 1974). Reproductive tillers

increase the yield but reduce the digestibility of herbage, the increase
and reduction being greater with longer regrowth periods.   Depending
on the stage of reproductive development, that is height of meristems,
the time of defoliation influences the number of reproductive tillers
in regrowth, and therefore the yield and quality of regrowth.
Similarly, different defoliation intensities will influence the number
of reproductive tillers in regrowth.

Because of stem growth, the response to cutting frequency is
different for reproductive and vegetative swards (Wilman *et al*, 1976a,c).
Doubling the defoliation interval (from 3,4 or 5 weeks to 6,8 or 10
weeks respectively) had a large positive effect on herbage yield during
the main period of stem development.   During the subsequent vegetative
period however, doubling the defoliation interval produced little extra
yield.   For example, doubling the defoliation interval from 5 to 10
weeks gave yields of 5.1 t DM/ha and 7.2 t DM/ha respectively during
reproductive growth, and 3.6 t DM/ha and 3.9 t DM/ha respectively during
the subsequent 10 weeks of vegetative growth.   Most of the response to
defoliation frequency in the reproductive period was attributable to
increased yield of stem and seedhead.

The effects of reproductive growth on herbage production in ryegrass
dominant swards has received little attention under grazing.   The
information reviewed was largely obtained from mowing experiments, and
experimenters have seldom investigated cutting height.   When other
criteria for defoliation frequency are studied, such as fixed time
intervals or light interception, the results can be profoundly influenced
by reproductive growth (Sheard and Winch, 1966), but frequently
reproductive growth is not mentioned.   A further problem is that research
has been conducted in environments with limited aftermath growth;   in
New Zealand growth can often continue through the winter.   Sheep and
cattle generally select leaf in preference to culm (Watkin and Clements,
1978), partly reflecting greater accessibility, and this preference could
influence the pattern of regrowth under grazing.

2.3.1.5 Residual shoots

In intensively grazed temperate pastures the primary growth unit
is the individual shoot and the pasture can be regarded as populations

of shoots (Mitchell and Glenday, 1958). In grasses, the shoots are
called tillers, and each tiller has axillary buds capable of developing
into further tillers (Langer, 1963). In white clover each stolon is
a shoot and new stolons (or an inflorescence) can develop from axillary
buds (Erith, 1924; Pascoe, 1973).

Factors controlling the growth of white clover, its performance
in grazed pastures and its ecological inter-relationships with other
species have recently been reviewed by Pascoe (1973) and Brougham *et al*
(1978). Since white clover formed only a small part of the pastures
studied and because its growth was not studied in detail, the factors
influencing stolon development will not be discussed further. The
relationship between tiller density (the number of grass shoots per
unit area) and regrowth, and the tiller dynamics of swards will be
reviewed.

2.3.1.5.1 Tiller density and regrowth

Regrowth is insensitive to tiller density over a wide range
(Jackson, 1973; Cocks, 1974) since a decrease in density is compensated
for by larger tillers (Kays and Harper, 1974; Ishida, 1975; Terai and
Kanda, 1979). In a given environment, ryegrass swards quickly reach
an equilibrium tiller density regardless of sowing rate; because at
low seed rates there is a high rate of tillering, and at high seed rates
there is a high rate of plant mortality (Holliday, 1953). The equilibrium
tiller density depends on species, time of year, soil fertility, moisture
availability, competition from other species, and defoliation regime
(Holliday, 1953; Mitchell and Glenday, 1958; Langer *et al*, 1964;
Huokuna, 1966; Harris and Brougham, 1968; Garwood, 1969; Harris, 1971;
Ishida, 1975; Hunt and Field, 1978; Pineiro and Harris, 1978b; Horst
and Nelson, 1979).

At very low tiller densities, not all light is intercepted by
tillers, and regrowth is positively correlated with density. Cocks
(1974) found that regrowth of *Lolium rigidum* (in terms of increase in
LAI after defoliation) increased with tiller density up to 10,000 tillers/
m^2, above which it changed little. Huokuna (1966) found that herbage
production was related to tiller density up to 3,200 tillers/m^2 in meadow
fescue swards but the influence of density depended somewhat on cutting

frequency.   When cut infrequently sparse swards produced more, but
when cut more often only dense swards gave high yields.   Variation in
tiller density has been shown by Lazenby and Rogers (1962) to account
for 94% of the variation in recovery after cutting of S24 perennial
ryegrass at different spacings.   Davies (1966) also found that regrowth
of S24 perennial ryegrass was related to tiller density between 5400
and 8700 tillers/m^2.   The critical density, below which growth is
positively correlated with density has not been established for perennial
ryegrass.

Any stress, or combination of stresses, which cause a decline in
tiller density may cause bare patches in the sward (Davies, 1977) there-
by reducing light interception and growth.   In mixed swards, white
clover or other volunteer species can establish in bare patches,
increasing light interception and reducing the effect of ryegrass
tiller density on sward growth.   The influence of ryegrass density on
regrowth of grass/clover swards could be expected to be greatest in cool
seasons when clover growth declines.

2.3.1.5.2 Tiller dynamics

Since the number of tillers present at any one time depends on the
relative rates of formation and death (Langer, 1963), the dynamics of
tiller populations determine sward persistence and botanical composition.
The effects of time of year, soil fertility, moisture availability,
competition and defoliation regime on tiller density, tillering and
tiller survival will be reviewed in this section.   The review is
restricted to field studies of swards where possible.

2.3.1.5.2.1 The seasonal pattern

Lamp (1952) reported that clonal plants of Bromegrass grown singly
without being cut showed two periods of active tillering.   The first in
spring, continued until internodal elongation started, and the second
began at anthesis and continued until winter.   A similar pattern of
tillering occurs in mown grass swards (Langer *et al*, 1964;   Huokuna,
1966;   Garwood, 1969;   Ito and Nakamura, 1975), though either period of
tillering may, at times, be absent.   Tiller death is normally greatest
during reproductive growth, initially due to death of vegetative tillers,

and then due to death of defoliated reproductive tillers.   In studies
at Palmerston North (Harris, 1971; Hill, 1971; Hunt and Field, 1978),
perennial ryegrass tiller density was greatest in late winter or early
spring, declined during reproductive growth, and then increased again
from autumn.   Early spring density is normally about double the minimum
density (Garwood, 1969; Hunt and Field, 1978).

The post-anthesis period of tillering is not always apparent from
density measurements, although it has been in some studies (Langer et al,
1964; Garwood, 1969), because decapitated reproductive tillers must
be replaced before an increase in density can occur.   Perennial ryegrass
swards closed for seed production normally have approximately 2000
(900-3200) reproductive tillers/m^2 (Hill, 1972; Spiertz and Ellen,
1972; Hebblethwaite and Burbridge, 1976; Hebblethwaite, 1977;
Hebblethwaite and Ivins, 1977, 1978), and grazed swards probably have
more due to secondary reproductive tiller development (Davies, 1969).

2.3.1.5.2.2 Reproductive growth

In ryegrass swards, the decline in density during reproductive
growth is mainly due to the death of vegetative tillers as reproductive
tiller density remains almost constant (Spiertz and Ellen, 1972;
Hebblethwaite and Ivins, 1977, 1978; Ong et al, 1978b).   Reduced
tillering and death of existing vegetative tillers both cause the decline.
Death of vegetative tillers is caused by failure of larger tillers
(mainly reproductive tillers) to supply assimilate to smaller heavily
shaded vegetative tillers (Ong et al, 1978b).   The decline in tillering
is due to the flowering axis exerting an inhibitory effect on the growth
of tiller buds (Jewiss, 1972; Laidlaw and Berrie, 1974).   Clifford
(1977) suggested that tiller bud suppression is influenced by movement
of inhibitory levels of auxin into buds from nearby elongating stem
internodes, whose growth in turn is controlled by the developing inflore-
scence and upper leaves.   The supply of mineral nutrients also appears
to be involved since continuous feeding of barley plants with a relat-
ively concentrated nutrient solutions prevented the decline in tillering
during stem elongation (Aspinall, 1961).

Defoliation during reproductive growth could be expected to increase
tillering by reducing apical dominance, and to increase vegetative tiller

survival in the improved light environment of the defoliated sward.
Defoliation of reproductive tillers can indeed advance the period of
rapid tillering from after anthesis to an earlier date (Asano and
Chujo, 1975; Krause and Moser, 1977). It is possible that just
grazing off part of the seedhead could stimulate tillering since removal
of florets from barley inflorescences increased tillering, the response
being more pronounced at low nitrogen levels (Aspinall, 1963). In
frequently cut swards of meadow fescue (Jewiss, 1966), cocksfoot
(Ito and Nakamura, 1975), and perennial ryegrass (Davies, 1977)
considerable numbers of vegetative tillers survived through reproductive
growth. This is in marked contrast to frequently cut swards of timothy
(Jewiss, 1966) and Italian ryegrass (Davies, 1977) where only a small
proportion of vegetative tillers survived through flowering. Less
frequent defoliation reduced the proportion of vegetative tillers
surviving reproductive growth (Jewiss, 1966; Williams, 1970) so that
persistence of the sward depended to a greater extent on tillering
after flowering. Although frequent defoliation can increase survival
of vegetative tillers, it does not always prevent a decline in density
(Langer, 1959; Anslow, 1967).

Decapitation of reproductive tillers stimulates development of new
tillers from previously dormant axillary buds on the basal nodes of
cut stubs (Gillet, 1973). Silsbury (1964), Williams (1970), and
Davies (1977) have also mentioned tillers originating from this source
in perennial ryegrass. Silsbury (1964) found that regrowth of ungrazed
perennial ryegrass, growing in the mediterranean-type environment of
South Australia after summer drought, was mainly due to the development
of tillers from dormant buds on the basal nodes of reproductive tillers.
Few vegetative tillers survived the drought and persistence depended
on dormant axillary buds. Sward death after cutting perennial ryegrass
swards at the head emergence stage has frequently been observed in crops
grown with high inputs of N fertilizer in the U.K. (Williams, 1970;
Jewiss, 1972) and is due to the failure of buds on cut reproductive stubs,
to regenerate. More frequent defoliation, by increasing survival of
vegetative tillers and decreasing the period of bud dormancy, prevents
sward death (Williams, 1970). Davies (1977) actually found that in
a S24 perennial ryegrass sward cut every three weeks few vegetative
tillers died between cuts (approximately 10%) and during the main flowering

period 34% of new tillers originated from cut stubs. In perennial ryegrass swards axillary buds on the basal nodes of defoliated reproductive tillers appear to be most important for sward persistence where defoliation is infrequent, expecially in high fertility or dry situations.

2.3.1.5.2.3 Effect of defoliation

Defoliation regime has a marked effect on tiller production, survival and density. Langer (1963), after reviewing several studies of the effect of cutting on tillering under controlled conditions, concluded that unless flowering stems were removed, defoliation was unlikely to increase tillering in single plants, although in a favourable environment the effect might only be temporary. He noted that in swards, defoliation also influenced the amount of mutual shading which Mitchell and Coles (1955) had suggested reduced tillering. Merely shading tiller bases, such as occurs in dense stands, can arrest tiller production, although dry weight per tiller is unaltered (Davies, 1977). Conversely, removing the base shade, as occurs with defoliation, permits resumption of tillering. Hunt and Field (1978) showed that after grazing perennial ryegrass swards, tillering was at first minimal, then increased, presumably as more assimilate became available, and eventually decreased as mutual shading had an effect. They also showed that initially after defoliation there was little tiller death, but soon after the canopy closed (95% light interception) tiller death increased greatly. Tiller death rate declined after a stable population was reached.

These results suggest that frequent close defoliation, although preventing mutual shading, reduces assimilation and hence tillering. Brougham (1959b) and Huokuna (1966) found that such a defoliation regime resulted in plant mortality and a low tiller density. Normally however, as a result of greater tiller appearance and survival, more frequent or closer defoliation result in a higher tiller density (Langer, 1959; Madison, 1962; Langer et al, 1964; Huokuna, 1966; Agyere and Watkin, 1967; Edmond and Hoveland, 1972; Beard, 1973; Harris, 1973; Ishida, 1975; Ito and Nakamura, 1975; Wilman et al, 1976b; Davies, 1977; Dobson et al, 1978; Pineiro and Harris, 1978b; Boswell and Crawford, 1978; Sheffer et al, 1978). Mitchell and Glenday (1958) and Monteath

et al (1977) have shown that ryegrass tiller density is greater in pasture grazed by sheep than in pasture grazed by cattle, partly as a result of closer and more frequent grazing.

2.3.1.5.2.4 Fertilizer

Pot experiments have demonstrated that tillering is greatly increased by raising the supply of mineral nutrients, notably nitrogen (Langer, 1966). In grass swards nitrogen fertilizer also increases the rate of tillering (Houkuna, 1966; Sampaio and Beaty, 1976) and tiller density (Lambert, 1962; Madison, 1962; Houkuna, 1966; Harris, 1973; Ishida, 1975; Wilman *et al*, 1976b; Beaty *et al*, 1977; Davies, 1977; Hebblethwaite and Ivins, 1977, 1978) but the response depends on defoliation frequency. Wilman *et al* (1976b) found that if defoliation of perennial ryegrass swards was frequent (every 3 or 4 weeks), nitrogen fertilizer increased density, but when defoliation was less frequent (every 8 or 10 weeks), nitrogen decreased density. The decrease was probably caused by the greater amount of shading in the fertilized swards. If phosphorus is limiting growth, the increase in tiller density with nitrogen fertilizer is greater if phosphorus is also applied (Harris, 1973).

2.3.1.5.2.5 Water supply

During summer drought, tiller density is normally greater in irrigated than dryland swards (Garwood and Williams, 1967), but when moisture becomes available again in autumn, dryland swards may become denser than previously irrigated swards (Horst and Nelson, 1979; Korte and Chu, unpublished data). Autumn density also depends on drought severity, since prolonged drought can result in death of ryegrass plants (Harris, 1971) and the recovery of depleted ryegrass swards would be expected to be limited. In the experiment of Horst and Nelson (1979) with tall fescue in Missouri, the difference in density observed in autumn was still evident the following spring. In pot studies, the amount and rate of tillering have been shown to be reduced under dry conditions (Olmsted, 1941; Chu, 1979), and in perennial ryegrass and timothy swards, resumption of tillering after flowering is delayed in the absence of rain or irrigation (Garwood, 1969).

2.3.2 Herbage death and decay

The death and decomposition of herbage have received relatively
little study in temperate grasslands (Mason, 1976), but both processes
have been considered to have an important influence on net herbage
production (Campbell, 1964; Brougham, 1962; Bean, 1964; Hunt and
Brougham, 1966; Anslow, 1966, 1967; Hunt 1970a,b; Morris, 1970;
Davies, 1971a; Tainton, 1974b; Wilman and Mares Martin , 1977;
Robson and Deacon, 1978; King *et al*, 1979).   The lack of knowledge
about death and decay is indicated by the largely unsuccessful attempt
of Sauer (1978) to model the dynamics of dead herbage.   Similarly,
the models of Sheehy *et al* (1979) and Okubo *et al.* (1977) predicted
considerably more dead herbage than was observed in the experiments
actually simulated.

In established swards the total dry weight above ground level at
any time includes a considerable quantity of dead material which is
continually being added to by senescence of green parts and reduced by
decay (Bean, 1964).   Campbell (1964) pointed out that dead herbage
intercepted light but had no photosynthetic capacity, so it probably
reduced pasture growth.   Dead herbage is generally avoided by grazing
animals in preference for green herbage (Arnold, 1964; McBride *et al*,
1967; Dudzinski and Arnold, 1973; Thomson, 1977) and is of lower
nutritive value than green herbage (Terry and Tilley, 1964; Wilman
et al, 1976d).   Rattray (1978) found that the *in vitro* digestability
of pasture in autumn was highly correlated (r = 0.98) with the proportion
of green herbage in the sward.

There is considerable difficulty in studying herbage death and
decay in pastures.   Wilman and Mares Martin (1976) noted that there
is no clear difference between 'living' and 'senescent or dead' tissue.
Herbage is normally classified as living when it is green and dead when
it is yellow or brown.   Quantitative data on the death and decomposition
rates has only been obtained in three studies (Hunt, 1970 a,b; Morris,
1970; Wilman and Mares Martin, 1977).   The death rate was obtained
by collecting dead herbage from fixed quadrats at frequent intervals
(normally every 3 days), and decomposition was estimated as the diff-
erence between litter accumulation (corrected for initial residues)
and herbage death.   Considerable time is required to separate litter

from green herbage in the field and this limits the size of any study.

The death rate has also been estimated from considering the average number of leaves per tiller, average leaf life, and mature leaf weight in a sward (Brougham, 1958b; Hunt and Brougham, 1966; Williamson, 1976) but this method can only provide information at the ceiling herbage mass. Campbell (1964) drew conclusions from fluctuations in net head matter yield, that is, dead herbage mass (Hodgson, 1979), but death and decomposition rates are confounded in this case. Gillingham (1978) measured litter fall in a high-stocked hill country pasture over a whole year but he undoubtedly underestimated the amount of herbage death since litter was collected infrequently (every two to seven weeks). Some decomposition would have occurred between litter collections, and since collections were made after grazing, litter consumed by sheep was not included in the estimate.

2.3.2.1 Factors affecting herbage death

Daily rates of herbage death of over 60 kg DM/ha/day in spring have been reported (Hunt, 1970a; Wilman and Mares Martin, 1977) indicating the importance of this process. Several factors have been suggested as influencing the rate of herbage death and these will be briefly reviewed.

2.3.2.1.1 Age of leaves

Leaves are organs of limited growth and, once they have reached their final size, they remain on the plant for a period and then die (Langer, 1979). Williamson (1976) found that the life-span of grass leaves in an undefoliated sward depended on species and time of year. In ryegrass, the rates of leaf appearance and death do not differ greatly, so that the number of living leaves per tiller is relatively constant; normally about three leaves per tiller in a closed vegetative sward (Hunt and Brougham, 1966; Davies, 1971b; Thomas and Norris, 1977). Hunt and Brougham (1966) found that in an undefoliated Italian ryegrass sward each tiller produced a new leaf every 8 to 18 days, in spring and winter respectively, so that the life of leaves was between 24 and 54 days. In another study (Brougham, 1958b), the life of white clover leaves was approximately 30 days during summer.

2.3.2.1.2 Stage of regrowth

The rate of leaf death is generally lowest shortly after defoliation
and it increases during regrowth (Huokuna, 1960; Bean, 1964; Agyare and
Watkin, 1967; Hunt, 1970 a,b; Wilman and Mares Martin, 1977).   This
increase in leaf death has been attributed to increased shading in the
later stages of regrowth.   Rodin and Bazilevich (1967) found that annual
litter fall in steppe meadows was proportional to the plant biomass,
and Duncan (pers comm) after re-analysing the data of Hunt (1970a) has
demonstrated a similar relationship during regrowth of ryegrass/clover
pasture.   Duncan found that approximately 0.8% of green herbage died
daily, regardless of either stage of regrowth or amount of shading of
lower leaves.   For example, the daily death rate of swards with 1000
and 6000 kg green herbage DM/ha would be expected to be 8 and 48 kg DM/
ha respectively.   Data in other sutdies where litter fall has been
measured (Morris, 1970; Wilman and Mares Martin, 1977) cannot be compared
because insufficient data was presented.

2.3.2.1.3 Defoliation regime

Herbage continually dies in undefoliated pasture stands (Brougham,
1962; Hunt and Brougham, 1966; Rodin and Bazilevich, 1967;
Williamson, 1976) but the defoliation regime can influence the amount
of death.   The influence of defoliation frequency can be judged from
the work of Hunt (1970 a,b) and Wilman and Mares Martin (1977) who both
studied dead herbage accumulation during regrowth.   Reports of Campbell
(1964) and Morris (1970) indicate that defoliation intensity has an
important influence on herbage death.

Anslow (1966) suggested that too long an interval between defoliations
could result in considerable loss of herbage through senescence and decay.
No experiments have compared litter fall in swards defoliated at different
frequencies under a constant defoliation intensity, but Wilman et al
(1976 a,c) reported that the amount of dead herbage harvested increased
markedly with less frequent defoliation.   For example, the amount of
dead leaf harvested over 30 weeks was 110 kg/ha and 1270 kg/ha from three
week and ten week cutting intervals respectively.   These results, and
those of Hunt (1970 a,b) and Wilman and Mares Martin (1977), suggest
that less frequent defoliation increase herbage death.

The influence of defoliation intensity on herbage death has not
been investigated, but Morris (1970) measured herbage death in swards
maintained at different LAI. Herbage death was greater at higher LAI,
for example, the daily death rate was 54 and 39 kg DM/ha/day in swards
maintained at average LAI of 4.6 and 3.1 respectively. As stocking
rate, and pasture utilization was increased, the amount of dead herbage
accumulating in dairy pasture during spring and summer was reduced
(Campbell, 1964). Similar results were obtained by Jagusch *et al*
(1978) under sheep grazing. These results suggest that herbage death
decreases with increasing defoliation intensity and level of herbage
utilization, a conclusion also reached by Beard (1973).

2.3.2.1.4 Climatic influences

Frost and drought are the main climatic factors influencing
herbage death. Several authors (Corbett, 1957; Wiegert and Evans,
1964; Agyare and Watkin, 1967) have noted that frost damage in winter
can result in leaf death. In his simulation model of biomass dynamics
for grassland, Sauer (1978) suggests that frost damage causes 25% of
green herbage to die if the minimum daily temperature falls below $7^{\circ}C$
for warm-season grasses and $3^{\circ}C$ for cool-season grasses.

Hunt (1968) concluded that from the limited information available,
moisture stress and high temperatures could be important factors
influencing leaf death rates. Chu (1979) reported that during a period
of water stress sufficient to prevent new leaves appearing, old leaves
died, reducing the leaf area. The reduction in leaf area was greater
at higher temperatures in plants maintained at the same level of moisture
stress. Sauer (1978) suggested that shoot death due to drought increases
linearly as soil-water potential drops below 20% of the permanent wilting
soil-water potential. Leaf death due to drought in summer would normally
be expected although the quantitative relationship has not been established
for ryegrass/clover pasture.

Although Gillingham (1978) undoubtedly underestimated herbage death
his results show the seasonal pattern. Litter fall was 380, 1430, 740
and 200 kg DM/ha during spring, summer, autumn and winter respectively
in perennial ryegrass/*Poa annua* dominated stockcamp pastures in hill
country. In winter and early spring litter was mainly leaf, but in late

spring senescing *Poa annua* plants formed the bulk of litter collected.
In summer, pastures became rank and litter was derived mainly from
shaded ryegrass, then in autumn the uneaten stalk material collapsed and
formed the bulk of the litter fall. Campbell (1964) found that dead
herbage accumulated during spring and summer, when only part of the
herbage available was consumed by dairy cows. Increasing the stocking
rate, or area of conserved pasture, reduced the amount of dead herbage.

These results suggest that the seasonal pattern of herbage death
in grazed pastures depends on pasture growth and utilisation, ungrazed
herbage shading plants and eventually dying. Drought during summer
accelerates the death of uneaten herbage. This is in marked contrast
to U.K. hill pastures, where frost seems to have the major effect. Dead
herbage accumulates during autumn and winter then gradually disappears
during summer (Eadie and Black, 1968). A component of dead herbage
which has received little attention is uneaten flowering tillers; most
research having concentrated on leaf death.

2.3.2.1.5 Nitrogen

The application of fertilizer nitrogen to pasture, besides increa-
sing herbage yield, increases herbage death (Morris, 1970; Wilman and
Mares Martin, 1977). Although the results of Wilman et al (1976 a,c)
are confounded by both herbage death and decomposition they also illus-
trate how nitrogen fertilizer can increase herbage death. With
infrequent defoliation (harvested every 10 weeks) more dead herbage
was harvested from ryegrass swards when nitrogen fertilizer was applied
(1160 and 2180 kg DM/ha for 0 and 525 kg N/ha respectively). The
increased herbage death is presumably due to the greater green herbage
mass or to the longer period of intense shading (2.3.2.1.2).

Wilman and Mares Martin (1977) also found that nitrogen fertilizer
tended to decrease the production of senescent and dead tissue in the
early stages of regrowth. The results of Wilman et al (1976 a,c)
also suggest that nitrogen fertilizer can reduce herbage death in the
first three weeks of regrowth. With frequent defoliation (every three
weeks) nitrogen increased total herbage yield from ryegrass swards, but
had no significant effect on dead leaf yield (Total herbage: 4730 and
10850 kg DM/ha; dead leaf: 100 and 110 kg DM/ha; for 0 and 525 kg DM/
ha respectively). Wilman and Mares Martin (1977) suggested that nitrogen

fertilizer increased yield in the early stages of regrowth by
increasing tiller density, but did not increase leaf death because few
of the new leaves would die within the first three weeks regrowth.

2.3.2.1.6 Pasture species

Differences in the amount of leaf death between various pasture
species reported by Wilman and Mares Martin (1977) may have merely
reflected different amounts of green herbage, and hence death.   In-
sufficient data is presented to test this hypothesis.

2.3.2.1.7 Biotic factors

Besides the factors already reviewed several other biotic factors
have been reported to influence herbage death.   Gillingham (1978)
observed that pulling of plants by grazing animals and urine scorch
increased pasture litter.   Herbage underlying dung patches quickly
dies and decays (MacDiarmid and Watkin, 1971).   Trampling of pasture
by the hooves of grazing animals also can result in herbage death.

Harper (1977) has described how surface-feeding slugs like
Agriolimax reticulatus chew through grass tillers at the base, leaving
the felled leaves uneaten on the soil to die.   Similarly, Porina
(*Wiseana spp*) larvae also chew foliage at ground level, leaving de-
foliated leaves to die, and Argentine stem weevil (*Hyperodes bonariensis*)
larvae damage grass tillers causing leaf death (Pottinger, 1973).
Root feeding invertebrates, notably grass grub (*Costelytra zealandica*)
larvae in New Zealand, reduce the root mass of pasture and can increase
the amount of dead herbage also.

Several species of rust fungi are commonly found in New Zealand
pasture, the species *Pucinia coronata* being most important (Blair, 1973).
Rust infected leaves die, infestation being most noticeable in summer
and autumn on perennial ryegrass.

2.3.2.2. Litter disappearance

Earthworms and micro-organisms are involved in removing litter from
pasture, but grazing animals also consume litter and may trample further
dead herbage into the soil.   Daily rates of litter disappearance up to

30 kg DM/ha have been reported for ryegrass/white clover pasture in New Zealand (Hunt, 1970b). The rate depends on the amount of litter present, the populations of earthworms and micro-organisms, and microbial activity. Syers *et al* (1970) reported that earthworms alone could remove up to 85 kg litter DM/ha/day from a ryegrass/clover pasture.

Generally two species of earthworm, both European in origin, *Allolobophora caliginosa* and *Lumbricus rubellus* predominate under ryegrass/ clover pasture in New Zealand, with the larger species *Octoclasium cyaaeum* and *Allolobophora longa* occurring infrequently (Sears and Evans, 1953; Waters, 1955). Both *A. caliginosa* and *L. rubellus* consume dung, dead roots, and dead leaf (Waters, 1955), reducing the herbage mass of pasture. *L. rubellus* has been reported to deposit up to 33 t/ha/yr of surface casts (Syers *et al,* 1979) and these casts can cover herbage. Although earthworms can reduce the herbage mass of pasture by removing large amounts of litter, due to improved nutrient cycling and improved soil physical properties they also improve the environment for plant growth (Barley, 1961; Stout *et al,* 1976).

Micro-organisms (mainly bacteria and fungi) are involved in the decomposition of litter both above and below the soil surface in pastures and turf (Bear, 1973; Hunt, 1977). Litter pH, litter carbon-nitrogen ratio, temperature and moisture are the main factors influencing the rate of decomposition (Hunt, 1977). Lime application and nitrogen fertilization can both increase the rate of litter decomposition (Beard, 1973). Warmer temperatures and moister conditions also increase decomposition (Hunt, 1977).

2.3.2.3 Litter disappearance and regrowth

Although less frequent and less intensive defoliations are expected to increase pasture growth, they are also expected to increase herbage death and disappearance. Morris (1970) clearly demonstrated the importance of this interaction between gross aerial growth and losses from litter disappearance. The maximum harvested yield was obtained by rotational defoliation to 3 cm every 4 weeks, but this was derived from the minimum gross aerial growth. Maximum gross aerial growth occurred under the simulated continuous grazing treatments maintained at a high LAI (4.6). The difference between gross and harvested yield was largely due to the death and subsequent decay of leaves, up to 50% of growth being lost. Morris (1970) concluded that, in practice, it

may be preferable to obtain less growth, but to harvest more of the
material grown, minimizing the losses through senescence and subsequent
decay.

2.4 CONCLUSION

Although defoliation intensity and frequency clearly influence
pasture growth, the optimum intensity and frequency of grazing is still
not clear from the literature.   It would help if the optimum grazing
management could be defined in terms of plant physiological parameters
such as leaf area index, stage of reproductive growth, reserve status,
or stubble quality.   Recommendations could then be made for farms
with different soil types, climates, fertilizer programmes, stocking
practice etc.   To obtain satisfactory conclusions, investigations must
be conducted under grazing with herbage sampling to ground level.
Since net herbage accumulation is the result of both growth and herbage
disappearance it is necessary to separate dead and live herbage.   In
this investigation defoliation intensity and frequency will be defined
by plant physiological parameters.

CHAPTER 3   TERMINOLOGY AND DEFINITIONS

The nomenclature and definitions recently published by Hodgson (1979) and Thomas (1980) are used in this thesis.   The more frequently used terms are presented for convenience in this chapter.

3.1 THE SWARD (Hodgson, 1979)

Herbage mass

the total mass of herbage per unit area of ground, measured to ground level (or to some reference height).

Herbage growth

the development and increase in weight of new leaf and stem tissue.

Herbage accumulation

(also referred to as net herbage accumulation); the change in herbage mass between successive instantaneous measurements, summed over time as appropriate.

Herbage consumed

the mass of herbage removed per unit area by animals at a single grazing or series of grazings.

Herbage harvested

the mass of herbage removed per unit area by mechanical means at a single harvest or series of harvests.

3.2 THE GRAZING PROCESS (Hodgson, 1979)

Degree of defoliation

the ratio of the amount of herbage consumed or harvested to the original mass.   The equivalent term defoliation intensity, is used also.

Residual herbage

the herbage remaining after defoliation.

Defoliation interval

the time between successive defoliations of an area.   The term defoliation frequency, the number of defoliations per unit time, is also used.

3.3 GRAZING MANAGEMENT (Hodgson, 1979)

Grazing period   the length of time for which a particular area of land is grazed.

Rest period   the length of time between the end of one grazing and the start of the next on a particular area.

Grazing cycle   the length of time between the beginning of one grazing and the beginning of the next, that is, the grazing period plus the rest period.

3.4 THE CANOPY (Thomas, 1980)

Leaf Area Index (LAI)   the area of green leaf (one side) per unit area of ground that is carried by a canopy. Only lamina was measured.

Tiller   aerial shoot of a grass plant. Tillers were only counted after they became apparent to the eye without the dissection of the plant.

Tiller appearance rate (TAR)   the rate at which tillers become apparent to the eye without dissection of the plant.

   (i) Absolute TAR   is given by $\dfrac{N_2 - N_1}{t_2 - t_1}$ where

t_1 and t_2 are the times at which counts are made of the number of live tillers (N).

   (ii) Proportional TAR   is given by $\dfrac{1}{N_1} \cdot \dfrac{N_2 - N_1}{t_2 - t_1}$

The TAR is *net* if N_2 is the number of live tillers at t_2, and *gross* if $N_2 = N_1 +$ (number of new tillers produced between t_1 and t_2).

Tiller death rate (TDR)   the rate at which tillers die. The gross *absolute TDR* and *proportional TDR* can be

calculated when the number of tillers dying between two dates is measured. The net TDR is the net TAR when $N_2 < N_1$.

3.5 REPRODUCTIVE DEVELOPMENT (Thomas, 1980)

Inflorescence emergence — the first appearance of the tip of a grass inflorescence at the mouth of the sheath of the flag leaf. Equivalent to ear emergence or head emergence.

Anthesis — flower opening.

CHAPTER 4   EFFECT OF LATE SPRING GRAZING INTENSITY AND
FREQUENCY ON THE HERBAGE PRODUCTION AND SHOOT
DENSITIES OF RYEGRASS DOMINANT PASTURE

4.1 INTRODUCTION

Several grazing management experiments concerned with defoliation
frequency and intensity have been reported in New Zealand.   Brougham
(1959b, 1960a) showed how botanical composition of pasture could be
altered by grazing regime and demonstrated that frequent close defol-
iation in summer greatly reduced ryegrass persistence and production.
Weeda (1965), Campbell (1969), Pineiro and Harris (1978a) and Holmes
and McClenaghan (1979) have all shown that less frequent defoliation
increases pasture growth but the optimum defoliation interval is still
not clear from these experiments.   Increasing the degree of defoliation
has been reported to increase (Holmes and McClenaghan, 1979), decrease
(Weeda, 1965) or have no effect on herbage production (Tainton, 1974b;
Marsh, 1978, 1979).   This study attempts to define the optimum grazing
intensity and frequency more clearly with reference to plant physiolo-
gical parameters.

Residual leaf area index (LAI) was chosen as the criteria for
defining the degree of defoliation (defoliation intensity) since many
studies have stressed the importance of light interception for pasture
growth (e.g. Brougham, 1956; Donald and Black, 1958).   Residual pasture
height and residual herbage mass have been used as criteria for defol-
iation intensity in grazing studies (e.g. Brougham, 1959b, 1960a;
Holmes and McClenaghan, 1979) but pastures of similar height or mass can
have different LAI depending on such factors as the ratio of live to
dead herbage and the ratio of leaf to non-leaf.   A high and low residual
LAI were compared to test whether this was an important criteria for
defining grazing regimes.   It was anticipated that continually leaving
a high residual LAI would reduce stubble quality (Hunt and Brougham,
1967; Jackson, 1974; Ollernshaw and Hodgson, 1977) so treatments with
alternating grazing intensities were included to maintain stubble quality
while having a higher light interception than the low residual LAI
treatment.   Two alternating intensity treatments were compared as the
timing of close grazings was expected to interact with the reproductive
growth of ryegrass.

Defoliation interval was also defined in terms of light interception. The optimum stage to defoliate pasture is uncertain, being either each time full light interception is reached (Tainton, 1974b) or each time the ceiling LAI is reached (Terai, 1977). More or less frequent defoliations have both reduced herbage production in mowing experiments (Wilson and McGuire, 1961; Sheard and Winch, 1966; Terai, 1977). Since much of the herbage accumulating in the later stages of regrowth is dead leaf (Hunt, 1970a; Tainton, 1974a), which is avoided by grazing animals (Arnold, 1964; McBride *et al*, 1967; Thomson, 1977), the production of live and dead herbage was measured.

As the grazing practice in one season can affect herbage production in subsequent seasons (Brougham, 1960a), the residual LAI treatments were only applied during late spring/early summer. To detect any residual effect all treatments were defoliated to the same degree in late summer and autumn. As recommended for ryegrass/clover pasture (Brougham, 1970), grazings were lax in summer and hard in autumn.

More intensive defoliation is expected to reduce herbage production (Donald, 1941; Alcock, 1964; Harris, 1978) and the reports of increased production from more intensive defoliation in mowing experiments (e.g. Reid, 1959, 1962; Boswell, 1977) may have been due to improved utilization of herbage from the base of the sward rather than increased growth (Tayler and Rudman, 1966). Similarly, part of the response to less frequent defoliation in mowing experiments could be due to improved utilization of herbage rather than growth (Anslow, 1967). To ensure that responses to defoliation were due to growth rather than utilization, herbage mass was measured to ground level from which new growth largely originates.

'Grasslands Nui' perennial ryegrass (Armstrong, 1977) was used in this study because it has been shown to be more persistent (Ritchie, 1975; Sheath *et al*, 1976; Lancashire *et al*, 1978) and higher producing than other perennial ryegrass cultivars both in mowing experiments (e.g. Sheath *et al*, 1976; Harris *et al*, 1977; Sithamparanathan, 1979) and in grazing experiments (Baars *et al*, 1976; Armstrong, 1977; Smith and Stiefel, 1977; Lancashire *et al*, 1978; Thomsen, 1978; Hayman, 1979). The marked advantage of "Nui" ryegrass production in ryegrass/clover swards is often offset to some extent by higher yields of

white clover in swards of other ryegrass cultivars.   Infestations of
stem weevil (*Hyperodes bonariensis* Kusch) can reduce the yield advantage
and persistence of Nui (Kain *et al*, 1977).   "Nui" has been available
to farmers since 1975 (Lancashire and Harris, 1977) and it appears to
be replacing other perennial ryegrass cultivars (Lancashire *et al*, 1978).

4.2   EXPERIMENTAL

4.2.1   The site

The experiment was conducted at Massey University's 'Tuapaka'
sheep farm 14 km east of Palmerston North (Plate 4.1).   The soil type of
the experimental site is a Tokomaru silt loam, of medium fertility in
its natural state, but poorly drained due to the presence of a fragipan
approximately 90 cm below the soil surface.   Drainage of the site was
adequate as a sub-surface drainage system had been installed for
several years.

Soil moisture determinations (% of dry weight at $105^{\circ}C$) for the top
15 cm of soil were made regularly from within the trial area (Appendix
I).   Monthly climatic data recorded at Palmerston North are presented
in Appendix II.   The summer of 1975-6 was wetter and cooler than normal
and except for a fortnight in late February the soil moisture level did
not drop below 20%, approximately equivalent to -100 kPa, the point at
which pasture growth is restricted (Scotter, *pers. comm.*).

4.2.2   Pasture establishment

After cultivation out of old pasture the area was sown on 25
March 1975 with a mixture of 16 kg/ha "Grasslands Nui" perennial
ryegrass (*Lolium perenne L.*) and 3 kg/ha "Grasslands Huia" white clover
(*Trifolium repens L.*).   Potassic superphosphate (6% P, 14% K) at a
rate of 380 kg/ha was broadcast following sowing and two further
applications of 225 kg/ha each were made in July 1975 and March 1976.
Lime at a rate of 1300 kg/ha was broadcast over the trial site in April
1975.   Soil quick-test analysis of samples taken in August 1975
indicated that pH, Ca, P, K and Mg levels were adequate for vigorous
plant growth.   During the establishment period the pasture was grazed
lightly in May, June and August 1975.   The experiment started on 12
September 1975.

Plate 4.1: A general view of some plots in December 1975.

Plate 4.2: The capacitance probe used in 1975/76.

4.2.3 The treatments

Initially it was envisaged that two pastures (main plots),
perennial ryegrass/white clover and tall fescue/white clover, be
compared under a range of grazing managements (sub-plots).   However,
the tall fescue failed to establish satisfactorily.   In August 1975
the ryegrass area was subdivided into 24 fenced paddocks each 15 m x 16 m
(Figure 4.1).   Eight grazing treatments were compared, two defoliation
intervals at four defoliation intensities arranged at random within three
block replicates.

The two defoliation interval treatments were:
    Frequent   (F),   grazed when the pasture canopy intercepted
                      95% of the photosynthetically active
                      radiation at noon;

    Infrequent (I),   grazed 2 weeks after the pasture canopy
                      intercepted 95% of the photosynthetically
                      active radiation at noon.
Light interception was measured with a "LI-COR" light meter with a
"QUANTUM" sensor (Lambda Instrument Corp. Nebraska), above the canopy
and under the canopy at several locations within the paddock at solar
noon.

The four defoliation intensity treatments were:
    Continuous hard (HH);
    Alternating hard and lax (HL);
    Alternating lax and hard (LH);
    Continuous lax (LL).
Grazing intensity was defined in terms of residual leaf area index
(LAI).   Hard grazing (H), to leave as low a LAI as possible left a
LAI between 0.1 and 0.6, while lax grazing (L) left some residual LAI,
between 1.5 and 2.5.   The grazing intensity treatments started on 25
October and the final one was completed on 11 January.

In late summer all treatments were lax grazed, and from March
onwards all treatments were hard grazed.   The defoliation interval
treatments were maintained throughout the experiment.   Table 4.1 shows
the actual defoliation regime for each treatment.   The experiment ended
on 21 July 1976.

Table 4.1: Defoliation regimes for Experiment 1

Dates refer to the grazing period and residual Leaf Area Indices are in brackets

	FREQUENT (F)				INFREQUENT (I)		
HH	HL	LH	LL	HH	HL	LH	LL
All plots hard grazed 10/9-12/9/1975 (0.8)							
Hard (0.9) 25/10-30/10	Hard (0.7) 27/10-1/11	Lax (1.7) 28/10-3/11	Lax (2.7) 25/10-30/10	Hard (0.4) 9/11-13/11	Hard (0.5) 13/11-18/11	Lax (1.5) 11/11-15/11	Lax (1.6) 8/11-12/11
Hard (0.2) 30/11-3/12	Lax (2.8) 28/11-30/11	Hard (0.3) 27/11-30/11	Lax (1.5) 22/11-26/11	Hard (0.4) 21/12-26/12	Lax (1.9) 28/12-31/12	Hard (0.2) 23/12-28/12	Lax (0.9) 12/12-15/12
Hard (0.1) 6/1-10/1	Hard (0.6) 14/12-17/12	Lax (3.0) 7/1-11/1	Lax (2.0) 28/12-31/12				
Lax (2.3) 15/2-20/2	Lax (2.5) 13/1-16/1	Lax (1.9) 29/1-2/2	Lax (2.2) 23/1-25/1	Lax (2.2) 4/2-6/2	Lax (1.0) 6/2-10/2	Lax (1.8) 13/2-17/2	Lax (1.9) 21/1-25/1
Lax (0.9) 14/3-18/3	Lax (2.9) 4.2-6/2	Lax (2.2) 23/2-25/2	Lax (1.2) 21/2-25/2	Lax (0.7) 12/3-15/3	Lax (0.8) 15/3-18/3	Lax (1.0) 22/3-25/3	Lax (1.5) 25/2-29/2
	Lax (1.3) 28/2-3/3	Lax (0.9) 22/3-25/3	Lax (1.2) 27/3-30/3				
Hard (0.4) 16/4-20/4	Hard (0.3) 16/4-20/4	Hard (0.3) 16/4-20/4	Hard (0.3) 12/4-16/4	Hard (0.3) 26/4-30/4	Hard (0.2) 30/4-5/5	Hard (0.2) 30/4-5/5	Hard (0.2) 12/4-16/4
Hard (0.5) 6/6-9/6)	Hard (0.8) 2/6-6/6	Hard (1.0) 2/6-6/6	Hard (0.3) 29/5-2/6	Hard (0.4) 23/6-27/6	Hard (0.5) 11/7-15/7	Hard (0.5) 15/7-19/7	Hard (0.5) 13/6-17/6
Experiment 1 ended 21/7/76							

42

Each grazing, by Romney sheep lasted 3 to 4 days, except at the first grazing of most treatments when insufficient sheep caused grazing to be extended to 5 days.

4.2.4 Measurements

Herbage mass was obtained immediately before and after grazing from at least 3 quadrats (0.23 m^2) per plot, cut to ground level with an electric shearing handpiece. Further samples were obtained in summer and autumn at approximately weekly intervals so that regrowth curves could be constructed. To reduce within-plot variation, quadrats were located within the plot at positions which gave an average capacitance probe (Plate 4.2) reading as suggested by Jones and Haydock (1970) after taking 25 readings per plot. Following cutting herbage was washed to remove soil and dung, and then weighed after draining. A 200-600g subsample was dried at 80°C for 14 hours to obtain the dry matter percentage. A second subsample was sorted into grass, white clover, other species and dead herbage. Emerged leaf lamina was then separated from the grass and white clover and the respective leaf areas measured on an automatic leaf area meter (Hayshi Denkoh Co. Ltd). Herbage which was no longer green was classified as dead. Partly dead leaves were separated into green and dead fractions. The fractions (including the leaf lamina) were dried separately at 80°C and weighed for calculation of herbage mass and leaf area index.

The densities of ryegrass tillers, Poa tillers, other grass species tillers and white clover shoots were determined from twenty (thirty after 1 May 1976) 20.3 cm^2 cores per plot taken before each grazing and again 8 days after grazing was completed using the technique of Mitchell and Glenday (1958).

4.2.5 Calculation of net herbage accumulation

Net herbage accumulation (P) was calculated for herbage component using the method of Campbell (1966) defined algebraically as:

$$P = \sum_i \left[B_i - A_i + \frac{(B_i - A_i)}{n_i} \ r_i \right]$$

A_i = herbage mass after grazing at the start of rest period i.

B_i = herbage mass before grazing at the end of rest period i.

n_i = number of days between grazings, or length of rest period i.

r_i = number of days sheep grazed at the end of rest period i.

i = number of grazing cycles that P is computed for.

If herbage cuts had been taken during a rest period P could be calculated for incomplete grazing cycles. The last term in the formula is a correction for growth during the grazing period.

4.2.6 Statistical treatment

Analyses of variance were done using the statistical computer programme "TEDDYBEAR" (Wilson, 1978) available on the Massey University Burroughs B6700 computer. Treatments were compared at the 5% significance level.

Despite all plots being treated similarly prior to the experiment, two plots in the ILL treatment had a significantly higher growth rate than the other ten I (Infrequent) plots in the first rest period (12 September to 10 November); viz 118 and 137 kg DM/ha/day compared with 80 ± 3 kg DM/ha/day. The frequency distribution of these twelve growth rates was also significantly skewed to one side (G1= -1.13), but the distribution was not significantly skewed when these two results were excluded (G1 = -0.32). The reason for the difference of these two plots was not a significantly higher stubble mass on 12 September (i.e. laxer grazing) or a significantly higher tiller population on 19 September, but perhaps a greater number of reproductive tillers per unit area. This last parameter was not measured. Net herbage accumulation for these two ILL plots were recalculated as missing plot values for the first rest period. In subsequent grazing cycles the measured yields were used to calculate net herbage accumulation for this treatment.

4.3   RESULTS

4.3.1   Herbage mass

4.3.1.1   Uninterrupted growth

The pattern of uninterrupted growth in spring was obtained from
herbage cuts (Table 4.2) taken from all plots after the first grazing
(12 September) and either from F plots before the grazing at 95%
light interception (26 October) or from I plots two weeks later (10
November).   It took approximately six weeks after grazing in September
for sufficient herbage (3730 kg DM/ha) to accumulate to intercept 95%
of sunlight at noon.   In the following two weeks a further 2250 kg DM/
ha accumulated, increasing the herbage mass to 5980 kg DM/ha on 10
November.   Herbage accumulation was largely green herbage but dead
herbage accumulated at a higher rate in the two weeks after 95% light
interception (35 kg DM/ha/day) than in the previous six weeks (4 kg
DM/ha/day).

Table 4.2:   Herbage mass (kg DM/ha ± SE) and accumulation rates
               (kg DM/ha/day) following grazing on 12 September 1975

	12 September	26 October	10 November
Herbage mass:			
Green herbage	670±30	3450±150	5180±20
Dead herbage	120±10	280± 20	800±70
Total	790±40	3730±160	5980±320
Accumulation rate:			
Green herbage		63	115
Dead herbage		4	35
Total		67	150

It was observed that stem elongation on reproductive tillers had
just commenced when F plots were grazed on 26 October.   Examination of
180 ryegrass tillers from herbage samples cut to ground level revealed
that 37% of ryegrass tillers had visible stem elongation and that the

highest nodes were up to 8 cm above ground-level (mean = 3.5 ± 1 cm).
When I plots were grazed in November many seedheads had emerged.

4.3.1.2 Subsequent regrowth

Changes in herbage mass, and its components, in each treatment
following the first rest period is presented in Figure 4.2.   Grass,
mainly ryegrass, is subdivided into emerged leaf lamina ("grass lamina")
and "grass stubble", which was mainly culms in late spring and mainly
leaf sheath and enclosed lamina in autumn.   The other component of
green herbage, presented as "other species", was mainly white clover,
but also a small amount of flat weeds (*Taraxacum officinale* Weber ex
Wiggers, *Leontodon taraxacoides* (Vill.) Merat, *Crepis capillaris (L).*
(Wallr.).   The last component in the sward was "dead herbage", which
initially was dead leaves, but following flowering also included dead
ryegrass culms.

4.3.1.2.1 Grass stubble

As can be seen from Figure 4.2 and Table 4.3 hard grazing, besides
removing almost all emerged lamina, also removed considerable quantities
of "grass stubble".   In contrast, lax grazing removed relatively
little "grass stubble".   Residual "stubble" either remained in the
sward until removed at a later grazing or until it died and was
classified as dead herbage.   During reproductive growth accumulation of
"grass stubble" was mainly due to culm growth.   The pattern of "stubble"
accumulation in any treatment depended on reproductive growth, residual
"stubble" death, and removal of reproductive meristems.

Table 4.3:   Degree of defoliation of herbage components
               (Expressed as a percentage)

Treatment Grazing period (1975)	FHH 30/11-3/12	FLL 26/11-26/11	IHH 21/12-26/12	ILL 12/12-15/12
"Grass lamina"	97	68	95	83
"Grass stubble"	72	11	46	23
Dead herbage	10	-27	-39	- 1
Total herbage	69	26	52	36

Figure 4.2: Hebage mass (t DM / ha) and accumulation rates (kg DM/ha/day)

92 ± 8	63 ± 6	81 ± 12	32 ± 4	6 ± 6	TOTAL
6 ± 4	-10 ± 3	13 ± 2	-9 ± 3	-20 ± 4	DEAD
86 ± 4	73 ± 4	68 ± 11	41 ± 3	26 ± 3	GREEN

IHH

86 ± 7	81 ± 3	66 ± 11	19 ± 8	-1 ± 4	TOTAL
10 ± 3	21 ± 11	9 ± 10	-20 ± 5	-20 ± 3	DEAD
76 ± 11	60 ± 14	57 ± 5	39 ± 6	19 ± 3	GREEN

IHL

63 ± 1	68 ± 10	56 ± 10	24 ± 6	5 ± 1	TOTAL
12 ± 8	-2 ± 5	26 ± 4	-17 ± 6	-17 ± 2	DEAD
51 ± 8	70 ± 5	30 ± 8	41 ± 6	22 ± 1	GREEN

ILH

105 ± 14	70 ± 7	76 ± 3	3 ± 14	-8 ± 2	TOTAL
33 ± 12	14 ± 8	-1 ± 3	-12 ± 17	-44 ± 3	DEAD
72 ± 14	56 ± 7	77 ± 6	15 ± 9	36 ± 2	GREEN

ILL

MASS

HERBAGE

N   D   J   F   M   A   M   J
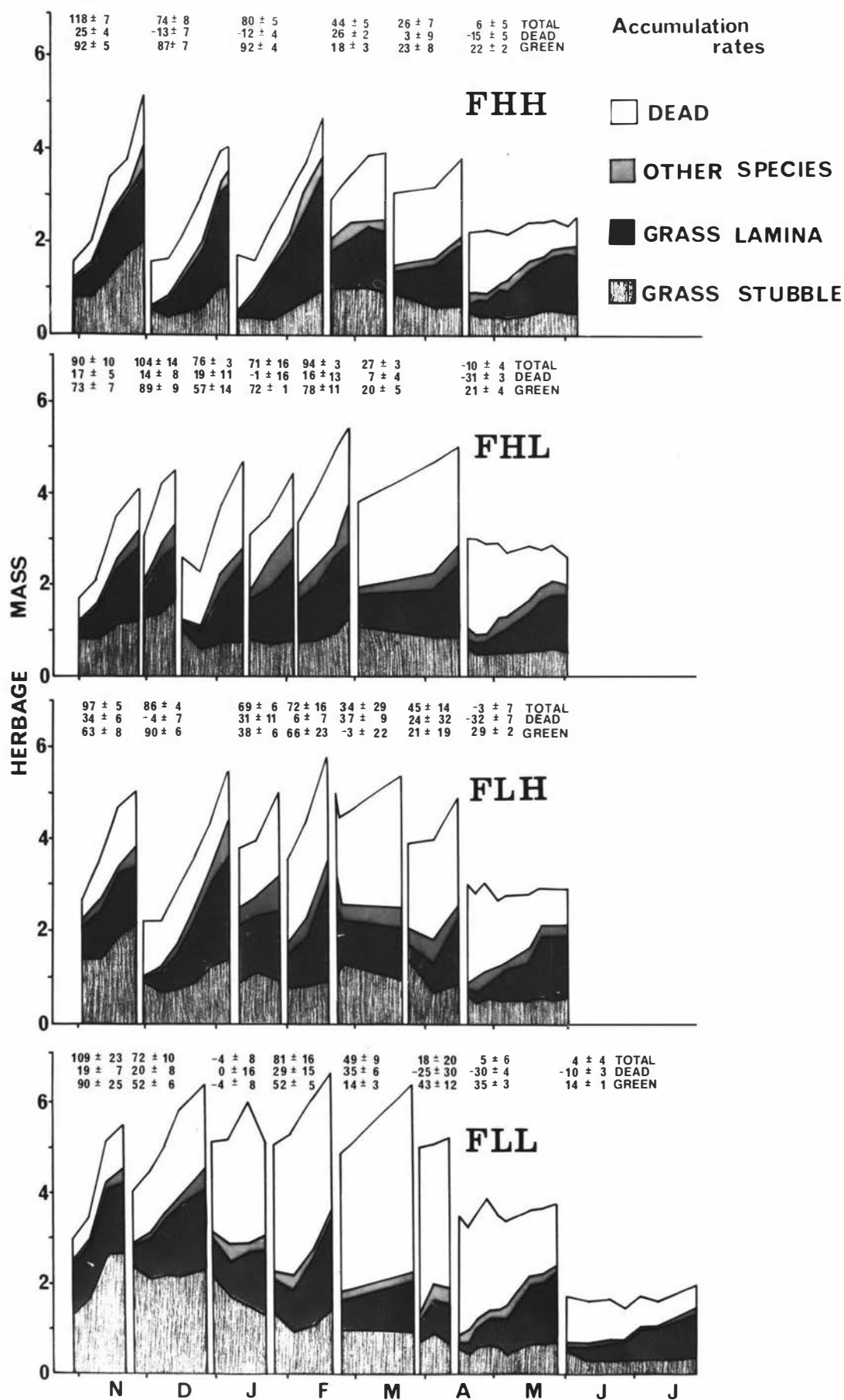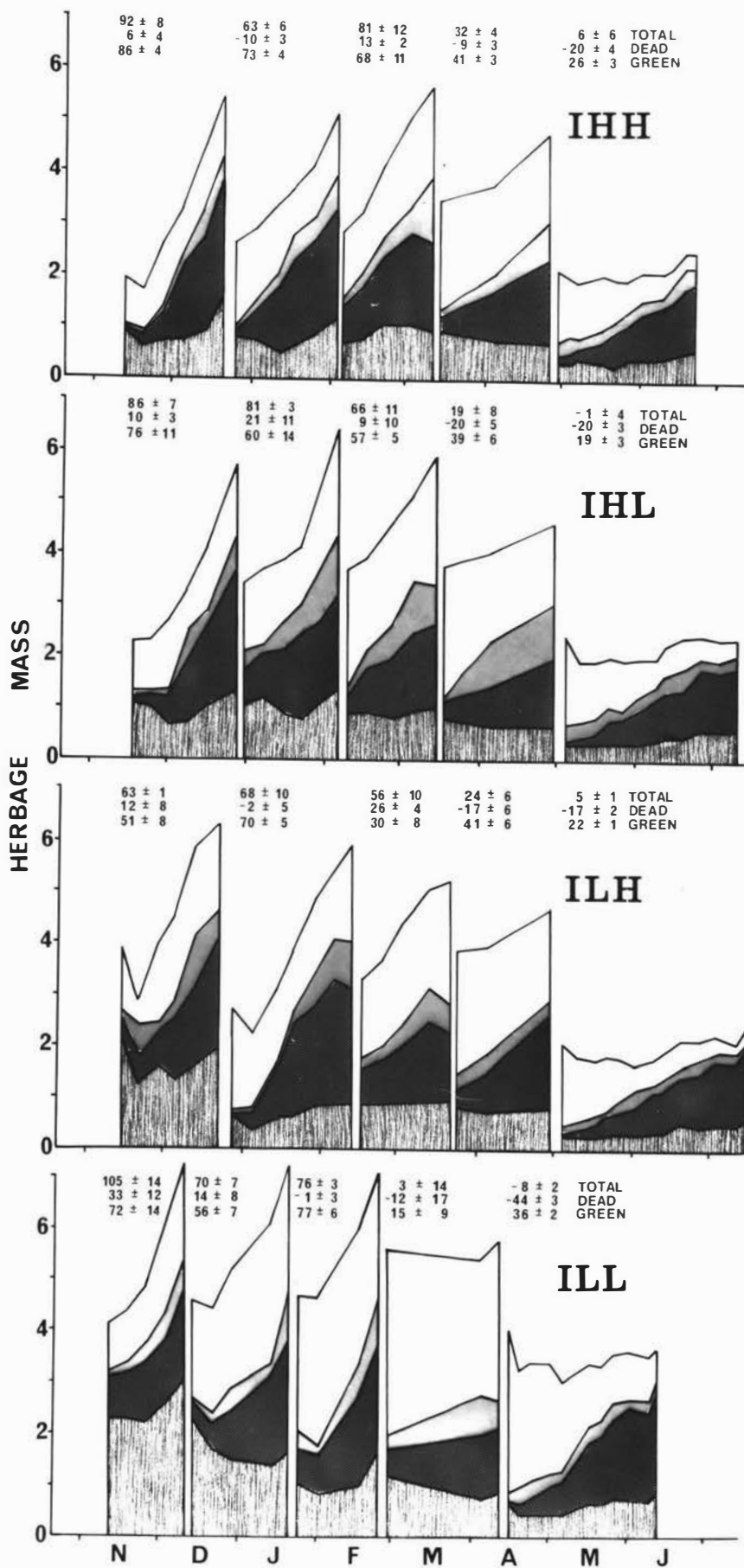
during rest periods for each treatment.

At the first grazing of FLL on 20 October, the reproductive
meristems were below the grazing height and culm growth continued
during the second rest period to 2.7 ± 0.2 t DM/ha (Figure 4.2).
A little "stubble"was removed in the next grazing period (0.3 ± 0.2
t DM/ha), almost entirely emerged inflorescence, and it was not until
January that the amount of "grass stubble" declined.   The decline was
not due to grazing by sheep, but rather the death and subsequent
reclassification of culms as dead herbage.   By the autumn there were
only occasional new reproductive tillers and the "grass stubble" was
almost entirely leaf sheath and unemerged leaf lamina.   A similar
pattern of change in the "grass stubble" component occurred on ILL,
except that many of the seedheads, but little culm, were removed in the
November grazing.

The first hard grazing of FHH and FHL on 25 October removed some
reproductive meristems, but left the later developing reproductive
tillers with intact meristems and these continued to grow in the second
rest period, accounting for most of the increase in grass stubble in
these treatments up to 1 December (Figure 4.2).   It was not until the
second hard grazing, on 1 December for FHH and on 16 December for FHL,
that these tillers were defoliated, and after this the swards remained
in a largely vegetative state with only occasional reproductive tillers
developing.   As on FLL, reproductive tillers continued to develop on
FLH after the first grazing, but on this treatment they were removed in
the hard grazing at the end of November, rather than remaining in the
sward to eventually contribute to dead herbage.

Reproductive tillers were also removed from the sward at the first
hard grazing of I plots which explains the lower levels of "stubble"
recorded after this grazing.   The decline in "stubble" after the first
hard grazing (15 November, IHH; 20 November, IHL; 25 December, ILH) was
caused by the reclassification of defoliated culms, which were up to
6 cm, as dead herbage as they died.   Hard grazing of vegetative swards
removed some "stubble" (e.g. IHH on 25 December) and this increased
again in the following rest period.

Plates 4.3 to 4.6 illustrate the different types of sward that
developed with hard and lax grazing.   On 10 December FHH and IHH were
leafy and vegetative, reproductive tillers having been killed by the

previous hard grazing.   In contrast, FLL and ILL were dominated by reproductive tillers, few reproductive meristems having been removed at previous lax grazings.

It was observed that at the end of rest periods in summer there were usually some ryegrass tillers with freshly emerged seedheads. These were particularly noticable on infrequently grazed plots and following hard grazings on F plots.   This partly explains the accumulation of "grass stubble" in the later stages of regrowth in summer. Where this occurred, the losses of old "stubble" in early regrowth were compensated for by new "stubble" growth within the same rest period.

4.3.1.2.2 Grass lamina

The herbage mass of "grass lamina" is shown in Figure 4.2 between "grass stubble" and "other species".   The amount of "grass lamina" increased in every rest period and the average level at the end of rest periods was 1.5 t DM/ha for F plots and 1.8 t DM/ha for I plots, although this depended on time of year.   In the last two weeks of the rest period in I plots, that is after 95% light interception had been attained, "grass lamina" generally continued to accumulate, generally at rates in excess of 20 kg DM/ha/day.   Leaf lamina was the main component of the vegetative sward to increase during rest periods.

4.3.1.2.3 Other species

"Other species" was a minor component of the sward except in slightly lower lying damper plots where white clover was more abundant. Two plots in particular, one in ILH and one in IHL, had an abundance of white clover in summer which partly accounts for the higher levels of other species in these two treatments.

4.3.1.2.3 Green herbage

The amount of green herbage in swards is shown in Figure 4.2 as the sum of "grass stubble", "grass lamina" and "other species".   Also the accumulation rate for each rest period is shown above the histograms in Figure 4.2.

Plate 4.3: FHH on 10 December 1975.
Seven days after hard grazing. Note the dead
grazed culms. Herbage mass (t DM/ha): Total 1.7,
Grass stubble 0.4, Dead 0.8; LAI = 1.0.

Plate 4.4: FLL on 10 December 1975.
Two weeks after lax grazing. Note the large
number of reproductive tillers. Herbage mass
(t DM/ha): Total 5.1, Grass stubble 2.2,
Dead 1.5; LAI = 3.0.

Plate 4.5:   IHH on 10 December 1975.
             Three days after 95% light interception was
             reached.   The tops of dead culms can be seen
             in the leafy sward.   Herbage mass (t DM/ha):
             Total 4.5, Grass stubble 0.9, Dead 1.2;   LAI = 4.8.

Plate 4.6:   ILL on 10 December 1975.
             Twelve days after 95% light interception was reached.
             The sward is strongly reproductive.   Herbage mass
             (t DM/ha): Total 7.3, Grass stubble 3.0, Dead 1.9;
             LAI = 5.7.   Two areas where herbage cuts have been
             taken can be seen in the foreground.

The pattern of accumulation of green herbage depended mainly on accumulation of "grass lamina" and "stubble". Although the amount of "lamina" always increased during rest periods, changes in the amount of stubble reflected growth of new "stubble" and senescence of culms.

The mean accumulation rate of green herbage for each rest period remained relatively constant during initial rest periods in FHH (92, 87, 92 kg DM/ha/day) whereas it declined in successive rest periods in FLL (90, 52, -4 kg DM/ha/day). Similarly in ILL, the accumulation rate of green herbage was lower than in IHH in the second rest period shown (56 and 73 kg green DM/ha/day respectively). These lower accumulation rates with lax grazing partly reflected stubble death, clearly apparent in January in FLL and in late December in ILL.

4.3.1.2.4 Dead herbage

"Dead herbage" was an important component in all treatments (Figure 4.2). As mentioned, laxly grazed ryegrass culms eventually died and were classified as "dead herbage", which explains the significantly higher amount of dead herbage on the LL treatments in both February and April (Table 4.4). In other treatments the ryegrass culms were eaten by sheep and little dead culm accumulated in the sward. However, not all "dead herbage" was ryegrass culm, there was also considerable accumulation of dead leaf, but as no separation into these two components was made it is not possible to assess the relative contribution of dead culm and dead leaf.

Table 4.4: Effect of grazing treatments on dead herbage mass (t DM/ha).

	4 February	5 April
Intensity Treatment:		
HH	1.04 c	1.64 b
HL	1.64 b	2.06 b
LH	1.50 b	2.12 b
LL	2.97 a	2.82 a
Frequency Treatment:		
F	1.73 a	2.27 a
I	1.85 a	2.05 a

Duncans multiple range test compares intensity or frequency treatments at each date.

The considerable amount of dead leaf that accumulated in swards during summer can be seen in Plates 4.8 and 4.9. Dead culms are also apparent.

Besides culm death, grazing and rust also appeared to increase the amount of "dead herbage". For example, the increase in "dead herbage" between 6 and 10 January on FHH (Figure 4.2) was during grazing and was presumably due to damage of herbage by trampling. Similar increases in "dead herbage" during grazing can be seen in other grazing periods. Also the negative values in Table 4.3 indicate that "dead herbage" accumulated during the grazing period. The increase in "dead herbage" in IHH and ILH at the end of the rest periods in March (Figure 4.2) was largely due to death of ryegrass "lamina" infected with rust (*Puccinia coronata*).

The hard grazings of autumn removed some "dead herbage", and remaining dead ryegrass culms were trodden down onto the soil surface. On all treatments a decline in the amount of "dead herbage" occurred following these hard grazings, with net rates of disappearance between 10 and 44 kg DM/ha/day (Figure 4.2). The amount of dead herbage in vegetative swards also declined following hard grazing of FHH and IHH in December, at rates of 13 and 10 kg DM/ha/day respectively.

4.3.1.2.5 <u>Total herbage</u>

Total herbage mass is shown in Figure 4.2 as the sum of "grass stubble", "grass lamina", "other species" and "dead", that is, the top of the histograms. The accumulation rate for each rest period is shown above the histograms.

Accumulation of total herbage reflected not only changes in green herbage, but also the accumulation or disappearance of dead herbage. Where dead herbage accumulated in the sward, the rate of accumulation of total herbage was greater than that for green herbage. This occurred in spring and summer, except after hard grazing, but in autumn the high disappearance rates of dead herbage substantially reduced the total herbage accumulation rate.

The variation in sward composition was greater on laxly grazed

Plate 4.7: FHH on 7 March 1976.
            Three weeks after lax grazing.   Herbage mass
            (t DM/ha): Total 3.2, Dead 1.5.

Plate 4.8: FLL on 7 March 1976.
            Three weeks after grazing.   Herbage mass (t DM/ha):
            Total 5.0, Dead 3.0.   Note the mat of dead herbage
            at the base of the sward.

plots possibly because of greater opportunity for selective grazing. Sampling of herbage became more difficult as patchiness developed with lax grazing and this explains the high coefficients of variation in accumulation rates following lax grazing. The hard grazings in autumn made the swards more uniform.

4.3.2 Net herbage accumulation

The experiment has been divided into two approximately equal periods for comparison of the effects of the treatments, *viz* a "spring/summer" period (12 September to 28 February) and an "autumn/winter" period (1 March to 28 July). During the 24 week "spring/summer" period 13.0 t DM/ha of herbage accumulated, compared with only 1.9 t DM/ha in the following 22 weeks. Since dead herbage accumulated in the first period and disappeared in the autumn, the difference between the two periods was smaller when the comparison was made on the basis of green herbage accumulation (11.5 and 3.4 t DM/ha respectively).

4.3.2.1 Grazing interval

The effect of the two grazing interval treatments on herbage accumulation is presented in table 4.5. Grazing interval did not significantly affect total herbage accumulation, but it did affect green and dead herbage accumulation.

With infrequent grazing significantly more green herbage accumulated (12% or 1.75 t DM/ha), but the difference was not evident as total herbage accumulation because of dead herbage disappearance. When compared during "autumn/winter" the difference between grazing frequencies was greater, with 57% (1.52 t DM/ha) more green herbage accumulating in I. This difference in green herbage accumulation in autumn resulted from significantly greater accumulation of both grass and white clover in I.

In "spring/summer" there was a significant interaction between grazing interval and grazing intensity for green herbage (and grass) accumulation (Table 4.6). There was no significant difference in green herbage accumulation between grazing intervals at three intensities (HH, HL, LH), but in LL significantly more green herbage accumulated with infrequent grazing.

Table 4.5:   Effect of grazing interval on net herbage
               accumulation (t DM/ha).

	Spring/summer		Autumn/winter		Whole experiment	
	F	I	F	I	F	I
GREEN HERBAGE:						
Grass	9.57 a	9.46 a	2.57 b	3.36 a	12.15 a	12.87 a
White clover	1.58 a	1.86 a	0.09 b	0.78 a	1.66 a	2.59 a
Other Species	0.21 a	0.29 a	0.00 a	0.04 a	0.22 a	0.33 a
Total	11.36 a	11.61 a	2.66 b	4.18 a	14.03 b	15.78 a
DEAD HERBAGE:	1.52 a	1.56 a	-0.85 a	-2.19 b	0.67 a	-0.64 b
TOTAL HERBAGE:	12.88 a	13.17 a	1.81 a	1.99 a	14.70 a	15.15 a

Duncans multiple range test compares F and I for each component

Table 4.6:   Net accumulation of green herbage in "spring/summer"
               (t DM/ha).   LSD (5%) = 1.34

	F	I
HH	13.82	12.97
HL	12.07	11.55
LH	10.90	9.95
LL	8.64	11.98

Table 4.7:   Net accumulation of "lamina" during summer
               (t DM/ha).   LSD (5%) = 0.91

	F	I
HH	6.28	6.24
HL	5.55	4.93
LH	4.97	5.02
LL	4.22	5.68

Accumulation of "lamina" (grass + clover) could only be calculated after 15 November as "lamina" was not separated in all treatments prior to this date. In summer (15 November to 28 February) there was a significant interaction between grazing interval and grazing intensity for "lamina" accumulation (Table 4.7). As with green herbage, there was no significant difference in lamina accumulation in HH, HL, or LH, but in LL significantly more "lamina" accumulated in I than F. In the "autumn/winter" period the interaction was not significant, and significantly more "lamina" accumulated in I than in F (3.77 and 3.33 t DM/ha respectively).

Significantly more dead herbage (1.31 t DM/ha) disappeared from the sward with infrequent grazing (Table 4.5). The difference in dead herbage disappearance occurred in the "autumn/winter" not in the "spring/summer" when grazing interval did not significantly influence the amount of dead herbage accumulating. At the beginning of autumn F and I had similar amounts of dead herbage (Table 4.4), approximately 2 t DM/ha. During the grazing periods of "autumn/winter" 0.74 t dead herbage disappeared from F, due presumably to eating and trampling into the soil, while 0.23 t DM/ha accumulated in I. Thus, the difference in net dead herbage loss during rest periods (Table 4.5) reflected a difference in the amount of herbage available for decay.

4.3.2.2 Spring/summer grazing intensity

The spring/summer grazing intensity treatments affected herbage accumulation in the "spring/summer" period, but had no significant residual effect in "autumn/winter", so that treatment differences in "spring/summer" were similar to those for the whole experiment (Table 4.8). The HH treatments accumulated 2.9 t DM/ha (20%) more herbage over the whole experiment than the LL treatments, and the two alternating treatments, HL and LH, were intermediate.

In "spring/summer" dead herbage accumulation was over four times greater on LL than on HH, and HL and LH were intermediate. Relatively large differences in dead herbage disappearance in "autumn/winter" were not significant, due mainly to the high variation in some treatments caused by the difficulty of measuring this component.

Table 4.8:   Effect of grazing intensity on net

herbage accumulation (t DM/ha)

	GREEN HERBAGE				DEAD	TOTAL
	Grass	White Clover	Other species	TOTAL	HERBAGE	HERBAGE
SPRING/SUMMER						
HH	11.70 a	1.25 a	0.44 a	13.40 a	0.53 b	13.93 a
HL	9.38 b	2.08 a	0.35 ab	11.81 b	1.88 a	13.70 ab
LH	8.44 .b	1.85 a	0.14 bc	10.43 c	1.51 ab	11.94 c
LL	8.54 b	1.69 a	0.08 c	10.31 c	2.22 a	12.53 bc
AUTUMN/WINTER						
HH	2.69 a	0.82 a	0.01 a	3.52 a	-0.95 a	2.57 a
HL	2.87 a	0.57 a	-0.02 a	3.42 a	-1.77 a	1.65 a
LH	3.05 a	0.05 a	-0.05 a	3.14 a	-0.88 a	2.26 a
LL	3.26 a	0.30 a	-0.03 a	3.59 a	-2.47 a	1.11 a
WHOLE EXPERIMENT						
HH	14.50 a	1.98 a	0.47 a	16.94 a	-0.40 a	16.54 a
HL	12.26 b	2.65 a	0.33 ab	15.24 b	0.08 a	15.32 ab
LH	11.48 b	1.90 a	0.19 b	13.57 c	0.63 a	14.20 bc
LL	11.80 b	1.98 a	0.11 b	13.89 c	-0.25 a	13.64 c

Duncans multiple range test compares intensity treatments for each component.

As mentioned in the previous section (4.3.2.1) there was a significant
interaction between grazing frequency and intensity treatments in green
herbage (Table 4.6), "lamina" (Table 4.7) and grass accumulation.   With
frequent grazing, a significantly higher amount of green herbage
accumulated with the HH treatment, and least with the LL treatment.   The
alternating intensity treatments, FHL and FLH, were not significantly
different and accumulated an intermediate amount of green herbage.
Accumulation of "lamina" and grass followed a similar response with
frequent grazing.   When grazing was infrequent, LH had the lowest green
herbage and grass accumulation, and there was no significant difference
between the three other intensity treatments.   "Lamina" accumulation in
summer with infrequent grazing was greatest in HH and there was no
significant difference between the other three intensity treatments.

Net green herbage accumulation was also calculated for the period when
the spring grazing intensity treatments were actually applied (26

October to 3 February). There was a significant (P < 0.05) correlation (r = 0.79) between the number of hard grazings (FHH = 3, FHL = 2, FLH = 1, FLL = 0) and accumulation. Each additional hard grazing in October-December resulted in a 20% (14 kg DM/ha/day) increase in daily accumulation rate with frequent grazing. This response reflects the decreased green herbage accumulation rates that occurred following lax frequent grazing (Figure 4.2, compare accumulation rates in FHH and FLL).

Net accumulation of white clover was not significantly affected by the intensity treatments. Accumulation of other species, a minor sward component, was greatest on HH and least on LL, with HL and LH being intermediate.

4.3.3 Leaf area index (LAI)

4.3.3.1 Residual leaf area index

Despite considerable variation in residual LAI following either hard or lax grazing in late spring/early summer, a contrast was maintained between treatments (Table 4.1). With lax grazing it was not possible to exactly control the consumption of herbage by sheep and this explains the variation in residual LAI following this type of grazing.

At the beginning of the second rest period all F or I plots had received similar pre-treatments so that the effects of different grazing intensities on regrowth could be investigated. The residual LAI ranged from 0.6 to 2.4 on F plots and from 0.3 to 2.0 on I plots. Correlation coefficients and linear regression equations were calculated for the net accumulation rate of herbage components and the residual LAI (Table 4.9). In the two weeks following grazing (20/10 to 3/11 in F or 10/11 to 24/11 in I) there was no significant correlation between residual LAI and the accumulation of total herbage, green herbage or dead herbage. Following the grazing in October of the F plots the accumulation rates of the components of green herbage, leaf lamina and non-leaf, were significantly correlated with residual LAI. A unit increase in residual LAI was associated with a decreased leaf accumulation rate of 15 $\pm$ 6 kg DM/ha/day and an increased non-leaf accumulatio

rate of 29 $\pm$ 9 kg DM/ha/day.   The non-leaf was mainly ryegrass culm
(4.3.1.2.1).   Although these two regressions were significant they only
accounted for 40-50% of the variation in accumulation rate.   Leaf
and non-leaf accumulation were not significantly correlated with LAI
after the November grazing of I plots.

Table 4.9:   Correlation coefficients between residual LAI and
accumulation rate (kg DM/ha/day) for different herbage
components measured over the first two weeks regrowth
in October (Frequent) or November (Infrequent)

	Frequent	Infrequent
Leaf lamina	-0.624*	-0.287 n.s.
Non-leaf	0.711**	-0.017 n.s.
Green herbage	0.467 n.s.	-0.150 n.s.
Dead herbage	0.131 n.s.	0.125 n.s.
Total herbage	0.529 n.s.	0.166 n.s.

Correlation coefficient significantly different from 0 at 1%**, 5%*,
or non-significant n.s.

4.3.3.2   LAI at 95% light interception

There was considerable variation in leaf area indices measured
at 95% light interception.   No consistent seasonal trends were apparent
within treatments so data has been pooled (Table 4.10).   Grazing
interval did not significantly influence the LAI measured at 95% light
interception.   In summer the LAI measured at 95% light interception was
affected by the previous grazing, being greater where the previous
grazing was hard.   For example, a LAI of 8.0 was measured at 95% light
interception in FHH on 6 January compared with 4.7 in FLL on 28 December.
Swards in FHH were vegetative with little "dead herbage" (560 kg DM/ha)
while swards in FLL contained more "dead herbage" (1780 kg DM/ha)
and considerable amounts of "stubble" (2330 kg DM/ha).   Much of the
"stubble" and "dead herbage" after lax grazing was ryegrass culm and
this also intercepted light above the measuring sensor (2.5 cm above
ground level).

Table 4.10:   LAI at 95% light interception (Pooled
                results for all treatments)

	F	I	LSD(5%)	Mean
SUMMER (Dec-Jan):				
Previous grazing hard	6.3	5.5	n.s.	6.0
Previous grazing lax	5.0	4.5	n.s.	4.8
L.S.D. (5%)	1.0	n.s.		0.8
Mean	5.6	5.0	n.s.	5.3
AUTUMN (Feb-March)	3.1	3.3	n.s.	3.2
WINTER (June)	2.9	3.0	n.s.	2.9

The LAI at 95% light interception was lower in autumn and winter
than in summer.   LAI measured in autumn were for swards containing
considerable amounts of dead herbage and this, together with the seasonal
decline in light intensity, accounts for the decrease between summer
and autumn.   During winter, the swards were vegetative with dead
herbage largely trampled below 2.5 cm, so the lower LAI reflected the
lower light levels of winter.

On infrequently grazed plots, the LAI continued to increase with
further accumulation of "lamina" (Figure 4.2) after 95% light inter-
ception had been reached.

4.3.4 Tiller populations

4.3.4.1 Sward development

Tiller cores taken during the experiment show changes which occurred
as the sward developed (table 4.11).   Both ryegrass and white clover
increased in percentage occurrence during the experiment due to tillering
and stolon growth.   White clover initially present in 20% of cores
increased to 65% presence by the end of the experiment.   Ryegrass was
more evenly distributed than white clover (initially 77% occurrence), and
eventually was present in almost all cores.   The continuing growth of
plants resulted in increased density of both ryegrass tillers and white
clover shoots.   *Poa* spp. (*P. annua* L. and *P. trivialis* L.) was the other

Table 4.11: Tiller and shoot densities (thousand/m^2), and percent species occurrence in cores (arcsin $\sqrt{}$ %, natural mean in parenthesis).

Sampling date:	1 Aug 75	19 Sept 75	21 Jan 76	1 Aug 76
Tiller and Shoot density:				
Ryegrass	3.0±0.4	5.3±0.3	7.1±0.2	6.6±0.3
Poa	n.a.	2.0±0.1	3.5±0.3	2.7±0.2
White clover	0.3±0.04	0.2±0.05	1.1±0.2	1.9±0.3
Occurrence:				
Ryegrass	1.07±0.02(*77*)	1.08±0.02(*78*)	1.33±0.03(*94*)	1.43±0.02(*98*)
Poa	0.76±0.03(*47*)	0.80±0.02(*57*)	1.06±0.03(*76*)	0.98±0.03(*69*)
Other grass species	0.50±0.02(*23*)	0.35±0.02(*12*)	0.27±0.04(*7*)	0.20±0.02(*4*)
White clover	0.48±0.03(*21*)	0.46±0.03(*20*)	0.75±0.04(*46*)	0.94±0.05(*65*)

n.a., not available

main component of the sward and this also increased in percent occurr-
ence with time.   Despite one third of tillers being *Poa* they contributed
little to production since ryegrass tillers were considerably larger.
Other grass species (mainly *Bromus mollis* L. *Glyceria fluitans* (L) R.Br.,
Agrostis tenuis Sibth., *Cynosurus cristatus* L. and *Holcus lanatus* L.)
were only a minor component of the sward.

4.3.4.2 Treatment effects

Although tiller cores were taken regularly before and after each
grazing, most of this data is not presented because of difficulties in
interpretation.   Besides the effect of treatments, there was considerable
seasonal variation in tiller populations which confounded responses
since data was not collected from all treatments on the same date.
Also, the densities measured before and after grazing were sometimes
greatly different.   Even at a given sampling, ryegrass tiller density
often had a coefficient of variation of 20% and occasionally 30%.
No distinction was made between vegetative and reproductive tillers
although it was observed that reproductive tillers often remained green
at the base for some time after growth had ceased.   Because of the
inaccuracies and the considered importance of tillering, it was decided
to examine this characteristic in detail in a later study.

4.3.4.2.1 Ryegrass tiller density

The effect of treatments on tiller density was compared on three
dates (September, January and August) when all treatments were sampled
within a short period of time (Table 4.12).   As expected, 8 days after
the start of the experiment (19 September) ryegrass tiller density was
not significantly affected by treatments.   In January, after the
grazing intensity treatments had been completed, it was found that
ryegrass tiller density was significantly affected by the intensity but
not frequency treatments.   Those treatments which had been hard grazed
were not significantly different, but the LL treatment had a lower tiller
density.   At the end of the experiment, 1 August, differences in
ryegrass tiller density were no longer significant.

To allow comparison with later experiments, ryegrass tiller density
for FHH and FLL at each grazing is presented (Figure 4.3).   To enable

Table 4.12: Effect of grazing treatments on ryegrass tiller
density (thousand tillers per m^2)

	19 Sept	21 Jan	1 Aug
Intensity treatment:			
HH	4.4 a	7.9 a	6.3 a
HL	4.9 a	6.8 ab	6.3 a
LH	5.3 a	8.0 a	7.0 a
LL	6.5 a	5.6 b	6.7 a
Frequency treatment:			
F	5.0 a	7.5 a	7.1 a
I	5.6 a	6.7 a	6.0 a

Duncans multiple range test compares intensity or frequency treatments for each date.

trends to be more easily seen the average density at each grazing
(before and after) has been plotted also.   Between late December and
March ryegrass tiller density was greater in FHH than in FLL.   During
April-June fluctuations in density from before grazing to 8 days after
grazing were considerably greater than the difference between FHH and
FLL.

4.3.4.2.2 *Poa* and white clover

White clover shoot density was not significantly affected by the
treatments in September, January or August.   *Poa* tiller density was not
significantly affected by the treatments in September or January, but in
August ILL had twice as many *Poa* tillers as other treatments (Table 4.13).

Table 4.13: Effect of treatments on *Poa* tiller density on
1 August 1976 (thousand tillers per m^2).
LSD (5%) = 2.0

	F	I
HH	3.1	1.5
HL	2.4	2.2
LH	2.2	2.9
LL	1.4	5.7
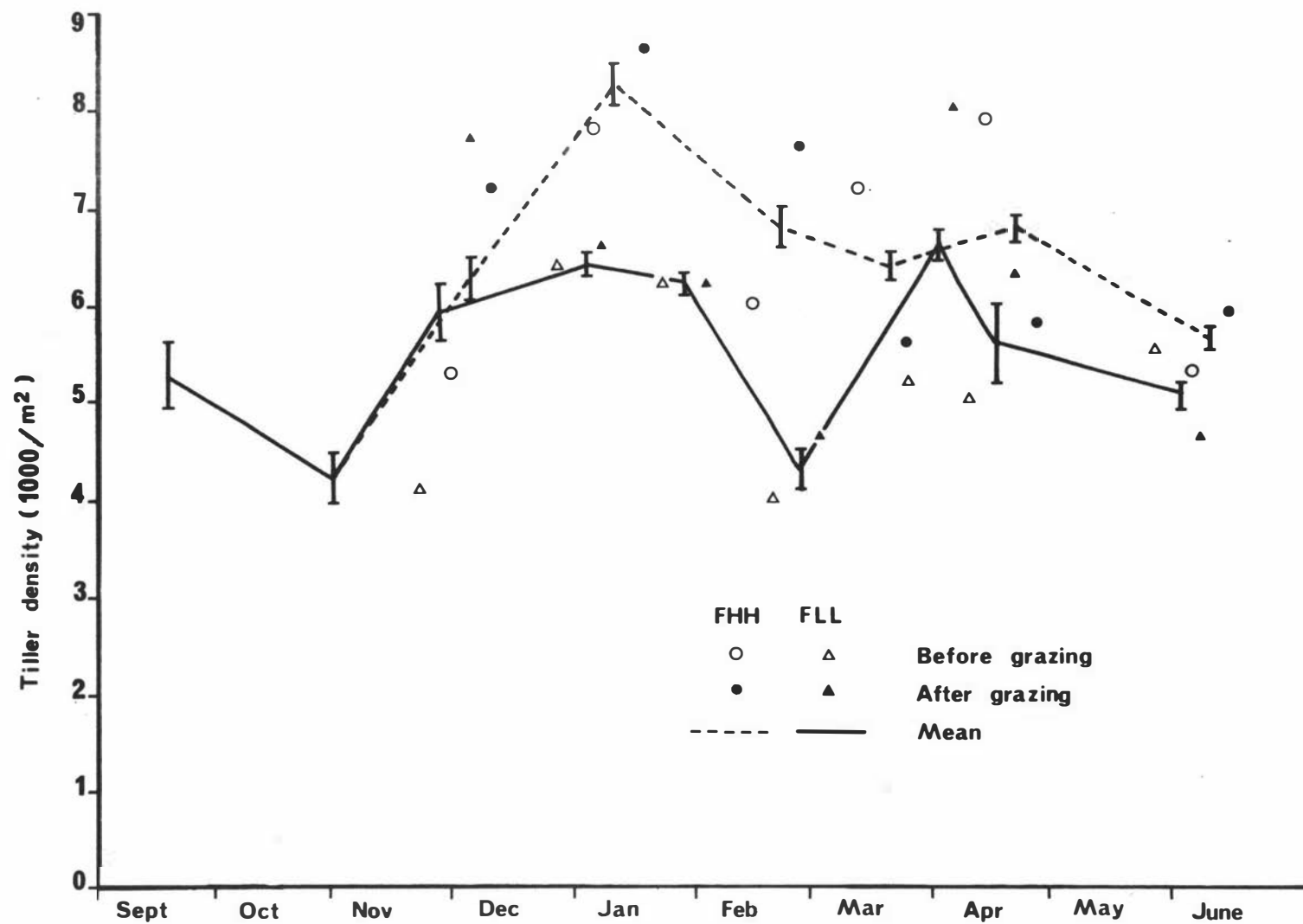
Figure 4.3: Ryegrass tiller density at each grazing in FHH and FLL.

4.3.4.3 Aerial tillers

It was observed that many defoliated reproductive ryegrass tillers developed aerial tillers on the residual nodes. Some of these rooted, but many were several cm above the soil surface. On 21 January, four 22 cm diameter cores were taken per plot and the number of aerial tillers per core counted to see if the presence of aerial tillers was affected by the treatments (Table 4.14). Aerial tillers occurred even in closely grazed pasture, but would not have been noticed by the casual observer because they were on the short (1-3 cm) culm bases left after grazing. Treatments which left more culm in the sward, and therefore more nodes above ground, resulted in more aerial tillers. Plots not grazed hard until the second grazing (LH) had significantly more aerial tillers than those grazed hard at the first grazing (HH and HL) because of the difficulty in forcing sheep to graze the more mature culm bases at a later date. Since sheep were able to largely avoid grazing culms in the LL treatment most aerial tillers were found in this treatment. Infrequently grazed swards had significantly more aerial tillers than frequently grazed swards, a reflection of the difference in culm development, especially at the first grazing.

Table 4.14: Effect of treatments on aerial tiller density
             (tillers/m^2)

	Density
Frequency treatment:	
F	170 b
I	260 a
Intensity treatment:	
HH	70 c
HL	70 c
LH	230 b
LL	490 a

Duncans multiple range test compares
intensity or frequency treatments,

4.4 DISCUSSION

4.4.1 The influence of reproductive growth

Light interception was used as a criterion for defoliation in this experiment, but during the late spring reproductive growth appeared to greatly influence the pattern of herbage accumulation. For example, in Table 4.9 a positive correlation between non-leaf accumulation and residual LAI after defoliation in October, but not after defoliation in November, probably reflected different stages of reproductive development at the time of grazing. In October stem elongation had just started in ryegrass, and hard grazing removed some apical meristems while few were removed by lax grazing. The positive correlation could have reflected different amounts of culm growth. In November, many seedheads had emerged and little further culm growth could be expected since even lax grazing resulted in meristems being removed. The lack of correlation between residual LAI and non-leaf accumulation could be interpreted as reflecting no culm growth on this occasion.

Tainton (1974b) compared two treatments during September, October, November, similar to IHH and ILL in this experiment and found no significant difference in total net production, but greater net green herbage production from lax grazing. He commented that this was not due to greater leaf area, but to the recovery of a greater proportion of older tillers in the sward. Since grazing occurred in mid-October when reproductive meristems could be expected to be defoliated by hard grazing, but not by lax grazing, the advantage was probably due to reproductive growth again. In this experiment the first grazing of IHH and ILL occurred in November at the head emergence stage when little recovery could be expected from older reproductive tillers. In fact, regrowth seemed to depend on the appearance of new tillers from grazed stubs of flowering tillers, most vegetative tillers having died.

Although IHH and ILL were clearly defined in terms of light interception by Tainton and in this experiment, different responses were obtained, reflecting the stage of reproductive development at grazing. Sheard and Winch (1966) also found that reproductive growth greatly affected herbage production when light interception was used as a criterion for defoliation. However, observations on reproductive

development were largely visual in this study so it was decided to examine reproductive growth in greater detail in a later study.

4.2.2 Dead herbage

Herbage was divided into live and dead components to show the optimum stage for defoliation but changes in the amount of dead leaf were mostly not obvious because of the presence of dead culm. This contrasts with other studies (Hunt, 1970 a, b; Tainton, 1974 a,b) where dead culm was absent and changes in dead leaf were obvious. In the first rest period of the experiment (Table 4.2) there was no dead culm and dead herbage accumulated at a higher rate after full light interception than before full light interception (35 and 4 kg DM/ha/ day respectively). Tainton (1974 a) also reported that the rate of leaf senescence increased rapidly from about the time that full canopy was attained.

The seasonal pattern of dead herbage accumulation and disappearance was similar to that reported by Campbell (1964). Dead herbage mass increased during summer and then decreased in autumn and winter. It is interesting to note that in autumn the total herbage accumulation rate was less than 10 kg DM/ha/day but green herbage accumulated at up to 36 kg DM/ha/day (Figure 4.2).

As shown by Rattray (1978), an increased proportion of dead herbage in the sward reduced the *in vitro* digestability (Figure 4.4). Continued lax grazing in late spring, by encouraging the accumulation of dead herbage (Table 4.4), can be expected to result in swards of low nutritive value. Conversely, continued hard grazing should result in swards of high nutritive value.

4.4.3 Grazing intensity

The intensity treatments were based on residual LAI and indeed where grazing was "hard" relatively little lamina remained after grazing compared with "lax" (Table 4.1). However, although "hard" grazings removed most lamina, the degree of defoliation for total herbage was often less than 50% (Figure 4.2 and Table 4.3). With "lax" grazings the degree of defoliation was even lower. Dead herbage was
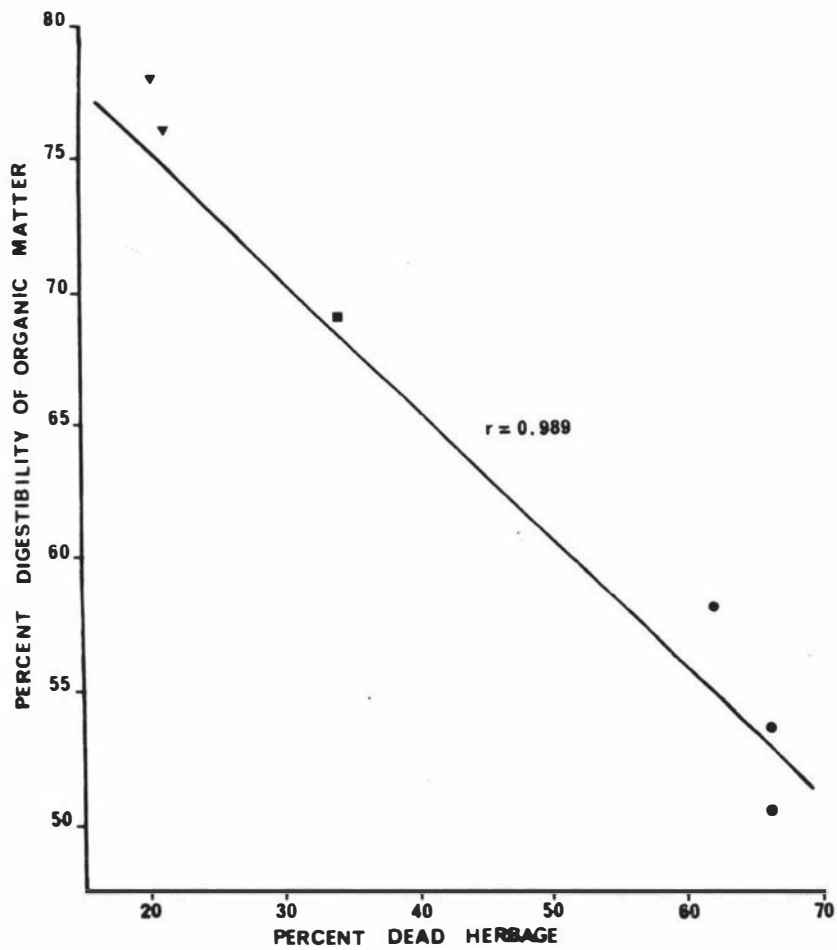
Figure 4.4: In vitro digestibility of organic matter and percent dead
herbage. Samples: ■ FHH, 2 Feb; 3 weeks after grazing.
                   ▼ IHH, 4 Feb; before grazing.
                   ● ILL, 2 Feb; 8 days after grazing.
Standard: in vivo digestibility 64%; in vitro 68%.

avoided, as also found by others (McBride *et al*, 1967; Thomson, 1977), and to increase the degree of defoliation it would have been necessary to force sheep to consume greater amounts of dead herbage.

There was a 20% advantage of close (HH) over lax (LL) grazing in herbage accumulation, mainly resulting from greater green herbage accumulation in spring/summer. No residual effect of spring grazing intensity was detected in the autumn/winter.

With frequent grazing significant relationships were established showing that increased residual leaf area reduced green herbage accumulation. There was a positive correlation between the number of hard grazings and green herbage accumulation, and in the two weeks following defoliation on 20 October there was a negative correlation between leaf accumulation and residual LAI (4.3.3.1). This result was surprising since the general finding had been that increased leaf area index causes greater light interception and accelerated growth rate (Brown and Blaser, 1968). Greater light interception may not have occurred with lax grazing because although the residual LAI was higher, the LAI at 95% light interception was lower (Table 4.10). For example, when the average LAI for FHH and FLL was calculated by numerical intergration for the period 25 October to 18 February no significant difference was found (3.3 and 3.4 respectively). Even if greater assimilation did occur with lax grazing, greater losses through death and decay (Morris, 1970), or greater translocation of assimilate to leafless culms (where it would presumably be lost in respiration), obscured this. Holmes and McClenaghan (1979) have also reported higher net pasture growth rates with closer grazing in spring.

During the spring/summer period more green herbage accumulated in IHH than in either IHL or ILH (Table 4.6), a pattern similar to that found with frequent grazing. ILL did not follow this pattern however, accumulating a similar amount of green herbage to IHH. This difference may have been due to greater secondary reproductive growth in ILL but this hypothesis cannot be confirmed because reproductive tillers were not separated from vegetative tillers.

The sampling of tiller populations in January was after most reproductive tillers had died and so it largely recorded vegetative

tillers. Despite the sward being relatively open in early spring
(Table 4.11) continued lax grazing reduced ryegrass tiller density
almost 30% compared with continued hard grazing (Table 4.12). These
results are similar to those from other grazing experiments (Tainton
1974 a; Boswell and Crawford, 1978) and are in accordance with the
conclusions of Langer (1963) and Davies (1977) who both noted that
close, but not too severe grazing, favoured tiller numbers.
Alternating grazing intensity treatments prevented the decline in tiller
population; a similar result to that of Ollerenshaw and Hodgson (1977)
with cut perennial ryegrass swards. With grazing intensities similar
between February and July the difference between treatments disappeared,
illustrating the dynamic nature of ryegrass tiller populations.

Except for greater invasion by *Poa* in ILL between January and
August there was no effect of treatments on botanical composition
measured as species occurrence in tiller cores. The reason for this
greater ingress of *Poa* was perhaps a combination of greater seeding
by *Poa* and lack of competition from ryegrass in ILL.

4.4.4 Grazing interval

A number of grazing experiments have shown that herbage production
was increased by doubling or tripling the grazing interval (Table 4.15).
In comparison to these other experiments both F and I in this
experiment were relatively infrequent and the difference between F and
I was relatively small. Tainton (1974 b) compared treatments
essentially the same as FHH and IHH. In contrast to this experiment
where no significant difference in herbage accumulation was detected
between F and I during the "spring/summer", Tainton (1974 b) obtained
12% greater herbage production from more frequent grazing. The difference
in results was due to the method of calculating production by Tainton.
This will be discussed further in Chapter 7 (7.1).

Tainton (1974 a,b) found that the rate of green herbage accumulation
declined quickly after 95% light interception was reached, explaining
the reduced production with less frequent grazing. The rate of green
herbage and grass "lamina" accumulation (also mentioned by Tainton)
only declined markedly after 95% light interception was reached in one
regrowth in eight during summer in this experiment (Figure 4.2). This
will be discussed in Chapter 7 (7.2.2.1).

Table 4.15:   Length of rest periods in some grazing
              experiments (days)

	Frequent	Infrequent
This experiment (average)		
HH	35	45
LL	32	43
Weeda (1965)	10	21
Campbell (1969)	7	28
Pineiro and Harris (1978 a)	14-28	28-56
Holmes and McClenaghan (1979)	10	21

The most notable effect of grazing frequency was in the "autumn/
winter" period when 57% more green herbage accumulated with infrequent
grazing.   Many of the regrowth curves for green herbage in "autumn/
winter" have a lower slope in early regrowth than in late regrowth,
especially where grazing was frequent (Figure 4.2).   Also there was
no marked decline in green herbage accumulation after 95% light
interception.   This suggests that the greater herbage accumulation in I
resulted from pasture being in the linear phase of growth longer.
This result is of considerable relevance to all-grass wintering systems
where infrequent defoliation (60-90 days depending on pasture growth)
is common in autumn and winter (Hook, 1978).   Considerably more herbage
can be accumulated by delaying grazing for two weeks after 95% light
interception, without significantly reducing tiller density or the
white clover content of the pasture.   Very long regrowths in autumn
and winter will however reduce both herbage accumulation and the clover
content of the sward (Brougham, 1970).   The optimum defoliation interval
for autumn and winter has yet to be defined, but it is at least two
weeks after 95% light interception.

3.4.5 Aerial tillers

The occurrence of aerial tillers on ryegrass have been reported
previously (Kydd, 1966; Hayes, 1971; Simons *et al*, 1974; Tainton,
1974b; Minderhound, 1978).   Although aerial tillering is not always

associated with flowering, Simons *et al* (1974) found that aerial
tillers frequently develop on the remains of flowering stems, and
the observations in this experiment (Table 4.14) suggest that most
aerial tillers were from this origin.   The persistence and production
of aerial tillers was investigated in a later study.

CHAPTER 5 THE EFFECTS OF THE TIMING AND INTENSITY OF SPRING GRAZINGS ON THE HERBAGE PRODUCTION AND TILLERING OF RYEGRASS DOMINANT PASTURE

5.1 INTRODUCTION

The previous experiment suggested that reproductive growth markedly influenced herbage production. As observations on stages of reproductive development were limited it was decided to relate defoliation treatments to stages of reproductive development in another experiment.

The interruption of reproductive development by mowing of pure grass swards has shown that interruption at anthesis will give the maximum annual herbage dry matter yield (Bird, 1943; Austenson, 1963; Bonin and Tomlin, 1968 a,b; Gillet, 1973; Corrall, 1974; Mislevy et al, 1977; Gervais and St Pierre, 1979; Corrall et al, 1979). However, the nutritive value of grass swards decline markedly during culm growth (Pritchard et al, 1963; Terry and Tilley, 1964) so that the advantage of defoliation at anthesis is reduced if herbage quality (annual yield of D.O.M., T.D.N., or protein) is considered. The mowing experiments mentioned above were all conducted overseas and there is little comparable local data for grazed ryegrass/clover swards. Besides possible differences in herbage production, botanical composition of ryegrass/clover swards could be altered by permitting different amounts of ryegrass reproductive growth.

The choice of grazing regime depends not only on annual herbage production, but also on the pattern of production. In the previous experiment pasture growth rate declined with successive lax grazings in early summer, whereas with successive close grazings it remained relatively constant (4.3.1.2.4). Extension workers (e.g. Hall, 1973) have observed that removal of reproductive tillers by close defoliation, or by mechanical topping (Matthews, 1975), will promote "vigorous leafy growth into a period when a pasture which has been allowed to seed will be in a phase of relatively poor vegetative growth". The following experiment examines the pattern of herbage production after different timings and intensities of grazing during the period of ryegrass

reproductive growth.

A possible reason for reduced growth from a pasture allowed to seed could be a reduced tiller density. Allowing reproductive growth normally results in a decline in vegetative tiller density (Spiertz and Ellen, 1972; Hebblethwaite and Ivins, 1977, 1978; Ong *et al*, 1978b) and decapitation of reproductive tillers could be expected to increase tillering (Asano and Chujo, 1975; Krause and Moser, 1977). In the following experiment the influence of differences in tiller density, resulting from different amounts of reproductive growth, on herbage production was investigated.

In the previous experiment it had been hoped that tiller cores taken before and after each grazing would show differences in tiller density between treatments. However, the amount of variation was often very high (coefficients of variation up to 30%) and because vegetative and reproductive tillers were not separated, interpretation of results was difficult. Variation was reduced in the following experiment by using fixed frames for tiller measurements, and by counting vegetative and reproductive tillers separately. A special study of aerial tillers was made to measure their importance to persistence and production.

5.2 EXPERIMENTAL

5.2.1 The site

The experiment was conducted between the 6 September 1976 and 1 June 1977 on the same site and pasture as the experiment described in Chapter 4. The experimental area was grazed on 6-10 August and again on 3-6 September, then 20 paddocks were chosen for the experiment. Potassic superphosphate (6% P, 14%K) at a rate of 567 kg/ha was broad-cast on all plots in September 1976. Insecticide to control Argentine stem weevil (*Hyperodes bonariensis*) was sprayed on all plots in October 1976 and March 1977.

Soil moisture determinations (% of dry weight at $105^{\circ}C$) for the top 15 cm soil were made regularly from within the trial area and are presented in Appendix I. Monthly climatic data recorded at Palmerston

North are presented in Appendix II. The autumn of 1976-7 was drier than the previous year with soil moisture levels being below 20% for approximately 10 weeks (February to April) and during this time pasture growth was slow.

5.2.2 The treatments

The following five treatments were arranged at random within four block replicates (Figure 5.1).

Control: Ungrazed after 6 September 1976.

T_1H: First grazed 21 October; mid-spring grazing hard.

T_1L: First grazed 21 October; mid-spring grazing lax.

T_2H: First grazed 15 November; late-spring grazing hard.

T_2L: First grazed 15 November; late-spring grazing lax.

T_1 and T_2, referred to as "time of grazing", were different stages of reproductive development at the first grazing. Grazing on 21 October 1976 (T_1) was when it was judged that many reproductive ryegrass meristems were within grazing height (3-4 cm above ground level) and grazing on 15 November (T_2) was when it was judged that 50% of ryegrass seedheads had emerged. The two grazing intensities were again based on residual leaf area index (LAI), and were designed to leave no leaf lamina (Hard: LAI = 0-0.7) or to leave some leaf lamina (Lax: LAI = 0.6-2.2).

All plots were laxly grazed during late summer and hard grazed during autumn as recommended by Brougham (1970). After the initial grazing (T_1 and T_2), subsequent grazings were either when the sward intercepted 95% of photosynthetically active solar radiation at noon or after 6 weeks, whichever was first. In late summer dry weather and in winter low temperatures reduced pasture growth so that 95% light interception was not reached after 6 weeks regrowth. All grazings were with Romney sheep and lasted 3 to 5 days. The actual grazing regime for each treatment is shown in Table 5.1.
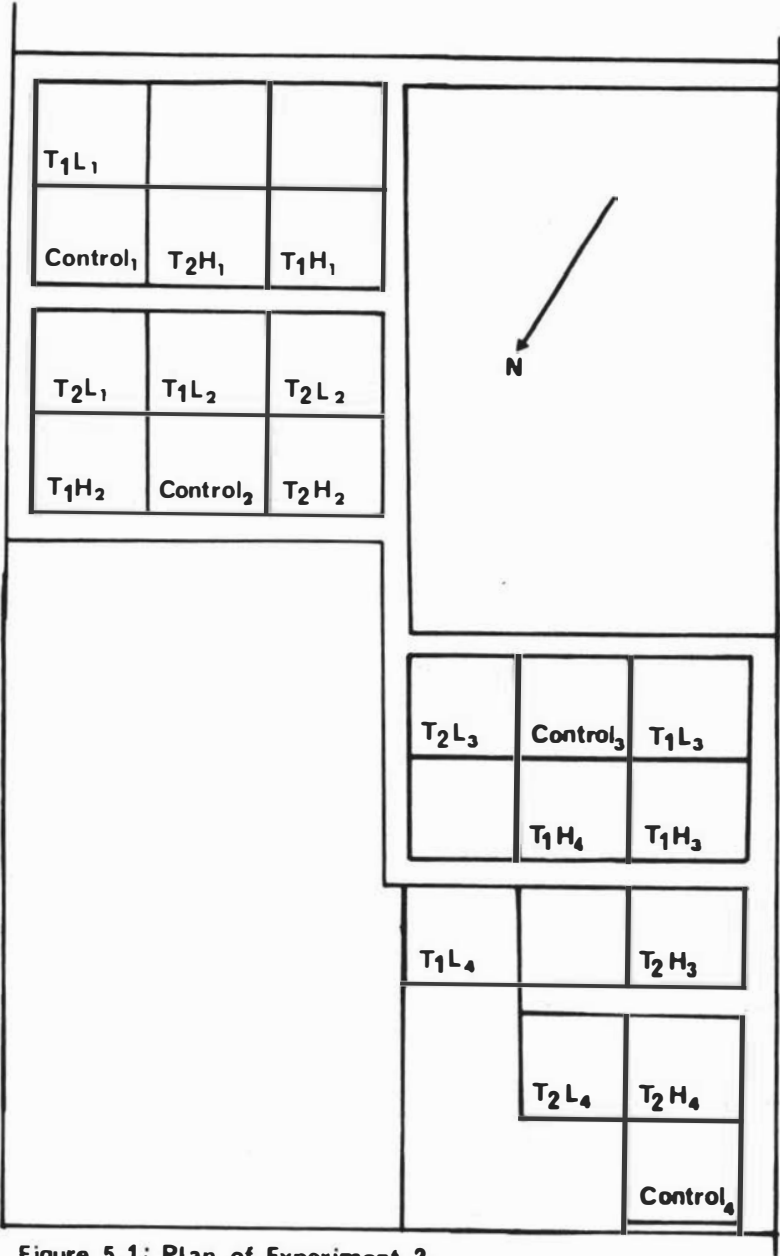
Figure 5.1: Plan of Experiment 2.

Table 5.1: Defoliation regimes for Experiment 2.   Dates refer
to the grazing period and the residual leaf area
indices are in brackets.

T_1H	T_1L	T_2H	T_2L
All plots HARD grazed 3/9 - 6/9/76 (0.6)			
Hard (0.7)	Lax (1.3)	Hard (0.0)	Lax (0.8)
21/10–25/10	21/10–25/10	15/11–20/11	15/11–20/11
Hard (0.1)	Lax (1.4)	Hard (0.1)	Lax (1.0)
20/11–23/11	10/11–15/11	16/12–20/12	11/12–15/12
Hard (0.2)	Lax (2.2)		
20/12–23/12	30/11–3/12		
	Lax (1.2)		
	17/12–20/12		
Lax (0.7)	Lax (1.8)	Lax (0.6)	Lax (0.8)
25/1–29/1	10/1–13/1	21/1–25/1	4/1–6/1
	Lax (0.7)		Lax (0.9)
	7/2–11/2		30/1–3/2
Hard (0.1)	Hard (0.3)	Hard (0.3)	Hard (0.2)
18/3–21/3	25/3–28/3	11/3–14/3	21/3–25/3
Hard (0.7)	Hard (0.2)	Hard (0.6)	Hard (0.4)
28/4–2/5	6/5–10/5	24/4–28/4	2/5–6/5
Experiment ended 1/6/77			

The Control treatment was ungrazed

5.2.3 Measurements

5.2.3.1 Herbage mass

Herbage measurements were similar to those in the first experiment (4.2.4) except that the capacitance probe was not used. The location of quadrats was random, although unusually long or unusually short areas of herbage were avoided. Sub-samples were dissected into ryegrass, white clover, other grasses, other species, and dead herbage. Dead ryegrass culms were separated from the dead herbage. Ryegrass was divided into three types of tillers: reproductive (those tillers with visible culm elongation), aerial (those tillers emerging from culm nodes), and vegetative. Emerged leaf lamina ("lamina") was again separated from the white clover and ryegrass fractions for leaf area measurement.

5.2.3.2 Tiller cores

Thirty 5 cm diameter tiller cores (Mitchell and Glenday, 1958) were collected from each plot at the beginning and end of the experiment. The number of ryegrass, *Poa*, other grass tillers and the number of white clover shoots per core was recorded.

5.2.3.3 Tiller marking

Following grazings in spring and summer four sampling areas per plot were obtained at random, but avoiding very long or very short areas of herbage. At each location a circular frame (10.2 cm diameter) was attached to the soil with wire and all live ryegrass tillers within the frame marked with short lengths of split plastic tubing (Plates 5.1 and 5.2). Vegetative, reproductive, and aerial tillers were separately marked with different coloured markers. Sampling areas were left undisturbed until immediately before the next grazing when they were removed for dissection. Tillers within each marked category, and those that had appeared during regrowth (unmarked), were cut at ground level and reclassified as vegetative, reproductive, aerial or dead. The number of tillers in each of the 15 possible categories was recorded and each indidivual tiller dried and weighed. New tillers that appeared but died before grazing were not counted.

Plate 5.1: A circular fixed frame used for tiller marking.
The yellow, red and blue plastic tubing marks
vegetative, reproductive and aerial tillers
respectively.

Plate 5.2: A circular frame used for tiller marking. The
wires were used to relocate frames at the end
of rest periods.

The ryegrass tiller density (Figure 5.5) for each category of tillers was calculated by averaging the densities in frames before and after each grazing.   Since bare areas of ground were avoided when placing frames, the tiller density obtained by this method was expected to be greater than that obtained from 5 cm diameter cores taken at random.   At the beginning of the experiment when both methods were used on 12 plots there was a 7% difference (Table 5.2). Approximately half the area per plot was actually measured with the non-random method (314 cm^2) compared with the random method (589 cm^2).

Table 5.2:   Ryegrass tiller density on 6 September as measured by different methods (thousand tillers/m^2)

Method	Density ($\pm$ SE)
4 x 10 cm diameter frames per plot (non-random)	6.4 $\pm$ 0.5
30 x 5 cm diameter cores per plot (random)	6.0 $\pm$ 0.5

The gross absolute tiller appearance rate (TAR) and gross absolute tiller death rate (TDR) were calculated as suggested by Thomas (1980).

$$TAR = \frac{\text{unmarked tillers}}{\text{rest period (days)}}$$

$$TDR = \frac{\text{marked tillers dead}}{\text{rest period (days)}}$$

5.2.3.4   Control plots

The control plots were left ungrazed after 6 September to allow uninterrupted reproductive growth.   The number of ryegrass seed-heads per unit area was measured at intervals over the spring.   Also, circular frames for tillering marking were placed in Control plots after grazing on 6 September and removed for dissection on 4 January.

5.2.4   Calculations and statistical analysis

Net herbage accumulation was again calculated using the same method as previously(4.2.5).   Statistical analysis were carried out on the

Massey University B6700 computer using the programme "TEDDYBEAR" written by Wilson (1978).

5.3 RESULTS

5.3.1 Development of the undefoliated flowering sward

5.3.1.1 Herbage accumulation

The pattern of herbage accumulation during uninterrupted reproductive growth was obtained from herbage cuts (Table 5.3) taken after the first grazing (6 and 21 September) and before the next grazing, either at T_1 (21 October) or at T_2 (15 November). Ryegrass was the main species, contributing 60-70% of the green herbage. 95% light interception was reached on 16 October and after this, that is, between 21 October and 15 November, the rate of dead herbage accumulation increased markedly. Stem elongation in ryegrass began in mid-September and as more tillers became "reproductive" the proportion of ryegrass in the "vegetative" category declined.

Table 5.3: Herbage mass (kg DM/ha) and rate of herbage accumulation (kg DM/ha/day) after grazing on 6 September 1976.

Date	6 Sept	21 Sept	21 Oct	15 Nov
Herbage mass				
Green herbage:				
Ryegrass				
Vegetative tillers	461 ± 35	1125 ± 47	864 ± 50	535 ± 41
Reproductive tillers	0	71 ± 17	1034 ± 87	2635 ±250
Total	461 ± 35	1196 ± 55	1898 ±118	3170 ±267
White clover	84 ± 8	217 ± 25	622 ± 58	1231 ±207
Other species	135 ± 22	341 ± 23	608 ± 61	1032 ± 94
Total	680 ± 45	1754 ± 40	3128 ± 90	5433 ± 97
Dead herbage:	230 ± 20	206 ± 18	532 ± 33	1076 ± 58
Total herbage:	910 ± 51	1960 ± 46	3660 ±103	6509 ±118
Accumulation rate				
Green herbage		72	35	92
Dead herbage		- 2	8	22
Total		70	43	114

5.3.1.2 Reproductive development

The final number of ryegrass tillers showing stem elongation
in the Control plots and classified as 'reproductive' was 2200 ±
100 per m^2. Tillers showing stem elongation first appeared in mid-
September and increased in percentage quickly during October (Figure
5.2). Herbage samples cut on 18 October, three days before T_1, were
examined and it was found that 26% of ryegrass tillers had visible stem
elongation, and of the remaining 74% with no visible elongation 20%
were found to have reproductive meristems when examined microscopically.
From this it was calculated that approximately 60% of the final number
of reproductive tillers showed visible signs of stem elongation on
18 October, a value similar to that finally obtained when more
reproductive tillers actually developed (T_1 in Figure 5.2).

Seadheads did not begin to appear until November and the number
quickly increased until early December. The sward lodged in mid-
December and the final seedhead count was from cut quadrats taken in
January. Examination of 180 reproductive tillers from 5 plots showed
that 34% of heads had emerged on 15 November when T_2 plots were first
grazed. This was similar to the proportion measured from seedhead
counts on control plots (T_2 in Figure 5.2).

Plates 5.3 and 5.4 show the control plots at T_1 and T_2.

5.3.1.3 Marked tillers

After grazing on 6 September tillers were marked in all
treatments. Table 5.4 presents the data obtained when frames
were removed on 21 October (from T_1), on 15 November (from T_2), and
on 4 January (from Control). Despite the variation between turfs,
reduced to some extent by covariance adjustment for the initial number
of tillers per circular frame, some trends were apparent.
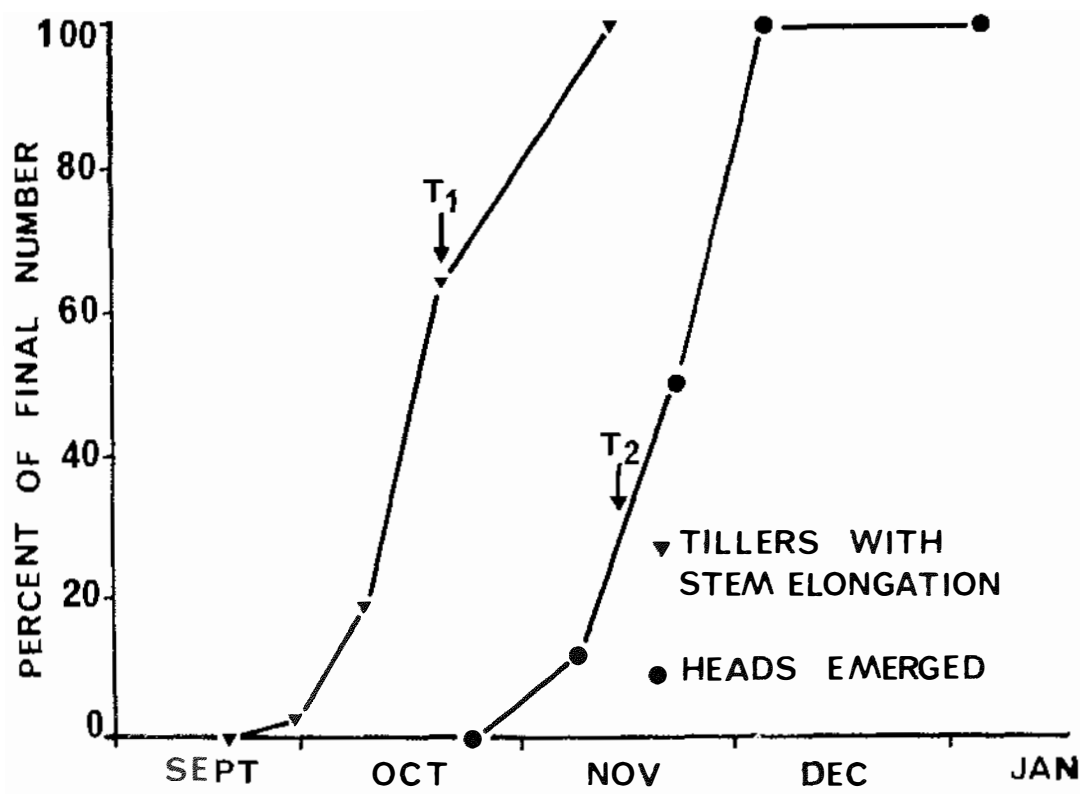
Figure 5.2: Reproductive development of ryegrass in the ungrazed Control plots.

Plate 5.3: A control plot at T_1 (21 October). A strip was mown out of the plot to show the sward structure.

Plate 5.4: A control plot at T_2 (15 November). A strip was mown to show the sward structure. Note the greater amount of reproductive development compared with Plate 5.3.

Table 5.4: Changes in ryegrass tiller density (100 tillers/m^2)
and tiller weight (mg/tiller) following grazing on
6 September

	6 Sept	21 Oct	15 Nov	4 Jan
Tiller density *				
Marked tillers:				
Vegetative	64 ± 5	41 ± 3	14 ± 2	9 ± 2
Reproductive	-	18 ± 2	27 ± 2	18 ± 2
Dead	-	5 ± 2	24 ± 2	38 ± 1
Unmarked tillers:				
Vegetative	-	15 ±12	4 ± 4	10 ± 7
Reproductive	-	1 ± 1	3 ± 1	1 ± 1
Mean tiller weight				
Vegetative tillers:				
Marked		26 ± 5	21 ± 3	27 ± 1
Unmarked	-	13 ± 2	17 ± 4	5 ± 1
Reproductive tillers:	-	67 ± 8	160 ±20	250 ± 25

* Adjusted by covariance for the number of tillers marked per
frame on 6 September.

The density of vegetative tillers declined with time as more tillers
became reproductive, and as marked tillers died. Tiller death
increased after 95% light interception was reached (16 October), and
the density of vegetative tillers declined from 5600 per m^2 on 21
October (T_1) to 1800 per m^2 on 15 November (T_2). By 4 January remaining
vegetative tillers were small and etiolated with 50% of the marked
vegetative tillers showing internode elongation. The meristems of
these etiolated tillers were examined and it was established that they
were not reproductive. Marked vegetative tillers with no internode
elongation on 4 January had a mean weight of 16 ± 3 mg/tiller but
including the tillers showing elongation increased the mean weight to
27 mg/tiller. New vegetative tillers (unmarked) were smaller than
older (marked) vegetative tillers. Over 90% of the reproductive
tillers were tillers present at the start of the experiment (i.e.
marked). Reproductive tillers increased in weight and grew to many
times the size of vegetative tillers.

Some aerial tillers appeared in the sward on 15 November and by
4 January 110 ± 60 aerial tillers per m^2 were present on Control plots.

5.3.2 Herbage mass

5.3.2.1 Whole sward

For simplicity and for comparison with the results in Chapter 4
the sward has been divided into grass (mainly ryegrass and *Poa*),other
species (mainly white clover), and the dead herbage (including dead
culm).   Changes in the herbage mass of these components for each rest
period is presented in Figure 5.3 and is similar to ryegrass (Figure
5.4) as ryegrass was the main pasture species.   The pattern of regrowth
in the first rest period (described in 5.3.1.1) is only drawn once
for T_1 and T_2.

5.3.2.1.1 Grass

The pattern of regrowth of grass (Figure 5.3) was similar to that
of ryegrass which will be described in detail (5.3.2.2).   The amount
of *Poa* was consistently greater under the lax grazing than the hard
grazing treatment in the spring/summer period (Table 5.5).   The
difference in the amount of *Poa* was established at the first hard or
lax grazing (at T_1 or T_2) and remained until all plots were hard grazed
in autumn.   The amount of *Poa* was not significantly influenced by the
"time of grazing" treatments.

5.3.2.1.2 Other species

White clover was the main component of the "other species" in
Figure 5.3, the remainder (flatweeds) rarely exceeding 50 kg DM/ha.
The amount of white clover increased during regrowth on all treatments
in spring and summer but in autumn there was less clover regrowth.
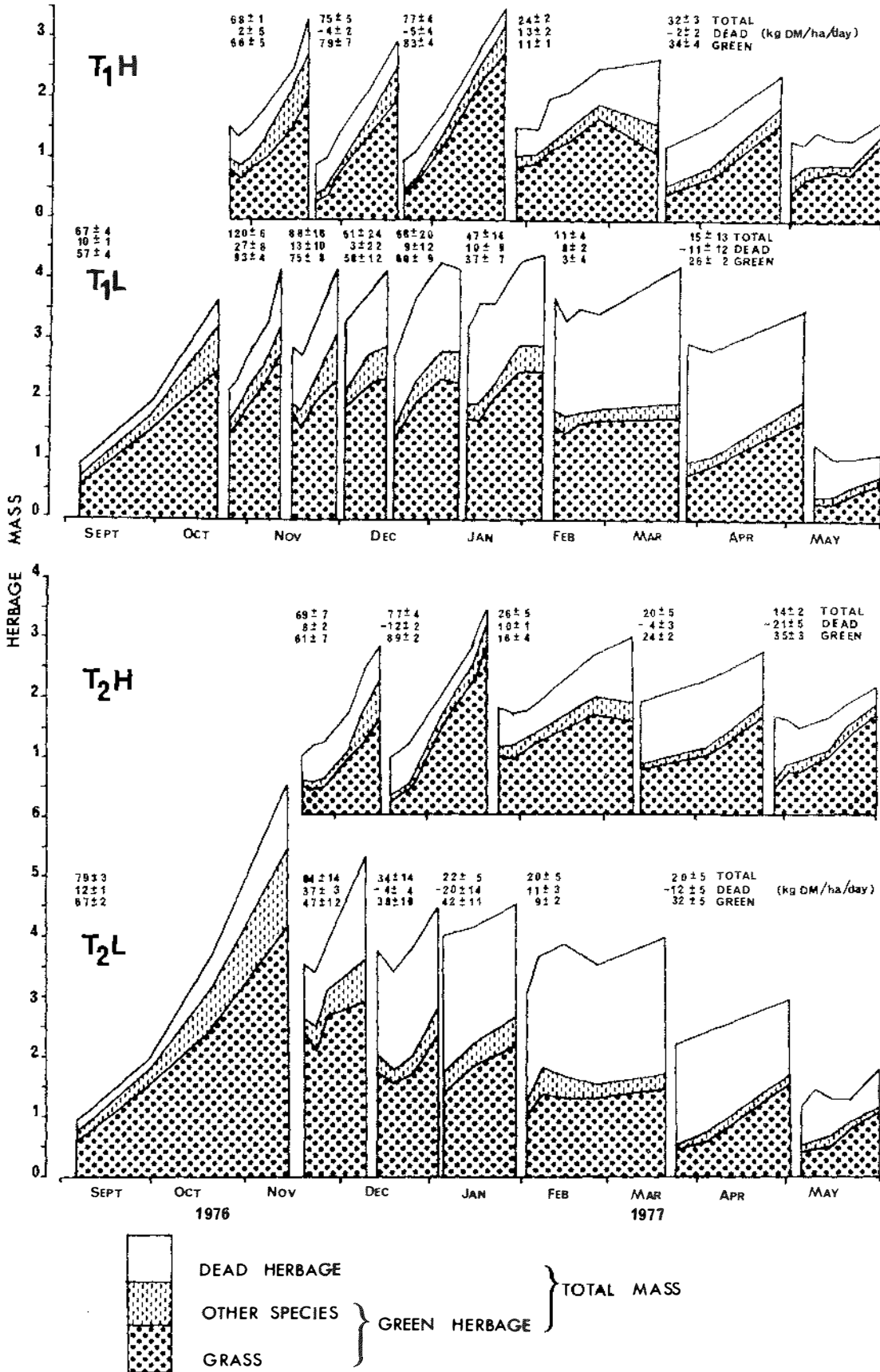
Figure 5.3: Herbage mass (t DM/ha) and accumulation rates (kg DM/ha/day) during rest periods.

Table 5.5: The effect of grazing intensity on the herbage mass
(kg DM/ha) of "other grass" (mainly *Poa*) at various
dates

Date	Hard	Lax
20 November	240 b	440 a
11 December	180 b	540 a
17 January	130 b	350 a
15 February	80 b	290 a
5 April	40 a	90 a
16 May	40 a	30 a

Duncans multiple range test compares Hard and Lax at each date.

5.3.2.1.3 Green herbage

The accumulation of green herbage ("grass" plus "other species")
was similar to the pattern for ryegrass (5.3.2.2). The average
accumulation rate for each rest period increased with successive hard
grazings (T_1H and T_2H) to approximately 85 kg DM/ha/day in January,
but declined to 37 kg DM/ha/day following successive lax grazings
in T_1L (Figure 5.3). It remained at approximately 40 kg DM/ha/day
on T_2L during the same period. Accumulation rates of green herbage
declined in the dry period during early autumn and then increased again
after rain.

5.3.2.1.4 Dead herbage

The accumulation of dead herbage reflected the accumulation of dead
ryegrass culm, described in 5.3.2.2, and the accumulation of dead leaf.
Dead leaf was the main component of dead herbage at all times (Table 5.6)
although dead culm accounted for over 40% of dead herbage in late summer
with lax grazing. Both dead leaf and dead culm were present in
significantly higher amounts in laxly grazed swards, but in the period
of dry weather in March when the amount of vegetative lamina declined
(Figure 5.4) the amount of dead leaf increased on previously hard
grazed plots, reducing this difference (Figure 5.3).

Table 5.6   The effect of grazing intensity on dead herbage
mass on various dates (kg DM/ha)

Date	Dead Leaf		Dead Culm		Total	
	Hard	Lax	Hard	Lax	Hard	Lax
20 Nov	500 b	900 a	*10 b	120 a	510 b	960 a
11 Dec	430 b	1080 a	170 b	310 a	500 b	1390 a
17 Jan	210 b	1120 a	70 b	680 a	280 b	1800 a
15 Feb	560 b	1100 a	130 b	790 a	690 b	1890 a
5 April	770 b	1100 a	150 b	590 a	920 b	1700 a
16 May	460 a	460 a	40 b	160 a	500 a	620 a

*Dead culm only present on T_1 on 20 November.
Duncans multiple range test compares H and L on each date for
each component.

5.3.2.2   Perennial ryegrass

Changes in the herbage mass of ryegrass vegetative tillers,
reproductive tillers and dead culm for each treatment over the
experimental period is presented in Figure 5.4.   Aerial tillers only
represented a small amount of herbage (generally less than 50 kg DM/ha
but occasionally up to 100 kg DM/ha) and so were not shown separately.
The first rest period was similar for both grazing intensity treatments
so it was only drawn once from T_1 and T_2.   Vegetative tillers are sub-
divided into "lamina" and "stubble".   Since reproductive tillers had
little "lamina" after the first grazing this is indicated by a dotted
line.   The amount of "lamina" on reproductive tillers is represented
below the dotted line (and above the vegetative tillers) and live
culm above the dotted line.

5.3.2.2.1   Reproductive tillers

Hard grazing on 21 October (T_1H) removed many reproductive meristems
and prevented further reproductive growth in those tillers.   With lax
grazing (T_1L) fewer meristems were damaged and reproductive growth
continued in the following rest period.   Subsequent hard grazings
(T_1H) also removed most of the reproductive herbage which had accumu-
lated so that relatively little dead culm accumulated in the sward on
T_1H.   In contrast, continued lax grazing (T_1L) mainly removed "lamina"
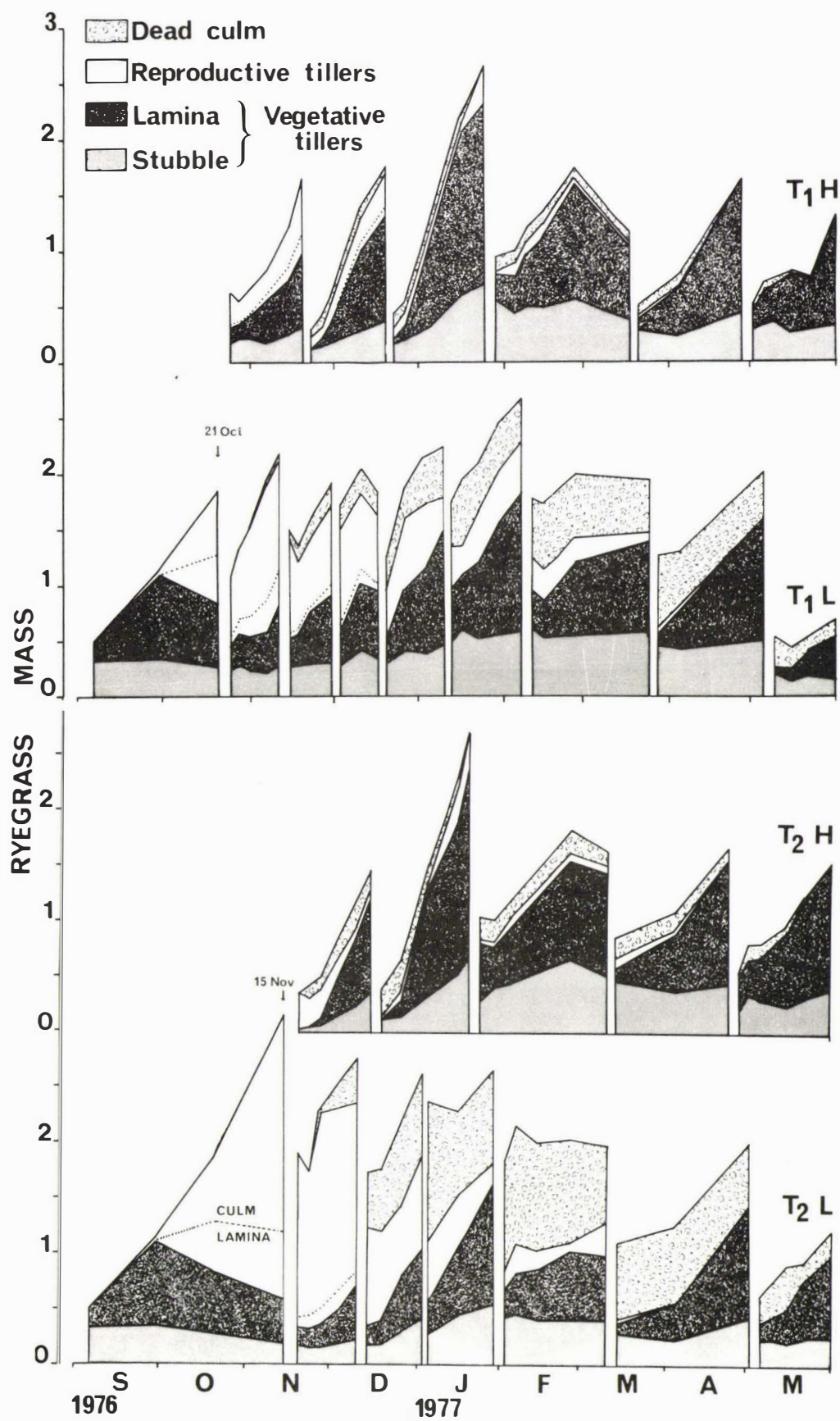
Figure 5.4: Ryegrass herbage mass (t DM/ha) during rest periods.

from reproductive tillers and culms continued to accumulate. At
first culm remained green, but later (January - March) died, increasing
the amount of dead culm.

Between 21 October and 15 November there was little further
accumulation of ryegrass "lamina" (60 ± 90 kg DM/ha) on T_2 plots and
ryegrass growth was almost entirely due to culm growth. Hard grazing
of largely reproductive swards on 15 November (T_2H) removed most
reproductive herbage and the residual culm died in the next 4 weeks.
A small amount of further reproductive growth occurred on T_2H in
January and the following lax grazing (21 Jan.), where sheep were able
to largely avoid culm, resulted in some dead culm accumulating. Lax
grazing on 15 November (T_2L) mainly removed "lamina" and left a
considerable quantity of culm (1540 ± 170 kg DM/ha). This culm was
largely avoided in subsequent grazings and died in December and January.

Ewes also avoided grazing dead culm which then disappeared from the
sward during autumn regrowths. Both T_1L and T_2L were hard grazed in
March but during this grazing little dead culm disappeared and it was
merely trampled onto the ground where it subsequently decayed (Figure
5.4).

Plates 5.5 and 5.7 illustrate how hard grazing removed considerable
amounts of culm compared with lax grazing (Plates 5.6 and 5.8) at both
T_1 and T_2. After grazing at T_1 (21 - 25 October) an area of sward in
T_1H and in T_1L was protected from grazing (Plates 5.9 and 5.10). The
protected areas show that the hard grazing on 21 - 25 October was largely
successful in preventing subsequent reproductive growth compared with
lax grazing (Plate 5.10) or no grazing (Plate 5.4).

5.3.2.2.2 Vegetative tillers

Except for the first rest period and a time in March, vegetative
tillers made a major contribution to herbage mass in all rest periods
(Figure 5.4). Hard grazing removed both "lamina" and "stubble" whereas
lax grazing mainly removed "lamina". The decline in vegetative
herbage mass in the first rest period was caused by the subsequent
reclassification of some of these vegetative tillers as reproductive
tillers and by the death of some vegetative tillers, especially
after 15 October in T_2 (Table 5.4).

Plate 5.5: T_1H after grazing on 27 October.
Many reproductive meristems were removed
in grazing. T_1L can be seen in the
background on the right.

Plate 5.6: T_1L after grazing on 27 October.
Note the greater amount of leaf and culm left
compared with T_1H above.

Plate 5.7: T_2H on 27 November, one week after grazing.
Note the limited number of vegetative
tillers recovering.

Plate 5.8: T_2L on 27 November, one week after grazing.
Consierable amounts of reproductive tillers
are still present.

Plate 5.9: T_1H on 27 November.
The area inside the bamboo stakes was hard
grazed on 21–25 October then protected from
grazing on 20–23 October (outside stakes).
Note the small amount of reproductive development
compared with T_1L in Plate 5.10.

Plate 5.10: T_1L on 27 November.
The area inside the bamboo stakes was lax
grazed on 21–25 October then protected from
grazing on 10–15 November (outside stakes).

The period of dry weather in March (Appendix I) resulted in desiccation of leaves and the decline in vegetative herbage mass particularly noticeable in T_1H and T_2H in March (Figure 5.4).

Hard grazed swards were largely vegetative whereas lax grazed swards contained more ryegrass culm. At the end of regrowth, when swards were intercepting 95% of noon sunlight, there was less vegetative herbage in previous lax grazed swards than in previously hard grazed swards (Table 5.7). Besides leaf, the culms which were mainly upright during summer, also intercepted light so that the greater vegetative herbage mass at 95% light interception in H reflected the smaller amount of light intercepting culms.

Table 5.7: Effect of grazing intensity on the herbage mass
(kg DM/ha) of vegetative ryegrass at 95% light
interception. (Pooled for regrowths in
November, December and January).

Previous grazing	Hard	Lax
Lamina	1180 a	740 b
Stubble	490 a	380 b
Total	1670 a	1120 b

Duncan's multiple range test compares H and L for each component.

5.3.3 Net herbage accumulation

Net herbage accumulation was calculated for two 19 week periods, *viz* Period I (6.9.76 - 17.1.77), and Period II (17.1.77 - 1.6.77). During Period I the rest periods followed hard and lax grazings, while in Period II all treatments were under similar grazing regimes. Total herbage accumulation for the whole experiment does not always exactly match the sum of Period I plus Period II because 17 January was part way through rest periods and this affected the correction for the following grazing period.

Averaged over all treatments a total of 12.7 t DM/ha of herbage accumulated during the 38 weeks of the experiment, of which 76% accumulated during Period I. Detailed results are presented in

in Appendix III and selected results in the following sections.

5.3.3.1 Time of spring grazing

Time of grazing did not significantly affect net accumulation of the main herbage components (Table 5.8).

Although net ryegrass accumulation was not significantly influenced by time of grazing, the accumulation of reproductive herbage and lamina before T_2 was (Table 5.9). T_2H and T_2L are not shown separately since both remained ungrazed until 15 November. Grazing at T_1 reduced reproductive ryegrass accumulation but increased vegetative ryegrass accumulation. Similarly, more lamina, but less stubble accumulated when reproductive growth was interrupted at T_1. These differences were apparent in accumulation for the whole experiment, but they were not significant (Appendix III).

5.3.3.2 Grazing intensity

Green herbage accumulation was influenced by grazing intensity (Table 5.10) and during the 38 weeks of the experiment 17% (0.9 t DM/ha) more green herbage accumulated in H than L. Although H was greater than L in both Period I and Period II, the difference was only significant in Period II. Because significantly more dead herbage accumulated in L than in H, and significantly less green herbage in L than H, the effect of grazing intensity on total herbage accumulation was non-significant.

Aerial tillers contributed significantly more to net herbage accumulation in L than in H (Table 5.11), particularly in Period I. However, the contribution was very small (approximately 3% of ryegrass in Period I) and appeared to decline over summer (Period II).

Table 5.11: Net herbage accumulation of the aerial tiller category (t DM/ha)

	Hard	Lax
Period I	0.02 b	0.13 a
Period II	0.00 a	0.05 a
Total	0.02 b	0.18 a

Duncans multiple range test compares H and L for each period.

2a

Table 5.8:   Effect of time of grazing on net herbage accumulation
(t DM/ha)

	Period I		Period II		Total	
	T_1	T_2	T_1	T_2	T_1	T_2
Ryegrass	5.48 a	5.24 a	2.93 a	3.30 a	8.41 a	8.43 a
Other grasses	1.13 a	1.16 a	-0.13 a	-0.04 a	1.00 a	1.12 a
White clover	2.12 a	1.86 a	0.33 a	0.36 a	2.51 a	2.21 a
Flatweeds	0.07 a	0.10 a	0.02 a	0.03 a	0.10 a	0.13 a
Green herbage	8.89 a	8.36 a	3.15 a	3.65 a	12.03 a	11.89 a
Dead herbage	1.06 a	1.07 a	-0.22 a	-0.33 a	0.85 a	0.73 a
Total	9.95 a	9.44 a	2.93 a	3.32 a	12.88 a	12.63 a

Duncans multiple range test compares T_1 and T_2 for each component.

Table 5.9:   Net accumulation of ryegrass and its components between
6 September and 15 November (t DM/ha)

	T_1H	T_1L	T_2
Vegetative tillers	0.8 a	0.7 a	0 b
Reproductive tillers	1.6 ab	1.0 b	2.7 a
Lamina	1.5 a	1.2 ab	0.8 b
"Stubble"	0.9 ab	0.5 b	1.9 a
Total	2.4 a	1.7 a	2.7 a

Duncans multiple range test compares T_1H, T_1L and T_2 for each component.

Table 5.10:   Effect of grazing intensity on net herbage accumulation
(t DM/ha)

	Period I		Period II		Total	
	Hard	Lax	Hard	Lax	Hard	Lax
Ryegrass	6.01 a	4.71 a	3.51 a	2.73 b	9.40 a	7.44 b
Other grasses	1.06 a	1.23 a	-0.04 a	-0.14 a	1.03 a	1.09 a
White clover	1.91 a	2.15 a	0.44 a	0.24 a	2.32 a	2.39 a
Flatweeds	0.10 a	0.08 a	0.05 a	0.01 a	0.14 a	0.09 a
Green herbage	9.08 a	8.17 a	3.96 a	2.84 b	12.91 a	11.01 b
Dead herbage	0.50 b	1.63 a	-0.14 a	-0.41 a	0.36 b	1.22 a
Total	9.59 a	9.80 a	3.82 a	2.43 a	13.27 a	12.23 a

Duncans multiple range test compares Hard L for each component.

Significantly more ryegrass leaf lamina accumulated in H than L, the difference being significant in Period I but not Period II (Table 5.12). White clover lamina accumulation was not significantly affected by grazing intensity.

Table 5.12: Effect of grazing intensity on net accumulation of lamina, (t DM/ha).

	Ryegrass		White Clover	
	Hard	Lax	Hard	Lax
Period I	3.86 a	3.11 b	0.95 a	1.12 a
Period II	2.97 a	2.75 a	0.27 a	0.22 a
Whole experiment	6.83 a	5.86 b	1.21 a	1.34 a

Duncans multiple range test compares H and L for ryegrass or clover in each period.

5.3.4 Leaf area index

5.3.4.1 Residual leaf area index

Residual leaf area indices (LAI) following each grazing are presented in Table 5.1. A reasonable contrast in residual LAI was maintained between treatments.

The effect of residual LAI on regrowth was investigated after grazing at T_1 and T_2 when plots had received similar pretreatments (Table 5.13). In the T_1 treatment (grazed 21 - 25 October) there was a significant correlation between residual LAI (0.5 - 1.8) and total net herbage accumulation over the following two weeks. This largely reflected the strong relationships between residual LAI and green herbage accumulation and between residual LAI and reproductive tiller accumulation. By contrast, in the T_2 treatment (grazed 15 - 20 November) the only significant relationship between residual LAI (0.01 - 1.2) and subsequent herbage accumulation was for dead herbage accumulating during the subsequent three weeks and the decline in vegetative tillers.

Table 5.13: Correlation coefficient between residual LAI and the components of net herbage accumulation following T_1 (25/10 - 7/11) and following T_2 (20/11 - 11/12).

	T_1	T_2
Vegetative tillers	-0.551 NS	-0.729*
Reproductive tillers	0.877 **	0.443 NS
Total ryegrass	0.799 *	-0.493 NS
Green herbage	0.910 **	0.076 NS
Dead herbage	0.314 NS	0.926 **
Total herbage	0.797 *	0.674 NS

5.3.4.2 Leaf area index at full light interception

Pasture was defoliated after six weeks regrowth in late summer and autumn, before 95% light interception was reached, so that the leaf area index at 95% light interception was measured only in summer (Table 5.14). Hard grazed pasture had a higher LAI at 95% light interception than laxly grazed pasture. Time of spring grazing treatments did not significantly affect the LAI at 95% light interception.

Table 5.14: LAI at 95% light interception in summer

Grazing intensity	LAI
Hard	4.6 a
Lax	3.7 b

a,b. Duncans multiple range test.

5.3.5 Tiller cores

To ensure that there were no differences in botanical composition between treatments tiller cores were taken at the start of the experiment. No significant differences between treatments were detected and pooled results are presented in Table 5.15. By the end of the experiment (Table 5.16), in June, ryegrass tillers occurred in slightly

more cores (93% cf 83%) and the density had increased. *Poa*
occurrence had declined, particularly under hard grazing, but
white clover occurrence had changed little (Table 5.16). The
ryegrass tiller density was 30% higher, and *Poa* tiller density
considerably lower where grazing had been hard in the previous spring/
summer, but white clover density was not significantly affected.
Time of spring grazing did not significantly affect the density of
any species in June.

Table 5.15: Tiller and shoot densities (thousand/m^2), and
percent species occurrence in cores (arcsin $\sqrt{}$%,
natural mean in parenthesis). in September 1976

	Occurrence	Density
Ryegrass	1.47 ± 0.10 (83)	6.2 ± 1.5
Poa	1.03 ± 0.18 (87)	2.8 ± 2.3
Other grass sp.	0.18 ± 0.16 (3)	–
White clover	0.84 ± 0.13 (65)	1.2 ± 0.6

Table 5.16: Effect of treatments on species occurrence in cores
(arcsin $\sqrt{}$%, natural mean in parenthesis) and shoot
densities (thousand/m^2 on 7 June).

	Grazing Intensity			Time of grazing		
	Hard	Lax		T$_1$	T$_2$	
Occurrence:						
Ryegrass	1.36(96)	1.44(88)	ns.	1.41(92)	1.39(94)	ns.
Poa	0.61(36)	0.91(73)	*	0.74(52)	0.78(57)	ns.
Other grass sp.	0.13(2)	0.11(1)	ns.	0.07(1)	0.16(3)	ns.
White clover	0.86(64)	0.89(72)	ns.	0.88(70)	0.85(66)	ns.
Density:						
Ryegrass	8.3	6.4	*	7.6	7.1	ns.
Poa	0.9	3.2	*	2.1	2.0	ns.
White clover	1.3	1.1	ns.	1.3	1.2	ns.

* significantly different at 5% level; or ns. non-significant.

5.3.6   Perennial ryegrass in fixed frames

5.3.6.1   Tiller density

As already mentioned (5.3.1.3) vegetative tiller density declined during uninterrupted reproductive development, so that at T_1 and T_2 there were 4800 and 2100 vegetative tillers/m^2 respectively (Figure 5.5).   Grazing at T_1 and T_2 resulted in a marked upsurge in vegetative tiller density.   Grazing intensity subsequently affected vegetative tiller density, with H having approximately 50% more tillers than L by the end of January.   The difference between H and L became apparent during December in T_1 and during January in T_2.

Reproductive tiller density was greatest at the first grazing (at either T_1 or T_2) and declined thereafter (Figure 5.5).   With lax grazing the decline was gradual as culms died, whereas after the first hard grazing a large reduction occurred, particularly following the first grazing of T_2H on 15 November.   For clarity standard errors are not shown for reproductive tillers in Figure 5.5.   They are presented in Figure 5.7.

Aerial tillers did not appear until after the first grazing at T_1 or T_2, and there was a consistently higher aerial tiller density in L than H.   Aerial tillers eventually did develop in the ungrazed control plots, but the density was comparatively low (100/m^2 on 4 January).   Standard errors for aerial tiller densities are presented in Appendix IV.

5.3.6.2   Tiller dynamics

5.3.6.2.1   Vegetative tillers

Differences in vegetative tiller density apparent in Figure 5.5 could have been due to differences in the absolute tiller appearance rate (TAR) or the absolute tiller death rate (TDR).   This data is presented in Figure 5.6.

The TAR and TDR marked by squares in Figure 5.6 were obtained from Table 5.4 (21 October and 15 November).   The method of calculation largely explains why the TAR on 11 October in T_2 was considerably less than the TAR on 29 September in T_1.   Many unmarked tillers died between
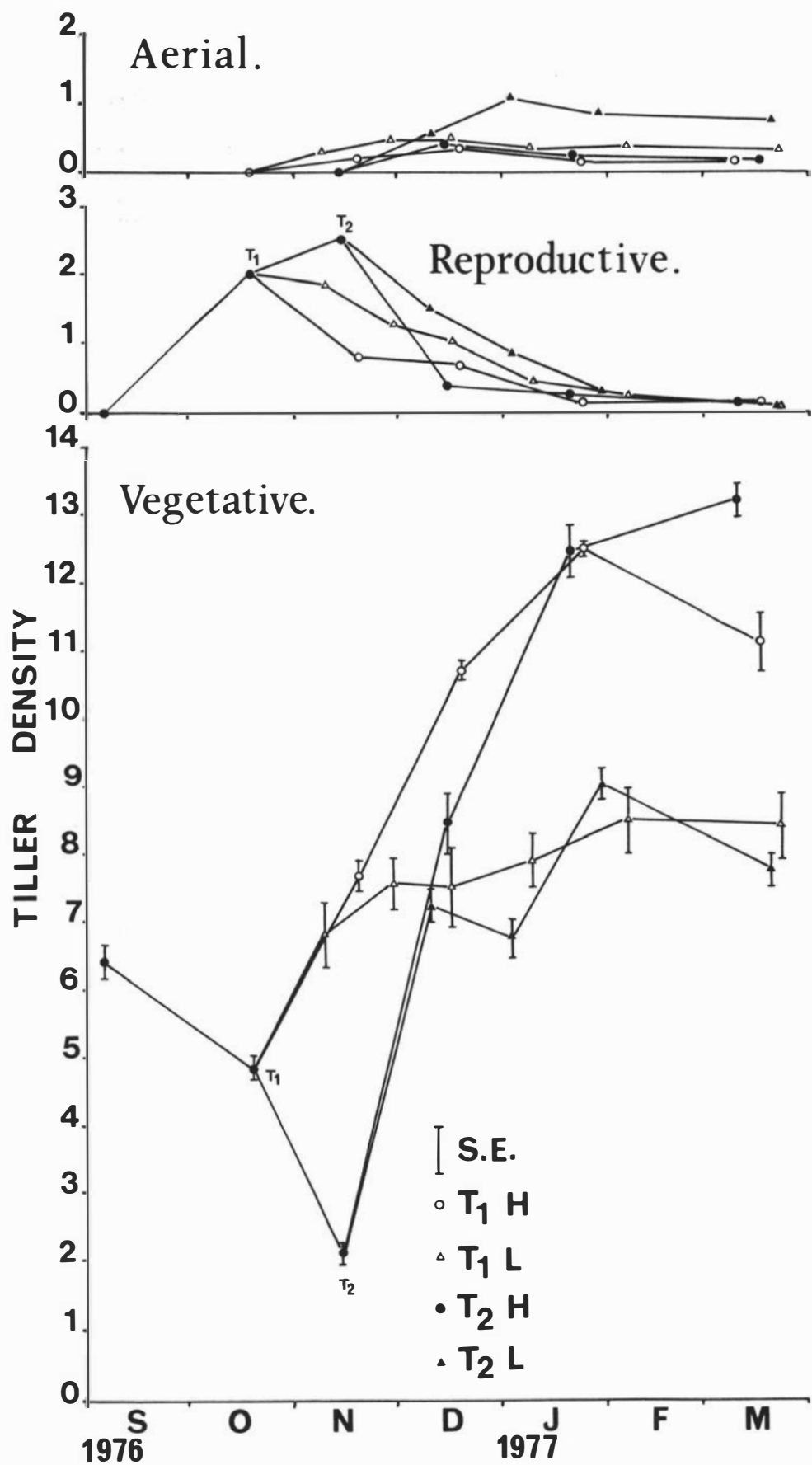
Figure 5.5: Ryegrass tiller density (1000/ m²) at each grazing.

21 October and 15 November (Table 5.4) and if these had been included a higher value for T_2 on 11 October would have been obtained. Similarly the TDR for T_2 on 11 October would be increased if unmarked tillers that died between 21 October and 15 November were included.

Although differences in TDR are apparent in Figure 5.6 they are of insufficient magnitude to account for the greater tiller density in H than L (Figure 5.5). However, it is interesting to note that the proportional TDR (2.4) was increased by laxer grazing. After T_1 and T_2 (indicated by arrows) the absolute TDR was significantly greater in L than H (Figure 5.6) and as the density at T_1 and T_2 was similar in both treatments (Figure 5.5) the difference was due to a greater proportional TDR in L. The greater absolute TDR during February-March in H than L (Figure 5.6) was due to a greater density in H than L, not a higher proportional TDR.

The TAR was relatively low during uninterrupted reproductive growth, but after grazing at T_1 and T_2 (indicated by arrows) increased dramatically, then declined rapidly during summer. After T_1 and T_2 the TAR was not significantly different in the H and L treatments, but after the next hard grazing, the TAR was significantly greater in H than L. Thus the greater vegetative tiller density in H than L (Figure 5.5) was largely due to a greater TAR in H than L during December (T_1) or January (T_2).

On 11 November the vegetative tiller density was considerably lower in T_2 than in T_1 (Figure 5.5) but this difference disappeared by January because the TAR was higher after T_2 than after T_1 (Figure 5.6). Vegetative tillers appeared either from the base of defoliated reproductive tillers or in the leaf axil of marked vegetative tillers. The relative contribution of each source of new tillers was not measured, but it was noticed that in October and November, when reproductive tillers were first defoliated, relatively more new tillers came from the base of reproductive tillers. This was most noticable after T_2 when few vegetative tillers had survived reproductive growth.
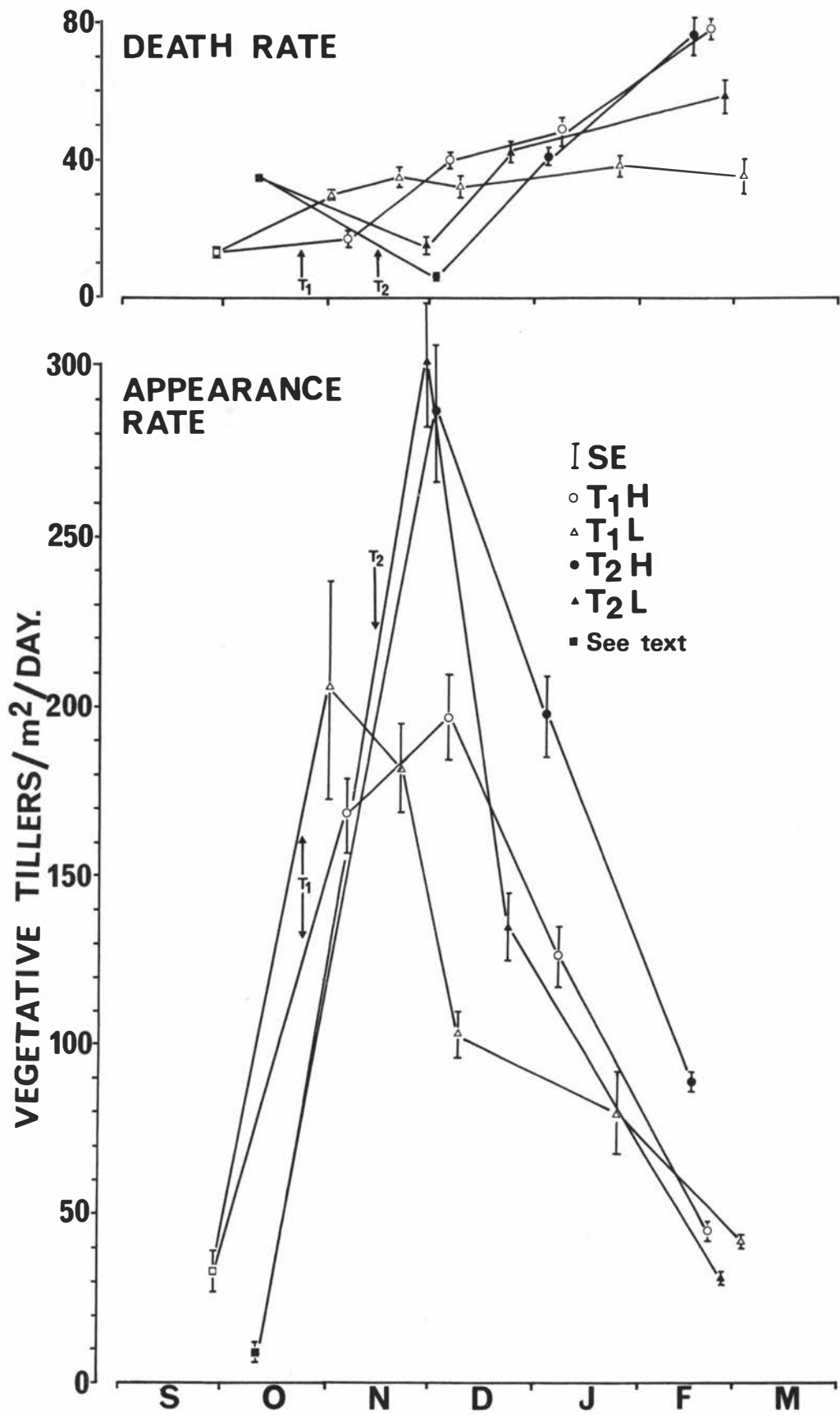
Figure 5.6: Absolute vegetative TDR and TAR during rest periods.

5.3.6.2.2 Reproductive tillers

The density of live and dead reproductive tillers at the end of each rest period is presented in Figure 5.7. Although most reproductive tillers had appeared by the first grazing (T_1 or T_2) further development occurred in all subsequent rest periods. These later reproductive tillers developed mainly from tillers marked as vegetative at the beginning of regrowth (95%), and the remainder from new tillers (5%). Most reproductive tillers died in the rest period following hard grazing, but many survived following lax grazing. This explains the faster decline in reproductive tiller density on T_1H and T_2H shown in Figure 5.5.

Dead reproductive tillers continued to accumulate, but since the number was lower than the number appearing, reproductive tillers must have decayed or have been removed during grazing.

5.3.6.2.3 Aerial tillers

Aerial tillers initially developed from the nodes of grazed culm. More aerial tillers appeared in L than in H, and more in T_2 than T_1 (Table 5.17). A large number of aerial tillers were removed during grazing (25% in T_1H and 85% in T_2H). Differences in aerial tiller density were therefore caused by differences in culm development and culm removal (and therefore sites for aerial tiller development), and by differences in aerial tiller removal during grazing.

Some aerial tillers occasionally developed into reproductive tillers. At the end of the second rest period on T_2L (4 January) three aerial tillers formed in the previous rest period (i.e. after the culms were grazed at T_2) developed an inflorescence. One of these is shown in Plate 5.11.

Table 5.17: Number of aerial tillers appearing and subsequently removed during grazing between October and the end of February (tillers/m^2). Full data is presented in Appendix IV

	T_1H	T_1L	T_2H	T_2L
Tillers appearing	600	1200*	1200	1800*
Removed in grazing	150 (25%)		1000 (85%)	

*Tillers were not marked for one regrowth cycle, reducing this total.
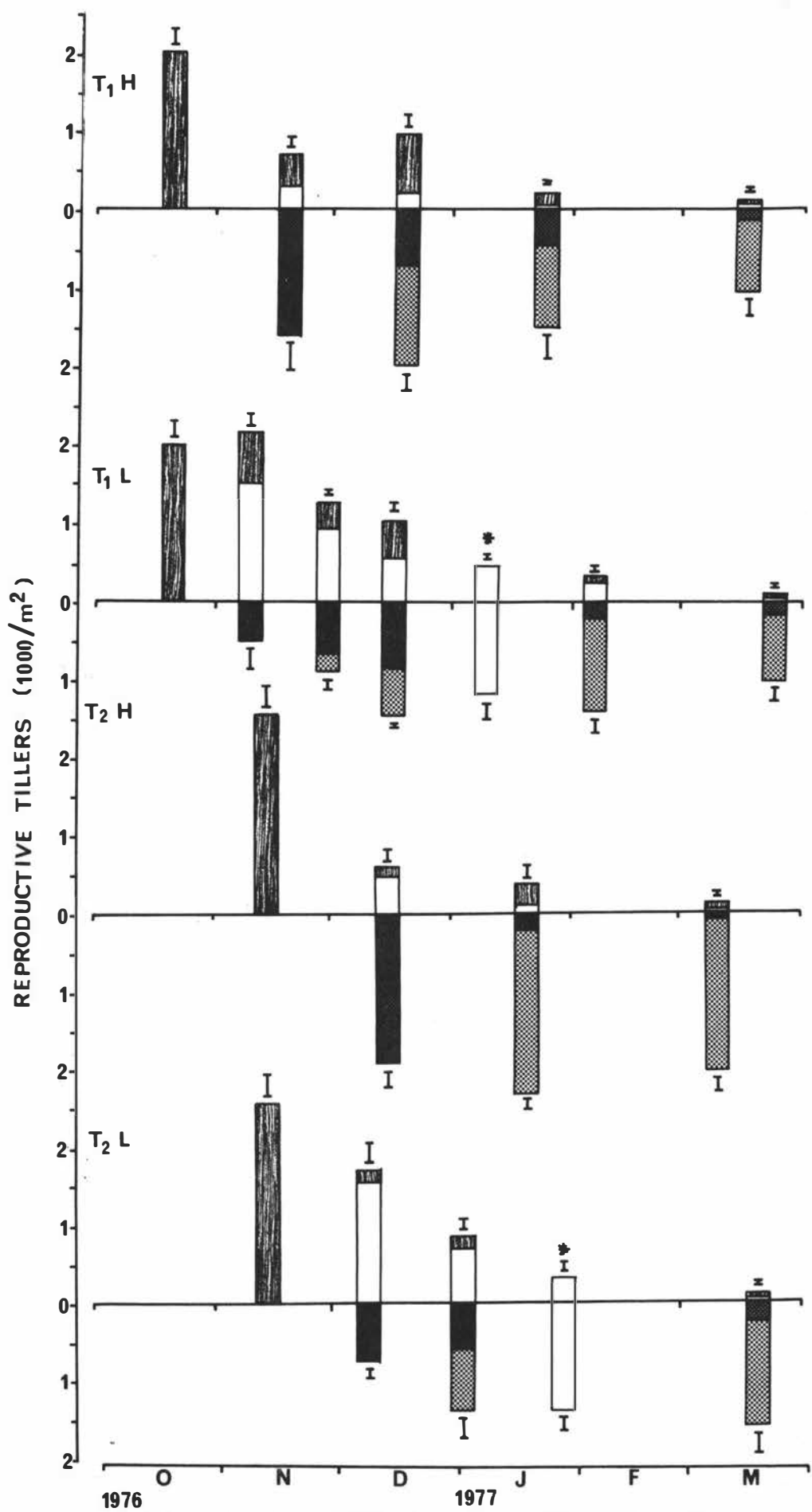
Figure 5.7: Reproductive tiller dynamics.

Live tillers {
▨ Appeared during rest period
□ Marked at start of rest period as reproductive

Dead tillers {
■ Died during rest period
▦ Dead at start of rest period

I S.E. of total live and dead

* No tillers marked in this rest period. Totals obtained from previous and subsequent rest periods.
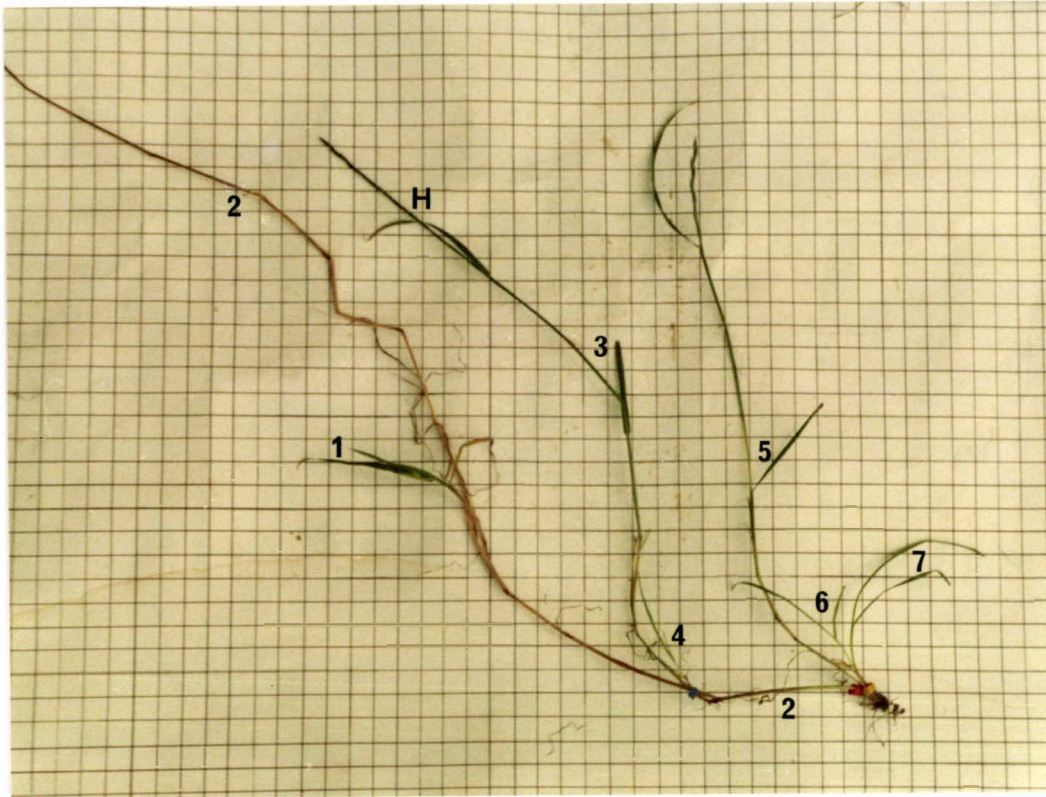
Plate 5.11: Flowering of an aerial tiller.   Sample from
T$_2$L on 11 December.

Tiller

1   Unmarked aerial tiller: appeared between
       20 Nov and 11 Dec.

2   Marked reproductive tiller: died between
       20 Nov and 11 Dec.

3   Marked aerial tiller: stem elongation
       between 20 Nov and 11 Dec.

4   Unmarked aerial tiller: appeared between
       20 Nov and 11 Dec.

5   Marked vegetative tiller: stem elongation between
       20 Nov and 11 Dec.

6+7   Unmarked vegetative tillers: appeared between
       20 Nov and 11 Dec.

H   Head on aerial tiller.
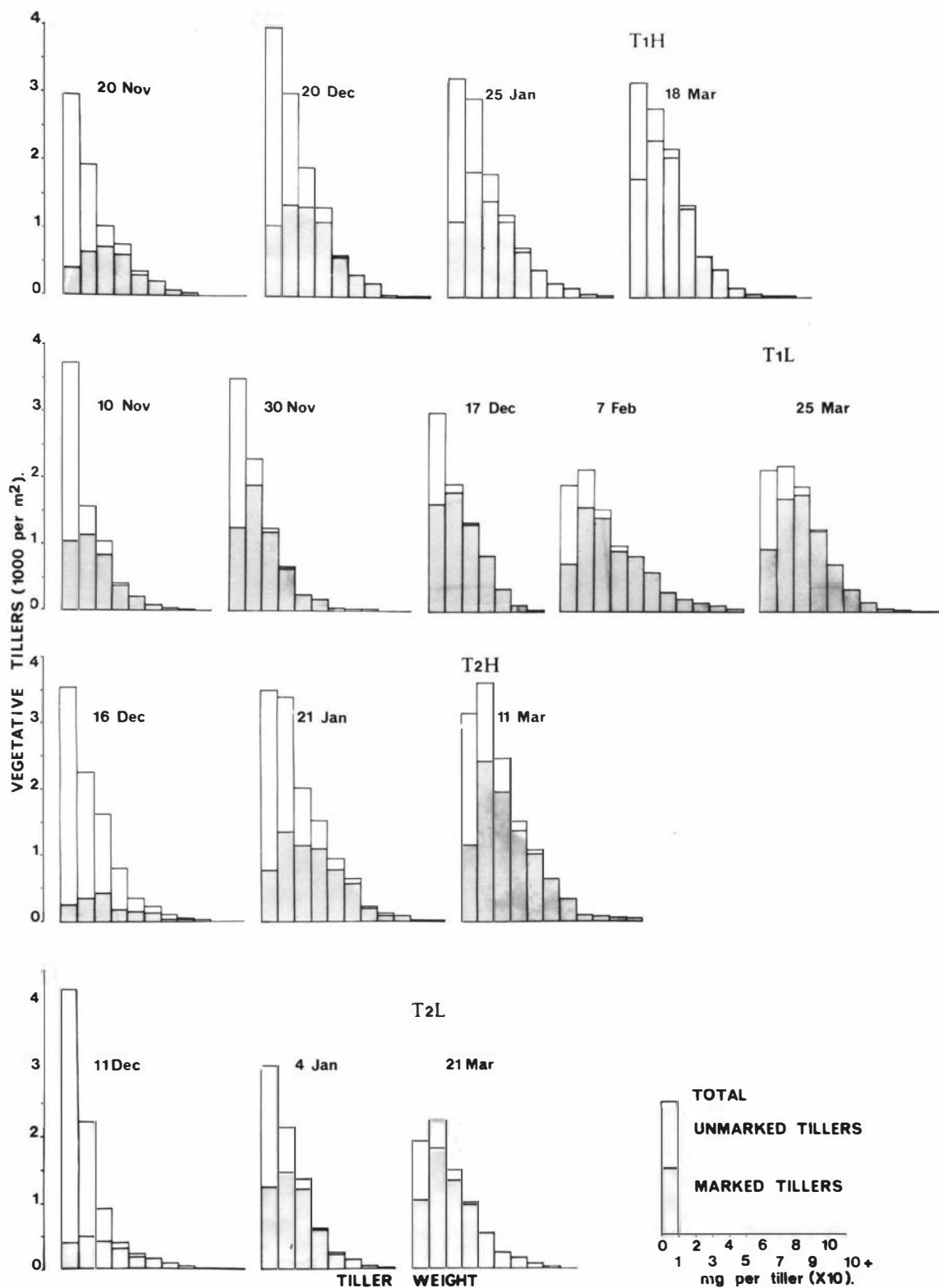
Figure 5.8: Frequency distributions of vegetative tiller weight at the end of rest periods.

5.3.6.3 Tiller weight

The weight of marked and unmarked vegetative tillers at the
end of rest periods are shown in Figure 5.8 and Table 5.18.
The mean weight of marked tillers was significantly greater than
the mean weight of unmarked tillers on all occasions. Generally
more than 50% of unmarked tillers were less than 10 mg and 80% less
than 20 mg, whereas only approximately 20% of marked tillers were less
than 10 mg and 40-50% less than 20 mg. Some marked vegetative
tillers were 100 mg or occasionally slightly heavier.

Table 5.18: Mean tiller weight and coefficient of skewness of
             marked and unmarked vegetative tillers before grazing

	Mean weight (mg)			Coefficient of skewness		
	Marked	Unmarked		Marked	Unmarked	
T_1H						
20 Nov	29	10	*	0.85	1.57	*
20 Dec	27	10	*	0.88	1.66	*
25 Jan	28	10	*	0.96	2.10	*
18 March	24	10	*	0.96	2.32	*
T_1L						
10 Nov	19	7	*	1.05	1.95	*
30 Nov	21	6	*	1.67	2.16	*
17 Dec	20	5	*	1.01	1.79	*
7 Feb	32	10	*	1.03	1.30	*
25 March	27	8	*	0.85	1.26	*
T_2H						
16 Dec	28	15	*	0.87	1.26	*
21 Jan	30	15	*	0.91	1.85	*
11 March	29	12	*	1.22	1.31	*
T_2L						
11 Dec	30	10	*	1.29	1.66	*
4 Jan	20	8	*	1.21	1.29	*
21 March	25	10	*	1.06	1.91	*

*Marked significantly (P< 0.05) different from unmarked

The coefficient of skewness calculated for vegetative tiller weight in each plot was positive and significant (P< 0.05) on all occasions for marked, unmarked and total (marked and unmarked) tillers. Unmarked tillers always had a significantly greater coefficient of skewness than marked tillers (Table 5.18).

5.3.6.4 Contribution of marked tillers to herbage mass

From the mean weight and number of tillers in each category the proportion of vegetative herbage mass contributed by marked and unmarked tillers was calculated (Table 5.19). In successive rest periods after the interruption of reproductive growth the unmarked tillers contributed a progressively lower proportion to the vegetative ryegrass herbage mass. This appeared to be related to tiller density because when the vegetative tiller population was relatively stable (e.g. T_1L after November - Figure 5.5) unmarked tillers were less important, contributing about 7% of vegetative herbage.

The proportion of reproductive herbage mass contributed by tillers marked at the start of the rest period as vegetative or reproductive was calculated (Table 5.20). The balance of reproductive herbage came from tillers appearing during the regrowth (unmarked) and occasionally from aerial tillers, but these two categories were less important. As might be expected on lax grazing treatments (T_1L and T_2L), reproductive tillers present at the start of regrowth contributed most reproductive herbage at the following grazing. However, on hard grazing treatments, the reproductive tillers marked at the start of regrowth largely died and tillers marked as vegetative (i.e. tillers with no stem elongation) rapidly developed to contribute most reproductive herbage at the following grazing. Because hard grazing resulted in a largely vegetative sward (Figure 5.4) vegetative ryegrass tillers reclassified as reproductive, although high in proportion, were actually quite low in amount.

5.4 DISCUSSION

5.4.1 Uninterrupted reproductive growth

Most reproductive tillers appeared in the first rest period
of the experiment (October and November) although further reproductive
tillers continued to appear until autumn.   The pattern of ryegrass
accumulation during this period of uninterrupted growth was similar
to that reported by Wilman *et al* (1976d), reproductive tillers making
the main contribution to herbage mass once culm elongation had begun.
Similarly, the decline in vegetative tiller density normally observed
during uninterrupted growth also occurred (Spiertz and Ellen, 1972;
Hebblewaite and Ivens, 1977, 1978; Ong *et al*, 1978b).   Thus, the
presence of 30-40% other species in the sward did not alter the pattern
of reproductive growth or tiller dynamics as observed in pure ryegrass
stands by overseas workers.

5.4.2 Interruption of reproductive growth

Later interruption of reproductive growth (up to anthesis) has
been shown to increase the amount of herbage harvested annually from
grass swards (Corrall, 1974; Mislevy *et al*, 1977).   For example,
Corrall (1974) harvested 13.4 t DM/ha and 16.4 t DM/ha from "Aberystwyth
S24" perennial ryegrass first cut at the leafy stage and the post-
anthesis stage respectively.   Both swards were subsequently cut after
5 weeks and then every 6 weeks.

Under grazing in this experiment later interruption of
reproductive growth, at the head emergence stage (T_2) compared with
the leafy stage (T_1), did not significantly increase herbage
accumulation (Table 5.8).   Delaying interruption until anthesis may
have increased herbage accumulation, but the increase would be expected
to be attributable to culm development (Wilman *et al*, 1976a), not lamina
development which almost stopped after 95% light interception (5.3.2.2.1).
The tendency for greater culm production and reduced lamina production
with later interruption of reproductive development was apparent in
this experiment (Table 5.9).   Between the start of the experiment and
head emergence (T_2) 53% (1 t DM/ha) less stubble and 88% (0.7 t DM/ha)
more lamina accumulated in T_1H than in T_2.

Cutting stemmy herbage for conservation is probably the most efficient method of harvesting pasture closed for long periods of uninterrupted reproductive growth. Although cattle may have consumed such herbage readily, the sheep used in this experiment showed reluctance to consume stem, especially the basal portion.

A period of rapid tillering occurred after grazing reproductive swards at both T_1 and T_2 (Figure 5.6). It is interesting to note that vegetative tillers appeared at the same rate when grazing was either hard of lax at both T_1 and T_2. Grazing presumably reduced apical dominance and base shading. Davies (1977) showed that merely shading tiller bases can arrest tillering, and conversely, tillering resumes when base shading is removed.

Considerably more reproductive meristems were removed by hard grazing than by lax grazing at both T_1 and T_2 (at least 80% in H compared with 25% at T_1 and 33% at T_2 in L). The proportion of reproductive meristems removed presumably had little effect on apical dominance as similar tiller appearance rates were measured after hard and lax grazing. Both hard and lax grazing removed lamina and it has been shown that removal of either the reproductive meristem or the expanding leaves in Italian ryegrass reduces apical dominance and allows tillering (Laidlaw and Berrie, 1974; Clifford, 1977). Also it was observed, although not measured, that lax grazing at T_2 resulted in removal of part of ryegrass seedheads and this may have been sufficient to stimulate tillering (Aspinall, 1964).

Head emergence in "Nui" perennial ryegrass occurs in October to November at Palmerston North, as does "Ruanui" (Wilson, 1959), so that the post-flowering period of tillering occurs between October and December, depending on when apical dominance is reduced by defoliation. This is in contrast to the United Kingdom where regularly defoliated swards resume rapid tillering in late summer or autumn (Langer *et al*, 1964; Garwood, 1969). In both cases tillering resumes after flowering, but flowering is earlier in New Zealand ryegrass (Table 5.21) so tillering resumes before rather than after summer. The period of reproductive development in "Manawa" ryegrass pastures is more prolonged than in perennial ryegrass pastures (Brougham, 1961), and this

could delay the appearance of post-flowering tillers in "Manawa" swards.

Table 5.21: Date of floral initiation (FI) and the post-flowering period of tillering (P) in relation to the longest day (LD). Data for S23 and S24 is from Garwood (1969).

	Sept	Oct	Nov	Dec	Jan	Feb
N.Z.	Sept	Oct	Nov	Dec	Jan	Feb
U.K.	Mar	Apr	May	June	July	Aug
Nui	FI		P	LD		
S23			FI	LD		P
S24		FI		LD	P	

5.4.3 Grazing intensity

Although enhanced regrowth could be expected from a higher residual LAI (Brougham, 1956), in fact greater net herbage accumulation occurred with a lower residual LAI. Net ryegrass accumulation was 25% greater in H than L (Table 5.10), a similar result to the previous year when green herbage accumulation was 20% greater in HH than LL. In contrast to Brougham (1956), who measured regrowth from a uniform sward mown to different heights, the above results were obtained over a number of rest periods from swards which became quite different in structure.

When Hunt and Brougham (1967) regularly trimmed a perennial ryegrass sward every seven days to a height which left sufficient herbage to intercept 90%-95% of noon sunlight they found that residual herbage contained progressively more dead herbage. A similar progressive accumulation of dead herbage occurred with lax grazing in this experiment and in the previous grazing experiment (Figures 4.2 and 5.3). This was because sheep removed lamina more readily than other herbage components, so that less than 50% of the total herbage (and little dead herbage) was removed.

Only after the first grazing at either T_1 or T_2 could the influence of residual LAI on herbage accumulation be investigated without confounding

influences from differences in sward structure, botanical composition, tiller density, etc (Table 5.13). Two similar comparisons were possible in the previous chapter (Table 4.9), and only in one of the four was total herbage accumulation significantly correlated with residual LAI. This one significant correlation (after T_1) appeared to be due to differential defoliation of reproductive meristems, which resulted in greater reproductive growth after lax grazing. It is therefore concluded that although a higher residual LAI may enhance regrowth (Brougham, 1956), this may not be reflected as greater herbage accumulation because of losses through death and decay. A greater residual LAI is associated with a greater green herbage mass, and, as discussed in the literature review (2.3.2.1.2), increased herbage death. Because of the activity of soil fauna dead herbage does not accumulate at the same rate as death occurs, but on one occasion (November 1976) dead herbage accumulation was significantly and positively correlated with residual LAI (Table 5.13). The negative correlation between vegetative herbage accumulation (leaf lamina accumulation in 1975) and increased residual LAI (Table 5.13 and 4.9 respectively) also reflects herbage death and disappearance.

The residual LAI of L was consistently greater than H (Table 5.1) but at 95% light interception the LAI of H was greater than L (Table 5.14). The greater amount of culm and dead herbage in L than H (Table 5.6), much of which intercepted light above the level of light measurement, was undoubtedly the cause of the difference in LAI between H and L at 95% light interception. The greater LAI of H at 95% light interception resulted in a smaller than expected difference in average LAI. For example, the average LAI, calculated by numerical integration of LAI measured at successive stages of regrowth, for T_1H and T_1L between 25 October and 18 December were not significantly different (2.2 and 2.8 respectively). As the average LAI of H and L were similar, the assimilation was probably similar also. The greater herbage accumulation measured with more intensive defoliation therefore must have reflected reduced herbage death and decay, that is, more efficient utilization of herbage before it was subjected to loss by decay.

Harder grazing, by removing culm and reproductive meristems, resulted in the reproductive tiller density declining more rapidly in summer. As in the previous year, continued lax grazing resulted

in a sward with large amounts of dead or dying ryegrass culm, while
hard grazed swards were leafy and vegetative.   The greater amount
of *Poa* in laxly grazed swards probably reflected *Poa* culm left at the
initial grazing at T_1 or T_2.   Besides the difference in leafiness,
as in the previous experiment, and as noticed by extension workers
(e.g. Hall, 1973) the pattern of herbage production was better in
H than L.   In January accumulation of green herbage was at
approximately 85 kg DM/ha/day in H compared with approximately 40 kg
DM/ha/day in L (Figure 5.3).

Hard grazed swards had a greater vegetative tiller density than
lax grazed swards by January in both 1976 and 1977 (30% and 50%
respectively), a result similar to that in other studies (e.g. Tainton,
1974a; Boswell and Crawford, 1978).   The difference in tiller density
was mainly attributable to a greater tiller appearance rate in H
than L, not at the first hard or lax grazing at T_1 or T_2, but subsequently
(5.3.6.2.1).   Several experiments have shown that tiller appearnce
can be reduced by artificial shading (Mitchell and Coles, 1955;
Bean, 1964; Thomas and Davies, 1978) and the greater amount of culm
and dead herbage in L than H (Table 5.6) probably reduced tiller
appearance in L by shading active photosynthetic tissue.   In 1976
a single hard grazing (which removed or trampled culm) was sufficient
to increase the tiller density to a level similar to a hard grazed
sward, also suggesting that shading by culm reduced tiller development
and appearance.

Differences in apical dominance or assimilate partitioning could
also have caused the greater tiller appearance rate in H than L.
During December and January there was considerably more green,
virtually leafless, culm in L than H (shown as "reproductive tillers"
in Figure 5.4).   Assimilate may have been translocated to these culms,
thereby reducing assimilate available for tillering in L.

In 1976 the difference in tiller density caused by hard and lax
grazing disappeared in autumn (Figure 4.3), but in 1977 the difference
was still apparent in June.   The main difference between years was
in autumn, 1976 being wetter and 1977 being drier (Appendix I).   It
would appear that hard grazing in autumn to clean up rank herbage from

the previous summer, as suggested by Hunt and Brougham (1967), can only be expected to remove the effect of previous lax grazing when sufficient moisture is available to permit tillering in autumn.

Despite all treatments being managed similarly between January and June (Period II), during this time swards previously hard grazed accumulated 25% more ryegrass than swards previously lax grazed. The difference was also reflected in green herbage accumulation, and was partly attributable to differences in ryegrass tiller density. There was a significant correlation ($r = 0.576$) between ryegrass accumulation in Period II and vegetative tiller density in March. In 1976, because differences in tiller density disappeared during the moister autumn, a similar residual response to previous grazing intensity was not observed. As Jackson (1973) commented, yield can be insensitive to tiller density over quite a wide range, but if density continues to fall yield is ultimately affected. From the results obtained in this experiment it appears that during autumn and early winter ryegrass accumulation can be reduced if tiller density drops below 8300 tillers/m^2 (Table 5.16). This is discussed further in the final chapter (7.2.4.1.1).

5.4.4 Aerial tillers

This experiment confirmed that aerial tillers develop from above ground axillary buds on grazed reproductive tillers. Different defoliation managements left different numbers of aerial axillary buds (or nodes), allowing different numbers of aerial tillers to develop. Aerial tillers contribute little to the persistance of ryegrass in pastures grazed by sheep since none of the marked aerial tillers rooted effectively and many were removed by grazing. Aerial tillers made a very small contribution to net herbage accumulation, even when grazing was lax and the number was greatest (0.2 t DM/ha over the whole experiment).

5.4.5 Tiller weight

Jones *et al* (1979) have measured the frequency distribution of tiller weights for tall fescue. As in this experiment, they found that tiller weights did not follow a normal distribution, but were

markedly skewed.   Jones *et al* (1979) found that the logs of individual tiller weights were not normally distributed either as suggested by the work of Koyoma and Kira (1956) and Obeid *et al* (1967).   As expected, the younger unmarked tillers were generally smaller than the older marked tillers (Table 5.18), although there was a large range in the weight of both categories of tillers (Figure 5.8).   Small tillers (less than 10 mg) were more likely to be new tillers, but a proportion were older, and presumably less vigorous.

Rapid tillering did not immediately result in a proportional increase in herbage production because the new tillers were considerably smaller than older tillers.   When the tiller density was stable new unmarked tillers contributed about 7% of herbage mass at the end of regrowth (5.3.6.4).   New tillers made a greater contribution to herbage mass and accumulation in November and December after reproductive growth had reduced the vegetative tiller density.   In the next chapter the relationship between tiller age and contribution to herbage production is investigated further.

Ong *et al* (1978b) reported that small tillers were most likely to die during periods of shading.   Although small tillers are most likely to be younger tillers, many established tillers (marked) were small even after several weeks regrowth.   Tiller death due to shading by larger tillers is therefore likely to affect both young and older established tillers.   Mean tiller weight is unlikely to be of value for interpretation of tiller dynamics because of the different tiller weight distributions caused by tiller age (Figure 5.8), and genotype (Jones *et al*, 1979).

CHAPTER 6: EFFECTS OF THE TIME OF CUTTING TO CONTROL REPRODUCTIVE DEVELOPMENT AND THE SUBSEQUENT CUTTING INTERVAL ON HERBAGE ACCUMULATION AND TILLER DYNAMICS OF RYEGRASS PASTURE

6.1 INTRODUCTION

Usually the vegetative tiller density of grass swards declines during reproductive growth (Spiertz and Ellen, 1972; Hebblethwaite and Ivins, 1977, 1978; Ong *et al*, 1978b). The experiment reported in Chapter 5 showed that defoliation during reproductive growth interrupted this decline and caused a period of rapid tillering. It would seem that different defoliation managements probably resulted in swards with different tiller age structures after flowering. Where stem development was permitted the vegetative tiller population was predominantly young, while earlier interruption of reproductive growth resulted in a mixture of preflowering and new tillers after flowering. Davies (1977) has shown that because of different proportions of vegetative tillers surviving flowering, S22 and S24 ryegrass swards have different tiller age structures.

Differences in age structure of tiller populations could only be implied from the grazing experiment because new sampling areas were chosen each rest period for tiller marking. To enable the same sampling areas to be observed through several rest periods, without the problems of animal treading, fouling, etc, a mowing experiment was designed. Defoliation regimes were chosen to produce a range of tiller age structures after flowering.

The grazing experiment described in Chapter 5 had shown that within any rest period the herbage production of ryegrass generally depended on tillers present at the start of regrowth, new tillers contributing little. In the following experiment the weight of tillers of different ages was measured to find their relative contribution to herbage accumulation.

6.2 EXPERIMENTAL

6.2.1 The site and sward establishment

The experiment was conducted between 5 September 1977 and 23 January 1978 at a site on the Massey University campus (Plate 6.1). The soil was an Ohakea silt loam (Cowie, 1974) which in its natural state is characterised by 1 m of poorly drained silt loam overlaying 2-5 m of weakly cemented gravels. Drainage was adequate at the site because a subsurface drainage system had been installed.

The experimental area was cultivated in February 1977 and then devided into 60 plots, each 2 m x 5 m, arranged in five block replicates (Figure 6.1). On 15 March "Grasslands Nui" perennial ryegrass (*Lolium perenne* L) was broadcast on 30 plots at a rate of 45 kg/ha. The other 30 plots were sown with "Grasslands Manawa" ryegrass (*Lolium x hybridum* Hausskn) but these were not used in the experiment. Ryegrass seedlings tended to emerge in rows, about 8 cm apart, corresponding to impressions left by a Cambridge roller used to consolidate the seedbed. Dicotyledon seedlings were controlled by spraying on 28 April 1977 (1.44 kg dichlorprop/ha, 90 g MCPA/ha, 0.13 kg dicamba/ha). The main weed grass was *Poa annua* L, largely in the inter-row areas. To encourage tillering, the sward was mown on 7 May, 28 May and 31 July before the experiment started.

6.2.2 Sward management

The experimental area was spray irrigated on four occasions (30 October, 9 December, 29 December and 15 January) when the amount of water in the top 15 cm of soil reached 20% of the dry weight. Pasture growth is limited by soil moisture if the soil moisture tension is less than -100 kPa (Scotter, *pers comm* .), 19% of the dry weight on this site.

Infestation by Argentine stem weevil (*Hyperodes bonariensis*) was anticipated so the experiment was sprayed with Oximal at 1 kg/ha on 22 September and 14 November. Little weevil damage was observed.

Fertilizer was applied to prevent plant nutrients from limiting growth (Table 6.1). Nitrogen was applied at approximately monthly

Plate 6.1: General view of the experiment on 7 November. The meterological station can be seen in the background. A 30 cm ruler is shown between A_5 and F_5 (Figure 6.1).

Plate 6.2: View of some plots on 7 November. Note A_5 and F_5 in the foreground, and E_4, B_4 and A_4 behind the 30 cm ruler. B_4 and F_4 were cut on 11 November.

intervals and during the measurement period 140 kg N/ha was applied.
Soil quick test values (Mountier *et al*, 1966) on soil samples (0-10 cm)
taken on 10 August 1977 indicated that nutrients were adequate for
vigorous plant growth (pH 5.6, K 7, Truog P12).

Table 6.1: Fertilizer application to the experimental area

Date	Fertilizer (N.P.K.)	Kg N/ha	Kg P/ha	Kg K/ha
7. 3.77	0. 6.14	-	23	53
9. 4.77	26. 0. 0	50	-	-
31. 8.77	12.10.10	48	40	40
4.10.77	12.10.10	25	21	21
9.11.77	26. 0. 0	90	-	-
9.12.77	26. 0. 0	60	-	-
3. 1.78	26. 0. 0	60	-	-
Total		238	84	114

6.2.3 Treatments

The experiment was mown on 5 September 1977 and then the following
six defoliation treatments compared (Figure 6.1):

A. Cut every three weeks

B. First cut after three weeks; subsequent cuts at 95%
    light interception

C. First cut when reproductive meristems were above cutting
    height; subsequent cuts every three weeks

D. First cut when reproductive meristems were above cutting
    height; subsequent cuts at 95% light interception.

E. First cut when reproductive meristems were above cutting
    height; subsequent cuts every 8 weeks.

F. First cut at head emergence; subsequent cuts at 95%
    light interception.

The actual cutting treatments and dates are shown in Table 6.2.
Because F was mown more frequently than expected the experiment ended
two weeks earlier than anticipated when available harvest areas were
exhausted in F.   Light interception was measured at solar noon in

treatments B,D and F with a 'LI-COR' light meter with the 2.5 cm high
'QUANTUM' sensor (Lambda Instrument Corp., Nebraska). All treatments
were cut to the same height with a modified reel mower which left a
stubble approximately 1-5 cm in length depending on tiller angle. For
all treatments the mean residual herbage mass after cutting was 600 $\pm$
100 kg DM/ha.

Table 6.2: Dates of cutting in each treatment. The cutting
interval is shown in parenthesis (W, weeks; 95%,
95% light interception; HE, head emergence; S,
when reproductive meristems were above cutting height).

Treatment A	Treatment B	Treatment C	Treatment D	Treatment E	Treatment F
5 Sept	5 Sept	5 Sept	5 Sept	5 Sept	5 Sept
26 Sept(3W)	26 Sept (3W)				
17 Oct (3W)		19 Oct (S)	19 Oct (S)	19 Oct (S)	
7 Nov (3W)	11 Nov (95%)	9 Nov (3W)			11 Nov (HE)
28 Nov (3W)		30 Nov (3W)	26 Nov (95%)		
	5 Dec (95%)				8 Dec (95%)
19 Dec (3W)		21 Dec (3W)		14 Dec (8W)	
	30 Dec (95%)		30 Dec (95%)		30 Dec (95%)
9 Jan (3W)		11 Jan (3W)			
23 Jan (2W)	23 Jan (95%)	23 Jan (2W)	23 Jan	23 Jan (5W)	23 Jan (95%)

6.2.4 Measurements

Each plot was divided into twenty 100 cm x 50 cm harvest areas
(Figure 6.2). Depending on the anticipated number of mowings,
sufficient areas were selected at random to allow one harvest before
and after each mowing; between 6 and 18 harvest areas were selected
in each plot. Each harvest area comprised a 0.18 m^2 quadrat for yield
estimation and an adjacent circular fixed frame (0.008 m^2 or 10.2 cm
diameter) for tiller marking.

6.2.4.1 Herbage mass

At each harvest, before and after mowing, one harvest area was
selected at random from each replicate to obtain the pre-mowing or post-
mowing herbage mass. The quadrat was cut to ground level with an
electric shearing handpiece. The cut herbage was washed to remove soil
and then dried at 80°C for at least 14 hours.

6.2.4.2 Tiller marking

The fixed frames were placed during August and all ryegrass tillers within each frame were marked with split coloured plastic 4 mm rings. Following the mowing on 5 September all frames were examined to mark unmarked tillers and remove rings from tillers that had died.   All 356 frames had been checked by 9 September.   After subsequent mowings these frames were again examined to mark new tillers and remove rings from dead tillers.   Since rings of different colours were used after each mowing, the rest period that a tiller had appeared in, could be seen from the colour of its plastic ring.   The number of rings of each colour removed from each frame and number of new tillers marked was recorded.

Vegetative tillers which were brown and withered, or had no live (greenish-white) leaves inside the sheath were classified as dead. Reproductive tillers were classified as dead when the defoliated stem was brown and sapless.   Because tillering is intravaginal in ryegrass new tillers were often enclosed in the marker ring of the parent tiller.   The largest tiller was classified as the parent tiller.

At each harvest, before or after grazing, one fixed frame (and the turf within it) per plot was removed with a spade and then examined in the laboratory.   Herbage within each frame was cut at ground level and divided into live ryegrass, dead leaf, dead ryegrass culm and other species.   Live ryegrass tillers were divided into different age categories (depending on colour of marker), and then further into reproductive tillers (those tillers with visible above-ground stem extension) and vegetative tillers.   The emerged leaf lamina was removed from each tiller to give leaf and stubble (the remainder) for each tiller category.   The dry weight of each herbage fraction was recorded to enable calculation of the proportion of herbage mass in each fraction. The number of tillers in each category and the number of unmarked tillers arising from each tiller category was recorded.

6.2.4.3 Seedhead counts

In treatment F an area was left in each plot which was not defoliated after 5 September and the number of seedheads per unit area was counted frequently through to 15 December.   After this lodging made

counts difficult.

6.2.5 Calculation of herbage accumulation

The total herbage mass before and after mowing was obtained from the cut quadrats (6.2.4.1) and the mass of each herbage component obtained by multiplying this total by the proportion measured in the fixed frame (6.2.4.2).   Herbage accumulation for each rest period was calculated as the difference between the herbage mass measured at the beginning and end of the rest period.   Detailed results are presented in Appendix V.

6.2.6 Statistical procedures

The statistical computer programme "TEDDYBEAR" (Wilson, 1978) was used for analysis of data.   Tiller density data (Tables 6.3, 6.5, 6.6 and 6.10) were compared using analysis of covariance, the number of tillers per frame at the time of tiller marking being the covariate.

6.3 RESULTS

6.3.1 Uninterrupted regrowth

6.3.1.1 During reproductive growth

Data obtained from different treatments, reflecting the un-interrupted growth and development of a reproductive sward is presented in Table 6.3.   On 5 September no reproductive tillers were apparent.   Three weeks later (26 September), stem elongation had just commenced and tiller density was increased by the appearance of new (unmarked) tillers.   The increase in herbage mass was mainly due to the increased weight of marked vegetative tillers, new tillers being considerably smaller.   Continued growth of marked tillers, both vegetative and reproductive, accounted for most of the increase in herbage between 26 September and 19 October.   Although reproductive tiller weight was not significantly different for these two dates, culm growth resulted in many previously vegetative tillers (16 mg) being classified as reproductive (93 mg) on 19 October.   The increase in herbage mass between 19 October and 11 November was due to the

Table 6.3: Herbage mass (t DM/ha), tiller density (hundred tillers/m^2), and tiller weight (mg/tiller) during uninterrupted growth after cutting on 5 September.

Date	5 Sept	26 Sept	19 Oct	11 Nov
TREATMENTS:	All	A + B	C,D,E	F
DAYS REGROWTH:	0	21	44	67
HERBAGE MASS:				
Ryegrass:				
Vegetative tillers	0.7 c*	1.2 b	1.8 a	1.4 b
Reproductive tillers	0 c	0 c	1.2 b	3.8 a
Total	0.7 d	1.2 c	3.0 b	5.2 a
Other species:	0.1 a	0.1 a	0.2 a	0.2 a
Dead herbage:	0.4 c	0.5 c	0.6 b	1.1 a
Total:	1.2 d	1.9 c	3.9 b	6.5 a
TILLER DENSITY:				
Vegetative tillers:**				
Marked	114	103 a	81 b	62 c
Unmarked		26 a	25 a	19 a
Total	114	129 a	106 b	81 c
Reproductive tillers:		1 b	16 a	22 a
Total alive:	114	130 a	122 a	103 b
Marked tillers dead:		11 c	17 b	30 a
MEAN TILLER WEIGHT:				
Vegetative tillers:				
Marked	9 c	16 b	24 a	26 a
Unmarked		5 b	10 a	13 a
Reproductive tillers		56 b	93 b	211 a

  * Duncans multiple range test compares dates.

 ** Adjusted by covariance for number marked on 5 September.

accumulation of dead herbage and further growth of reproductive tillers. The decline in vegetative tiller herbage mass after 19 October was associated with a decline in the number of vegetative tillers and no significant increase in tiller weight. By 11 November reproductive tillers were eight times heavier than marked vegetative tillers. Reproductive tiller density did not increase significantly after 19 October and a final density of 1730 ± 150 tillers/m^2 was reached (Mean of treatments C,D,E and F in Table 6.3).

Seedheads began emerging in late October and continued to appear until December (Table 6.4). At the first cut of Treatment F on 11 November 39% of heads had emerged. Plates 6.1 and 6.2 show treatment F four days before mowing on 7 November.

On 26 September when treatments A and B were cut, there were few reproductive tillers with stem elongation (70 ± 30 tillers/m^2) and changes in tiller density during the subsequent regrowth (Table 6.5) were similar to those described for the regrowth starting on 5 September (Table 6.3). The number of vegetative tillers again declined as tillers were reclassified as reproductive tillers, and as vegetative tillers died. Significantly ($P < 0.05$) fewer new tillers appeared in the first three weeks regrowth after cutting on 26 September compared with the first three weeks after 5 September (2600 and 1200 tillers/m^2 respectively).

Table 6.4: Head emergence during uninterrupted growth on the undefoliated part of F.

Date	Heads/m^2 (± SE)	% Head emergence
5 Sept	0	—
19 Oct	0	—
28 Oct	30 ± 10	2
4 Nov	160 ± 20	10
10 Nov	590 ± 70	39
21 Nov	1220 ± 120	81
15 Dec	1550 ± 230	100

Table 6.5: Tiller density during uninterrupted growth after cutting on 26 September (hundred tillers/m^2, adjusted by covariance for number of tillers marked on 26 September).

Date	26 Sept	17 Oct	11 Nov
TREATMENT	A and B	A	B
DAYS REGROWTH:	0	21	46
LIVE TILLERS:			
Vegetative tillers:			
Marked	122	102 a	79 b
Unmarked	–	12 a	7 a
Marked and unmarked	122	114 a	85 a
Reproductive tillers:	1	10 a	21 a
Total	123	124 a	106 a
DEAD TILLERS (marked):	–	11 a	23 a

Duncans multiple range test compares dates.

6.3.2.1 During vegetative growth

When treatments C,D and E were cut on 19 October 1600 ± 200 tillers/m^2 had visible stem elongation (reproductive tillers in Table 6.3). Cutting removed meristems from 1200 ± 100 tillers/m^2, and effectively controlled reproductive development. Data obtained from treatments C,D and E after cutting on 19 October is presented in Table 6.6.

After cutting on 19 October the sward was mainly vegetative because reproductive tillers with defoliated meristems died and few further reproductive tillers appeared. Herbage accumulation was mainly due to increasing weight of vegetative tillers, and after 95% light interception (26 November) to dead herbage accumulation. Vegetative tillers continued to increase in weight after 95% light interception (to 50 mg) and the number did not change significantly during the eight weeks regrowth. This is in contrast to the reproductive sward (Table 6.3) where vegetative tillers (25 mg) did not increase significantly in weight and declined in number after 19 October, when the sward was also at full light interception.

Table 6.6: Herbage mass (t DM/ha), tiller density (hundred tillers/m^2, adjusted by covariance for the number of tillers marked on 19 October) and tiller weight (mg/tiller) during uninterrupted growth after cutting on 19 October.

Date	19 Oct	9 Nov	26 Nov	14 Dec
TREATMENT:	C,D,E	C	D	E
DAYS REGROWTH:	0	21	38	56
HERBAGE MASS:				
Ryegrass:				
Vegetative tillers	0.5 d*	0.9 c	2.2 b	4.3 a
Reproductive tillers	0.3 a	0.3 a	0.6 a	0.6 a
Total	0.8 d	1.2 c	2.7 b	4.8 a
Other species	0.1 a	0.1 a	0.1 a	0.3 a
Dead herbage	0.5 b	0.6 b	0.6 b	1.2 a
Total	1.4 d	1.9 c	3.5 b	6.4 a
TILLER DENSITY:				
Vegetative tillers:				
Marked	106	92 a	89 a	87 a
Unmarked		9 b	28 a	33 a
Total	106	101 a	114 a	120 a
Reproductive tillers:	16	11 a	6 a	6 a
Total alive	122	112 a	120 a	126 a
Marked tillers dead		19 a	29 a	29 a
MEAN TILLER WEIGHT:				
Vegetative tillers:				
Marked	6 c	14 c	31 b	50 a
Unmarked		6 b	6 b	18 a
Reproductive tillers:	21 c	36 c	94 b	146 a

*Duncans multiple range test for herbage mass was with transformed (square root) data.   The natural means are shown.

Duncans multiple range test compares dates,

6.3.2 Net herbage accumulation

Treatment A was mown every three weeks so the seasonal pattern of herbage accumulation was apparent (Table 6.7). Accumulation was greatest in early December when vigorous vegetative growth occurred. Vegetative growth was comparatively low during late October but the average soil temperature (Table 6.7) and other meterological data (Appendix VI) collected 50 m from the experiment suggest that the period of lowest herbage accumulation was not due to temperature or moisture limitations, as the plots were irrigated.

Table 6.7: Net ryegrass herbage accumulation in treatment A
(3 weekly cut) and the average 10 cm soil
temperature for each rest period.

Regrowth cycle*	Temperature (°C)	Ryegrass accumulation (t DM/ha)		
		Vegetative	Reproductive	Total
5 Sept – 26 Sept	7.8	0.6 cb	–	0.6 cb
26 Sept – 17 Oct	10.5	0.8 b	0.3	1.1 b
17 Oct – 7 Nov	12.1	0.3 c	0.2	0.5 c
7 Nov – 28 Nov	14.1	0.9 b	0.1	1.0 b
28 Nov – 19 Dec	15.8	1.5 a	0.3	1.8 a
19 Dec – 9 Jan	16.2	1.0 b	–	1.0 b

* Last cut omitted because only two weeks regrowth.
Duncans multiple range test compares cycles.

The treatments had a marked effect on net herbage accumulation when compared at the end of the experiment (Table 6.8 and Figure 6.3) and as expected ryegrass contributed over 90% of herbage. The most frequently cut treatment accumulated least herbage (A : 6.8 t DM/ha) and treatment F accumulated 80% more herbage (F : 12.5 t DM/ha).. Differences in herbage accumulation were largely explained by the number of cuts during the experiment and the amount of reproductive growth that occurred. Figure 6.3 shows that in treatments A,C,D and E herbage accumulation was highly correlated with the number of cuts during the experiment (r= -0.924 with 18 d.f.). Treatments B and F had considerably higher accumulation than would be expected from the number of cuts, but this can be explained by reproductive growth.

Comparing treatments B,D and F (Table 6.8), all mown at 95% light interception (Table 6.2), shows the effect of reproductive growth on herbage accumulation. Preventing reproductive growth by mowing at the leafy stage (D) reduced ryegrass and dead herbage accumulation compared with allowing reproductive growth to continue until 39% head emergence (F). The greater amount of dead herbage in F than in D accumulated during the later stages of reproductive growth, that is, after 95% light interception was reached (Appendix V). The mowing of B on 26 September removed few reproductive meristems and reproductive growth continued until 95% light interception was reached on 11 November. This explains why herbage accumulation in treatment B was greater than would be expected from the number of cuts (Figure 6.3).

Table 6.8: Net herbage accumulation for each treatment between 5 September and 23 January (t DM/ha).

Treatment	A	B	C	D	E	F
Ryegrass:						
Vegetative	5.7 b	7.1 a	5.3 b	7.9 a	8.0 a	7.4 a
Reproductive	0.8 c	2.6 ab	1.5 bc	1.2 c	1.8 bc	3.8 a
Total	6.5 c	9.7 ab	6.8 c	9.1 b	9.8 ab	11.2 a
Other species	0.3 a	0.6 a	0.5 a	0.4 a	0.2 a	0.3 a
Dead herbage	0 b	0.2 b	0 b	0.3 b	1.1 a	1.0 a
Total herbage	6.8 c	10.5 b	7.4 c	9.8 b	11.1 ab	12.5 a

Duncan multiple range test compares treatments for each component.

The effect of cutting frequency on net herbage accumulation can be seen by comparing A and B or C,D and E (Table 6.8 and Figure 6.3). Less herbage accumulated when cutting was every three weeks compared with cutting at 95% light interception (compare A and B, or C and D). Comparing D and E indicates that the response to increased regrowth length beyond 95% light interception in a vegetative sward was largely from increased dead herbage accumulation (Table 6.8).

The other species component of the sward was mainly *Poa* but at the start of the experiment the following species occurred (% occurrence in 30 fixed frames): ryegrass (100), *Poa* (77), *Trifolium repens* (17)

Juncus bufonius (13), *Bellis perennis* (10), *Veronica* sp (10), *Coronopus didymus* (3), *Geranium* sp (3) and *Taraxacum officinale* (3).

6.3.3 Tiller dynamics

Data on ryegrass tiller density, tiller appearance and tiller death in the sward was obtained from the three fixed frames per plot destructively sampled at the last two dates for each treatment, that is, 23 January and at the penultimate mowing. In Figure 6.4, tillers marked at the start of the experiment are labelled I, and new tillers marked at successive mowings, II – VIII. In Table 6.9, the number of total tillers, new tillers, and dead tillers are equivalent to the sum of all tiller categories (I – VIII), the number of marked tillers and the tillers dying during regrowth (I – VII) respectively. The number of reproductive tillers at each date (Table 6.9) was recorded from fixed frames removed at each mowing, not the same frames used to calculate tiller density, appearance and death.

6.3.3.1 Tiller density

Ryegrass tiller density at the beginning of the experiment was not significantly different for the six treatments ($P < 0.05$) although it ranged from 9700 to 11700 tillers/m^2 (treatments B and F respectively), all tillers being vegetative. In September the tiller density increased due to rapid tillering, but declined again during the period of reproductive growth in October (A and C Figure 6.4). These changes are not apparent in other treatments because of less frequent sampling. During October and early November reproductive growth was interrupted and a period of rapid tillering occurred, increasing the tiller density. In most treatments the density declined during the last few weeks of the experiment.

Treatments were compared in early December when the peak density was reached, and again at the end of the experiment (Table 6.10). Treatment E, mown on 14 December, was excluded from the first comparison. In December density was greatest on C and F and least on A and D; but at the end of the experiment no difference could be detected between treatments.

Table 6.9: Ryegrass tiller density at each mowing (hundred
tillers/m^2)

	Reproductive tillers	Dead tillers	New tillers	Total tillers
TREATMENT A:				
5 September	0			112 bc*
26 September	0	9 c	24 b	127 a
17 October	10	7 c	7 cd	127 a
7 November	13	16 b	2 d	113 bc
28 November	4	22 ab	36 a	127 a
19 December	6	17 b	12 c	122 ab
9 January		23 a	11 c	110 c
23 January				105 c
TREATMENT B:				
5 September	0			97 c
26 September	1	8 d	25 b	114 b
11 November	21	14 c	9 d	108 b
5 December	1	26 a	40 a	123 a
30 December	4	24 a	12 cd	111 b
23 January		19 b	17 c	109 b
TREATMENT C:				
5 September	0			110 c
19 October	14	14 b	41 a	137 ab
9 November	10	26 a	6 c	117 c
30 November	1	13 b	38 a	143 a
21 December	4	20 ab	13 bc	136 ab
11 January		22 a	17 b	131 ab
23 January				129 b
TREATMENT D:				
5 September	0			117 c
19 October	14	17 a	26 a	126 b
26 November	7	21 a	30 a	135 a
30 December	1	24 a	16 b	127 b
23 January		18 a	26 a	136 a
TREATMENT E:				
5 September	0			104 a
19 October	19	13 b	34 a	125 a
14 December	5	31 a	29 a	123 a
23 January		43 a	43 a	124 a
TREATMENT F:				
5 September	0			117 cd
11 November	24	32 a	17 b	103 d
8 December	0	30 a	77 a	150 a
30 December	3	27 a	13 b	137 ab
23 January		35 a	25 b	127 bc

* Duncans multiple range test compares observations between cuts within treatments.

Table 6.10: Effect of treatments on tiller density (hundred
tillers/m^2, adjusted by covariance for the number
of tillers marked on 5 September).

Treatment	A	B	C	D	E	F
1 December *	126 b	133 ab	143 a	131 b	–	145 a
23 January	103 a	117 a	128 a	131 a	128 a	122 a

*A: 28/11, B: 5/12, C: 30/11, D: 26/11, F: 8/12
Duncans multiple range test compares treatments on 1 Dec or 23 Jan.

6.3.3.2 Tiller appearance

Treatment A, and treatment C after 19 October, were both mown
every three weeks and showed similar tiller appearance patterns
(Table 6.9).   Two periods of rapid tillering occurred, the first
before stem elongation (5-26 September) and the second after defoliation
of reproductive tillers.   Mowing in October defoliated many reproductive
tillers, but it was not until after the next mowing (7 or 9 November)
that the period of most rapid tillering occurred (Table 6.9).
Tillering was significantly reduced in treatment A during the period
of stem elongation (26 September to 7 November).   A similar period of
reduced tillering occurred in treatment C (19 October to 7 November).
After the late November peak, tillering declined to a level intermediate
between the previous extremes in A and C.

Although not apparent from Figure 6.3, in the less frequently
mown treatments (B,D,E,F) tillering was also rapid before stem
elongation began and relatively slow during stem elongation (Table 6.3).
After defoliation of reproductive tillers in treatments B,D and F
(11 November, 19 October and 11 November respectively) rapid tillering
occurred (Figure 6.3).   Rapid tillering also occurred in treatment
E after defoliation of reproductive tillers (Table 6.6).

When treatments C,D and E were mown on 19 October it was found
from the 15 frames removed before mowing and the 15 frames removed
after mowing that 51% of reproductive tillers had new unmarked tillers
attached compared with 11% of vegetative tillers (Table 6.11).   From
Table 6.11 it was calculated that reproductive tillers had 0.9 new

tillers per tiller compared with 0.2 for vegetative tillers.
Since reproductive tillers were less numerous than vegetative tillers,
56% of new tillers were attached to reproductive tillers.

Table 6.11: Number of new (unmarked) tillers per marked
            vegetative and reproductive tiller on 19
            October (Treatments C,D and E).

New tillers/marked tiller	Number of marked tillers		
	Vegetative	Reproductive	Total
0	1636	188	1824
1	147	88	235
2	46	60	106
3	10	36	46
4	2	7	9
5	0	1	1
Total	1841	380	2221

By contrast, when treatment F was cut for the first time
(11 November), reproductive tillers had 0.6 new tillers/tiller and
vegetative tillers 0.1 new tillers/tiller (detailed data not presented).
Also, a greater proportion of new tillers were attached to reproductive
tillers (72%) than to vegetative tillers.

Swards were largely vegetative after mid-November (Table 6.9) but
late reproductive tillers continued to contribute new tillers (Table
6.12). The defoliated culm bases of mown reproductive tillers (cut
stubs) also produced new tillers, in F contributing 35% of new tillers
on 8 December. At later dates, when fewer stubs were present, a
greater proportion of new tillers came from vegetative tillers. A
similar trend is apparent in other treatments. Where frequent mowing
reduced reproductive dominance (A and C) the proportion of new tillers
contributed by reproductive tillers (cut and uncut) was reduced.

Table 6.12: Proportion (%) of new tillers appearing from
vegetative, reproductive and defoliated reproductive
(cut stubs) tillers at each cut.

	Vegetative tillers	Reproductive tillers	Cut stubs
TREATMENT A:			
28 November	84	6	10
19 December	86	10	4
9 January	80	5	14
23 January	98	0	2
TREATMENT B:			
5 December	66	3	31
30 December	81	12	7
23 January	95	0	5
TREATMENT C:			
30 November	88	4	7
21 December	90	5	5
11 January	89	1	10
23 January	99	0	1
TREATMENT D:			
26 November	59	24	17
30 December	78	10	12
23 January	93	0	7
TREATMENT E:			
14 December	57	18	25
23 January	74	0	26
TREATMENT F:			
8 December	64	1	35
30 December	74	7	19
23 January	99	0	1

The tillering rate of vegetative tillers (Table 6.13) was
influenced by tiller age and time of year. Data was highly variable,
mainly because the number of tillers observed in each category was
low. Each frame contained about 100 tillers, subdivided into several
categories (I-VIII). Established tillers (I) tillered at different
rates in each rest period, but generally at higher rates than the newest

tillers (e.g. in A comare I with III on 7 Nov, I with V on 19 Dec, I with IV on 9 Jan). During the period of more rapid tillering however, this difference between category I tillers and more recent tillers was reduced (i.e. A on 28 Nov, B on 5 Dec, C on 30 Nov, D on 26 Nov, F on 8 Dec). Apparent differences between treatments at similar dates were partly attributable to different periods of time between cuts.

Table 6.13: Tillering rate (tillers/100 tillers) for each category of vegetative tillers

Category	I	II	III	IV	V	VI
TREATMENT A:						
7 November	4	1	*0**			
28 November	43	46	*61*	*50*		
19 December	26	24	*18*	*10*	*0*	
9 January	14	13	*7*	*0*	6	*1*
TREATMENT B:						
5 December	47	53	*33*			
30 December	9	18	*17*	6		
23 January	20	*9*	*22*	*10*	*5*	
TREATMENT C:						
30 November	34	41	*29*			
21 December	18	20	*20*	1		
11 January	16	18	*6*	3	1	
TREATMENT D:						
26 November	29	15				
30 December	17	16	1			
23 January	29	24	13	5		
TREATMENT E:						
14 December	25	8				
23 January	30	*72*	45			
TREATMENT F:						
8 December	88	86				
30 December	11	11	4			
23 January	*24*	*66*	26	*39*		

*Numbers in italics indicate less than 100 marked tillers in category.

6.3.3.3 Tiller death

In treatment A tiller death was lowest at the beginning of the experiment and increased after 17 October when defoliated reproductive tillers died (Table 6.9). Similarly, defoliated reproductive tillers contributed to the greater death rate of Group I tillers between 19 October and 9 November apparent in treatment C (Figure 6.3). Similarly reproductive tillers defoliated on 11 November in treatments B and F contributed to the period of faster tiller death of Group I tillers apparent in Figure 6.3. During December and January few reproductive tillers appeared (and therefore died after mowing) but tiller death did not decline significantly in treatments A,C,D and F (Table 6.9).

6.3.4 Mean tiller weight

6.3.4.1 Reproductive tillers

The weight of reproductive tillers during the main period of reproductive growth was presented in Tables 6.3 and 6.4.

6.3.4.2 Vegetative tillers

The mean weight of vegetative tillers in each age category is presented in Table 6.14. Generally, mean tiller weight was increased by longer regrowths. For example, in treatments A and C category I tillers averaged 19 (12-25) mg, in treatments B, D and F 35 (28-44) mg and in treatment E 52 (49-54) mg after average regrowths of 3,5 and 7 weeks respectively. Where considerable reproductive growth occurred (e.g. B on 11 November) vegetative tillers were lighter and such data is excluded in the comparison above. It is also interesting to note that on 7 November in treatment A, the re-growth with low herbage accumulation (Table 6.7) category I tillers were of a similar weight to previous regrowths (Table 6.14).

The influence of tiller age on tiller weight at mowing can be seen by comparing tillers in different age categories on a given date (Table 6.14). In 24 out of 27 comparisons (89%) the youngest category of tillers (e.g. VII on 9 January in A) was significantly (P < 0.05)

Table 6.14: Mean weight of vegetative tillers before mowing (mg)

Age Category	I	II	III	IV	V	VI	VII
TREATMENT A:							
26 September	13 a	3 b*					
19 October	13 a	10 b	4 c				
7 November	12 a	10 ab	9 ab	6 b			
28 November	24 a	27 a	25 a	23 a	4 b		
17 December	25 b	26 b	31 b	47 a	14 c	9 c	
9 January	19 bc	20 b	26 a	–	15 bc	13 c	6 d
TREATMENT B:							
26 September	19 a	7 b					
11 November	19 a	16 ab	8 b				
5 December	36 ab	40 a	31 b	11 c			
30 December	33 a	33 a	31 a	25 a	8 b		
23 January	36 ab	36 ab	43 a	30 b	21 b	10 d	
TREATMENT C:							
19 October	25 a	10 b					
9 November	16 a	11 b	6 c				
30 November	24 a	27 a	24 a	5 b			
21 December	24 b	26 ab	30 a	14 c	4 d		
11 January	21 a	24 a	15 b	14 bc	11 c	5 d	
TREATMENT D:							
19 October	22 a	8 b					
26 November	36 a	28 a	6 b				
30 December	39 ab	42 a	29 b	15 c			
23 January	33 a	34 a	28 b	22 c	9 d		
TREATMENT E:							
19 October	24 a	10 b					
14 December	49 a	52 a	18 b				
23 January	54 a	55 a	46 a	20 b			
TREATMENT F:							
11 November	26 a	13 b					
8 December	44 a	44 a	13 b				
30 December	31 ab	37 a	21 b	9 c			
23 January	28 a	33 a	28 a	28 a	8 b		

*Duncans multiple range test between categories on a line.

lighter than the older categories of tillers. The hypothesis that tillers of different ages present at the start of regrowth have a similar mean weight at the end of regrowth (e.g. categories I - VI on 9 January in A) was true in 10 out of 21 comparisons (48%). The hypothesis was true less frequently where cutting was most frequent (3 out of 9 comparisons in A and C (33%) and 2 out of 2 in F (100%)). Where the hypothesis was false there was a tendancy for younger groups of tillers to be lighter.

6.4 DISCUSSION

6.4.1 Herbage accumulation

This experiment again illustrated that less frequent defoliation increased ryegrass herbage accumulation (Anslow, 1967; Boswell, 1977). Delaying interruption of reproductive growth until 39% head emergence (Treatment F) increased herbage accumulation compared with earlier interruption (Treatments B and D), and further delaying interruption until anthesis could have undoubtedly increased accumulation even further (Austenson, 1963; Gillet, 1973; Corrall, 1974; Mislevy *et al*, 1977). In the vegetative sward, defoliation prior to 95% light interception reduced herbage accumulation (Treatments A compared with B, and C compared with D), largely due to a reduction in vegetative tiller weight (6.3.4.2). Delaying defoliation until after 95% light interception (Compare treatments D and E) resulted in little increase in ryegrass accumulation and greater dead herbage accumulation (Table 6.8). These results support the conclusion of Tainton (1974a) that there is little advantage in delaying grazing after 95% light interception has been reached. However, where a pasture is closed for conservation, delaying defoliation beyond this stage will increase herbage accumulation (because of the continued growth of reproductive tillers) provided closing is not too late, thereby reducing the number of reproductive tillers.

The seasonal pattern of ryegrass accumulation was similar to that reported by Brougham (1959a), except that between 17 October and 7 November there was a period of unexpectedly low growth. Treatment A

was actually continued until September 1979 and a similar period of
low growth was measured between 17 October and 7 November 1978.
As previously mentioned (6.3.2) low temperatures and lack of moisture
was unlikely to have caused the lower growth.   The reduced vegetative
tiller accumulation in this rest period could have been due to reduced
tiller density or reduced tiller weight.   Tiller weight was not
significantly lower in this rest period than in previous rest periods
(Table 6.14), but vegetative tiller density was lower (Table 6.9).
These results suggest that frequent close defoliation during the
reproductive period reduces herbage production because of reduced
reproductive tiller growth and because of low rates of tillering.

As in the previous experiment (Table 5.19), an increase in tiller
density did not immediately result in an increase in herbage production
because newly emerged tillers were considerably smaller (Table 6.14).
New tillers continued to increase in weight after their first
defoliation and where cutting was less frequent, tillers of different
ages (excluding the newest) often had a similar mean weight (Table
6.14).   This result requires further investigation because tiller
groups have a highly skewed weight distribution (Figure 5.8) so
similar mean weights may have arisen from a few large tillers in a
category.   Category I tillers (tillers marked at the start of the
experiment) contributed most to yield in this experiment because (i)
most reproductive tillers came from this category, (ii) this
category was most numerous (iii) tillers did not decline markedly in
weight with age during the experiment (Table 6.14).   Each cutting
reduces tiller weight and tillers will decline in weight with age
if the rate of regrowth declines in successive rest periods.

6.4.2 Tiller dynamics

Tiller density (Figure 6.4) followed a similar seasonal pattern
to that observed under grazing (Figure 5.5) and by others in the U.K.
(Langer *et al*, 1964; Garwood, 1969).   Vegetative tiller density
declined during the period of reproductive growth, but not to the same
extent as in the grazing experiment, then recovered quickly after
defoliation of reproductive tillers.   In the grazing experiment
vegetative tiller density declined to 2100 tillers/m^2 at 34% head

emergence, compared with 8100 tillers/m^2 at 39% head emergence, in
this cutting experiment (Table 6.3).   As discussed in more detail
in the final chapter (7.2.4.2.3 and 7.2.4.2.4), the difference in
vegetative tiller density at head emergence could have been due to
nitrogen fertilization and/or the absence of white clover in the
mowing experiment.   Because tiller density did not decline as much as
expected the defoliation regimes did not produce the expected range
of tiller age structures after flowering.

Differences in tiller density of the sward were detected in
December (Table 6.10) and these largely reflected different numbers
of new tillers (Figure 6.4), that is, tillers appearing after removal
of reproductive meristems.   At the end of the experiment the
differences were no longer significant because new tillers had died
at a greater rate than older (preflowering) tillers (6.4.3).   Hunt
and Field (1978) also found that defoliation frequency had little
effect on tiller density in summer compared with the late winter/
early spring when less frequent defoliation markedly reduced density.
The similarity of all treatments suggest that under conditions of
adequate moisture and nutrients, the tiller dynamics of "Nui" perennial
ryegrass are little influenced by defoliation frequency during summer.

In reproductive swards the mean tiller weight of vegetative
tillers failed to increase significantly after 95% light inter-
ception (Tables 5.4 and 6.3), but in a vegetative sward mean tiller
weight continued to increase after 95% light interception (Table 6.6).
These tables also show that after 95% light interception is reached
tiller density declined in reproductive swards but not in the
vegetative sward.   These differences are presumably due to competition
for light and assimilates.   Vegetative tillers can be shaded by
taller reproductive tillers and Ong *et al* (1978b) demonstrated that
the larger reproductive tillers do not translocate assimilates to
smaller heavily shaded vegetative tillers.   In a vegetative sward
assimilates are translocated from unshaded to shaded tillers and
shaded tillers can survive for up to five weeks provided the rest of
the plant receives adequate light (Ong and Marshal, 1979).   Eventually
some plants will dominate the vegetative sward as skewness of the
population increases (Harris, 1971) and tillers on shaded plants will

die.   Data presented by Hunt and Field (1978) showed that in autumn
tiller death did not increase substantially until three weeks after
95% light interception was reached.   Where nutrients are limiting,
tiller death is unlikely to be related to light interception
(Davies, 1971b).

6.4.3 Prediction of tiller death

Data presented in Figure 5.4 was used to determine if there was
a relationship between tiller density and the tiller death rate (TDR).
A simple relationship between density and TDR would be useful for
simulation modelling of tiller dynamics.   Insufficient data was
collected to allow the relationship between density and the tiller
appearance rate to be investigated in similar detail.

Data from each age category (I-VIII) was considered separately
and data was excluded where a large number of tillers died.   Within
each treatment, tillers were classified as appearing either before
flowering or after flowering (e.g. in F preflowering tillers were
categories I and II, and post-flowering tillers were categories III-
V).   Variables were defined as follows:

> TDR;   density of dead tillers of a given category
>   (I-VII) at the end of the rest period
>   divided by the number of days regrowth (dead
>   tillers/m^2/day).
>
> N;   tiller density within a given category (I-VIII)
>   at the start of the rest period (marked tillers/m^2).

Linear regressions were calculated between TDR and N (Table 6.15).
The regression coefficient is equivalent to the proportional tiller
death rate.

By comparing treatments C,D and E after 19 October the effect of
cutting interval (3, 4.6, and 6.9 weeks average respectively) was
investigated (Table 6.15).   The proportional TDR, that is, the linear
regression coefficient, was not significantly different for the three
cutting intervals.   Had treatment E been permitted to grow longer than

Table 6.15: Predictive equations for tiller death rate (TDR) from tiller density (N).

Factor	Equation	Slope*	df	r^2
Cutting interval				
Treatment C	TDR = 0.006 N	p	57	0.46
Treatment D	TDR = 0.006 N-3	p	37	0.76
Treatment E	TDR = 0.007 N-7	p	22	0.77
First mowing				
Treatment B	TDR = 0.004 N+8	p	62	0.54
Treatment D	TDR = 0.004 N+3	p	42	0.63
Treatment F	TDR = 0.008 N+4	q	37	0.47
**Tiller age ** **				
Preflowering	TDR = 0.004 N+3	p	101	0.56
Postflowering	TDR = 0.008 N+4	q	41	0.43

*Duncans multiple range test comparing the regression coefficients.   All regression coefficients were significantly greater than zero (P < 0.01).

**Treatments B,D and F.

7 weeks the TDR may have been higher in this treatment because of accelerated tiller death at the end of very long regrowths (Hunt and Field, 1978).

Treatments B,D and F were compared to test the effect of date of first cut (Table 6.15).   Only data from rest periods cut at 95% light interception was included.   The proportional TDR was significantly higher in F than B or D.   This reflected a greater number of post-flowering tillers, which had a greater proportional TDR than older pre-flowering tillers.   There were 9060 post-flowering tillers/m^2 in treatment F compared with 5150/m^2 and 4550/m^2 in B and D respectively.   This data suggests that tiller death can be linearly related to density for a given age category of vegetative tillers. It then follows that a given age category of tillers will decay

exponentially with time and half lives can be calculated.
From Table 6.15 it can be calculated that vegetative tillers
present before flowering had a half life of 173 days and those
appearing after flowering a half life of 87 days.

Modelling of tiller populations will be possible when (i)
it is shown that decay curves are indeed exponential; the present
experiment was too short; (ii) seasonal patterns of tiller
appearance are more clearly defined over the whole year and under
different conditions; (iii) half lives are calculated for tillers
apppearing at different times of the year; (iv) reproductive
activity of tillers appearing at different times of the year is
known (Hill and Watkin, 1975).

CHAPTER 7: OVERALL DISCUSSION OF RESULTS

7.1 MEASUREMENT OF HERBAGE PRODUCTION

Before discussing the results further it is worthwile considering the technique used to measure herbage production.   In both the grazing and mowing experiments different management systems were assessed in terms of net herbage accumulation, that is, summation of differences in total herbage mass between the beginning and end of rest periods.

As emphasised in the literature review, herbage accumulation reflects growth of new plant material less losses due to senescence and decomposition.   As discussed by Korte and Sheath (1978) herbage harvested in mowing experiments does not always equate with net herbage accumulation.   The technique used by Sears (1951) has been used in New Zealand to measure pasture production in grazing experiments (Brougham 1959b, 1960a; Pineiro and Harris, 1978a), but this measure is not necessarily the same as net herbage accumulation.

With the Sears' technique, protection cages are placed in paddocks at the time of grazing.   After grazing, herbage within the cages is removed with handshears, or by hand plucking, in an attempt to copy the irregular defoliation pattern made by grazing animals.   Herbage removal from the cages is used as a measure of herbage production.

Over several grazings the Sears' technique should give similar results to net herbage accumulation measurements, uneaten herbage eventually dying and decomposing.   Lynch and Mountier (1954) demonstrated this when they compared the Sears' technique and the Australian difference technique, which measures net herbage accumulation, and did not detect a significant difference in annual herbage production.   However, at any grazing, the amount of herbage removed by grazing will not necessarily equal the amount of herbage that accumulated in the previous regrowth. For example, herbage accumulating in the previous regrowth (net herbage accumulation), plus herbage left after the previous grazing, could be consumed and measured by the Sears' technique.   It is concluded that the seasonal distribution of pasture production could be confounded by the degree of defoliation when measured by the Sears' technique.

"Trim" techniques for measurement of pasture production
(Lynch and Mountier, 1954) have been widely used in New Zealand
(Weeda, 1965; Radcliffe and Lynch, 1974). A motor-mower cuts
pasture to a uniform height at the beginning ("trimming cut") and end
(for measurement of growth) of each rest period. Although Lynch and
Mountier (1954) concluded that a "trim" technique was to be preferred
for most types of investigation it does not measure net herbage accu-
mulation of the surrounding untrimmed pasture. Trimming can be
expected to alter both the rate of growth and decomposition, by
removing photosynthetic tissue and herbage that otherwise could have
decayed.

Tainton (1974b) used yet another method for calculating net
production in pasture. He calculated net production as the difference
between total herbage mass (living and dead) at the end of the rest
period and living herbage mass (excluding dead) at the beginning of
the rest period. If dead herbage accumulates in successive rest
periods, as it did in both grazing experiments (Figures 4.2 and 5.3),
then it could be counted more than once as production using this
method. When accumulation is calculated as the difference between
total herbage mass (living and dead) at both the end and
beginning of the rest period, different results and conclusions are
reached (Table 7.1).

Table 7.1: Average rates of herbage accumulation (kg DM/ha/day)
after 1 September 1972 as presented by Tainton (1974b)
and after recalculation from data presented in figures

Herbage component	Living	Dead	Total
Tainton (1974b):			
Treatment 1*			103.4
Treatment 2			92.6
SE			4.2
Recalculated:			
Treatment 1	74	–	74
Treatment 2	71	7	78

* Treatment 1: Grazed to 2.5cm at 95% light interception.
 Treatment 2: Grazed to 2.5cm two weeks after 95% light intercepetion.

Tainton (1974b) concluded that "in terms of the net production of material available to the animal, Treatment 1 showed a substantial advantage over Treatment 2". The recalculated results show little difference in living and total herbage accumulation for the two treatments, but greater dead herbage accumulation where grazing was delayed until two weeks after the canopy intercepted 95% of the incoming light (Treatment 2). These results will be discussed further (7.2.1).

In the grazing experiments an allowance was made for growth during the grazing period. It is generally recognised that with a prolonged grazing some allowance should be made for growth during the grazing period (Green, 1949; Linehan *et al*, 1952; Hodgson, 1979). If the grazing period is less than 3 days such growth is generally ignored. However, occasionally grazing lasted five days when insufficient sheep were available to consume the required amount of herbage in three days.

The method of Campbell (1966) was used to calculate accumulation during the grazing period (4.2.5). This method assumes that the accumulation rate is the same during the grazing period as measured in the previous rest period. There is no *a priori* reason, except ease of calculation and precedent, for this assumption. The accumulation rate during grazing could have been equated with the accumulation rate in the subsequent rest period, or a combination of rates in the previous and subsequent rest periods. A more accurate assessment of herbage removal could have been obtained if protection cages had been placed during the grazing period (Linehan *et al*, 1952).

7.2 MANAGEMENT OF REPRODUCTIVE SWARDS

Perennial ryegrass dominant pasture has two distinctive periods of growth, reproductive and vegetative, each requiring management according to different criteria. Before discussing the role of light interception, stage of reproductive development and tiller dynamics as criteria for management of reproductive swards, the timing of reproductive growth will be considered.

7.2.1 Timing of flowering

In all three experiments reproductive development was synchronised by closing swards in early September. The reproductive development observed was very similar to that reported for "Grasslands Ruanui" perennial ryegrass growing in pots (Wilson, 1959) and in rows for seed production (Hill, 1971). Floral initiation occurred in late August and September, and head emergence began in late October. Culm elongation started approximately three to four weeks before heading. As discussed before (3.3.1.4.1), the timing of reproductive development is influenced by climate and grazing management.

Floral initiation is largely controlled by daylength (Evans, 1964) and grazing has no obvious effect (Hill, 1971). Initiation in "Grasslands Ruanui" perennial ryegrass is unaffected by temperature over the range 4 to 14°C, and occurs at daylengths of approximately 11 hours (Aitken, 1966). An 11 hour daylength is reached at slightly different dates at different latitudes, for example, on 21 August, 28 August and 1 September at Kaitaia (Latitude 35°S), Palmerston North (40°S) and Invercargill (46°S) respectively (Gerlach, 1974).

Reproductive development after floral initiation is hastened by warmer temperatures (Cooper, 1952; Evans, 1964; Aitken, 1966; Keatinge et al, 1979) so that culm elongation will occur earlier and more rapidly in a warm spring than in a cool spring. In the mowing experiment it was found that later closing of swards delayed reproductive development and similarly Brougham (1961) found that culm elongation was later in a continuously grazed sward than in a rotationally grazed sward. Thus paddocks within a farm would be expected to be at various stages of reproductive development at any time in spring because of differences in previous grazing. However, examination of reproductive tillers in any paddock will show the stage of reproductive development and enable prediction of responses to grazing management.

Most reproductive tillers (about $2200/m^2$) appeared in an initial group, but further reproductive tillers continued to develop until late autumn, although at a much lower rate. A similar result was obtained by Brougham (1961) who found that in a "Grasslands Ruanui" perennial ryegrass sward relatively few seedheads appeared after December.

By contrast, in a grazed "Grasslands Manawa" ryegrass (*Lolium x hybridum* Hauss kn) sward, the period over which stem elongation occurred was more prolonged, with many seedheads appearing up to February.

7.2.2 Light interception as a criteria for defoliation

Light interception was used to determine both the stage of development for defoliation and defoliation intensity.   Few problems were encountered in identifying 95% light interception, the critical leaf area index as defined by Brougham (1958a).   On windy days with broken cloud, rapid fluctuations in the light flux above the canopy occasionally prevented measurement, but on clear or overcast days the light flux was sufficiently constant.   Grazing intensity treatments with different residual LAI provided low (hard grazed) and high (lax grazed) percent light interception after grazing.

Increased light interception, through higher residual LAI, was expected to result in greater herbage accumulation due to accelerated growth rates (Brougham, 1956;   Brown and Blaser, 1966).   Also, the rate of herbage accumulation was expected to increase after grazing, as light interception increased, until 95% light interception when further increases in LAI would not greatly increase light interception or growth.   Thus in both grazing experiments herbage mass was expected to accumulate exponentially with respect to time during the rest period.

Figures 4.2 and 5.3 clearly showed that herbage mass did not accumulate exponentially between grazing and 95% light interception, the relationship often appeared to be almost linear, at least after the initial stages.   It is unlikely that replication in time (as well as in space), to separate climatic effects from stage of regrowth, would have changed the observed pattern.   Temperatures and radiation increased in spring, and this would be expected to accentuate the predicted exponential pattern.   These results do not prove that pasture growth was not influenced by light interception, but rather that herbage accumulation was not.

In an experiment simulating defoliation by sheep Morris (1970) found that the harvested yield (equivalent to herbage accumulation in

this thesis) was not an accurate reflection of the growth which had
taken place, since a large and variable proportion of the herbage was
never harvested, but grew, died and decayed untouched.   The changes
in herbage mass shown in Figures 4.2 and 5.3 do not represent pasture
growth, they also include herbage death and decay.

The negative correlation between vegetative herbage accumulation,
or leaf accumulation, and increased residual LAI (Tables 4.9 and 5.13)
suggested that much of the residual leaf died and decayed soon after
defoliation in the grazing experiments.   When Brougham (1956) showed
that the rate of pasture growth increased until complete light
interception was approached he measured increases in herbage mass above
a 2.5 cm cutting height, so that his measurements avoided herbage
disappearance at the base of the sward.   As shown in Plate 4.8 and
by Jackson (1976) most dead herbage is concentrated at the base of the
sward.   Also, Brougham's experiment began in September, when swards
have least dead herbage (Campbell, 1964), again reducing herbage losses.

A relatively small range of residual LAI was investigated in
the grazing experiments.   In the study of Brougham (1956) the residual
LAI ranged up to 5, whereas it never exceeded 3 in the grazing
experiments.   A very low level of utilization would have been required
to leave higher residual LAI.   Reduced utilization would have
increased dead herbage accumulation and reduced herbage accumulation.

In the grazing experiments the advantage of increased residual
LAI was most obvious when laxer grazing resulted in fewer reproductive
tillers being defoliated (Tables 4.9 and 5.13).   The observed
increased herbage accumulation was most likely a result of increased
reproductive growth, not increased light interception.

7.2.2.1 Defoliation frequency

In the mowing experiment, defoliating every three weeks, before
95% light interception was reached, reduced herbage accumulation
compared with defoliating at 95% light interception (Table 6.8).
Similar results have been obtained elsewhere (Wilson and McGuire,
1961; Sheard and Winch, 1966; Mitamura, 1972).

Both the first grazing experiment (Table 4.5) and the re-calculated results of Tainton (Table 7.1) showed that during late spring defoliation at either 95% light interception or two weeks after 95% light interception resulted in a similar herbage accumulation (living plus dead).   This was because no consistent exponential growth phase (2.3.1) was detected and because rapid herbage accumulation continued after 95% light interception (Figure 4.2).

During uninterrupted growth of reproductive swards, lamina accumulated until 95% light interception was reached, after which further herbage accumulation was largely due to rapid culm and dead leaf accumulation, with little further lamina accumulating (Figure 5.4 and Table 6.8).   A similar pattern was observed by Tainton (1974a, b) and this explained why greater dead leaf accumulation occurred when grazing was two weeks after 95% light interception compared with grazing at 95% light interception (Table 7.1).   This pattern also explained why more lamina accumulated when reproductive growth was interrupted at a leafy stage compared with at 30% head emergence (Table 5.9).

In the first grazing experiment dead herbage accumulation was similar for treatments grazed at 95% light interception and grazed two weeks after 95% light interception.   In that experiment dead herbage included both dead leaf and dead culm, not just dead leaf as in the experiment of Tainton (1974b).   More dead leaf could have accumulated when defoliation was delayed until two weeks after 95% light inter-ception, but this was undoubtedly obscured by culm death and decay in the first grazing experiment.

7.2.2.2 Defoliation intensity

The residual LAI treatments used in both grazing experiments were designed to result in different light interceptions.   Differences in residual LAI were achieved, but differences in light interception by leaves (the photosynthetically active part of the canopy) were considerably smaller than expected because of culm development.

Lax grazing permitted culm development, while close grazing reduced culm development and also resulted in trampling of dead

culms to the bottom of the canopy. Standing culms (dead and dying) intercepted light so that at 95% light interception, instead of the LAI being similar for lax and close grazing, the LAI was considerably greater in close grazed swards (Table 4.10 and 5.14). As mentioned previously (4.4.3 and 5.4.3), this resulted in the average LAI during rest periods, and therefore light interception by leaves, being similar in lax and hard grazed swards.

In the first grazing experiment herbage accumulation in "spring/ summer" was greatly influenced by the residual LAI treatments despite light interception by leaves being similar for high and low residual LAI treatments. It was concluded in previous discussion (4.4.3 and 5.4.3) that the greater herbage accumulation with hard grazing, also found by Holmes and McClenaghan (1979), was more likely to have been the result of reduced losses through death and decay than the result of greater growth.

The rate of herbage accumulation declined with successive lax grazings in early summer, while it remained considerably higher and relatively constant with hard grazing (Figures 4.2 and 5.3). This confirms the observations of Saxby (1948) and Hall (1973) that close grazings in late spring will promote vigorous leafy growth compared to pasture that has been permitted to become rank and stemmy. The decline in accumulation rate in rank pasture was not a result of water stress, both stemmy and leafy pastures were growing under similar conditions, but was probably due to greater herbage losses through death and decay. Rank pasture also has the disadvantage that much of the herbage offered to grazing animals, being dead, is of low nutritive value (Rattray (1978) and Figure 4.4).

The "hard" grazings in late spring that largely prevented the accumulation of stemmy material were not particularly severe. "Hard" grazings in the first grazing experiment seldom resulted in removal of more than 50% of the herbage and the residual herbage mass was at least 1.5 t DM/ha (Figure 4.2). "Hard" grazings were slightly more severe in the second grazing experiment (Figure 5.3). In comparison, Jagusch *et al* (1978) reported that during spring in a farmlet experiment at Ruakura, sheep (21 ewes/ha) removed 52% of herbage offered and the

residual herbage mass was 1.6 t DM/ha.

7.2.3 Stage of reproduction development as a criteria for defoliation

Stage of reproductive development was used as a criteria for defoliation because culm development had a marked effect on pastures, herbage accumulation rates of over 100 kg DM/ha/day being measured during this period. Different stages of interruption of reproductive growth and defoliation to reduce reproductive growth were investigated.

7.2.3.1 Stage of growth at interruption

Two stages of interruption of reproductive growth were compared, the late leafy stage (when culm elongation was beginning and many reproductive meristems could be defoliated) and the head emergence stage (34% heads emerged in the second grazing experiment and 39% heads emerged in the mowing experiment). Both mowing and hard grazing at the leafy stage removed many reproductive meristems (5.3.6.1 and 6.3.3.3). The consequence of interrupting reproductive growth at the leafy stage compared with the head emergence stage seemed to depend on the fertility level, which influenced the size of reproductive tillers. In the grazing experiment similar herbage accumulation was obtained when interruption was at either stage, but in the mowing experiment, later interruption increased accumulation (Table 5.8 and 6.8). Much of the increase in accumulation in the mowing experiment was contributed by reproductive tillers. Similar reproductive tiller densities were measured ($2200/m^2$) but reproductive tillers were heavier in the mowing experiment than in the grazing experiment (211 mg and 120 mg respectively at head emergence). Nitrogen fertilizer was applied in the mowing experiment, but not in the grazing experiment. The greater nitrogen availability in the mowing experiment may have resulted in heavier reproductive tillers (Wilman *et al*, 1977).

Although interruption of reproductive growth at the leafy or the head emergence stage produced variable results in terms of herbage accumulation, the relative accumulation of lamina and culm was consistently affected. Culm accumulation was increased and lamina

accumulation decreased by delaying interruption after the leafy stage. As found by others (e.g. Wilman *et al*, 1976d) this was because the ceiling leaf mass was reached at the late leafy stage and further uninterrupted growth was largely culm (Figure 5.4). Defoliation at the leafy stage permitted further leaf accumulation and reduced culm accumulation if reproductive meristems were also defoliated.

Later interruption of reproductive growth, up to anthesis (Austenson, 1963; Gillet, 1973; Corrall, 1974; Mislevy *et al*, 1977), could be expected to increase annual herbage production under fertile conditions. Also, a high herbage mass, up to 10-12 t DM/ha (Corrall *et al*, 1979), largely comprising culms could be expected where reproductive growth continued uninterrupted until anthesis. In the second grazing experiment difficulty was encountered in forcing sheep to consume the basal portion of culms when swards had reached a herbage mass of 6 t DM/ha and this problem would be greater in swards at anthesis. As discussed previously (5.4.2), mechanical harvesting of reproductive herbage for hay or silage is the most effective method of utilising a high herbage mass.

7.2.3.2 Interruption of reproductive growth

Reproductive tillers were killed by removal of their meristems. Also, with very frequent defoliations (Treatment A in the mowing experiment) culm growth was largely suppressed. In this treatment many reproductive tillers, having a fixed number of leaves at floral initiation, may have actually died without any culm development occurring, once all the leaves had developed.

It was shown, in both the second grazing experiment and the mowing experiment, that a carefully timed hard grazing or mowing could largely end reproductive growth at an early stage of culm development. The timing of this defoliation depended on the position of developing seedheads relative to defoliation height. This can be determined by inspecting the larger tillers in the sward. The developing seedhead can be felt within the leaf sheath by squeezing each tiller between thumb and forefinger after stripping back the basal leaves.

7.2.4 <u>Tiller density as a criteria for defoliation</u>

It was observed in the literature review (2.3.1.5.1) that re-
growth is insensitive to tiller density over a wide range since a
decrease in density is compensated for by larger tillers. Also, in
mixed swards, a decrease in density of one species is quickly
compensated for by an increase in density (and growth) of other species.
It can therefore be concluded that over a wide range of conditions tiller
density will have little value as a criteria for defoliation.

However, it was found in the second grazing experiment that tiller
density could influence herbage accumulation. Herbage accumulation
had previously been found to be affected by tiller density in perennial
ryegrass swards over the range 5400 to 8700 tillers/m^2 (Davies, 1966).
Ryegrass tiller density was within this range in June 1977, 6400 and
8300 tillers/m^2 in lax and close grazed swards respectively, and this
difference in density resulted in a significant difference in herbage
accumulation. This result shows that management during the reproductive
period of growth, by affecting tiller density, can influence herbage
production. Thus, although tiller density normally has little value
as a criteria for defoliation, it should be considered during late
spring/early summer when a reduction in density below a critical
level can reduce subsequent herbage production.

7.2.4.1 <u>The relationship between tiller density and herbage
production</u>

7.2.4.1.1 <u>The critical density</u>

The critical tiller density, below which growth is positively
correlated with density, depends on sward purity, season, and tiller
weight. In mixed swards, white clover and other species can compensate
for low ryegrass tiller density. During summer low ryegrass tiller
density is unlikely to restrict herbage production, either rapid white
clover growth compensating (Brougham, 1959a) or dry soil conditions
masking any effect.

The second grazing experiment showed that the critical tiller
density in autumn was at least 8000 tillers/m^2 for infrequently grazed

ryegrass dominant pasture.   Presumably, below this density tiller
size and other species could not compensate sufficiently.   In more
frequently grazed pasture of similar botanical composition a higher
critical density could be expected (Huokuna, 1966), less time being
available for tillers to increase in weight, and compensate for low
density.

A lower critical density would be expected in spring than in
autumn because ryegrass grows more rapidly during reproductive growth
and because reproductive tillers have a higher potential weight than
vegetative tillers.   For example, Wilman et al (1976d) harvested
8 tDM/ha from Italian ryegrass swards with a tiller density of 3400
tillers/m^2 after 11 weeks uninterrupted growth.   Again, the critical
density would be expected to be higher where more frequent defoliation
interrupted reproductive development.

More research is required to establish the critical tiller density
for ryegrass/clover pasture at different times of the year and under
different defoliation regimes.   Until this information is available
tiller density measurements are unlikely to be useful in predicting
the potential for herbage production in a particular rest period.
However, Lazenby and Rodgers (1952, 1964) found that annual herbage
production was highly correlated with tiller density in perennial
ryegrass grown under one management.   They noted that with greater
variability within a population tiller density would become a less
reliable parameter of annual herbage production.

7.2.4.1.2 Tiller weight and tiller age

Both the second grazing experiment and the mowing experiment
showed that an increase in tiller density did not always result in an
increase in herbage production because newly emerged tillers had a
considerably smaller weight than other tillers.   However, where mowing
was infrequent, tillers of different ages (excluding newly emerged
tillers) generally had similar weights at the end of regrowth (Table 6.14).
Thus, juvenility only influenced the contribution of tillers to herbage
production for the first few weeks after appearance.

This conclusion is possibly an over-simplification because the frequency distribution of tiller weights is highly skewed (Figure 5.8, Jones *et al*, 1979). Similar mean weights of different tiller age categories could arise from a small change in the proportion of larger tillers. Also, it is possible that under grazing, recently emerged tillers, or in fact small tillers in general, being at the base of the sward are less intensively defoliated than larger tillers. Grass tillers can survive for three years under frequent defoliation (Jewiss, 1966) but more work is required to define their contribution to herbage accumulation at different ages. Obviously both mean tiller weight and the frequency distribution of tiller weight need to be measured for tillers of different ages over several rest periods to show if the conclusion in the previous paragraph is true.

7.2.4.1.3 Post-flowering tillers and growth

A period of rapid tillering was found to occur between October and December, depending on when apical dominance was reduced by defoliation of reproductive tillers. The contribution of these post-flowering tillers to herbage production and sward persistence is not clear. However, the mowing experiment showed that post-flowering tillers were actually well established by January under irrigation (Table 6.14), often being as heavy as preflowering tillers. Vegetative tillers that survive until atuumn, as well as tillers that appear up to early September, can be expected to flower the following spring in.grazed swards, and contribute to herbage production.

These results are in marked contrast to those of Hill and Watkin (1975) in seed production studies. They found that few summer formed tillers survived and that autumn tillers contributed most of the reproductive tillers the following spring, and therefore considerable spring herbage. In seed crops vegetative tillers are shaded and have to compete with the larger reproductive tillers for nutrients, so that few survive. Surviving vegetative tillers after heavy competition are small and etiolated.

It is concluded that autumn tillering is important after seed crops or drought have depleted tiller populations. However, it was unexpected to find that close grazing in autumn, which removed or

trampled dead culms, was largely unsuccessful in encouraging recovery
of tiller density in previously lax grazed swards in 1977.   By contrast
in 1976, hard grazing in autumn successfully encouraged tillering in
previously lax grazed swards.   The main difference between years was
the amount of autumn rainfall, 1976 being wet and 1977 being dry
(Appendix I).

Thus before ryegrass can tiller in response to hard grazing in
autumn, sufficient moisture must be available.   This requires further
investigation, but until more evidence is obtained, it would appear
that to prevent autumn growth being reduced, tillering should be
encouraged in early summer in preference to autumn.   Obviously any
dead herbage should also be removed by autumn to encourage growth and
tillering.   Because close grazing reduces growth in autumn (7.3.2)
it may be better to have a "clean-up" grazing, as suggested by Hunt
and Brougham (1966), before autumn rains.

7.2.4.2 Factors influencing tiller density

In this section the factors influencing tillering and tiller
density in ryegrass dominant swards during the reproductive period of
growth will be discussed.   Defoliation will be discussed in terms of
interruption of reproductive growth and defoliation intensity.   Nitrogen,
the main nutrient that seemed to influence results, and the presence
of other species will be discussed.   Little can be added to previous
comments on the affect of moisture on tiller density (2.3.1.5.2.5).

7.2.4.2.1 Interruption of reproductive growth

During uninterrupted reproductive growth vegetative tiller density
declined, as also observed by others (Spiertz and Ellen, 1972;
Hebblethwaite and Ivins, 1977, 1978; Ong *et al*, 1978b), to 2100
tillers/m^2 at 34% head emergence in the second grazing experiment.
The decline was due to reduced tillering and death of vegetative tillers
as described previously (2.3.1.5.2.2).

Delaying interruption of reproductive growth beyond 34% head
emergence would be expected to decrease vegetative tiller density further,
and perhaps result in sward death (Williams, 1970).

Sward death as a result of prolonged reproductive growth has not been reported in New Zealand.

Where vegetative tiller density has been markedly reduced by long periods of uninterrupted reproductive growth, regeneration and growth depends largely on tillering from buds on the cut stubs of reproductive tillers (Williams, 1970). Even where considerable numbers of vegetative tillers are present after interruption of reproductive growth, buds on cut stubs contribute a large number of tillers. In Treatment F of the mowing experiment, where after interruption of reproductive growth at 39% head emergence there were 8100 vegetative tillers/m^2, 35% of new tillers ($2700/m^2$) originated from cut stubs (Table 6.12).

Although tillering declines during reproductive growth it normally resumes either after anthesis (Lamp, 1952) or earlier where reproductive tillers have been defoliated (Asano and Chujo, 1975; Krause and Moser, 1977). The latter situation was illustrated in the second grazing experiment where grazing, even laxly at a leafy stage of reproductive development permitted resumption of tillering. Lax grazing at the leafy stage only removed the apex from approximately 15% of the developing reproductive tillers.

7.2.4.2.2 Defoliation intensity

It has frequently been observed that more intensive defoliation of perennial ryegrass swards results in increased tiller density (Harris and Thomas, 1970; Tainton, 1974a; Davies, 1977; Boswell and Crawford, 1978) and this result was obtained in both grazing experiments (Table 4.12 and Figure 5.5). However, as already discussed (5.4.2), both hard and lax grazing to interrupt reproductive development were equally effective in encouraging the resumption of tillering. The differences in density which eventually developed seemed to be due to a higher rate of tiller appearance in hard grazed swards later in the season.

As discussed (7.2.4.2.1), tillering recommences after defoliation of reproductive tiller apices. Also, merely shading tiller bases can arrest tillering, and conversely, removing base shade permits tillering (Davies, 1977). However, in the second grazing experiment, similar tiller appearance rates were measured after hard and lax grazing were used to interrupt reproductive development. This was despite more reproductive tillers dying and more light reaching the base of the sward after hard grazing. Either grazing removed the limiting effect of shading and apical dominance or some other factor was restricting tillering during reproductive growth.

Clifford (1977) suggested that in *Lolium multiflorum* tillering was suppressed by movement of inhibitory levels of auxin into buds from nearby elongating stem internodes, whose activity in turn was controlled by the developing inflorescence and upper leaves. Wheeler (1980) reported that removing the lamina of the flag leaf from wheat reduced internode elongation. As both hard and lax grazing removed leaves from reproductive tillers this may have reduced internode elongation and permitted the resumption of tillering.

7.2.4.2.3 <u>Nitrogen fertilization</u>

Nitrogen fertilization could have affected tiller density and tillering in the mowing experiment. Nitrogen fertilizer was applied in this experiment, but not in the second grazing experiment, and greater availability of nitrogen could partly explain the higher vegetative tiller density measured at head emergence in the mowing experiment (8100 and 2100 tillers/m^2 in the mowing and second grazing experiment respectively). Work in the U.K. on perennial ryegrass closed for seed production has shown that nitrogen fertilizer applied

at the time of floral initiation markedly increases vegetative
tiller density in the early stages of reproductive growth
(Hebblethwaite, 1977; Hebblethwaite and Ivins, 1977).

In the U.K. work nitrogen did not significantly effect
reproductive tiller density.   However, largely as a consequence of
a greater proportion of vegetative tillers dying where higher amounts
of nitrogen fertilizer had been applied, in the period between 50%
ear emergence and anthesis the differences in vegetative tiller
density disappeared or reversed.   Thus, depending on the stage of
growth, nitrogen fertilizer may first increase, and then decrease,
vegetative tiller density during uninterrupted reproductive growth.
Higher levels of nitrogen fertilizer can be expected to accentuate this
pattern and to predispose the sward to failure to regenerate after
long periods of uninterrupted reproductive growth (Williams, 1970).

Results from the mowing experiment suggested that later
interruption of reproductive growth (at ear emergence compared with at
the start of internode elongation) increased the subsequent amount of
tillering, and tiller density, but this trend was not apparent in the
second grazing experiment.   The greater availability of nitrogen in
the mowing experiment could have explained this difference also.

From the limited evidence available it appears that defoliation
and nitrogen, through their effects on competition between vegetative
and reproductive tillers, interact strongly during reproductive growth
in affecting tiller density and tiller dynamics.

7.2.4.2.4 Other species

In the mowing experiment the sward was almost pure ryegrass with
other species, mainly *Poa*, filling gaps between ryegrass.   In the
grazing experiments the sward was also predominantly ryegrass, with
white clover and *Poa* contributing approximately 30% of the green
herbage.   The presence of white clover probably affected tillering and
tiller density in the grazing experiment.

The higher vegetative tiller density measured at early head
emergence, and the greater amount of tillering after later interruption

of reproductive growth, in the mowing experiment compared with the second grazing experiment could have been caused either by white clover and/or nitrogen availability (7.2.4.2.3). Harris (1971) found that perennial ryegrass growing in association with white clover had a lower tiller density than when growing in monoculture. It was suggested that this was caused by intense shading of the base of the mixed sward, arising from the horizontal arrangement of white clover laminae, reducing the rate of tillering (Davies, 1977) and/or tiller survival. Although white clover may have altered the magnitude of fluctuations in tiller populations, the same patterns observed in monoculture were apparent.

7.2.5 Management and botanical composition

Grazing management in late spring/early summer had little effect on botanical composition of pasture. However, in both grazing experiments, *Poa* tiller density was significantly greater during winter in pasture which had been particularly stemmy the previous summer (ILL in 1976 and L in 1977, Tables 4.13 and 5.16). The greater invasion of *Poa* into lax grazed pasture could have been due to a greater amount of *Poa* seeding and/or reduced competition from ryegrass.

7.2.6 Root growth

Although plant roots were not measured they could have influenced the results. In field studies a decrease in the rate of initiation of new roots together with increased senescence and decay of older roots has been noted during the period of reproductive growth (Troughton, 1957; Garwood, 1967). Interruption of reproductive growth, besides encouraging tillering, may have encouraged initiation of new roots. Also, compared with rank stemmy swards, leafy swards may have had more vigorous root growth. However, during dry weather in February and April 1977 (Appendix I) herbage accumulation in leafy and stemmy swards was similarly restricted by lack of moisture (Figure 5.3).

7.2.7 Management recommendation

The two grazing intensity treatments compared in 1976 and 1977 resulted in swards with different structures, leafy swards from close grazing and stemmy swards from lax grazing. Providing moisture is available, leafy swards are preferable to stemmy swards because of higher growth rates in December and January, higher nutritive value, and higher tiller density (which can influence autumn growth). However, close grazing of the whole farm is not normally possible during reproductive growth because the pasture growth rate is greater than animal requirements. As was recently discussed (Matthews *et al*, 1979), leafy growth can still be obtained by combinations of grazing, closing paddocks for conservation and mechanical topping.

7.2.7.1 Forage conservation

Closing paddocks for forage conservation will increase the stocking rate on the rest of the farm, making it possible to graze the remainder of the farm closer. Pasture growth not utilised by grazing animals should be harvested as hay or silage, thereby reducing death and decay. Herbage left ungrazed for feeding during summer drought will be largely stem, which will die and decline in nutritive value. These stems may also reduce autumn growth.

As higher yields can be obtained from reproductive crops than from vegetative crops (Leafe *et al*, 1974), paddocks should preferably be closed before grazing has removed reproductive meristems. The optimum stage of growth for cutting reproductive crops depends on the nutritive value of conserved forage required (Green *et al*, 1971).

Another consideration may be the encouragement of post-flowering tillers. In the second grazing experiment post-flowering tillers established quickly after close grazing in October and November, but many farmers cut hay in December. Tillers appearing after December haymaking may not survive drought as well as older and therefore larger tillers. Langer (1963) suggested that small tillers will die first in drought.

7.2.7.2 Mechanical topping

Removing stemmy herbage by mechanical topping will encourage leafy growth and tillering, but unless toppings are conserved, cut herbage will be wasted. The litter resulting from topping could encourage the growth of *Pithomyces chartarum*, increasing the risk of facial eczema (Brook, 1963). Litter could also increase the risk of ryegrass staggers (Keogh, 1978). As might be expected, Holmes and McClenaghan (1979) showed that topping only increased pasture production when herbage was long and stemmy at the time of topping. Topping leafy pasture did not increase pasture growth.

Provided reproductive meristems are above the cutting height, the timing of topping is probably not critical. In the first grazing experiment the alternating grazing intensity treatments (HL and LH) had a similar tiller density to the HH treatment and were leafy in January. Topping before reproductive meristems are above cutting height only removes leaf, and stem growth could still occur.

It should be noted that lax grazing, which did not prevent stemmy growth, encouraged tillering at both the leafy and head emergence stage (Figure 5.6). Tillering was restricted later in the season, when culms died. Thus mechanical topping will have most benefit after pasture has become rank.

7.2.7.3 Grazing

It is difficult to generalise about the optimum grazing regime for the reproductive period of growth from the experiments reported in this thesis. Many factors (such as stocking rate, type of farm, pasture species, etc) will have a considerable effect on decisions. However, a reasonable objective for late spring management, besides feeding livestock fully, is to control reproductive growth and maintain leafy swards.

Longer rotations during reproductive growth could undoubtedly increase herbage production, but would probably reduce herbage quality. Many dairy farmers have rotations of approximately 3 weeks during spring (e.g. Matthews *et al*, 1979) and longer regrowths were shown to increase

herbage accumulation in the mowing experiment. Since much of the
extra production would be culm, especially with the laxer grazing
of cattle, herbage could be more difficult to utilise and, if not
grazed off, would decline in quality.

7.3 MANAGEMENT OF VEGETATIVE SWARDS

The main objective of this thesis was to study grazing management
during the period of reproductive growth in late spring/early summer.
The amount of information obtained on the vegetative period of growth
was therefore relatively limited. However, some comments about the
pattern of vegetative herbage accumulation and about autumn grazings
can be made.

7.3.1 The pattern of vegetative herbage accumulation

It was shown in the mowing experiment (6.3.1.2) that during
uninterrupted vegetative growth herbage accumulation was mainly due
to increasing weight of tillers present at the start of regrowth,
plus, after 95% light interception, the dead herbage accumulation.
This pattern was similar to that observed during reproductive growth,
but the patterns of lamina accumulation and tiller death were different
during reproductive growth.

As discussed previously (7.2.2.1) during uninterrupted reproductive
growth lamina accumulated until 95% light interception when a ceiling
was reached. This contrasts to vegetative growth where lamina
continued to accumulate after 95% light interception (Figure 4.2).
Increased weight of reproductive tillers after 95% light interception
was mainly due to increased culm weight. Vegetative tillers, consisting
almost entirely of leaves, increased in weight by increasing leaf weight,
the number of leaves being relatively constant (Hunt and Brougham, 1966;
Davies, 1971b; Thomas and Norris, 1977). Eventually a ceiling herbage
mass is reached in vegetative swards (Brougham, 1959a).

After 95% light interception was reached tiller density declined
rapidly in reproductive swards but not in vegetative swards (Tables
6.3 and 6.6). Results from the first grazing experiment also showed
that delaying grazing until two weeks after 95% light interception did
not significantly reduce tiller density compared with grazing at 95%
light interception (Table 4.12). Data presented by Hunt and Field
(1978) showed that in autumn, tiller death did not increase substantially
until three weeks after 95% light interception. Shaded tillers survive

in vegetative swards because the larger unshaded tillers translocate assimilates (Ong and Marshal, 1979), whereas in reproductive swards little translocation to shaded tillers occurs (Ong *et al*, 1978b). Eventually some plants will dominate the sward (Harris, 1971) and tiller density will decline (Hunt and Brougham, 1966) as tillers on shaded plants die.

7.3.2 Grazing interval

In the first grazing experiment it was found that during "autumn/winter" 57% more green herbage accumulated when grazing was two weeks after 95% light interception compared with grazing at 95% light interception. The reason suggested for this (4.4.4) was that the rate of green herbage accumulation increased during the rest period, especially when grazing was at 95% light interception, so that the swards remained at a higher accumulation rate longer with less frequent grazing.

The results of the grazing experiment and other grazing trials (Brougham, 1959b; Tainton, 1974b) all show that less frequent and less intensive grazing during autumn markedly increases herbage accumulation. Brougham (1959b) found that frequent hard grazings in autumn reduced herbage yields by approximately 20% compared with infrequent lax grazings. Tainton (1974b) obtained considerably higher herbage production from swards alternately hard and lax grazed than from swards continually hard grazed. This result was also true when net herbage accumulation was calculated as described in 7.1. The optimum stage of growth for grazing in "autumn/winter" is at least two weeks after 95% light interception is reached.

Both Mitamura (1972) and Terai (1977) concluded that to maximise the amount of herbage harvested from vegetative cocksfoot swards the optimum time to defoliate was when the sward reached the ceiling LAI, that is, some weeks after 95% light interception was reached. Such infrequent defoliation of ryegrass dominant swards could be expected to reduce tiller density, and perhaps subsequent herbage growth, especially if more frequent defoliation was adopted later. Also, the conclusions of Mitamura (1972) and Terai (1977) were based on relatively short experiments.

It would seem worthwhile to investigate further the otpimum stage of growth for grazing in autumn/winter. At this time of the year infrequent grazing is often practised in an effort to accumulate herbage for early spring when animal demand for forage normally exceeds pasture growth. It is therefore important to determine if long rest periods can be adopted, that is, grazing at the ceiling LAI, without

reducing spring growth.

7.4 CONCLUSION

At the beginning of this thesis it was suggested that defoliation should be based on plant physiological criteria, and various criteria were investigated. The research emphasises that harvested herbage (net herbage accumulation) reflects two processes, herbage growth and herbage death. Increased light interception, reproductive growth and high tiller density can increase herbage growth, but may not increase herbage harvested because of losses.

In particular, increased light interception, although presumably resulting in greater herbage growth, also resulted in greater losses, and no overall advantage in net herbage accumulation. This conclusion requires further investigation under a wider range of conditions. If grazing had been considerably more frequent in the grazing experiments, as occurs on farms in spring (Matthews *et al*, 1979), then close grazing could have reduced growth to such an extent that net herbage accumulation was reduced also.

The relationship between pasture growth and pasture losses due to senescence, decay, pests and pathogens needs to be clearly established before the effects of physiological criteria on net herbage accumulation can be accurately assessed. Seldom has pasture growth been measured, although several techniques are available (Sestak *et al*, 1971), agronomists normally measuring the amount of herbage harvested mechanically or by grazing animals. Since grazing animals selectively eat the photosynthetically active herbage from the canopy and avoid dead material, it is important that the realtionship between growth, death and decomposition be established under grazing.

APPENDIX I: Soil moisture (% dry weight at 105°C) in the top 15cm soil.
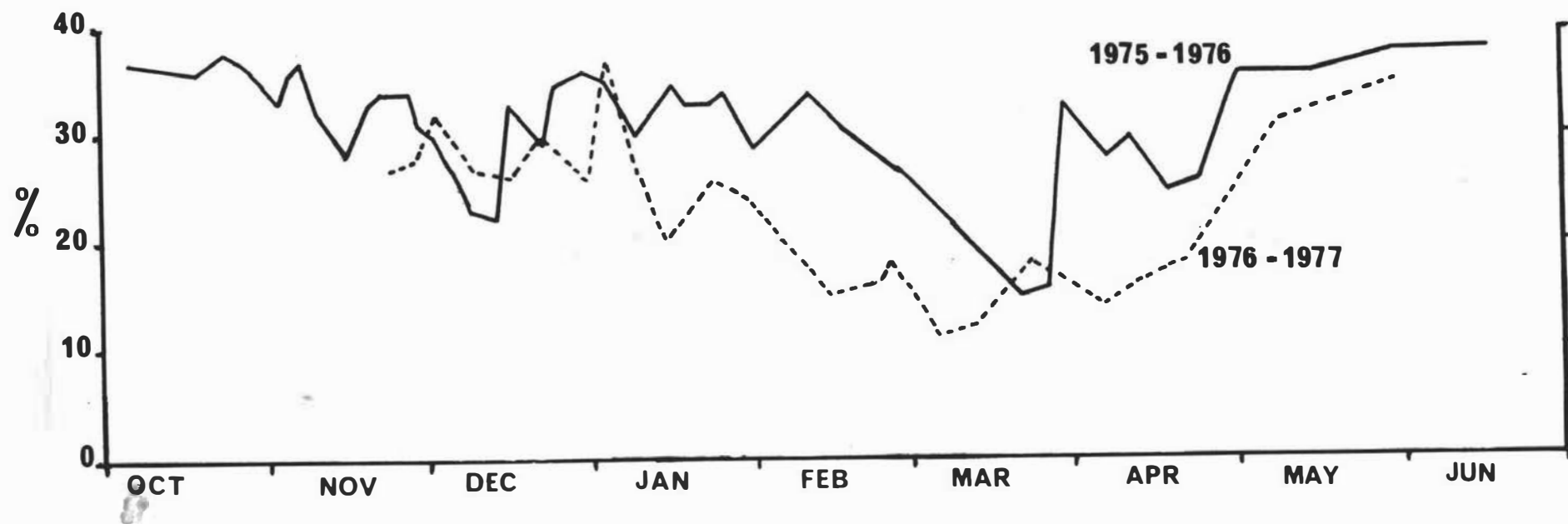
APPENDIX II: Meteorological Measurements, D.S.I.R., Palmerston North

	Sept	Oct	Nov	Dec	Jan	Feb	Mar	April	May	June	July
Rainfall (mm)											
1975-76	54	83	53	103	89	61	79	51	109	215	120
1976-77	78	140	65	75	67	45	52	67	113	109	80
1928-75 Mean	73	87	76	94	81	70	67	79	89	97	87
Daily Max. Temp (^{o}C)											
1975-76	14.4	16.7	17.0	19.3	20.9	19.0	21.2	18.2	14.3	11.9	11.7
1976-77	14.3	16.1	17.3	20.2	20.2	22.4	22.1	18.1	13.3	12.3	12.4
1928-75 Mean	14.8	16.6	18.6	20.6	22.0	22.4	20.9	18.2	15.0	12.6	11.9
Daily Min. Temp (^{o}C)											
1975-76	7.0	9.8	9.5	11.1	14.0	10.4	11.9	10.4	6.4	4.4	4.6
1976-77	7.1	7.9	8.7	12.8	12.3	12.8	12.2	9.4	4.9	5.5	5.1
1928-75 Mean	6.6	8.3	9.8	11.6	12.7	12.8	11.6	9.5	6.8	4.6	3.9
10 cm Soil Temp (^{o}C)											
1975-76	9.5	12.7	13.5	15.4	17.6	14.8	14.5	13.0	9.2	6.9	7.0
1976-77	9.4	12.2	13.1	16.0	15.9	17.1	15.8	12.6	7.7	7.2	6.6
1928-75 Mean	9.9	12.5	15.2	17.5	18.7	18.3	16.4	13.2	10.2	7.7	6.6

Appendix III: Net herbage accumulation in the second grazing
               experiment

(a) Effect of time of grazing.

(b) Effect of grazing intensity.

(a) Effect of time of grazing on net herbage accumulation (t DM/ha)

	Period I		Period II		Whole Experiment	
	T_1	T_2	T_1	T_2	T_1	T_2
Green herbage:						
Grass:						
Ryegrass:						
Vegetative tillers	3.74 a	2.59 b	2.77 a	3.29 a	6.57 a	5.80 a
Reproductive tillers	1.60 a	2.54 a	0.16 a	-0.04 a	1.70 a	2.46 a
Aerial tillers	0.07 a	0.08 a	0.00 a	0.05 a	0.07 a	0.13 a
Total*	5.48 a	5.24 a	2.93 a	3.30 a	8.41 a	8.43 a
Poa and other grass	1.13 a	1.16 a	-0.13 a	-0.04 a	1.00 a	1.12 a
Total	6.61 a	6.40 a	2.80 a	3.26 a	9.41 a	9.55 a
White clover	2.21 a	1.86 a	0.33 a	0.36 a	2.51 a	2.21 a
Flat weeds	0.07 a	0.10 a	0.02 a	0.03 a	0.10 a	0.13 a
Total	8.89 a	8.36 a	3.15 a	3.65 a	12.03 a	11.89 a
Dead herbage:						
Ryegrass culm	0.31 a	0.13 a	0.46 a	-0.43 a	-0.13 a	-0.32 a
Dead leaf	0.75 a	0.94 a	0.24 a	0.10 a	0.98 a	1.05 a
Total	1.06 a	1.07 a	-0.22 a	-0.33 a	0.85 a	0.73 a
Total herbage:	9.95 a	9.44 a	2.93 a	3.32 a	12.88 a	12.63 a

*Total includes fragments not classifiable as vegetative, reproductive or aerial.

Duncans multiple range test compares T_1 and T_2 within a period for each component.

(b) Effect of grazing intensity on net herbage accumulation (t DM/ha)

	Period I		Period II		Whole experiment	
	Hard	Lax	Hard	Lax	Hard	Lax
Green herbage:						
Grass:						
Ryegrass:						
Vegetative tillers	3.72 a	2.60 b	3.24 a	2.82 a	6.95 a	5.42 b
Reproductive tillers	2.19 a	1.94 a	0.27 a	−0.14 a	2.36 a	1.80 a
Aerial tillers	0.02 b	0.13 a	0.00 a	0.05 a	0.02 b	0.18 a
Total*	6.01 a	4.71 a	3.51 a	2.73 b	9.40 a	7.44 b
Poa and other grass	1.06 a	1.23 a	−0.04 a	−0.14 a	1.03 a	1.09 a
Total grass	7.07 a	5.94 a	3.47 a	2.59 b	10.43 a	8.53 b
White clover	1.91 a	2.15 a	0.44 a	0.24 a	2.32 a	2.39 a
Flat weeds	0.10 a	0.08 a	0.05 a	0.01 a	0.14 a	0.09 a
Total	9.08 a	8.17 a	3.96 a	2.84 b	12.91 a	11.01 b
Dead herbage:						
Ryegrass culm	−0.04 b	0.48 a	−0.28 a	−0.61 a	−0.29 a	−0.16 a
Dead leaf	0.54 a	1.15 a	0.14 a	0.20 a	0.65 b	1.38 a
Total	0.50 b	1.63 a	−0.14 a	−0.41 a	0.36 b	1.22 a
Total herbage:	9.59 a	9.80 a	3.82 a	2.43 a	13.27 a	12.23 a

*Total includes fragments not classifiable as vegetative, reproductive or aerial.

Duncans multiple range test compares H and L within a period for each component.

Appendix IV: Aerial tiller density (tillers/m^2) at the end of each rest period in the second grazing experiment.

Treatment	Rest Period	Live tillers			Dead tillers
		Unmarked	Marked	Total	
T_1H					
	25/10 - 20/11	105± 76	–	105± 76	–
	23/11 - 20/12	383±151	158± 38	540±188	68±31
	23/12 - 25/1	53± 31	68± 50	120± 78	128±58
	29/1 - 18/3	60± 21	150± 50	210± 56	45±19
	Total	601			241
T_1L					
	25/10 - 10/11	255±175	–	255±175	–
	15/11 - 30/11	398±132	255± 94	653±201	6C±41
	3/12 - 17/12	158± 43	315±114	473±147	23± 8
	13/1 - 7/2	188± 53	293± 83	480± 80	60±27
	12/2 - 25/3	180± 32	150± 44	330± 70	128± 35
	Total*	1179			271
T_2H					
	20/11 - 16/12	840± 274	–	84C± 274	–
	20/12 - 21/1	33C± 244	68± 33	390± 259	15± 9
	25/1 - 11/3	23± 14	128± 70	150± 84	8± 8
	Total	1193			23
T_2L					
	20/11 - 11/12	743± 222	–	243± 222	
	15/12 - 4/1	843± 172	263± 132	1125± 299	30± 17
	3/2 - 21/3	240± 59	525± 51	765± 98	338± 63
	Total*	1846			368

* Note that the total is reduced because tillers were not marked for one rest period.

In Table 5.17 the number of tillers removed during grazing:

Removed = Total marked - total live - total dead.
e.g. T_1H 601 - 210 - 241 = 150.

Appendix V: Net herbage accumulation (t DM/ha) in the mowing experiment.

	Ryegrass			Other species	Dead herbage	Total herbage
	Vegetative	Reproductive	Total			
TREATMENT A:						
26 Sept	0.6	–	0.6	–	–	0.7
17 Oct	0.8	0.3	1.1	0.2	–	1.3
7 Nov	0.3	0.2	0.5	0.1	–	0.6
28 Nov	0.9	0.1	1.0	0.2	0.1	1.3
19 Dec	1.5	0.3	1.8	-0.1	–	1.7
9 Jan	1.0	–	1.0	0.2	-0.2	1.0
LSD (5%)	0.5	0.3	0.5	0.3	0.3	0.3
TREATMENT B:						
26 Sept	0.6	–	0.6	–	0.1	0.7
11 Nov	0.7	2.5	3.2	0.3	0.1	3.7
5 Dec	1.8	-0.2	1.6	0.2	0.1	1.9
30 Dec	1.9	0.2	2.2	0.1	-0.1	2.2
23 Jan	2.1	–	2.0	–	-0.1	2.0
LSD (5%)	0.5	0.4	0.6	0.3	0.2	0.7
TREATMENT C:						
19 Oct	1.1	1.3	2.4	0.1	0.2	2.8
9 Nov	0.3	0.1	0.4	–	0.1	0.5
30 Nov	1.3	–	1.3	–	-0.1	1.2
21 Dec	1.1	0.1	1.2	0.3	–	1.4
11 Jan	1.2	–	1.3	0.1	-0.3	1.0
LSD (5%)	0.4	0.4	0.3	0.2	0.2	0.3
TREATMENT D:						
19 Oct	1.1	0.9	2.0	0.3	0.1	2.4
26 Nov	1.7	0.3	1.9	-0.1	0.1	2.0
30 Dec	3.0	0.1	3.0	0.1	0.1	3.2
23 Jan	2.1	–	2.1	–	–	2.2
LSD (5%)	0.7	0.4	0.6	0.2	0.2	0.7
TREATMENT E:						
19 Oct	1.2	1.5	2.7	0.1	0.2	3.0
14 Dec	3.8	0.3	4.1	0.2	0.7	4.9
23 Jan	2.9	–	2.9	–	0.2	3.1
LSD (5%)	1.0	0.6	1.0	0.2	0.5	1.4
TREATMENT F:						
11 Nov	0.7	3.8	4.4	0.1	0.7	5.3
8 Dec	2.6	0.3	2.3	0.1	–	2.4
30 Dec	2.0	0.2	2.2	–	-0.1	2.2
23 Jan	2.1	0.1	2.2	0.1	0.3	2.7
LSD (5%)	0.6	1.1	1.1	0.4	0.4	1.0

Appendix VI: Meterological measurements, Massey University (1977-1978)

	Temperatures (^{o}C)			Bright sunshine (hr).
	Daily Av.	Grass min.	10cm soil	
5 Sept - 26 Sept	8.3	0.9	7.8	78
26 Sept - 17 Oct	10.9	4.3	10.5	98
17 Oct - 7 Nov	11.8	4.0	12.1	115
7 Nov - 28 Nov	13.7	6.7	14.1	148
28 Nov - 19 Dec	15.3	7.9	15.8	82
19 Dec - 9 Jan	14.8	7.1	16.2	164

BIBLIOGRAPHY

AGYARE, J.A. and Watkin, B.R. (1967).   Some effects of grazing management on the yield and its components of some pasture grasses.   Journal of the British Grassland Society. 22: 182-191.

AITKEN, Y. (1966).   The flowering responses of crop and pasture species in Australia.   I.   Factors affecting development in the field of *Lolium* species (*L. rigidum* Gaud., *L. perenne L.*, *L multiflorum* Lam).   Australian Journal of Agricultural research. 17: 821-839.

ALBERDA, Th (1977).   Perennial Ryegrass.   Crop photosynthesis: methods and compilation of data obtained with a mobile field equipment.   Agricultural Research Report 865, Centre for Agricultural Publishing and Documentation, Wageningen p.4-11.

ALBERDA, T. and Sibma, L. (1968).   Dry matter production and light interception of crop surfaces.   Actual herbage production in different years as compared with potential values. Journal of the British Grassland Society. 23:206-215.

ALCOCK, M.B. (1964).   The physiological significance of defoliation on the subsequent regrowth of grass-clover mixtures and cereals. In Grazing in terrestrial and marine environments.   British ecological society symposium No. 4 Editor B.J. Crisp. pp322.

ANSLOW, R.C. (1965).   Grass growth in midsummer.   Journal of the British Grassland Society 20: 19-26.

ANSLOW, R.C. (1966).   The rate of appearance of leaves on tillers of the Gramineae.   Herbage Abstracts 36: 149-155.

ANSLOW, R.C. (1967).   Frequency of cutting and sward production. Journal of Agricultural Science.   68: 377-384.

ANSLOW, R.C. and Green, J.O. (1967).   The seasonal growth of pasture grasses.   Journal of Agricultural Science 68: 109-122.

APPADURAI, R.R. and Holmes, W. (1964).   The influence of stage of growth, closeness of defoliation and moisture on growth and productivity of a ryegrass-white clover sward.   I.   Effect on herbage yields.   Journal of Agricultural Science 68: 377-384.

ARMSTRONG, C.S. (1977).   'Grasslands Nui' perennial ryegrass (*Lolium perenne* L.).   N.Z. Journal of Experimental Agriculture 5: 381-384.

ARNOLD, G.W. (1960).   Selective grazing by sheep of two forage species at different stages of growth.   Australian Journal of Agricultural Research.   11: 1026-1033.

ARNOLD, G.W. (1964). Factors within plant associations affecting the behaviour and performance of grazing animals. In Grazing in terrestrial and marine environments. Editor, D.J. Crisp. British Ecological Society symposium No. 4.

ASANO, H. and Chujo, H. (1975). The effect of removal of main stem on appearance of tillers and heading in some temperature grasses. Journal of Japanese Grassland Science. 21: 259-264.

ASPINALL, D. (1961). The control of tillering in the barley plant. I. The pattern of tillering and its relation to nutrient supply. Australian Journal of Biological Science 14: 493-505.

ASPINALL, D. (1963). The control of tillering in the barley plant. II. The control of tiller bud growth during ear development. Australian Journal of Biological Science 16: 285-304.

AUSTENSON, H.M. (1963). Influence of time of harvest on yield of dry matter and predicted digestibility of four forage grasses. Agronomy Journal 55: 149-153.

BAARS, J.A. *et al* (1976). An evaluation of 'Grasslands Nui' perennial ryegrass in the Waikato. Proceedings of the Ruakura Farmers' Conference 1976. p 62-64.

BARLEY, K.P. (1961). The abundance of earthworms in agricultural land and their possible significance in agriculture. Advances in Agronomy 13: 249-268.

BARNARD, C. (1964). Form and Structure. In Grasses and Grasslands. Edited by C. Barnard, Macmillan and Co Ltd., London p 47-72.

BARRY, R.G. and Chorley, R.J. (1971). Atmosphere, Weather and Climate. Methuen & Co Ltd., London.

BARTHOLOMEW, P.W. and Chestnutt, D.M.B. (1977). The effect of a wide range of fertilizer nitrogen application rates and defoliation intervals on the dry matter production, seasonal response to nitrogen, persistance and aspects of chemical composition of perennial ryegrass (*Lolium perenne* cv. S24). Journal of Agricultural Science 88: 711-721.

BEAN, E.W. (1964). The influence of light intensity upon the growth of an S37 cocksfoot (*Dactylis glomerata*) sward. Annals of Botany (N.S.) 28: 427-443.

BEARD, J.B. (1973). Turfgrass Science and Culture. Prentice-Hall, Englewood Cliffs, New Jersey. pp 658.

BEATY, E.R. *et al.* (1977). Yield, leaf growth, and tillering in Bahiagrass by N Rate and season. Agronomy Journal 69: 308-311.

BEHAEGHE, T.J. (1974). Experiments on the seasonal variations of grass growth. Proceedings of the 12th international Grassland Congress, Moscow. 1: 268-281.

BEHAEGHE, T.J. (1978). The seasonal discrepancies between potential and actual grass growth. An essay of explanation by eco-physiological constraints. Seventh general meeting of the European Grassland Federation, Gent. p 2.1-2.20.

BINNIE, R.C. and Harrington, F.J. (1972). The effect of cutting height and cutting frequency on the productivity of an Italian ryegrass sward. Journal of the British Grassland Society 27: 177-182.

BIRD, J.N. (1943). Stage of cutting studies: I. Grasses. Journal of the American Society of Agronomy 33: 845-861.

BLACK, J.N. (1963). The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (*Trifolium subterraneum* L.). Australian Journal of Agricultural Research 14: 20-38.

BLAIR, I.D. (1973). Pasture plant diseases. In Pastures and Pasture Plants; editor: R.H.M. Langer; A.H. and A.W. Reed, Wellington.

BONIN, S.G. and Tomlin, D.C. (1968a). Effects of nitrogen on herbage yields of timothy harvested at various developmental stages. Canadian Journal of Plant Science 48: 501-509.

BONIN, S.G. and Tomlin, D.C. (1968b). Effects on nitrogen on herbage yield of reed canarygrass harvested at various developmental stages. Canadian Journal of Plant Science 48: 511-517.

BOOYSEN, P. deV. and Nelson, C.J. (1975). Leaf area and carbohydrate reserves in regrowth of Tall Fescue. Crop Science 15: 262-266.

BOSWELL, C.C. (1977). Effects of cutting regime on pasture production. N.Z. Journal of Experimental Agriculture. 5: 403-408.

BOSWELL, C.C. and Crawford, A.J.M. (1978). Changes in the perennial ryegrass component of grazed pastures. Proceedings of the N.Z. Grassland Association 40: 125-135.

BROOK, P.J. (1963). Ecology of the fungus *Pithomyces chartarum* (Berk & Curt) M.B. Ellis in pasture in relation to facial eczema disease of sheep. N.Z. Journal of Agricultural Research 6: 147-228.

BROWN, K.R. (1980). Seed production in N.Z. ryegrasses. I. Effect of grazing. N.Z. Journal of Experimental Agriculture 8: 27-32.

BROWN, R.H. and Blaser, R.E. (1968). Leaf area index in pasture growth. Herbage abstracts. 38: 1-9.

BROUGHAM, R.W. (1955).   A study in rate of pasture growth.
    Australian Journal of Agricultural Research 6: 804-812.

BROUGHAM, R.W. (1956).   Effect of intensity of defoliation on
    regrowth of pasture.   Australian Journal of Agricultural
    Research.   7: 377-387.

BROUGHAM, R.W. (1958a).   Interception of light by the foliage of pure
    and mixed stands of pasture plants.   Australian Journal of
    Agricultural Research.   9: 39-52.

BROUGHAM, R.W. (1958b).   Leaf development in swards of white
    clover (*Trifolium repens* L.). N.Z. Journal of Agricultural
    Research 1: 707-718.

BROUGHAM, R.W. (1959a).   The effects of season and weather on
    the growth rate of a ryegrass and clover pasture.
    N.Z. Journal of agricultural research 2: 283-296.

BROUGHAM, R.W. (1959b).   The effects of frequency and intensity
    of grazing on the productivity of a pasture of short-rotation
    ryegrass and red and white clover.   N.Z. Journal of Agricultural
    Research.   2: 1232-1248.

BROUGHAM, R.W. (1960a).   The effects of frequent hard grazings at
    different times of the year on the productivity and species
    yields of a grass-clover pasture.   N.Z. Journal of Agricultural
    Research 3: 125-136.

BROUGHAM, R.W. (1960b).   The relationship between critical leaf area,
    total chlorophyll content, and maximum growth-rate of some pasture
    and crop plants.   Annals of Botany (N.S.) 24: 463-474.

BROUGHAM, R.W. (1961).   Some factors affecting the persistency of
    short rotation ryegrass.   N.Z. Journal of Agricultural Research
    4: 516-522.

BROUGHAM, R.W. (1962).   The leaf growth of *Trifolium repens* as
    influenced by seasonal changes in the light environment.
    Journal of Ecology 50: 449-460.

BROUGHAM, R.W. (1970).   Frequency and intensity of grazing and their
    effects on pasture production.   Proceedings of the New Zealand
    Grassland Association 32: 137-144.

BROUGHAM, R.W. (1977).   Some trends in grassland farming in Europe.
    Proceedings of the N.Z. Grassland Association 39: 5-19.

BROUGHAM, R.W. *et al.* (1978).   The ecology and management of white
    clover-based pastures.   In Plant Relations in Pastures.   C.S.I.R.O.,
    Melbourne.   Editor J.R. Wilson.   p 309-324.

BURGER, A.W., Jackobs, J.A. and Hittle, C.N. (1962).   The effect of
    height and frequency of cutting on the yield and botanical
    composition of Smooth bromegrass and Orchardgrass mixtures
    Agronomy Journal 54: 23-26.

BUTLER, G.W., Greenwood, R.M., Soper, K (1959). Effects of shading and defoliation on the turnover of root and nodule tissue of plants of *Trifolium repens*, *Trifolium pratense* and *Lotus uliginosus*. N.Z. Journal of Agricultural Research 2: 415-426.

CALDER, D.M. (1966). Inflorescence induction and initiation in the Gramineae. In The growth of cereals and grasses. Edited by F.L. Milthorpe and J.D. Ivins. Butterworths, London. p 59-73.

CAMPBELL, A.G. (1964). Grazed pasture parameters: Dead herbage, net gain and utilization of pasture. Proceedings of the N.Z. Society of Animal Production 21: 17-28.

CAMPBELL, A.G. (1966). Grazed pasture parameters. I. Pasture dry-matter production and availability in a stocking rate and grazing management experiment with dairy cows. Journal of Agricultural Science 67: 199-210.

CAMPBELL, A.G. (1969). Grazing interval, stocking rate, and pasture production. N.Z. Journal of Agricultural Research 12: 67-74.

CHESTNUTT, D.M.B. *et al*. (1977). The effect of cutting frequency and applied nitrogen on production and digestibility of perennial ryegrass. Journal of the British Grassland Society 32: 177-183.

CHU, A.C.P. (1979). Aspects of water deficit and vegetative growth in selected pasture and forage grasses. Ph D thesis, Massey University.

CHU, A.C.P. and Robertson, A.G. (1974). The effects of shading and defoliation on nodulation and nitrogen fixation by white clover. Plant and Soil 41: 509-519.

CLIFFORD, P.E. (1977). Tiller bud suppression in reproductive *Lolium multiflorum* Lam. cv. Westerwoldicum. Annals of Botany 41: 605-615.

COCKS, P.S. (1974). Potential production of grass and clover monocultures in a Mediterranean-type environment - An experimental approach. Australian Journal of Agricultural Research 25: 835-846.

COLLINS, D.P. and McCarrick, R.B. (1969). Effect of time and frequency of cutting on total and seasonal production of herbage. Irish Journal of Agricultural Research 8: 29-40.

COOPER, J.P. (1951). Studies on growth and development in *Lolium* II. Pattern of bud development of the shoot apex and its ecological significance. Journal of Ecology 39: 228-270.

COOPER, J.P. (1952). Studies on growth and development in *Lolium* III. Influence of season and latitude on ear emergence. Journal of Ecology 40: 352-379.

COOPER, J.P. (1960). The use of controlled life-cycles in the forage grasses and legumes. Herbage Abstracts 30: 71-79.

CORBETT, J.L. (1957). Studies on the extension of the grazing season. I. Evaluation of selected strains of some grass species for winter grazing. Journal of the British Grassland Society. 12: 81-96.

CORRALL, A.J. (1974). The effect of interruption of flower development on the yield and quality of perennial ryegrass. Vaxtodling 29: 39-43.

CORRALL, A.J. et al. (1979). Grass species and varieties. Seasonal patterns of production and relationships between yield, quality and date of first harvest. Grassland Research Institute Technical Report No. 26.

COWIE, J.D. (1974). Soils of Palmerston North City and Eivnrons, New Zealand. N.Z. Soil Survey Report No. 24.

DAVIDSON, J.L. (1968). Growth of grazed plants. Australian Grasslands Conference. 2: 125-137.

DAVIDSON, R.L. (1978). Root systems - the forgotten component of pastures. In Plant Relations in Pastures, Edited by J.R. Wilson, C.S.I.R.O. Melbourne. p 86-94.

DAVIDSON, J.L. and Donald, C.M. (1958). The growth of swards of subterranena clover with particular reference to leaf area. Australian Journal of Agricultural Research 9: 53-72.

DAVIDSON, J.L. and Milthorpe, F.L. (1966a). Leaf growth in Dactylis glomerata following defoliation. Annals of Botany. 30: 173-184.

DAVIDSON, J.L. and Milthorpe, F.L. (1966b). The effect of defoliation on the carbon balance in Dactylis glomerata. Annals of Botany. 30: 185-198.

DAVIES, A. (1966). The regrowth of swards of S24 perennial ryegrass subjected to different pretreatments. Journal of Agricultural Science. 67: 139-144.

DAVIES, A. (1971a). Growth rates and crop morphology in vernalized swards of perennial ryegrass in spring. Journal of Agricultural Science. 77: 273-282.

DAVIES, A. (1971b). Changes in growth rate and morphology of perennial ryegrass swards at high and low nitrogen levels. Journal of Agricultural Science 77: 123-134.

DAVIES, A. (1977). Structure of the grass sward. Proceedings international meeting on animal production from temperature grassland, Dublin. Editor, B. Gilsenan. p 36-44.

DAVIES, I. (1969). The influence of management on tiller development and herbage growth. Welsh Plant Breeding Station, Aberystwyth, Technical Bulletin No 3.

DAVIES, I. (1976). Developmental characteristics of grass varieties in relation to their herbage production. 2. Spring defoliation of Dactylis glomerata: the fate of reproductive tillers which are cut, but whose stem apex is retained. Journal of Agricultural Science 87: 33-38.

DAVIES, I; Davies, A; Troughton, A; Cooper, J.P. (1971). Regrowth in grasses. Report of the Welsh Plant Breeding Station for 1971, 79-94.

DEINUM, B. (1976). Photosynthesis and sink size: An explanation for the low productivity of grass swards in autumn. Netherlands Journal of Agricultural Science. 24: 238-246.

DOBSON, J.W. et al. (1978). Tall fescue yield, tillering, and invaders as related to management. Agronomy Journal. 70: 662-666.

DONALD, C.M. (1941). Pastures and Pasture Research, University of Sydney.

DONALD, C.M. and Black, J.N. (1958). The significance of leaf area in pasture growth. Herbage Abstracts 28: 1-6.

DUDZINSKI, M.L. and Arnold, G.W. (1973). Comparison of diets of sheep and cattle grazing together on sown pastures on the Southern Tablelands of New South Wales by principal components analysis. Australian Journal of Agricultural Research 24: 899-912.

EADIE, J. and Black, J.S. (1968). Herbage utilisation on hill pastures. Occasional Symposium No. 4, British Grassland Society. 191-195.

EDELSTEN, P.R. and Corrall, A.J. (1979). Regression models to predict herbage production and digestability in a non-regular sequence of cuts. Journal of Agricultural Science. 92: 575-585.

EDMOND, D.B. and Hoveland, C.S. (1971). A study of position of grass growing points in two species under different systems of management. N.Z. Journal of Agricultural Research 15: 7-18.

ERITH, A.E. (1924). White clover: a monograph. Duckworth, London.

EVANS, L.T. (1964). Reproduction. In Grasses and Grasslands. Edited by C. Barnard. Macmillan and Co. Ltd., London. p 126-153.

EVANS, P.S. (1971). Root growth of Lolium perenne L. II. Effects of defoliation and shading. N.Z. Journal of Agricultural Research. 14: 552-562.

EVANS, P.S. (1977). Root distribution and water-withdrawal patterns of some crop and pasture species. Proceedings of Soil and Plant Water Symposium, Plamerston North, 1976. D.S.I.R. Information Series No 126: 186-190.

FRAME, J. (1966). The evaluation of herbage production under cutting and grazing regimes. Proceedings of the 10th International Grassland Congress, Helsinki. p 291-297.

FRAME, J. (1976). A comparison of herbage production under cutting and grazing (including comments on deleterious factors such as treading. Pasture utilization by the grazing animal. Occasional Symposium, British Grasslands Society 8: 39-49.

FRAME, J. and Hunt, I.V. (1971).   The effects of cutting and grazing systems on herbage production from grass swards.   Journal of the British Grassland Society 26:   163-171.

GARWOOD, E.A. (1967).   Seasonal variation in appearance and growth of grass roots.   Journal of the British Grassland Society. 22:   121-130.

GARWOOD, E.A. (1969).   Seasonal tiller populations of grass and grass/ clover swards with and without irrigation.   Journal of the British Grasslands Society 24:   333-344.

GARWOOD, E.A. and Williams, T.E. (1967).   Soil water use and the growth of a grass sward.   Journal of Agricultural Science 68: 281-292.

GERLACH, J.C. (1974).   Climatographs of N.Z.   Ruakura Agricultural Research Centre Reserach Bulletin 74-1, Hamilton.

GERVAIS, P. and St-Pierre, J.C. (1979).   Influence du stade de croissance a la premiere recolte sur le rendement, la composition chimique et les reserves nutritives de la fleole des pres. Canadian Journal of Plant Science.   59:   177-183.

GILLET, M. (1973).   Influence du mode d'exploitation au printemps sur la production, en quantite et en qualite, des graminees fourrageres.   Fourrages 55:   15-76.

GILLINGHAM, A.G. (1978).   Phosphorus cycling in grazed, steep hill country.   PhD thesis, Massey University.

GRABER, L.F. *et al* (1927).   Organic food reserves in relation to the growth of alfalfa and other perennial herbaceous plants. Bulletin 80.   University of Wisconsin agricultural experimental station 3-128.

GREEN, J.O. (1949).   Herbage sampling errors and grazing trials. Journal of the British Grassland Society 4:   11-16.

GREEN, J.O. *et al.* (1971).   Grass species and varieties.   Relationships between stage of growth, yield and forage quality.   Grassland Research Institute technical report No. 8, Hurley pp 81.

HALL, A.M. (1973).   The principles of pasture growth.   Dairyfarming Annual 25:   102-105.

HARPER, J.L. (1977).   Population biology of plants.   Academic Press, London.

HARRIS, A.J. *et al* (1977).   Performance of four ryegrass cultivars under cutting.   N.Z. Journal of Experimental Agriculture 5:   391-395.

HARRIS, E.A. (1979).   N.Z. Official Year book 1979 84:   349.

HARRIS, W. (1968).   Pasture seeds mixtures, competition and productivity. Proceedings N.Z. Grasslands Association.   30:   143-153.

HARRIS, W. (1971). The effects of density, cutting height and white clover (*Trifolium repens L.*) on the structure of a ryegrass (*Lolium* spp.) population. Journal of Agricultural Science 77: 385-385.

HARRIS, W. (1973). Competition among pasture plants. IV Cutting frequency, nitrogen and phosphorus interactions, and competition between two ryegrass cultivars. N.Z. Journal of Agricultural Research. 16: 399-413.

HARRIS, W. (1978). Defoliation as a determinant of the growth, persistence and composition of pasture. In Plant Relations in Pastures, Edited by J.R. Wilson, C.S.I.R.O., Melbourne. p 67-85.

HARRIS, W. and Brougham, R.W. (1968). Some factors affecting change in botanical composition in a ryegrass-white clover pasture under continuous grazing. N.Z. Journal of Agricultural Research. 11: 15-38.

HARRIS, W. and Thomas, V.J. (1970). Competition among pasture plants. I. Effects of frequency and height of cutting on competition between two ryegrass cutlivars. N.Z. Journal of Agricultural Research 13: 833-861.

HAYES, P. (1971). Stoloniferous perennial ryegrass (*Lolium perenne*) in Northern Ireland paddocks. Record of Agricultural Research 19: 63-64.

HAYMAN, J.M. (1979). New Zealand perennial ryegrass cultivars in mid-Canterbury. Proceedings of the N.Z. Grassland Association 41: 116-122.

HEBBLETHWAITE, P.D. (1977). Irrigation and nitrogen studies in S23 ryegrass grown for seed. I. Growth, development, seed yield components and seed yield. Journal of Agricultural Science 88: 605-614.

HEBBLETHWAITE, P.D. and Burbidge, A. (1976). The effect of maleic hydrazide and chlorocholine chloride on the growth, seed yield components and seed yield of S23 ryegrass. Journal of Agricultural Science 86: 343-353.

HEBBLETHWAITE, P.D. and Ivins, J.D. (1977). Nitrogen studies in *Lolium perenne* grown for seed. I. Level of application. Journal of the British Grassland Society. 32: 195-204.

HEBBETHWAITE, P.D. and Ivins, J.D. (1978). Nitrogen studies in *Lolium perenne* grown for seed. II. Timing of nitrogen application. Journal of the British Grassland Society. 33: 159-166.

HILL, M.J. (1971). A study of seed production in "Grasslands Ruanui" perennial ryegrass (*Lolium perenne L.*), "Grasslands Kahu" timothy (*Phleum pratense L.*) and Praire grass (*Bromus unioloides H.B.K.*). PhD thesis, Massey University.

HILL, M.J. (1972). The effects of time of application of nitrogen on seed yield of 'Grasslands Ruanui' ryegrass (*Lolium perenne L.*) Proceedings of the Agronomy Society of N.Z. 2: 5-10.

HILL, M.J. and Watkin, B.R. (1975).   Seed production studies on
    perennial ryegrass, timothy and prarire grass.   I.   Effect
    of tiller age on tiller survival, ear emergence and seedhead
    components.   Journal of the British Grassland Society.   30:   63-71.

HODGSON, J. (1979).   Nomenclature and definitions in grazing studies.
    Grass and Forage Science 34:   11-18.

HOLLIDAY, R. (1953).   Agronomic research in grassland husbandry
    problems.   Agricultural Progress 28:   109-123.

HOLMES, C.W. and McClenaghan, R.J. (1979).   Grazing management and
    growth of pasture.   Dairyfarming Annual 31:   79-80.

HOOK, P.J. (1978).   Recent advances in grassland management in
    Eastern Southland and West Otago.   Proceedings of the N.Z.
    Grassland Association 40:   17-24.

HORST, G.L. and Nelson, C.J. (1979).   Compensatory growth of tall
    fescue following drought.   Agronomy Journal 71:   559-563.

HUNT, W.F. (1968).   Some aspects of leaf death during the regrowth of
    a perennial ryegrass (Lolium perenne L.) White clover (Trifolium
    repens L.) sward.   M.Agr.Sc. thesis, Massey University.

HUNT, W.F. (1970a).   The influence of leaf death on the rate of
    accumulation of green herbage during pasture regrowth.   Journal
    of Applied Ecology 7:   41-50.

HUNT, W.F. (1970b).   Leaf death and decomposition during pasture
    regrowth.   N.Z. Journal of Agricultural Research 14:   208-218.

HUNT, H.W. (1977).   A simulation model for decomposition in grasslands.
    Ecology 58:   469-484.

HUNT, L.A. and Brougham, R.W. (1966).   Some aspects of growth in an
    undefoliated stand of Italian ryegrass.   Journal of Applied
    Ecology 3:   21-28.

HUNT, L.A. and Brougham, R.W. (1967).   Some changes in the structure
    of a perennial ryegrass sward frequently but leniently defoliated
    during the summer.   N.Z. Journal of Agricultural Research
    10:   397-404.

HUNT, W.F. and Field, T.R.O. (1978).   Growth characteristics of
    perennial ryegrass.   Proceedings of the N.Z. Grassland Association
    40:   104-114.

HUOKUNA, E. (1960).   The effect of differential cutting on the
    growth of cocksfoot.   Proceedings of the Eighth International
    Grassland Congress: 429-433.

HUOKUNA, E. (1966).   Tillering in meadow-fescue swards.   Proceedings
    of the Tenth International Grassland Congress, Helsinki p 129-134.

ISHIDA, R. (1975).   Vegetational structure of sown grassland.   V.
    Changes of the number of tillers per unit area and relation
    between number of tillers and yields in some grass species.
    Journal of Japanese Society of Grassland Science 21:   47-51.

ITO, M. and Nakamura, T. (1975).   The effects of cutting frequency
    upon the seasonal fluctuations of tiller population and the life
    history of tillers in a Orchardgrass sward of a single clone.
    Journal of Japanese Society of Grassland Science 21:   1-8.

JACKSON, D.K. (1973). Efficiency in grass production for grazing Report of the Welsh Plant Breeding Station for 1973 p 111-115.

JACKSON, D.K. (1974). Some aspects of production and persistancy in relation to height of defoliation of *Lolium perenne* (Var. S23). Proceedings XII International Grassland Congress Moscow. Part I, p 273-284.

JACKSON, D.K. (1976). The influence of patterns of defoliation on sward morphology. Proceedings of a symposium on Pasture utilization by the grazing animal. British Grassland Occasional Symposium No 8: 39-49.

JACKSON, M.V. and Williams, T.E. (1979). Response of grass swards to fertilizer N under cutting or grazing. Journal of Agricultural Science 92: 549-562.

JAGUSH, K.T. *et al*. (1978). The dynamics of pasture production under sheep. Proceedings of the N.Z. Society of Animal Production 38: 129-138.

JAMESON, D.A. (1963). Response of individual plants to harvesting. Botanical Review 29: 532-594.

JEWISS, O.R. (1966). Morphological and physiological aspects of growth of grasses during the vegetative phase. In The Growth of Cereals and Grasses. Edited by Milthorpe, F.L. and Ivins, J.D.; Butterworths, London. p 39-55.

JEWISS, O.R. (1972). Tillering in grasses - its significance and control. Journal of the British Grassland Society 27: 65-82.

JEWISS, O.R. and Woledge, J. (1967). The effect of age on the rate of apparent photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Annals of Botany. 31: 661-671.

JONES, L.I. (1959). Varietal characteristics of herbage plants in relation to their agronomic assessment. In The Measurement of Grassland Productivity. Edited by J.D. Ivins; Butterworths Scientific Publications, London.

JONES, M.J. (1933). Grassland management and its influence on the sward. Empire Journal of Experimental Agriculture 1: 43-57, 122-127, 223-234, 361-367.

JONES, R.J. *et al*. (1979). Seedling selection for morphological characters associated with yield of Tall Fescue. Crop Science 19: 631-634.

JONES, G.G. and Haydock, K.P. (1970). Yield estimation of tropical and temperate pasture species using an electronic capacitance meter. Journal of Agricultural Science 75: 27-36.

KAIN, W.M. *et al*. (1977). Effects of stem weevil on grazed swards of perennial ryegrass in Wairarapa and Manawatu. Proceedings N.Z. Weed and Pest Control Conference. 30: 192-197.

KAYS, S. and Harper, J.L. (1974). The regulation of plant and tiller density in a grass sward. Journal of Ecology 62: 97-105.

KEATINGE, J.D.H. *et al*. (1979). The influence of climatic factors on physiological development in perennial ryegrass. Grass and Forage Science 34: 55-59.

KEOGH, R.G. (1978). Development and control of ryegrass staggers in sheep. Proceedings of the N.Z. Society of Animal Production 38: 47-52.

KING, J. *et al*. (1979). Regrowth of ryegrass swards subject to different cutting regimes and stocking densities. Grass and Forage Science. 34: 107-118.

KORTE, C.J. and Sheath, G.W. (1978). Herbage dry matter production: the balance between growth and death. Proceedings of the N.Z. Grassland Association. 40: 152-161.

KOYOMA, H. and Kira, T. (1956). Intraspecific competition among higher plants. VIII. Frequency distribution of individual plant weight as affected by the interaction between plants. J. Inst. Polytech. Osaka City Univ. D8, 161-178.

KRAUSE, J.W. and Moser, E.E. (1977). Tillering in irrigated smooth bromegrass (*Bromus inermis* Leyss.) as affected by elongated tiller removal. Proceedings of the XIII International Grassland Congress, Leipzig. p. 37-42.

KUNELIUS, H.T. and Calder, F.W. (1978). Effects of rates of N and regrowth intervals on yields and quality of Italian ryegrass grown as a summer annual. Canadian Journal of Plant Science 58: 691-697.

KYDD, D.D. (1966). The effect of intensive sheep stocking over a five-year period on the development and production of the sward. I. Sward structure and botanical composition. Journal of the British Grassland Society 21: 284-288.

LAIDLAW, A.S. and Berrie, A.M.M. (1974). The influence of expanding leaves and the reproductive stem apex on apical dominance in *Lolium multiflorum* Annals of applied Biology. 78: 75-82.

LAMBERT, D.A. (1952). A study of growth in swards of timothy and meadow fescue. III The effect of two levels of nitrogen under two cutting treatments. Journal of Agricultural Science. 59: 25-32.

LAMP, H.F. (1952). Reproductive activity in *Bromus inermis* in relation to phases of tiller development. Botanical Gazette. 113: 413-438.

LANCASHIRE, J.A. and Harris, A.J. (1977). Evaluation of new herbage cultivars. Proceedings of the N.Z. Grassland Association. 39: 108-120.

LANCASHIRE, J.A. *et al.* (1978). Perennial ryegrass cultivars. Proceedings of the N.Z. Grassland Association 40: 114-124.

LANGER, R.M.H. (1959). A study of growth in swards of timothy and meadow fescue. II The effects of cutting treatments. Journal of Agricultural Science 52: 273-281.

LANGER, R.H.M. (1963). Tillering in herbage grasses. Herbage Abstracts 33: 141-148.

LANGER, R.M.H. (1966). Mineral nutrition of grasses and cereals. In The Growth of Grasses and Cereals, editors Milthorpe and Ivins Butterworths, London,p216-226.

LANGER, R.M.H. (1979). How Grasses Grow. Second Edition. Edward Arnold, London.

LANGER, R.M.H., *et al.* (1964). The changing plant and tiller populations of timothy and meadow fescue swards. Journal of Applied Ecology 1: 197-208.

LAZENBY, A. and Rogers, H.H. (1962). Selection criteria in grass breeding. I. Journal of Agricultural Science 59: 51-66.

LAZENBY, A. and Robers, H.H. (1964). Selection criteria in grass breeding. II. Effect on *Lolium perenne*, of differences in population density, variety and available moisture. Journal of Agricultural Science 62: 285-298.

LEAFE, E.L. (1971). Micro-environment, carbon dioxide exchange and growth in grass swards. In Crop Processes in Controlled Environments, Editors Rees, A.R. *et al.* Academic Press. p 157-174.

LEAFE, E.L. *et al.* (1974). Physiological processes influencing the pattern of productivity of the intensively managed grass sward. Proceedings XII International Grassland Congress, Moscow 191-205.

LEAFE, E.L. *et al.* (1979). The growth of the grass sward under grazing. Annual Report 1978, Grassland Research Institute, Hurley. p 49-51.

LE CLERC, M.H. (1976). Effects of nitrogen and rest periods on the seasonal production of a pure grass sward. I. Dry matter production. Irish Journal of Agricultural Research. 15: 247-255.

LEVY, E.B. (1970). Grasslands of New Zealand. 3rd Ed. Government Printer, Wellington. 347 p

LINEHAN, P.A. *et al.* (1952). The output of pasture and its measurement. Part III. Journal of the British Grassland Society 7: 73-98.

LYNCH, P.B. and Mountier, N.S. (1954). Cutting techniques in grassland experiments. N.Z. Journal of Science and Technology 36A: 375-385.

MAC DIARMID, B.N. and Watkin, B.R. (1971). The cattle dung patch. I. Effect of dung patches on yield and botanical composition of surrounding and underlying pasture. Journal of British Grassland Society 26: 239-245.

MADISON, J.H. (1962). Turfgrass Ecology. Effects of mowing, irrigation, and nitrogen treatment of *Agrostis palustris* Huds., 'Seaside' and *Agrostis tenuis* Sibth., 'Highland' on population, yield, rooting and cover. Agronomy Journal. 54: 407-412.

MARSH, R. (1978). Effect of exclosure cages on the growth rate of pastures at different times of the year. N.Z. Journal of Experimental Agriculture 6: 115-117.

MARSH, R. (1979). Effect of herbage DM allowance on the immediate and longer term performance of young Friesian steers at pasture. N.Z. Journal of Agricultural Research 22: 209-219.

MASON, C.F. (1976). Decomposition. The Institute of Biology's Studies in Biology No. 74. Edward Arnold, London.

MATTHEWS,P.N.P.(1975), Pasture and forage crops in perspective. Dairy Farming Annual 27: 27-39.

MATTHEWS,P.N.P.*et al* (1979). The management of spring pasture. Dairyfarming Annual 31: 73-94.

MAY, L.H. (1960). The utilization of carbohydrate reserves in pasture plants after defoliation. Herbage Abstracts 30: 239-245.

McBRIDE, G. *et al*. (1967). Ecology and behaviour of domestic animals. Proceedings of the Ecological Society of Australia 2: 133-165.

McCREE, K.J. and Troughton, J.H. (1966). Non-existance of an optimum leaf area index for the production rate of white clover grown under constant conditions. Plant Physiology 41: 1615-1622.

MILTHORPE, F.L. and Davidson, J.L. (1966). Physiological aspects of regrowth in grasses. In The Growth of Cereals and Grasses. Editors Milthorpe, F.L. and Ivins, J.D. Proceedings of the 12 Easter school in agricultural science, University of Nottingham, 1965. p 241-255.

MINDERHOUD, J.W. (1978). Pseudostolons and aerial tillers: morphological phenomena of *Lolium perenne* L. Seventh General Meeting of the European Grassland Federation, Gent. p 10.31-10.39.

MISLEVY, P. *et al*. (1977). Influence of Plant Stage at Initial Harvest and Height of regrowth at cutting on forage yield and quality of Timothy and Orchardgrass. Agronomy Journal 69: 353-356.

MITAMURA, T. (1972). The effect of cutting on the dry matter production of Orchardgrass sward (*Dactylis glomerata* L.). Bulletin of Institute for Agricultural Research, Tohoku University 24: 55-93.

MITCHELL, K.J. (1956). Growth of pasture species under controlled environment. I. Growth at various levels of constant temperature. New Zealand Journal of Science and Technology 38A : 203-216.

MITCHELL, K.J. and Coles, S.T.J. (1955). Effects of defoliation and shading on short-rotation ryegrass. N.Z. Journal of Science and Technology A36: 586-604.

MITCHELL, K.J. and Glenday, A.C. (1958). The tiller population of pastures. N.Z. Journal of Agricultural Research 1: 305-318.

MONTEATH et al. (1977). Effects of animals on pasture production. I. Pasture productivity from beef cattle and sheep farmlets. N.Z. Journal of Agricultural Research. 20: 23-30.

MORRIS, R.M. (1970). The use of cutting treatments designed to stimulate defoliation by sheep. Journal of the British Grassland Society 25: 198-206.

MORTIMER, G.B. and Ahlgren, H.L. (1936). Influence of fertilization, irrigation and stage and height of cutting on yield and composition of Kentucky Bluegrass (Poa pratensis L.). Journal of the American Society of Agronomy 28: 515-533.

MOUNTIER, N.S. et al. (1966). Sources of error in advisory soil tests. I. Laboratory sources. N.Z. Journal of Agricultural Research 9: 328-338.

MOUSTAFA, E.; Ball, R.; Field, T.R.O. (1969). The use of acetylene reduction to study the effect of nitrogen fertilizer and defoliation on nitrogen fixation by field-grown white clover. New Zealand Journal of Agricultural Research. 12: 691-696.

OBEID, M. et al. (1967). Influence of density on plant to palnt variation in fiber flax Linum usitatissimun L. Crop Science. 7: 471-473.

O'BRIEN, J.A. et al. (1977). The effect of management and competition on the uptake of [32]Phosphorus by ryegrass, meadow fescue and their natural hybrid. Journal of Applied Ecology 4: 513-520.

OKUBO, T. et al. (1977). A model for seasonal changes in productivity and solar energy utilization of grazing pasture. Japan Agricultural Research Quarterly 11: 221-227.

OLLERENSHAW, J.H. and Hodgson, D.R. (1977). The effects of constant and varying heights of cut on the yield of Italian ryegrass Lolium multiflorum Lam.) and perennial ryegrass (Lolium perenne L.) Journal of Agricultural Science 89: 425-435.

OLMSTED, C.E. (1941). Growth and development in range grasses. I. Early development in Bouteloua curtipendula in relation to water supply. Botanical Gazette. 102: 499-519.

ONG, C.K. and Marshall, C. (1975). Assimilate distribution in
    Poa annua L. Annals of Botany 39: 413-421.

ONG, C.K. and Marshall, C. (1979). The growth and survival of
    severely-shaded tillers in *Lolium perenne* L. Annals of Botany
    43: 147-155.

ONG, C.K. *et al.* (1978a). The fixation of labelled carbon
    dioxide by the inflorescence of *Poa annua* L. and *Lolium perenne* L.
    Annals of Botany 42: 855-862.

ONG, C.K. *et al.* (1978b). The physiology of tiller death in grasses .
    2. Causes of tiller death in a grass sward. Journal of the
    British Grassland Society. 33: 205-211.

PASCOE, W.B. (1973). Effects of grazing on the growth and development
    of white clover (*Trifolium repens* L.). M.Agr. Sc. Thesis, Massey
    University.

PINEIRO, J. and Harris, W. (1978a). Performance of mixture of
    ryegrass cultivars and praire grass with red clover cultivars under
    two grazing frequencies. I. Herbage production in the
    establishment year. N.Z. Journal of Agricultural Research.
    21: 83-92.

PINEIRO, J. and Harris, W. (1978b). Performance of mixtures of
    ryegrass cultivars and praire grass with red clover cultivars
    under two grazing frequencies. II. Shoot populations and
    natural reseeding of praire grass. N.Z. Journal of Agricultural
    Research. 21: 665-673.

POTTINGER, R.P. (1973). Pests of grassland and small seed crops.
    In Pastures and Pasture Plants; Editor: R.H. Langer; A.H.
    Reed, Wellington p 367-406.

PRITCHARD, G.I. *et al.* (1963). The *in vitro* digestibility of whole
    grasses and their parts at progressive stages of maturity.
    Canadian Journal of Plant Science 43: 79-87.

RADCLIFFE, J.E. and Lynch, P.B. (1974). The influence of regional
    climate and soil on pasture production in N.Z. XII International
    Grassland Congress, Moscow. p 501-514.

RATTRAY, P.V. (1978). Pasture constraints to sheep production.
    Proceedings Agronomy Society of N.Z. 8: 103-108.

RAYMOND, W.F. (1970). The nutritive value of forage crops.
    Advances in Agronomy. 7: 1-108.

REID, D. (1959). Studies on the cutting management of grass clover
    swards. I. The effect of varying the closeness of cutting
    on the yields from an established grass-clover sward. Journal
    Agricultural Science. 53: 299-312.

REID, D. (1962). Studies on cutting management of grass-clover swards. III The effects of prolonged close and lax cutting on herbage yields and quality. Journal of Agricultural Science 59: 359-368.

RICKARD, D.S. and Radcliffe, J.E. (1976). Seasonal distribution of pasture production in New Zealand. XII Winchmore, Canterbury Plains dryland and irrigated pastures. N.Z. Journal of Experimental Agriculture 4: 329-335.

RITCHIE, I.M. (1975). 'Grasslands Nui' ryegrass. Annual Report of Research Division, N.Z. Ministry of Agriculture and Fisheries p 144-145.

ROBINSON, R.R., Sprague, V.G. and Lueck, A.G. (1952). The effect of irrigation, nitrogen fertilization and clipping treatments on persistance of clover and on total and seasonal distribution of yield in a Kentucky Bluegrass sod. Agronomy Journal 44: 239-244.

ROBSON, M.J. (1973). The growth and development of simulated swards of perennial ryegrass II. Carbon assimilation and respiration in a seedling sward. Annals of Botany. 37: 501-518.

ROBSON, M.J. and Deacon, M.J. (1978). Nitrogen deficiency in small closed communities of S24 ryegrass. II Changes in weight and chemical composition of single leaves during their growth and death. Annals of Botany 42: 1199-1213.

RODIN, L.E. and Bazilevich, N.I. (1967). Production and Mineral Cycling in Terrestrial Vegetation. English translation by G.E. Fogg. Oliver and Boyd, Edinburgh.

RYLE, G.J.A. (1970). Distribution patterns of assimilated ^{14}C in vegetative and reproductive shoots of *Lolium perenne* and L. *tenulentum*. Annals of applied biology. 66: 155-167.

SAMPAIO, E.V.S.B. and Beaty, E.R. (1976). Morphology and Growth of Bahiagrass at three rates of nitrogen. Agronomy Journal 68: 379-381.

SAXBY, S.H. (1948). Pasture production in New Zealand. Bulletin No 250, N.Z. Department of Agriculture, Wellington 203p.

SAUER, R.H. (1978). A simulation model for grassland primary producer phenology and biomass dynamics. In Grassland simulation model ed G.S. Innis, pp 55-87. Springer Ecological Studies 26. Springer-Verlag, New York.

SEARS, P.D. (1951). The technique of pasture measurement. N.Z. Journal of Science and Technology 33A: 1-29.

SEARS, P.D. and Evans, L.T. (1953). Pasture growth and soil fertility. III. The influence of red and white clovers, superphosphate, lime, and dung and urine on soil composition, and on earthworm and grass-grub populations. N.Z. Journal of Science and Technology. Volume 35A, Supp 1: 42-52.

SESTAK, Z. *et al*. (1971). <u>Plant photosynthetic production:</u>
<u>manual of methods</u>. Dr W. Junk N.V. Publishers, The Hague,
The Netherlands.

SHEARD, R.W. and Winch, J.E. (1966). The use of light interception,
gross morphology and time as criteria for the harvesting of
timothy, smooth brome and cocksfoot. <u>Journal of the British</u>
<u>Grassland Society</u> 21: 231-237.

SHEATH, G.W. *et al*. (1976). An evaluation of several grass and
legume cultivars under dryland and irrigation in North Otago.
<u>Proceedings N.Z. Grasslands Association</u> 38 : 140-150.

SHEEHY, J.E. *et al*. (1979). The growth of perennial ryegrass:
A model. <u>Annals of Botany</u> 43: 335-354.

SHEFFER, K.M. *et al*. (1978). Effect of mowing height on leaf angle,
leaf number, and tiller density of 62 Kentucky Bluegrasses.
<u>Agronomy Journal</u> 70: 686-689.

SIBMA, L. and Louwerse, W. (1977). The effect of changes in crop
structure on photosynthesis, dry matter production and chemical
composition of *Lolium perenne*. Proceedings of the 13th
International Grassland Congress, Leipzig. Section 1: 2-12.

SILSBURY, J.H. (1964). Tiller dynamics, growth, and persistency of
Lolium perenne L. and *Lolium rigidum* Gaud. <u>Australian Journal</u>
<u>of Agricultural Research</u>. 15: 9-20.

SILSBURY, J.H. (1965). Interrelationships in the growth and development
of *Lolium*. I. Some effects of vernalisation on growth and
development. <u>Australian Journal of Agricultural Research</u>.
16: 903-913.

SIMONS, R.G. *et al*. (1974). The effect of cutting height and mulching
on aerial tillering in two contrasting genotypes of perennial
ryegrass. <u>Journal of Agricultural Science</u> 83: 267-273.

SITHAMPARANATHAN, J. (1979). Seasonal growth patterns of herbage
species on high rainfall hill country in northern North Island.
I. Temperature grasses. <u>N.Z. Journal of Experimental</u>
<u>Agriculture</u>. 7: 157-162.

SMITH, R.G. and Dawson, A.D. (1976). Hill Country Grazing Management.
<u>Proceedings of the N.Z. Grassland Association</u> 38: 47-55.

SMITH, R.G. and Stiefel, W. (1977). Pasture and lucerne research on
sand country. <u>Proceedings of N.Z. Grasslands Association</u>.
39: 61-69.

SPIERTZ, J.H.J. and Ellen, J. (1972). The effect of light intensity
on some morphological and physiological aspects of the crop
perennial ryegrass (*Lolium perenne* L. var. 'Cropper') and its
effect on seed production. <u>Netherlands Journal of Agricultural</u>
<u>Science</u> 20: 232-246.

STERN, W.R. and Donald, C.M. (1961). Relationship of radiation, Leaf area index and crop growth-rate. Nature 189: 597-598.

STERN, W.R. and Donald, C.M. (1962). The influence of leaf area and radiation on the growth of clover in swards. Australian Journal of Agricultural Research. 13: 615-623.

STOUT, J.D. *et al*. (1976). Decomposition processes in New Zealand soils with particular respect to rates and pathways of plant degradation. In The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. 17th Symposium of the British Ecological Society 1975. ed. Anderson, J.M. and Macfadyen, A.

SYERS, J.K. *et al*. (1979). Cycling of nitrogen by surface-casting earthworms in a pasture ecosystem. Soil Biology and Biochemistry 11: 181-185.

TAINTON, N.M. (1974a). A comparison of different pasture rotations. Proceedings of N.Z. Grassland Assocation. 35: 204-210.

TAINTON, N.M. (1974b). Effects of different grazing rotations on pasture production. Journal of the British Grassland Society. 29: 191-202.

TAYLER, J.C. and Rudman, J.E. (1966). The distribution of herbage at different heights in "grazed" and "dung patch" areas of a sward under two methods of grazing management. Journal of Agricultural Science 66: 29-39.

TERAI, K. (1977). Judgement of artificial grassland productiveness (2) - Influence of plant density and cutting time on dry matter production of orchard grass sward (*Dactulis glomerata* L.). Reports of the Institute for Agricultural Research, Tohoku University. 28: 9-27.

TERAI, K. and Kanda, M. (1979). Mortal response and growth of individual plants in a population of orchardgrass (*Dactulis glomerata* L.). III. Relationship between tiller density and tiller weight. Journal of Japanese Society of Grassland Science. 24: 270-276.

TERRY, R.A. and Tilley, J.M.A. (1964). The digestibility of the leaves and stems of perennial ryegrass, cocksfoot, timothy, tall fescue, lucerne and sainfoin, as measured by an *in vitro* procedure. Journal of the British Grassland Society 19: 363-372.

TESAR, M.B. and Ahlgren, H.L. (1950). Effect of height and frequency of cutting on the productivity and survival of Ladino Clover (*Trifolium repens* L.). Agronomy Journal 42: 230-235.

THOMAS, H. (1980). Terminology and definitions in studies of grassland plants. Grass and Forage Science 35: 13-23.

THOMAS, H. and Davies, A (1978). Effect of shading on the regrowth of *Lolium verenne* swards in the field. Annals of Botany 42: 705-715.

THOMAS, H. and Norris, I.B. (1977). The growth responses of *Lolium verenne* to the weather during winter and spring at various altitudes in mid-Wales. Journal of Applied Ecology 14: 949-964.

THOMSEN, E. (1978). Grass species under sprinkler irrigation. Annual Report of Research Division, N.Z. Ministry of Agriculture and Fisheries, p 117-118.

THOMSON, N.A. (1977). Factors affecting animal production: intake and utilization by ewes grazing grass/clover and lucerne pastures. Proceedings of the N.Z. Grassland Assoication 39: 86-97.

TROUGHTON, A. (1957). The Underground Organs of Herbage Grasses. Commonwealth Bureau of Pastures and Field Crops, Bulletin No. 44. pp 163.

TROUGHTON, A. (1978). The influence of reproductive development upon the root system of perennial ryegrass and some effects upon herbage production. Journal of Agricultural Science 91: 427-431.

WATERS, R.A.S. (1955). Numbers and weights of earthworms under a highly productive pasture. N.Z. Journal of Science and Technology 36A: 516-525.

WATKIN, B.R. and Clements, R.J. (1978). The effects of grazing animals on pastures. In Plant Relations in Pastures, Edited by J.R. Wilson, C.S.I.R.O. Melbourne p 273-289.

WATSON, D.J. (1947). Comparative physiological studies on the growth of field crops. I. Variations in net assimilation rate and leaf area between species and varieties and within and between years. Annals of Botany (N.S.). 11: 41-89.

WEEDA, W.C. (1965). The effects of frequency and severity of grazing by cattle on the yield of irrigated pasture. N.Z. Journal of Agricultural Research. 8: 1060-1069.

WEINMANN, H. (1948). Underground development and reserves of grasses - A review. Journal of the British Grassland Society. 3: 115-140.

WHEELER, A.W. (1980). Effects of removing ears and leaves on responses of Barley and Wheat to Chlormequat Chloride and Gibberellic Acid. Annals of Botany 46: 379-381.

WHEELER, J.L. (1962). Experimentation in grazing management. Herbage Abstracts 32: 1-7.

WIEGERT, R.G. and Evans, F.C. (1964). Primary production and the disappearance of dead vegetation on an old field in S.E. Michigan. Ecology 45: 49-63.

WILLIAMS, R.D. (1970).   Tillering in grasses cut for conservation,
    with special reference to perennial ryegrass.   Herbage
    Abstracts.   40: 383-388.

WILLIAMSON, P. (1976).   Above-ground primary production of chalk
    grassland allowing for leaf death.   Journal of Ecology 64:
    1059-1075.

WILMAN, D. et al . (1976a).   The effect of interval between harvests
    and nitrogen application on the proportion and yield of crop
    fractions in four ryegrass varieties in the first harvest year.
    Journal of Agricultural Science.   86: 189-203.

WILMAN, D. et al. (1976b).   The effect of interval between harvests
    and nitrogen application on the number and weights of tillers and
    leaves in four ryegrass varieties.   Journal of Agricultural
    Science 87: 45-57.

WILMAN, D. et al. (1976c).   The effect of interval between harvests
    and nitrogen application on the proportion and yield of crop
    fractions and on the digestibility and digestable yield and nitrogen
    content and yield of two perennial ryegrass varieties in the second
    harvest year.   Journal of Agricultural Science.   87: 59-74.

WILMAN, D. et al. (1976d).   Nitrogen and Italian ryegrass.   3. Growth
    up to 14 weeks: yields, proportions, digestibilities and nitrogen
    contents of crop fractions, and tiller populations.   Journal
    of the British Grassland Society 31: 73-79.

WILMAN, D. et al. (1977).   The effect of interval between harvests
    and nitrogen application on initiation, emergence and longevity
    of leaves, longevity of tillers and dimensions and weights of
    leaves and 'stems' in Lolium.   Journal of Agricultural Science
    89: 65-79.

WILMAN, D. and Mares Martins, V.M. (1977).   Senescence and death of
    herbage during periods of regrowth in ryegrass and red and white
    clover, and the effect of applied nitrogen.   Journal of Applied
    Ecology 14: 615-620.

WILSON, D.B. and McGuire, W.S. (1961).   Effects of clipping and nitrogen
    on competition between three pasture species.   Canadian Journal
    of Plant Science 41: 631-642.

WILSON, J.B. (1978).   TEDDYBEAR statistical programme.   Technical
    Report T_5, Edition 2.4.   University of Otago computing Centre.   89pp.

WILSON, J.R. (1959).   The influence of time of tiller origin and
    nitrogen level on the floral and ear emergence of four pasture
    grasses.   N.Z. Journal of Agricultural Research 2: 915-932.

WOLEDGE, J. (1977).   The effects of shading and cutting treatments on
    the photosynthetic rate of ryegrass leaves.   Annals of Botany
    41: 1279-1286.

WOLEDGE, J. (1979). Effect of flowering on the photosynthetic capacity of ryegrass leaves grown with and without natural shading. Annals of Botany. 44: 197-207.

WOLEDGE, J. and Jewiss, O.R. (1969). The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). Annals of Botany 33: 897-913.

WOLEDGE, J. and Leafe, E.L. (1976). Single leaf and canopy photosynthesis in a ryegrass sward. Annals of Botany. 40: 773-783.

YOUNGER, V.B. (1972). Physiology of defoliation and regrowth. In The Biology and utilization of grasses. Edited by V.B. Youngner and C.M. McKell, Academic Press, London.