

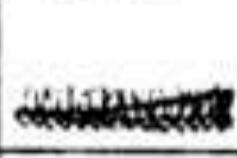
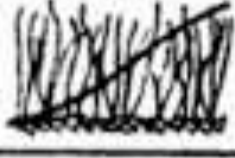



	SHORT GRAZED PASTURE	LONGISH SPELLS BETWEEN GRAZING	EXCESSIVE SPELLS BETWEEN GRAZING	CHOU MOLLIER	MAIZE EQUIVALENT (JOHNSTON GRASS ETC.)
GROWTH FORM AND LIGHT INTERCEPTION CURVE	HEIGHT 2-3in 	HEIGHT 9-15in 	HEIGHT 9-15in 	5ft 	10ft 
MAXIMUM LEAF AREA INDEX	4-5	10	12	6	16
PEAK SUMMER DAILY AIR REQUIREMENT	185 acre/ft	340 acre/ft	230 acre/ft	440 acre/ft	685 acre/ft
VENTILATION	EXCELLENT	FAIR-GOOD	POOR	GOOD	EXCELLENT
POTENTIAL ANNUAL PRODUCTION PALMERSTON NORTH (lbs/DM/acre)	12000	22000	15000	26000	42000

FIGURE 8. Inter-relationships between crop structure and potential production. Mitchell (1960).

These differences in temperature and moisture content of the soil profile arising from different types of vegetation cover may have immediate effects on the availability of nutrients (Mitchell 1957) and, on a longer term, on the balance between various directions of soil type development.

ASPECTS OF LIGHT UTILIZATION, LEAF DEVELOPMENT AND SENESCENCE AND GRAZING ON GRASS-LEGUME BALANCE AND PRODUCTIVITY OF PASTURES

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In this paper it is intended to describe some aspects of leaf development and leaf canopy structure of communities of two species of importance to New Zealand agriculture in relation to the light environment, then to illustrate some effects grazing has on the grass-legume balance and productivity of pastures.

Two species that have been studied in some detail at Grasslands Division are white clover (*Trifolium repens*) and the ryegrasses (*Lolium* spp.). The first is a stoloniferous type with individual leaves developing from the terminal

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buds of the stolons. When fully formed each leaf comprises a petiole supporting a lamina which is usually orientated horizontally. The *Lolium* spp. have a markedly different leaf development pattern with new leaves developing from the apex of the tiller unit and orientating themselves, when in a closed community, much more vertically. It is of importance to this discussion that these different leaf development patterns result in marked differences in the development and structure of the leaf canopy at certain times of the year and in turn significantly influence productivity.

Stands of the different species have been looked at in two ways. Leaf growth and leaf canopy development have been studied in undisturbed pure stands of each species in separate investigations. In addition pure stands of the species have been investigated in terms of leaf growth and canopy development following defoliation.

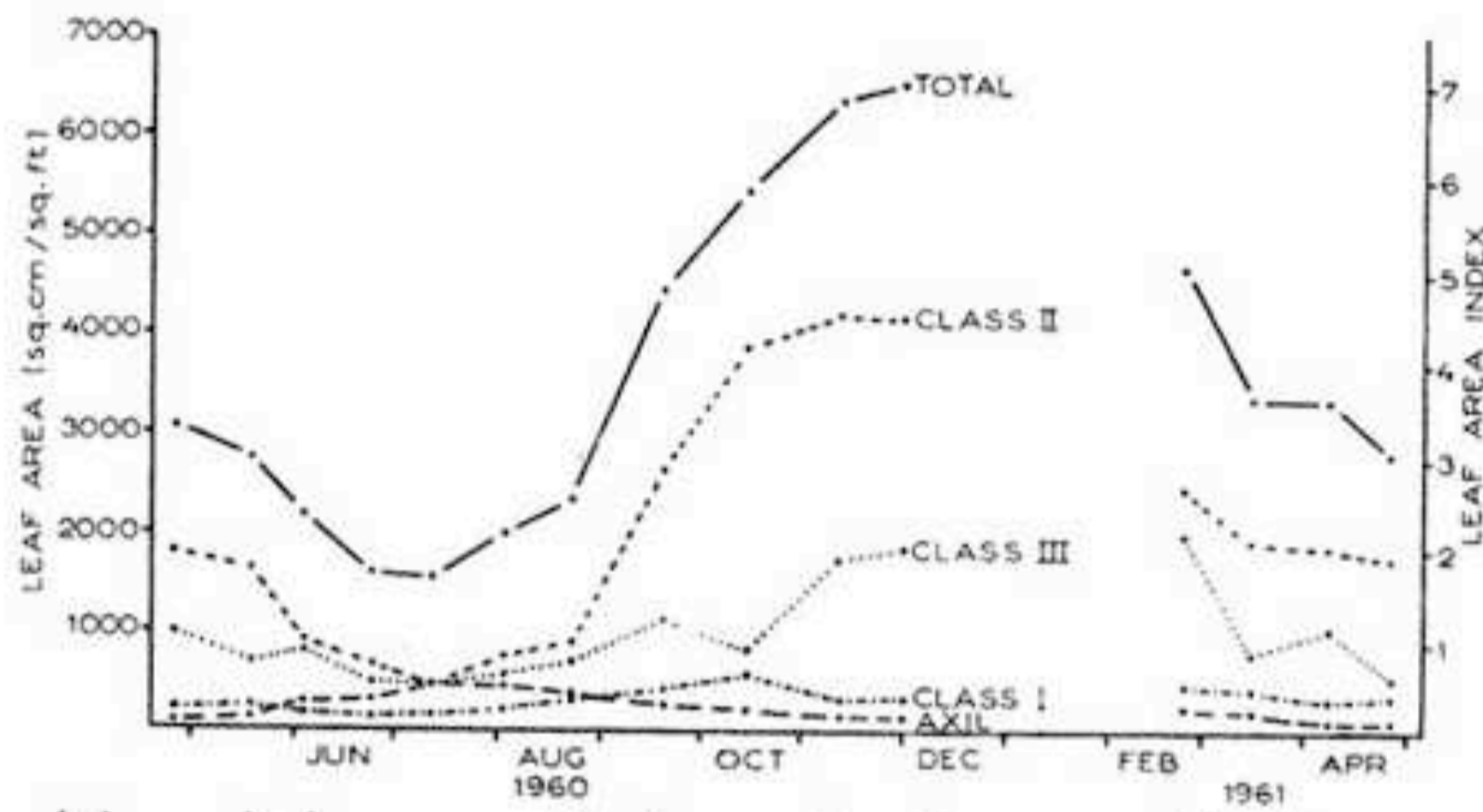


FIGURE 1. Seasonal changes in the amounts of leaf present in various stages of development and senescence.

The results presented in Figure 1 show the seasonal changes that occur in the amounts of leaf present in various stages of development and senescence in undisturbed stands of white clover.

The total areas of leaf in the stand showed marked seasonal changes ranging from 1500 sq. cm./sq. ft. (1 sq. ft. = 929 sq. cm.) in mid-winter (July) to 6,500 sq. cm./sq. ft. in late spring. For all seasons except the winter, the main component of the leaf canopy was fully opened main leaves originating from terminal buds (Class II in the diagram), and to a lesser extent, leaves in various stages of senescence (Class III).

The areas of unopened main or terminal bud leaves (Class I) developing under the main leaf canopy amounted to 0.5 L.A.I.* units, except during the late autumn and winter when the areas recorded were approximately one-third of those obtained at other seasons of the year. An opposite trend is shown for the areas of leaf developing from axillary buds, the mid-winter value of 0.5 L.A.I. units being approximately three times those recorded during the remainder of the year and being equal to the mid-winter value of both main and senescing leaves.

These values were a function of the rate of development and the number of leaves per unit area in the different classes. This is illustrated in Figure 2 where lamina weights

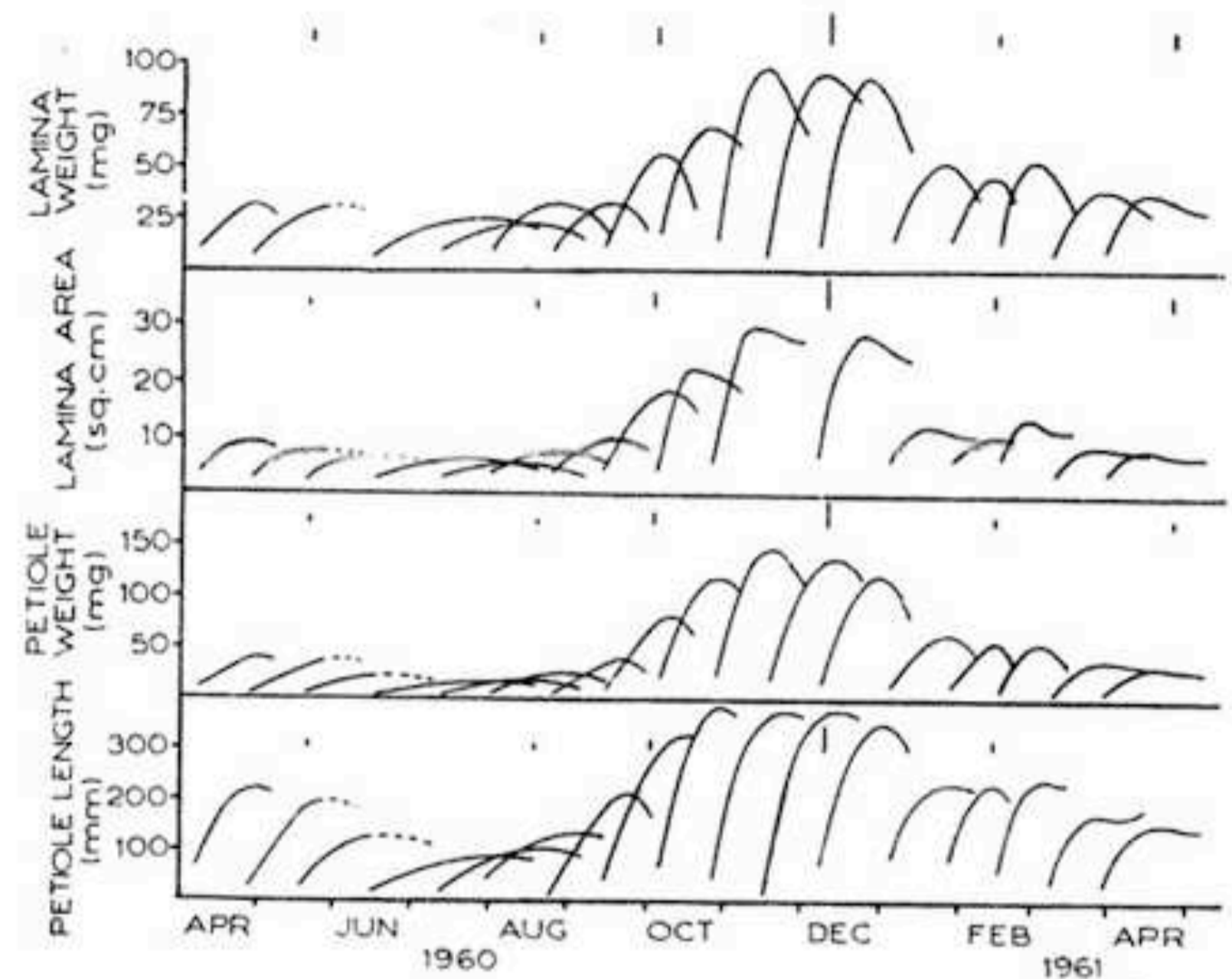


FIGURE 2. Fitted polynomial showing the relationship between leaf age and leaf dimensions for the successive groups of leaves throughout the year. Average standard errors of estimates are shown by vertical bars (two S.E.'s in length).

and areas and petiole weights and lengths of individual leaves, whose life histories were followed at approximate 3 week intervals throughout the year, are shown. The estimates were obtained by marking separate groups of terminal bud leaves with petioles less than 30 mm. in length, across the width of each plot of the stands with the least disturbance possible. At intervals of 2 or 3 days from the marking date until leaf death occurred, 6-10 of the marked leaves were harvested and lamina area and dry weight and petiole length and dry weight determined. The marking and harvesting procedure was repeated at 3 or 4 week intervals throughout the year.

As can be seen, the smallest leaves at maturity were those developing during the winter period, although the interval from marking to death was approximately twice as long as that found for the largest leaves. These latter developed during the late spring and were four to five times as large in all dimensions except that of petiole weight in which an approximate nine-fold difference between the smallest and largest was found.

A striking feature of the four series of curves is the large increase shown in the maximum dimensions attained by leaves marked in the

* The ratio of leaf area to ground area occupied.

early spring compared with those marked eight weeks earlier in mid-winter. Equally striking are the rapid decreases recorded during a four week period in December because of the drier conditions that prevailed.

The marked seasonal differences in the height reached by the uppermost leaves in the canopy (stage II leaves) were paralleled by similar fluctuations in the height from ground level at which particular intensities of light were recorded (see Figure 3). In July, the 3,000 ft. candle level was only slightly below

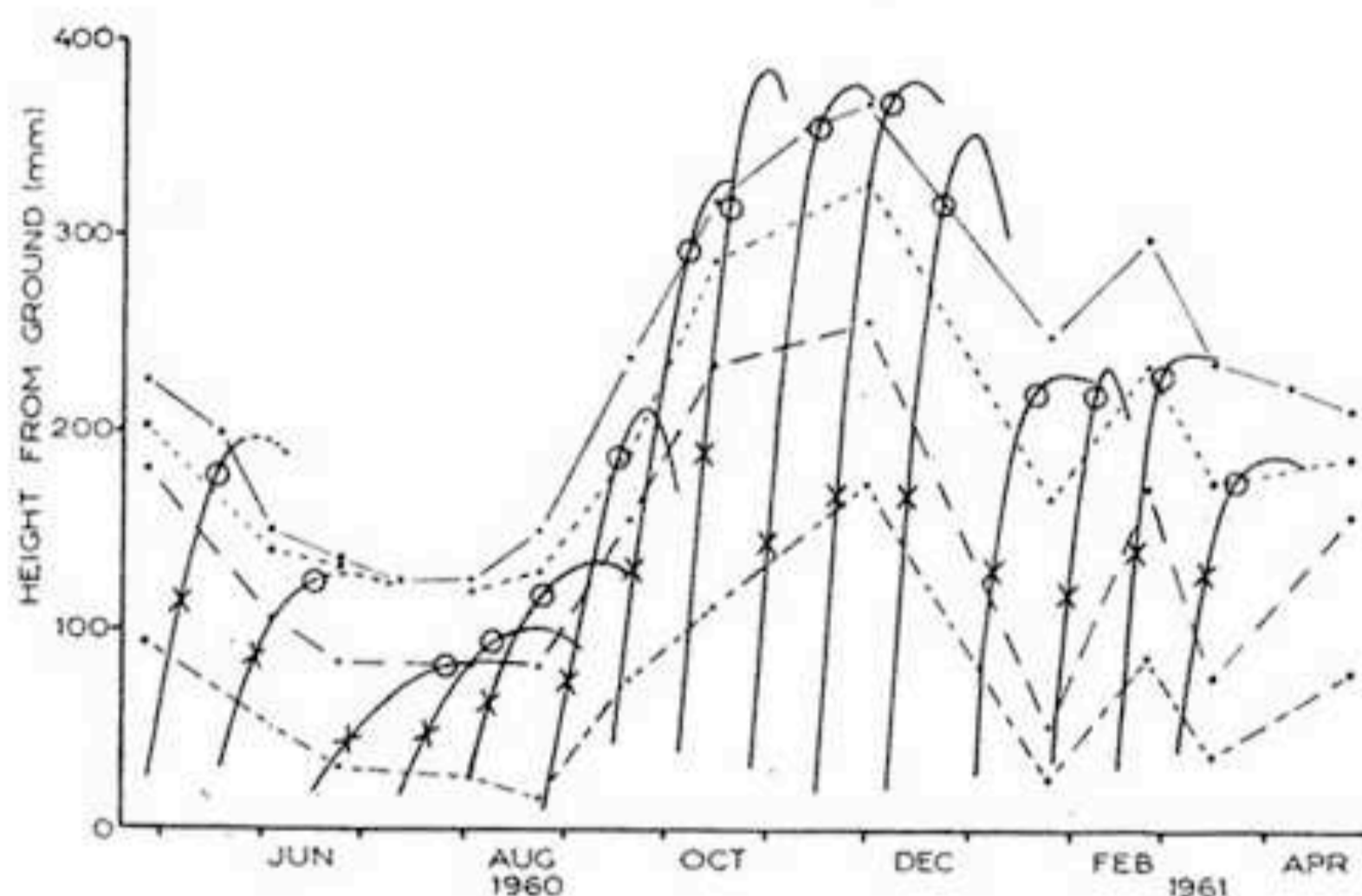


FIGURE 3. *Petiole development of successive groups of leaves in relation to seasonal changes recorded in the light environment (X denotes the height at which unfolding of laminae occurred and O denotes the height at which laminae expansion ceased).*

· — · — · upper leaves;
 · · · · · 3,000 ft. candle level
 · — — — · 500 ft. candle level;
 · · · · · 100 ft. candle level.

the level of the uppermost leaves, whereas the 100 ft. candle level was close to the ground. In the late spring, the 3,000 ft. candle level was recorded approximately 50 mm. below the level of the uppermost leaves, but at this time when the canopy was much taller and more dense, the 100 ft. candle level was midway between the ground and the height of the uppermost leaves. The intensity of light close to the ground was very low.

These results together with some not presented on rate of petiole elongation and lamina expansion suggest that the overall effect of the many physiological processes involved in leaf development of undisturbed white clover stands resulted in the maintenance of a state of dynamic equilibrium between the environment

and leaf growth, such that a high proportion of light was continually intercepted by green leaf. The maintenance of this equilibrium was also associated with a continued pattern of leaf death and renewal.

The results presented so far demonstrate the magnitude of the effects of changes in environmental factors on the various growth processes involved in the development of leaf canopies of undisturbed stands of *Trifolium repens*. They show that all were effective in controlling growth, with temperature and moisture setting the extreme limits within which changes in the intensity, duration and quality of light were effective.

Defoliation of stands such as those described above, results in marked physiological changes in leaf growth. This is illustrated by the results shown in Figure 4.

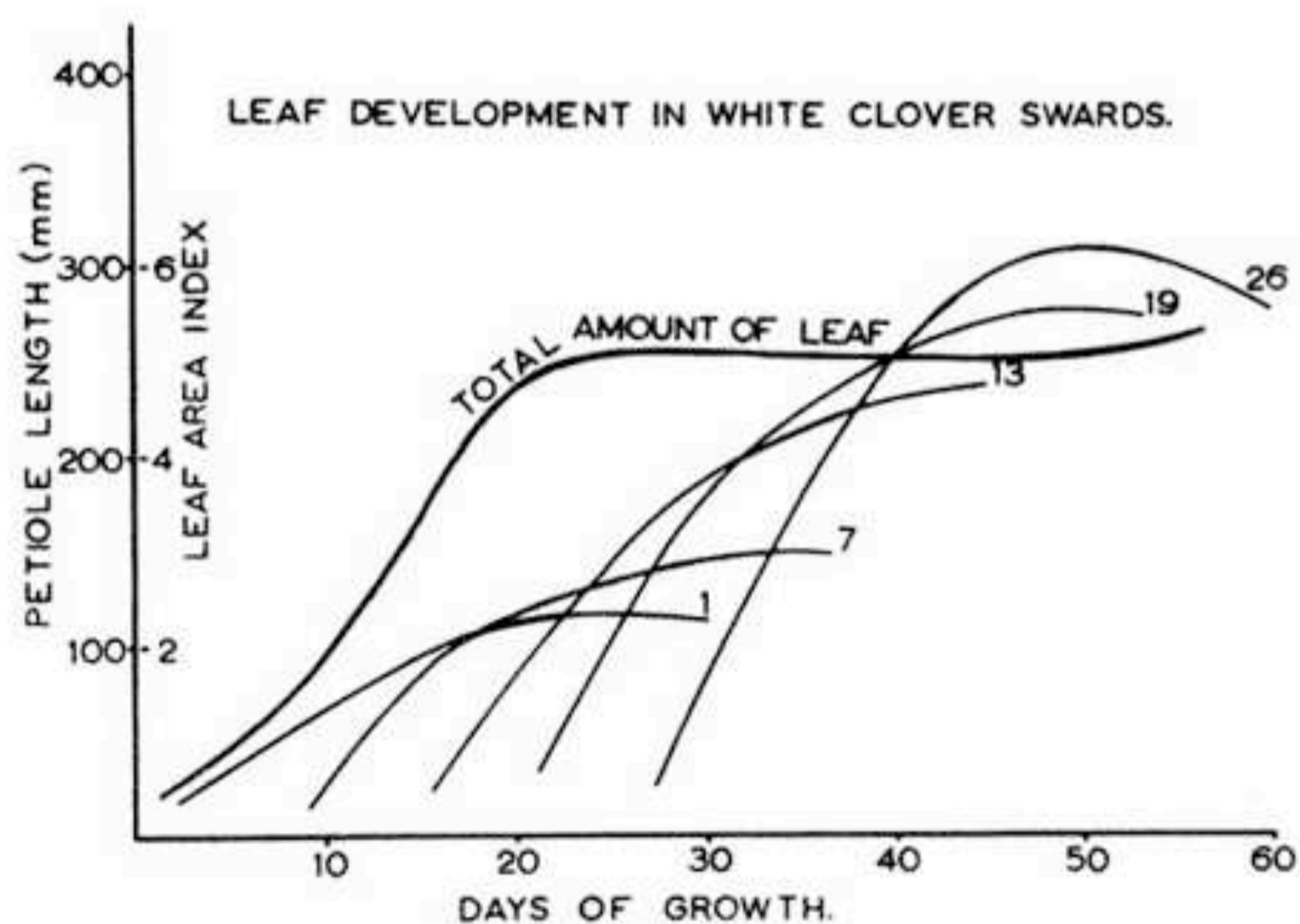


FIGURE 4. *Leaf growth in white clover stands following defoliation, showing petiole development of leaves marked at successive intervals from defoliation and progressive measurements of the total amount of leaf present expressed as Leaf Area Index.*

In this stand, defoliation was to 1 in. from ground level. As this would not result in the removal of terminal growing points the effects shown are probably a reflection of light interactions on leaf growth. The first formed leaves of the terminal growing points were relatively small in all dimensions including petiole length. The next crop of leaves reached slightly larger dimensions and over-topped the first formed, this procedure being repeated until the leaf canopy readjusted to a state of equilibrium with the light environment. The

environmental factors involved in this pattern of development would be similar to those involved in leaf development of the undisturbed stands previously discussed. During the relatively short period of readjustment, marked increases in dry matter accumulation occur. However, once the state of equilibrium is again reached, further dry matter gains are negligible.

From results obtained at Palmerston North (Hunt and Brougham 1966) a pattern of leaf and canopy development similar to that outlined above occurs during the vegetative growth of undisturbed stands of *Lolium multiflorum* Lam. However, because of differences between white clover and Italian ryegrass in the pattern of reproductive growth, a much more complex picture emerges for the ryegrasses during this phase. These differences arise because flowering heads of ryegrass are produced by the terminal growing points; continued production of leaves depends on the activity of lateral buds. In white clover, flowers are produced laterally whereas new leaves are produced continually by the apex. The results presented in Table 1 together with those already presented illustrate the marked differences between the two species where it is shown that the amount of new leaf produced by Italian ryegrass falls off rapidly after the onset of flowering. However, there is a progressive increase from mid-winter to the end of the experiment in the amounts of mature leaf present per unit area of stand. This could be a reflection of an increase in the depth of penetration of light into the leaf canopy associated with seasonal increases in daylight intensity or of the effect

of particular environmental factors on the size of mature leaves. Although these data are not presented size of these leaves increased until October. In addition the position of leaves in the canopy of ryegrass stands after the onset of flowering is such that they are not over-topped strongly by those formed later. Because of this, senescence would not be so markedly induced by shading as it is in white clover stands, or in ryegrass during the vegetative period. The life expectancy of ryegrass leaves is also normally much longer than that of white clover.

Because of differences in morphological development and in the structure of leaves and leaf canopies throughout the year, the two species react differently to grazing pressures. The effects are the result of three different actions of the grazing animal: In foraging, the animal first selects then bites, it walks considerable distances each day exerting relatively large pressures on rather delicately constructed leaf surfaces, and it returns, by dung and urine, concentrated applications of plant nutrients. Each of these three actions of the grazing animal have pronounced differential effects on the components of *Lolium* and white clover associations, the effects being more pronounced at some times of the year than at others. Each will be discussed separately although it should be realised that under field conditions there is often an interplay of all factors.

Selection and Biting

Under New Zealand conditions, observations indicate that at most times of the year, the

TABLE 1. Seasonal trends in composition and size of the herbage canopy (g./m.²) of an undisturbed stand of *Lolium multiflorum*.

(1 g./m.²=9 lb./acre)

Date of sampling	Young leaf	Mature leaf	Sheath	Stem	Ear	All living material
24 May	63 ± 5	64 ± 7	45 ± 5	—	—	171 ± 10
7 June	74 ± 7	64 ± 8	45 ± 5	—	—	174 ± 12
21 June	66 ± 6	65 ± 6	45 ± 5	—	—	175 ± 10
5 July	69 ± 6	68 ± 7	51 ± 5	—	—	189 ± 11
19 July	68 ± 6	79 ± 5	58 ± 5	—	—	205 ± 14
2 August	63 ± 5	80 ± 4	70 ± 6	—	—	213 ± 13
16 August	55 ± 5	88 ± 5	56 ± 6	45 ± 5	—	245 ± 13
30 August	71 ± 5	75 ± 7	59 ± 6	88 ± 7	—	294 ± 14
13 September	76 ± 6	68 ± 7	59 ± 6	115 ± 12	—	317 ± 17
27 September	85 ± 4	65 ± 5	59 ± 6	287 ± 19	—	496 ± 19
11 October	66 ± 2	89 ± 7	60 ± 6	407 ± 26	2 ± 1	632 ± 31
25 October	40 ± 1	121 ± 8	93 ± 8	525 ± 27	10 ± 2	788 ± 38
8 November	37 ± 1	138 ± 8	130 ± 8	594 ± 31	19 ± 2	899 ± 43

TABLE 2. Leaf numbers per unit area and maximum dimensions of main and axillary leaves in undisturbed and continuously defoliated stands of white clover in the autumn.

Dimensions	Axillary leaves	Main leaves	Axillary leaves	Main leaves
No. of leaves sq. ft.	275	405	710	550
<i>Petioles</i>				
Length (mm.)	90 ± 28	190 ± 33	40 ± 10	75 ± 13
Weight (mgm.)	5.2 ± 0.9	33.0 ± 1.1	1.3 ± 1.1	5.5 ± 1.1
<i>Laminae</i>				
Area (sq. cm.)	1.6 ± 0.16	7.2 ± 0.16	0.7 ± 0.16	2.6 ± 0.16
Weight (mgm.)	3.3 ± 1.36	26.0 ± 1.36	1.7 ± 1.36	11.0 ± 1.36

grazing animal shows some preference for the clover component of mixed associations. Under intensive grazing systems, this usually results in overgrazing of the clover and is manifested by the removal of varying proportions of the terminal growing points of clover stolons. Regrowth is then characterised by increased development of axillary meristematic zones followed by an increased number of leaves per unit area of sward. Most of the developing leaves are much smaller in all dimensions, particularly in petiole length, than those occurring in swards where overgrazing does not occur. The results presented in Table 2 illustrate this for pure stands of white clover subjected to two different grazing systems.

In mixed pastures the smaller leaves of clover are soon overtopped by the more vigorous ryegrass component when spelling occurs and this is very pronounced during the colder months of the year. Used intelligently however, hard grazings of pasture communities at particular times of the year are of value in changing dominance to species that tolerate the subsequent climate (Brougham 1960).

During the late spring, summer and early autumn, when reproductive activity in ryegrasses occurs, overgrazing may also markedly alter the botanical composition of pastures to one of clover dominance. At this time, active stem elongation of tillers occurs. Depending on the variety of ryegrass, the extent of activity can be high (see Figure 5). The percentages of tillers of two varieties of ryegrass with growing points elevated above two different heights from ground level are shown for two systems of management over the reproductive period.

TABLE 3. Total and species yields of a ryegrass, cocksfoot, red and white clover pasture under two systems of summer management.

Both pastures received the same treatment until the beginning of summer.

Treatment	Total yield	Ryegrass	Cocksfoot	Red clover	White clover	Other species
Frequent lax grazings	1990	1390	265	65	185	85
Frequent hard grazings	3960	1480	1000	745	545	190

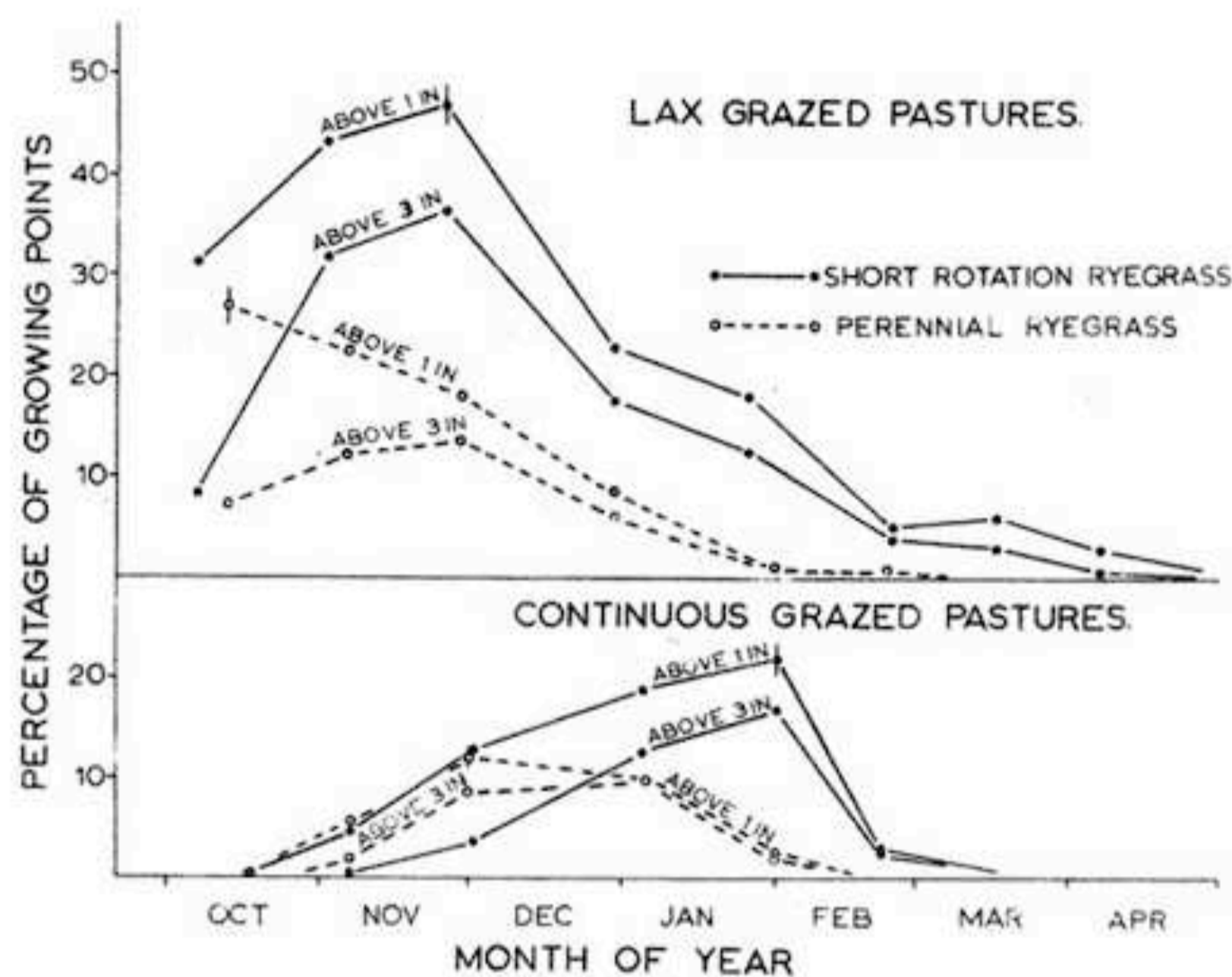


FIGURE 5. Percentage of tillers with growing points elevated above two levels from the ground in pure stands of perennial and short-rotation ryegrass under lax and continuous grazing.

Removal of the growing point of a tiller results in death, and in pastures where a high proportion of growing points are elevated, overgrazing will strongly reduce tiller numbers and productivity of ryegrass. The results presented in Table 3 illustrate this for a mixed ryegrass, cocksfoot (*Dactylis glomerata* L.) and red and white clover pasture. Until the beginning of summer both pastures received the same treatment and were then subjected to two different grazing systems for a period of three months. The data shown are the yields and botanical composition obtained over the three month period (see Brougham 1960).

The significance of removal of growing points in determining the persistency of species and in altering botanical composition has also been demonstrated by Branson (1953) and more recently Booyesen *et al.* (1963) have discussed it in a review.

Treading

Depending on the intensity of stocking, hooves of grazing animals may have marked and specific effects on the growth of component species in pasture associations, resulting in large changes in the balance between grass and legume. These effects are direct as is evident from work carried out in New Zealand by Edmond (1958a, 1958b, 1962, 1963, 1964), and are attributable to differential damage of the photosynthetic surfaces of different species, to damage of stem and leaf apices as reflected by decreases in tiller and leaf number (Lancashire 1961), and to changes in the root environment through soil compaction. This last factor is aggravated by pugging and poor aeration in wet soil (Edmond 1963).

The significance of treading in altering botanical composition and yields of component species is shown in Table 4. These unpublished data of Edmond indicate a small but significant change in botanical composition resulting from one treading at a rate of 18 sheep equivalent per acre applied 60 days before the figures shown were obtained. Before the treading treatment was applied both trodden and untrodden pastures were defoliated to a height of 1 in. and then spelled for measurement.

The cumulative effects of numbers of grazings applied to pasture associations throughout the year may result in large changes in botanical composition. However, because of seasonal changes in the response of different species to treading damage (Edmond 1964) the effects are sometimes not additive so that the balance between grass and legume in these associations may vary throughout the year from grass to clover dominance.

Excretion

During grazing, animals return to confined areas of the pasture highly concentrated dress-

ings of plant nutrients. Because of differential responses of pasture species to the nutrients returned in this manner, and to a lesser extent to direct damaging effects to photosynthetic surfaces by the highly concentrated nutrient solutions (Doak 1954), changes in the growth and composition of species in pastures can be dramatic. These effects have been intensively studied and discussed by several groups of workers (Sears 1953; Walker 1956) and for this reason only one example will be outlined here.

In New Zealand where animals are outdoors throughout the year, it has been a common dairy-farm practice, particularly in the colder months, to resort to systems of farm management in which animals are kept in close proximity to the dairy shed during the evenings and at the back of the farm during the day. In terms of convenience to the farmer, this system has much to commend it. Unfortunately, however, the dairy animal eats about three-fifths of its daily feed supply during the day and only two-fifths during the evening. The excretion behaviour is such that only two-fifths of the total daily amount of nutrients is excreted during the day and the remainder during the evening (Goodall 1957). This results in a marked transfer of fertility from day paddocks to night paddocks, and of importance to this discussion night paddocks become strongly grass dominant through high nitrogen return and day paddocks much more clover dominant because of a lowering of soil nitrogen.

The cumulative effect of the above three actions of the grazing animal together with modifications in the environment of plant associations brought about by different grazing management systems is demonstrated by the results presented in Tables 4 and 5. Table 4 shows the marked effect these cumulative actions may have on altering the genotypic structure of plant populations. In this experiment areas of an established short rotation ryegrass and red and white clover pasture were subjected to four different management systems (see Brougham 1959) for a period of

TABLE 4. Botanical composition of two areas of a ten-year-old pasture, 60 days after one area was trodden at 18 sheep equivalent per acre in the winter.

Treatment	Perennial ryegrass	Poa spp.	White clover	Other species
Trodden at 18 sheep equivalent when soil was moist	75.1 ± 1.8	7.7 ± 0.9	14.0 ± 1.8	3.2
Not trodden	81.8 ± 1.7	6.2 ± 0.9	10.3 ± 1.6	1.7

Prior to treading there were no significant differences in the botanical composition of the two areas.

two years. This grass species is a hybrid of *L. perenne* and *L. multiflorum* and genetically is rather widely based (Corkill 1956). After two years of differential management significant changes in the genotypic structure of the ryegrass populations remaining in the different pastures occurred. Table 5 shows some of these changes for two of the treatments.

TABLE 5. Percentages of fluorescent tillers remaining in the pastures after two years of different management.

Treatment	Percentage fluorescence and standard errors
Frequent hard grazings	62.5 ± 4.4
Long-spelled lax grazings	85.8 ± 3.1
Sown line of seed	78.8 ± 2.0

The above tests were carried out on 120 randomly selected plants from two pastures and from germinated plants of the sown line of seed.

Based on measurements of fluorescence these results indicate that frequent and intensive grazings caused a greater death of fluorescent plants (Italian types) than of non-fluorescent types (perennial types). Under systems of management where grazings were less intensive and less frequent a greater death of perennial types has occurred (see Brougham *et al.* 1960).

These changes together with alterations in the balance between grass and legume induced by the different frequencies and intensities of grazing resulted in marked changes in the productivity of the two pastures (see Table 6).

Yields shown are those obtained in the second year of the experiment.

In the above discussion many other factors that are of importance in determining the balance between grass and legume have not

been mentioned. The availability of water in relation to differences in root penetration of the different species may be a major determinant of botanical balance in some environments, as can be the abilities of different species to take up water and soil nutrients under different intensities of defoliation (Jantii and Kramer 1956). Marked species differences in susceptibility to damage by insects, pests and fungal activity are also important. For example, in New Zealand the more annual types of ryegrass are much more susceptible to attack from grass grub (*Costelytra zealandica*) and Argentine stem weevil (*Hyperodes bonariensis*) than are the perennial types and white clover. Under certain circumstances strongly clover-dominant associations may result from attacks by these insects. Another factor of importance in determining the ability of species to persist in associations is that of availability of carbon dioxide within the profiles of plant associations. Recent unpublished work carried out by E. R. Lemon of Cornell University, U.S.A. suggests that the leaf and canopy structure of some plants in associations may markedly influence the availability of carbon dioxide to other species in the association, thus influencing rate of growth and botanical composition.

Thus there are many factors that can act against high productivity and the growth of the components in *Lolium*-clover pastures. A large number of these factors are associated with the behaviour of the grazing animal and its effect through biting, treading and excreting. However, through an appreciation of the way in which these factors operate both separately and in combination desirable balances between grass and legume can be maintained resulting in high productivity.

TABLE 6. Total and species yields (lb.D.M./acre) obtained from the pastures under two systems of management during the second year of the experiment (December 1956-end November 1957).

Special yields Treatment	No. of grazings	Total yield	Ryegrass	Red clover	White clover	Other grasses	Other species
Frequent hard grazings	12	11,230	5,570	70	4,620	620	350
Long-spelled lax grazings	11	14,270	11,750	560	1,860	30	—
Sig. diff. at 5% level		1,475	2,225	200	1,175	—	70

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SOME PEDOLOGICAL FACTORS OF IMPORTANCE TO THE PASTURE ECOSYSTEM IN THE SOUTH ISLAND

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It should not be necessary to emphasise to ecologists the importance of the soil in the pasture ecosystem. Yet it is true that ecologists are not always aware of the limitations of soils with respect to the ecosystem. This is in part because soils are not as easily observed as plants or animals, and in part because of the lack of a course in pedology in the training of ecologists.

If we were able to construct or breed pasture soils, what would be the specifications we would ask for? They are many and would include: Mineral assemblages supplying readily available plant nutrients, non-fixing clays, medium texture, adequate root space, free drainage, fine but stable granular structure, medium density, high structural stability, high bearing capacity under wet conditions, and high moisture storage. Soils of the natural tall grasslands of Asia and North America, the prairie and chernozems, are the closest naturally occurring soils to this ideal, but very few soils of the

South Island even approach it. Our soils with good physical properties usually have nutrient problems and vice versa. Most of our soils depart in more than one respect from the ideal specification; for example, most have only weakly (some moderately) developed structure, and are easily compacted when dry and puddled when wet. Several contributions to this symposium cover the problems of soil chemistry, and this paper will therefore be restricted to some of the more important physical properties of soils as they affect the pasture ecosystem.

SOIL FACTORS LIMITING MOISTURE STORAGE AND AVAILABILITY

Many soils have low available water storage. The first class of these are the shallow and stony soils (associated with yellow-grey earths and brown-grey earths) widespread on the plains of Canterbury and Otago. Many hold less than 2 inches of available water in the