THE LIGHT FACTOR IN GRASS AND CLOVER SWARDS.

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1.0.0. GENERAL INTRODUCTION.

Competition begins with a shortage of an essential factor and leads to a relationship of dominance and suppression. In plant populations, such competition is manifest by a reduction of individual plant yield and changes in botanical composition, and with high plant populations by the attainment of ceiling yields and a decline in plant numbers. Although there have been many investigations in which the water and nutrient supply was regulated, these studies have often failed to distinguish between various forms of competition or to evaluate the degree of competition. Because of its ubiquitous nature, light has not often been considered to be in short supply and this factor was not sufficiently well understood to manage it effectively in agriculture. In this thesis, light was the principal factor examined in studying the competition between pasture plants.

Measurements of plant stature, of leaf area distribution and of light intensity profiles are pertinent to any analysis of competition for light and there are comparatively few such data for pasture. An association of species of contrasting growth habits provides a suitable starting point for studies of the nature of the light distribution in swards and of competition for light between individuals. However, competition for other factors may proceed simultaneously with competition for light, and any treatment favouring the stature and leaf growth of one member of an association of herbage plants is likely to give it an advantage with respect to light interception over other members in the same community, although this difference in stature or leaf area may be small initially. In order to understand the role of light in mixed herbage associations it is necessary to appreciate, in the broadest possible terms all the factors which govern the balance between species, and a discussion along these lines introduces the literature review. Light relationships are influenced by the seed mixture, by environmental factors such as temperature and moisture, and by the effects of defoliation and nitrogen. Although there are numerous studies involving these factors, there are few light records amongst them. A catalogue of the available light measurements in pastures is therefore presented, and this is followed by a discussion of the role of light in pasture growth. Finally the literature review covers the techniques of studying competition for light, and of measuring light intensities in pastures.

An account of the programme of investigation expressing the philosophy of the work done follows the literature review. The experimental programme comprised

1) A study of the distribution of vegetation, leaf area profile and light gradient in a range of grass and clover swards.
2) A study of the recovery of clover swards from varying periods of shading by grass.
3) An examination of the growth of individual plants and leaves in swards of subterranean clover of different initial densities.

The methods, results and discussion deal with each experiment in turn, and a general discussion concludes the thesis.

2.0.0. LITERATURE REVIEW.

2.1.0 Factors influencing the grass clover balance.

There are countless examples of changes in botanical composition of pasture and these are usually attributed to competition of one kind or another. In this section of the literature review, some of the factors which influence the grass clover balance are examined, giving consideration to the possible role of light in the competition between species.

The succession in sown pasture varies a great deal and is dictated by the environment, e.g. moisture, temperature or nutrient supply, and management (Martin Jones 1933, Headley 1946, Blaser et al 1950, Willoughby 1954, Walker 1960). Small changes in the environment can bring about marked changes in the balance between grass and clover and the reasons for this will become apparent as the analysis develops. The factors examined are:

(a) Seed rates of grass and clover: this affords the initial control of botanical composition.

(b) The influence of season: this deals with some dominant environmental factors over which there is virtually no control.

(c) The influence of defoliation: a potent factor in modifying botanical composition.

(d) The influence of applied nitrogen: this provides a means of modifying the botanical composition and increasing overall production per unit of land.

(e) The influence of nutrients other than nitrogen: the necessity of including certain elements to ensure the presence of clover.

(f) Grazing simultaneously checks and promotes pasture growth, and so generates changes in botanical composition. Because many processes operate simultaneously under grazing this section will be a synthesis of the points previously raised.

(a) The influence of seed rates on the botanical composition of mixed pasture.

The initial control of botanical composition in sown pasture may be achieved by adjusting the seed mixture, but those species which emerge and develop rapidly, draw on the light, water, and mineral nutrient supply, to an extent which depresses the development of the associate species (Donald 1946). Species are usually rated for aggression on the basis of vigour of emergence and seedling growth, and both may be modified by management i.e. nitrogen applications, time of sowing and depth of sowing (Blaser et al 1952, O'Brien 1960). Because of their faster growth rate, grasses are generally more aggressive than legumes (Caputa 1948, Blaser et al 1956a, Brougham 1959).

Where the nutrient supply is adequate the rapid early development of grass roots, followed by increasing tiller numbersat about four weeks from sowing, generally gives grass a strong competitive advantage in mixed sowing with clover. High early yields of grass lead to a reduction of clover yield. Brougham (1954a) examined sowing mixtures 0, 10, 15, 20, 30, 40 and 60 pounds per acre of short rotation ryegrass with 4 pounds of red and 3 pounds of white clover. Over a period of twelve months there were no differences in total yield between treatments, but the clover content declined with increasing seed rates of ryegrass. The number of clover plants surviving six months after sowing decreased with increasing seed rates of ryegrass (Fig. 1) and this was explained on the basis of competition for light.

The factors which may lead to clover suppression when sowing down pasture are:

(a) a heavy sowing of grass to establish a larger grass population;
(b) faster emergence of grass seedlings;
(c) faster seedling growth by grass;
(d) heavy tillering by grass.

(b) Some environmental factors which may modify the grass clover balance.

Good management is based on a sound appreciation of the seasonal production of pasture in a particular environment. Blackman (1933) stressed the relevance of the seasonal productivity curves of individual species in a sward, to interpret changes in botanical composition. Total annual production may not vary greatly, provided no

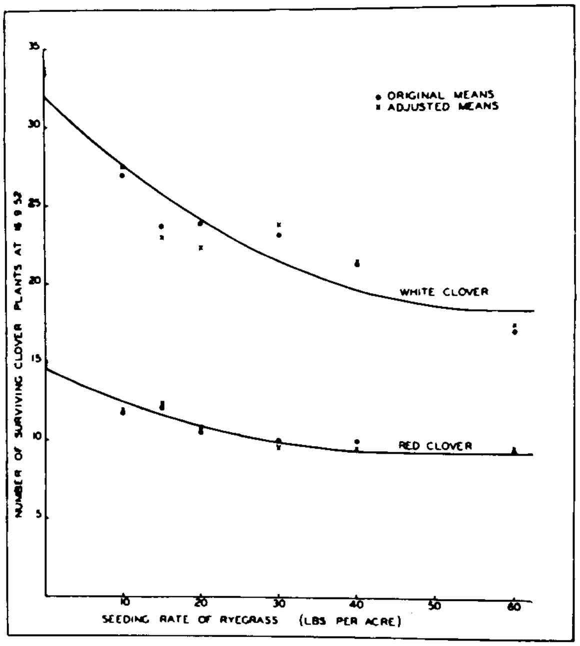

Fig. 1. - The number of clover plants surviving in mixture with varying seeding rates of ryegrass (after Brougham 1954a).

extremes in season are encountered (Brougham 1960), but botanical composition can change markedly from year to year.

Soil Moisture: The soil moisture status may alter the balance between species (Ahlgren and Fuelleman 1950, Peterson and Hagan 1953). A good moisture supply may counteract the adverse effects of defoliation or high nitrogen dressings on the clover content of mixed pasture (Robinson, Sprague and Lueck 1952, Low and Armitage 1959). Where the severity of competition for moisture can be reduced by tillage practices, clover may be retained in the pasture (Calder 1952). In Southern Australia a large proportion of sown pastures consist of the annual self-regenerating subterranean clover and annual grasses and these do not germinate until the opening of the growing season in autumn. If rain falls early while temperatures are still high, the pasture tends to be clover dominant; if late, temperatures are low, and the pasture will be grass-dominant (Tiver 1954).

Temperature in the presence of applied nutrients may be quite important in promoting early growth of grass or clover and so incline the balance either way. In Southern New South Wales, the application of nitrogen and phosphorus to mixed pasture at the beginning of the season increased clover yields more, than applications three months later. Willoughby (1954) attributed this to the more effective competition by clover for these nutrients before temperatures fell. At Jealott's Hill Blackman (1936) found that nitrogen applied in very early spring while temperatures were rising, increased yield at the beginning of the season (Table 1), and brought forward the first grazing by a number of days.

Table 1

Relative Growth Rates of pastures with varying temperatures (after Blackman 1936)

Mean soil temperature (9 a.m. @ 4")	nitrogen applied	nil nitrogen
42°	no growth	no growth
42-44°	0.024	0.009
44-47°	0.026	0.021
47°	0.039	0.039

The effect of applied nitrogen was greatest in the soil temperature range from 42-47°F, because of the differential growth of grass and clover at these temperatures. These examples from Willoughby's and Blackman's work illustrate the same phenomenan i.e. the uptake of nitrogen by grass at low temperature, during the winter in New South Wales and during very early spring in the United Kingdom.

Mitchell's studies (Mitchell 1953, 1954, 1955, 1956, Mitchell and Coles 1955), isolated the responses of the important species of New Zealand sown pasture plants to the dominant environmental factors, particularly light and temperature. In grazing studies with a ryegrass, white and red clover pasture Brougham (1959b) obtained clover dominance in the late summer and autumn, and grass dominance during early summer, spring and winter: the changes in botanical composition are explained in terms of the differential temperature and light tolerance between species demonstrated by Mitchell.

Photoperiod: By influencing stature or modifying the distribution of plant parts of individual species, photoperiod may alter the competitive capacity of clover and grass (Robinson and Sprague 1947, Keller and Peterson 1950).

Light: In reviewing the influence of varying light intensity on the growth of herbage plants, Black (1957a) emphasised that there were no measurements to show how one species altered the light to another in a pasture association. Since the publication of this review there were two further contributions on the influence of light intensity on the growth of herbage plants. Gist and Mott (1957) subjected Medicago sativa, Trifolium pratense and Lotus corniculatus to three light intensities and four levels of watering, at four temperatures and the

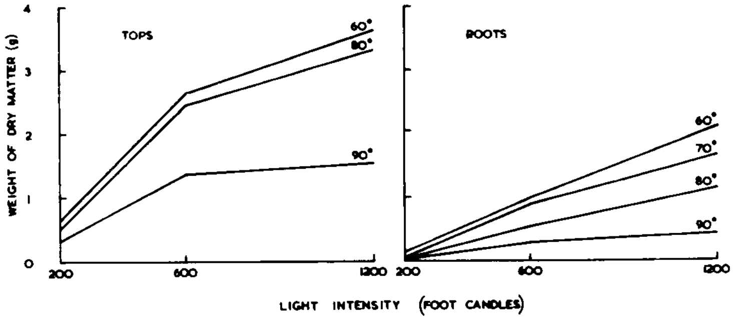

Fig. 2. - The interaction of light intensity and temperature on the growth of temperate legumes (derived from Gist and Mott 1957).

experiment was harvested at 45 days.

The results for the three species were pooled as they showed similar trends and are presented in Fig. 2. Decreasing light intensity reduced growth of both roots and tops. The interaction between light and temperature was more marked with top growth than with root growth. When moisture was varied, only a very small response to increasing soil moisture was noted at low light intensities: that is, the response to light was only fully realised when soil moisture was adequate. The results showed:-

(a) that the comparatively large top growth of red clover at low light intensities was not accompanied by root development.

(b) that the drought tolerance of lucerne developed only after the seedlings had been exposed to high light and had formed an extensive root system.

Although the highest light intensities in this experiment did not approach values generally encountered in the open, they were of an order which might be expected where shading from a taller growing grass occurs.

In a clover and ryegrass pasture, Brougham (1959a) found that ceiling yields, and the time required to reach them, were positively correlated with light and temperature. In winter the growth rate was dominated by ryegrass and in late summer and early autumn by clover. Increases in the growth rate of ryegrass were associated with decreases in the growth rate of clover and Brougham argued that the changes in botanical composition depended on species temperature tolerance and inter-species competition for light.

(c) The influence of defoliation on the botanical composition of mixed swards.

Defoliation is known to exert a strong influence in modifying the botanical composition of mixed pasture. Quite apart from any other effects, the act of removing vegetation changes the light microclimate in a sward. Although botanical changes can be attributed to causes other than light intensity, it is likely that the balance between species depends in considerable measure on the light microclimate. It is difficult to generalise on the effects of defoliation without specifying the nature of the defoliation because a pasture may be defoliated in many ways and to varying degrees. Defoliation by mowing removes the vegetation abruptly and completely but with grazing the process takes place more gradually and involves the return of nutrients and growth-promoting substances to the pasture. In examining the effects of defoliation on the botanical composition of pasture we are concerned with

(a) the proportion of each botanical component in the pasture at defoliation,

and (b) the regrowth of each botanical component between defoliation.

The growth of a species after defoliation is influenced in part by the energy stored in the residual tissues, by the amount of assimilating leaf surface that remains or can be developed within a short time after defoliation, by the number of points available to resume growth, and by the relative growth rates of the species.

Let us now examine the effects of treatments in which the frequency and intensity of defoliation are varied in a pasture consisting of two species, one erect, e.g. ryegrass and the other prostrate e.g. white clover. For the time being let the growth rates of the species be identical and constant throughout. The <u>frequency</u> of defoliation refers to the recurrent reduction in height of pasture, and is in inverse relation to the intervals between defoliations - i.e. the periods of regrowth. If defoliation is frequent, the taller species repeatedly loses its tissues and is unable to develop full stature because the period of regrowth is cut short; in this way the prostrate species contributes an increasing proportion of the residual tissues at each defoliation. If defoliation is infrequent, the periods of regrowth are prolonged and the taller species overshadows the prostrate species; competition for light gradually suppresses the prostrate species and the taller species forms an increasing proportion of the residual tissue at each successive defoliation. Thus by varying the frequency of defoliation, differences in residual tissues between species may develop, to bring about changes in the botanical composition of a simple mixture.

Intensity of defoliation refers to the height of pasture remaining at defoliation. Severe defoliation removes the bulk of the taller species and the prostrate species forms most of the remaining tissues. If defoliation is lax, shading of the prostrate species is intensified as the taller species regains stature. Lax and infrequent defoliations accentuate competition for light, and can be expected to have similar effects. With intense defoliation the light relationships between species change drastically and quickly, and for this reason intensity-of-defoliation-treatments are likely to show more striking effects on botanical composition than frequency-of-defoliation-treatments, in which differences in the light relationships between species develop more gradually.

Needless to say, growth rates vary considerably between species and respond differently to climatic influences or artificial treatments, and species and strains show great variations in growth habit - grasses are not always erect nor are clovers always prostrate. Nitrogen promotes the growth of grasses. Consequently the relationships between species in simple mixture discussed so far are further modified by differential growth rates, which are constantly changing. It is not surprising therefore to find changes in botanical composition attributed to dominant environmental or seasonal factors which have a strong influence on the growth rate of species.

Let us now examine the effects of intensity and frequency of defoliation on the botanical composition of a number of pastures and begin with those studies in which both were varied at the same time.

Martin Jones (1933) demonstrated changes in botanical composition on swards which were initially similar and consisted principally of ryegrass and white clover. The treatments, and the nature of the changes were:

(a) very close grazing throughout the growing season resulted in clover dominance;

(b) very light grazing in spring brought about grass dominance;

(c) intensive rotational grazing to 2 ins. in winter,

4 ins. in spring and autumn,
and 5 ins. in summer,
reduced the invasion by weeds, and maintained a desirable balance between grass and clover;

(d) overgrazing in winter and spring and light grazing in summer and autumn, which were normal farm practice, resulted in a reasonable balance between grass and clover but a heavy weed infestation.

Blackman (1933) explained fluctuations in the red clover content in a number of pastures on the basis of shading by the grass component of the pasture, and referred to differences in time (frequency) and severity (intensity) of grazing as critical factors in bringing about changes in botanical composition.

Beruldsen and Morgan (1936) in Victoria varied the frequency of cutting on a pasture consisting mainly of perennial ryegrass, cocksfoot, prairie grass, white clover and strawberry clover. Table 2 shows the percentage composition of the total dry matter and the change over from clover to grass dominance.

A rest period of about a month maintained clover in the sward, and increased grass production, especially from late autumn to early spring.

Table 2.

The Change in botanical composition
by varying the interval between cuts.
(Beruldson and Morgan 1936).

Treatment	Grasses	Legumes	Weeds
Cut weekly	40.2	59.3	0.5
" fortnightly	48.3	50.8	0.9
" 3-weekly	48.7	50.2	1.1
" 4-weekly	51.6	46.8	1.6
" 5-weekly	58.8	39.6	1.6
" 8-weekly	66.7	31.8	1.5
" for hay then " 3-weekly	81.7	16.4	1.9

Peterson and Hagan (1953) showed that the proportion of grasses increased with frequent cutting. The plots were cut back to 2 inches and the average heights on cutting were:

Table 3

Cutting treatments and grass content of a mixed pasture consisting of several legumes and grasses. (Peterson and Hagan 1953).

Interval between cuts	Average height when cut (inches)	Grass in mixture July cut (per cent.)	September cut (per cent.)
2	6-8	20	40
3	9-12	16	34
4	11-20	9	15
5	10-26	4	8

The table shows that frequent cutting prevented the pasture from achieving full stature between cuts. The shorter pastures tended to be white clover dominant and the taller ones lucerne dominant. Lucerne was a strong competitor in these mixtures by virtue of its rapid and erect growth after mowing. Clover was affected adversely (Wagner 1952b), and clover content was reduced by infrequent cutting, cutting high or applying nitrogen

(Sprague and Garber 1950). Conversely clover dominance developed with frequent and early cutting (Wagner 1952a).

Recent work by Brougham (1959b) showed that infrequent grazing favoured grass growth and reduced the white clover content of mixed pasture; hard grazing suppressed red clover, but not infrequent grazing. White clover dominance in autumn was followed by reduced ryegrass growth in winter. Weed invasion was greatest with hard grazing. Walker _et al_ (1954) suggested that in order to obtain the highest yields of dry matter, grasses should not be allowed to grow beyond a certain stage i.e. they should not be allowed to absorb all the incident light (Brougham 1956).

Intense defoliation generally favours the retention of clover in mixed pasture. This may vary with the species of grass in the mixture (Burger _et al_ 1958) and with the amount of nitrogen applied (Robinson and Sprague 1947, Robinson, Sprague and Lueck 1952, Reid 1959).

In recent work Brougham (1960) emphasised the harmful effects of overgrazing during periods of low pasture production on botanical composition and total yield. Hard grazing in summer reduced the amount of grass and increased the proportion of white clover impairing the subsequent production of the pasture. Hard autumn grazing reduced clover yields without adverse effect to botanical composition over the whole year and was recommended to change dominance from clover to grass, and to encourage tillering in grass.

Most of the experimental data examined are consistent with the suggestion that the principal effect of defoliation are due to changes in the light microclimate within the sward. Yet the published comments on the changes in the botanical composition are often no more than "Competition for light", "Competition for nutrients" or "Competition for water, light and nutrients", without evidence in support of these statements. It would seem that many observations recorded in this section could have been put on a sounder basis had they been interpreted in terms of light intensity readings and measures of L.A.I.

(d) The influence of applied nitrogen on the botanical composition of mixed pastures.

To appreciate fully the effects of nitrogen fertilizer this practice needs to be considered in relation to the function of clover in the pasture. Increasing nitrogen fertilizer:

(a) reduces the effectiveness of the clover-rhizobium symbiosis (Young 1958, Allos and Bartholomew 1959) and hence the contribution of clover nitrogen,

and (b) promotes the growth of grass preferentially, intensifying the competition for light between species (Blackman 1938, Blackman and Templeman, 1938).

Dealing with the nitrogen contribution by clover first. Estimates of the nitrogen contribution by clover range from 500-600 pounds of nitrogen per acre per annum (Sears, 1953, Walker <u>et al</u> 1954, 1956) under very favourable circumstances in New Zealand, to average values of 200 pounds of nitrogen per acre per annum in the British Isles (Holmes and MacLusky 1955, Herriott and Wells 1960) to 100 pounds per acre per annum or less in Australia, where low fertility and strong seasonal influences are not wholly favourable for the clover-rhizobium symbiosis. Utilization of symbiotic nitrogen depends on:

(a) the annual pattern of the contribution,
(b) the uptake by grass in different seasons,
(c) the retention in the soil of unused nitrogen (Allison 1955) and its availability at a later date.

Fertilizer nitrogen should be regarded only as a means of supplementing the supply of symbiotic nitrogen to grass (Young 1958) if the balance between grass and clover is to be maintained. The form in which nitrogen is applied is not important (Walker <u>et al</u> 1953). Walker, Orchiston and Adams (1954) established a relationship to determine the fate of nitrogen from various sources (including fertilizer nitrogen) in pastures and soil.

$$G_n = 0.67\ (C_n + F_n) + K$$

where

G_n	=	G_n	-	G_{n_o}
Yield of applied N in grass		Yield of N in grass with applied N where fertilizer rate is N_x		Yield of N in grass without applied N

and similarly for the other symbols, where C_n is the yield of nitrogen in clover and F_n is fertilizer nitrogen. The factor 0.67 varies slightly from trial to trial and K is a constant for any particular trial. These authors made a number of assumptions to derive the equations and these were:

(a) all the available soil nitrogen was taken up by the grass;

(b) all the nitrogen in the legume was fixed symbiotically;

(c) the accretion of nitrogen in grass in mixed swards, above the level of nitrogen in pure grass swards was due to nitrogen in the legume;

(d) the ratio of tops to roots was
3:1 in mature clover
and 2:1 in mature grass;

(e) the nitrogen equilibrium in soil outside roots, is a balance between contributions by free-living organisms and rain, and uptake of mineralized nitrogen in the herbage and losses by leaching;

(f) the rate of net mineralization is proportional to the amount of organic matter present.

Several key assumptions can only apply in a uniform and continuously favourable environment, and while they may be reasonable approximations for New Zealand conditions they are not universally acceptable. Therefore the equation given is of limited value only.

In Table 4, a comparison is made of grass swards with and without nitrogen, and with clover (Holmes and MacLusky 1955); moderate nitrogen dressings on the mixed pasture did not eliminate clover from the sward and slightly improved total yields. The data in the Table 4(b) suggest, and other evidence has confirmed, that light dressings of nitrogen on mixed pasture - up to about 60 pounds per acre do not seem to have any marked effect on production or botanical composition (Wheeler 1958). Unless the extra herbage can be converted to animal products it is uneconomic to apply nitrogen. Woodman and Underwood (1932) found that a single dressing at the beginning of the season gave the most effective recovery of nitrogen. But the concensus

Table 4

The influence of clover on the yield of pasture and the effect of nitrogen on the yield of a mixed sward.

(derived from Holmes and MacLusky 1955).

(a) Comparison of combined nitrogen and clover.

	Pure grass swards 1949-53			Clover and grass 1949-53
Pounds Nitrogen per acre annually	Nil	140-208 in 4-6 dressings	350-416 in 5-6 dressings	Nil
Average Yield (Pounds per acre)	2180	5940	8300	4630

(b) Nitrogen on a mixed grass and clover sward

1949-51 : no nitrogen
1951-53 : nitrogen treatments as shown

Pounds Nitrogen per acre annually	Nil	35 in spring 35 in late summer	140-208 in 4-6 dressings
Average Yield (Pounds Per acre)	5780	6340	7240
Effect on sward	High clover content	Clover depressed by some grasses	Clover further depressed by those grasses
		Clover content maintained in presence of timothy and fescue	

of opinion is that split dressings are more desirable to maintain the balance between grasses and clover (Walker <u>et al</u> 1953, Hughes and Evans 1951, Nelson and Robins 1956). The intensive system of grassland management (Greenhill 1930) involves frequent nitrogen dressings to mixed pasture and grazing the additional herbage by rotating the stock. 85 per cent. of the nitrogen ingested by the grazing animal is returned to the pasture (McDonald 1960) and the return of nutrients in dung and urine influences botanical composition (Sears 1949, Sears and Thurston 1953). Sears (1949) estimated that mature sheep on productive pastures returned in urine the equivalent of 2000 pounds per acre of sulphate of ammonia and in dung 700 pounds. Wheeler (1958) found that the effect of animal excreta on botanical composition was related to its content of readily available nitrogen (Table 6), but that it had no appreciable effect on total yield. Where nitrogen was applied (Table 5) the clover content declined with increasing rates of nitrogen application but more readily where dung and urine were returned to the pasture. The values in Table 5 are means for two years. Herbage yields were significantly increased by urine in combination with fertilizer nitrogen, as shown in the last column of Table 5. The plots which received

Table 5

The influence of increasing nitrogen fertilizer and return of excreta on mixed pastures (from Wheeler 1958).

Annual Nitrogen Application pounds/acre	Clover content of pasture per cent.		Additional herbage production due to urine
	No return	Full return	pounds/acre
Nil	44	25	55
52	43	18	955
about 170	16	2	1865
about 290	2	-	2455

urine contained about 13 per cent. less clover than the plots which received no urine. Nitrogen dressings have to be matched with heavier stocking to maintain an even grazing pressure, otherwise grass dominance develops and competition for light will again control the balance between species.

The suppression of clover from mixed associations to which nitrogen has been applied is now ascribed to light and all previous theories can be safely disregarded. Blackman (1938) and Blackman and Templeman (1938) reported a series of experiments which included two levels of of shading and various nitrogen treatments on pure stands of grass and clover. Clover was not depressed by nitrogen applications, but there were significant reductions in yield due to shading. With frequent defoliation and shading, leaf growth of grasses was depressed by the addition of nitrogen but the leaf growth of clover at successive defoliations remained unaffected by additional nitrogen. Unlike clover, grasses at low light intensities still actively absorbed nitrogen. In the course of this work Blackman had come to accept the view "that the balance between legumes and grasses is dependent upon competition for light", and this is discussed at length in these papers.

The boost which applied nitrogen gives to grass in mixed pasture (Blackman and Templeman 1938) without a parallel stimulus to the already nitrogen rich clover, considerably accentuates the shading of clover by the taller growing grass. Thus, where defoliation is absent or infrequent, fertilizer nitrogen rapidly promotes and sustains shading of clover and in this way exerts a distinct influence on the botanical composition of the pasture.

On the other hand, where intense or frequent defoliation is practiced, the role of nitrogen in influencing the balance between species will in part be determined by the extent to which nitrogen applications may aid the grass to overcome the adverse effects of defoliation, relative to the recovery of the clover. With reductions in light intensity, frequent defoliation and the application of nitrogen, Blackman and Templeman (1940) showed an effect on root development, and a transfer of carbohydrates from roots to leaves with a concommitant reduction of protein synthesis in leaves. The question is asked to what extent the interval between defoliations can modify the depressing effect of high nitrogen, at low light intensities? In pure stands of coastal Bermuda grass at low light intensities and high nitrogen dressings, yields relative to unshaded plots, continued to decline in spite of progressively longer periods between defoliations Burton _et al_. 1959).

(e) The influence of nutrients other than nitrogen on the botanical composition of grass and clover swards.

The growth of clover is severely reduced where nutrient deficiencies are acute, and the following general remarks apply to the grass clover balance under these conditions:

(a) Clover is more sensitive than grass, and therefore does not contribute much to yield.

(b) Grass is able to develop a better root system and therefore has a competitive advantage over clover.

The tremendous increase in the acreage of sown pasture in Southern Australia is due almost entirely to the use of the annual self-regenerating pasture legume subterranean clover, and to the correction of a number of soil nutrient deficiencies (Stephens and Donald 1958).

In Australia phosphorus is deficient in nearly all agricultural soils and this may be remedied by applying superphosphate at the rate of 3-4 cwt. per acre on new pasture, and following this with annual or biennial dressings of 2 cwt. per acre. Pasture on potassium deficient land lacks vigour, contains little clover, and is often invaded by weeds (Brown and Rouse 1953). Clover growth can be restored by applying 1-2 cwt. per acre of potassium fertilizer followed by applications of ¼-½ cwt. per acre (Newman 1956). Calcium ions are essential for the satisfactory nodulation of subterranean clover (Loneragan 1959). The Sulphur requirement is partially met by applications of superphosphate. Hilder and Spencer (1954) obtained large increases in the production of natural pasture with rising Sulphur levels as a result of better legume yield in the pasture. Millikan (1953, 1958) has described deficiency symptoms in clover and Stephens and Donald (1958) have given an account of the major deficiencies in Australian soils, illustrating it with

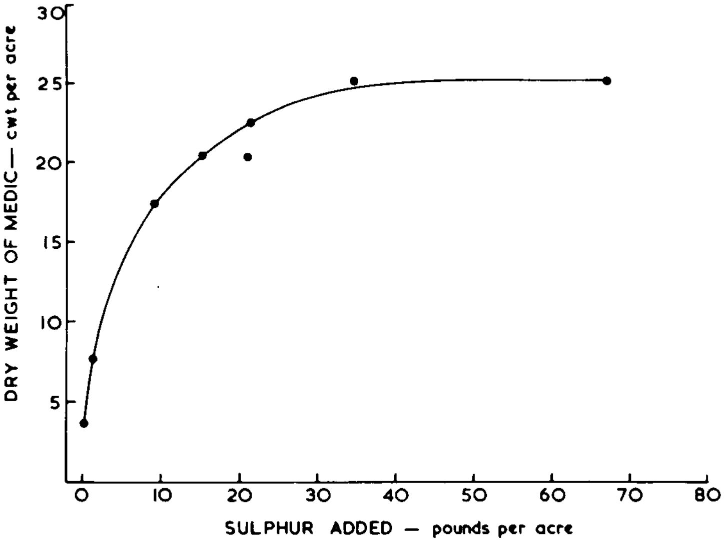

Fig. 3. - The yield of medics with increasing sulphur levels in the fertilizer.

some data on pasture responses. These show how the yield of clover is depressed in the absence of an essential nutrient. Copper deficiency is always associated with phosphorus deficiency, and commonly with zinc, molybdenum, and potassium deficiencies. Copper was necessary for the establishment of legumes (Riceman and Donald 1938) and the average percentage of subterranean clover in pastures increased from 27 per cent. to 58 per cent. on applications of 15-20 pounds Bluestone per acre (Jones and Elliott 1945). Molybdenum is required by the Rhizobium (Anderson 1956) for effective nitrogen fixation. Grasses showed no response (Anderson and Thomas 1946). Zinc was also critical for the establishment of subterranean clover (Riceman 1948).

Where deficiencies are not acute, the nutrient status may also influence botanical composition. The use of diverse species in an association initiates competition for nutrients, (Walker 1960), especially during the early stages of growth. If these differences are allowed to develop they ultimately affect the balance between grass and clover in a mixed association. In this regard Mouatt and Walker (1959) commented that light competition from the fast growing grass was "implemented before phosphate deficiency was felt by the clover". Trumble and Shapter (1937) studied the effect of applied phosphate and nitrogen in sand culture and found that for every increase in the level of nitrogen, grass responded to higher applications of phosphate; clover was depressed by an increase in the available nitrogen and to a lesser extent by a decline in the available phosphate. These results may be attributed to the interaction of competition for light and for nutrients. Willoughby (1954) found that the decline of the grass component in sown pasture was due to competition with clover for nitrogen and phosphorus early in the season and a rising clover density. Superphosphate in the presence of sulphate of ammonia increased grass yields without reducing clover yields, but that additional superphosphate alone improved clover yields only.

Donald (1958) has shown how competition for even a single factor involved competition for another factor, albeit indirectly. Where there is competition for light between grass and clover the clover has a reduced capacity to exploit its own nutrient supply. Where there is competition for nutrients, the grass intrudes into the nutrient supply of clover and thus the clover has a reduced capacity to exploit is its own light supply. (See Table 9 p. 83).

(f) The influence of grazing on the botanical composition of grass and clover swards.

The season, the frequency and the intensity of defoliation have been shown to influence the balance between species in mixed pasture. The return of animal excreta was also shown to be important and in addition the animal may exert an influence by selective grazing (Norman 1957), treading (Edmond 1958) and damage to plants (Davies 1946, Scott 1956). Because of the inter-relationship of so many factors, some investigators consider that an equilibrium exists between soil fertility, pasture production and the output of animal products (Sears 1953). In effect it is an equilibrium of the nitrogen which the soil can retain and supply for pasture growth. Equilibrium nitrogen may be maintained at a high level in some environments and under some systems of management, but is susceptible to unfavourable environmental circumstances and is readily altered by agronomic practices (Willoughby 1954, Allison 1955).

In examining the effects of grazing on the botanical composition of pasture it is appropriate to begin with a brief statement on management studies. The adjustment of grazing pressures and intensities to the year-round growth of pasture affords some control over seasonal conditions. If varied in accordance with the growth cycle of the important components of the pasture it is possible to regulate botanical composition. Grazing pressure is the proportion of pasture growth eaten by animals (Davies 1946) and grazing intensity is the height of herbage remaining after each grazing (Brougham 1959b).

In a comparison of continuous grazing with a 4-week and 8-week rotation, Moore, Barrie and Kipps (1946) found that the summer-growing lucerne was lost from the pasture under continuous grazing, and retained on the 8-week rotation making a substantial contribution to yield; in the 4-week rotation the position was intermediate. Under continuous grazing Phalaris and subterranean clover formed a stable pasture and using these species Willoughby (1959) showed that animal production increased as grazing parallelled pasture growth; neither the time nor the intensity of grazing greatly influenced botanical composition. This must be qualified, because consumption by animals at all levels of stocking did not exceed the growth rate of pasture, i.e. grazing pressure was less than 100 per cent. at all times.

In New Zealand, frequent hard grazing in spring reduced total dry matter yields, but had no long term effects on botanical composition. Brougham (1960) suggested that annual pasture yield may be increased 45 per cent. by adopting the following key practices:

(a) Moderate grazing during the period immediately before the trough in the annual production curve, (January to March) to maintain a desirable balance between species.

(b) Intensive grazing during late autumn and and early winter to bring about a rapid change from clover dominance in summer to grass dominance in autumn and winter; a desirable balance between species was maintained in spring, because the grass made better growth than clover in the previous winter.

In these studies no animal responses were recorded: to deplete the pasture to the height required for each treatment within 24-28 hours, Brougham (1959b) varied the stock numbers at each grazing. It may be argued that there was no real adjustment of grazing pressure to the seasonal growth rate of pasture and that the only valid conclusions therefore were those based on results obtained during the trough of pasture production. Since Brougham's recommendations were to graze intensively during the low ebb of seasonal production the question of the method of stocking in these experiments does not arise.

Wheeler's data (1960, in press) showed that gang-mowing (Chippindale and Merricks 1956) in the spring was better than grazing, to maintain a desirable botanical composition; in other words, the regular and even removal of herbage was preferable to selective grazing and excessive consumption by animals. Gang-mowing also reduced pasture to a uniform height (Reid and MacLusky 1960) when the differences in the growth rates between species were greatest, thus preventing one species from overshadowing another.

Sears (1953) summarized his own work in New Zealand in which he considered the pattern of pasture and soil fertility development under grazing. The inclusion of clover not only increased the total production of herbage but also the yield and nitrogen content of the associate grass. In some cases total herbage yields increased by over 500 per cent. with a concommitant increase of over 100 per cent. in the yield of grass. Red clover was not nearly as effective as white clover but on the other hand it enhanced the value of the pasture as summer feed. Changes in botanical composition attendant on fertilizer application were closely associated with soil fertility, initially favouring the clover and subsequently the grass. With complete return of dung and urine Sears (1953) found that total hernage production was increased and that there was a better spread of seasonal production. Additional nitrogen in the soil stimulated the growth of ryegrass in the spring and winter. With nil nitrogen Wheeler (1958) did not obtain any significant increase in herbage production (Table 6) but he obtained a similar effect as Sears, where small amounts of nitrogen were added to the pasture. Sears found that with the

Table 6

Botanical composition of mixed pasture with and without return of excreta (after Sears 1949 and Wheeler 1958).

	Av. Annual Dry Matter	Botanical Composition per cent.		Percentage Growth in Winter
	pounds per acre	Clover	Grass	
Palmerston North, New Zealand (1941-45).				
No return of dung or urine	10600	51	49	9.0
Return of dung and urine	14000	28	72	12.3
Lincoln, New Zealand (1945-48).				
No return of dung or urine	9500	66	34	1.9
Return of dung and urine	9600	24	76	6.3
Wye, United Kingdom (1954)				Other species
No return of dung or urine	6740	50	47	3
Dung alone	6430	51	45	4
Urine alone	6510	43	54	3
Dung and urine	6940	38	58	4
L.S.D. within columns at P 0.05	1940	11	9	4

complete return of nutrients, clover did not disappear from the pasture, and this is attributed to nitrogen losses from the cycle.

Undoubtedly the animal benefits from the presence of the legume in a pasture mixture. (Hein and Cook 1937, Blaser et al 1956(b), Davis and Bell 1957, Van Keuren and Heinemann 1958, Heinemann and van Keuren 1958, I.C.I. 1959(a). Yet it is difficult to foresee how a desirable balance can be sustained over a period of time, in the presence of the grazing animal whose influence disturbs the equilibrium between species. Limitations to animal production do not necessarily synchronise with the limitations to pasture productions (Lambourne 1958, Willoughby 1959) and consequently rapid changes in grazing pressure may develop. This will have repercussions on the botanical components in the pasture, and the nature of the botanical changes will depend on the time at which grazing pressure is most intense (Martin Jones 1933).

Conclusion. The foregoing review shows that a complex of factors influences the grass clover balance and though changes in botanical composition of mixed pastures have been interpreted in terms of photoperiod, temperature, moisture regime, nitrogen supply, other nutrients and defoliation, they have not been examined in terms of the light supply. The influence of light is generally accepted but the nature of light competition in limiting yield and influencing survival of species in mixed association needs to be better understood if the light supply is to be managed effectively for a desirable grass clover balance.

2.2.0. Light Intensity in Pastures.

2.2.1. Records of Light Intensity in Pastures.

Studies of micro-environment have been conducted in many types of vegetation, ranging from naturally occurring to planted communities and from pasture to tall forest. Of the factors involved, light is the one which has been measured least, mainly because appropriately calibrated instruments have only recently become available and partly because of the problems involved in measuring light within a plant community. These problems may be accentuated in pasture due to the small distances involved and the difficulties in locating instruments without seriously disturbing the leaf cover. Before examining the available records of light measurements in pastures let us consider the features which distinguish pastures from other forms of vegetation in respect to the problem of light measurement.

(a) The diversity of pastures. A pasture generally consists of several species of differing morphological form present in varying proportions; other species may invade the pasture and modify it still further. Pastures are seasonal in character and are frequently disturbed by grazing, mowing or trampling. They may be rendered even more diverse by simple treatments, such as fertilizer application.

(b) The dimensions of pastures. Pastures are generally short and until recently, recording instruments have not been sufficiently small for use in pastures. However as the area of the sensitive surface on a photocell is reduced, so the problem of calibration is increased.

(c) The changing nature of pastures. Because of their seasonal character, pastures rapidly change in structure and dimensions. In addition diurnal movements (of nastic, pulvinal or phototropic origin) of individual plants are apt to bring about changes in environmental conditions over very short distances.

In Table 7 data from a number of sources are assembled so that an assessment can be made of the contribution of each paper to the general understanding of the light regime within pasture swards. Some caution, however, is necessary in drawing inferences from one publication to the next since there was no single underlying concept which prompted these observations, and consequently they differ in nature and in the way in which they were made; sporadic interest in the subject itself is evident from the dates of publication.

Ångström (1925) was interested in measuring the physical properties of ground and atmosphere particularly in regard to radiation and in comparing the performance of the pyrheliometer with that of the pyranometer; the values shown in the Table 7 represent some of the readings recorded. The values of light intensity at various

Table 7.

A summary of previous records of light intensity in pastures.

Worker and Location	Time of year	Instrument	Nature of Vegetation and any Special Circumstances	Height of measurement	Findings
Ångström (1925) Stockholm	26-6-1925 13-8-1925 18-8-1925	Pyranometer			
	Late Summer		Pasture sward of *Phleum pratense* and *Dactylis glomerata* approx. 100 cms high	Above Sward 50 cms. 10 cms. Ground level	100 per cent. of incident light energy 1.08g/cal./cm^2/min. 96 per cent. 26 per cent. 18 per cent.
Steiger (1930) Lincoln, Nebraska	1928	Clements Photometer	Upland prairie and in particular under *Psoralea floribunda* *Amorpha canescens*	Ground level and under bushes	General vegetation reduced light intensity to 20 per cent. at ground level 8 - 12 per cent. under *P. floribunda* 6 per cent. on grass under *P. floribunda* 4 per cent. under *A. canescens*.
			Low prairie		Usually 5 - 10 per cent. at ground level and 1 - 2 per cent. in dense vegetation Absence of upland species due to competition for light

Worker and Location	Time of year	Instrument	Nature of Vegetation and any Special Circumstances	Height of measurement	Findings
Rübel (1932) Pontresina	Probably June or August		*Trisetum flavescens*	At various leaf positions and ground level	At upper leaves 60 to 70 per cent. lower leaves 40 per cent. ground level 0.7 to 0.25 per cent.
			Poa pratensis		Under flowers 83 per cent. At upper leaves 70 to 75 per cent.
			Avena pubescens		Under leaves 50 per cent. Ground level 20 to 25 per cent.
			Polygonum bisterta		At surface 100 per cent. At leaves 70 per cent. Ground level 0.7 per cent.
Flory (1933) Lincoln, Nebraska	15-7-1933	Clements Photometer	*Andropogon scopiarus* *Stipa sparta* *Koelaria cristata* *Poa pratensis*) Association L.A.I. of this prairie was 6.3	33 cms. 16 cms. Ground level	At 33 cms. 100 per cent. 16 cms. 24 per cent. Ground level 5 per cent.
Sauberer (1937)	May-June	13 types of cells examined a number of filters tested	The paper includes a study of the specteral composition of light in plant stands. Measurements made in forests, in shrubs, crops and pasture.		
		Photocell with: Ilford Filter - - Green - Red Agfa Filter - 83 -84	Cloudiness rated at 10	Ground level	With Ilford Green 12.7 per cent. Red 10.9 per cent. Agfa - 83 23.0 per cent. - 84 32.2 per cent.
	6-5-1935	Photocell	Measurements throughout the day in the open, in a clover sward and in crops of barley and rye. Clover Swards 25 cms. - 30 cms. tall.	Ground level	Maximum light intensity recorded at midday and in crops shortly afterwards. Direction of sowing of some significance in crops. At ground level 3 to 7 per cent.

Worker and Location	Time of year	Instrument	Nature of Vegetation and any Special Circumstances	Height of measurement	Findings
Pohjakallio (1952) (Vik and Mudusniemi Experiment Stations) Finland	Mean values for the year - 1951	Lunelund Potassium Photocell	Red clover 30 cms. tall. Young shoots of *Phleum pratense* 30 cms. tall. of "Flagging" of Mitchell and Calder .	Ground level	In red clover 1 per cent in direct sunlight. In timothy 18 per cent in diffuse light.
Monsi and Saeki (1953) near Tokyo	May to Sept. 1949 and April to July 1950	Photocell or Eder-Hechtschen Wedge Photometer	Forest Associations Meadows at low alititudes) mainly Meadows at high altitudes) *Miscanthus* dominant *Phragmites* communities	Light intensities at approx. 10 cm. intervals	Photographs of light pattern at ground level, in 6 contrasting communities. Diagrams showing how lightintensity changes with height and vertical leaf distribution in one community on 8 sampling occasions. Light intensity profiles and vertical distribution of vegetative material in a number of plant communities. The relationship between light intensity and leaf area index is examined in some detail. Theoretical light extinction and the minimum light intensity observed in some communities. Theoretical considerations relating these observations to productivity.
Brougham (1956) Palmerston North New Zealand	16-9-1954		(*Lolium perene* x *L. multiflorum*)) Association *Trifolium repens*) *Trifolium pratense*) Swards initially defoliated to 1", 3" and 5".	2.5 cm.	Light interception plotted against L.A.I. gave a consistent relationship regardless of initial intensity.of defoliation.
Shul'gin (1956) Zvenigorod Biological Station, U.S.S.R.	18-7-1954	Yanishevskii Pyranometer	Readings taken in natural and sown pastures, in crops and in forest.	10 cms.	In sown grasses 43 per cent. meadow 43 per cent. grass mixture 18 per cent.

Worker and Location	Time of year	Instrument	Nature of Vegetation and any Special Circumstances	Height of measurement	Findings
Alekseenko (1958) Leningrad Agric. Inst.	1956-1957 (May-July)	Not stated	*Phleum pratense*) Grown singly *Festuca pratensis*) and in *Dactylis glomerata*) associations *Trifolium pratense*) *Medicago sativa*) The structure of perennial pasture stands was examined 4-6 times in 2 seasons. Profiles of light intensity, air temperature and relative humidity measured at 20 cm. intervals. Transpiration in clover and photosynthesis in lucerne measured.	60 cms. 40 cms. 20 cms. G.L.	Light intensity (per cent) as swards enter reproductive phase (July 1st). Timothy / Lucerne / Clover / Timothy and Lucerne / Clover and Timothy Above sward 100 100 100 100 100 At 60 cms. 48 47 100 46 52 At 40 cms. 21 14 6 9 13 At 20 cms. 11 5 1 3 3 At G.L. cms. 4 2 1 1 1 Relative volume of vegetative mass of a species is greater in mixture than in pure sowing. L.A.I., Relative Humidity and Total rate of photosynthesis greater in mixtures than in pure sowings. Rate of photosynthesis of a species is less in mixture than in pure sowing. Some structures give better yield than other structures.
Black (1958) Adelaide South Australia	May-August 1957		Dense swards of *Trifolium subterraneum* of 2 different initial seed sizes, sown singly and together	Vertical interval of 2 cm. up to 34 cms.	Most of light is absorbed by the uppermost leaves of the canopy. In the earlier stages of growth, light absorption is greatest in plants originating from large seed.
Brougham (1958) Palmerston North New Zealand	4-12-1956 to 5-1-1957		Light readings at 2.5 cms. and Leaf Area Index of regrowth at 4 day intervals up to 32 days, after initial mowing to 2.5 cms. Associations examined were 1. *Lolium perenne* 2. (*L. perenne* x *L. multiflorum*) 3. *Phleum pratense* 4. *Trifolium repens* 5. *T. repens* and (*L. perenne* x *L. multiflorum*)	2.5 cm.	Difference in form of light interception pattern with increasing Leaf Area Index for the different species.

Worker and Location	Time of year	Instrument	Nature of Vegetation and any Special Circumstances	Height of measurement	Findings
Brougham (cont.)	19-12-1956 23-1-1957 21-1-1957		Hourly readings throughout the day on regrowth 15 days old in December and January and 11 days old in February. Associations examined were: 1. *Lolium perenne* 2. (*L. perenne* x *L. multiflorum*) 3. *Trifolium repens* 4. *T. repens* and (*L. perenne* x *L. multiflorum*)	2.5 cms.	Patterns of light interception throughout the day, were alike, in general, but differed in magnitude and in particular detail. These differences were due to angle of elevation of the sun and to differences in leaf area and form.
Mitchell and Calder (1958) Palmerston North New Zealand	January to May 1956	1.8 cm. x 1.1 cm. Barrier - layer *Selenium photocell*	Eight assorted summer pastures and five assorted autumn pastures consisting mainly of *Lolium* spp. *Trifolium repens* and *Trifolium pratense*.	For seven pasture types readings at 5 cm. intervals and for six types at 2.5 cm. intervals.	Three distinct patterns of light penetration established depending on the species and partly on the development of the pasture.
Black (1960) Adelaide South Australia	April-June 1959		Mixed swards consisting of 2 strains of *Trifolium subterraneum*. Three strains of different petiole lengths were used and sown in mixed cultures, and pure cultures as controls.	Vertical interval of 2 cms. up to 26 cms.	Strains with longer petioles intercepted most of the incident light and hence suppressed growth of the companion strain. The degree of suppression was determined by extent of shading.
Saeki (1960) Central Japan			*Miscanthus sacchariflorus* community	Vertical interval 12.5 cms. up to 240 cms.	Light intensity at height can be expressed as a function of L.A.I. $\frac{I}{I_o} = K e^{-\frac{KF}{1-m}}$ I = light intensity received by the leaves at height I_o = incident light F = L.A.I. K = extinction coefficient m = leaf transmissibility This equation tends to overestimate where leaves are erect in the upper layers.

levels conform to the general pattern of light interception in grasses established later but suggest a thin stand; another possible explanation for the higher values is that leaves readily transmit radiation of wavelength higher than 0.7 , and a pyranometer is more sensitive to these values than a photocell. Steiger (1930) made an ecological study of upland and lowland prairie in Nebraska, and measured soil moisture, temperature, evaporation and light intensities at various sites. Under dense cover the light values ranged from 1 to 5 per cent. and under sparse cover they were of the order of 10 to 20 per cent. Steiger considered that light was important in the development of seedlings of prairie plants. Rübel's (1932) main interest was in ecological plant geography and he reported isolated readings among grasses in discussing the light micro-climate in vegetation. His data showed intense light reductions below leaves, and it is interesting to note that he recorded reductions in light intensity of up to 17 per cent due to inflorescences alone. Flory (1933) made a general comparison of the micro-climate in a prairie and in a nearby field of maize. The light readings given were limited to those shown in Table 7. These data are used again by Weaver and Flory (1934). Sauberer (1937) dealt with a number of aspects of light measurements in vegetation and his paper shows a consciousness of some of the problems involved. He used a range of measuring instruments and indicated their shortcomings. He considered light penetration and the spectral composition of light in vegetative stands. In reporting measurements throughout the day in several stands he referred to cloudiness, the elevation of the sun and the position of leaves. He does not discuss the significance of these measurements in relation to the biological material handled. Pohjakallio (1952) compared radiation in Northern with that in Southern Finland and dealt briefly with light intensity under young crop and pasture. The table from which the readings were taken compared light intensity on clear and cloudy days.

Monsi and Saeki (1953) examined the light distribution in a number of communities in relation to the distribution of leaf "aphotosynthetic" material, and the number of stalks at vertical intervals of 10 cm. They show how the light is distributed within the vegetation, and this is the first study of its kind; in this respect this is an original and significant contribution.

Brougham's interest in light in pastures arose from previous work on the rate of pasture growth. In this study Brougham (1956) measured light intensity 1 in. above ground level in well-established swards initially defoliated to 1, 3 and 5 ins. Light intensities at 1 in. were related to the amount of leaf material present. He showed that the rate of pasture regrowth increased until complete light interception was approached and that thereafter an almost constant maximum rate was sustained; the more intense the defoliation, the longer it took to achieve complete light interception. Shul'gin (1956) recorded an assortment of light intensity readings in forest, crops and pastures on isolated occasions. The patterns were not adequately described and it is not clear why he chose to read light intensities from 10 cm. from the ground.

In the U.S.S.R. Alekseenko (1958) studied

(a) The structure of some perennial grasses in pure stands and in mixtures.

(b) The micro-environment within the swards.

(c) The influence of structure on the micro-environment and the effect of the latter on some physiological processes and yield of plants.

Unfortunately the full text of Alekseenko's findings is embodied in a thesis and only fragments of his light intensity data are available. The data shown in Table 7 were obtained from several sources, but mainly from the publication by the U.S.S.R. Ministry of Agriculture. In general, his results showed that in pure grass stands the greatest light reductions within the swards occured during the period of maximal tiller development. At tillering, leaf concentration in timothy was greatest in the zone from 40 to 70 cm, and in cocksfoot and fescue from 10-40 cm. For this reason light intensities above 40 cm. in timothy were less than in the other two species, but greater at ground level. The values of light intensity were less in profiles of grass-legume mixtures than in pure grass stands. Pure clover stands showed abrupt reductions in light intensity near the top of the swards but this was not so marked in lucerne. Legumes in mixed stands accentuate light reductions within the swards, especially in the region of their upper leaves. In mid-summer, reductions in light intensity of 50 per cent. were recorded near the top of the grass swards.

Black (1958a) in South Australia demonstrated the suppression, in swards of subterranean clover, of plants which grew from small seeds when sown in mixture with large seeds. By apportioning the light intensity received within each 2 cm. layer between plants from large and small seed he showed that the small-seeded plants were growing in progressively increasing shade until they received only 2 per cent. of daylight at their surface. This experiment followed earlier work by Black (1957a) in which he showed that larger-seeded plants reached a critical Leaf Area Index* before smaller-seeded plants.

Brougham (1958a) wished to examine how the L.A.I. for maximum light interception, previously reported as 5 (Brougham 1956) varied,

(a) with different pastures, and

(b) for the same pasture, at different times of the year, particularly when the L.A.I. was similar on the different occasions.

Once again he measured light intensity at 1 in., and L.A.I. at 4-day intervals over a period of 32 days during regrowth after mowing to 1 inch. He established different patterns of light interception for swards consisting of plants of different configuration, with clover swards at one extreme and grass swards on the other (Fig. 4). From these data it is clear that the L.A.I. at which 95 per cent. light interception (defined by Brougham as the critical L.A.I.) differed for different stands. He also examined changes in percentage light penetration with time of day for four types of pastures on three occasions about a month apart. From these results Brougham suggested seasonal differences in critical L.A.I. values.

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* The Leaf Area Index (L.A.I.) is the leaf area per unit of land (Watson 1947).

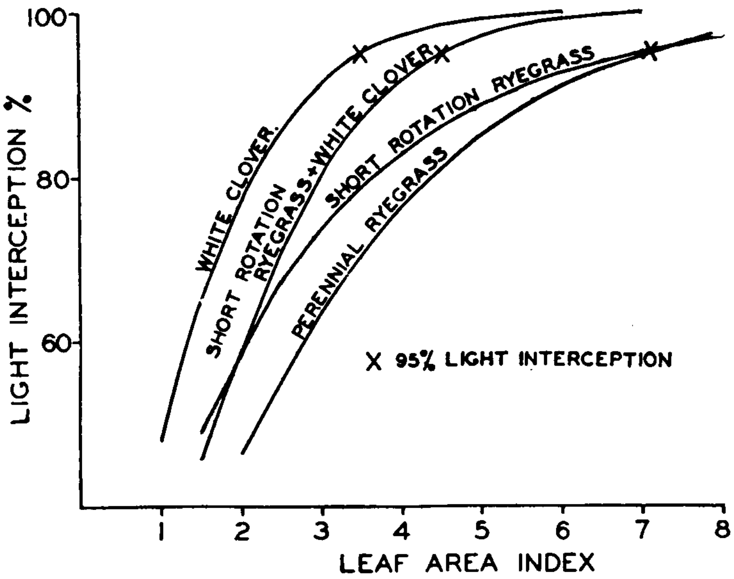


Fig. 4. - The relationship between light interception and L.A.I. (after Brougham 1958).

The work of Mitchell and Calder (1958) supplements the foregoing results of Brougham, and showed the light interception patterns in different kinds of pastures at any one time. They examined eight summer pastures, some of which were grass-dominant others clover-dominant and a number of mixed swards, all of which were at different stages of growth. These pastures varied in form and the height ranged from 3.5 ins. to 19.0 ins. Three patterns of light interception are distinguishable (Fig. 5). It is clear from work already quoted that L.A.I. and light interception are closely linked and that the pattern of light interception can be expected to vary with the structure of a pasture. The comment by Mitchell and Calder to the effect that the standard errors of the light readings were at a maximum at the centre, may be interpreted to mean that the greatest variation in light readings occurred where there was the greatest variation in the position at leaves were held above ground level. The conclusions that can be drawn from their results must be limited while they remain unsupported by data of leaf distribution profiles. Furthermore these readings were taken on a single occasion only, and consequently have temporal value only. Black (1960) studied the effect of differences in petiole length on the component yield, when two strains of differing petiole lengths were sown in mixture. Though no data were given for petiole lengths, these may be inferred from Fig. 5 in Black's paper in which the spatial organisation of leaf area is shown in the six experimental swards. The light intensity profiles at 60 days (the final sampling occasion) showed marked differences between strains in the height at which light extinction occurred. In pure sowings these were

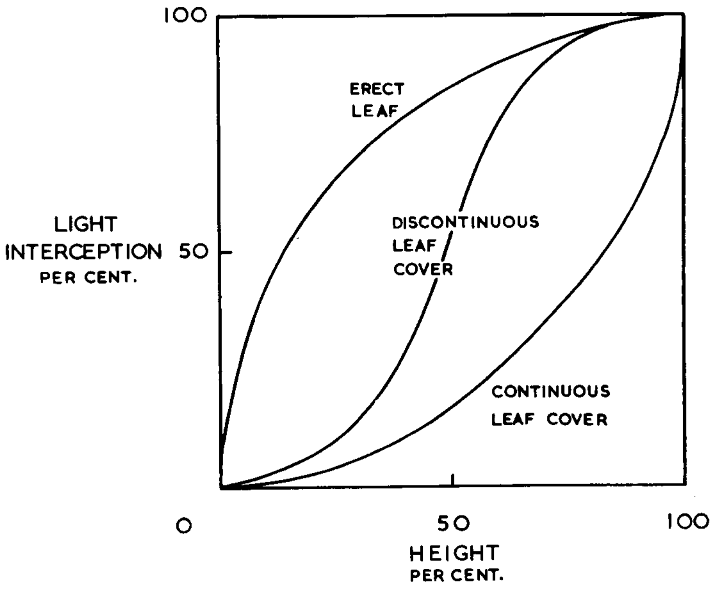


Fig. 5. - The influence of height of pasture and the nature of the pasture canopy on the percentage light interception (derived from Mitchell and Calder 1958).

Tallarook	4 cm. above ground level
Bacchus Marsh	10 cm. " " "
Yarloop	16 cm. " " "

The percentage of incoming light apportioned between the components of mixed swards consisting of Tallarook and Yarloop showed that Tallarook (shortest petioles) was completely shaded by Yarloop (longest petioles) within a month of emergence. From the data it is possible to deduce that equal L.A.I. values do not necessarily bring about equal light reductions, and in fact, light is reduced more where an equivalent L.A.I. is concentrated in a short vertical interval. Saeki (1960) restates and refines the equations previously formulated by Monsi and Saeki (1953) concerning light intensity, L.A.I. and photosynthesis. The noteworthy contribution of these papers is that the relationship between L.A.I. and production is established through the medium of light distribution in a plant community, and the demonstration that the L.A.I. -light relationship may be modified in accordance with leaf configuration.

Conclusion. Interest in light intensity in pastures is increasing and more records are becoming available. The data available so far suggest that the L.A.I.-light relationship is not a constant one but, is nevertheless amenable to formulation. A thorough investigation of the relationship between L.A.I. and light intensity might well begin with artificial models in a photometric laboratory.

2.2.2. The Significance of Light Intensity and L.A.I. in Pasture Growth

In a regular environment, the relationship of yield and L.A.I. with time usually takes a form which satisfies the differential equation

$$\frac{dW}{dt} = k W \left(1 - \frac{W}{A}\right)$$

where k and A are constants. (Davidson and Philip 1956, Shinozaki and Kira 1956, Nelder, Austin, Bleasdale and Salter 1960). This is a logistic curve, but a decline in yield or L.A.I. may be recorded if the experiment is allowed to proceed long enough (Davidson 1954, Ničiporovič and Strogonova 1957) or where irreversible checks (Nelder *et al* 1960) occur. In the study of yield, the interdependence of incident radiation, leaf area index, and growth has now come to be recognised (Monsi and Saeki 1953, Brougham 1956, Davidson and Philip 1956, Ničiporovič 1956, Donald and Black 1958, Iwaki 1958, Watson 1958, Pearsall 1959, Blackman and Black 1959, de Wit 1959, Saeki 1960, and Nelder *et al.* 1960) and where a complete canopy of foliage develops during the vegetative phase of growth - as in mesophytic pasture - the following propositions require consideration:

(a) the density and disposition of foliage determine the relationship between light intensity and L.A.L.;

(b) in swards the level of production depends on the incident radiation, and competition for light sets a ceiling to yield;

(c) the relationship of optimum L.A.I. to the light gradient within the foliage.

Light intensity and L.A.I. In the absence of crop about 80 per cent. of the sun radiation which is transmitted by the atmosphere is absorbed by the ground. Where a crop is grown, the amount of radiation absorbed by the crop depends on the amount of leaf tissue. Figure 6 may be compared with Fig. 4 in which the relationship of L.A.I. and light interception of ryegrass and clover are shown.

Light intensity within a stand. The light intensity and profile within a sward may be expressed by Beer's Law (Monsi and Saeki 1953, Davidson and Philip 1956, Brougham 1958a, Nelder et al 1960).

$$I = I_0 \, e^{-kA} \qquad \ldots\ldots\ldots \; (1)$$

where I = actual light intensity under an L.A.I. of A

I_0 = incident light value

k = coefficient of extinction which ranges from 0.3 - 0.5 in communities with erect leaves, and from 0.5 - 1.0 in communities with horizontal leaves.

Values reported were:

Perennial ryegrass	0.27	(Brougham 1958)
Short rotation ryegrass	0.46	(Brougham 1958)
White clover	0.69	(Brougham 1958)
Miscanthus	0.5-0.6	(Monsi and Saeki 1953)
Helianthus	0.8-0.9	(Monsi and Saeki 1953)
Subterranean Clover	0.90	(Davidson and Philip 1956)

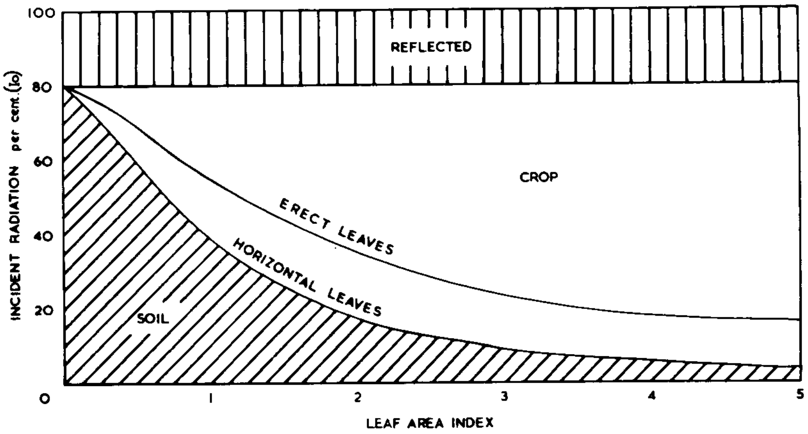


Fig. 6. - Distribution of incident radiation in a growing crop (after Ničiporovič 1956).

The relationship may be expressed as $\frac{I}{Io} = e^{-kA}$

where $\frac{I}{I_o}$ is the mean relative light intensity or the daylight factor (see page 99)

The relationship is not valid where the form of growth changes with the stage of growth (Brougham 1958, Nelder et al 1960) and the value of k may be modified by stalks, or a concentration of leaves in a short vertical interval.

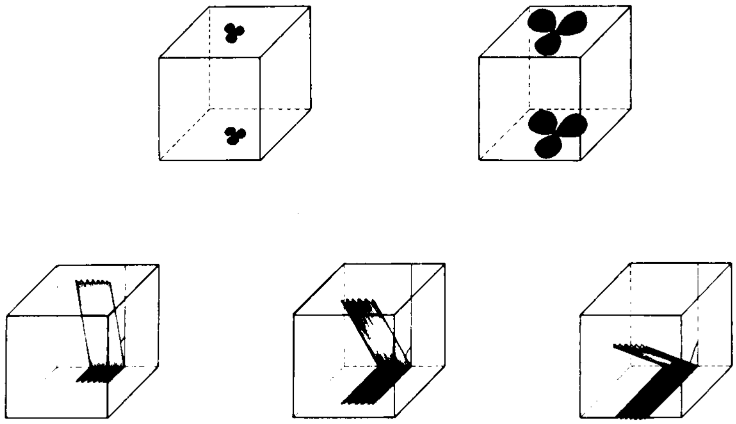
Transmission in leaves may alter the extinction coefficient, and the inclusion of a factor "m" for light transmission through leaves (Kasanaga and Monsi 1954) gives the relationship (Saeki 1960)

$$\frac{I}{I_o} = k\,e^{-\frac{kA}{(1-m)}} \qquad \ldots\ldots\ldots\ldots (2)$$

<u>Disposition of leaves</u>. Monsi and Saeki (1953) discuss in some detail the quantitative aspects of leaf disposition and show how this may influence the coefficient of extinction k. In the cases of leaves horizontally disposed where the area of one side of the cube is S and leaf area is a. (Fig. 7)

$$K \rightarrow 1 \quad \text{as} \quad (a\,/\,S) \rightarrow 1$$

i.e. the coefficient of extinction approaches 1 as the area of leaf increases. For leaves such as grass leaves which make an angle with the vertical $k \rightarrow 1$ as the angle approaches 90^o, or the leaf becomes horizontal. In fact the greatest change in the coefficient of extinction takes place as the leaf moves from 0^o to 45^o from the vertical (Fig. 7). The light intensity beneath a given L.A.I. will vary according to the disposition of the foliage and Fig. 8 shows



α = 10° from vertical

α = 30° from vertical

α = 70° from vertical

Fig. 7. - The diagrammatic presentation of the effect of increasing leaf area or increasing leaf angle on the coefficient of extinction.

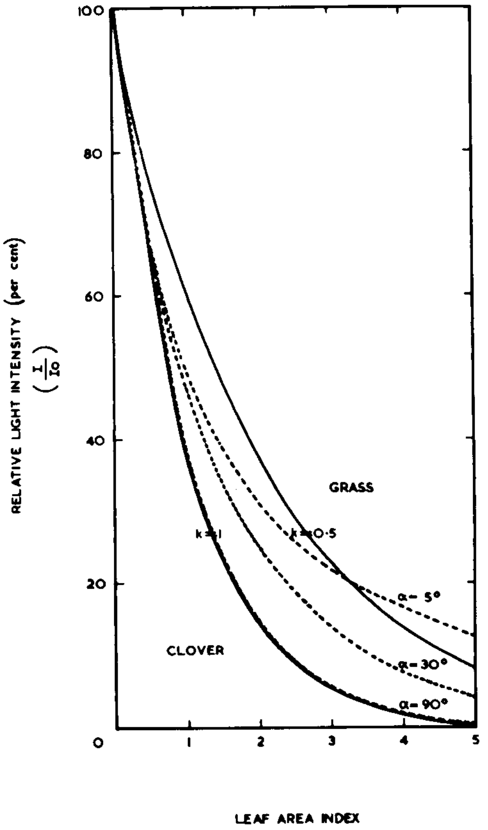


Fig. 8. - The relationship between L.A.I. and light intensity with varying k values, and varying leaf angles (derived from Monsi and Saeki 1953).

this relationship for varying k values and various leaf angles. The calculated values of the extinction coefficient agree reasonably well with the observed values, i.e. where there were no problems associated with the measurement of leaf angle and leaf disposition. Reductions in light intensity are very rapid as k approaches unity. Thus the relationship between the light profile in the sward and L.A.I. is not constant but varies with incident radiation, depth of canopy, and angle of foliage.

<u>Ceiling yield</u>. The current record yields of pasture are of the order of 15 tonnes/hectare (Sears 1949, de Wit 1959) but estimates based on theoretical considerations (de Wit 1959) and experimental evidence (Brougham 1959a) suggest that annual production of the order of 24 - 35 tonnes/hectare may be possible. Watson (1952) attributed variations in the net assimilation rate to changes in external factors (especially light and temperature) and stated that increases in L.A.I. were the most effective means of increasing production. He did not think it likely that photosynthetic efficiency could be improved. On the other hand, Ničiporovič (1956) expressed the view that higher yields may be obtained firstly by increasing photosynthetic efficiency (i.e. by a greater rate of photosynthesis and a longer duration of photosynthesis) and hence net assimilation, and secondly by developing more leaf tissue early. For the assimilation of one atom of Carbon, four quanta of light energy are required, and since the absorption of energy takes place mainly in the leaves it seems that the most efficient means of raising productivity is to expose as much leaf tissue for as long as possible (daily and seasonally) to incoming light.

When this is achieved it is likely that CO_2 will become limiting. It is patently clear that any discussion of ceiling yields must always be in relation to Blackman's principles of limiting factors (Blackman 1905) and the magnitude of the factors involved should be considered relative to one another.

Yield of dry matter and light intensity. The relative growth rate is approximately a linear function of the log of light intensity (Black 1957b) and the interception of light by foliage approximates Beer's Law; these relationships satisfy the conditions for a logistic expression of yield of dry matter with time (Nelder *et al* 1960). The reviews of Black (1957b) and Donald and Black (1958) and Blackman and Black (1959) indicate that provided temperature is not limiting and water and nutrients are in adequate supply the rate of growth is dependent on diurnal radiation when most of the incident light is intercepted by the foliage. Brougham (1959a) in New Zealand found that radiation values fluctuated by as much as 40 per cent. of the mean daily total received, and mean temperature showed weekly fluctuations of 10° F. On pasture that was cut fortnightly to 1 in., he showed the following changes in weekly growth rates with changes of one unit of climatic factor. The analysis of Brougham's data in these terms (Glenday 1959) depends on a roughly constant growth rate; only the data for the first 6 weeks of growth were used, those from 6 to 14 weeks being discarded because they were too variable. The lack of any response of clover to radiation may be due to the fact that light intensities were not measured at the surface of clover and seriously affects the validity of the conclusions. An estimate based on his previous work (Brougham 1958a) would suggest reductions in light intensity at the surface of clover of the order of 15-25 per cent. in 14 days.

Table 8

The relation between growth rate and climatic factors.

	Total Herbage pounds dry matter/week	Ryegrass pounds dry matter/week	Clover pounds dry matter/week
Radiation gm cals cms^{-2}	1.0	1.3	-
Temperature Range °F	17.0	19.0	-
Maximum Temperature °F	-	-	40.0
Season	Winter Spring	Winter Spring	Summer Early Autumn

The light intensity determines the efficiency of production as can be seen from these figures taken from Ničiporovič (1956).

Light Intensity K cal/m^2/hour	Utilisation of Energy per cent.
700 - 800	0.75
100 - 200	2.5 - 3.0
100	decreases to 0

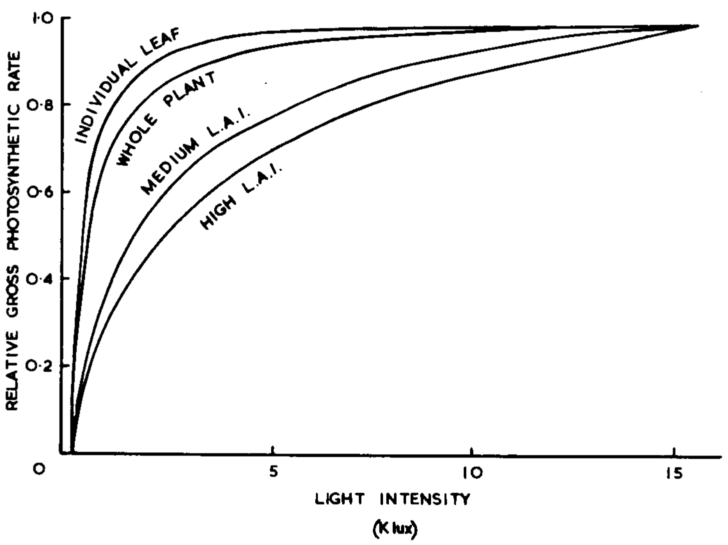


Fig. 9. - The relation between illumination and photosynthetic rate for individual leaves, whole plants, and swards. (after Davidson and Philip 1956).

The compensation point is usually in the vicinity of 20-30 K cal/m^2/hour. While photosynthesis at normal CO_2 concentrations of air is largely influenced by light intensity, the dominant influences on respiration are temperature and the concentration of substrate. In a crop, the rate of photosynthesis is normally 5-10 times the rate of respiration. (Thomas and Hill 1949). With mutual shading the rate of photosynthesis of individual leaves will depend on their location with respect to the incident light (Saeki 1959); consequently with increasing L.A.I. the rate of photosynthesis of the entire stand will be less than the rate of individual leaves which are fully exposed to light (Fig. 9). Clearly then the gross photosynthesis of a sward depends on the nature of the light gradient within the stand. The natural increase in leaf area with time (Monsi and Saeki 1953, Hodgson and Blackman 1956, Black 1958(a), 1960(a) or increasing density (Hodgson and Blackman 1956, Saeki and Kurowa 1959) modify the light profile; the magnitude and direction of the incident light also influences the light gradient. Consequently the L.A.I. which reduces the light intensity to the compensation point for the lowest leaves will vary.

This L.A.I. has been termed the "marginal compensation area" by Davidson and Philip (1956), and $F_{opt.}$ by Kasanaga and Monsi (1954) and by Saeki (1960) who gives a family of curves for different values of k (See Fig. 10). This changing relationship was recognised by Brougham (1958(a) when he said that "complete utilisation of available light will be obtained by a smaller amount of foliage in winter than in summer". Similarly (Black 1958(a) showed that the L.A.I. required for complete light absorption increased from about four in mid-June to

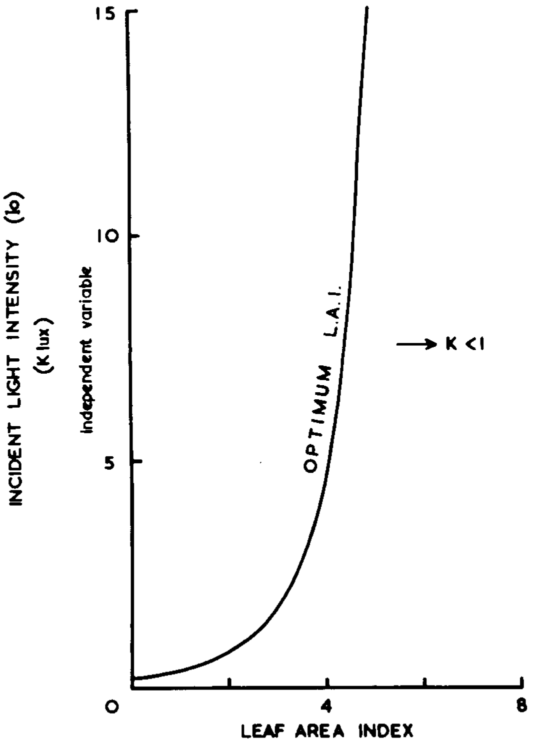


Fig. 10. - The optimum L.A.I. at various light intensities k approx. = 1. (after Davidson and Philip 1956).

about seven in mid-August. The records of mean insolation (I.C.I. 1959b) were subsequently examined and it was noted that the mean insolation increased from 210 to 324 g cal cm^{-2} per day - a ratio of 4 to 6.5. This seems to provide an adequate explanation of Black's observation. Therefore as the optimum L.A.I. - at which the rate of dry weight increase is greatest - is approached, competition for light within the sward will become more intense. Increases in leaf area beyond the optimum L.A.I. signify an inefficient utilisation of the incoming radiant energy for dry matter production, and in this way competition for light sets a ceiling to yield.

<u>Leaf Area Index and Growth</u>. Watson (1952) considered that there was little opportunity for increasing the net assimilation rate and that the development of successful crop husbandry largely depended on "discovering empirically the optimal conditions for leaf area production in a particular environment". Others claim that there is scope for improving the photosynthetic efficiency of crops (Ničiporovič 1956) and breeding for net assimilation rate (Morley 1958). It is rash to predict the conditions for maximum production because of the danger of oversimplification, but from density experiments it is known that an intermediate number of plants is capable of producing ceiling yields (Kiesselbach 1925, Clements, Weaver and Hanson 1929, Donald 1951) and it might therefore be expected that an optimum relationship exists between L.A.I. and the weight of dry matter for a stand of homogeneous plants (Shinozaki and Kira 1956). By definition, the net absolute contribution of the sward to dry matter is maximal at optimum L.A.I. (Donald and Black 1958). With dense swards of subterranean clover,

absolute growth rate was found to be greatest at about L.A.I. 4-5 and to fall away to zero at L.A.I. 8.7. (Davidson and Donald 1958). Brougham (1956) on the other hand, found that approximately constant rates of dry matter increase were maintained when the L.A.I. was sufficient to absorb all the incident light. In experiments with kale, Watson (1958) obtained an optimum L.A.I. of about 3, but with sugar beet the range of L.A.I. tested (L.A.I. 1-6) was not adequate to determine optimum L.A.I.

Watson (1958) suggested that the opportunity to increase kale yields was in the early growth stages when L.A.I. was below the optimum value. The continuous removal of small amounts of herbage about the optimum L.A.I. was considered by Davidson and Philip (1956) to be the most efficient system of pasture production. Saeki (1960) stated that "daily maximum surplus production $P_{max.}$ is performed by 'optimum L.A.I.'". He showed the dependence of $P_{max.}$ on I_o and k and this led him to conclude that maximum yields depended on the incident radiation and the disposition of leaves. Watson and Witts (1959) considered that the disposition of leaves of cultivated beet gave a more uniform illumination of the whole leaf area than in wild sugar beet, and that this accounted for differences in the net assimilation rate between the two types.

The interdependence of factors. During the vegetative phase and until the optimum L.A.I. is reached, increases in L.A.I. and weight of dry matter are dependent on the same environmental factors - the τ of Nelder et al (1960) - albeit at different rates. Good correlations between yield of dry matter and L.A.I. might therefore be expected over short experimental periods (Brougham 1956). The fact that the growth rate becomes steady (Brougham 1956) or declines (Davidson and Donald 1958) at optimum L.A.I. is an expression of the fact that competition for light is becoming severe. From then on the vital relationships are:

(a) the light intensity - L.A.I. profiles of the vegetation (Kasanaga and Monsi 1954).

and (b) the relationship of L.A.I. with time (Ničiporovič 1956).

<u>Where two species are grown together</u>. There are very few studies in which competition between species has been studied in terms of light intensity, L.A.I. and growth. Iwaki (1959) demonstrated the suppression of green gram from a mixed stand of green grams and buckwheat due to reduced photosynthesis and increased respiration as a result of shading by buckwheat. The effects of shading on growth have been studied by the Oxford school in the last 25 years; a brief summary was given by Blackman (1956) and those findings which apply to pastures were reviewed by Black (1957b). The grass clover balance lends itself to the study of competition for light between two species in terms of L.A.I., light intensity and growth, and this was the basis for two experiments in this thesis.

2.3.0. Procedures in studies of competition for light in pastures.

There are several ways in which competition for light in pastures may be analysed, and these will be discussed in this section of the literature review. Changes in the environment commonly lead to changes in plant form and plant number and it is therefore appropriate to begin with a discussion of census studies.

Census Studies.

A quantitative analysis of population changes may often direct attention to limiting environmental influences or indicate when these become limiting. Census studies are of two kinds. In the first instance the number of individuals in the population is studied from germination to maturity and in the second, the morphological characters such as tiller number, leaf number, etc. are classified on an individual and a population basis. The usefulness of census studies was summarised by Watson (1952) when discussing variations in leaf area. "General descriptions of the changes in plant population and in the morphology of the crop plants can be amplified and made quantitative by means of census and development studies, but they give no information on the physiological causes of variation in leaf area". Census and growth measurements should be supported by data concerning the dominant environmental influences.

Plant numbers from germination to maturity. There are a number of studies which have examined plant numbers in pastures. Under monoculture Langer (1956) followed the life histories of individual tillers of timothy in relation to growth and nutrition.

He emphasised the continuous nature of tiller production i.e. the formation of new and the death of old ones. From an analysis of the tiller population of timothy and meadow fescue Langer (1958, 1959) showed a decline in tiller number from April to June which was reduced by frequent defoliation in a wet summer. He also showed that the response to cutting treatment was related to the stage of development of the species. Mitchell and Glenday (1958) review the methods which have been used to assess botanical composition in pastures and suggest that tiller counts are preferable to weight estimates because they are independent of the immediate past history of the pasture.

In clover swards Black (1958b) observed "that wherever planting density is high, plant numbers decline rapidly as complete light absorption approaches, finally settling down between about 12 to 20/100 cms.^2 "Kira (1956) and his colleagues refer to this as "autoregulation", and say "In a plant community which started growth under very high density, part of the initial population is successively eliminated as plants grow due to the competitive interaction between neighbouring individuals". These authors examine competition in terms of the C-D (Competition-Density) effect and its derivative Y-D (Yield-Density) effect, and assume that

(a) that the growth of a plant can be described by a logistic curve

and (b) that at higher densities final yield per unit area is constant regardless of density.

The complex analysis is based on the equation

$$y = \frac{r}{Ar + B}$$

where y = yield

r = density

and A and B are assumed to be independent of density; this is not always the case, as these authors point out.

Holliday (1960) makes essentially the same assumptions as the Japanese workers and subjects yield and plant population data for single crops to a similar analysis. The only difference in his treatment is that he makes allowance for the number of plants lost and takes it for granted that yield is compensated by the surviving plants. He suggests that this form of analysis may be useful in examining more complex situations where two or more species are in competition. de Wit and Ennick (1958) extended to pastures an analysis of seed sown and seed harvested in successive generations of mixed sowings of barley and oats consisting of 2 species. Constant growing conditions were assumed for the analysis. The relative reproductive rate for each species in the pasture may be determined from the number of growing points surviving from one dormant period to the next. They introduced a special factor in the equation for cases where one species may have a beneficial effect on its associate, e.g. a legume on a grass. Although the authors attempted some assessment of "mutual competition" between associated species, the form which this competition might take is not considered, in sufficient detail, and so long as they think of competition as an abstract phenomenon the analysis has little merit. de Wit is continuing his studies with further experimental work in environmental cabinets. Black (1960b) reported a decline in plant numbers in pure and in mixed stands of red clover (*T. pratense*) and lucerne (*M. sativa*) at a range of planting densities. Seedling mortality was much higher in lucerne than in clover. He referred to Biswell and Graham (1956) and Schulze and Sommerfeldt (1958), as the only other workers who examined plant numbers in pastures, in the course of their studies.

Morphological studies. The census studies with cotton (Balls 1953) and cereals (Watson 1952) which reached a peak in the years from 1920-1940 attempted to relate vegetative characters to yield. The comment by Russel and Watson (1940) is appropriate and reflects on the usefulness of such studies. "In general it may be said that all growth attributes which have been discussed are related to yield, and the nearer the time of observation to harvest the closer is the relation". Where yield is composed of the entire crop, as in pastures it is perhaps more significant to *analyse* the morphological changes with time, rather than to *relate* morphological characteristics to yield. There are comparatively few studies of morphological changes due to competition during the experimental period. If plant losses occur as has been indicated, it is only reasonable to expect some rather significant changes in plant form. If surviving plants compensate for those which have been lost then the individuals to be examined will range from vigorous ones to the remnants of plants which have died or are about to die. In other words, a loss in plant numbers is accompanied by an increasing variability of the morphological characteristics of individual plants, and expresses the fact that competitive stresses within the aggregate population are becoming more severe. It is therefore better to have a frequent sampling programme to show up the dominant trends with time rather than sample less frequently and more extensively. Few workers have set out to examine in this way, the individuals in an aggregate population of pasture plants.

Evans (1942, 1949) examined the formation and growth of leaves in Kentucky bluegrass and the longevity of fertile and infertile tillers, but this work does not seem to have been published in its entirity. Langer (1956) made a detailed study of tiller development in timothy grown at a density of 30 plants/100 cm^2. For each tiller an examination was made of the position, number of dead and living leaves, the height of the stem, the time of appearance of the flag leaf and inflorescence and the length of the inflorescence. Knight and Hollowell (1959) examined the effect of stand density in crimson clover on height, number of vegetative stems, number of seed heads per plant, number of florets per head, and forage yield. In most of this work the emphasis is on the reproductive parts. Mitchell (1954, 1955, 1956) examined in detail the growth of a number of New Zealand pasture species and made frequent observations of

(a) tiller number and position of each new tiller
(b) number of leaves
(c) rate of elongation of successive leaves on the main stem.

The plants were not grown under sward conditions but were subjected to a range of light and temperature treatments. The influence of density on the growth form of subterranean clover plants is illustrated by Davidson (1954) in a series of photographs taken regularly but no data are given in the text of changes in leaf number per plant. Davidson and Donald (1958) record the number and size of leaves per plant in subterranean clover swards sown at four densities and subjected to four defoliation treatments. In an analysis of competition between plants of different initial seed sizes in swards of subterranean clover Black (1958a) distinguished between the growth of the individuals and the growth of the aggregate population. A steady decline in plant numbers occurred in all swards, and in the swards of mixed initial seed size it was due entirely to the loss of small seeded plants. Leaf distribution in vertical intervals of 2 cm. and number of leaves per plant were examined.

Growth Analysis.

Yield, L.A.I. and Light Intensity. The yield of pasture is usually expressed as the dry weight of the botanical components at a single cut. Occasionally a number of cuts are made and thus a curve of seasonal productivity may be obtained. The analysis of competition for light in terms of yield alone leads to speculation concerning the light micro-environment and is therefore unsatisfactory. Donald (1951) studied the growth of Wimmera Ryegrass and subterranean clover sown at a range of densities, on the basis of aggregate yield and yield per plant and attributes competitive effects in grasses to competition for nitrogen and in subterranean clover to competition for light. In further work (Donald 1958) a technique was developed to isolate competition for light and for nitrogen between two species of grass growing together, and by successfully isolating these factors yield was an adequate criterion in the analysis of competition. Bleasdale

(1956) suggests that the onset of competition between two species growing together may be shown by plotting the log of yield of one against the other. If the points fall about a curve of the hyperbolic type, the inflection signifies the onset of competition. He states that the data of Mann and Barnes on ryegrass and clover may be examined in this way. This however still does not give any information on the nature of competition.

Yield and its derived functions have been reviewed in detail by Watson (1952) and it is not intended to dwell on the methods of classical growth analysis except to discuss them in relation to the analysis of competition for light. Watson deals at length with the limitations of the concept of N.A.R. and shows that in general, dry matter yield depends more on variation in leaf area than in N.A.R. Though Watson regards the leaf area as a measure of the photosynthetic system of a crop he does not at this stage consciously consider competition for light. Ničiporovič (1956) on the other hand reviews much the same field in a series of lectures entitled "Photosynthesis and the theory of high crop yield" and sets out to show how yields might be increased if the absorption of light by crops can be improved. "Once the optimum leaf development is attained, further increases in yield can only be obtained by increasing either the efficiency of photosynthesis or the transfer of material to the economic parts of the plants". Donald and Black (1958) have stated the importance of measuring L.A.I. in studying pasture growth and have approached this from the point of view of light competition. "The ultimate criterion of the efficiency of the agriculture could be well expressed in terms of the proportion of the incoming light energy utilised by crops or pastures. In turn this will depend in considerable measure on the area of photosynthetic tissue displayed for the interception of light energy, in particular the area of leaf".

Since yield of dry matter and L.A.I. are significant growth attributes of pasture it is appropriate to discuss how they may be used to examine competition for light. In the first place it is desirable to obtain during a cycle of growth, as many values as possible, of yield (Klages 1933) and L.A.I. of each botanical component of the pasture. The primary considerations with respect to yield are whether a ceiling has been achieved and whether the botanical components are present in desirable proportions. The optimum and ceiling values of L.A.I. of the pasture (Donald and Black 1958) should be determined, and also whether the optimum has been reached in the shortest possible time (Ničiporovič 1956). Though the measurement of leaf area was tedious at one time, several rapid and reliable methods are now available (Milthorpe (Chap. 15) 1956, Donovan, Magee and Kalbfleisch 1958, Batyuk, Rybalko, Okanenko 1958, Jenkins 1959, Warren Wilson 1959) and these have facilitated the determination of L.A.I.

Yield and L.A.I. have been related in a number of ways. Davidson and Donald (1958) related the rate of dry matter production to L.A.I. and found that it reached a maximum about L.A.I. 4-5 and fell as the L.A.I. increased to 8-9. This is attributed to reductions in light intensity within the sward to below the compensation point, and rendering a portion of the sward "parasitic". The rate of leaf growth was reduced more than the rate of stem growth. In defoliation treatments it was shown that the increase in total weight in the sward in the ensuing four weeks was influenced by the L.A.I. at the beginning of this period, and this is again attributed to the L.A.I.-light relationship. Unfortunately light intensities were not recorded in this experiment. Langer (1959) in his studies of grass swards suggests competition for nutrients and tentatively for light, but provides no data in support of either. There is no doubt that competition for light exists in his swards of timothy and meadow fescue when he says "the leaf canopy will gradually tend to be raised". He shows that the weight of leaf per unit area remaining after cutting, influenced the rate of increment of living tissue after each cut. Brougham (1956) studied pasture during a month of regrowth after mowing to determine when the leaf surface was no longer efficient in absorbing all the incident light. He first examined the light being intercepted by the pasture during regrowth after it had been mown to different heights. Then he plotted

(a) a regression of L.A.I. on yield (Fig. 3);

(b) leaf efficiency index (rate of increase of herbage yield per L.A.I.) against time (Fig. 4);

(c) the daily dry matter increment on L.A.I. (Fig. 6).

The regression of L.A.I. on yield showed that in each treatment the rate of leaf area increase was similar to the rate of yield increase. With moderate defoliation the maximum leaf efficiency coincided with the complete light interception and with intense defoliation leaf efficiency was higher. The dry matter increment data showed that approximately constant rates were maintained when enough foliage had been formed to intercept most of the light.

Davidson and Philip (1956) working on Davidson's data (1956) and making certain assumptions, concerning light penetration in a pasture profile, a constant environment, constant respiration rate, etc., derived curves relating L.A.I. and N.A.R. (Fig. 9 in Davidson and Philip) and a family of curves relating the efficiency of production (Fig. 8 in Davidson and Philip) to L.A.I. The relationship between L.A.I. and N.A.R. showed a sharp initial rise of N.A.R. at L.A.I. values less than 2, and gradually falling away as L.A.I. increased. Watson (1958) examined the relation of L.A.I. and N.A.R. for kale and for sugar beet between L.A.I. values of 1 and 5, and for potatoes between L.A.I. 2 and 3; he plotted linear regressions in each case. The family of curves for the efficiency of production given by Davidson and Philip (1956) suggest that the rate of growth is greatest at certain light intensities and L.A.I. values and that the efficiency falls as the light intensity or L.A.I. departs from these values. Although this form of analysis may be quite valid with dry matter data, it may be more rewarding to apply it to data of gas exchange in sward. The comment by Monsi and Saeki (1953) "there exists for the production of the plant association at a defined light intensity an optimum amount of leaf, which in the final instance is also determined by the light intensity" underlines the importance of the changing interrelationship between light and L.A.I. In discussing productivity of photosynthesis as a factor in crop yield capacity Ničiporovič (1956) used N.A.R. and L.A.I. to calculate growth rates. He makes a prognosis of the optimum development of L.A.I. and N.A.R. and from these calculated the daily increment in dry matter which should be possible and also the optimum course of dry matter accumulation. He does not at any time relate L.A.I. and yield directly but discusses their relationship through light intensity.

The evidence clearly suggests that although the trends of yield and L.A.I. with time may describe the growth of a pasture, it is also necessary to record light intensity within the pasture to study competition for light. Since the area of leaves and their distribution determine the light gradient in the sward, these should be measured simultaneously. Monsi and Saeki (1953) were the first to attempt this with any degree of precision and studied the "productive structure" of a *Phragmites/Sanguisorbia* community by stratified cuts at intervals of 10 cm. and measured the light intensity at the surface of each layer. Monsi and Saeki use their results to discuss production under conditions of varying light intensity and infer competition for light between species in the association. Several workers in Japan have adopted the methods of Monsi and Saeki in the study of crop ecology. Similarly Alekseenko (1958) cut pastures in 10 cm. layers and took light readings at 20 cm. intervals. He merely recorded the structure of pasture without analysing growth. In a sward of subterranean clover consisting of a mixture of two contrasting seed sizes Black (1958a) (in a study already referred to) showed that plants originating from small seeds had their uppermost leaves located in an unfavourable light environment which was created by the plants from large seeds. The critical data were the leaf distribution expressed as the L.A.I. profile of the sward together with the light intensity profile of the sward.

The components of Leaf Area Index. While the analysis of leaf distribution in pasture clarifies the relationship between L.A.I. and light intensity, it does not provide any information concerning the nature of L.A.I. or its development and persistence in swards. In discussing the physiological analysis of variation in leaf area Watson (1952) draws attention to the fragmentary information within a species concerning

(a) increase in the number of growing points,

(b) leaf expansion,

(c) senescence and death.

The relative importance of each of these with regard to competition for light in pasture is of particular relevance to this review. The above points have been examined by Langer (1957) for grasses but not in relation to the light micro-environment. He investigated the growth of Timothy (Phleum pratense) and showed that the decline in the area of leaf of a whole plant began before maximum dry matter production was achieved, and that additional leaf area - from the continued production of tillers - was not enough to compensate for the loss through death.

The suggestion of a continuous turnover of leaves in clover swards (Brougham 1958a, Davidson and Donald 1958, Black 1958b) was examined by Brougham (1958b) who followed the development of individual leaves in swards of white clover, at different stages of growth after defoliation. Terminal bud leaves were labelled at six-day intervals, on seven occasions after defoliation. Thereafter a number of marked leaves were harvested every two days over a period of five weeks. The leaves were grouped in six categories according to their condition and colour and the following data were collected:

(a) individual petiole length;

(b) dry weight of the total number of petioles in each category;

(c) dry weight of the total amount of leaf lamina in each category;

(d) mean area per leaf in each class - derived from the leaf area/leaf weight ratio of various discs.

These studies were made with random samples of leaves and not on individual plants, and therefore are relevant to points (b) and (c) only, raised by Watson. They do not throw any light on the interrelationship between the individual plant and the entire population, but show the average trend in petiole and lamina development during a short period of regrowth in a dense clover sward, as competition for light becomes more severe.

There is still scope to study leaf initiation, expansion senescence and death and to investigate further the role of shading on the useful life, and ageing of a leaf in swards. Since grass has a determinate habit of growth in contrast to clover which has an indeterminate habit they will have to be studied separately.

Techniques.

The purpose of this section is to examine ways in which competition for light may be studied and outline some general principles to be kept in mind in planning an investigation. It is important to record light intensities within the sward in each experiment, and the problems of light measurements in pastures are discussed in section 2.4.0.

of the thesis. The way in which light readings are to be used, ought to be clearly understood at the outset of the investigation. It is not enough to show that light intensities are reduced, but necessary to indicate how competition for light occurs. Useful primary data is generally obtained if light readings are made at frequent intervals, both in space and in time. Monsi and his co-workers in Japan, Brougham in New Zealand and Black in South Australia have all made effective use of their light meters. Alekseenko, and Mitchell and Calder on the other hand have merely recorded light intensities.

Turning now to the plant material under examination. While directing attention to competition for light, care should be taken not to overlook simultaneous competition for other factors. The moisture characteristics of the soil need to be understood, the nutrient supply should be catered for, especially where relative uptake between species may differ and give one a competitive advantage over the other. The genetic background of the species under study and the response to temperature and photoperiod should be known. The best agronomic practices regarding planting material, method of planting etc. must be observed. Where an artificial treatment such as shading is imposed every precaution should be taken to guard against side effects: e.g. filtering of light, undesirable reflections, change in the temperature regime. In order to bring more factors under control, there has been a tendency to conduct competition studies with uniform plant material, using smaller plots, and to plant experiments in large containers (Caputa 1948, Black 1958a, Langer 1957). This degree of refinement is unnecessary where a high degree of uniformity of the plant material can be achieved in the field (Glenday 1955, 1959). If the analysis of competition for light is the sole objective, then the distinction between intra- and inter-specific competition is resolved into a study of competition with like and unlike growth forms.

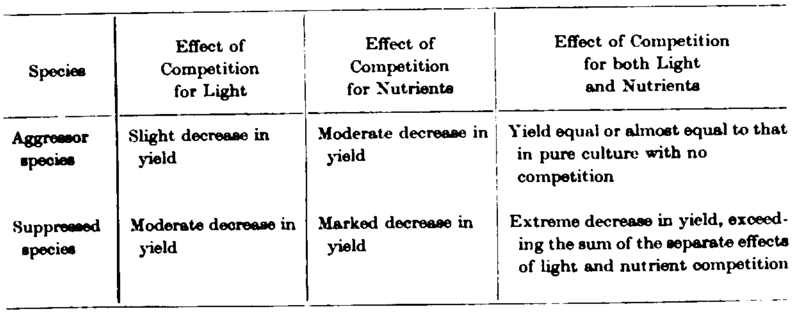
In pure cultures. The obvious means of bringing about different degrees of competitive stress in swards of a single species is to manipulate density at planting. Donald (1951) studied subterranean clover swards at 8 densities, Wimmera ryegrass at 10 densities and *Bromus* at 6 densities. Davidson (1954) studied subterranean clover swards at 5 densities. In the clover swards the effects observed are attributed to competition for light between individuals, and in the grasses to competition for nitrogen. Black (1957a) studied the growth of subterranean clover swards grown from seed of varying size. The relative growth rate of each sward slowed down as it approached an L.A.I. 4 and fell progressively until the swards reached a common ceiling yield. Light interception was deemed complete at L.A.I. 4. Previous work on the influence of seed size is discussed and the comment made that intra-specific competition was not a major consideration in these studies. The crucial argument in Black's paper is that the pattern of dry matter production of a sward depends on the initial cotyledon area per unit of ground - however this may be achieved - and this determines the time at which complete light interception occurs. Lawson and Rossiter (1958) sowed large and small seeds of two strains of subterranean clover at constant seeding rates per unit area and found no effect on the growth rate of the swards, i.e. seed size *per se* had no effect and total cotyledonary area was the criterion as in Black's study. These authors do not examine their results in terms of competition for light and suggest that consideration should be given to the early growth of roots. Black (1958a) sowed large and small seeds together and showed how large seeded plants suppressed small seeded plants. Similar effects of intra-specific competition may be obtained by manipulating the germination in swards so as to obtain a delay in establishment of a portion of the population - either by differential depth of sowing, or by different rates of germination amongst individuals.

Studies of this kind are dependent on the constancy of the relative growth rate in the absence of competition, and this condition only applies to genetically pure material. These studies also depend on a simple seed morphology and where the seed is almost wholly "embryo" without endosperm, as in the self-pollinating subterranean clover, a high degree of uniformity between plants from seed of the same size may be achieved. In other species, uniform seed size does not necessarily imply uniform relative growth rates, but there is no decisive evidence on this point.

<u>In mixed culture</u>. Mixed culture may mean the association of similar forms such as two clovers or two grasses, or the association of contrasting forms such as a clover and a grass. Whether the association be of like or unlike forms, the photoperiodic response of the species chosen for study should be kept in mind, so that any observed effects may be correctly attributed to competition for light without qualification in respect to photoperiodic effects. A uniform planting pattern is desirable so that the effects of competition for light may be evenly distributed throughout the association. Black (1960a) grew three swards of subterranean clover each consisting of two strains sown at high

densities; he examined petiole lengths, light profiles and vertical leaf distribution, and concluded that strain differences in petiole length determined the success of a strain under competition. That is, the success of a strain in a mixture depended on the relative location of foliage in respect to the incident light.

Donald (1958) discussed a technique to study competition for light and competition for nutrients and applied this to a study of competition between *Lolium* and *Phalaris*. A distinction is made between single factors and groups of factors, direct effects and indirect effects and the nature of interactions was examined. The findings were summarised qualitatively in the following way (Table 9):



Species	Effect of Competition for Light	Effect of Competition for Nutrients	Effect of Competition for both Light and Nutrients
Aggressor species	Slight decrease in yield	Moderate decrease in yield	Yield equal or almost equal to that in pure culture with no competition
Suppressed species	Moderate decrease in yield	Marked decrease in yield	Extreme decrease in yield, exceeding the sum of the separate effects of light and nutrient competition

The methods outlined for pure cultures can also be applied in mixed cultures. The density of the associate species may be varied. Black (1960b) grew lucerne and red clover in mixed stands in all combinations of 50, 250, 1250 and 6250 plants per square metre, i.e. in 16 combinations. Unfortunately there were only two harvests 17 days apart and the first one was made six weeks after emergence. Because of the shallow containers in which the swards were grown and in the absence of light readings, the analysis of these results is difficult and open to considerable speculation. Brougham's experiments with mixed herbage are concerned with regrowth after mowing, and they are not of sufficient duration to study the effects of competition between species. However, Brougham (1954, a, b, c) made use of this principle in earlier work, by varying the density of the component species in the mixture.

The only investigations where competition for light in associations of contrasting species was studied by examining the vertical distribution of L.A.I. and vegetative material in conjunction with the light profile, are those of Monsi and his school (1953, et seq.) in Japan. A *Phragmites/Sanguisorbia* association was selected for detailed study and cut on half a dozen occasions during the season. Although these authors claim that shading by *Phragmites* suppressed the *Sanguisorbia* the evidence is not sufficiently clear-cut to rule out the effect of an adverse photoperiodic influence in *Sanguisorbia*. Alekseenko (1958) cut sown pasture in horizontal layers on a number of occasions during a season and these were determined by the stage of development of the sward. He made no attempt to relate his findings to the analysis of growth, or competition for light.

Conclusion. A number of general conclusions may be drawn from this review. The first, is that an array of factors unrelated to light may influence procedure, and this must be considered if competition for light is to be successfully demonstrated. A standard planting is desirable in competition studies, and though this is most easily achieved by conducting experiments in large containers, it is possible also to obtain a high degree of uniformity in field plantings. Refinements in procedure will permit a reduction in plot size and possibly lead to a greater number of observations; the value of simple observations which are outlined in the text, such as changes in plant number during the course of an experiment, should not be underestimated. A prior evaluation of the nature of light competition may reveal some rewarding methods for measuring light within the experimental swards, and these will enhance the value of any growth data recorded. Growth analysis to be applied should be considered with some caution for while the rate of photosynthesis is dependent on light, the rate of respiration is not, and dry weights can only estimate the net result of these two processes. It may well be that gas analyses are the most effectual way of measuring the effects of competition for light on plants - but in the meantime much may be learnt by using the existing methods at our disposal.

2.4.0. The measurement of the light profile in a pasture.

A number of problems in ecological photometry need to be considered in relation to the measurement of light intensity in pastures. The earlier work has been summarised by Klugh (1925) but he does not deal with pastures. The factors involved in measuring light intensity in pasture can be conveniently grouped into photometric problems and ecological factors.

Photometric problems. The primary aim in measuring the light intensity in pasture is to assess the use of the incoming energy. In addition to measuring the amount of light, it is necessary to assess the quality of the light. Plant material acts as a selective filter and the wave-lengths therefore alter as the light percolates through the sward. The light energy depends on the colour of the light, and the reflection, absorption and transmission within the sward will influence the energy distribution. The wave-lengths most effective in photosynthesis have been established (0.3 - 0.76μ), but a variety of relations can exist between wave-length and photosynthetic efficiency, depending on anatomical structure, the nature and distribution of the pigments in the plant, and the energy content of the light absorbed. (Roussel 1953, Wassink and Stolwijk 1956). It is difficult to measure the light intensity available for photosynthesis, because there is no standard response curve for a plant in the same sense as there is a "standard eye", which enables illumination engineers to determine whether there is adequate lighting.

Since it is convenient to measure and express the light energy in pastures in units of visual photometry, it is important to specify the spectral sensitivity of the measuring apparatus (Mestre 1935) and to assess the response of the instrument to equal energy input at various wave-length within the range 0.3 to 0.76 μ . If this is done the results obtained by various workers can be converted to energy units and compared. It should also be possible to define a mean response curve for plants and this has already been attempted by Schulze (1956) (Fig. 11). Trickett, Moulsley and Edwards (1957) say that such a definition "must await the development of large controlled chambers with suitable lighting and the measurement of the spectral response absorption and transmission characteristics of living plant foliage in bulk". In the meantime much is to be gained by recognising an empiric relationship even if it has to be modified from time to time. Furthermore if the response curve were expressed in terms of absolute energy rather than illumination units it would clear up the confusion at present existing between illumination flux and energy distribution. If an arbitrary response curve of the anabolic process in assimilation as a function of wave-length were accepted it would lead to a clearer concept of the distribution and use of radiant energy in plant communities.

Consideration should be given to the direction of the incident light. Sunlight penetration into a sward depends on the angle of elevation of the sun, but diffuse radiation which is always present is a further source of energy. (Bleksley 1954, Jacobs 1955, Drummond 1958). The estimate of illumination also depends on the amount of diffuse radiation received, which is related to atmospheric turbidity and cloudiness (Smithsonian Tables 1951, Roussel 1953) and the type of

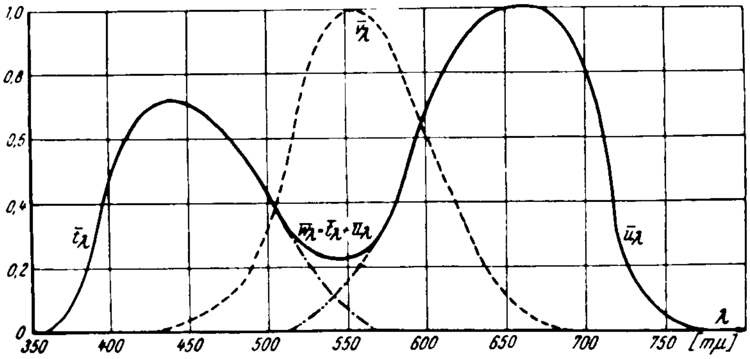


Fig. 11. - **Curves of CO_2 assimilation and eye sensitivity.** (after Schulze 1956).

receiving surface on the photocell and the plane in which the sensitive surface is exposed (Atkins, Poole and Stanbury 1937, Giovanelli 1953, McCree 1955, Trickett, Moulsley and Edwards 1957, Richardson 1959). The sensitivity of a flat-surface instrument falls off as the angle between the normal and incident beam increases (Walsh 1953, Keitz 1955) where as a spherical meter gives "an unambiguous estimation of the influx into a space" (Wassink and Scheer 1951, Wassink 1954). These authors attempted to relate daylight readings taken with a spherical instrument with those taken by a flat surface type of instrument and found that the conversion factor altered during the day. It is doubtful whether a correlation is warranted because the instruments do in fact measure the light intensities in different circumstances. Richardson (1959) showed that a spherical meter was less sensitive than a flat one to changes in the direction of light, but more sensitive to changes in light intensity due to vegetation. Atkins, Poole and Stanbury (1937) consider that a small sphere might be the best form of sensitive surface to measure the total illumination available for photosynthesis.

In photometry it is necessary to avoid measuring reflected light which is not ordinarily present and which may result from a disturbance of the system, such as the insertion of a photocell into a dense sward, or by bringing a reflecting surface close to the photocell.

Sunflecks within the canopy (Evans 1956) occur as light penetrates between leaves and are a source of variation of light readings. Light intensity may also vary where there are differences in plant density. Roussel (1953) reports studies which examined the shadow pattern in gaps occuring in forest canopies. The formula and diagrams he presents related the size and shape of the gap, the height of the trees, and the apparent motion of the sun. Such calculations can readily be made for any situation (Phillips 1951), but the circumstances must be adequately specified. In assessing the average light conditions in a pasture sward it is difficult to decide how readings are to be interpreted, especially if the incidence of sunflecks is high. Evans and Coombe (1959), by means of hemispherical photography, have developed a method by which sunlight penetration into forests can be examined in relation to the apparent motion of the sun and canopy characteristics. This makes it possible to determine whether any selected area is typical. It may be difficult to develop such techniques for pasture work but the existence of miniature cameras may make this possible.

Photocells may show a hysteresis effect with respect to temperature and this is often dependent on previous temperature history; the extent of this response also varies with the type of photocell (Sauberer 1958). Under humid conditions the photocell may deteriorate very quickly.

A number of photocells permanently placed on a grid system and connected to continuously recording devices would be the best apparatus for measuring the distribution of light intensity within a sward, for such readings would take into consideration day to day changes due to the angular distribution of daylight, diurnal movement of the leaves in the sward, and would indicate the incidence and distribution of sunflecks. A number of practical difficulties arise in such an arrangement: prolonged exposure of the photocell may cause a drift in the response which may presist for some time.

An interesting alternative is the use of chemical methods for measuring light (Leighton and Forbes 1930) and since these methods integrate the light received with respect to time, they might be readily adapted to studies of light in pastures. Their apparent advantages are independence from a directional effect of sunlight, economy, ease of handling, and the fact that readings can be made under a variety of climatic conditions. The spectral response of, and the effect of temperature on the reactions involved would need to be known. One of the difficulties for pasture work is that the vials would have to be small enough to be positioned with the minimum of disturbance to the sward. Dore (1958) notes a method which could have some application for pasture work.

The construction and calibration of small, portable and durable photocells is far easier today than it has been in the past. Although there are a number of problems associated with their use, these will be resolved as the methods of photometry are applied more widely. The important points that should be observed by the pasture ecologist are

(a) to define the spectral sensitivity of the apparatus used

and (b) to test the photocell under a standard light each time before taking it into the field.

Ecological Factors. The structure of a sward depends amongst other things on the species content, the density of sowing and the age of the pasture. In the early stages, leaf material predominates, but with further growth, stem development begins in the lower layers (Monsi and Saeki 1953, Alekseenko 1958). In a clover-dominant sward the leaf material forms the surface and is generally concentrated in a relatively narrow band with petiole and stem below. The leafy layer deepens as growth continues, and as a result the petioles and growing point may eventually be located in total darkness (Black 1958a, 1960a). After some time a residue of dead leaves and petioles litter the ground (Brougham 1958b). In grass pasture infloresences eventually dominate the surface of the pasture, shading the leafy layer beneath. Grass in mixed pasture may bring about significant reductions in light intensity due to stem and infloresence even at high angles of elevation of the sun. Though the surface of pasture may be homogeneous, it cannot be considered to be horizontal or uniform. It reflects, transmits and diffuses the light falling upon it; the patterns of the diffusion and reflection indicatrix depend on the angle of incidence of the light source and the nature and extent of the "crests" and "troughs" of the surface. In this regard a grass sward will obviously exhibit greater irregularities than a clover sward. The depth of the "troughs" and their direction with respect to the light source can create some apparent anomalies in light readings, and areas of high luminance may result from multiple reflection. The extent of this will in part depend on the reflecting and transmitting properties of the boundary planes i.e. the leaves, which cannot be regarded as being stationary.

Light absorption by leaves has been studied extensively and though individual results vary tremendously the magnitudes are generally of the same order (Moss and Loomis 1952, Kleshnin and Shul'gin

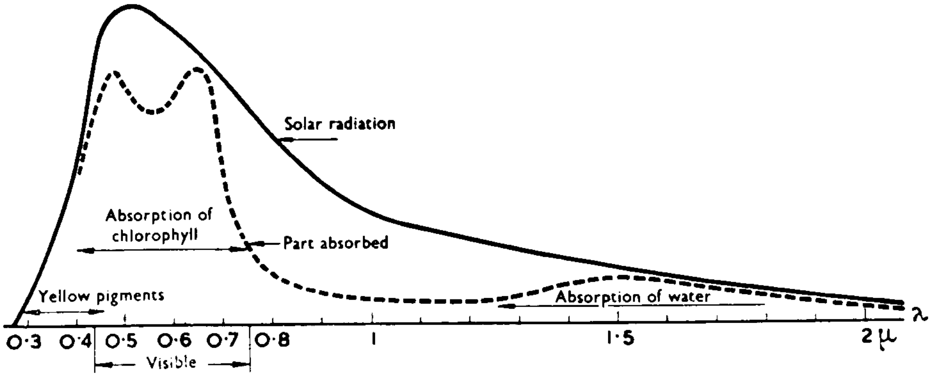


Fig. 12. - Composition of solar radiation and proportion absorbed by a leaf in each spectral region (after Terrien, Truffaut and Carles 1957).

1959). Approximately 30 per cent. of the incident light is reflected and transmitted and 70 per cent. absorbed. Absorption is greatest in the shorter wave-lengths (around 0.47μ), and Fig. 12 shows the amount of the incoming solar radiation absorbed by a leaf in the different wave-lengths. It is obvious that as the incoming energy passes through more and more leaves its composition will alter in favour of the higher wave-lengths (around 0.67μ). Sauberer (1937) suggested that readings taken in dense stands could be in serious error unless the instrument used is appropriately calibrated. Egle (1937) studied the distribution of the light intensity in deciduous forest during leaf development and found that the reduction in intensity is proportionately less in the red wave-lengths than in the blue. This applied to pasture as well, and was dependent on the angle of incidence of the light. Similarly, Coombe (1957) made the point that estimates of the daylight factor (page 99) could differ significantly, when instruments of different spectral sensitivity were used. Terrien, Truffaut and Carles (1957) attributed the difficulties in measuring the radiation dispersed by leaves to the insensitivity of the available measuring devices, and referred particularly to the radiation at higher wave-lengths. The published evidence indicates that most of the incoming radiant energy useful for assimilation can be absorbed by two leaves superimposed on each other (Knuchel 1914, Seybold 1932, Sidorin 1945, Rabideau, French and Holt 1946, Kasanaga and Monsi 1954). This will not be strictly true as the distance between leaves is increased or as leaf movement takes place. Shul'gin and Kleshnin (1959) claimed that the optical properties of leaves did not change when the chlorophyll concentration exceeded 3 mgm 100 cms^{-2} of leaf surface.

The movement of foliage could result from a number of stimuli. "Plant movements taking place under natural conditions result from a combination of the effects of both tropic (directional) and nastic (diffuse) stimuli". (Stiles 1936). The nyctinastic movements of leaves (so described because of their association with onset of night) are for the most part attributed to photonasty. Although this form of movement is very pronounced in the families Oxalidaceease and Leguminoseae, it can occur even in the Gramineae and Darwin (1880) has described circumnutation in Phalaris canariensis. Most grasses exhibit an involute curling of the upper leaves during periods of relative moisture deficiency, and some authors have expressed the view that all diurnal movements are in part attributable to this hydronasty. Bünning (1959) concludes that the light-dark change is the most important single factor leading to diurnal movements of leaves. Such movements lead to changes in the configuration of the pasture and, concurrently with the changes in the angular distribution of daylight, differences in the pattern of light penetration can be expected. The day to day differences in these patterns may be small and could be modified by existing conditions, but over longer periods, such as a month they may become significant. Daylength, azimuth and altitude of the sun at three latitudes in the southern hemisphere are tabulated for the 21st day of each month in Table 10. The differences in azimuth and altitude are of sufficient magnitude to influence the amplitude of the directional movement of leaves while changes in daylength would alter the duration or "rhythm" of these movements. (Bünning 1959, Holdsworth 1959).

Table 10

The daylength azimuth and altitude of the sun for the 21st day of each month.

(data kindly supplied by Mount Stromlo Observatory 1960).

At latitudes -30° (N.S.W. and Queensland border, and North of Perth) and
-35° (Albany, Adelaide, Canberra) and
-40° (North Island, New Zealand).

	Jan. 21st	Feb. 21st	Mar. 21st	April 21st	May 21st	June 21st	July 21st	Aug. 21st	Sept. 21st	Oct. 21st	Nov. 21st	Dec. 21st
Daylength												
-30°	13^h 46	12^h 59	12^h 07	11^h 12	10^h 31	10^h 13	10^h 29	11^h 12	12^h 06	12^h 59	13^h 46	14^h 05
-35°	14^h 07	13^h 10	12^h 06	11^h 01	10^h 11	9^h 48	10^h 09	11^h 01	12^h 06	13^h 11	14^h 08	14^h 30
-40°	14^h 32	13^h 24	12^h 08	10^h 48	9^h 46	9^h 20	9^h 45	10^h 48	12^h 05	13^h 23	14^h 33	15^h 01
Azimuth *												
-30°	66	77	90	104	114	118	114	104	91	78	67	62
-35°	65	76	90	105	115	119	116	105	91	77	65	61
-40°	63	75	90	106	117	122	118	106	91	76	63	58
Maximum Altitude **												
-30°	80	71	60	48	40	37	39	48	59	71	80	83
-35°	75	66	55	43	35	32	34	43	54	66	75	78
-40°	70	61	50	38	30	27	29	38	49	61	70	73

* At all longitudes between 100° E and 180° E
Rise: From S. over E. Set: From S. over W.

** between 11^h 44 and 0^h 16 local mean time

As seasonal changes take place, especially in radiation (de Wit's Fig. 14 1958), so leaf movement becomes more or less pronounced. With increasing leaf folding or rolling, shading by leaf laminae becomes less, and the shading by stems and petioles becomes more important. In winter, the uppermost leaves of a sward hardly fold or roll during the day and light penetration is negligible, but in summer leaf folding or rolling is more pronounced and the angle of elevation of the sun is greater. Consequently the light intensity within a sward is higher in summer than in winter (Brougham 1958a). This view is supported by the data of Monsi and Saeki (1953) which showed the dependence of the extinction coefficient (k) on the leaf angle and how at given L.A.I., the light intensity decreased as the leaf angle from the vertical increased (See Figs. 7 and 8). Fortanier (1954) showed that in <u>Arachis Hypogea</u> leaf movement was less pronounced at low light intensities than at high light intensities, but emphasised that this was a complex phenomenon depending not only on prevailing conditions, but also on the intensity, colour and duration of the preceding illumination (or period of darkness).

A generalisation on the influence of environmental factors on the light regime in pastures is difficult, without taking into account the time of the year, topographical features of the site, the stage of growth of the pasture and the instrument used in measuring the light intensities. Here, I only wish to refer to daily or topical changes that may modify a set of readings and which have to be considered in interpreting results that are obtained. In humid weather, the photocell may be unreliable and every care has to be taken to ensure that it continues to register. Water on the surface of vegetation alters the reflection and consequently absorption of light; this varies with the nature of the vegetation and depends on whether it is overcast (Smithsonian Tables 1951). On windy days, leaf movement increases the variability of light readings and where the vegetation is short substantial errors in light intensity readings may occur. Solar altitude and sky conditions may alter the relative spectral distribution of radiation. Table 11 shows the mean relative cloudiness of each month, at the Waite Institute, Adelaide. This ranges from 36 per cent. in mid-summer to 68 per cent. in mid-winter. During this period daylength becomes 4 hours shorter, the angle of elevation of the sun falls by 42°, and the azimuth changes by 52°.

Table 11

Mean relative cloudiness for each month at the Waite Institute (average for the years 1925-59 incl.). The values are mean daily hours under cloud, expressed as a percentage of daylength.

Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
36	36	39	50	61	67	68	59	51	49	44	42

Hisdal (1959) has shown that the relative spectral distribution of radiation appears to remain reasonably constant in a narrow waveband around 0.46μ and that the greatest variation occurs at wavelengths of about 0.34 μ and 0.59 μ .

It is nevertheless possible to outline some guiding principles to obtain readings which are significant in ecological studies, and which can be related to one another.

Most light measurements in ecology are expressed as the "daylight factor", which is "the ratio of the illumination measured at a point inside the vegetation to that on a horizontal plane in the open, under an unobstructed hemisphere of sky of uniform luminance" (Walsh 1953). Although light intensity readings expressed as percentage of full daylight may show variations of the order of 5-10 per cent. during a day, or under varying sky conditions, it is none the less a satisfactory way of describing the average lighting conditions within an ecological association (Atkins, Poole and Stanbury 1937, Monsi and Saeki 1953). With a thoroughly diffuse sky, there is no marked directional effect of sunlight, abberant reflections and the incidence of sunflecks are reduced to a minimum, leaf movement is less pronounced and consequently the light regime within the vegetation is less variable and easier to measure. On such days the light intensities are lower, more within the range of a sensitive photocell, and the dependence of the photocell on angular response is minimised. Consequently less errors are likely to accrue in assessing a light profile in pastures by taking readings within an hour of local noon on days when the light is uniformly diffused. When it comes to measuring light intensity in pastures there is little scope for controlling the ecological variables. The best that can be done is to be consistent in applying the methods of photometry to ensure that the sample of vegetation being examined is normal for its particular stage of development. Mestre (1953) makes the point that "first approximation" data on biological material of "indeterminate physiological states" is not as valuable as a general agreement on instrumental methods. While this may be partly true intelligent measurements can still be made if the performance of the instrument is adequately defined. Similarly the physiological state of the biological material should be described so that some assessment may be made of the use of the incoming energy.

Concluding Remarks. The importance of light in ecological studies has long been recognised (Salisbury 1929, Shirley 1935, 1945, Burkholder 1936) but in view of the difficulties in measuring the average light conditions in natural vegetation, studies of this kind have not always been fully developed. Black (1957b) has reviewed the literature on the influence of varying light intensity on the growth of herbage plants, and it is evident that a great deal more is to be learnt about the light microclimate in pastures. The techniques at present available can give accuracy of the order of 5 per cent. under the *best* experimental conditions (Brougham's Table 1, 1958a), but accuracy of a lower order, say 10 to 15 per cent. is often adequate to describe the role of light in the ecology of pasture associations. In practice many of the sources of error can be minimised and provided the results are reproducable, it may be said that the existing techniques of light measurement can be applied to pasture studies with some degree of confidence, so long as the circumstances in which these measurements are made are clearly recognised.

3.0.0. THE PROGRAMME OF INVESTIGATION.

In this section a brief account is given of the philosophy behind the specific experiments presented in this thesis.

3.1.0. The extent to which one species alters the light to another in mixed culture.

Where two species are grown in close association, the extent to which one alters the light to the other may vary as the height and form of each species changes during the growing season. In Experiment A, four nitrogen treatments were applied to mixtures which consisted initially of equal numbers of grass and clover plants, resulting in an almost pure clover stand on the one hand and an almost pure grass stand on the other, with two intermediate mixtures. Thus, it was possible to study the light micro-climate within pastures of varying botanical composition, and to examine the nature and degree of competition for light between grass and clover in swards to which various levels of nitrogen had been applied.

3.2.0. The light gradient in clover swards.

Pure stands of pasture plants of varying initial densities may eventually reach similar yields (Donald 1951) and L.A.I. values (Davidson 1954). Because of differences in the course of development, differences in leaf arrangement within swards may be expected, and consequently differences in the penetration of incident light. In Experiment C, the light profiles in clover swards at three densities were compared at certain times, and again at similar L.A.I. values independently of time.

3.3.0. The recovery of clover swards from varying periods of shading by grass.

Shading of clover by grass in a mixed pasture is often of a temporary nature only. Whilst clear-cut effects on the growth of individual species have been shown in shading and transfer studies (Blackman and Wilson 1951, Blackman and Black 1959) it is not known what degree of shading clover in mixed swards can tolerate or how it recovers when adequate light is again available, after varying periods of shade. In Experiment A, clover showed a temporary set-back only at one level of nitrogen (N 3) but was almost completely eliminated from the swards at a higher level of nitrogen (N 4), due to the effects of shading by grass.

In Experiment B, competition between grass and clover was restricted to competition for light, by separating the underground growth of species. Clover was transferred from mixed association to pure clover stands on several occasions as the experiment progressed, and the growth of clover was examined while shaded by grass, and subsequently after transfer to a more favourable light environment. The shading of clover for varying periods can be considered as "light shortage treatments" of different duration and may be likened in some respects to different degrees of water stress in soil moisture studies.

3.4.0. A study of individual plants and leaves in pure stands of subterranean clover.

In applying L.A.I. concepts to problems of pasture growth, significant changes within swards were postulated at optimum and ceiling

L.A.I. (Donald and Black 1958). Essentially, these ideas conceive the continuous formation of new leaves and a loss of older ones, beginning with the attainment of optimum L.A.I.; as L.A.I. rises above the optimum, an increasing number of older leaves die until at ceiling L.A.I., an equilibrium is reached between leaf initiation and expansion on the one hand and leaf death on the other. The proposals arose from studies with swards of subterranean clover and had to be confirmed by detailed investigation. An experiment was designed to examine the course of L.A.I. development in terms of new leaves, of leaf expansion, and senescence and death of leaves, in conjunction with the light profile in the sward.

In Experiment C, subterranean clover swards were grown at three densities for five months after emergence when flowering began. Every new leaf was labelled on a number plants selected at the beginning of the experiment, for detailed study in each density. At frequent intervals a few of these plants were harvested and analysed. The area of each leaf lamina was measured, petiole lengths were measured and the leaves were weighed individually. It was thus possible to break down L.A.I. into its component parts, and to examine the growth and development of individual plants in the swards.

Since this experiment was conducted, Brougham (1958b) published a study in which the L.A.I. of white clover swards was examined in terms of new and atrophying leaves, and the longevity of clover leaves was determined. Additional features of Experiment C were the account of the sequence in which leaves were developed on individual plants and the position at which they were held in the sward. In this experiment leaf development was examined from the viewpoint of competition, principally competition for light, and this gave a difference in emphasis between the two studies.

4.0.0 METHODS.

The major experiments were undertaken out-of-doors during the growing season from May to November in the years 1957, 1958 and 1959. The sequence of presentation is not chronological and has been adopted to introduce the three major experiments in logical order. Experiments A and B were performed in 1957 and 1959 respectively, and examine a number of aspects of the associated growth of grass and clover (see sections 3.1.0 and 3.3.0). Experiment C was conducted in 1958 and deals with the growth of individual plants in pure clover swards. All the experiments involved detailed analyses of the plant material and for this reason as many variables as possible were controlled. The soil conditions were carefully managed by conducting the experiments in large boxes or arrangements of boxes; the packing of the soil, the nutrient and water supply were adjusted as desired. All seed was sieved and further grading for specific gravity in one experiment ensured uniformity in the initial planting material. Depth of sowing was carefully regulated at all times. In Experiment A harvesting techniques were developed to cut the vegetation at short, equal, vertical intervals. In Experiment B techniques were evolved to allow the plants above ground to grow in intimate association but at the same time to eliminate competition underground and to study independently competition for light between species. In Experiment C, a similar arrangement of long narrow boxes was used to study the development of individual plants in a sward. The labelling of individual leaves was an important feature of the methods used in this experiment. The species used in these experiments were subterranean clover (*Trifolium subterraneum*) and Wimmera Rye Grass (*Lolium rigidum*). They are frequently grown together in sown pasture, and have proved suitable for studies of this kind.

Daylight readings were made with a Weston Illumination Meter Model 756 and light intensity in the pasture profile was measured with a small selenium barrier layer cell developed at the Dominion Physical Laboratory in New Zealand (Barrowman 1956). The same light meter and photocell were used in all the experiments; during 1958 a bubble was fitted to the photocell to ensure that it was exposed horizontally at all times.

4.1.0. Experiment A: The influence of nitrogen on grass and clover swards.

4.1.1. Outline of experiment.

In this study, initially identical grass/clover swards were subjected to varying nitrogen treatments with a view to developing swards of different botanical composition. The resulting swards ranged in a graded series from clover dominance to grass dominance. The swards were harvested in horizontal layers 3.5 cm deep to determine the vertical distribution of foliage and dry matter of the component species. Profile measurements of light intensity were made frequently during the experiment to assess how one species varied the light to the other. So as to eliminate unnecessary soil variation and to ensure good control over the swards the experiment was conducted in large boxes.

4.1.2. Details of experiment.

Sixteen boxes about 75 cm square and 45 cm deep were filled with a soil mixture containing 10 per cent. of Urrbrae Loam and 90 per cent. of Plympton sand, each known to be low in nitrogen. A basal dressing of phosphorus, potassium, sulphur, calcium, magnesium and the minor elements copper, zinc, boron, molybdenum applied in dilute solutiona as shown in Table 12.

The soil was levelled and a wire grid was placed on the surface to delimit plot and boundary areas (see Plate 1). There were five harvest strips each 10 cm x 60 cm with buffer zones 4 cm wide between them; each strip was divided into 3 "quadrats" of 10 cm x 20 cm.

Table 12.

Basal fertilizer dressing in Experiment A showing the element form in which applied and quantity.

Element	Equivalent of element in pounds per acre	Form applied	Quantity per box in gms.
P	75	KH_2PO_4	17.0
Ca	360	$CaCl_2 \cdot 6H_2O$	127.2
S	100	K_2SO_4 and in minor elements	14.6
K	175	Applied as KH_2PO_4 & K_2SO_4	
Mg	40	$MgSO_4 \cdot 7H_2O$	28.3
Cu	1.8	$CuSO_4 \cdot 5H_2O$	0.458
Zn	1.6	$ZnSO_4 \cdot 7H_2O$	0.458
Bo	0.6	H_3Bo3	0.229
Mo	2 ozs/acre Ammonium Molybdate		0.0081
Mn	3.5	$MnSO_4 \cdot 4H_2O$	0.916

All nutrients were applied on July 5th except P which was applied on June 28th and Ca which was applied on July 8th.

Plate 1. A single large box in experiment A at planting, showing wire grid resting on soil surface.

Thus 15 "quadrats" 10 cm x 20 cm (or about $\frac{1}{2}$ square link) were available in each box (See Fig. 13).

On July 10th excess seed of Tallarook subterranean clover (7.93 mgm per seed, $<$ 2.50 mm $>$ 2.25 mm diameter) and of Wimmera Rye Grass (2.60 mg per seed, $<$ 20.0 x 1.0 mm and $>$ 20.0 x 0.75 mm) was sown. Emergence took place on July 23rd and the stand was thinned on July 30th to 24 seedlings per dm^2 of each species. Each "quadrat" and the buffer zones were sown separately to obtain an even distribution of plants over the whole box, and the seed was covered with approximately 0.5 cm of sand. Each replicate of each nitrogen treatment (Table 13) was in a separate box, and the 16 boxes were arranged in a Latin Square. (Fig. 13, Plates 2a, 2b). The boxes in the experiment were:

$$\begin{pmatrix}\text{Levels of}\\ \text{nitrogen}\\ \\ 4\end{pmatrix} \times \begin{pmatrix}\text{Replicates}\\ \\ \\ 4\end{pmatrix} = 16 \text{ boxes}$$

In each box a harvest was made on five occasions, so that the harvests were:

$$\begin{pmatrix}\text{Levels of}\\ \text{nitrogen}\\ \\ 4\end{pmatrix} \times \begin{pmatrix}\text{Replicate}\\ \text{boxes}\\ \\ 4\end{pmatrix} \times \begin{pmatrix}\text{Harvest}\\ \text{Occasions}\\ \\ 5\end{pmatrix} = 80 \text{ Harvests}$$

The four nitrogen treatments are shown in Table 13.

Each harvest of each nitrogen treatment comprised one strip 60 cm x 20 cm and the strips were harvested serially. Each box in a replicate was harvested from a different direction as shown in Figure 13. At each harvest, two of the three "quadrats" within the strip were cut in successive horizontal layers 3.5 cm deep and the remaining

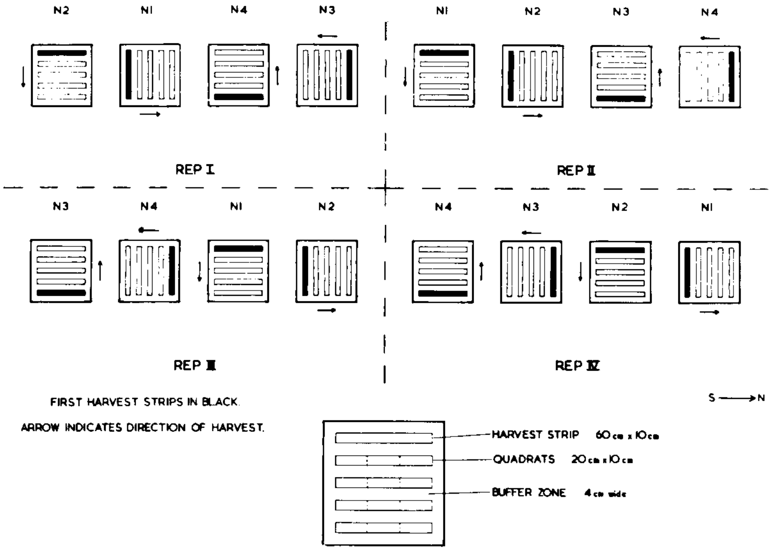


Fig. 13. - The Layout of Experiment A.

one was harvested by a single cut at ground level. This quadrat will be referred to as "the whole-plant-quadrat".

Table 13.

Nitrogen treatments in Experiment A, showing the amount applied at each dressing.

Treatment	Ammonium Nitrate g per box				Total Nitrogen applied	
	Days from sowing			Total	pounds/acre	$g\ m^{-2}$
	36	44	52			
N 1	-	-	-	-	Nil	Nil
N 2	2.3	2.3	-	4.6	22.4	2.5
N 3	6.9	6.9	-	13.8	67.2	7.5
N 4	13.8	13.8	13.8	41.4	201.6	22.5

Table 14 shows the number of layers harvested for each species on each sampling occasion.

In order to eliminate edge effects due to lateral illumination, frames consisting of arc mesh covered by a double thickness of hessian were used as a border around the swards (see Plate 2b); they were progressively raised so that the upper edges were level with the surface of the sward. After a strip was harvested a frame on the side of the exposed border was moved to the new boundary.

Table 14.

The number of horizons harvested for grass and for clover, on each of the five sampling occasions.

Days from sowing	67		84		99		113		133	
Date	Sept. 14th		Oct. 1st		Oct. 16th		Oct. 30th		Nov. 19th	
Treatment	Clover	Grass	Clover	Grass	Clover	Grass	Clover	Grass	Clover	Grass
N 1	2	2	3	4	7	8	10	12	14	17
N 2	2	3	3	4	7	8	11	13	15	19
N 3	2	4	4	6	8	10	11	14	17	21
N 4	3	5	5	9	10	15	11	21	11	26

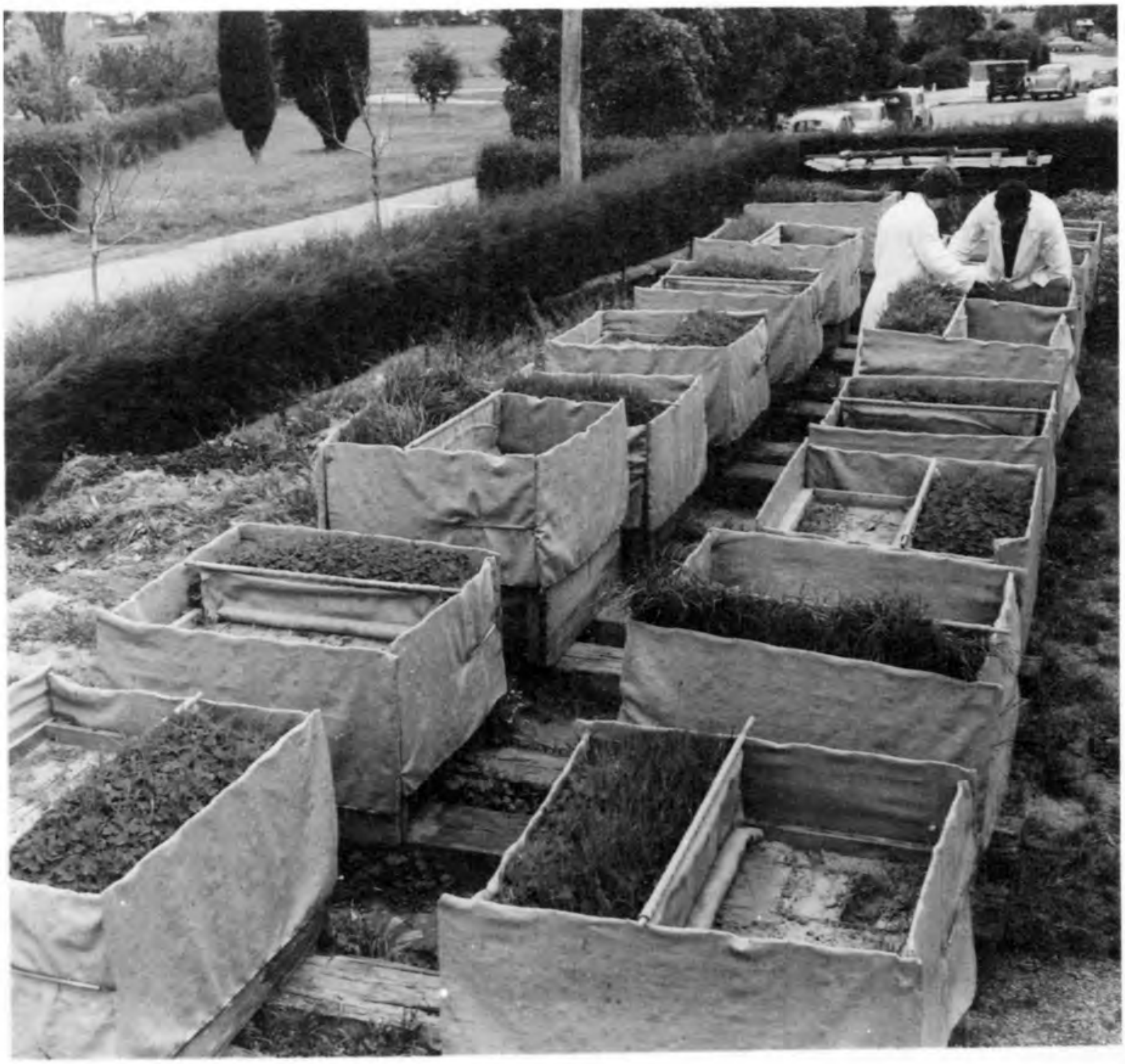
Plate 2. A general view facing North, of Experiment A.

(a) On the day of sowing - July 10th, 1957.
The numbers on the boxes refer to
nitrogen treatments.


2
1
4
3
3

Plate 2. A general view facing North, of Experiment A.

(b) At harvest 3 on October 17th, 1957. Note the side-covers to prevent lateral illumination.



To ensure accurate cutting at the desired heights above ground level, a series of special wire frames were used (see Plate 1). The area of these was 10 cm x 20 cm (the size of a "quadrat") and they were supported by four legs which fitted onto the wire grid resting on the surface of the soil. The tallest frame was 52.5 cm high, and the fifteen frames decreased in height at intervals of 3.5 cm; i.e. the dimensions of the frames were 10 cm x 20 cm x 3.5 (x) cm where X is the number of the frame. For cuts above 52.5 cm the shorter frames rested on the tallest frame. A frame was selected which when placed in position, was within 3.5 cm of the top of the foliage; the vegetation was then cut back level with the surface, as shown in Plate 3a, 3 b. The next frame which was 3.5 cm shorter was then placed in position and the protruding vegetation was again cut, and so on until the last cut was made at ground level.

A pair of hand shears was modified by glueing and bolting $\frac{1}{4}$ inch rubber to the blades (see Plate 4); the rubber held the vegetation which was severed with each cut, and, loss of plant material was negligible even under windy conditions.

For the first two harvests, the material obtained in this way was separated into grass and clover and sub-sampled to determine the proportion of leaf and stem. The procedure was modified as quantity of material to be handled increased. From the third harvest onward, a subsample was obtained from each sample and was separated into grass and clover. The replicates of the grass and clover which had been separated in the sub-sample from each layer were then pooled within layers and further subsampled for determination of leaf, stem, dead leaf

Plate 3. Close-up views of the technique of harvesting in layers, in Experiment A.

(a) A frame in position on the "quadrat" with shears resting on the surface of the frame, ready to cut the protruding vegetation.

Plate 3. Close-up views of the technique of harvesting in layers, in Experiment A.

(b) Showing how the plant material is held by the shears after being cut.

Plate 4. Hand-shears with 0.65 cm rubber fitted to the blades to hold cut vegetation. Metal supports are braised to the edge of the blades near the points to hold the rubber firmly in position.

and dead stem. The samples from the whole-plant-quadrats were separated into grass and clover, plant counts made, and the weight of dry matter determined. These weights served as a check on the aggregate yield of the material which had been harvested in many layers.

Leaf area determinations were made on the leaf fractions described above, using the airflow planimeter described by Jenkins (1959). With this method both whole leaves and leaf fragments were dealt with satisfactorily.

Some assessment of the angle of disposition of grass leaves in each layer was attempted; assuming an accurate vertical cut at 3.5 cm interval, the angle of the grass leaf from the vertical may be calculated from a measurement of the length of the piece of leaf, cut at both ends. This method was sufficiently accurate to measure differences greater than 15° in the slope of leaves, but because of the very high densities used in the experiment the angle at which the grass leaves were subtended was almost vertical and consequently no real differences could be established. These results are not presented.

Light intensity in the sward was measured at intervals of 3.5 cm upward from the ground surface (i.e. at the surface of each layer that was cut) at five positions in each sward, at approximately weekly intervals during the experiment. Barrowman (1956) has described the apparatus, and the way in which it was used followed very closely the method outlined by Black (1958) (See Plate 8).

4.2.0. Experiment B: The recovery of clover from varying periods of shading by grass.

4.2.1. Outline of experiment.

A study was made of the recovery of clover from progressively longer periods of shading by grass. Mixed grass and clover swards were grown in discrete narrow boxes which were held together by clamps (Plates 5a, 5b), and which could be rearranged without destroying the swards or the necessity of transplanting. A number of clover boxes were removed from the mixed swards each week for eight weeks; their growth was recorded prior to transfer, and after transfer in the absence of grass shading. The density of clover plants was held constant throughout the experiment. By growing grass and clover in separate boxes, competition for water and nutrients between species was eliminated and it was feasible to study the light factor independently. Pure clover swards were grown under similar conditions as a control.

Light profiles were measured during the experiment to determine the light intensity in mixed culture at the surface of the clover.

Weight of dry matter and L.A.I. of the component species, plant number and leaf number in clover were the primary data collected.

4.2.2. Details of experiment.

These boxes hereafter referred to as "panels" consisted of wood with galvanised iron sides. The timber framework consisted of pieces 2.5 cm x 2.5 cm planed all round, 45.0 cm long for the base, and

Plate 5. A close-up view of a mixed sward in Experiment B.

(a) June 1st, 1959 - 15 days from sowing. Showing the arrangement of alternate grass and clover panels. The internal dimensions of the panels are 2.5 cm x 40 cm. Matchsticks 8 cm from the edge indicate borders.

Clover - 11 days after emergence.
Grass - 3 days after emergence.

Plate 5. A close-up view of a mixed sward in Experiment B.

(b) June 29th, 1959 - 43 days from sowing. Showing growth of grass and clover in intimate association. The edges of the panels are just discernible at the bottom and at the top of the photograph.

Clover - 39 days after emergence.
Grass - 31 days after emergence.

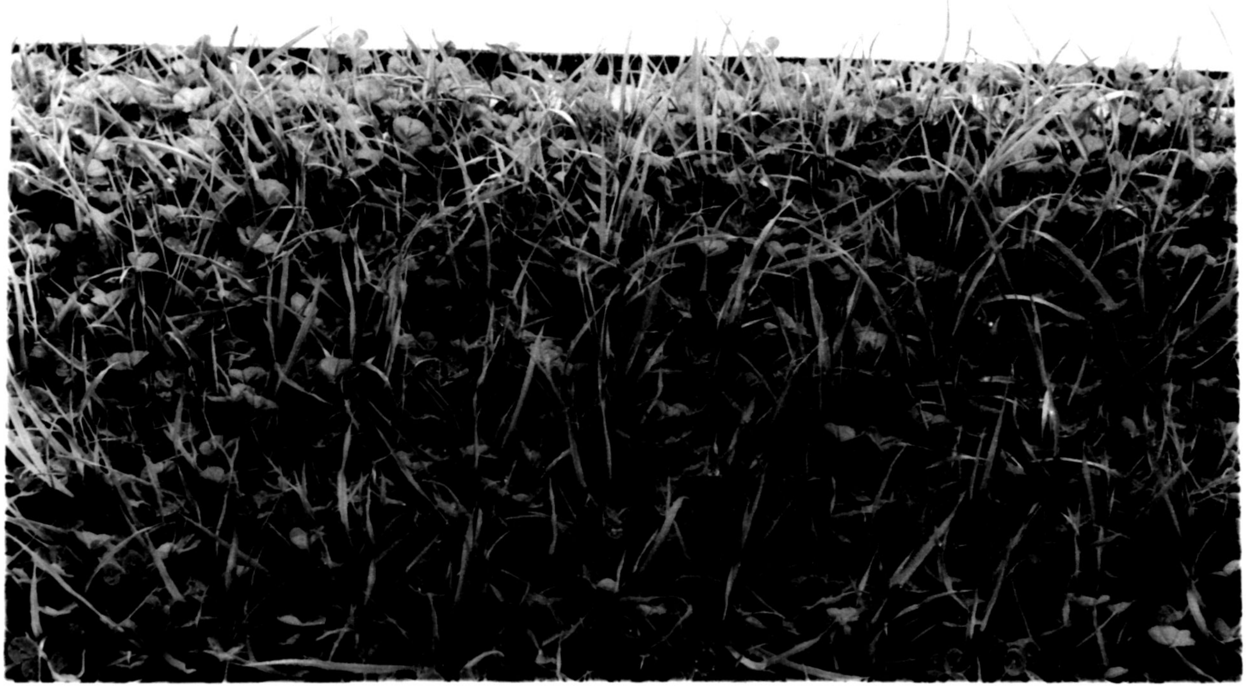


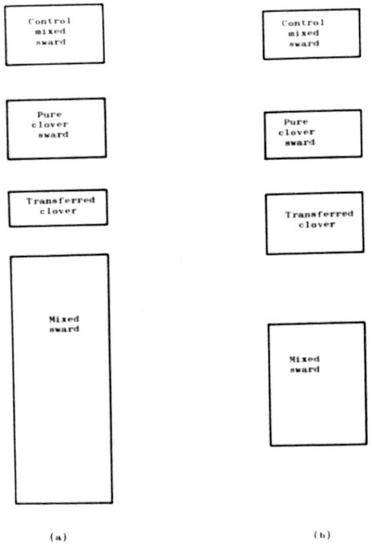
Plate 6. A general view facing North of two replicates in Experiment B.

(a) June 1st, 1959. - 15 days from sowing. The match-sticks (8 cm from the edge of each panel) which define the sampling area can be clearly seen in many of the panels.

(b) July 23rd, 1959. - 67 days from sowing. "Jutex" side-cover protect the swards against wind.

Rep. 1

on left hand side of both photographs



KEY TO BOTH PLATES

43.0 cm long for the two verticals; the other two sides of the panel were made up of 24 gauge galvanised iron 45.0 cm x 45.0 cm fixed to the timber with flat headed nails. The internal dimensions of each panel were 2.5 cm x 40 cm and 43 cm deep, giving a surface soil area of 100 cm^2. The border at each end of the sward was made up of a pair of panels twice as wide as those in the swards, i.e. 5.0 cm x 40.0 cm each. All panels were painted inside and out with a clear lead-free paint.

For ease of handling the panels were arranged in their respective groups before being filled with soil. The groupings within each replicate represent the main treatments and were as follows:

(a) Control pure sward: consisting of clover panels only.

(b) Control mixed sward: consisting of alternate grass and clover panels (Plate 7) from which regular harvests were made.

(c) Mixed sward:

  i. Also consisted of alternate grass and clover panels, but about two months after sowing clover panels were transferred weekly from this sward for eight weeks and the accompanying grass panels were discarded.

  ii. On transfer, the clover panels from (i) were grouped into a pure clover sward in the absence of grass. The initial requirement of this second group were border panels of pure clover.

At the beginning of the experiment each replicate consisted of clover panels and grass panels arranged in three groups as shown and a set of separate borders to which clover panels were transferred later. (See Plate 6a). Each group of panels was held together with carpenter's clamps and piping as shown in Plates 6a and 6b. The panels were stood in troughs 10 cm deep, which could be filled with water, or drained as required.

There were three replicates in the experiment.

The soil was a sterilized potting compost. To prevent bulging of panels and to ensure uniform packing of soil one third of the weight of soil destined for each panel was placed in alternate panels, beginning from the middle and working outwards, and was tamped to fit into a determined volume. Soil was then added to the intermediate panels and this procedure was continued until all the panels were filled to within 2.5 cm of the surface. 4.3 Kg of oven-dry soil was added to each of the narrow panels and 8.6 Kg to each of the larger ones, giving a soil density of 1.03. Frequent watering prior to planting allowed the soil to settle.

The moisture characteristics of the soil in these panels had been determined in the previous year for Experiment C. Tests with tensiometers of a modified design (Sedgley and Millington 1957) showed that when the panels were saturated at the surface and allowed to drain for 24 hours, the approximate suction in the middle of each panel was in the range indicated in Fig. 14. Inspection of Fig. 14 suggests that within the range shown neither air nor water would have had much influence in limiting growth. On days when evaporation was higher than usual the troughs in which the panels were standing were filled with water, generally for not longer than 12 hours at a time.

The panels were filled with soil on May 11th and the appropriate

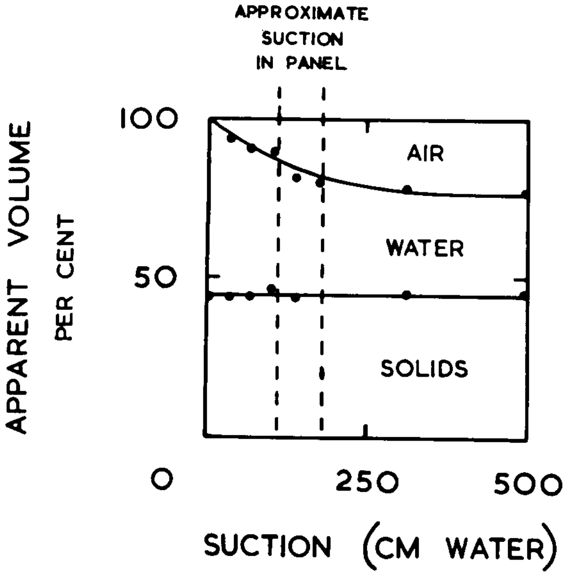
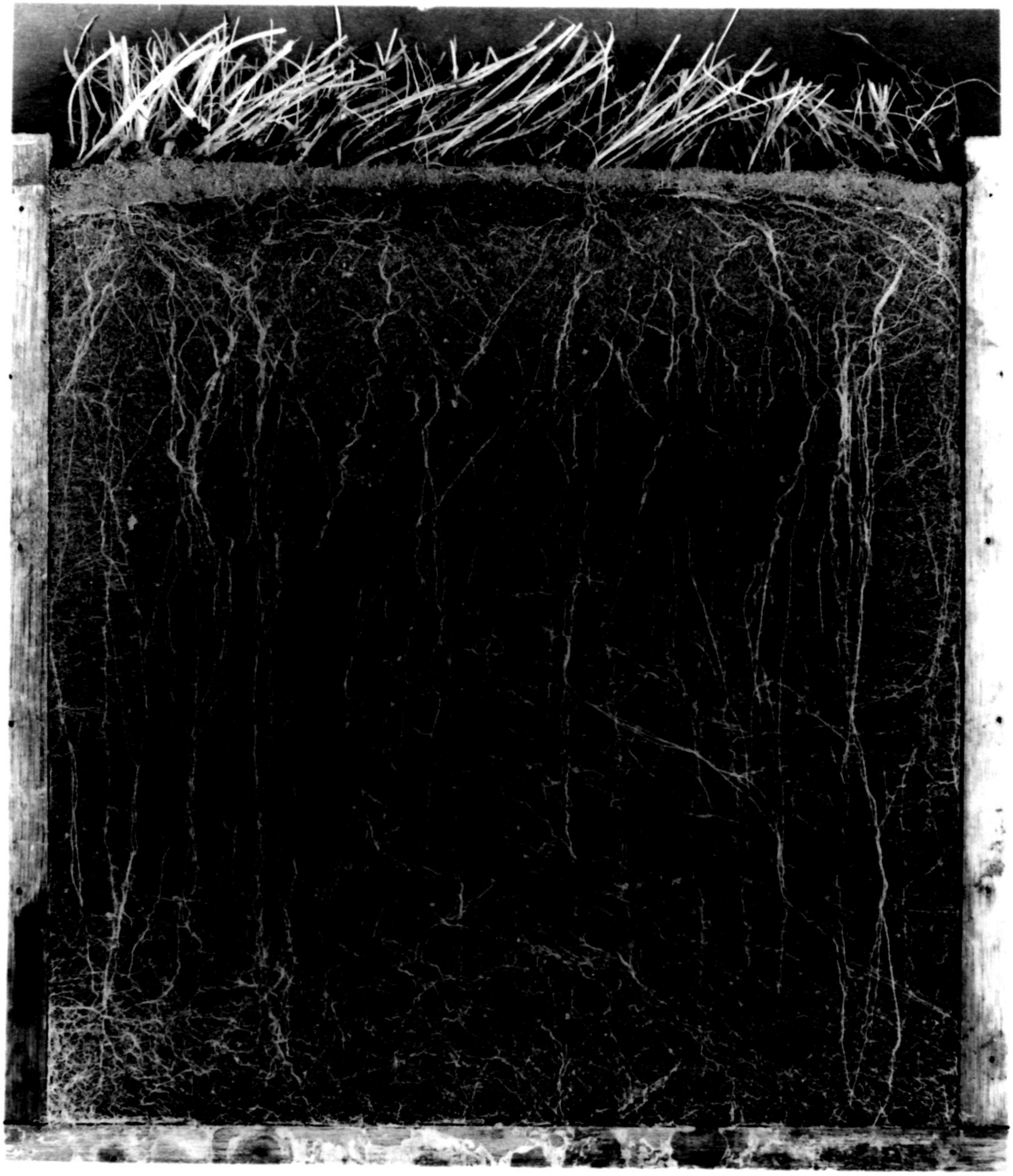


Fig. 14. - Moisture characteristics of the soil in Experiment B. A panel filled with water and allowed to drain for 24 hours contained approximately 45 per cent. solids, 36 per cent. water and 18 per cent. air by volume. The suction in the panel was in the range of 110-180 cm water.

Plate 7. Root growth in Experiment B.

September 14th, 1959. - 120 days from sowing. One side of a border panel sown to grass and clover was removed to expose the roots in the soil. The internal dimensions of the panel are 40 cm wide and 43 cm deep.



rhizobial culture applied on May 13th. On May 14th and 15th, an excess of Bacchus Marsh subterranean clover seed (10.5 mgm per seed) was sown in the appropriate panels. Clover emerged on May 21st and was thinned to give a stand of 28 plants per panel. On May 18th, an excess of Wimmera Rye Grass seed (2.695 mg per seed) was sown, this emerged on May 29th and was thinned to give a stand of 33-34 plants per panel. Soon after emergence, markers were placed in all the panels 8 cm from each end (Plate 6a) to define a sampling area in each panel 24 cm x 2.5 cm, i.e. 60 cm^2. In view of the staggered planting, May 17th, 1959 may be considered the mean sowing date. This corresponds closely with the sowing date of Experiment C, and provides a basis for comparing the results from these two experiments without the necessity of considering any possible photoperiodic effects.

The number of plants per panel in each clover box is intermediate between the two higher densities used in Experiment C (Section 4.3.0., Page 132) and it could be expected that mortality of plants in pure stands of clover at this density would not begin until 110-120 days from sowing. This was an important consideration in designing the experiment, for if suppression of clover due to overshadowing by grass were to be demonstrated, it was important that the decline in number of clover plants was not initially due to intra-specific competition.

Ammonium nitrate in solution was applied separately to each panel as shown in Table 15. The dressing to clover was a moderate one, served as a mild boost, and corrected a temporary nutrient imbalance which appeared during the experiment.

Although an adequate border of plants was provided in each treat-

Table 15.

The time of application and the amount of nitrogen applied to individual panels in Experiment B.

Days from sowing	Ammonium Nitrate g per panel	
	Grass	Clover
22	0.184	-
33	0.184	-
40	-	0.184
47	0.184	-
60	0.184	-
68	0.184	-
80	0.184	-
Total	1.104	0.184
N applied Pounds per acre	286.3	47.7
$g\ m^{-2}$	32.10	5.35

ment, protective side covers of a heavy grade of material commercially known as "Jutex" were erected with the dual purpose of preventing damage by excessive wind, and reducing side illumination into the sward. These covers were first raised about 6 weeks from sowing and further raised as required. (See Plate 6b).

The main group of treatments in the experiment were outlined when describing the arrangement of panels. The harvest and transfer details in a replicate are set out in Table 16. Because the times of transfer were fixed and because of the time involved in rearranging the swards, harvests were staggered so that the work was evenly distributed over the experiment. In the pure clover swards there were 11 harvests which were made by harvesting and removing a panel at random from the sward. In the control mixed sward a clover panel and an adjacent grass panel were removed at each harvest. Although there was provision for more harvests, only 9 were made, because the clover had died as a result of shading by grass. In the mixed swards the grass was only used as a shading agent and 8 treatments of shading of progressively longer duration were obtained by transferring clover panels at different times. The transfers were made at 58, 65, 72, 79, 85, 93, 100, 107 days from sowing, the clover having been shaded by grass for most of the time up to the date of transfer. The growth of clover was recorded after transfer.

The sequence of removing panels from swards, both for harvest and for transfer, was randomised before the experiment began.

From the mixed swards, 8, 6, 3, 3, 4, 4, 4, 4 clover panels were transferred on the respective transfer occasions as shown in Table 16. Harvests after transfer were made from this group and recovery was followed by harvests extending over a minimum period of 6 weeks (transfers 3, 4 and 8). Although it would have been more desirable to have less harvests in the post-transfer period in transfers 1 and 2 and more harvests after transfers 3 and 4, the values obtained were adequate to show growth after transfer.

In order to maintain a reasonable area of sward and minimise advective effects in the later stages of the experiment, all the panels (including the borders) in the three replicates were moved together 107 days from sowing to make up a sward of pure clover and another of the control mixed sward. The replicates of the clover panels which had been transferred were also moved together 128 days from sowing.

The data collected in the experiment were:

(a) Plant numbers.

(b) Number of green leaves in clover.
Number of live tillers in grass.

(c) Weight of dry matter of grass and clover.

(d) L.A.I. of grass and clover.

(e) Weekly measurements of

i. Height of grass and clover

ii. Light intensity at vertical intervals of 2 cm in the mixed sward (Plate 8)

From these it was possible to determine the average light intensity at the surface of the clover.

Initially (b) and (d) were determined on the entire sample, but as the plants grew larger, a sub-sample was obtained from each replicate until eventually it consisted of no less than 15 per cent. of the main sample.

4.3.0. Experiment C: The analysis of L.A.I. in terms of individual plants and leaves.

4.3.1. Outline of experiment.

The sequence of leaf development and the contribution of individual leaves to the L.A.I. of subterranean clover swards were investigated at three densities; these were intended to maintain numbers in one treatment, to secure plant mortality in another, and to provide an intermediate density.

The experimental procedures permitted:

(a) an examination of the leaf development of individual plants in a sward,

(b) measurements of the position of individual identified leaves in the swards,

and (c) frequent harvests of individual plants, with only a temporary disarrangement of swards, except at the end of the experiment. At the last three harvests the structure of the sward was more easily disturbed.

At the beginning of the experiment, plants were selected for detailed study in each treatment, and their leaves were labelled as they formed. A number of labelled plants was harvested regularly in each density, and the following data were recorded: individual lamina areas, lamina weights, petiole lengths, and the dry weight of roots and of the total plant. In each sward, the light gradient was measured weekly.

4.3.2. Details of experiment.

Planting the experiment. Three experimental areas were provided by arranging three groups of fifty panels, of the kind described in Experiment B. (See Plate 9a). All panels were 40 cm long and 43 cm deep. One area of 40 cm x 250 cm ($= 1m^2$) was made up of 50 panels 5 cm wide and was sown to subterranean clover at a density of 4 plants per dm^2 or 8 plants per panel. The other two areas were 40 cm x 125 cm ($= 0.5m^2$) and consisted of 50 panels 2.5 cm wide; these were sown at densities of 16 and 36 plants per dm^2 respectively, i.e. 16 and 36 plants per panel. Graded seeds of Bacchus Marsh subterranean clover (7.30 mg/seed $<$ 2.50 mm, $>$ 2.25 mm) which had been soaked overnight were sown. Every seed was individually placed in each panel to give an even stand at each density. Simultaneously with the general planting, seed were sown in separate pots at the appropriate densities, and the seedlings were used to replace retarded or damaged plants. Sowing was on May 14th, 1958, emergence took place on May 20th, and replacements were transplanted on May 22nd. This experiment was set up in the same manner as Experiment B and this was described in section 4.3.0.

For ease of daily access to individual plants no side covers were erected as in the other experiments (see Plate 9b), since the borders were considered adequate.

Labelling of plants. Within a fortnight of emergence a number of plants were chosen at random from within the central 25 cm of each panel and were designated for detailed study, by attaching large labels to the base of the stem. In the density 4 plants per dm^2

4 plants in each panel were marked in this fashion and in the densities 16 and 36 plants per dm^2, 6 plants were marked in each panel. At the outset of the experiment 144 individual plants in each density were reserved for detailed study.

Labelling of leaves. Every new leaf on plants selected for detailed study, was identified as it unfolded by means of a small numbered label attached to its petiole. The task of labelling was continuous as new leaves unfolded, and was interrupted only by harvests or by inclement weather. The number of new leaves labelled between harvests and which were subsequently harvested, is shown in Table 17. All labels were waterproof and were cut from P.V.C. sheets 0.25 mm thick; they were perforated near one edge and slit from the perforation to the edge to facilitate attachment to the plant or petiole. The labels identifying whole plants were 1.5 cm x 2.5 cm, and the labels identifying leaves were approximately 0.8 cm x 0.5 cm in size. Although the number of unharvested plants was less at each successive harvest, the number of leaves to be labelled did not diminish until September (Table 17), because of the great increase leaf numbers per plant; several difficult periods occurred when there was an upsurge of leaf development at all densities, and more than 600 leaves had to be labelled in a week. Although frequently disturbed, the swards resumed a normal appearance after an undisturbed period of a day or two. Mislabelling, the occasional tearing of a leaf or damage to petioles were amongst the hazards of labelling, but this occurred only occasionally and was not serious. As the swards aged, labelling became more involved and time consuming because leaves were inter-twined and the hazards of labelling increased.

Table 17

The number of individual leaves labelled during the inter-harvest periods, in Experiment C.

Interval between harvests	Number of new leaves labelled during this interval
May 22nd - June 3rd	414
June 4th - June 10th	378
June 11th - June 17th	342
June 18th - June 24th	306
June 25th - July 1st	444
July 2nd - July 8th	606
July 9th - July 15th	252
July 16th - July 23rd	696
July 24th - July 29th	300
July 30th - Aug. 6th	600
Aug. 7th - Aug. 13th	444
Aug. 14th - Aug. 26th	382
Aug. 27th - Sept. 9th	258
Sept. 10th - Sept. 23rd	264
Sept. 24th - Oct. 7th	144
Oct. 8th - Oct. 21st	6

Table 18.

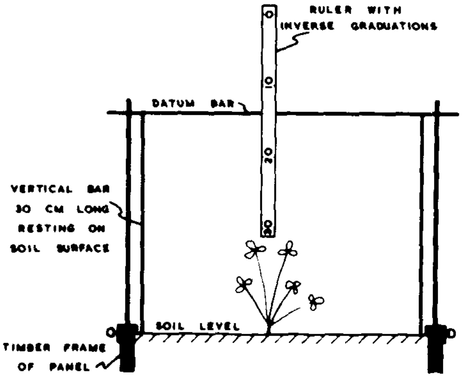
The number of plants in each density harvested on each occasion, and the average number of leaves labelled on each up to the time of harvest. (All the leaves labelled on a plant were not necessarily present at harvest, some were dying and some had died to leave only leaf scars on the stem).

Harvested		Density 4/dm^2		Density 16/dm^2		Density 36/dm^2	
Harvest number	Days from sowing	Number plants harvested	Approx. number of leaves per plant labelled up to date of harvest	Number plants harvested	Approx. number of leaves per plant labelled up to date of harvest	Number plants harvested	Approx. number of leaves per plant labelled up to date of harvest
			WEEKLY HARVESTS				
1	20	12	1	12	1	12	1
2	27	12	2	12	2	12	2
3	34	12	3	12	3	12	3
4	41	12	4	12	4	12	4
5	48	12	6	12	6	12	5
6	55	12	10	12	9	12	6
7	62	6	12	6	11	6	6
8	69	6	19	6	13	6	9
9	76	6	23	6	15	6	9
10	83	6	30	6	18	6	12
11	90	6	35	6	22	6	14
			FORTNIGHTLY HARVESTS				
12	104	6	45	6	22	6	16
13	118	6	52	6	25	6	16
14	132	6	60	6	30	6	16
15	146	6	69	6	32	12	16
16	160	6	70	12	32	12	16
Total		132		138		144	

Harvests. There were sixteen harvests in this experiment and the first was made on June 3rd, twenty days from sowing. Table 18 shows the harvest occasions, the number of plants harvested at each density and the approximate number of leaves on each plant. At the beginning of the experiment twelve labelled plants from each density were harvested every week. From the sixth harvest onwards this was reduced to six plants because it was no longer possible to handle twelve plants as well as continuing to label new leaves, in the time available. For similar reasons the inter-harvest interval was lengthened to 14 days in mid-August. These compromise decisions were made reluctantly, because a greater variability between plants was expected as the experiment progressed.

A harvest was made by removing a panel, and clamping the remaining panels together to reconstitute the sward. The order in which panels were withdrawn from the swards was randomised prior to the experiment, but it was so arranged that successive removals were at least five panels apart. In this way plants selected for late harvest were not disturbed repeatedly.

On the day prior to harvest a datum bar was adjusted at 30 cm above ground level and the height of labelled leaves above ground was measured.



ARRANGEMENT TO MEASURE LAMINA HEIGHT

The plants in the panel selected for harvest were carefully parted from the rest of the sward, the panel was loosened and withdrawn, and the remainder of the sward was then pushed together. It was found that the leaves from the two fresh faces were normally intermingled in a day or so. The panels which had been withdrawn were moved to the laboratory. The labels from leaves which had atrophied were recovered, to account for all the leaves which had been labelled.

The next operation was to remove a side from the panel to expose the soil (Plate 6) and wash out each labelled plant with its root. The plants were then held in a large pot of water in a refrigerator until they could be examined in detail.

The petiole and mid-rib length of each leaf was measured; each leaf lamina, and the remnants from each plant were packeted separately; the roots were cut off at ground level and also packeted. All packets were dried in a forced draught oven at 85-90° for 24 hours, and their contents weighed. During the experiment a total of 414 plants and some 6,000 individually labelled leaves were examined.

The lamina area was determined from mid-rib length measurements using the relationship

$$A = 2.16 \times L^{2.1}$$

given by Black (1958a), and where A and L are in cm^2 and cm respectively.

Senescent leaves were placed in five categories according to colour, using the standards in a Munsell colour chart (1929).

Healthy				Quite dead
1	2	3	4	5
GY/5/6 GY/4/6	GY/5/8 GY/6/6 Y-GY/7/8	Y/7/8 Y/6/8	Y/4/1 Y/5/4	Y/3/2 Y/2/2

Towards the end of the experiment some plants died, especially at the highest density, and a number of root systems with only a stump above ground were recovered.

Plate 8. Measuring the light intensity profile in Experiment B.

The photocell is inserted into the sward and held level with the aid of the bubble. The photograph shows the photocell which is fitted with a sheath that exposes 5 per cent. of the sensitive surface. This affords protection when using the cell at high light intensities. Another sheath exposing 10 per cent. of the sensitive surface was also used.

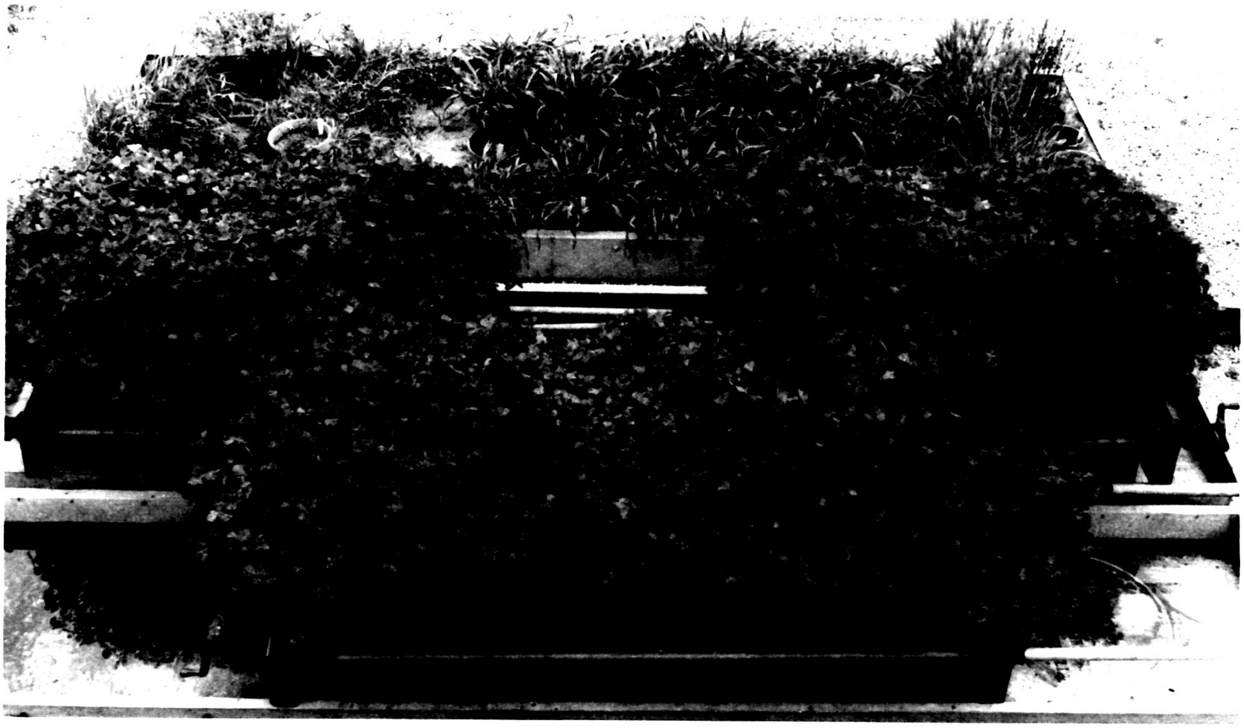
Plate 9a. A general view of Experiment C facing North taken on June 10th, 27 days from sowing.

Density 4 plants per dm^2 in lower half of photograph
Density 16 plants per dm^2 in upper left hand corner
Density 36 plants per dm^2 in upper right hand corner

Maximum and minimum thermometers protected by shields, recorded daily temperatures at the site of the experiment, and were situated in border panels which were not used.

Plate 9b. A general view of Experiment C facing North taken on September 23rd, 132 days from sowing.

The swards had recently been disturbed to label individual leaves.



5.0.0. RESULTS.

5.1.0. Experiment A. The influence of nitrogen on grass and clover swards.

5.1.1. Yield.

(a) Total yield of dry matter of swards.

The total yield of the swards at each nitrogen level on successive harvest dates is given in Table 1. At the early harvests, the differences were significant in favour of high nitrogen, but disappeared by the last harvest, despite considerable variation in botanical composition between the nitrogen treatments.

Table 19

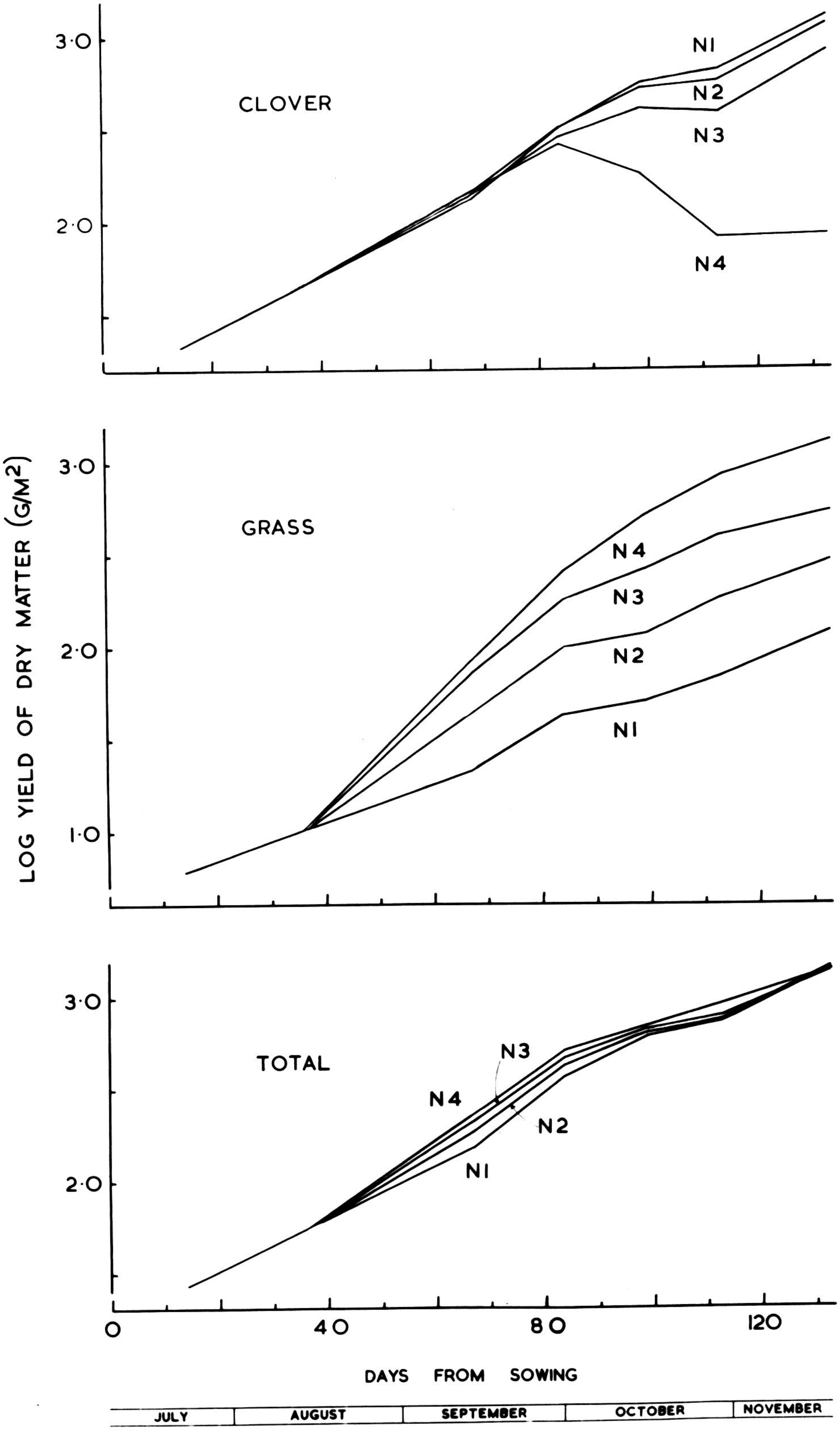
Mean yield of total dry matter of tops at successive harvests (g dm^{-2})

	Sept. 14th	Oct. 1st	Oct. 16th	Oct.30th	Nov. 19th
N 1	1.49	3.64	6.03	7.17	13.99
N 2	1.83	4.20	6.40	7.49	14.40
N 3	2.09	4.63	6.60	7.76	13.48
N 4	2.27	5.12	6.89	9.11	13.69
Significance	xxx	xxx	x	xx	N.S.
L.S.D. in each column at					
$P < 0.05$	0.24	0.51	0.52	0.85	2.61
< 0.01	0.35	0.73	0.75	1.22	3.75
< 0.001	0.51	1.07	1.10	1.80	5.52

The log of total yield of dry matter is plotted against time in Fig. 15c

Fig. 15. - The influence of nitrogen treatment on the relative growth of the swards.

(a) Clover component only.
(b) Grass component only.
(c) Total yields.


CLOVER
N1
N2
N3
N4
3·0
2·0
GRASS
N4
N3
N2
N1
3·0
2·0
1·0
LOG YIELD OF DRY MATTER (G/M^2)
TOTAL
N3
N4
N2
N1
3·0
2·0
0
40
80
120
DAYS FROM SOWING
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER

(Figs. 15a and 15b are discussed later) and shows that nitrogen treatments had only a slight influence on the course of total dry matter production. All swards reached approximately the same maximum yield, and this may be considered as the ceiling under the conditions of this experiment.

During the latter half of September the crop growth rate (g dm^{-2} per day) increased with higher nitrogen levels, as shown in Table 20. In early October and November this was reversed and during the latter half of October no obvious pattern could be discerned. During November the crop growth rate was higher in the clover-dominant swards as they were approaching ceiling yields.

Table 20

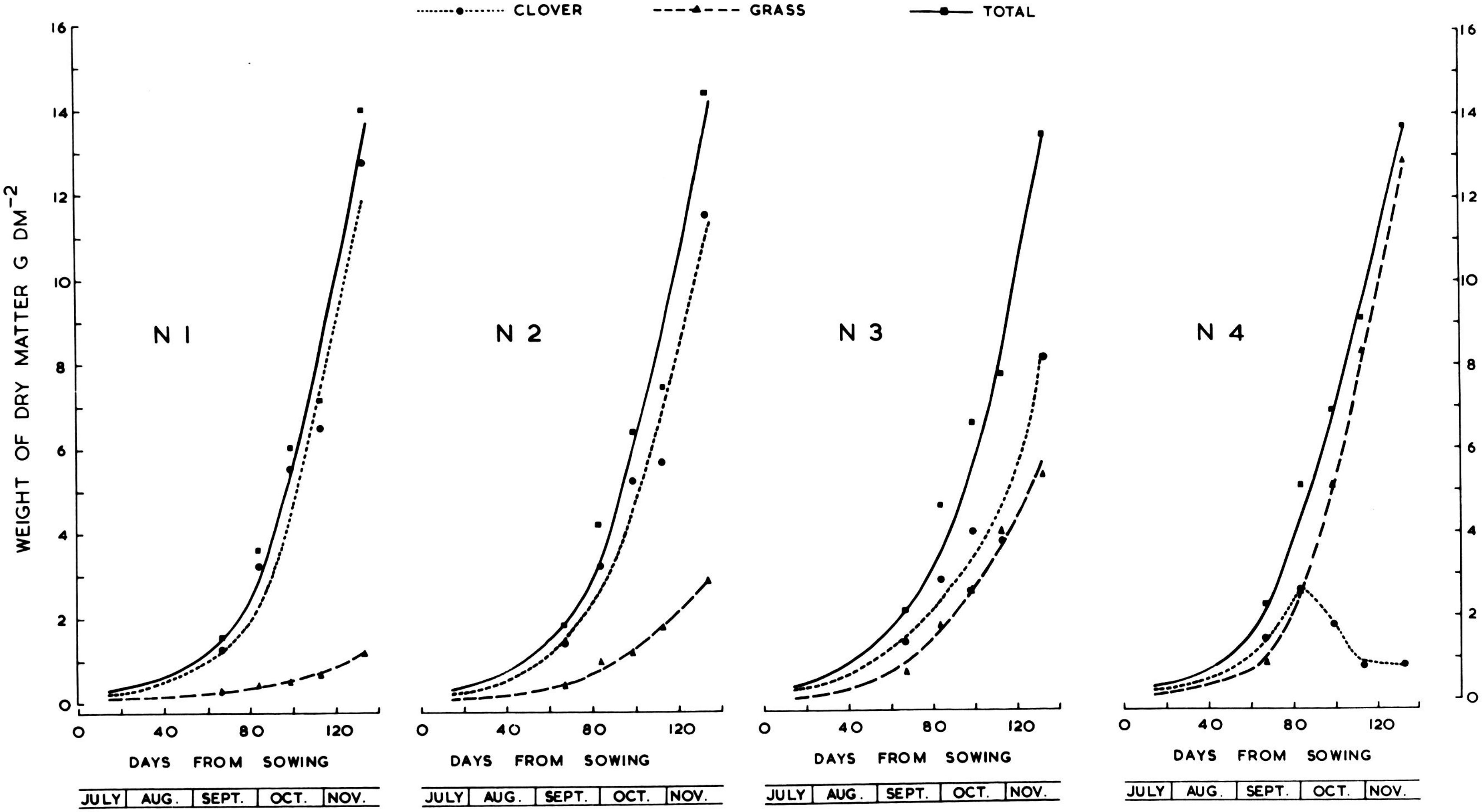
Mean crop growth rate of tops between harvests (g dm^{-2} per day)

	Sept. 15th to Oct. 1st	Oct. 2nd to Oct. 16th	Oct. 17th to Oct. 30th	Oct.31st to Nov.19th
N 1	0.126	0.159	0.081	0.341
N 2	0.139	0.147	0.078	0.346
N 3	0.149	0.131	0.083	0.286
N 4	0.168	0.118	0.159	0.229

(b) Yield of the botanical components of the swards.

The course of clover yields was similar up to about 80 days (Fig. 15a) irrespective of the nitrogen treatment while the course of grass yield was dependent, even at 40 to 50 days, upon

Fig. 16. - The weight of dry matter of swards in the four nitrogen treatments. Clover is represented by a dotted line, grass by a broken line and total yields by a continuous line.


CLOVER
GRASS
TOTAL
WEIGHT OF DRY MATTER G DM^{-2}
0
2
4
6
8
10
12
14
16
N 1
N 2
N 3
N 4
0
40
80
120
DAYS FROM SOWING
JULY
AUG.
SEPT.
OCT.
NOV.

the amount of nitrogen applied (Fig. 15b). There were marked differences in the botanical composition of the four swards (Fig. 16). At the final harvest they ranged from 90 per cent. clover in N 1 to only 5 per cent. clover in N 4. Thus, the treatments succeeded in producing a clover dominant sward, a grass dominant sward and two swards of intermediate composition (80 per cent. clover and 58 per cent. clover).

Clover development was similar in N 3 and N 4 until about October 1st, and the difference after this date was quite spectacular. Early in the experiment a delicate balance existed between grass and clover in both the N 3 and N 4 treatments; though it was maintained in N 3, and in N4 it changed in favour of grass under the influence of the higher nitrogen applications.

The aggressor species developed similarly in both clover and grass-dominant swards, but the companion species behaved differently. In the clover-dominant N 1 the amount of grass increased throughout the experiment, but in the grass-dominant N 4 the yield of clover rose to a peak on October 16th, and fell again to yield less than 1 g dm^{-2}. Some values are shown in Table 21.

The variability (Appendix, page 311) recorded in the yields of dry matter, was low with the exception of clover in N 1, N 2 and N 3 at the last harvest. This was due to the extensive runner development in clover between the fourth and fifth harvests.

Table 21

The yield of the component species in the clover-dominant N 1, and the grass-dominant N 4 swards.
g dm^{-2}.

	N 1		N 4	
	Aggressor (Clover)	Suppressed (Grass)	Aggressor (Grass)	Suppressed (Clover)
Sept. 14th	1.27	0.21	0.83	1.43
Oct. 16th	5.53	0.50	5.11	1.78
Nov. 19th	12.81	1.18	12.86	0.83

These features are also clear from Fig. 16.

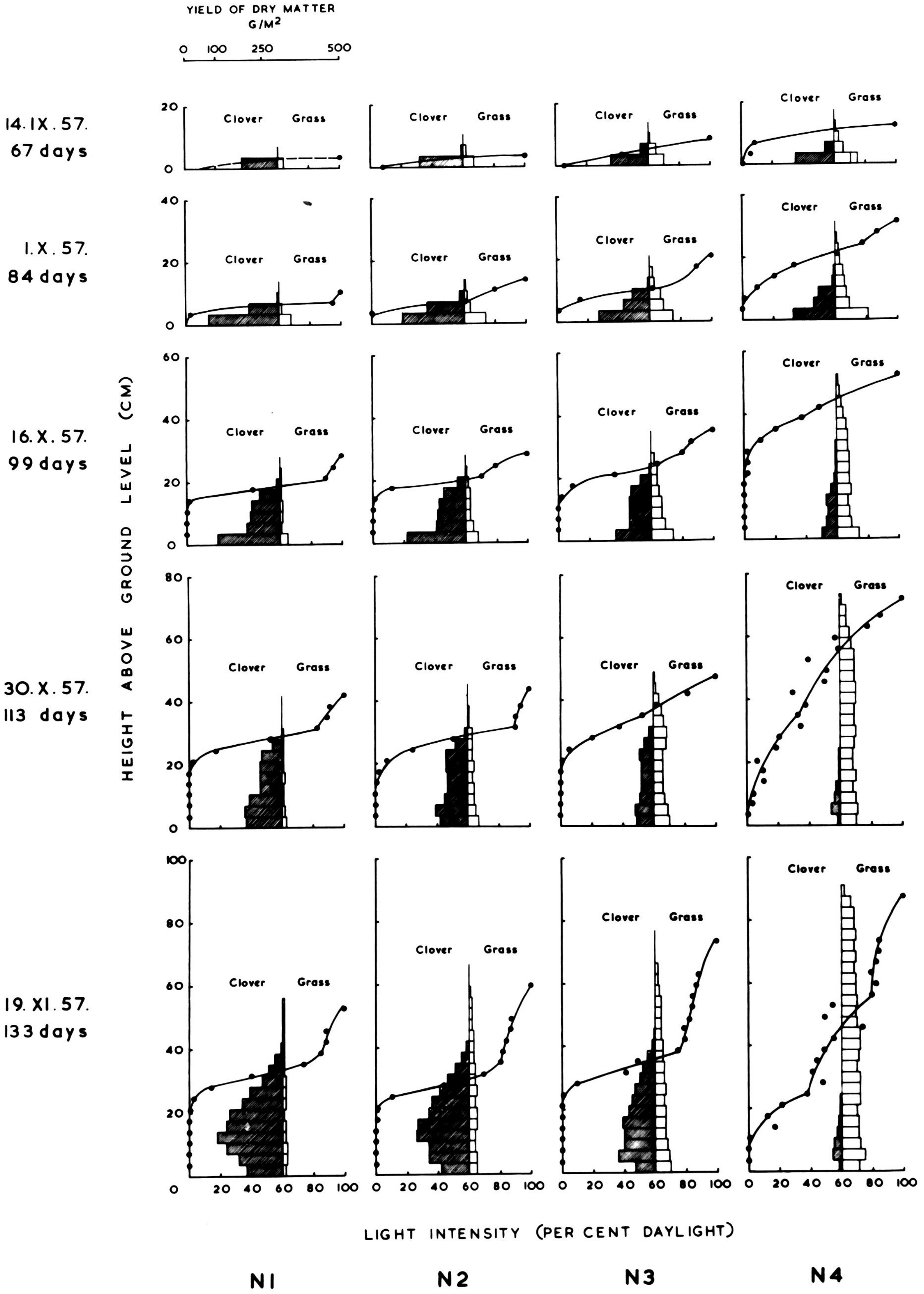
(c) The vertical distribution of yields.

Figure 17 illustrates the distribution of dry matter of grass and clover in the vertical span of the sward at intervals of 3.5 cm for each treatment and on each harvest occasion. Grass had a greater stature than clover and more horizons were harvested of grass than of clover (see Table 14).

The yield per unit of height was greater in clover (0.62 g/cm) than in grass (0.26 g/cm). The largest yields of clover in any horizon were recorded in N 1 (2.23 g dm^{-2} at 0 to 3.5 cm at 84 days, and 2.12 g dm^{-2} at 10.5 to 14.0 cm at 133 days), and for grass in N 4 (1.06 g dm^{-2} at 0 to 3.5 cm at 84 days, and 0.76 g dm^{-2} at 3.5 to 7.0 cm at 133 days).

The nature of the vertical distribution of dry matter changed

Fig. 17. - Each graph shows the vertical distribution of dry matter and the light profiles within the sward on all occasions and at all levels of nitrogen. The vertical line represents the height of the sward; the distribution of clover yields is shown to the left and the grass yields to the right of this line. The scale for the histograms is given in the top left hand corner. The scale for light intensity is shown along the ordinate and the actual values at each horizon is indicated by a solid dot.


YIELD OF DRY MATTER G/M²
0 100 250 500
14.IX.57. 67 days
1.X.57. 84 days
16.X.57. 99 days
30.X.57. 113 days
19.XI.57. 133 days
Clover
Grass
HEIGHT ABOVE GROUND LEVEL (CM)
0 20 40 60 80 100
LIGHT INTENSITY (PER CENT DAYLIGHT)
0 20 40 60 80 100
N1
N2
N3
N4

during the course of the experiment but differently with each species. As the grass increased in height the vartical distribution remained uniform, but with clover the bulk of the vegetation remained close to ground level except at the last harvest when it was mainly distributed from 10.5 to 17.5 cm. This difference of grass and clover was to be expected because grass elongated, while clover developed new leaves and petioles from branches and runners near the ground.

There was no appreciable difference in the vertical distribution of the clover between N 1 and N 2, or even of the depressed clover yield in N 3. This is shown in Table 22 where the amount of clover in each 7 cm horizon (2 layers) is expressed as a percentage of the entire clover yield for that treatment. As clover yields were negligible in N 4, the values are not included in Table 22.

The petioles and stems of the clover formed an increasing proportion of the dry weight of the sward and the laminae tended to be carried upwards as growth of the sward proceeded. This may be seen from Table 23 which shows for the N 1 treatment the leaf laminae expressed as a percentage of the clover weight in each horizon. From about 80 days onwards, clover leaf laminae constituted 70 per cent. or more of the yield in the upper 10 to 14 cm of the sward.

Table 22.

Weight of clover at 113 and 133 days in each 7 cm (2 layers) of vegetation, expressed as a percentage of the total clover yield.

(0 cm is ground level)

Height above ground level cm	113 days			133 days		
	N 1	N 2	N 3	N 1	N 2	N 3
49 - 56						0.3
42-49				0.1	0.2	0.6
35-42		0.1	0.3	2.3	3.0	4.0
28-35	0.4	2.3	4.0	8.1	9.6	10.3
21-28	14.5	19.0	19.7	16.9	18.2	16.5
14-21	21.9	22.4	21.5	26.1	25.3	22.5
7-14	27.1	23.5	23.7	28.2	25.3	23.8
0-7	36.1	32.8	30.8	18.3	18.4	22.0
	100.0	100.0	100.0	100.0	100.0	100.0

Table 23

Leaf laminae as a percentage of the clover yield within each 3.5 cm vertical interval in N 1. (At heights above the bar, all horizons have 70 per cent. or more of leaf laminae).

Height above ground level cm	Days from sowing.				
	67	84	99	113	133
42.0 - 45.5					97.5
38.5 - 42.0					79.4
35.0 - 38.5					78.0
31.5 - 35.0					74.3
28.0 - 31.5				96.7	65.9
24.5 - 28.0				92.1	68.4
21.0 - 24.5				84.0	68.5
17.5 - 21.0			97.8	73.2	59.9
14.0 - 17.5			89.0	56.1	51.2
10.5 - 14.0			75.4	54.3	58.9
7.0 - 10.5		98.4	58.0	46.4	42.8
3.5 - 7.0	100.0	82.6	44.7	33.5	42.5
0 - 3.5	30.8	37.8	23.5	0	0

5.1.2. Leaf area index

(a) The total L.A.I. of swards.

The development of L.A.I. of the swards and that of each of the component species is shown in Fig. 18. The curves were drawn by eye.

The maximum values of L.A.I. recorded in the four nitrogen treatments were as follows:

N 1 Nov. 19th	N 2 Nov. 19th	N 3 Nov. 19th	N 4 Oct. 30th
14.7	11.6	11.2	11.0

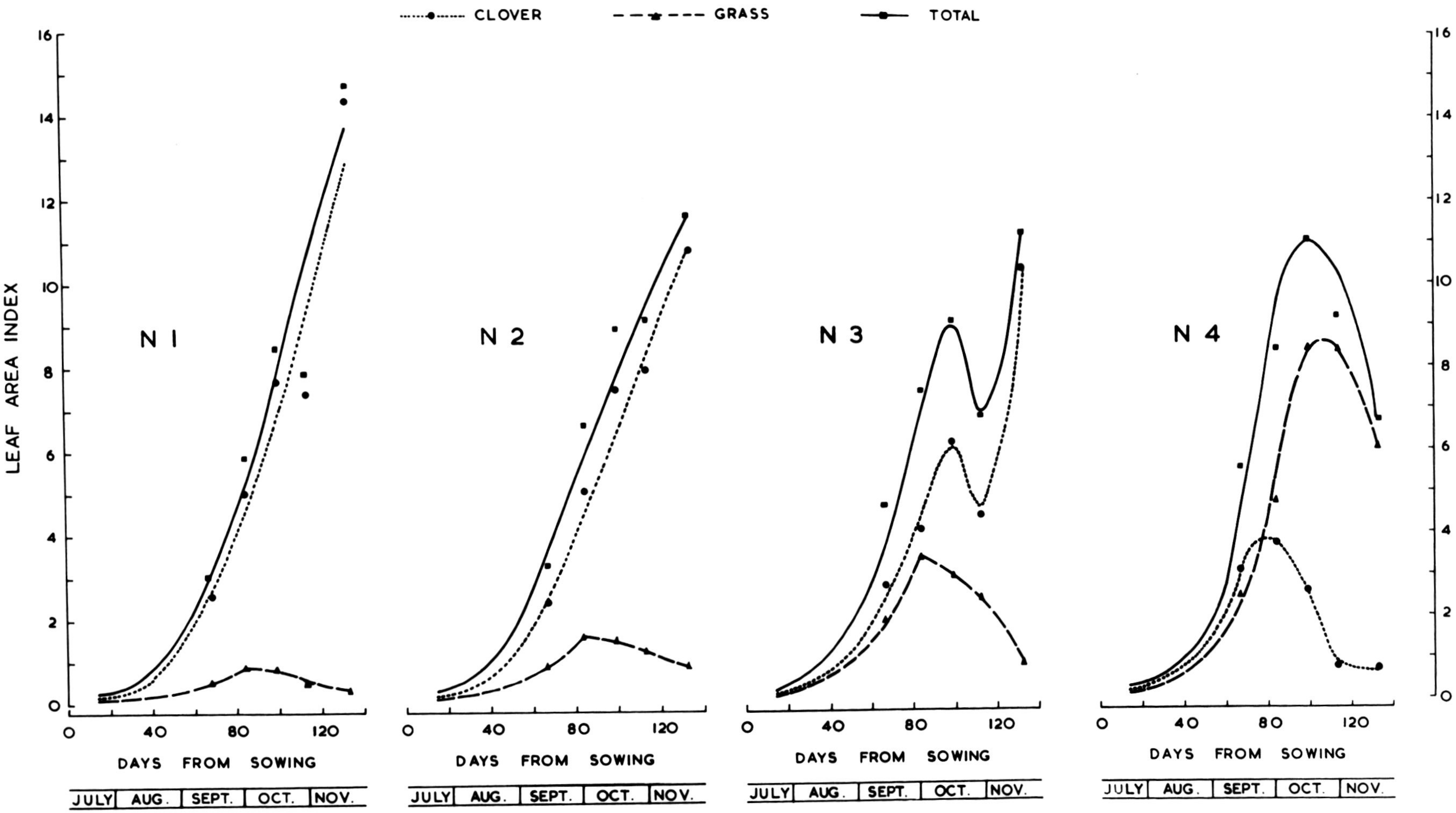
With the exception of the N 1 treatment these values were approximately equal, and were higher than any values for annual pastures previously reported.

The total L.A.I. of N 1 and N 2 was still rising at the end of the experiment. In N 3 the depression on October 30th is an expression of the reduction of clover and grass L.A.I. at this harvest. In N 4 it reached a peak during mid-October. These aspects are discussed more fully under the L.A.I. of the botanical components.

The rates at which the total L.A.I. developed in the four nitrogen treatments is shown in Table 24.

The rate of L.A.I. development was lower in all swards during the latter half of October. In N 1 and N 2 there was a decline in clover leaf development. In N3 and N 4, the simultaneous depression of clover L.A.I. due to shading by grass and the fall in grass L.A.I. which coincided with the onset of flowering, led to high negative rates.

Fig. 18. - The Leaf Area Index in the four nitrogen treatments. Clover is shown by a dotted line, grass by a broken line and total L.A.I. by a continuous line.


CLOVER
GRASS
TOTAL
LEAF AREA INDEX
0
2
4
6
8
10
12
14
16
N 1
N 2
N 3
N 4
0
40
80
120
DAYS FROM SOWING
JULY
AUG.
SEPT.
OCT.
NOV.

This decline persisted in N 4 but not in N 3 where the clover recovered during November. Where clover dominated, there was an increase in the rate of leaf development from October 1st to November 19th. A moderate nitrogen dressing stimulated leaf development in N 2 between the first and second harvests.

Table 24.

Mean rate of development of L.A.I. between harvests (unit per day)

	Sept. 14th to Oct. 1st	Oct. 2nd to Oct. 16th	Oct. 17th to Oct. 30th	Oct. 31st to Nov. 19th
N 1	0.17	0.18	-0.05	0.34
N 2	0.20	0.15	0.02	0.12
N 3	0.16	0.11	-0.17	0.22
N 4	0.17	0.17	-0.13	-0.12

The values of L.A.I. recorded at the final harvest in N 1, N 2 and N 3 were due to clover, and may be somewhat high for the following reasons. Up to the time that runner development had taken place borders were adequate, but once runners formed, they passed from the quadrat through the border areas and enjoyed peripheral conditions, even though they were enclosed within the hessian side-covers. The procedure was to harvest all plants seeded in a given area, and this included some complete runners which had numerous clusters of one or two leaves, which had formed late, in the axils of the primary runners.

(b) The L.A.I. of the botanical components.

In every nitrogen treatment there was a clear demonstration in terms of L.A.I. of dominance and suppression of the component species. The L.A.I. of the aggressor and suppressed species diverged after October 1st and the L.A.I. values at this date are shown in Table 25.

Table 25

The L.A.I. of the botanical components in each nitrogen treatment on October 1st (84 days from sowing) and the light intensities to which the leaves of the suppressed species were exposed.

Nitrogen treatment	Aggressor		Suppressed		
	Species	L.A.I.	Species	L.A.I.	Light regime
N 1	Clover	5.02	Grass	0.85	62% L.A.I. exposed to 4% daylight
N 2	Clover	5.01	Grass	1.59	74% L.A.I. exposed to 61% daylight 33% L.A.I. exposed to 2% daylight
N 3	Clover	4.06	Grass	3.37	74% L.A.I. exposed to 63% daylight 40% L.A.I. exposed to 15% daylight 10% L.A.I. exposed to 2% daylight
N 4	Grass	4.71	Clover	3.74	100% L.A.I. exposed to 34% daylight 50% L.A.I. exposed to 2% daylight

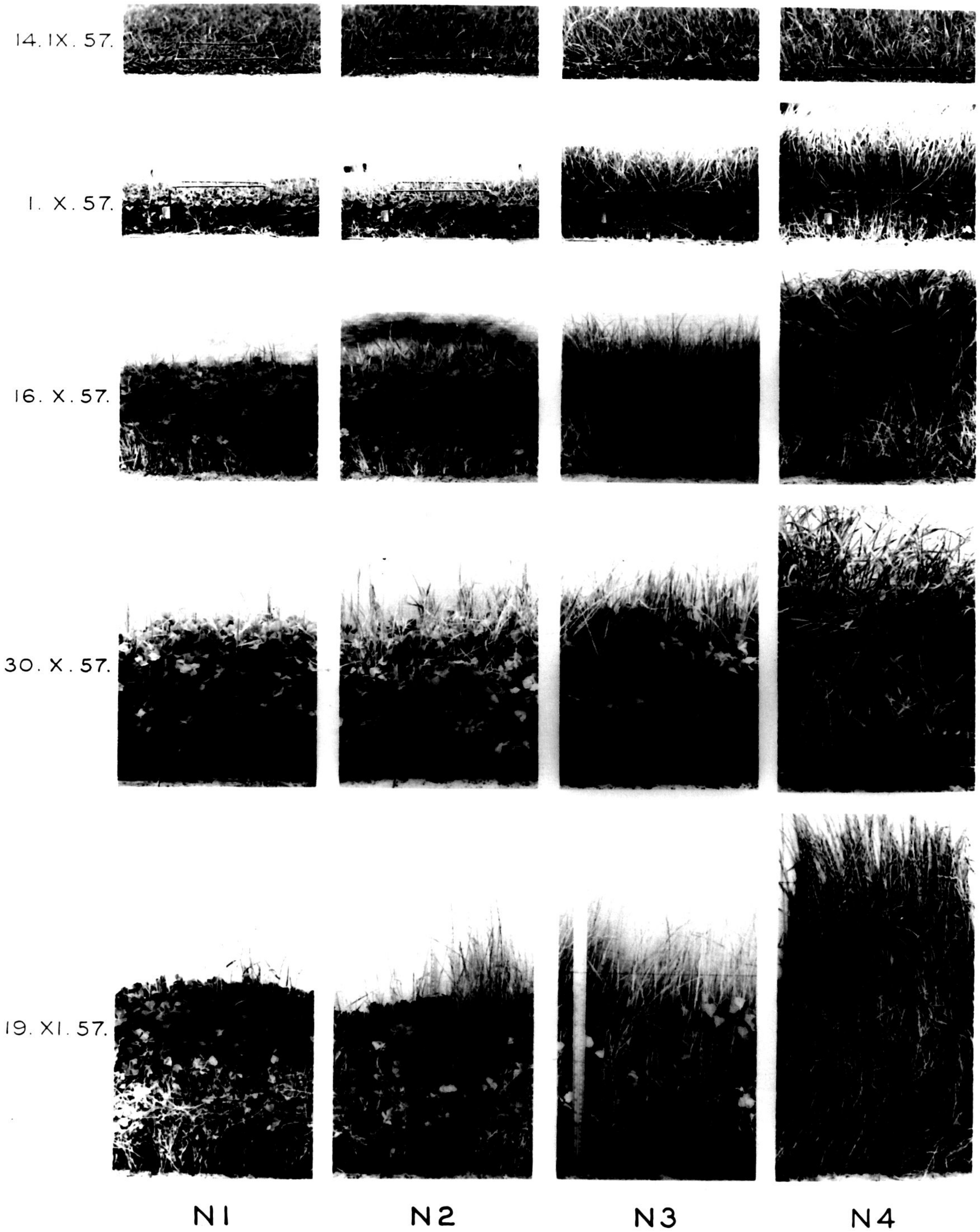
The decline of grass L.A.I. in N 1, N 2 and N 3 began slowly during the first fortnight of October and proceeded more rapidly after this. The decline in clover L.A.I. in N 4 was rapid from October 1st onwards. This may be seen by inspecting Figure 18. The lowest L.A.I. values reached were 0.70 for clover in N 4, and 0.35, 0.86, 0.85 for grass in N 1, N 2 and N 3 respectively.

The N 3 treatment presents an interesting situation because dominance was not absolute. The yields of dry matter of grass and clover were approximately equal, but it was the clover which eventually became dominant. Although the grass L.A.I. declined as shown in Fig. 18 the dry weight continued to rise steadily and kept pace with the dry matter increase of clover as shown in Fig. 16. In spite of the steady and continued decline of grass L.A.I. in the N 3 treatment the grass overtopped the clover throughout the experiment and this may be seen from Plate 11. When shading was severe, it led to a temporary depression of clover L.A.I. and a retardation of the rate of dry weight increase between approximately 100 and 120 days. With the elongation of grass from days 120 to 130, more light was admitted and the clover again increased in leaf area. (Figs. 18, 20).

The maximum grass L.A.I. in each treatment was related to the quantity of nitrogen applied as shown in Fig. 19. It seems that a ceiling L.A.I. for grass was not reached in this experiment and that greater values might have been attained with higher nitrogen applications.

A decline of grass L.A.I. is to be expected as older leaves begin to senesce in a plant of determinate habit of growth, and as

Plate 11. Pasture profiles in each nitrogen treatment at all harvests. The lay-out of this plate matches Figs. 17 and 20, in which the vertical distribution of dry matter and L.A.I. are depicted. In the later harvests, the paler leaves beneath the upper part of the canopy in the clover-dominant N 1 and N 2, indicate the depth of the dark zone. The rapid suppression of clover where heavy nitrogen dressings were applied to the sward is clearly shown in the N 4 series.


14. IX. 57.
1. X. 57.
16. X. 57.
30. X. 57.
19. XI. 57.
N1
N2
N3
N4

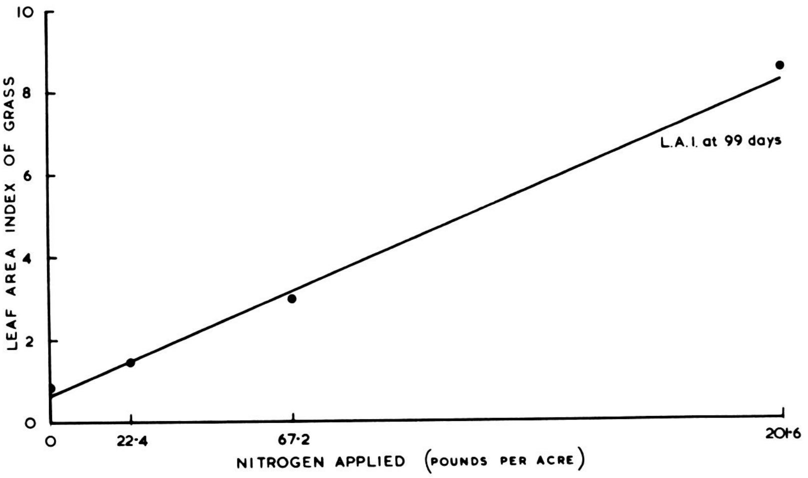
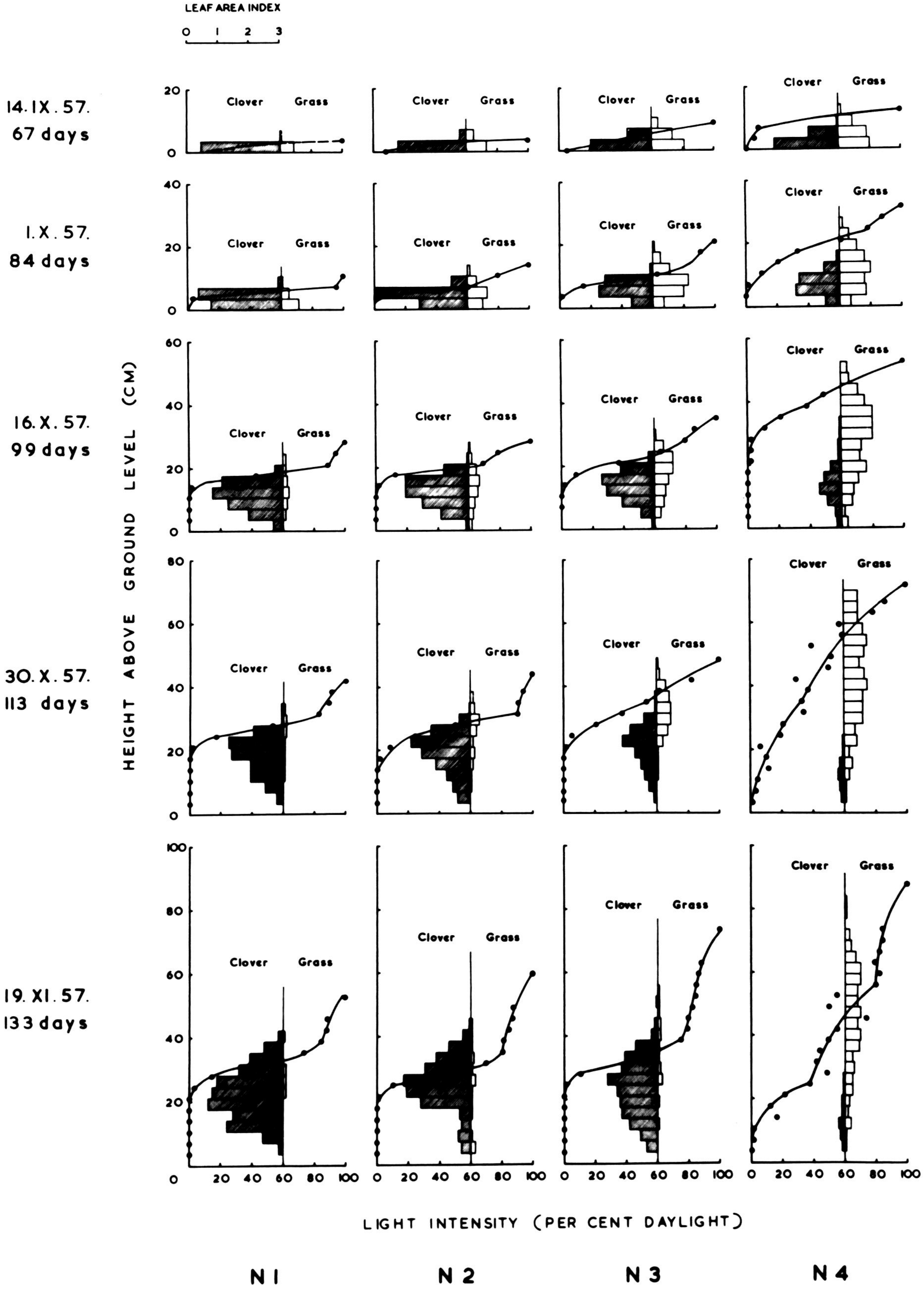


Fig. 19. - The relationship between the amount of nitrogen applied and grass L.A.I.

Fig. 20. - The vertical distribution of Leaf Area Index for clover and for grass, is superimposed on graphs showing the light gradient within each sward on successive harvest occasions. The vertical lines represent the height of the swards, and the distribution of clover L.A.I. appear to the left, and the grass L.A.I. to the right of this line. The scale for the histograms is given in the top left hand corner.


LEAF AREA INDEX
0 1 2 3
14. IX. 57.
67 days
1. X. 57.
84 days
16. X. 57.
99 days
30. X. 57.
113 days
19. XI. 57.
133 days
Clover
Grass
HEIGHT ABOVE GROUND LEVEL (CM)
0
20
40
60
80
100
LIGHT INTENSITY (PER CENT DAYLIGHT)
0 20 40 60 80 100
N 1
N 2
N 3
N 4

tiller numbers begin to fall because of high sowing density. The decline in grass L.A.I. began at 84 days in N 3 and at 108 days in N 4. This delay in the fall of leaf area in N 4 may have been due to the higher level of nitrogen as well as the later application (Table 13).

(c) The vertical distribution of L.A.I.

Figure 20 illustrates the vertical distribution of L.A.I. at intervals of 3.5 cm for each treatment and each harvest occasion. The main difference between the vertical distribution of dry matter and of L.A.I. was in the greater symmetry about the modal height of the L.A.I. distribution and this may be seen at a glance by comparing Figs. 17 and 20. This is to be expected because of the greater contribution of stem and petioles in the lower layers.

The largest values of total L.A.I. recorded in each nitrogen treatment at each harvest in any horizon are shown in Table 26. At the beginning of the experiment the maximum values of L.A.I. harvested in any horizon were almost equal for the four nitrogen treatments, and the grass and clover values tended to complement each other. This may be seen at 67 and 84 days; although similar total values were recorded, the ratio of grass L.A.I. to clover L.A.I. varied very greatly. As the experiment progressed the vertical dispersion of leaf material became greater especially in grass. The nitrogen treatments stimulated growth of grass and this characteristically has its foliage spread over a greater vertical interval than has the clover. The values in Table 26 indicate that an L.A.I. of 3.00 to 3.50 per 3.5 cm of vertical interval, or 0.85 to 1.00 per 1 cm of vertical interval, is a maximum concentration of leaf in a pasture sward in this environment.

Table 26

The maximum values of total L.A.I. recorded within any horizon in each nitrogen treatment on successive harvests. (The values are partitioned for clover and for grass).

Days from sowing	Treatment	Height of horizon cm	L.A.I. within horizon		
			Clover	Grass	Total
67	N 1	0 - 3.5	2.56	0.42	2.98
	N 2	0 - 3.5	2.19	0.63	2.82
	N 3	0 - 3.5	1.96	1.05	3.01
	N 4	0 - 3.5	2.08	1.02	3.10
84	N 1	3.5 - 7.0	2.67	0.26	2.93
	N 2	3.5 - 7.0	2.99	0.66	3.65
	N 3	3.5 - 7.0	1.73	0.99	2.72
	N 4	3.5 - 7.0	1.41	0.85	2.26
99	N 1	10.5 - 14.0	2.25	0.20	2.45
	N 2	14.0 - 17.5	2.07	0.36	2.43
	N 3	14.0 - 17.5	1.68	0.47	2.16
	N 4	17.5 - 21.0	0.32	0.80	1.12
113	N 1	21.0 - 24.5	1.76	0.07	1.83
	N 2	21.0 - 24.5	1.88	0.12	2.00
	N 3	21.0 - 24.5	1.08	0.22	1.30
	N 4	42.0 - 45.5	-	0.76	0.76
133	N 1	17.5 - 21.0	2.40	0.03	2.43
	N 2	24.5 - 28.0	2.16	0.14	2.30
	N 3	24.5 - 28.0	1.61	0.13	1.74
	N 4	63.0 - 66.5	-	0.49	0.49

The points made in connection with the vertical distribution of dry matter apply also to the vertical distribution of L.A.I.

(a) Grass has a greater stature than clover.

(b) Clover has a greater L.A.I. per unit of height.

(c) The nature of the vertical distribution changes differently with each species.

Dealing with each of these points in turn.

Some grass leaf was always disposed above the surface of clover even though it was not always possible to measure it. (Plate 11, Fig. 20). The amount increased with increasing nitrogen level and the L.A.I. of grass above the clover canopy was greatest at 113 days. This is discussed in Section 5.1.6. (b) and the points made here are illustrated in the upper half of Fig. 24.

The relative contribution of leaf area and dry weight in the same vertical interval may be different. In Table 27 the relative proportion of grass above clover in N 4 is expressed on the basis of height, L.A.I. and weight of dry matter. Thus the L.A.I. of grass in the 14 cm above clover in N 4 at 84 days was 0.91, or 19.3 per cent. of the total L.A.I. of the grass. The grass yield in the same 14 cm was 0.268 g dm^{-2} - only 10.1 per cent. of the total yield of the grass at this harvest. These and the corresponding values for the 99th day are shown in Table 27, and it is evident that there are several criteria of stature.

The largest L.A.I. of one species in any horizon was in clover at 84 days. A value of 2.99 was recorded in N 2, and 2.67 in N 1. The highest value for grass was 1.14 in N 3 at 84 days, and the next

Table 27

The proportion of grass above the clover in N 4 calculated on the basis of height, L.A.I. and weight of dry matter.

Days from sowing	On the basis of height per cent.	On the basis of L.A.I. per cent.	On the basis of weight per cent.
84	44.4	19.3	10.1
99	33.3	32.8	16.2

highest were 1.02 at 67 and 99 days, and 0.99 at 84 days in N 4. Assuming under the conditions of this experiment maximum L.A.I. values of 3.0 for clover and 1.0 for grass per horizon of 3.5 cm harvested, then the maximum leaf area per cubic centimetre of canopy is 0.86 cm^2 for clover and 0.29 cm^2 for grass, giving 3:1 ratio of foliage density of clover:grass. A comparison of dry weights on this basis gives a ratio of 9:4.

The difference in the nature of the vertical distribution of clover and grass is illustrated by the change in height of the modes. Table 28 shows the height of the mode of the L.A.I. distribution of each species. This may also be seen by inspection of Fig. 20 where the heights are shown on the ordinates.

Elongation was taking place in the grasses after October 16th and the effect can be seen in Fig. 20. In N 4 the grass L.A.I. remained at 8.4 from October 16th to October 30th in spite of an increase in height of the sward from 55 cm to 75 cm.

Table 28

Height above ground level of the mode of the L.A.I. distribution (cm)

Days from sowing	N 1		N 2		N 3		N 4	
	Clover	Grass	Clover	Grass	Clover	Grass	Clover	Grass
67	2	2	2	2	2	2	2	2
84	5	2	5	5	7	7	7	12
99	12	12	14	14	14	23	12	33
113	23	30	23	30	23	33	12	47
133	19	26	25	26	26	26	12	47

5.1.3. Census data.

(a) Plant numbers.

The number of plants per dm^2 is shown in Table 30. The aim was to establish 24 plant per dm^2 of each species, but thinning was carried out soon after the first emergence and as delayed germination subsequently took place, a larger number of plants actually became established.

Clover. Between the first and second harvests there was a slight but significant increase in clover numbers at all levels of nitrogen and this remained static between the second and third harvests. The numbers did not show any significant trends in N 1 and N 2 from the second harvest onwards. The drop in clover numbers in N 3 between the third and fifth harvests, though small, was significant;

Table 30.

Mean density of plants at each harvest.
(number per dm^2)

Days from sowing	N 1		N 2		N 3		N 4	
	Clover	Grass	Clover	Grass	Clover	Grass	Clover	Grass
67	28.1	30.9	27.7	29.6	25.7	29.4	25.4	25.1
84	31.5	33.4	29.6	30.5	29.0	31.5	28.8	29.9
99	32.3	23.9	32.3	30.5	30.7	34.8	25.9	32.3
113	29.5	18.2	29.5	32.5	24.6	33.9	10.2	32.0
133	26.9	12.2	27.2	30.5	22.9	38.4	5.9	35.8

Clover: (a) Least Significant Difference between any nitrogen treatment on any harvest occasion.

$P < 0.05$ 3.2
< 0.01 4.3
< 0.001 5.8

Grass: (a) Least Significant Difference between any nitrogen treatment on any harvest occasion.

$P < 0.05$ 6.4
< 0.01 8.8
< 0.001 12.0

(b) Least Significant Difference between harvest occasions at one level of nitrogen.

$P < 0.05$ 5.8
< 0.01 7.8
< 0.001 10.2

a sharp decline from 26 to 6 plants occurred in N 4 during this period.

Grass. A significant decline in numbers from the second harvest onwards, occurred in N 1. Numbers in N 2 remained static throughout, but there was a slight increase in N 3 and N 4 with later harvests which may have been due to a combined effect of delayed germination, nitrogen applications, or errors of counting as a result of increased tillering.

(b) Tiller numbers in grass.

Tiller numbers were determined on the whole-plant-quadrats and are presented in Table 31.

Table 31

Number of grass tillers per dm^2.

Days from sowing	N 1	N 2	N 3	N 4
67	46.5	62.2	73.5	66.5
84	43.4	58.0	81.9	98.7
99	23.9	35.1	47.0	77.5
113	18.2	32.5	39.0	49.6
133	12.2	30.5	38.4	41.2

There was an increase in tiller numbers from the first to the second harvest in N 3 and N 4, due to increased tillering on individual plants. Otherwise tiller numbers declined as a result of death of plants in N 1, and a loss of tillers per plant in N 2, N 3 and N 4. Inter-plant competition was intense in N 1, while intra-plant competition was operative at the higher levels of nitrogen.

(c) Leaf numbers in clover.

The number of green clover leaves were determined on the whole-plant-quadrats, except at the last harvest, when runner development had begun. The numbers of green clover leaves per dm^2 at the second, third and fourth harvests are given in Table 32.

Table 32

Number of green clover leaves per dm^2.

Days from sowing	N 1	N 2	N 3	N 4
84	297.7	257.5	261.0	259.2
99	269.7	279.4	205.7	119.2
113	156.4	165.2	111.9	14.4

The maximum number of green leaves was attained in the clover dominant swards (300 leaves per dm^2) and this is higher than the values obtained with Bacchus Marsh in other experiments (Davidson 1954, Black 1958b, Davidson and Donald 1958). It could be explained on the basis of a greater potential leaf development in Tallarook (Donald and Smith 1937, Aitken & Drake 1940, Black 1960a) which was the variety used in this experiment. The decline in leaf numbers between 99 and 113 days was due to a loss of leaves per plant as well as a decline in plant number, the greatest loss occurring in the N 4 treatment.

5.1.4. Light intensity.

(a) Light intensity readings in the swards.

The light intensity profiles for all swards at each harvest are shown in both Figs. 17 and 20. The abscissae show the light intensities from 0 to 100 per cent. daylight and the ordinates the height in cm. Light intensities were measured at the surface of each horizon harvested, i.e. every 3.5 cm. The light profiles changed with time, and differed according to nitrogen treatments. (It is suggested that the contrast in light profiles from N 1 to N 4 can be seen very clearly, if the figure is turned on its side). There were a number of characteristic or recurring features which make some generalisations possible.

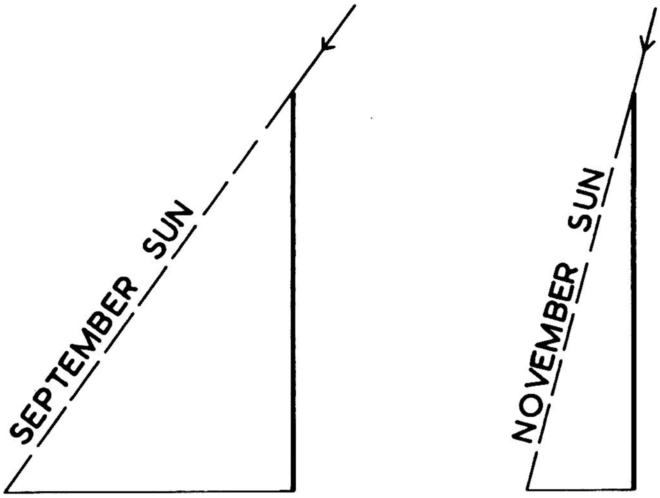
(i) The reductions in light intensity were abrupt in the clover-dominant swards but much more gradual in the grass-dominant swards. Table 33 shows the biggest reductions of light intensity in any interval of 3.5 cm, at each nitrogen level on successive harvests. More light was absorbed within 3.5 cm of foliage at the beginning of the experiment when foliage was dense and close to the ground than later, when the swards had developed statures. In a mature clover-dominant sward as much as a third of the incoming light was absorbed in a vertical interval of 3.5 cm, while in a grass-dominant sward the maximum amount of light absorbed in the same interval was one sixth to one fifth daylight. This is not surprising in view of the different vertical distribution of foliage in the two species.

Table 33.

The largest reductions in light intensity in any single interval of 3.5 cm, in each nitrogen treatment on successive harvests
(Light intensity reductions expressed as a percentage of full daylight)

Days from sowing	N 1		N 2		N 3		N 4	
	Height interval cm	Light reduction per cent.	Height interval cm	Light reduction per cent.	Height interval cm	Light reduction per cent.	Height interval cm	Light reduction per cent.
67	-	-	3.5 - 0	92	7.0 - 3.5	54	10.5 - 7.0	89
84	7.0 - 3.5	92	7.0 - 3.5	59	10.5 - 7.0	48	21.0 - 17.5	28
99	21.0 - 17.5	47	21.0 - 17.5	57	24.5 - 21.0 21.0 - 17.5	27	49.0 - 45.5	18
113	31.5 - 28.0	30	28.0 - 24.5	26	31.5 - 28.0 28.0 - 24.5	17	63.0 - 59.5	11
133	35.0 - 31.5	33	28.0 - 24.5	33	31.5 - 28.0	30	28.0 - 24.5	16

(ii) The presence of grass inflorescences and stem above the canopy of foliage caused a reduction in light intensity of the order of 15 to 20 percent. even where grass was poorly developed. At 133 days in the N 1 treatment, the grass had no leaf but there was a very small amount of dry matter which consisted mainly of stem and inflorescence standing 17 to 18 cm above clover. The extent of shade is dependent on the amount and height of the vegetative material present and the direction of the incident light. The noon alititude of the sun at latitude - 35° is 54° in September and 75° in November resulting in greater shading with a September sun for the same amount of material.



(iii) The majority of leaves in the swards were heavily shaded and Table 34 shows the percentage of all leaves exposed to light intensities below 40 per cent. daylight in each treatment. The peak values occur earlier at the higher nitrogen levels.

Table 34

The percentage of the leaf area in each sward exposed to light intensities below 40 per cent. of full daylight.

Days from sowing	N 1	N 2	N 3	N 4
67	-	-	64.0	74.5
84	47.4	31.1	51.3	89.2
99	69.8	58.7	68.1	83.8
113	83.7	73.9	68.0	51.6
133	76.4	46.0	65.7	30.4

The degree of self shading within the sward is evident from Table 34.

(iv) Whereas individual grass leaves traversed several harvest layers, clover leaves were usually horizontally disposed within a single layer. In view of the marked changes in light intensity over short distances, an individual grass leaf was exposed to extreme differences in illumination, but it was unlikely that individual clover leaves encountered such variation over their surface. This point is illustrated in Plate 12 which shows the profiles of the N 1 and the N 4 swards at 84 days.

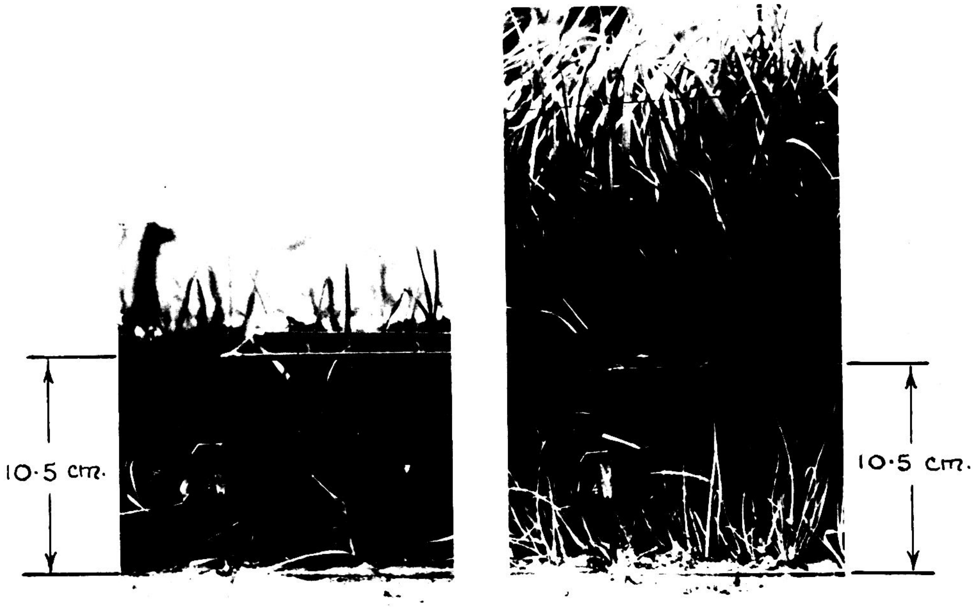


Plate 10. Pasture profiles of the clover-dominant N1, and the grass-dominant N4 swards on October 1st, illustrating

(a) the severity of shading within the swards,

and (b) the horizontal disposition of clover leaves within a single layer, and the vertical disposition of the grass leaves.

The height of the frame is 10.5 cm. Yields at this time were $3.64 g\ dm^{-2}$ in N1 and $5.12 g\ dm^{-2}$ in N4.

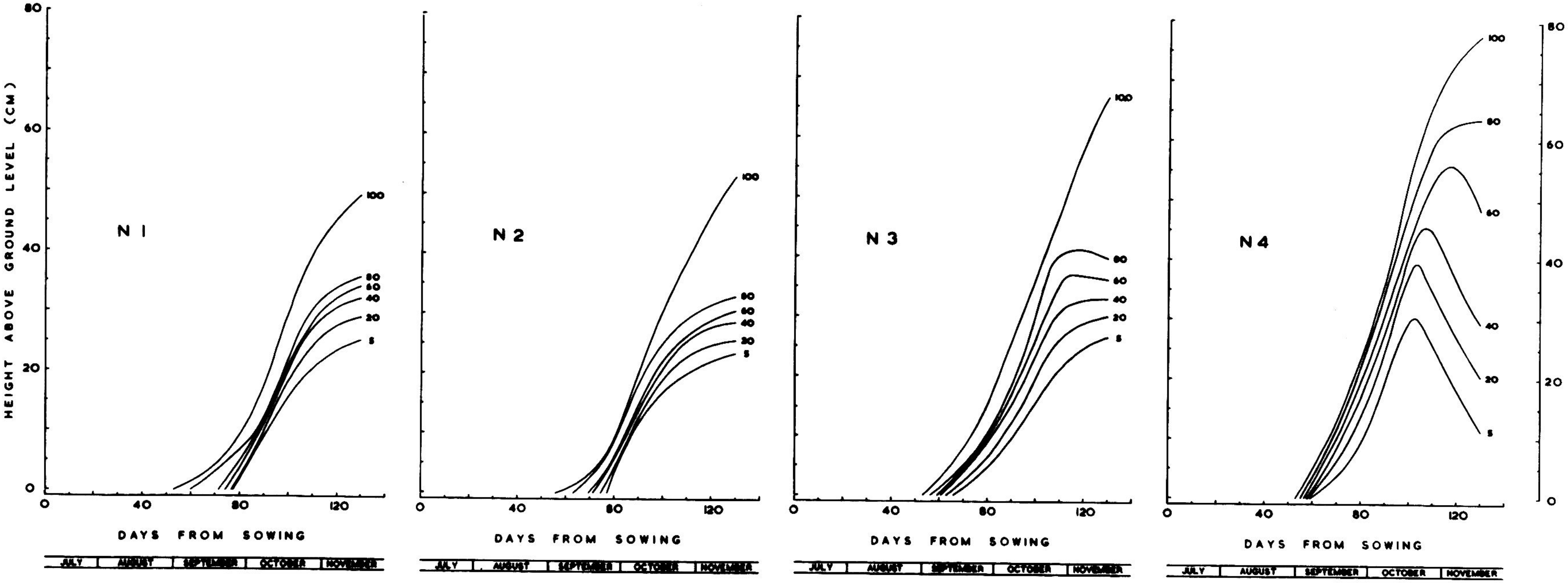
(b) Isopleths of light intensity.

The weekly and the occasional bi-weekly records of light intensity were plotted against height for each nitrogen treatment. From these figures it was possible to obtain the heights for the following light intensities (expressed as a percentage of full daylight): 100, 80, 60, 40, 20, and 5. Five per cent. was arbitrarily selected as a light intensity at which respiratory losses may exceed photosynthetic gains (Boysen Jensen 1932). From the data now available, i.e. days from sowing, and height of the selected light intensity values, it was possible to construct isopleths of light intensity during the course of the experiment. The curves were fitted by eye and smoothed to eliminate irregularities, and are presented in Fig. 21. Ideally, a network of instruments permanently placed in the sward and fitted with automatic recording devices is needed to establish such sets of curves. Meanwhile the presentation in Fig. 21 clearly shows the nature of the changing light patterns and indicates the distinctive features of the light penetration into the four types of swards in this experiment. Initially, light reached the ground, but beginning at about

78 days in N 1
77 days in N 2
66 days in N 3
59 days in N 4

95 per cent. or more of the light was absorbed by the vegetation, mostly by the leaves near the surface. By mid-October (100 days from sowing) the lower half of all swards were at light intensities of

Fig. 21. - The pattern of light interception in each nitrogen treatment during the experiment. The abscissa represent time and the ordinates are height. With the aid of the isopleths of 100, 80, 60, 40, 20 and 5 per cent. daylight, the light gradient at any time during the experiment may be determined. The 100 per cent. line represents the top of the sward.


HEIGHT ABOVE GROUND LEVEL (CM)
80
60
40
20
0
N 1
N 2
N 3
N 4
100
80
60
40
20
5
0
40
80
120
DAYS FROM SOWING
JULY
AUGUST
SEPTEMBER
OCTOBER
NOVEMBER

5 per cent. daylight or less. A comparison of the 100 and 80 per cent. isopleths in the N 1 and N 2 treatments indicates the nature of the light reductions caused by small amounts of grass above the surface of the clover. The proximity of the lines in the N 1 and N 2 treatments clearly shows the compactness of the leaf layer in the clover dominant swards and how effective they are in light interception. Grass, on the other hand, allowed a deeper penetration of light into the sward. In Table 35 the depth from the surface at which 95 per cent. interception occurred, and Fig. 22 expresses this in units of L.A.I.

Table 35

The depth from the surface at which 95 per cent. light interception occurred in the clover-and-grass-dominant swards.

(cm)

Days from sowing	Clover dominant N 1	Grass dominant N 4
80	7.5	14.0
100	14.5	23.5
120	22.0	55.5

The grass dominant swards developed stature earlier than the clover dominant swards. Similarly N 2 swards were slightly ahead of the N 1 swards due to the early stimulus of applied nitrogen. The loss of grass leaves in N 3 and in N 4 led to a fall in the isopleths after 100 days; in N 3 the isopleths of 40, 20 and 5 per cent. did not fall because of the presence of clover.

5.1.5. Light intensity in relation to L.A.I.

Figure 22 shows the relationship of L.A.I. and light intensity for N 1 and N 4 at 99 and 113 days. The abscissa represent the cumulative values of L.A.I. from the surface of the sward; these were obtained by adding downwards the values obtained in each horizon. The ordinate is the corresponding light intensity at the surface of the following horizon. The figures illustrate clearly the greater capacity of clover foliage to intercept light and show how this persisted as the swards matured. In spite of increasing L.A.I. more light penetrated the swards at 113 days than 99 days and this is due partly to elongation and partly to a higher angle of elevation of the sun.

5.1.6. Derived data.

(a) The leaf area duration of grass above clover in relation to nitrogen applied.

The leaf area duration has been defined (Watson 1958) as the integral of leaf area index during a growth period. From the data presented in Fig. 20 it was possible to obtain the L.A.I. of grass, above the upper surface of the clover canopy during the latter part of the experiment and the data are shown on the upper half of Fig. 24. From these, the L.A.D. values of grass above clover were calculated at 20-day intervals and plotted against the nitrogen applied. This is shown in Fig. 23. Increases in grass L.A.D. above the clover with time were negligible in N 1 and N 2, approximately constant in N 3 and progressively larger in N 4. The grass-above-clover L.A.D. values of

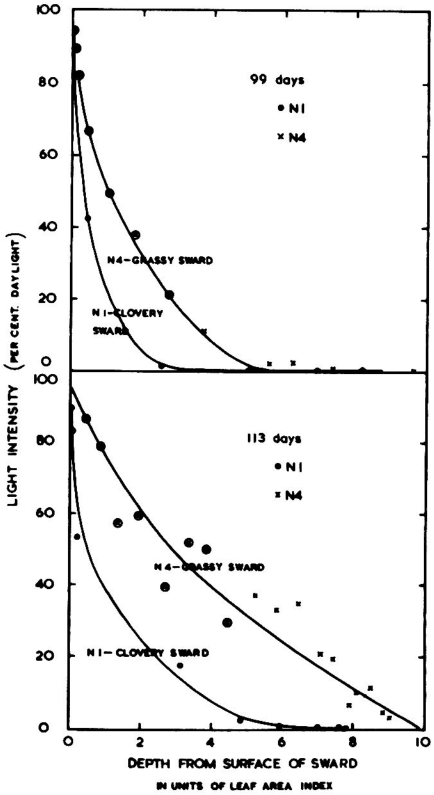


Fig. 22. - The relationship between Leaf area index and light intensity in the clover-dominant N 1, and the grass-dominant N 4 swards, at the third and fourth harvests.

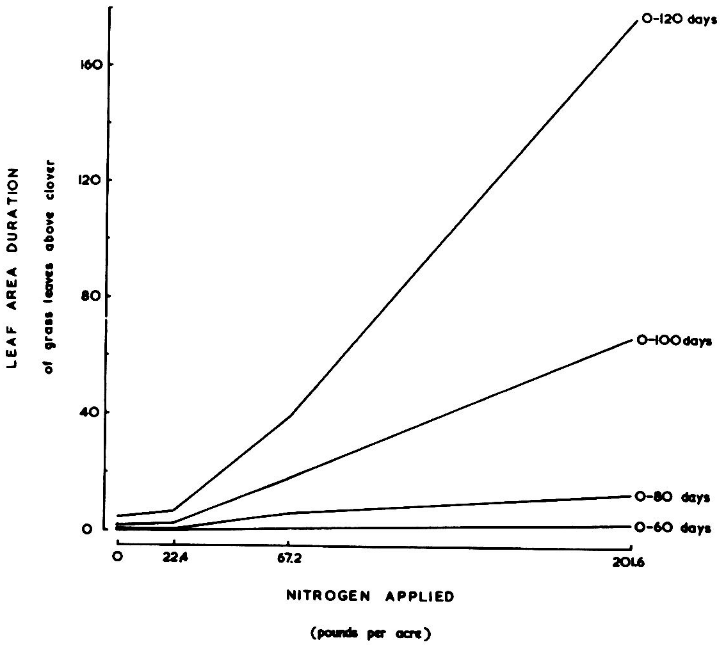


Fig. 23. - The influence of applied nitrogen in promoting the growth of grass leaves above clover. The abscissa represents the quantity of nitrogen applied and the ordingate shows the Leaf Area Duration of grass leaves above clover for 0-80, 0-100 and 0-120 days.

N 3 and N 4 began to diverge at about 100 days (October 17th) onwards and by 120 days (November 6th) the L.A.D. in N 4 was almost $4\frac{1}{2}$ times as great as in N 3. Figure 23 illustrates a principal difference between the nitrogen treatments as they develop during the course of the experiment. Since high values of L.A.D. for grass-above-clover indicate continued and intensified shading of the clover, the differences in clover growth in the four swards will be examined more closely in relation to the light intensities at the surface of clover.

(b) The L.A.I. of grass above clover and the light intensity at the surface of clover.

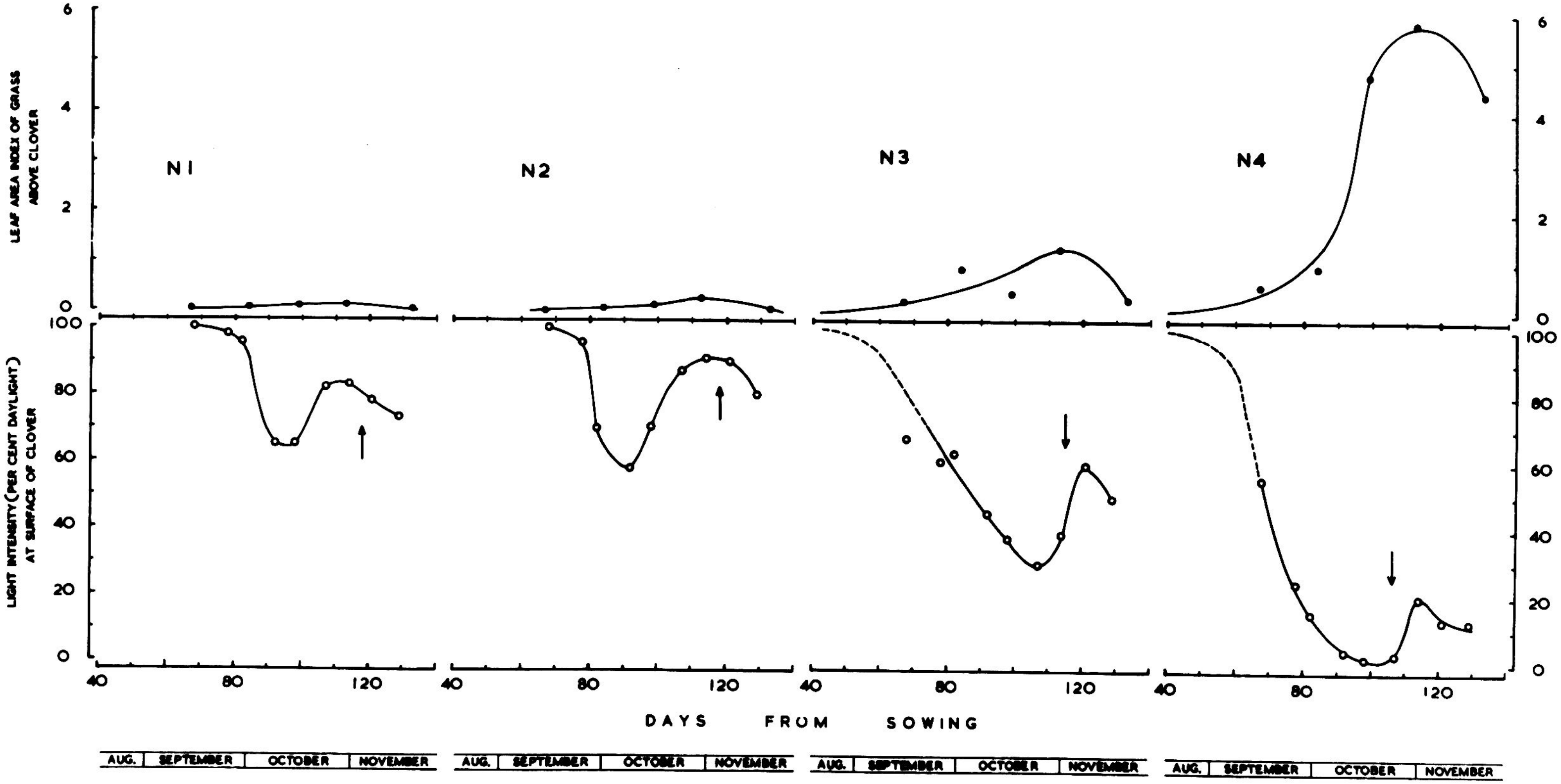
In the upper half of Fig. 24 the L.A.I. values of grass-above-clover are shown for each nitrogen treatment at successive harvests, and in the lower half the changes of light intensity at the surface of the clover canopy are plotted against time. The highest L.A.I. values of grass-above-clover occurred at the fourth harvest (113 days) and these were:

N 1	0.13
N 2	0.27
N 3	1.28
N 4	5.80

In all the nitrogen treatments light intensities fell to a minimum and the lowest values recorded at the surface of the clover canopy were:

N 1 65 per cent. of daylight at about day 95
N 2 58 per cent. of daylight at about day 92
N 3 29 per cent. of daylight at about day 107
N 4 2 per cent. of daylight at about day 98

Fig. 24. - The development of grass-above-clover L.A.I. at each nitrogen level is shown in the upper half of the figure, and in the lower half the light intensity at the surface of the clover is plotted against time. The days on which light readings were made do not correspond to the harvest dates. The arros indicate that heading was general.

LEAF AREA INDEX OF GRASS ABOVE CLOVER
LIGHT INTENSITY (PER CENT DAYLIGHT) AT SURFACE OF CLOVER
N1
N2
N3
N4
0
2
4
6
0
20
40
60
80
100
40
80
120
DAYS FROM SOWING
AUG.
SEPTEMBER
OCTOBER
NOVEMBER

Thus, the shading by grass was most severe about mid-October, just before the maximum L.A.I. values of grass-above-clover was attained.

Although the L.A.I. values of grass-above-clover in N 1 and N 2 were small, they strongly reduced the light intensities at the surface of the clover canopy, for a short period in mid-October. In N 3, the balance between grass and clover was delicate, and the zoning of leaves of the two species was not distinctive; it was therefore difficult to define the L.A.I. of grass-above-clover, and the points recorded for the second and third harvests fall 0.4 units of L.A.I. above and below the line drawn. Although these points may be real, the line represents the general trend, and is adequate for the comparison of treatments. In N 4, the suppression of clover was clear-cut.

The light intensity at the surface of the clover canopy fell more rapidly in N4 than in N 3, and reached a lower value. There was a noticeable increase in light intensity at the clover surface as heading began and the L.A.I. of grass declined; the subsequent fall in light intensity was due to an increased density of seed heads of grass, and this is apparent from the data showing the vertical distribution of dry matter on November 19th. (Fig. 17).

(c) Clover yields, and the mean daily radiation at the clover surface.

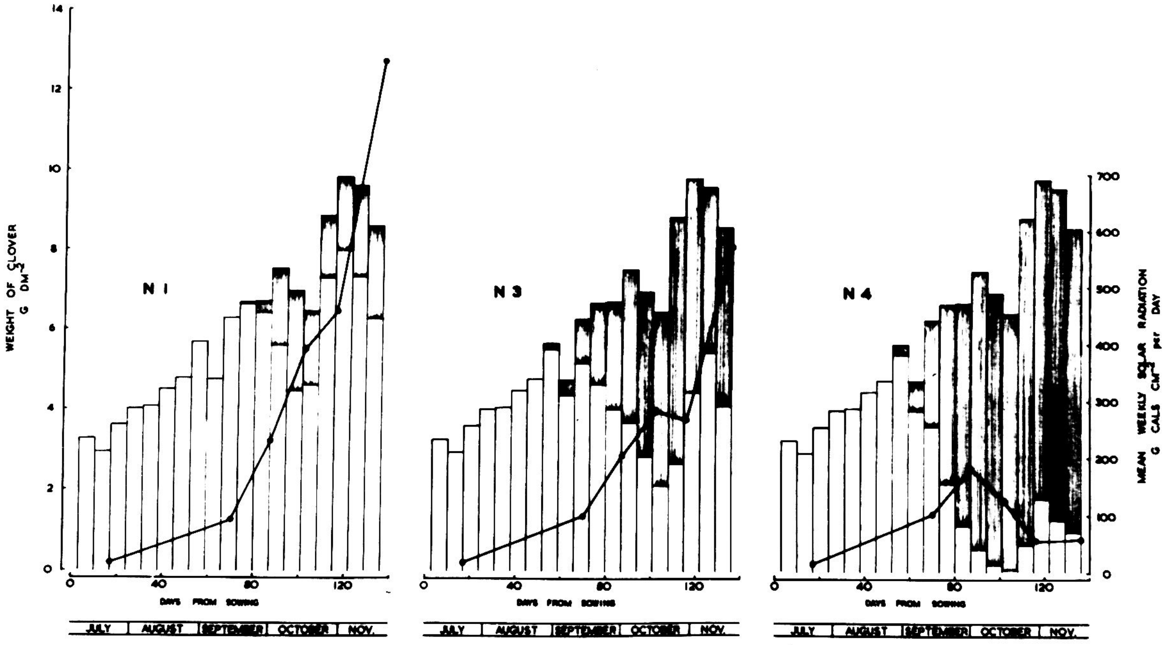
(i) The mean daily radiation at weekly intervals during the experiment.

N 1, N 4 and N 3 were representative of clover dominance, suppression and an intermediate situation, and the clover yields in these treatments are considered in relation to the radiation available to the clover. In Fig. 25 the mean weekly solar radiation was expressed as g cals cm^{-2} per day and was plotted in a series of histograms. The hatched portions show the radiation absorbed by grass-above-clover, and the clear portions the amount of radiation at the surface of the clover. The nearest solarimeter at the time of the experiment was located at Dry Creek, 20 miles North of the Waite Institute, and a comparison of the hours of bright sunshine between the two stations led to the belief that these records (I.C.I. 1959) were a reasonable approximation of the solar radiation at the site of the experiment. Accepting the constancy of the daylight factor (see page 99), the light intensity values in Fig. 24 were used to partition the radiation between that absorbed by the grass-above-clover, and that available at the surface of the clover. The weight of dry matter of clover in each treatment were plotted on the same graphs, and Fig. 25 illustrates the effect of a diminishing light supply on clover yields. The main features concerning the clover yield have already been discussed in section 5.1.1. (b) (page 145).

(ii) The radiation at the surface of clover fourteen days before harvest.

The daily radiation at the surface of clover was obtained by applying the light intensity data in Fig. 24 to the radiation data from Dry Creek. In Fig. 26(a) the mean daily radiation at the surface of clover during fourteen days before a harvest (abscissae), is plotted against the yield of clover (ordinates), for harvests I to IV inclusive. Because of the difficulty of measur-

Fig. 25. - The mean solar radiation at weekly intervals during the experiment, showing the amount absorbed by grass-above-clover (hatched), and the radiation available to clover (clear). Clover yield in each treatment is also shown.

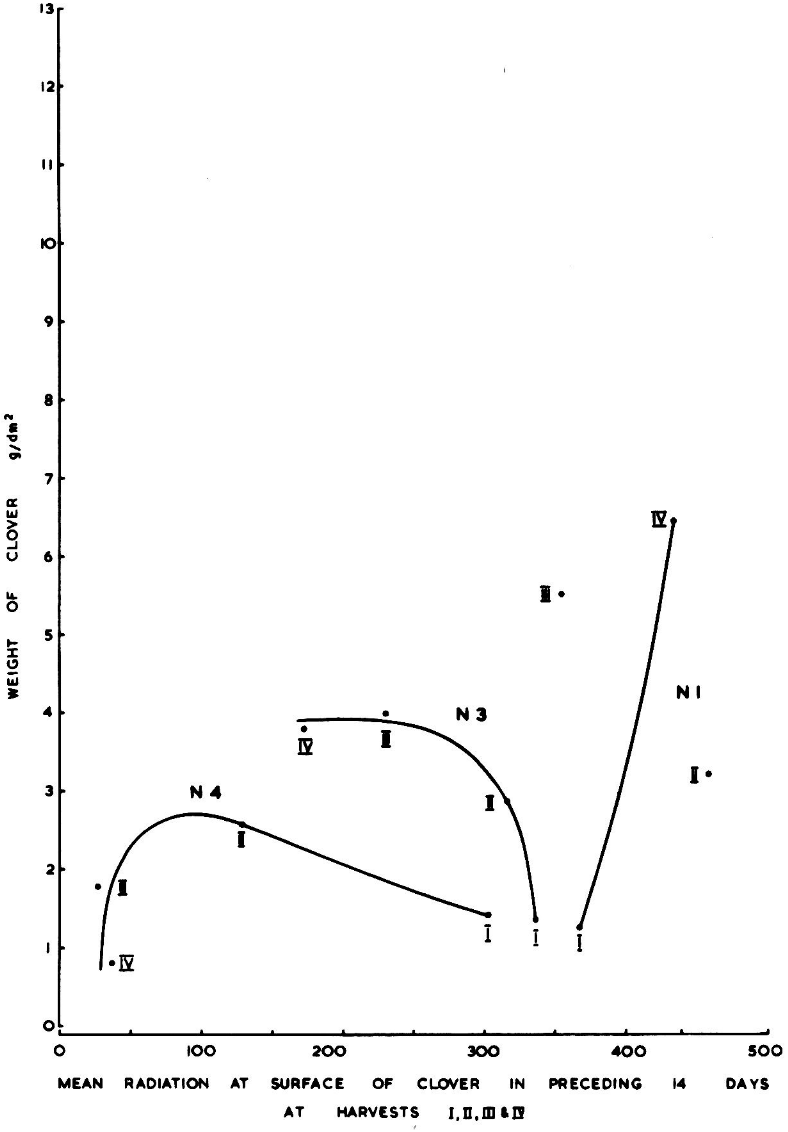

WEIGHT OF CLOVER
G DM^{-2}
14
12
10
8
6
4
2
0
N 1
N 3
N 4
0
40
80
120
DAYS FROM SOWING
JULY
AUGUST
SEPTEMBER
OCTOBER
NOV.
MEAN WEEKLY SOLAR RADIATION
G CALS CM^{-2} per DAY
700
600
500
400
300
200
100
0

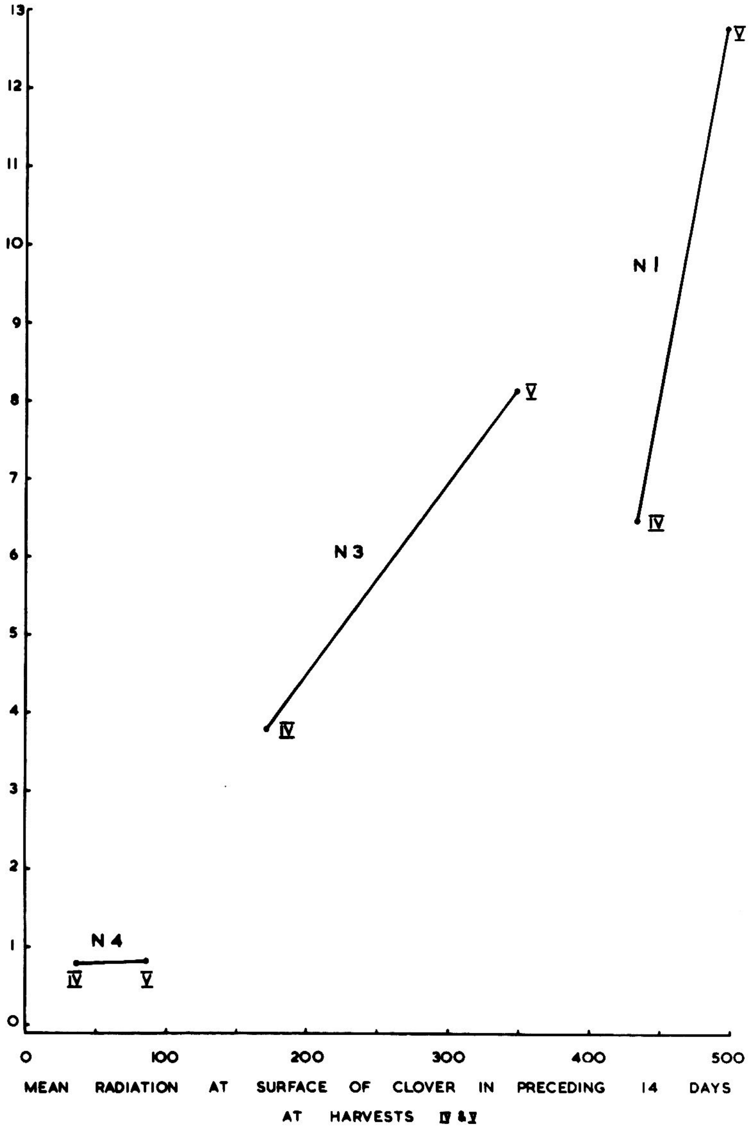
uring partial shading by a very small amount of grass with a small flat photocell (see section 2.4.0.), the radiation data for N 1 were erratic, but they may be improved by using the incident radiation data without conversion. In N 3 and N 4 the entire clover surface was shaded and this difficulty did not arise. Figure 26 (a) shows that mean radiation fell more gradually in N 3 than in N 4, and was not as severe. The important differences in clover yield between N 3 and N 4 occurred between harvests II and III, as the mean daily radiation fell from 316 to 230 in N 3, and from 128 to 27 in N 4. The yield of clover in N 4 began to decline, when the mean daily radiation at the surface of clover fell below 80 g cal cm^{-2} per day.

Between harvests IV and V the height of grass increased, the L.A.I. of grass fell, the maximum altitude of the sun rose and the light intensity at the surface of clover increased appreciably (Figs. 20 and 24). With higher radiation, the clover which had been suppressed to different degrees up to harvest IV in the three treatments, responded differently to the more favourable light conditions. This is shown in Fig. 26 (b). Between harvests IV and V clover yield in N 1 rose by 6.3g dm^{-2}, in N 3 it increased by 4.4g dm^{-2} but in N 4 by only 0.03g dm^{-2}. The corresponding increases in radiation were 63, 178 and 49g cal cm^{-2} per day respectively. Further results of this nature are given in Experiment B (page 217).

Fig. 26. - The mean radiation at the clover surface during 14 days before a harvest, and clover yields.

(a) during the vegetative period.
(b) after the grass had flowered, and the light intensity at the clover surface had increased.


WEIGHT OF CLOVER g/dm²
0
1
2
3
4
5
6
7
8
9
10
11
12
13
N 4
N 3
N 1
I
II
III
IV
0
100
200
300
400
500
MEAN RADIATION AT SURFACE OF CLOVER IN PRECEDING 14 DAYS
AT HARVESTS I, II, III & IV


0
1
2
3
4
5
6
7
8
9
10
11
12
13
N 4
N 3
N 1
IV
V
0
100
200
300
400
500
MEAN RADIATION AT SURFACE OF CLOVER IN PRECEDING 14 DAYS
AT HARVESTS IV & V

5.2.0. Interim discussion of the results of Experiment A.

The influence of applied nitrogen in modifying the proportion of grass and clover in swards, initially identical in botanical composition, was striking. One of the objectives of the experiment was to study changes as they developed. In this discussion the influence of nitrogen is evaluated, an appraisal is made of the salient features of the light micro-environment and the growth data are considered, giving particular attention to the nature of clover suppression.

The influence of applied nitrogen. Soil nitrogen was initially low and fertiliser was the chief source of nitrogen for the swards. There was a slight response by clover to nitrogen early in the experiment, but most of the nitrogen was taken up by the grass. Increasing nitrogen applications maintained the grass population, encouraged tillering, and stimulated leaf development and height of grass. Grass thus gained several advantages with added nitrogen, particularly in respect to leaf area and height. The low nitrogen dressing in N 2 had little influence, and the difference between N 1 and N 2 were comparatively small. Unfortunately no pure cultures of grass were grown, because of the limited number of treatments which could be handled, but it would be reasonable to assume from the work of Trumble and Shapter (1937) that the grass yield in this experiment was not depressed to any appreciable extent by the presence of clover. In this experiment the amount of available nitrogen limited the further growth of grass, and grass in N 1 and N 2 may be regarded as weakly aggressive, and moderately aggressive in N 3.

The effect of these changes in grass growth on the balance between species, will be discussed in greater detail after the light micro-environment has been considered.

The light micro-environment. The light profiles of grassy and clovery swards were different. In accord with the findings of other workers light intensity was reduced more in the upper layers of clover than grass swards, and 95 per cent. light reduction occurred at lesser depths in clover than in grass. The relationship between L.A.I. and light intensity is similar to the relationship between L.A.I. and light interception established by Brougham (1958a). Whereas Brougham's data were derived from repeated measurements of light intensity at ground level and the L.A.I. of swards during a month of regrowth, the data in Experiment A were obtained from the profiles of light intensity and L.A.I. on a single occasion.

Apart from the data of Monsi and Saeki (1953) there is no previous record of how these relationships change with time, in swards of varying botanical composition. It was shown in the literature review, that changes in leaf area per unit volume (leaf concentration), or in the disposition of leaves (leaf angle) altered the light profile in the sward (Figs. 7, 8). In this experiment the maximum leaf concentration was 0.86 cm^2 per cm^3 for clover and 0.29 cm^2 per cm^3 for grass; leaf concentration varied with nitrogen treatment and with time, and changes in the light profiles resulted. The isopleths of light intensity were not so crowded together in N 4 as in N 1, and the light was even more gradually reduced when grass was elongating in N 3 and N 4. Measurements of the disposition of grass leaves showed that young leaves were held at angles of 20 to 30° from the vertical (α in Fig. 7) and that changes in disposition were small, because of the high densities of stand. In Experiment A, the angle at which leaves were held, was not a major factor influencing the light gradient in the swards.

There were characteristic reductions in light intensity by inflorescences. Though the amount of inflorescence in N 1 was small, the light reductions due to inflorescence were almost as great as in N 4.

Light reductions by the uppermost leaves of the sward were also considerable. In a number of cases where light intensities of 60-70 per cent. full daylight were measured a little below the surface of the sward, aggregate L.A.I. values of only 0.5 units were recorded at this height. Observation in the field has shown that shadow patterns due to very slight differences in height are frequently discernible at the surface of an apparently uniform sward; this is particularly noticeable at low angles of elevation of the sun. In this experiment light intensities were measured with a horizontally disposed photocell, and these light reductions might not have been so pronounced if a spherical cell had been used.

The light intensities at the surface of clover were critical measurements in this experiment. It is clear that the grass leaf disposed above clover was primarily responsible for the reductions in light intensity, but it was surprising to find how severe the reductions were in the N 1 and the N 2 treatments; as has already been explained, this may be due to the use of a flat-surface photocell. The light intensity data were used to determine the amount of radiation available to clover in each of the swards, and thus it was possible to assess clover growth in terms of the light supply.

Growth Data. There was a gradation in sward composition from N 1 to N 4, nevertheless all swards attained the same total yield at the end of the experiment, and the values appear to be ceiling yields under the conditions of this experiment. This suggests full exploitation of the light environment and the light data support this view.

One feature of the growth data is the dominance of one species and the suppression of the other. It occurred in each nitrogen treatment in terms of L.A.I.: in N 4, clover declined after the second harvest and at the end of the experiment grass dominance was absolute; in N 1, N 2 and N 3 the L.A.I. of grass declined after the second harvest. Senescence of grass leaves set in after the fourth harvest in the grass-dominant N 4, and was accelerated in the other three nitrogen treatments. Though some grass leaves were disposed above clover in N 1, N 2 and N 3, the shading of most of the leaf tissue was an important factor in accelerating ontogenetic senescence. The loss of leaves in clover resulted in a significant fall in the dry weight. A decline in L.A.I. is therefore of serious consequence while clover remains in an indeterminate[1] stage of growth. In N 4, clover yield was severely depressed and in N 3 it received a temporary set-back only. The manifestations of clover suppression are:

(a) loss of leaf (Figs. 18, 20, Table 26),

(b) loss of yield (Figs. 16, 17, Table 21),

and (c) a decline in plant numbers (Table 30).

Attention has already been focused on the reductions in light

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[1] Indeterminate: growth not limited or stopped by the development of a terminal inflorescence; indefinite prolongation and subdivision of an axis.

intensities which may take place at the clover surface in the presence of even small amounts of grass. The use of radiation values permits an evaluation of clover growth in terms of the available radiation in each of the nitrogen treatments. The increments of yield become less as the compensation point is approached, and when radiation falls below the compensation point, yield declines slowly at first, but then more rapidly until small reductions in radiation lead to the elimination of clover. The resumption of growth in N 3 when the radiation at the clover surface increased at the end of the experiment, and the failure of clover to recover in N 4 despite increased radiation, suggested that there may be a threshhold radiation value between the compensation point and complete light extinction, from which clover might recover. This was the subject of further experiment and the results of Experiment B follow.

5.3.0. Experiment B.

5.3.1. Growth Data.

(a) Yield and L.A.I. of pure clover swards.

Eleven harvests were made in the pure clover swards, which consisted of clover panels only. (See Table 16). Yield and L.A.I. are plotted against time in Fig. 27a. This is a record of clover production in pure stands during this experiment; the ceilings achieved were 8.06 g dm^{-2} for weight of dry matter and 11.4 for L.A.I. The growth rate increased steadily up to 72 days, levelled off during August and rose again between 107 and 114 days. Similarly the L.A.I. rose to 8.2 was depressed at 93 days and then rose again to 11.4 Dur-

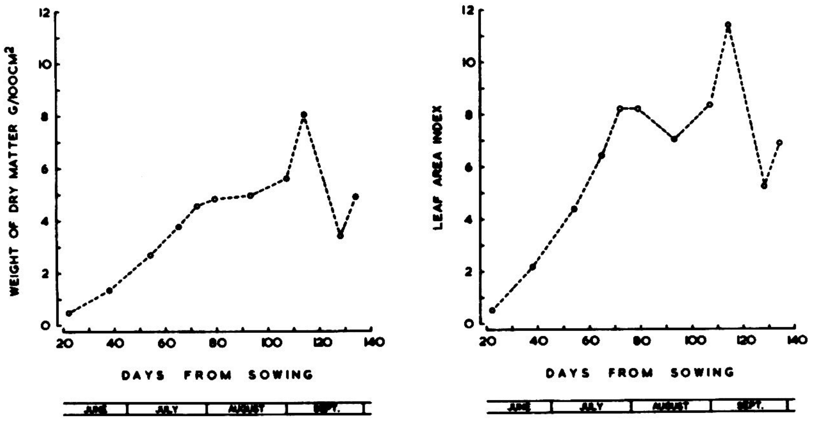


Fig. 27a - The yield, and L.A.I., of pure clover swards.

ing the August plateau (72 to 107 days) the number of leaves per plant was declining and individual leaves were expanding (See Table 41).

Plants from the border panels were encroaching on the sample panels at the last two harvests, and this resulted in death of plants in the sample panels, and there was consequently a greater variability between replicates. This appears to be the only reasonable explanation for the fall and rise at 128 and 134 days respectively.

(b) Yield and L.A.I. of control mixed swards.

The control mixed swards consisted of alternate grass and clover panels. Contributions by grass and clover were rising simultaneously and the total yield of the sward increased four-fold during the period from 38 to 65 days (Fig. 27b). The rate declined as the contribution by clover fell during the period from 65 to 107 days. The reduction in grass yield at the last harvest (121 days) was due to the death of tillers; as in the case of the pure swards, this may have resulted from the encroachment of plants in the border panels on plants in the sample panels. Only a few grass tillers were elongating at the conclusion of the experiment. During the first three weeks of August the L.A.I. of the entire sward remained above 12.0, due mainly to the increasing leaf area of grass. During the same period the L.A.I. of the pure clover swards was about 8.0.

At the first three harvests clover yielded more than grass, and at the first two harvests it developed a greater L.A.I. than grass, but at no time did it have an advantage in height. From the fourth harvest onwards, clover steadily declined in yield and L.A.I., and at the penultimate harvest (107 days) it was eliminated from the swards. When

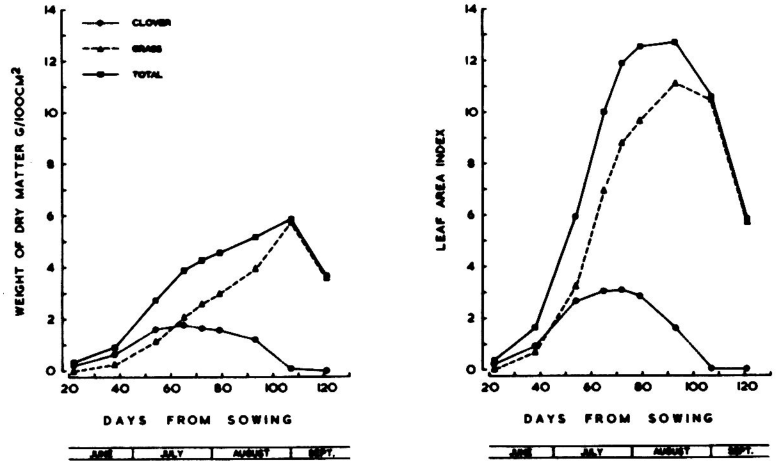


Fig. 274- The yield, and L.A.I. of the control mixed swards.

calculated on the basis of the entire sward area, grass reached a ceiling yield of 5.76 g dm^{-2} at 107 days and a ceiling L.A.I. of 11.1 at 93 days. The yield and L.A.I. of clover in mixed swards shown in Fig. 27 6. were calculated on the area of the entire sward. However, for a comparison between clover in pure and mixed stands, the calculations have to be based on the areas of individual panels. Thus the best yield of clover in mixture with grass was 3.60 g dm^{-2} of dry matter and the highest value of L.A.I. was 6.2.

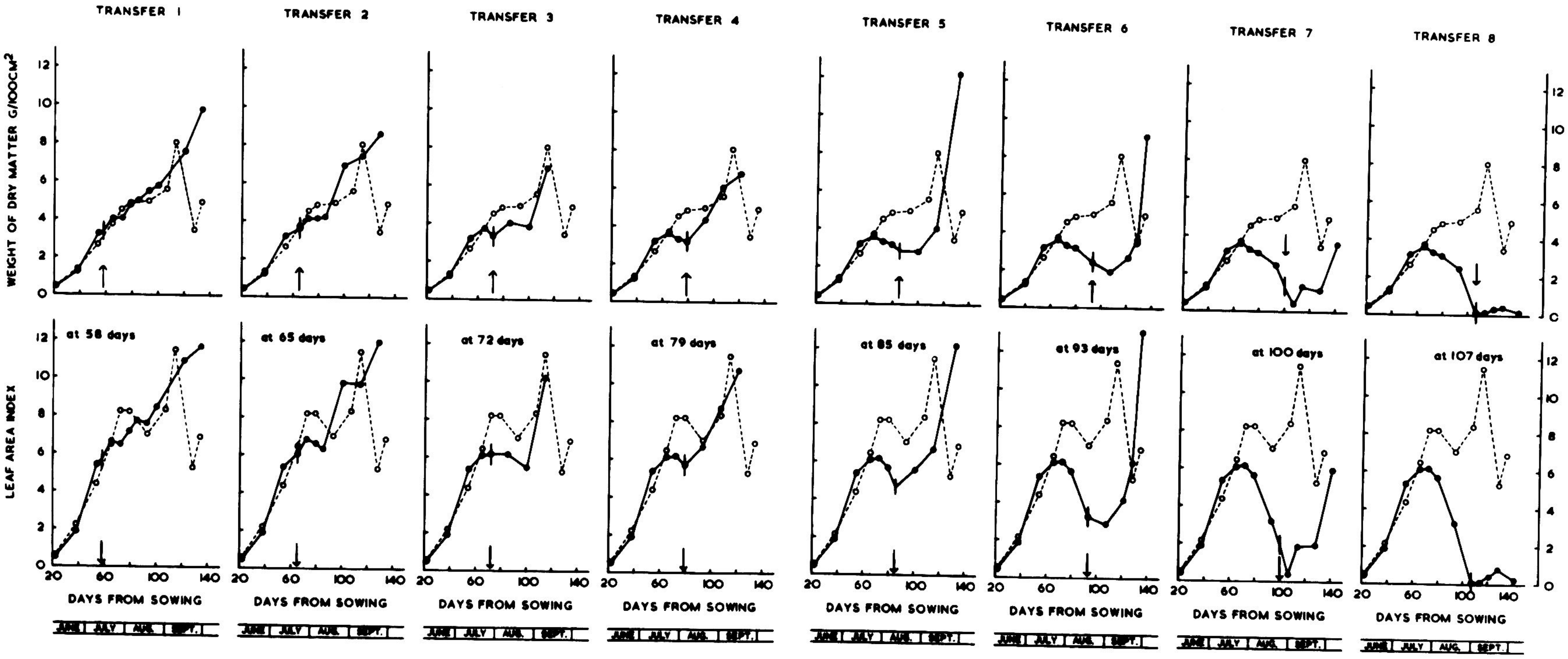
(c) The yield and L.A.I. of clover transferred from mixed swards.

(i) Yield and L.A.I. at transfer.

Clover panels were grown amongst grass panels and transferred at 58, 65, 72, 79, 85, 93, 100 and 107 days from sowing (See Table 16). After transfer, they were grown as pure stands of clover by placing the panels from a transfer alongside the panels from the previous transfer; the density of clover was held constant throughout the experiment. The weight of dry matter, and L.A.I. of clover at each harvest, before and after transfer, are shown as a series of graphs in Fig. 28. The dotted lines are for clover in the control pure swards and the continuous lines are for clover in mixed culture. The results were calculated on the areas of single panels.

On the whole, yield and L.A.I. showed similar responses and there was a continuing trend from transfer to transfer. On days 58 and 65 there was no measurable set-back to clover in the mixed swards, but at the third transfer, on day 72, clover in mixed stand differed significantly from clover in pure stand and this

Fig. 28 - The yield (above), and L.A.I. (below), of clover before and after transfer from mixed swards are shown by continuous lines. The transfer occasion (1 to 8) is indicated at the top of the graphs; the time in days is shown between the upper and lower series of graphs; it is also marked by a vertical line on the graph, and an arrow on the abscissae. The broken lines represent the yield and L.A.I. of pure clover swards.


TRANSFER 1
TRANSFER 2
TRANSFER 3
TRANSFER 4
TRANSFER 5
TRANSFER 6
TRANSFER 7
TRANSFER 8
WEIGHT OF DRY MATTER G/100CM^2
LEAF AREA INDEX
0
2
4
6
8
10
12
at 58 days
at 65 days
at 72 days
at 79 days
at 85 days
at 93 days
at 100 days
at 107 days
20
60
100
140
DAYS FROM SOWING
JUNE
JULY
AUG.
SEPT.

difference became larger at each successive transfer. This is shown in Table 36 and is clear from Fig. 28.

Table 36

A comparison of the yield, and L.A.I., of clover in pure stand and in mixture.

Transfer number	Days from Sowing	Yield of dry matter g dm^{-2}		L.A.I. of clover	
		in pure stand	in mixture	in pure stand	in mixture
-	22	0.46	0.47	0.5	0.5
-	38	1.36	1.29	2.2	1.9
-	54	2.69	3.21	4.4	5.4
1	58	-	-	-	-
2	65	3.77	3.60	6.4	6.1
3	72	4.55	3.33 ^{x}	8.2	6.2
4	79	4.84	3.18 ^{xx}	8.2	5.7
5	85	-	-	-	-
6	93	4.96	2.44^{xxx}	7.0	3.2
7	100	-	-	-	-
8	107	5.60	0.18	8.3	0.07
-	114	8.06	-	11.4	-

L.S.D. between clover in pure and in mixed stands, within each harvest

at $P < 0.05$ is 1.07
$P < 0.01$ 1.46
$P < 0.001$ 1.99

(ii) Yield and L.A.I. after transfer.

Transfer 6 was the first in which a decline of clover was recorded after transfer; in transfer 7, this decline continued until yield and L.A.I. fell to almost zero. Clover failed to recover after transfer 8.

<u>Total increase in 6 weeks</u>: A harvest at about 6 weeks after transfer was common to all treatments (except transfer 8 which only had 5 weeks), and from these data the initial comparisons were made of clover recovery from varying periods of shading by grass. The total increment in weight of dry matter and the L.A.I. in each treatment during this period are shown in Table 37.

Table 37

The growth of clover during 6 weeks after transfer.

Transfer number	Weight of dry matter (g dm^{-2})		Leaf Area Index	
	at transfer	increase during ensuing 6 weeks	at transfer	increase during ensuing 6 weeks
1	3.36	2.45	5.6	2.8
2	3.60	3.57	6.1	3.7
3	3.33	3.65	6.2	4.1
4	3.18	3.61	5.7	5.0
5	2.86	7.67	4.6	10.3
6	2.44	6.67	3.2	9.9
7	1.31	2.31	1.6	4.3
8	0.18	-0.04*	0.1	0.2*

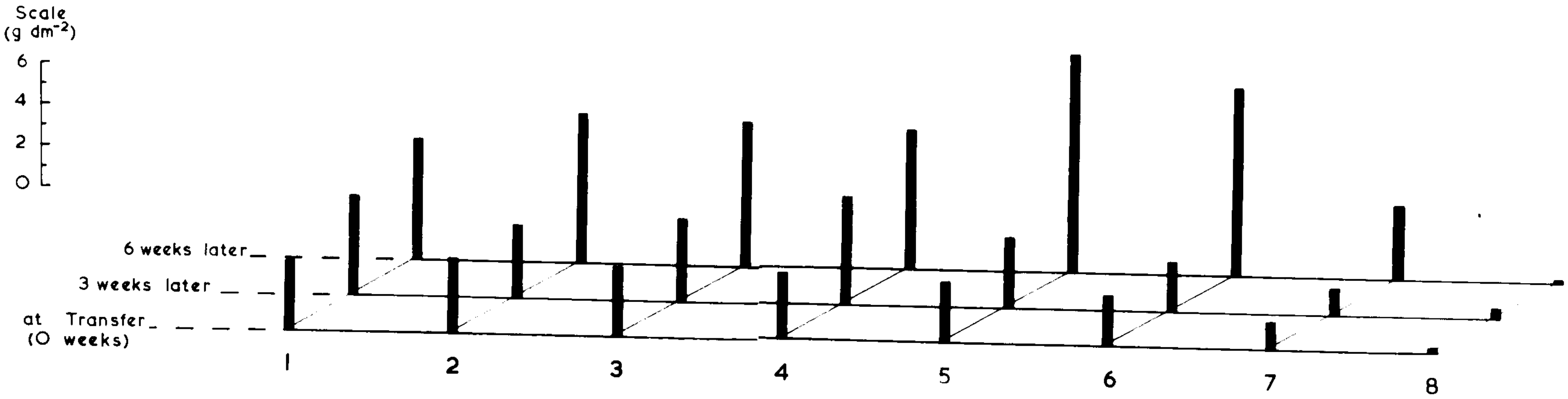
* Data at the end of 5 weeks.

After transfer 1, the weight increment was 2.50 g dm^{-2} and this was similar to the increase in dry weight of pure clover swards during the corresponding period. After transfers 2, 3 and 4 the increment was about 3.6 g dm^{-2} and after transfers 5 and 6 it was between 6 and 7 g dm^{-2}. The L.A.I. increases during the 6 weeks ranged from 3 to 5 units of L.A.I. for transfers 1 to 4 and transfer 7, and in transfers 5 and 6 the increases were of the order of 10 units.

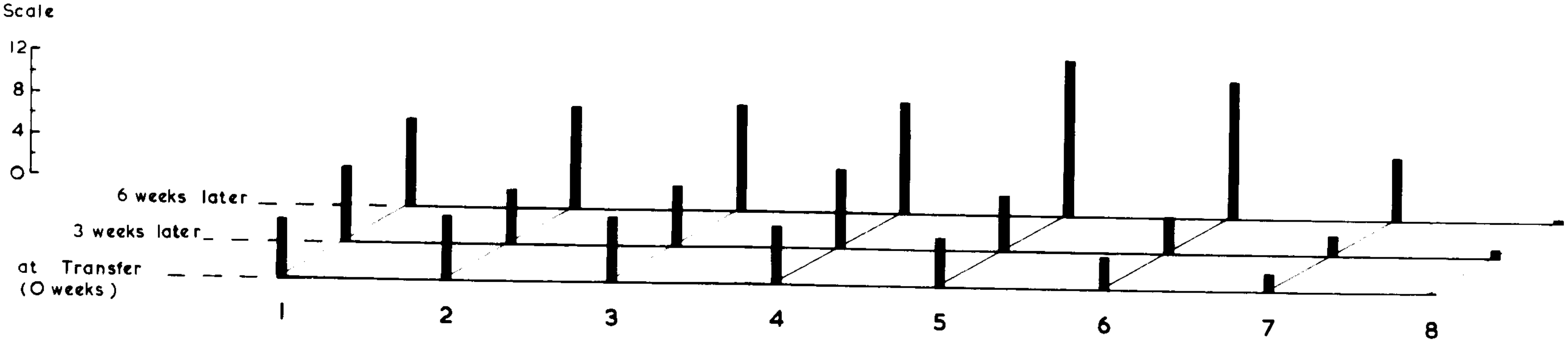
At 3 - week intervals after transfer: It was pointed out in section 4.2.0. (Page 130) that the harvests in this experiment were staggered to cope with the programme, and consequently it is difficult to make comparisons of the growth after transfer between treatments by using the original data. Scrutiny of the results showed that cardinal differences were beginning to develop at about 3 weeks after transfer, and since values at six weeks were already common to all treatments, it seemed logical to deal with the data at 0, 3 and 6 weeks from transfer. To do this, each replicate was plotted, and values interpolated where necessary; the means are shown in Fig. 29, which is in effect another presentation of the post-transfer data in Fig. 28. There are two time scales in Fig. 29: the weekly transfers appear from left to right on the horizontal axes, and the 3 - and 6 - week occasions after transfer are on the diagonal axes. Yield and L.A.I. are plotted vertically on each occasion and the scale is shown on the left hand side.

The yield and L.A.I. data were converted to logs (see Tables 58 & 59 in the Appendix) because of the nature of the variation, and also to examine the relative effects between transfers and after transfer. However, the variability between replicates at 6 weeks after transfer was high, and there was some doubt as to the reality of the much greater

Fig. 29. - The yield (above), and L.A.I. (below), of clover at 3 -weekly intervals after transfer. The transfer numbers are shown on the horizontal areas and the time intervals on the diagonal axes. The values are plotted vertically, and the scales are shown on the left hand side of the diagrams.



WEIGHT OF DRY MATTER
(G DM^{-2})



LEAF AREA INDEX

increases in yield and L.A.I. in transfers 5 and 6. To test this, the log-transformed data were treated as follows:

(a) Transfers 7 and 8 were omitted from the analysis because the values at transfer and after transfer were considerably lower;

(b) Generally the results at 6 weeks were significantly different from those at 0 and 3 weeks, and the differences between values at 0 and 3 weeks were not significant. Therefore occasions 0 and 3 weeks were grouped together and compared with the results at 6 weeks, using a weighted analysis;

(c) Transfers 1-4 and 5-6 were grouped and compared.

By using a two-way table,

Transfers

		1 2 3 4	5 6
	6	Group C	Group D
Weeks after transfer	3 0	Group A	Group B

and the appropriate tests, the interaction between groups was found to be highly significant: the variance ratios were

$$F^{1}_{12/24} = 16.72 \text{ for the log of yield}$$

$$F^{1}_{12/24} = 17.97 \text{ for the log of L.A.I.}$$

Table 38 summarises the levels of significance which were found when analysing the increase in log of yield and L.A.I. during the second three weeks within each transfer, i.e. when comparing (0 and 3) and 6 weeks along the diagonal time axes in Fig. 29.

Table 38

The levels of significance in a comparison of (0 and 3) and 6 weeks after transfer, within each transfer.

Levels of significance	Log Yield	Log L.A.I.
P 0.001	Transfers 5,6	Transfers 5, 6
P 0.01	Transfers 2,3	-
P 0.05	Transfer 4	Transfers 2, 3
Not significant	Transfer 1	Transfers 1, 4

Variability between panels was large, especially at the later harvests in each transfer. It would appear that small differences at transfer may develop into large differences subsequently, and an examination of the data, replicate by replicate and panel by panel suggests that yield may have been strongly influenced by the position of a panel. Where a neighbouring panel was better than average, yield was often below average and vice versa. This situation may have been affected by aspect, and also by the fact that there were not enough panels to form an adequate sward after each transfer; in some cases plants from earlier transfers may have encroached on plants from a later transfer.

5.3.2. Census Data.

(a) The density of clover plants.

(i) A comparison of clover density in pure stand and in mixture.

The initial density of clover plants in each panel was 28 per dm^2. Differences between clover in pure stand and in mixture appeared 13 weeks from sowing; while the numbers declined slowly in pure stands, they fell sharply in mixed stands. It is conceivable that death of clover plants in mixed stands would have begun earlier, had grass and clover roots occupied the same soil. Table 39 shows the density of clover in pure and in mixed culture. Between 93 and 107 days the clover numbers in mixed culture fell sharply, while the number in pure culture fell at about 18 to 130 days.

(ii) Plant numbers from transfer onwards.

Table 40 shows the mean number of plants in each transfer at 0, 3 and 6 weeks from transfer. Transfers 7 and 8 were excluded from the analysis of variance. The overall analysis indicated that in the first interval after transfer there was a significant (at $P < 0.05$) fall in plant numbers which did not continue into the second interval. In transfers 6 there was a significant (at $P < 0.001$) decline in plant number from 0 to 3 weeks and this is also apparent in transfer 7. This suggests that the light stress prior to transfers 6 and 7 had some effect which carried on after transfer, and that this was a phenomenon of accelerated senescence.

The increase in plant number from 2.8 at transfer 8, to 6.1 three weeks later is not real and is due to a larger number of plants surviving in one replicate only.

(b) The mean number of leaves per plant, and the mean area per leaf.

(i) A comparison of clover in pure stand, and in mixture.

Table 39

The number of clover plants per dm^2 in pure stands and in mixture

Days from sowing	54	58	65	72	79	85	93	100	107	114	128	134
Transfer number	-	1	2	3	4	5	6	7	8	-	-	-
Clover in pure stand	27.8	-	27.8	28.3	27.2	-	28.8	-	25.5	25.0	17.2	18.3
Clover in mixture	28.8	-	27.8	28.3	28.3	-	25.5	-	1.7	0	-	-

Analysis of Variance from 54 to 93 days (inclusive).

L.S.D. between and within treatments, at

$P < 0.05 = 3.0$
$< 0.01 = 4.2$
$< 0.001 = 5.6$

Table 40

The number of plants per dm^2 in the post-transfer period.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6	Tr7	Tr8
At transfer (0 weeks)	28.3	27.8	28.3	28.3	27.2	25.6	13.9	2.8
3 weeks later	28.4	26.1	26.7	27.2	25.0	21.7	9.4	6.1
6 weeks later	26.1	26.1	25.6	26.1	25.0	20.6	9.5	2.2

Analysis of variance from Transfer 1 to Transfer 6 (inclusive)

L.S.D. between times		L.S.D. between transfer	
at $P < 0.05$ =	1.4	at $P < 0.05$ =	2.0
< 0.01	1.9	< 0.01	2.7
< 0.001	2.5	< 0.001	3.6

The mean number of unfolded green leaves per plant in pure and in mixed culture is shown in Table 41. The mean area of leaves is also shown.

Table 41

The mean number of leaves per plant and the mean area per leaf in pure and in mixed culture.

Days from sowing	Clover in pure stand		Clover in mixture	
	Number of leaves per plant	Mean area per leaf (cm^2)	Number of leaves per plant	Mean area per leaf (cm^2)
38	2.6	3.0	2.8	2.5
54	5.0	3.2	6.5	2.9
65	8.0	2.9	8.9	2.6
72	7.6	3.8	7.7	2.8
79	8.4	3.6	7.4	3.0
93	6.1	4.0	5.1	2.9
107	4.6	7.0	1.4	2.0
114	5.3	8.6	-	-
128	3.6	8.6	-	-
134	3.4	10.9	-	-

At 38, 54 and 65 days, leaf number per plant was greater for clover in mixture, than for clover in pure stand. In pure culture, the number of leaves per plant rose until day 79 and then fell; as leaf number fell the mean area per leaf increased. In mixture, the leaf number began to fall after day 65, and in contrast to the pure stand the mean area of leaves remained reasonably constant; after 93 days when leaf mortality became heavy the mean leaf area diminished.

(ii) Leaf number and leaf area from transfer onwards.

In Table 42 the number of unfolded green leaves per plant and the mean area per leaf are shown from transfer onwards.

Table 42

The number of unfolded green leaves per plant and the mean area per green leaf at 3 weekly intervals from transfer onwards.

Transfer number	At transfer		Three weeks after transfer		Six weeks after transfer	
	Number of leaves per plant	Mean area per leaf (cm^2)	Number of leaves per plant	Mean area per leaf (cm^2)	Number of leaves per plant	Mean area per leaf (cm^2)
1	7.7	2.6	8.9	3.1	7.5	5.1
2	8.8	2.6	8.2	2.6	7.6	5.7
3	7.7	2.8	6.7	3.4	7.7	5.8
4	7.4	3.0	7.0	4.1	6.7	5.3
5	6.4	2.9	6.1	3.2	9.8	6.0
6	5.0	2.9	5.1	3.1	9.2	5.7
7	3.1	2.0	4.8	3.4	9.8	4.8
8	1.4	0.8	2.9	1.6	5.0[x]	2.4[x]

x Data at the end of 5 weeks

During the first three weeks after transfer the number of unfolded green leaves per plant was approximately steady. However in this experiment leaves were not labelled and it is likely that the leaf population at three weeks consisted of a new generation of leaves - especially in the later transfers where leaves were senescing rapidly at transfer. At six weeks, leaf number per plant increased markedly in transfer 5 to 8, indicating that meristems were actively forming on surviving plants.

The leaf areas rose from 2.7 cm^2 at transfer to 3.3 cm^2 three weeks later, and to 5.5 cm^2 at six weeks. (These means exclude the values recorded for transfer 8)

(c) The mean number of unfolded green leaves per dm^2, from transfer onwards.

Leaf number per unit area is the product of number of plants per unit area and leaf number per plant. In the controls, a peak of 230 leaves per dm^2 in pure swards was reached at 79 days and in the mixed swards the peak was 246 leaves per dm^2 at 65 days. It is of interest to consider these data for the post-transfer period, since they are a measure of clover recovery after transfer. The data are shown in Fig. 30. An inspection of the figure shows that there was a slight decline in leaf numbers after transfers 2, 3, 4. In transfers 5 and 6 leaf number fell in the first three weeks and then rose sharply in the second three weeks. The increase in leaf number per dm^2 was quite spectacular after transfers 5, 6 and 7 and where there was no significant loss in plant stand, high values were restored. The numbers at six weeks in transfers 5, 6 and 7 were 246, 185 and 124 respectively.

The log transformed data were analysed in the same manner as the yield and L.A.I. (See Table 60 Appendix) and a significant (at $P < 0.01$) interaction was found in the two way table set out on page 202. At (0 and 3) weeks there was a significant (at $P < 0.001$) fall in numbers from transfers (1-4) to transfers (5-6). Within

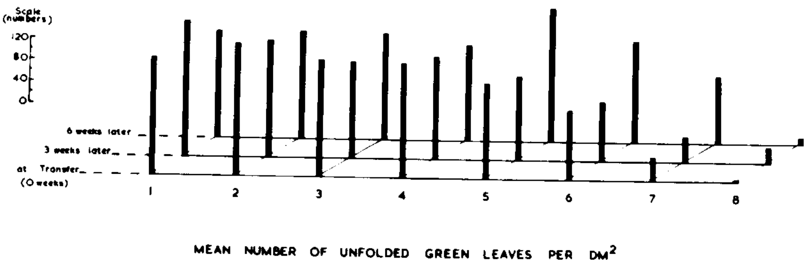


Fig. 30. - The mean number of unfolded green leaves per unit area, at three-weekly intervals from transfer onwards.

transfers the difference between (0 and 3) weeks and 6 weeks was not significant in the group of transfer (1-4), but was significant in the group of transfers (5-6).

5.3.3. Light intensity at the surface of clover.

The data for Fig. 31 were obtained from regular measurements of the light gradient and the height of clover in mixed swards. In 9 weeks the light intensity fell from full daylight to almost nil, the greatest reduction occurring in June. The light intensities at the surface of clover at transfer are shown in Table 43.

Table 43

The light intensity at the surface of clover in mixed swards at each transfer.

Transfer	Light intensity (per cent. daylight).
1	28.5
2	21.5
3	15.5
4	11.0
5	7.5
6	4.0
7	2.0
8	0.5

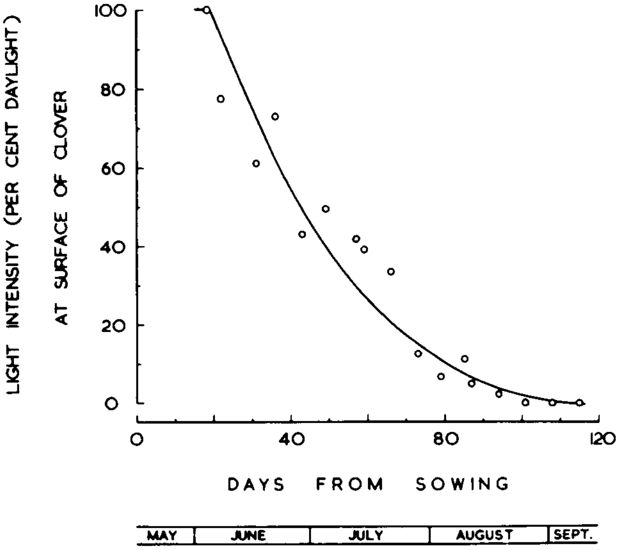


Fig. 31. - The light intensity at the surface of clover in mixed swards, in Experiment B.

5.3.4. Derived Data

(a) A comparison of the leaf area / leaf weight ratio of clover in pure and in mixed swards.

As the light intensity falls, or the L.A.I. increases, the leaf area to leaf weight ratio rises (Blackman 1956, Davidson and Donald 1958). In this experiment the ratio was initially higher for clover in pure culture and this was reversed at about 70 days. The divergence between treatments, even though the ratio was rising both in pure stands and in mixtures, is shown in Table 44. The light intensity at the surface of clover in mixed stands at the time of sampling is also shown.

Table 44

The leaf area/leaf weight ratio of clover in pure and in mixed stands. The light intensities in the last column were shown in Table 43.

Days from sowing	Leaf/area/Leaf weight ratio (cm^2/g)			Light intensity at the surface of clover in mixed stand (per cent. day-light)
	Clover in pure stand A	Clover in mixture B	Significance	
22	167	156	N.S.	93.0
38	260	232	A B ^{x}	58.7
54	323	326	N.S.	33.4
65	400	394	N.S.	21.5
72	411	474	B A ^{xxx}	15.5
79	448	483	B A ^{xx}	11.0
93	431	513	B A ^{xxx}	4.0

L.S.D. within a row or within a column,
at $P < 0.05 = 3.0$ $< 0.01 = 4.2$ $< 0.001 = 5.6$

(b) Clover yields, and the mean daily radiation at the clover surface.

(i) The mean daily radiation at weekly intervals during the experiment.

In Fig. 32 the mean daily radiation received at weekly intervals at the site of the experiment and at the surface of clover in pure and in mixed culture are shown. During 1959 radiation was recorded at the Waite Institute, about 200 metres from the site of this experiment. The procedure of applying the light intensity data to the radiation data was similar to that outlined for Experiment A, on page 184 and Fig. 32 may be compared with Fig. 25 on page 185.

(ii) The radiation at the surface of clover fourteen days before harvest.

Clover yields and mean daily radiation in the control mixed swards: In Fig. 33 the mean daily radiation at the surface of clover over a period of 14 days before a harvest, is plotted against the yield of clover in the control mixed swards at nine harvests. In this experiment the yield of clover declined rapidly when the mean radiation at the surface of the clover was reduced to below 60 g cal~~s~~ cm^{-2} per day. In three weeks from July 21st to August 18th the radiation diminished from 54 to 14 g cal~~s~~ cm^{-2} per day and yield fell from 3.60 g dm^{-2} to 2.45 g dm^{-2}. After August 18th, the yield of clover fell to almost zero within a fortnight. These data suggest that the compensation point for clover in this experiment was somewhere about 60 g cal~~s~~ cm^{-2} per day, at a time when the insolation at the site of the experiment was approximately 180 g cal~~s~~ cm^{-2} per day. An

Fig. 32. - The histograms show solar radiation, as daily averages at intervals of a week. The radiation at the clover surface is represented by the clear portion of the histograms and the shaded portion indicates the amount of radiation absorbed by grass. The continuous lines show the yield of clover in pure stands (left hand side) and in mixed stands (right hand side).
(Cf. Fig. 25).

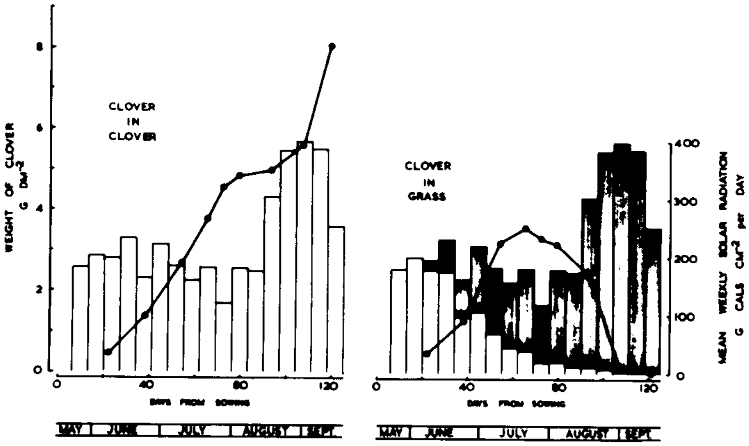
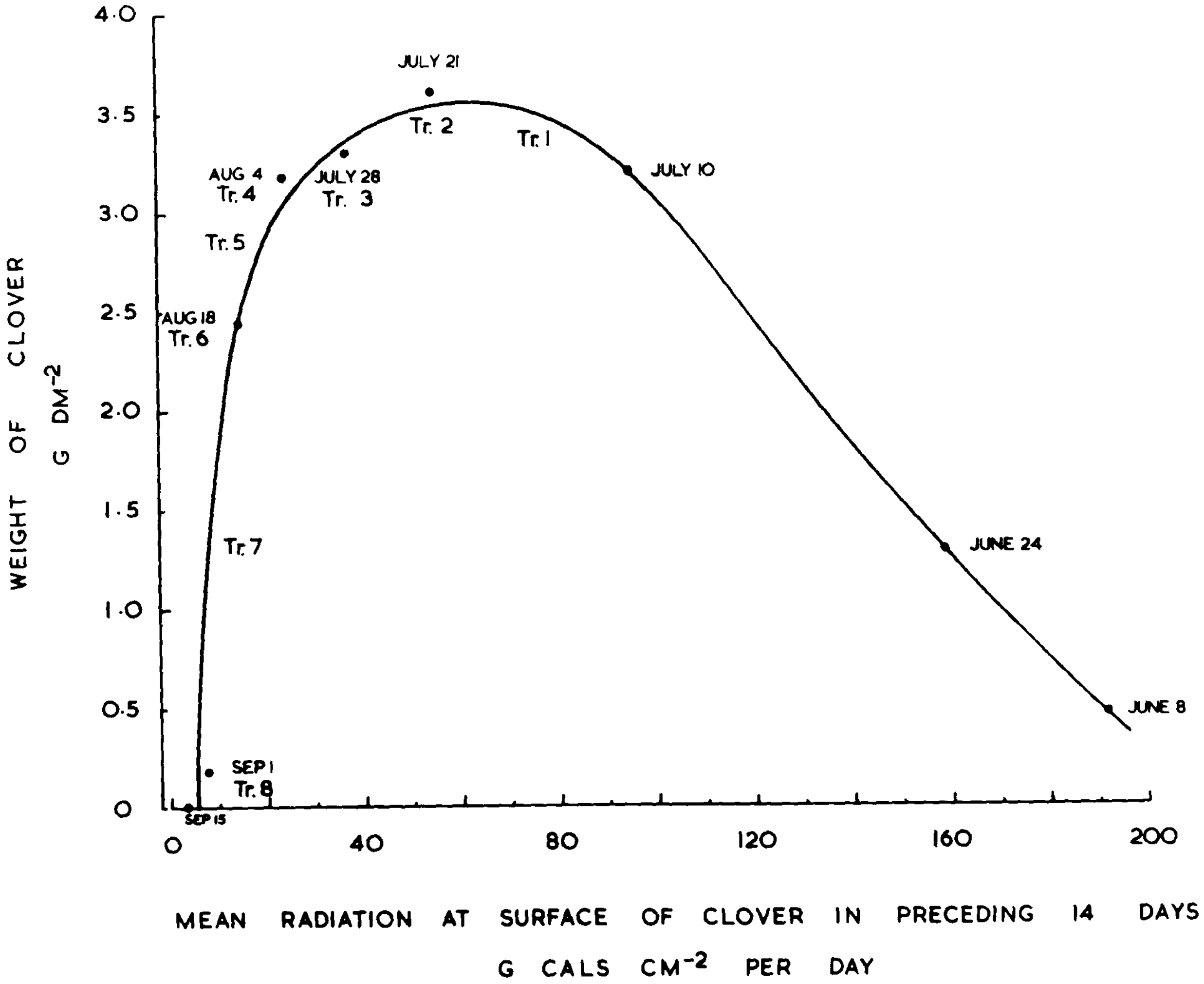

WEIGHT OF CLOVER G DM-2
0
2
4
6
8
CLOVER IN CLOVER
0
40
80
120
DAYS FROM SOWING
MAY
JUNE
JULY
AUGUST
SEPT
CLOVER IN GRASS
0
40
80
120
DAYS FROM SOWING
MAY
JUNE
JULY
AUGUST
SEPT
MEAN WEEKLY SOLAR RADIATION G CALS CM-2 per DAY
0
100
200
300
400

Fig.33. - The relationship between the radiation received at the surface of clover in mixed swards and the yield of clover in Experiment B. Harvest dates and the occasions of transfer are shown on the figure.

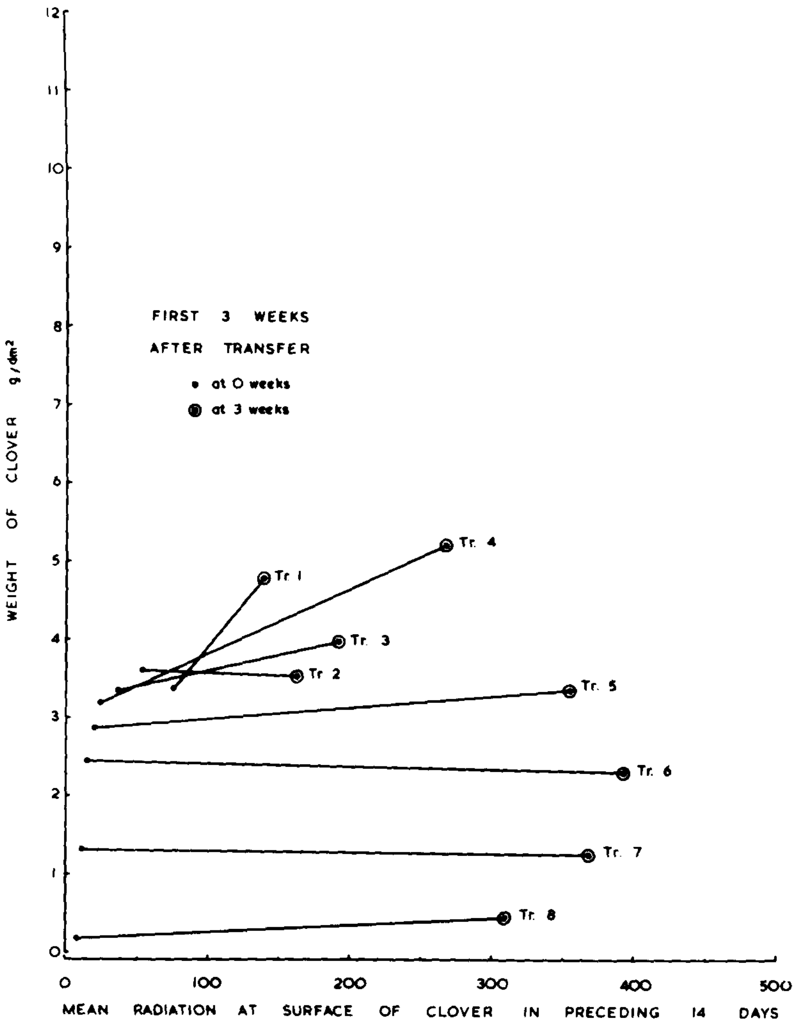

4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
WEIGHT OF CLOVER
G DM-2
0
40
80
120
160
200
MEAN RADIATION AT SURFACE OF CLOVER IN PRECEDING 14 DAYS
G CALS CM-2 PER DAY
JULY 21
Tr. 2
Tr. 1
JULY 10
AUG 4
Tr. 4
JULY 28
Tr. 3
Tr. 5
AUG 18
Tr. 6
Tr. 7
JUNE 24
JUNE 8
SEP 1
Tr. 8
SEP 15

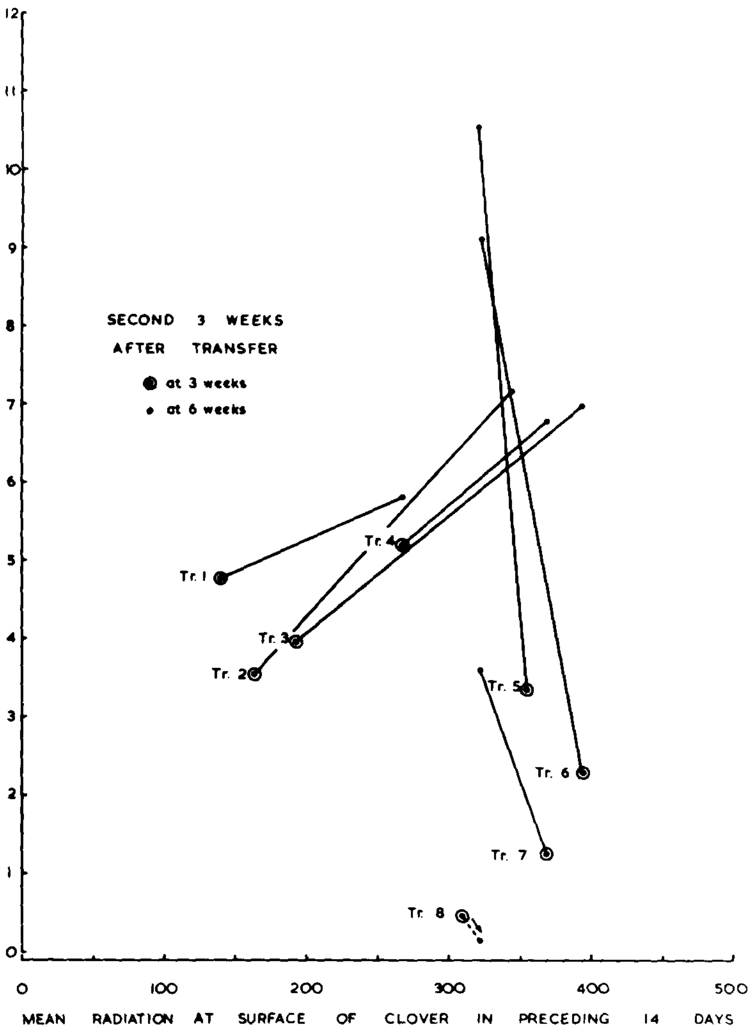
examination of the daily values of radiation at the surface of the clover showed that 60 g cals cm^{-2} was not reached after July 20th and that this value was exceeded on only 9 days during the whole of July.

Clover yields and mean daily radiation from transfer onwards: The yield of clover (ordinate) is plotted against the mean daily radiation at the surface of clover in the 14 days preceding a harvest (abscissae). The values during the first 3 weeks after transfer are shown in Fig. 34a, and during the second 3 weeks after transfer in Fig. 34b. In the first 3 weeks a large increase in the daily radiation at the surface of clover had only a slight influence on the growth of clover in transfer 1-4 and none in transfers 5-8. It was shown in Table 39 that a real decline in plant numbers in the mixed swards was beginning at the time of transfer 6. During the second interval, yield continued to rise in transfers 1-4 during a period of moderate increase in radiation, but in transfers 5-7 there was a marked increase in yield despite a slight reduction in the radiation received. Transfer 8 showed a very small decline in yield at a high level of radiation.

Fig. 34. - Showing the influence of radiation on yield, from transfer onwards:

(a) during the first 3 weeks after transfer,
(b) during the second 3 weeks after transfer.


FIRST 3 WEEKS
AFTER TRANSFER
• at 0 weeks
◉ at 3 weeks
WEIGHT OF CLOVER g/dm²
MEAN RADIATION AT SURFACE OF CLOVER IN PRECEDING 14 DAYS
0
1
2
3
4
5
6
7
8
9
10
11
12
0
100
200
300
400
500
Tr. 1
Tr. 2
Tr. 3
Tr. 4
Tr. 5
Tr. 6
Tr. 7
Tr. 8


SECOND 3 WEEKS
AFTER TRANSFER
◉ at 3 weeks
• at 6 weeks
MEAN RADIATION AT SURFACE OF CLOVER IN PRECEDING 14 DAYS
0
1
2
3
4
5
6
7
8
9
10
11
12
0
100
200
300
400
500
Tr. 1
Tr. 2
Tr. 3
Tr. 4
Tr. 5
Tr. 6
Tr. 7
Tr. 8

5.4.0. Discussion of the results of Experiment B.

In this experiment the grass was used as a shading agent only, and frequent nitrogen dressings encouraged tillering and leaf growth. Clover was rapidly shaded before grass had begun to elongate and was totally suppressed from the mixed swards. The relationship between radiation and clover yield proposed for N 4 in Experiment A was confirmed, and the results can be explained in terms of the level of radiation prior to transfer.

The first transfer was made before there was any serious reduction in radiation: transfer 2 took place when the clover was near the compensation point, and transfers 3, 4 and 5 were made as the radiation at the clover surface was rapidly diminishing below the compensation point; the remaining three transfers were made when radiation at the surface of clover was very low. Two transfers, instead of one, between transfers 6 and 8 would have been advantageous.

The clover that was transferred recovered from the effects of light stress in the following ways:

(a) After six weeks, clover in transfers 1-6 had recovered fully. The growth of clover after transfers 1-4 was similar to the growth in the unshaded control swards, except for a slight set-back before transfers 3 and 4. After transfers 5 and 6, a quiescent period of 3 weeks was followed by rapid growth during the next 3 weeks. During this latter interval, the relative growth in these treatments were the largest in the experiment.

(b) Transfer 8 failed to recover as a result of a severe reduction in plant stand.

(c) The relative growth of the surviving plants after transfer 7 was similar to transfers 5 and 6, but the plant stand had been reduced, and consequently the recovery per unit area at 6 weeks was intermediate between (a) and (b) above.

Severe and prolonged shade resulted in the death of clover plants. The fall in plant number was approximately 10 per cent. at transfer 6, but by transfer 7 a week later, 50 per cent. of the stand had died. Where radiation fell below the compensation point, and there was a recession in growth without death of plants, the clover recovered rapidly after a quiescent period.

Growth after transfer may be interpreted in terms of leaf survival and development. The mean number of unfolded green leaves is a compound measure of the number of plants and their leaf primordia. In this experiment the response of this measure was similar to the response of yield and L.A.I. In general it may be argued that the nature of the recovery depends on the stage of growth at which the stress is applied. In this experiment, shading was continuous from the beginning, and transfers 5 and 6 were subject to greater light stress than transfers 1-4; yet transfers 5 & 6 made a better recovery in six weeks. The only reasonable explanation appears to be that new leaf primordia continued to form as light stress became progressively more severe; when the light stress was removed, the simultaneous growth of all these primordia, though slow at first, eventually resulted in exceptionally rapid growth. Where the light stress was severe enough to prevent the formation of primordia, plants died, as in transfers 7 and 8.

This interpretation is based on the evidence gained in Experiment C, in which individual leaves were studied throughout the life of clover swards, grown at three densities.

5.5.0. Experiment C

5.5.1. The sward as a whole

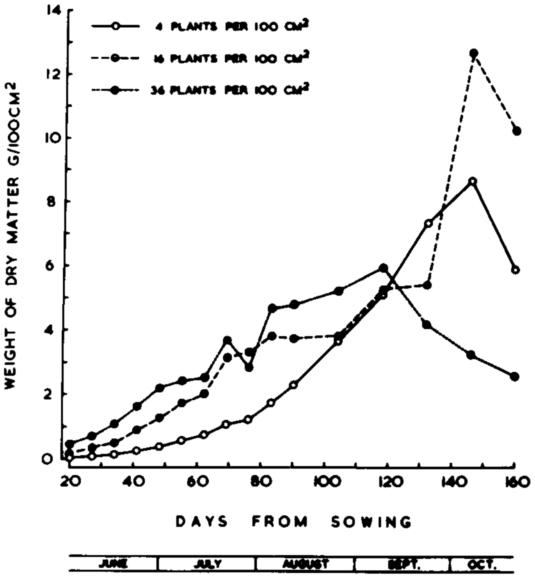
(a) Yield of tops and L.A.I.

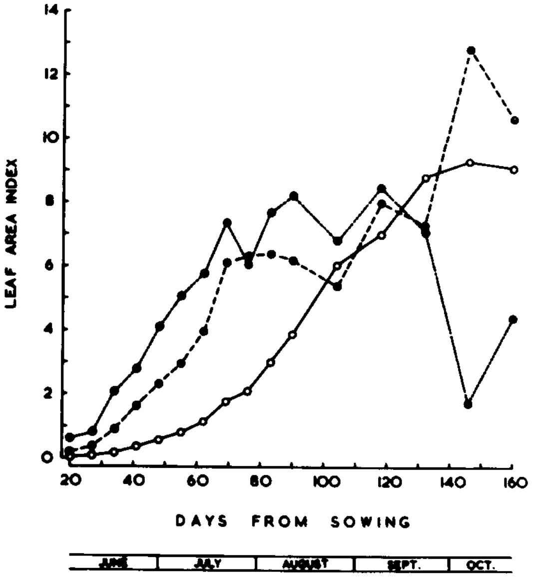
(i) With time

The yield of the above-ground parts and the L.A.I. of the swards are shown in Fig. 35. At 118 days the yields were 5.1, 5.3 and 5.9 g dm^{-2} and the L.A.I. values were 7.0, 8.0 and 8.5 for stands at 4, 16 and 36 plants per dm^{2} respectively. The development of yield and L.A.I. was slow at the lowest density, rapid at the highest density and intermediate in the middle density. At the low and high densities the curves of yield and L.A.I. are continuous, and at the middle density (16 plants per dm^{2}) there is a plateau between 69 and 104 days. A similar plateau was recorded between 72 and 109 days in the pure clover swards (28 plants per dm^{2}) of Experiment B (Fig. 26). Davidson (1954), also recorded one at 25-62 plants per dm^{2} and a minor one at 6.2 plants per dm^{2}. This phenomenon is thought to be real and was probably associated with branching, and leaf development on these branches.

At 90 days, the densest sward first attained L.A.I. of 8 and this then oscillated between 7 and 8 until 132 days, i.e. for a period of about 6 weeks. During this period the yield showed a steady upward trend, rising to a maximum at 118 days, and then declining. The fluctuating L.A.I. suggests/that when the L.A.I. reached a certain value, leaves died, and that the L.A.I. was restored when new leaves formed. Clearly then, a ceiling L.A.I. was reached at about 100 days in the high density. In the low density, the L.A.I. rose to a peak of 9.3 at 146 days, and this date coincided with the maximum yield in this density. In the

Fig. 35. - The yield and L.A.I. of pure clover swards grown at three densities.


4 PLANTS PER 100 CM²
16 PLANTS PER 100 CM²
36 PLANTS PER 100 CM²
WEIGHT OF DRY MATTER G/100CM²
0
2
4
6
8
10
12
14
20
40
60
80
100
120
140
160
DAYS FROM SOWING
JUNE
JULY
AUGUST
SEPT.
OCT.


LEAF AREA INDEX
0
2
4
6
8
10
12
14
20
40
60
80
100
120
140
160
DAYS FROM SOWING
JUNE
JULY
AUGUST
SEPT.
OCT.

middle density the marked fluctuations prevent a satisfactory evaluation of the situation, but the data suggest that ceiling yield was first reached at about 123 days. Though the yield data do not show a decline at the last two harvests, some plants in the sward had died, and yield would have declined had the experiment continued.

The yield and L.A.I. of the swards were computed from individual plant data, and the values for the middle density at the last two harvests in Fig. 35 should be considered with some caution because of the high variability between individuals (See Fig. 41). Two points on the yield and L.A.I. curves are considered to be aberrant. They are those at 76 days in density 36 plants per dm^2 and at 146 days in density 16 plants per dm^2. Although the plants harvested were uniform within each panel, several aspects of the data lead to the conclusion that the plants were below average at 76 days in the high density, and above average at 146 days in the middle density.

The crop growth rates $\frac{dw}{(dt)}$ were calculated from the curves in Fig. 35 and are tabulated in the Appendix (Table 71 A plot of these values against L.A.I. revealed a rise and fall in crop growth rate as the L.A.I. increased from emergence to ceiling L.A.I. This was followed by a cyclic pattern at about ceiling L.A.I. In the first phase of growth before the cyclic patterns developed, peak crop growth rates were distinguished and these are recorded in Table 45. By definition (page) the L.A.I. values corresponding to these growth rates are optimum L.A.I.'s. These varied with density as shown in Table 45. In the second phase of growth the amplitude of the cycles also varied with density.

Table 45

The initial* peak in the crop growth rate and the corresponding L.A.I.

Density (Plants per dm^2)	Days from sowing	L.A.I.	Peak crop growth rate (g dm^{-2} / day)
4	86	3.8	0.124
16	66	5.2	0.107
36	40	2.7	0.079

* The growth rates fluctuated above and below this value.

(ii) Yield and density.

Figure 36 depicts the relationship between the yield and density at 20, 55, 90 and 118 days, i.e. at two five-week, and one four-week interval. At 20 days when the first trifoliate leaf had formed but was still folded, the relationship was linear. From 25 to 55 and from 55 to 90 days, yield increases were larger at the high density, but from 90 to 118 days, they were less at the high density. Thus a curve of near-asymptotic form was obtained at 118 days. These curves form a similar pattern to the ones presented by Donald (1951).

(b) Yield of roots.

The yield of roots per unit of ground surface is shown for each harvest in Table 46. The trends of the root yields are similar to the trends in the above-ground parts depicted in Fig. 35. At 118 days, root yields were approximately equal in all three densities. When top growth was approaching a ceiling at about 120 days, the yield of roots was about 0.80 g dm^{-2} giving a top/root ratio of approximately 6.

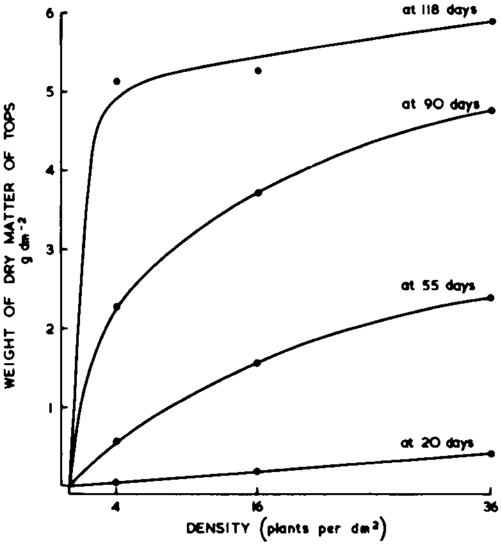


Fig. 36. - The yield per unit area plotted against density at the 1st, 6th, 11th and 13th harvests.

Table 46.

Dry weight of roots per unit of ground surface in each density at each harvest.

Days from sowing	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
4 plants per dm^2	0.02	0.04	0.07	0.10	0.19	0.23	0.32	0.43	0.41	0.49	0.54	0.85	0.80	1.23	1.05	0.97
16 plants per dm^2	0.11	0.15	0.22	0.31	0.45	0.53	0.58	0.64	0.64	0.70	0.65	0.67	0.80	0.89	1.66	1.28
36 plants per dm^2	0.22	0.31	0.40	0.53	0.59	0.52	0.63	0.76	0.51	0.75	0.77	0.82	0.88	0.72	0.83	0.78

There was a different pattern in each density in the rate of root growth. At the lowest density the rate of root growth gradually increased to reach a peak at 62 days and then oscillated with high values at 96 and 124 days and low values at 73, 112 and 140 days. In the high density, the highest rate was recorded at 36 days and this rapidly declined to fluctuate slightly at a low level. The pattern in the middle density was intermediate between these two. The data are included in Table 71 in the Appendix.

In Fig. 37 the proportion of roots is expressed as a percentage of the total dry weight of the plant (including roots) and this is plotted against time. The general trends are similar in the three densities - falling at first and then levelling; the fall was initially more rapid at the high density. The middle and the high density fell to 16 per cent. at 69 days. In the low density the proportion of roots remained at about 30 per cent. until 69 days, and then declined to the same value as the other two densities at 118 days. The values at the low and the middle densities remained together until the end of the experiment,

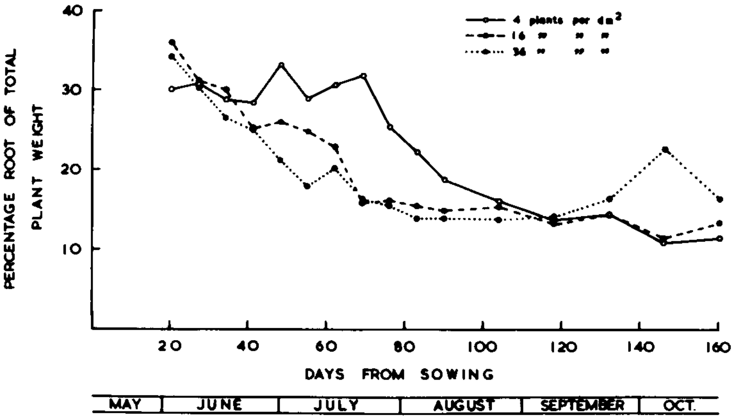


Fig. 37. - The proportion of root, as a percentage of the total yield of the sward, in three densities.

but the proportion of root in the high density increased, mainly because the top weight was rapidly falling.

(c) Leaf number per unit area.

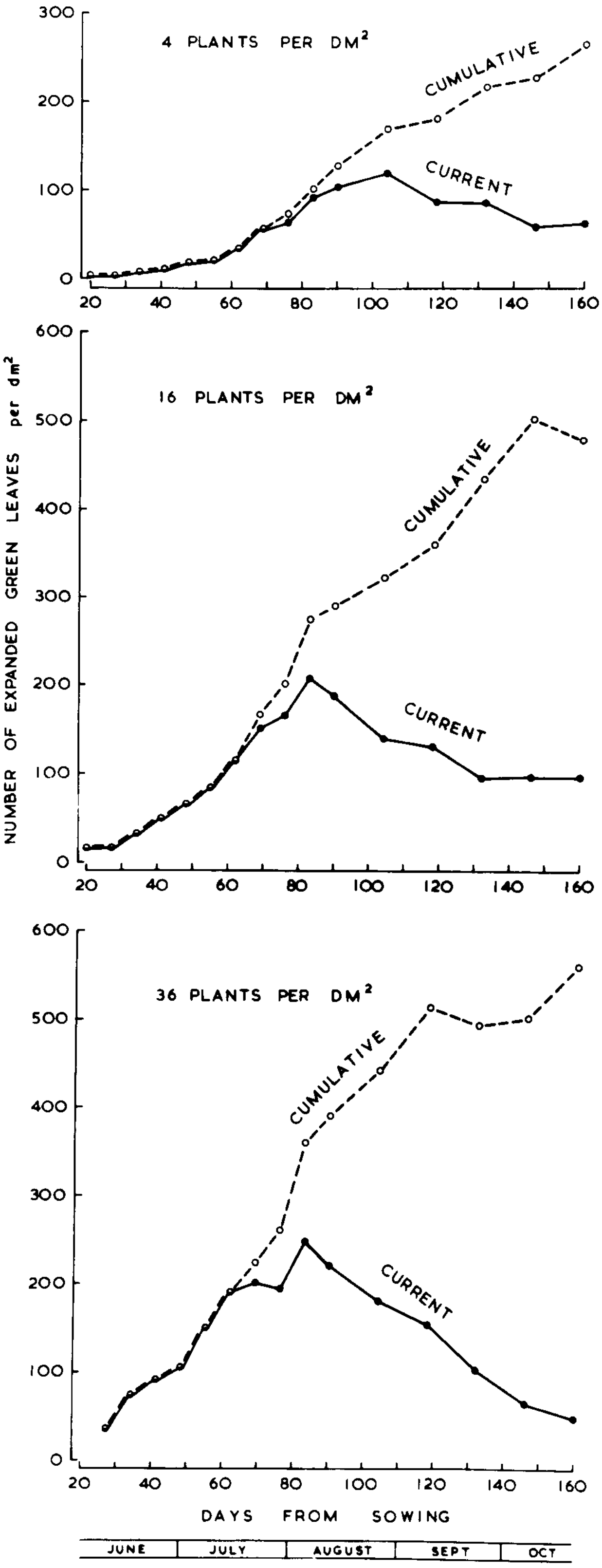
In Fig. 38 the number of expanded leaves per dm^2[★] are plotted for each density. The green leaves currently attached to the plants are distinguished from the cumulative totals. At first, the number of leaves produced was dependent on the number of plants in the stand. Up to 55 days the relationship of the number of plants per dm^2 to density was linear but after this time it rapidly changed. A peak of current expanded leaves was reached at 104 days at the low density, and at 83 days in the middle and high densities. These peaks and the corresponding L.A.I. values were:

	4 plants per dm^2	16 plants per dm^2	36 plants per dm^2
L.A.I.	6.0	6.4	7.7
Number of expanded green leaves per dm^2	120	208	248

The cumulative data in Fig. 38 reflect the changes which occurred in plant stand. At the low density all plants survived and the cumulative totals were still rising at the end of the experiment. In the middle density a few plants died between 146 and 160 days, and at the high density plant stand fell by more than 40 per cent. between 130 and 160 days. As plant stand was reduced the cumulative totals levelled off.

[★] plants per dm^2 x number of expanded green leaves per plant.

Fig. 38. - The number of expanded green leaves per dm^2 in each density. The current leaf population is shown as continuous black lines and the cumulative totals are plotted as broken lines. The irregularities in the cumulative values arise from the fluctuations in numbers of labelled expanded leaves, between panels.


4 PLANTS PER DM²
CUMULATIVE
CURRENT
0
100
200
300
20
40
60
80
100
120
140
160
16 PLANTS PER DM²
CUMULATIVE
CURRENT
NUMBER OF EXPANDED GREEN LEAVES per dm²
0
100
200
300
400
500
600
36 PLANTS PER DM²
CUMULATIVE
CURRENT
DAYS FROM SOWING
JUNE
JULY
AUGUST
SEPT
OCT

5.5.2. The individual plant in the sward.

(a) Total plant weight.

(i) Total weight per plant, roots included.

The mean weight per plant in each density is shown for nine selected harvests in Table 47 and for the first six harvests in the inset of Fig. 40. Since plant deaths complicated the mean weight of individual plants at the last few harvests, the mean values at 118 days may be considered as the ultimate account of treatment differences. At 20 days, the dry weight of all plants in the experiment was similar (Table 61 and 62 Appendix). Treatment differences were not established until 34 days, and by 41 days these were highly significant. As the experiment progressed, individual plant weight became increasingly a function of density, and this is illustrated in Fig. 39.

In the upper half of Fig. 40 the range of individual plant weights was depicted by joining all the highest and lowest points respectively of each harvest. At each of the first six harvests there were 10 intermediate values between the "largest" and the "smallest" plant. in each density, and 4 in each of the next ten harvests. The variability of individual plants was examined and in the lower part of the figure the values of the Coefficient of Variation ($\frac{\text{Standard Deviation}}{\text{Mean}}$ x 100) corresponding to each harvest are shown. The variation increased with rising density. Thus, the population is more variable where competition is strong, than where it is weak.

The "largest" plant in the low density reached an upper limit of yield at approximately 2900mg; yield in the middle density was still rising at 1400 mg and in the high density it rose to 360 mg and then fell. Even the "largest" plant of the high density failed

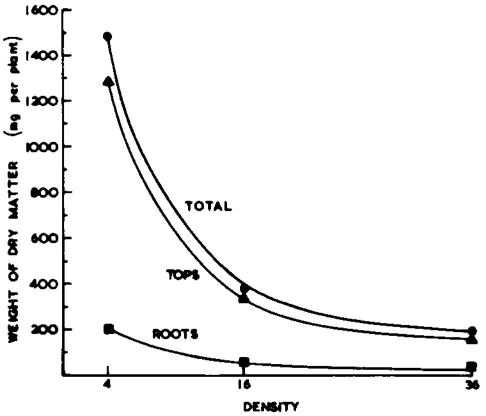
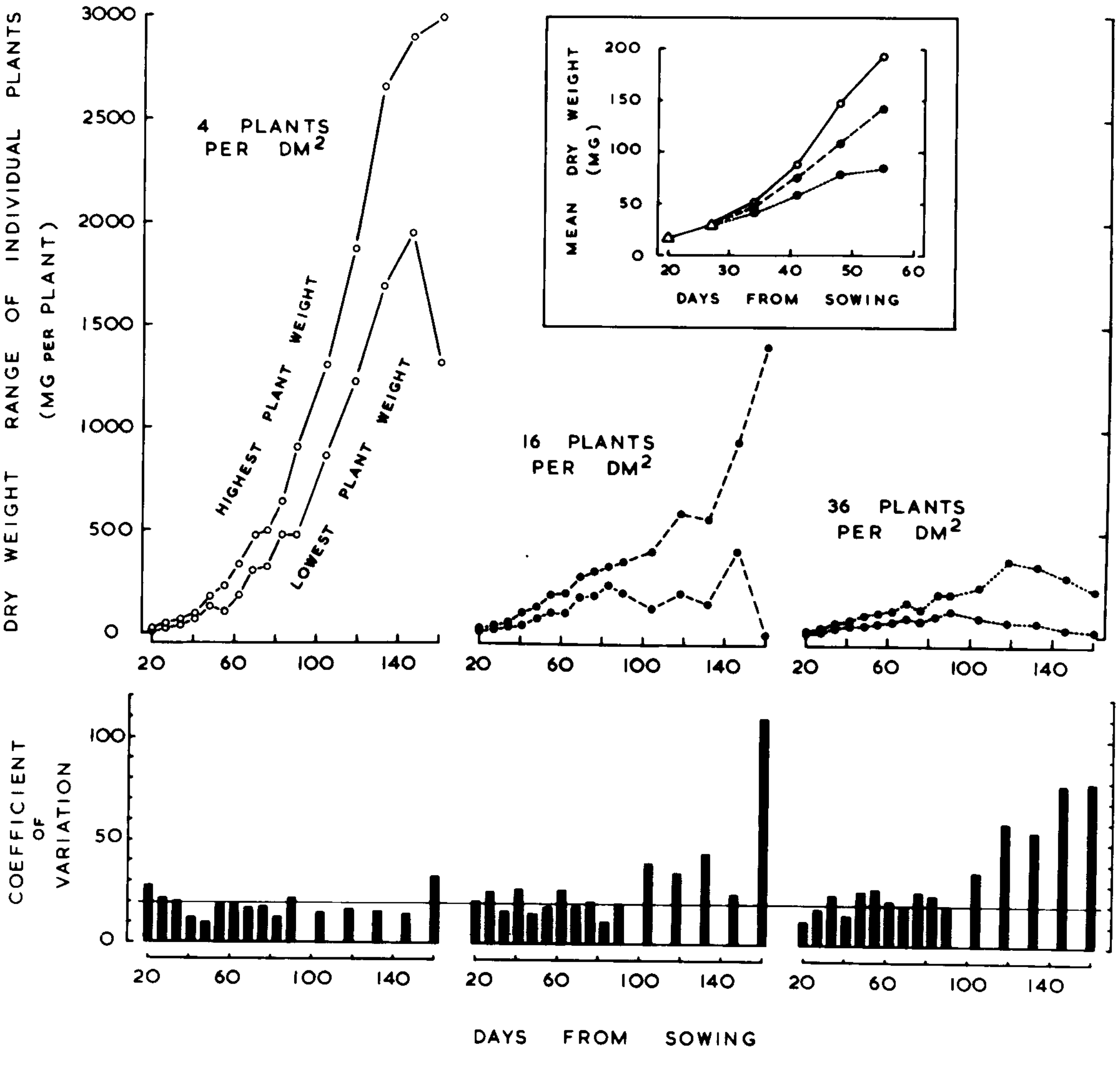


Fig. 39. - The mean yield of the entire plant, and of tops and roots, as a function of density, at 118 days.

Fig. 40. - Individual plant data.

In the upper part of the figure, the range of dry weights of individual plants is shown by plotting the lowest and highest values recorded at each harvest. The mean values from 20 to 55 days are plotted in the inset (the triangles represent overlapping points). In the lower part of the figure the Coefficient of Variation at each harvest in each density is represented by a vertical bar. An arbitrary line is drawn at 19 per cent. (See text).



DRY WEIGHT RANGE OF INDIVIDUAL PLANTS
(MG PER PLANT)
3000
2500
2000
1500
1000
500
0
4 PLANTS PER DM²
HIGHEST PLANT WEIGHT
LOWEST PLANT WEIGHT
16 PLANTS PER DM²
36 PLANTS PER DM²
MEAN DRY WEIGHT (MG)
200
150
100
50
0
20
30
40
50
60
DAYS FROM SOWING
20
60
100
140
COEFFICIENT OF VARIATION
100
50
0
DAYS FROM SOWING

to develop a full complement of leaves during the course of the experiment. In every density the dry weight of the "lowest" plant fell after reaching a peak: this occurred at 146 days in the low density, at 90 days in the high one, and was not so well-defined at the middle density. In the high density, the weight fell to 20 mg and most of this was composed of root.

The increasing weight of the "heaviest" plants and the progressive decline of the "lowest" plants, illustrated in Fig. 40 is typical of the relation of a dominant to a suppressed member of an association (See Fig. 16).

The coefficient of variation lay between 10 and 30 per cent. except for 10 values. After 90 days the rise in the coefficient of variation was greater at the high density than at the middle one; at the low density it remained steady except at the last harvest. These large increases were a reflection of declining weights in some plants. The arbitrary line through 19 per cent. was drawn to separate the values at the low density (below the line) from those at the high density, (above the line) during the period from 41 to 83 days. The greater variability of individual plant weight at this early stage suggests that there were already some important competitive stresses within the high density swards. This difference between the variability of the low and the high density was not so well-defined when the variability of the top and root weights were examined separately (Tables 64 and 65 Appendix).

(ii) The weight of tops and roots of each plant.

A summary of the early differences between densities in top and root weight is incorporated in Table 47. Significant differences in the mean top weights were established at 41 days and in the mean root weights at 34 days. This coincided with a fall in growth rate

Table 47.

The mean dry weight (mg) of the entire plant (including roots), and of tops and roots, at 9 harvests. These harvests were selected to show the initial and the ultimate differences between densities. (The L.S.D.'s were weighted according to the S.E.'s).

Individual plant data.

Weight per plant	Plants per dm^2	DAYS FROM SOWING												
		20	27	34			41			55	76	90	118	146
TOTAL	4	17.3	32.0	51.9			89.0			192.3	405.6	704.3	1483.7	2432.9
	16	18.4	30.6	46.5			75.9			141.7	263.0	273.7	379.4	815.9★
	36	17.2	28.3	42.0			58.6			85.5	95.7	163.6	189.3	118.1
	Levels at P <			0.05	0.01	0.001	0.05	0.01	0.001					
	Comparisons			L.S.D.			L.S.D.							
Significance	4 & 16		N.S.	8.7	12.3	17.9	14.5	20.5	29.3					
	16 & 36		N.S.	8.4	11.9	17.3	13.8★	19.5	27.9					
	4 & 36		N.S.	9.9★	14.1	20.3	9.0	12.6	18.1★					
TOPS	4	12.2	22.0	35.4			63.7			136.9	302.9	569.5	1282.9	2166.5
	16	11.7	20.9	32.6			56.8			108.2	220.3	233.3	329.5	722.0
	36	11.2	19.7	30.6			44.0			70.2	81.1	141.0	164.7	98.8
	Levels at P <						0.05	0.01	0.001					
	Comparisons						L.S.D.							
Significance	4 & 16		N.S.	N.S.			10.8	15.2	21.7					
	16 & 36		N.S.	N.S.			10.6★	14.9	21.3					
	4 & 36		N.S.	N.S.			6.8	9.6	13.8★					
ROOTS	4	5.2	10.0	16.5			25.3			55.4	102.7	134.9	200.8	266.4
	16	6.6	9.7	13.8			19.1			33.4	42.7	40.5	49.9	93.9
	36	6.0	8.6	11.3			14.6			15.2	14.6	22.6	24.6	25.7
	Levels at P <			0.05	0.01	0.001	0.05	0.01	0.001					
	Comparisons			L.S.D.			L.S.D.							
Significance	4 & 16		N.S.	3.6	5.1	7.4	4.2★	5.9	8.4					
	16 & 36		N.S.	2.7	3.8	5.5	3.6★	5.1	7.3					
	4 & 36		N.S.	4.2★	5.9	8.6	2.9	4.1	5.8★					

$(\frac{dW}{dt})$ of the highest density swards at 40 days in the tops, and at 36 days in the roots. During this period the growth rate of the tops and roots in the low density swards was rising.

At 27 days, the ratio of tops to roots was 2.2 to 2.3 in all treatments, and increased more rapidly at the high and middle densities to reach approximately equal values of 6.4 to 6.7 at 118 days in all densities.

(b) Branching on individual plants.

There were obvious differences between densities in the number of branches on individual plants. Branching began at about 40 days, just as the 4th and 5th leaf were forming. In most cases, the 5th leaf arose from the first branch and the 8th leaf from the second. Between 83 and 90 days there were 2, 3, and 6 branches per plant at the high, middle and low densities, respectively. At the low density all the branches survived, and at the other two densities the number of branches per plant declined, as shown in Table 48.

Table 48

The mean number of branches per plant, at 4 harvests approximately 3 weeks apart.

Plants per dm^2	Days from sowing			
	48	69	90	118
4	-	4.0	6.0	6.2
16	0.4	2.2	3.2	2.3
36	0.3	1.7	2.0	0.8

5.5.3. The individual leaves in the sward.

(a) Introduction.

The occurrence of leaves on individual plants is examined in part (b) of this section. Parts (c), (d) and (e) deal with lamina weight, petiole length and lamina height for chosen groups of leaves, and in part (f) the lamina weight and petiole length of L 1 to L 4 are compared in the three densities; in part (g) the visual criteria of senescence are compared with lamina weight changes. Mean leaf areas were omitted from the text, because leaf weights depict the trends adequately. The means of each leaf group are tabulated in Tables 66, 67, 68 & 69. in the Appendix, and the curves in Figs. 42, 43 and 44 were fitted by eye.

Two independent examinations were made to decide the leaf groupings. In the first, the mean dates of leaf appearance, unfolding and the onset of senescence were plotted on a time scale and certain natural leaf groupings in each density became apparent. In the second examination, mean lamina weight and height, and mean petiole length were plotted for every leaf in each density, and similar curves were grouped. The results obtained by these two methods were similar, and there was no difficulty in deciding on the groupings to be adopted in each density.

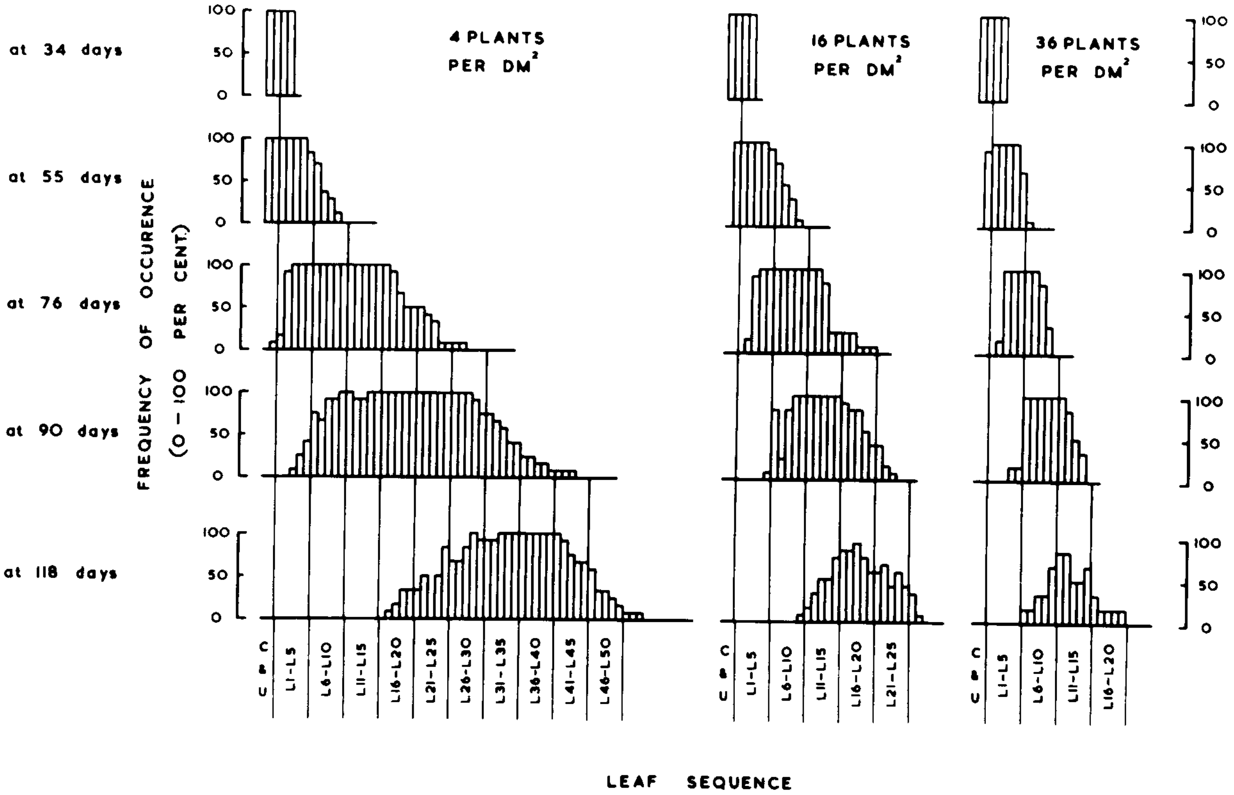
(b) The frequency distribution of individual leaves.

Leaf distributions at five harvests approximately three weeks apart, are presented for all three densities in Fig. 41. The abscissae show the leaf sequence from the cotyledons to the last-formed leaf, and the ordinates show the frequency of occurrence of a particular leaf. The horizontal base lines show the number of leaves produced at each date and density; the portion occupied by the histogram represents the number of expanded green leaves. The base-line to the left of the histograms represents dead leaves, and to the right, those that formed and were still folded. At 34 days the position was similar in all three densities. Within each density the movement of the modes of the distributions from left to right was greatest at 4 plants and least at 36 plants per dm^2. Excluding the cotyledons and unifoliate leaves, each plant at 118 days had lost 16, 9 and 5 leaves at 4, 16 and 36 plants per dm^2 respectively. The shape of the distributions was more symmetrical when the formation of new leaves kept pace with the death of old ones, i.e. at about ceiling L.A.I. The modes of the distributions reached 100 per cent. in all cases, except at the two higher densities on day 118, i.e. certain leaves were absent from some plants, either through death or they were not being initiated. At this stage some plants were being suppressed because they failed to produce new leaves, while others continued to grow and form new leaves, thus gaining dominance. In Fig. 41 this is expressed by a slight extension in the range of leaf sequence and a fall in the modal frequency at the highest density between 90 and 118 days.

In each distribution the following leaves were chosen as modes, since they are the central leaves of the frequency distribution (Fig. 41).

Days from sowing	Plants per dm^2		
	4	16	36
34	L 1-2	L 1-2	L 1-2
55	L 2-3	L 2-3	L 2-3
76	L 8-11	L 7-10	L 4-7
90	L18-21	L11-14	L 7-10
118	L33-36	L16-19	L10-13

Fig. 41. - The frequency of occurrence of expanded leaves, presented as a sequence for each density, at the 3rd, 6th, 9th, 11th and 13th harvests. (C & U stand for cotyledons and unifoliate leaves, and L1, L2 etc. for the 1st, 2nd, etc. trifoliate leaves).



4 PLANTS PER DM^2
16 PLANTS PER DM^2
36 PLANTS PER DM^2
at 34 days
at 55 days
at 76 days
at 90 days
at 118 days
FREQUENCY OF OCCURENCE (0 – 100 PER CENT.)
100
50
0
C & C
L1-L5
L6-L10
L11-L15
L16-L20
L21-L25
L26-L30
L31-L35
L36-L40
L41-L45
L46-L50
LEAF SEQUENCE

The character of the leaves at the mode was examined more closely. In Table 49 the mean lamina area and weight, and the petiole length and lamina height of the above modes are presented, and each of these attributes is considered in turn.

Table 49.

The mean lamina area and mean lamina weight, and the mean petiole length and mean lamina height, of the modal leaves at the 3rd, 6th, 9th, 11th and 13th harvests.

(a) Lamina area (cm^2)

Days from sowing	Plants per dm^2 4	16	36
34	2.5	2.9	2.9
55	4.6	4.1	3.9
76	3.5	3.6	2.9
90	4.1	3.2	3.4
118	8.4	5.5	4.5

(b) Lamina weight (mg)

Days from sowing	Plants per dm^2 4	16	36
34	6.7	5.7	5.8
55	15.0	11.1	8.9
76	7.0	6.6	5.0
90	9.0	6.2	5.1
118	20.8	11.7	8.1

(c) Petiole length

Days from sowing	Plants per dm^2 4	16	36
34	2.0	2.4	2.5
55	4.7	5.4	6.8
76	5.7	8.7	7.6
90	8.9	10.2	12.4
118	16.5	16.6	15.7

(d) Lamina height

Days from sowing	Plants per dm^2 4	16	36
34	1.0	2.0	2.5
55	1.8	2.8	4.1
76	3.7	6.3	6.1
90	5.4	9.1	11.8
118	10.3	9.3	10.6

Lamina area: The increase in lamina area between 90 and 118 days was greater at the low than at the other two densities, and began earlier. Otherwise, the differences between densities and harvests were only small.

Lamina weight: The lamina weights at 55 days were large and were of the same order as the weight at 118 days. It will be shown later that in all densities, L2, L3 and L4 were the largest leaves to form for some time, and at 55 days L2 was at the peak and L3 was approaching the peak of development. Leaf weight declined with rising density, and at 118 days the modal leaves at the low density were more than twice as heavy as the modal leaves at the high density. Differences in lamina area were not as great and consequently the Leaf Area/Leaf Weight ratio is higher in the dense swards, as might be expected.

Petiole length: The trends within the Table 49 show an increase in petiole lengths from 34 days to 118 days and from the lowest density to the highest one. At 118 days petioles attained similar lengths of 16 cm in all densities. The difference at the early harvest suggests that there was already competition for light between leaves at the higher densities leading to greater petiole length and leaf height. This became more acute, as time went by, occurring later at the lower densities.

Lamina height: It follows from the petiole length data that the height of the modal leaves rises more rapidly with increasing density. This was in fact the case, and an approximately similar height of 10 cm was reached at 118 days. A comparison of Tables 49 (c) and (d) shows that from the beginning the petioles were more nearly vertical at the high density than at the other two.

(c) Mean lamina weight.

In Fig. 42 the mean lamina weights in each density are plotted against time. A rise and fall in weight was recorded in nearly all leaves which completed their normal life cycle before the end of the experiment. The lamina weights were greater at the low density than at the high one as shown in the following examples.

4 plants per dm^2		16 plants per dm^2		36 plants per dm^2	
L 2-3	14.9	L 2-5	10.5	L 3	9.1
L 4-8	9.1	L 6-8	7.6	L 4-6	6.6

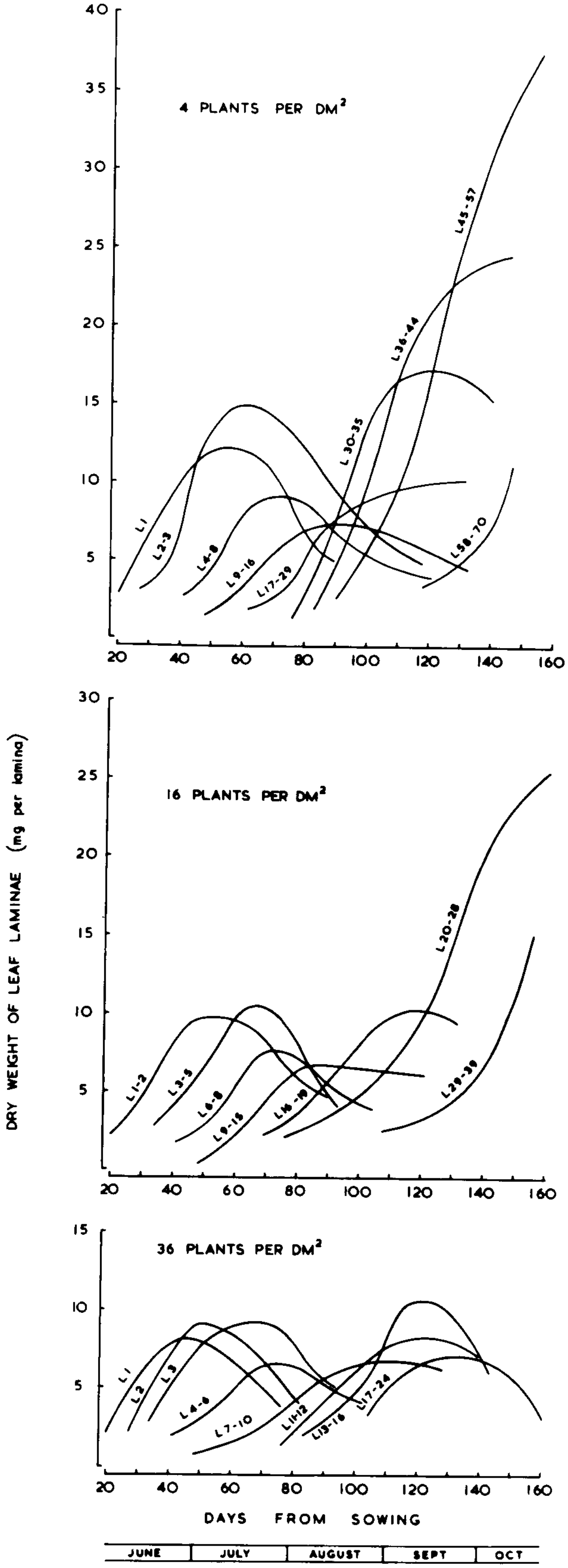
Initial leaf size was smaller between 30 and 60 days (i.e. mid-June to mid-July). One possible explanation is that initial size of early leaves became smaller on later branches. Branches developed rapidly after 45 days and L 5 was the first leaf on the first branch and L 8 was the first on the second.

It was noted in the primary data that successive leaves on a single branch increased in size - except for the axilary leaves which were obviously smaller. This conforms with Mitchell's findings (1956).

The simultaneous formation of leaves on different branches resulted in a periodicity in leaf development. At the low density there were 6 branches per plant and periodicity was strong. At the high density one and at most two branches developed, and consequently the periodicity was weak. There is no simple expression of this, but it was manifest in several ways and this will be discussed in section 5.6.0.

There is a similarity in the shape of the curves in their position on the time scale between certain groups of leaves in the low and middle densities; this may best be seen by superimposing the

Fig. 42. - The mean lamina weight of successive leaf groups in swards of subterranean clover grown at three densities.


DRY WEIGHT OF LEAF LAMINAE (mg per lamina)
4 PLANTS PER DM²
40
35
30
25
20
15
10
5
L1
L2-3
L4-8
L9-16
L17-29
L30-35
L36-44
L45-57
L58-70
20
40
60
80
100
120
140
160
16 PLANTS PER DM²
30
25
20
15
10
5
L1-2
L3-5
L6-8
L9-15
L16-19
L20-28
L29-39
20
40
60
80
100
120
140
160
36 PLANTS PER DM²
15
10
5
L1
L2
L3
L4-6
L7-10
L11-12
L13-16
L17-24
20
40
60
80
100
120
140
160
DAYS FROM SOWING
JUNE
JULY
AUGUST
SEPT
OCT

graphs over a light table. It was also noted in all densities that L 3 was the largest leaf to develop for some time.

At 90 days there was a large array of leaves present, resulting in a confluence of lines in Fig. 42 and this is particularly noticeable at the low density. A summary of the leaves present at 45, 90 and 135 days, and a range of their weights is given in Table 50. The range fell and rose in the low and middle densities, and in the high density it kept on falling.

Table 50

The leaves present in each density 45, 90 and 135 days is shown in the column "leaf sequence". The mean lamina weight of the smallest and the largest leaf, and the difference between them, is shown in the column "weight range".

	Days from sowing					
	45		90		135	
	Leaf sequence	Weight range (mg)	Leaf sequence	Weight range (mg)	Leaf sequence	Weight range (mg)
4 plants per dm^2	L 1-18	3.3 - 11.2 Range: 7.9	L 2-57	4.7 - 9.4 Range: 4.7	L 30-70	5.9 - 28.2 Range: 22.3
16 plants per dm^2	L 1-8	2.2 - 9.4 Range: 7.2	L 3-28	3.4 - 6.8 Range: 3.4	L 20-39	5.3 - 17.9 Range: 12.6
36 plants per dm^2	L 2-6	2.4 - 8.4 Range: 6.0	L 1-16	3.0 - 5.6 Range: 2.6	L 11-24	7.0 - 8.7 Range: 1.7

The weight of laminae was increasing rapidly at the end of the experiment, as for example L 36-44 and L 45-57 at the low density and

L 20-28 and L 29-39 at the middle density. In the highest density, the weight increase in the group L 13-16 was as at first similar to the curve for L 20-28 in the middle density, but at about 115 days it rapidly turned into a decline.

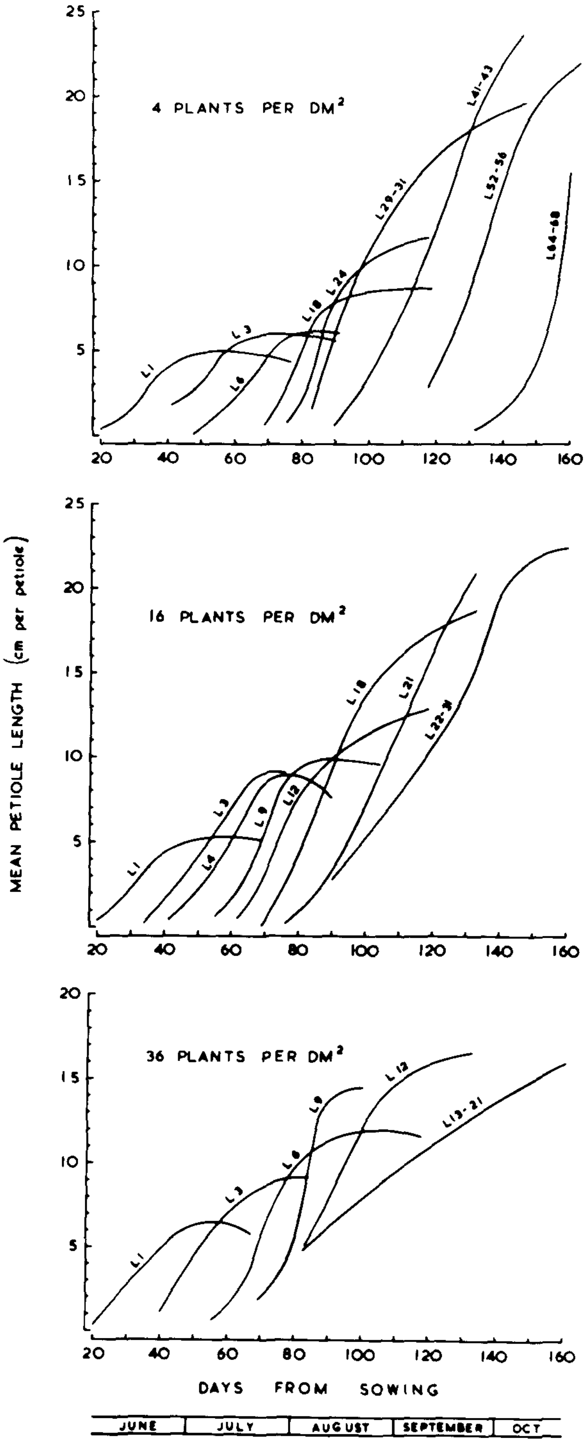
The longevity of leaf groups varied between densities and within densities. In many cases it was possible to continue recording lamina weight until a leaf became detached from the plant or could no longer be identified. Normally laminae unfolded when approximately 40 per cent. of their maximum weight was first recorded, and they began to lose colour when they had fallen to approximately 75 per cent. of their maximum dry weight. Generally 5-6 weeks elapsed between unfolding and visual senescence and this is a good approximation of the life span of an individual leaf.

(d) Petiole length.

In general, petioles continued to elongate until they reached a maximum length and this is shown in Fig. 43. The declines recorded after the peak length was reached were not significant. The longest petioles at 40, 60, 80, 100 and 120 days are identified and their lengths are shown in Table 51. At first, the petioles in the densities 16 and 36 plants per dm^2 were longer than the petioles at 4 plants per dm^2, and at 120 days the longest petioles were approximately equal in all densities. However petioles in the low density continued to lengthen, while those in the high density had become more or less stationary.

The rate of petiole elongation gradually increased with successive leaves and slowed down again at the end of the experiment in the high (e.g. L 12) and the middle density (e.g. L 21). There were some steady periods, when either the rate of elongation or the ultimate

Fig. 43. - The mean petiole length of representative leaves or groups of leaves, in swards of subterranean clover grown at three densities.


4 PLANTS PER DM²
16 PLANTS PER DM²
36 PLANTS PER DM²
MEAN PETIOLE LENGTH (cm per petiole)
DAYS FROM SOWING
L1
L3
L6
L18
L24
L29-31
L41-43
L52-56
L64-68
L1
L4
L3
L9
L12
L18
L21
L22-31
L1
L3
L6
L9
L12
L13-21
25
20
15
10
5
20
40
60
80
100
120
140
160
JUNE
JULY
AUGUST
SEPTEMBER
OCT

length attained or both, were similar for a wide range of leaves; e.g. L 18 to L 31 at 4 plants, and L 4 to L 18 at 16 plants per dm^2.

Table 51

The longest petiole, and its length in each density on five occasions during the experiment.

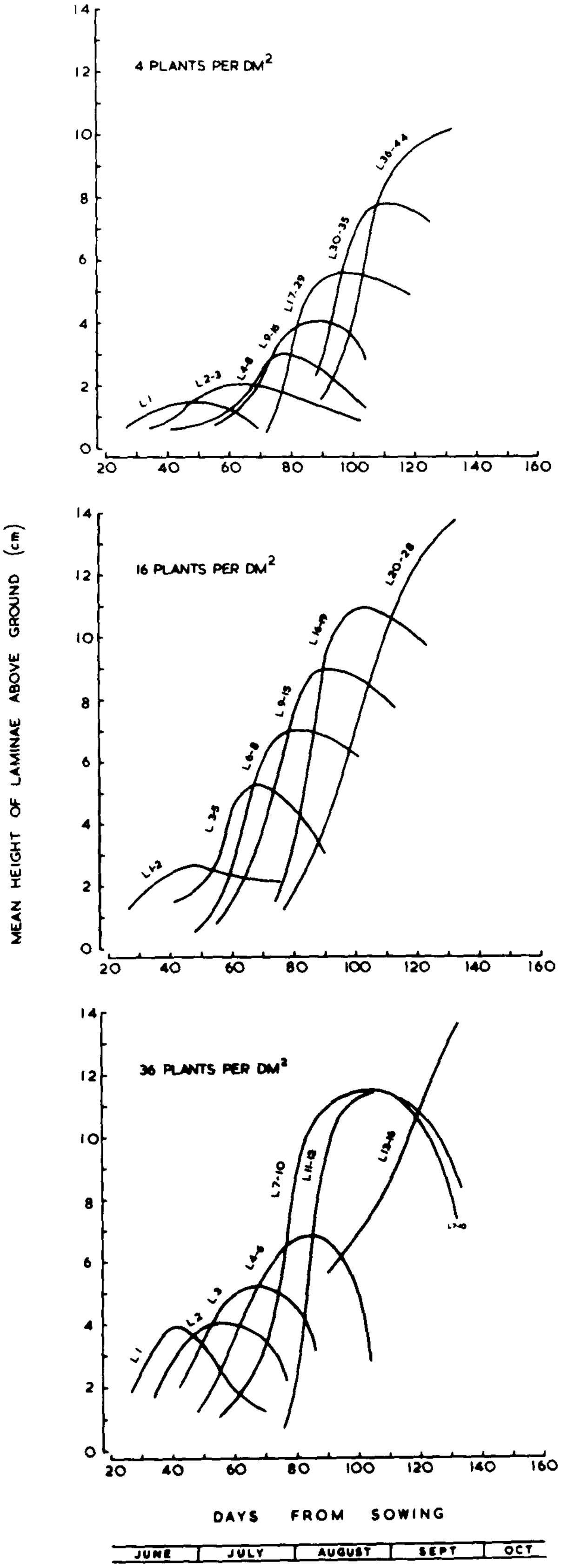
		Days from sowing				
		40	60	80	100	120
4 Plants per dm^2	Leaf group	L 1	L 3	L 3 & L 6	L 29-31	L 29-31
	Length (cm)	4.0	5.3	6.1	10.9	16.5
16 Plants per dm^2	Leaf group	L 1	L 3	L 9	L 18	L 18
	Length (cm)	4.4	7.0	9.3	13.8	17.5
36 Plants per dm^2	Leaf group	L 1	L 3	L 6	L 9	L 12
	Length (cm)	4.9	7.0	9.8	14.5	15.9

(e) Mean lamina height.

The average height of leaf groups is plotted in Fig. 44. There were fewer observations of this attribute than of lamina weight or petiole length.

Laminae reached the top of the canopy and were overtopped by later leaves. As successive leaves attained new heights, the older leaves receded into the body of the sward. This is clearly depicted in Fig. 44 and applies without reservations at the low and middle densities, but at the high density a few exceptions were noted. For example L 7-10 overtopped L 4-6 before these attained their maximum height, and L 11-12 barely reached the height attained by L 7-10. At the later harvests in the high density, lamina position varied tremendously. The

Fig. 44. - The mean height at which groups of laminae were held in swards of subterranean clover grown at three densities.



4 PLANTS PER DM^2
L1
L2-3
L4-8
L9-16
L17-29
L30-35
L36-44
16 PLANTS PER DM^2
L1-2
L3-5
L6-8
L9-15
L16-19
L20-28
36 PLANTS PER DM^2
L1
L2
L3
L4-6
L7-10
L11-12
L13-16
L7-10
MEAN HEIGHT OF LAMINAE ABOVE GROUND (cm)
0
2
4
6
8
10
12
14
20
40
60
80
100
120
140
160
DAYS FROM SOWING
JUNE
JULY
AUGUST
SEPT
OCT

curves in Fig. 44 portray the average situation and instances of individual laminae failing to reach the top of the canopy were noted in the primary data.

The leaf canopy rose more rapidly where the leaf population was greater. The rise was continuous in the low and middle densities, and sporadic in the high density, resulting in greater irregularities in the surface of the sward. Later on, especially in the low and middle densities, a leaf occasionally rose well above the general level of the canopy because long petioles were forming on the extremities of branches. These leaves reduced the light intensity at the top of the canopy and therefore exaggerated the impression of height as expressed in the light profiles of Fig. 47. On the other hand, the values given in Fig. 44 and Table 52 probably under-estimated lamina height, because there was a tendency for a downward movement of the sward surface as a result of the frequent handling necessitated by labelling.

Table 52

The tallest leaf and the height at which the lamina was held, in each density on five occasions during the experiment.

		Days from sowing				
		40	60	80	100	120
4 Plants per dm^2	Leaf group	L 1	L 2-3	L 9-16	L 30-35	L 36-44
	Height (cm)	1.3	2.0	3.8	6.7	9.6
16 Plants per dm^2	Leaf group	L 1-2	L 3-5	L 9-15	L 16-19	L 20-28
	Height (cm)	2.4	4.5	7.5	10.9	12.2
36 Plants per dm^2	Leaf group	L 1	L 3	L 7-10	L 7-10	L 11-16
	Height (cm)	3.9	5.9	8.7	11.4	11.0

The heights of the tallest leaves at 40, 60, 80, 100 and 120 days were read from Fig. 44 and are shown in Table 52. A comparison of petiole lengths (Table 51) and laminae heights (Table 52) shows that the values of petiole length are consistently larger. In the high density the difference was not as great as in the other two.

While petioles are elongating, the relative height of laminae in a sward may be determined from petiole length; but after the petioles have elongated fully, the leaves recede into the sward, and petiole length is no longer an adequate measure of lamina height. Furthermore the petioles at lower densities do not necessarily arise from the base of each plant and they are not always erect. It may be concluded that petiole length is not an acceptable measure of lamina height.

(f) Comparison of lamina weight and petiole length of L 1 to L 4 in each density.

The cotyledons, the unifoliate leaf, and L 1 to L 4, developed simultaneously in all densities and had reached their maximum weight before the L.A.I. of the swards was very large. These early leaves were contemporaneous on all plants and this permitted a precise comparison of the lamina weights and petiole lengths in the three densities. Lamina weights are plotted in Fig. 45 and petiole lengths in Fig. 46.

Early differences in lamina weight between densities are obvious from the graphs and even the cotyledons and unifoliate leaves declined in weight more rapidly at the highest density. With increasing density, senescence set in earlier, but the time lag was small. However, the most striking differences occurred during the period of weight increase, and this is illustrated by these figures of (lamina weight in mg) for L 1 and L 2 at 41 days:

Fig. 45. - The mean lamina weights of the cotyledons, the unifoliate leaf and L 1 to L 4 during their entire life cycle in swards of subterranean clover at 3 densities. The 3 densities are plotted on each graph. U shows the time of opening of the young leaf and S the onset of senescence (criterion 2 on page 139).

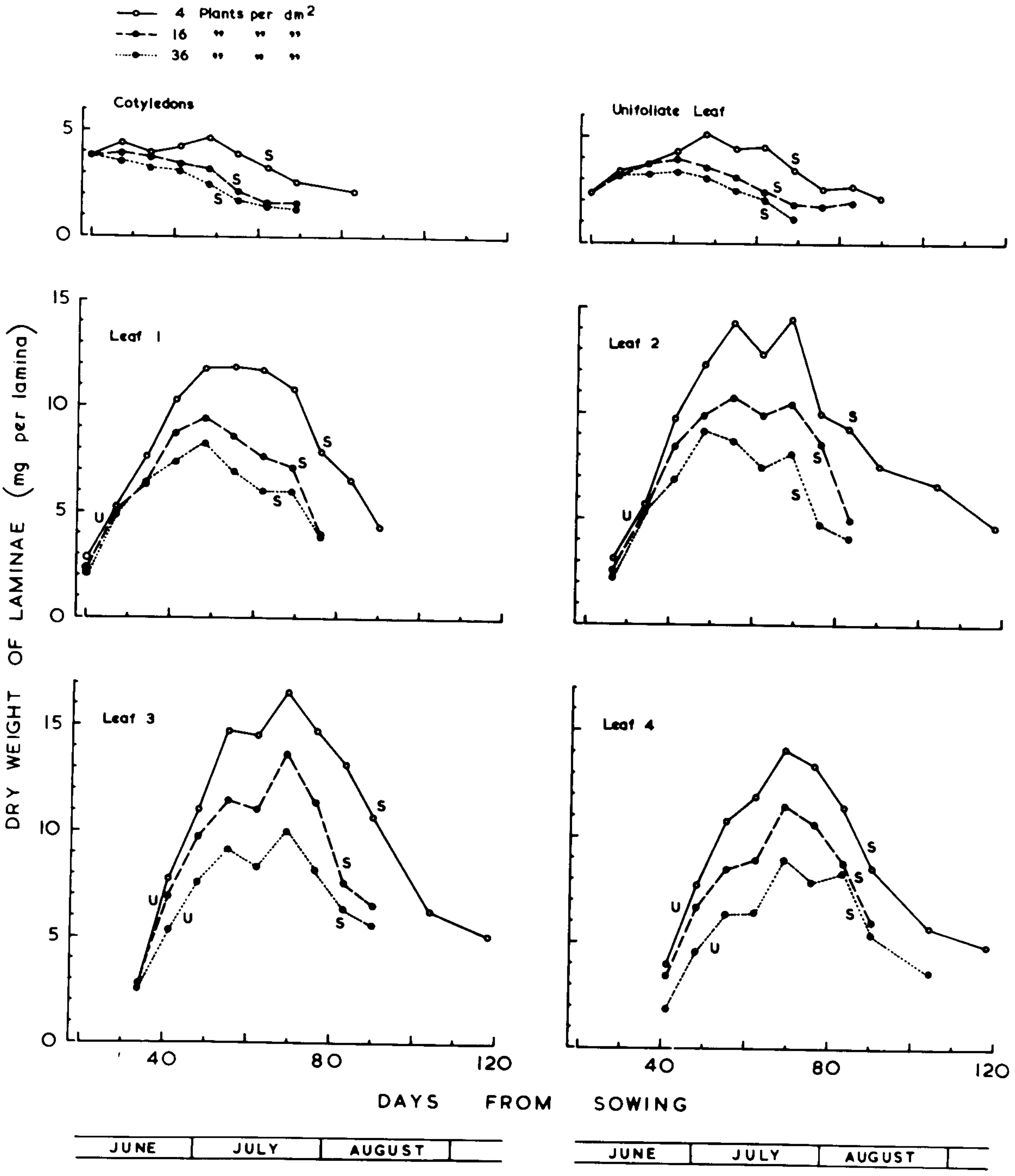
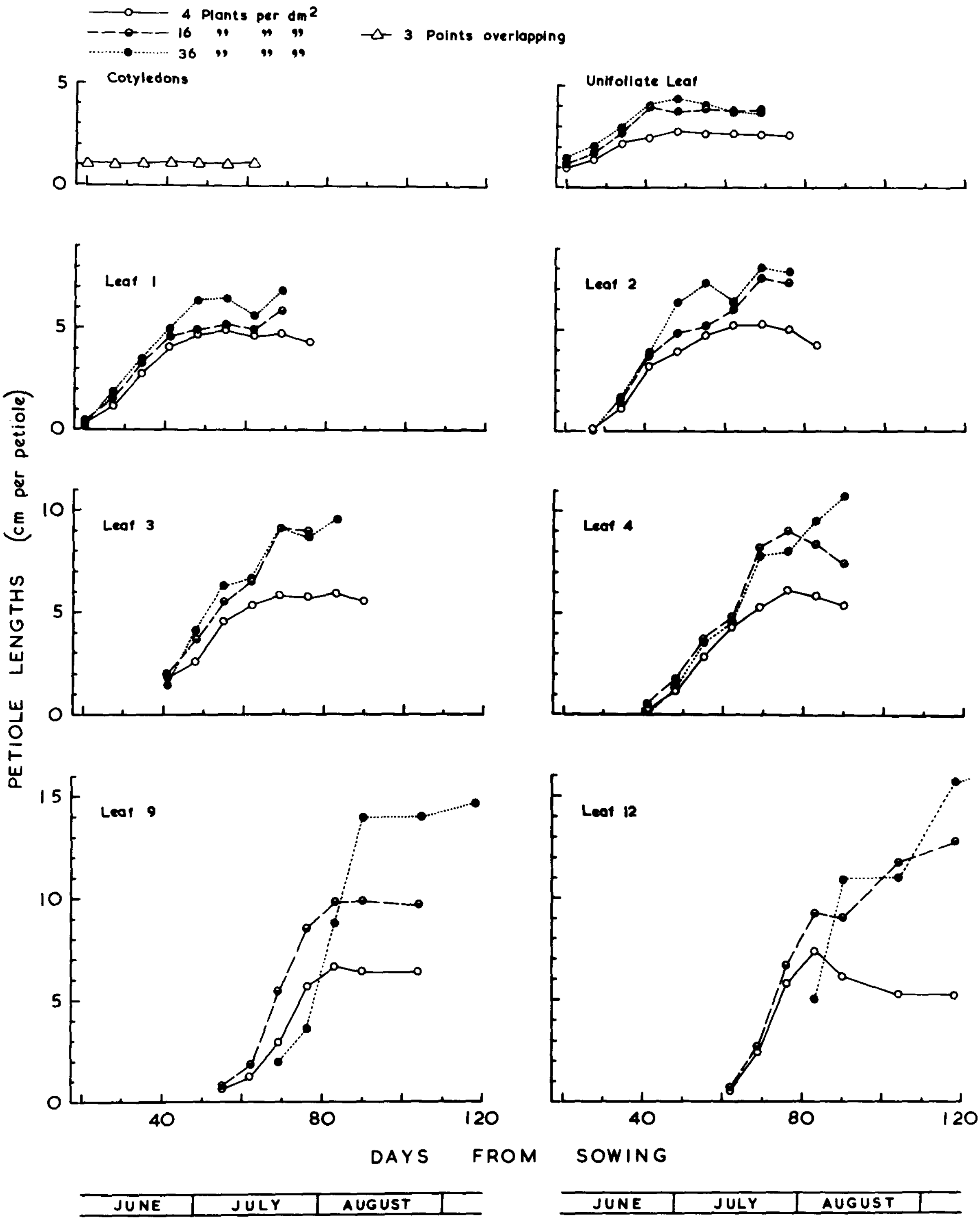

4 Plants per dm²
16 " " "
36 " " "
Cotyledons
Unifoliate Leaf
Leaf 1
Leaf 2
Leaf 3
Leaf 4
S
U
0
5
10
15
40
80
120
DRY WEIGHT OF LAMINAE (mg per lamina)
DAYS FROM SOWING
JUNE
JULY
AUGUST

Fig. 46. - The mean petiole lengths of the cotyledons, the unifoliate leaf, L 1 to L 4, and L 9 and L 12 in swards of subterranean clover at 3 densities.



4 Plants per dm²
16 " " "
36 " " "
3 Points overlapping
Cotyledons
Unifoliate Leaf
Leaf 1
Leaf 2
Leaf 3
Leaf 4
Leaf 9
Leaf 12
PETIOLE LENGTHS (cm per petiole)
0
5
10
15
40
80
120
DAYS FROM SOWING
JUNE
JULY
AUGUST

		4 plants per dm^2	16 plants per dm^2	36 plants per dm^2
41 days	L 1	10.3	8.8	7.4
	L 2	9.8	8.4	6.9

At 41 days the difference in lamina weight between densities was about 1.5 mg. for L 1 and L 2; differences were apparent also in L 3 and L 4 at this time, and these leaves were still folded or about to open. Here then, was the basis for the significant difference in top weight first recorded at 41 days (Table 46).

The difference in petiole length was also striking. At first the high and the middle densities separated from the low one and this may be seen most clearly in L 3 and L 4; but by the time L 9 and L 12 were developing, the differences between densities were well defined and their additional leaves are included. The development of individual leaves had moved out of phase between densities and consequently with increasing density there was a displacement from left to right along the abscissa, as well as a vertical displacement along the ordinate. Maximum lamina weight is reached at the same time as maximum petiole length.

(g) Senescence of individual leaves.

The meaning of senescence is not explicit in botanical parlance (Molisch 1938, Comfort 1954). It may be regarded as a continuous process which ends in death, and the word is best defined in terms of the starting point. Since visual criteria are subjective, the following definition is preferred: senescence begins with a loss in weight of the fully expanded leaf. But this can only be determined by harvest. Since the dry weight and colour of individual leaves were both recorded in this study, a comparison of these criteria is possible.

The laminae were classed in five specified colours which are listed on page 139. These may be described as follows:

1) full green colour of a healthy subterranean clover leaf;

2) pale green to greenish yellow;

3) brownish yellow;

4) olive and olive grey: at this stage the lamina is shrivelled;

5) dark brown: leaf form cannot be recognised.

In practice, these categories do not differ greatly from the classes (II to IV) arbitrarily chosen by Brougham (1958b).

A comparison of the weight, colour and condition of a lamina was made on several leaves, and the data are presented in Table 70 of the Appendix.

One example of a typical leaf is given on page 254. Points to be noted are:

(a) When a lamina opens, it weighs 30 to 50 per cent. of the maximum weight that it attains. The average estimate of several leaves is 40 per cent.

(b) Leaf weight is continually changing, either increasing or declining. There is no protracted period of maximum weight.

(c) It is not possible to determine from appearance whether a leaf has started to lose weight.

(d) A lamina loses approximately 15 to 35 per cent. of its maximum dry weight before the onset of senescence can be distinguished visually. The average estimate of several leaves is about 25 per cent.

Density 4 plants per dm^2 - L 4

Days from sowing	Lamina weight (mg)	Percentage of the maximum weight	Leaf colour and condition
41	4.0	28	lamina folded
48	7.7	55	lamina open, colour 1
55	10.8	77	lamina open and leaf expanding, colour 1
62	12.0	85	leaf expanding, colour 1
69	14.1	100	maximum area and weight, leaf fully expanded, colour 1
76	13.4	95	leaf fully expanded, colour 1
83	11.4	81	slight shrinkage in area, leaf decreasing in weight, colour 1
90	8.6	61	80 per cent. of laminae have colour 2
104	5.7	40	laminae have colour 4 and are shrivelled
118	4.8	34	only 50 per cent. of laminae are still attached to the plant, and these are not recognisable.

5.5.4. Light Intensity Data.

The light interception in these swards was similar to the patterns already established for clover (sections 2.2.1 and 5.1.0) and the only aspects of the light data to be considered in this section are the light gradients at optimum L.A.I. and the increasing depth of the dark zone in the three swards. Zero light readings at ground level were first recorded at about

83 days from sowing at density 4 plants per dm^2
62 days from sowing at density 16 plants per dm^2
and 41 days from sowing at density 36 plants per dm^2

From these times onwards all the incident light was intercepted by the swards. It was shown earlier (Table 45) that the optimum L.A.I. in the three densities occurred at about 86, 66 and 40 days respectively and the coincidence of these dates with those listed above is self-evident. The light profiles in the three densities are depicted at 41, 61, 83, 116 and 156 days in Fig. 47.

When foliage intercepts all the light, a zone of darkness develops and this increases in depth as the sward grows. To ascertain the extent of this darkened layer, the height was recorded at which light extinction occurred at various dates in each density. These data, for 28-day intervals from the first record of zero light at ground level, are shown in Table 53.

Zero light at ground level first occurred when the L.A.I. was about 2.9 at the high density and 4.0 at the low and middle densities. The L.A.I. of 2.9 occurred about June 25th, which is close to the shortest day of the year (see Table 10) and the other values were recorded 3 weeks later for the middle density, and 8 weeks later for the low one. The depth of the dark zone in the middle and high densities increased from 0 to 9 cm as the L.A.I. rose to 8. At 156 days, the dark

Fig. 47. - The light profiles in 3 densities. The first occasion in each density is at optimum L.A.I. The height of the dark zone is hatched in.

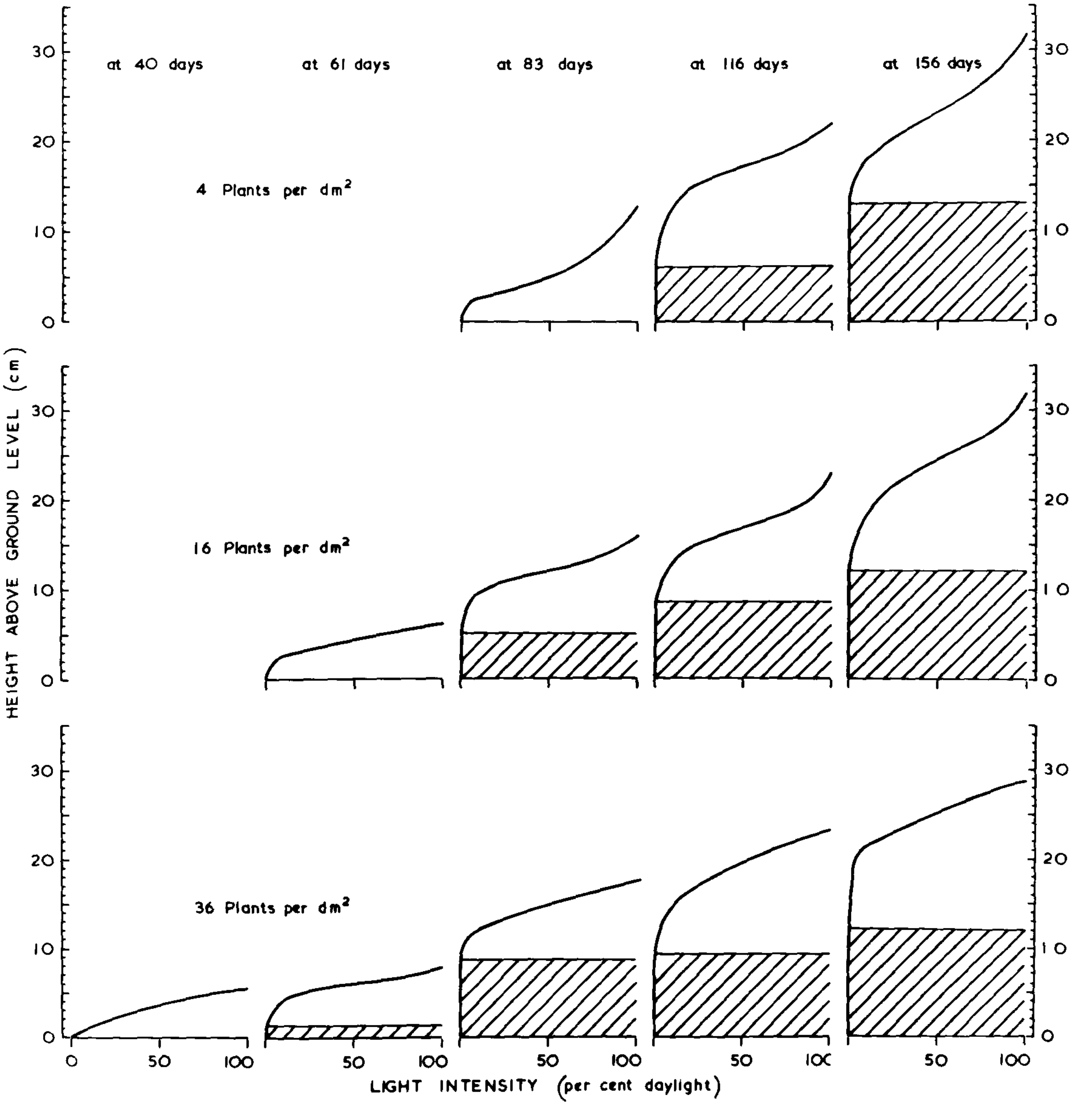

at 40 days
at 61 days
at 83 days
at 116 days
at 156 days
4 Plants per dm²
16 Plants per dm²
36 Plants per dm²
HEIGHT ABOVE GROUND LEVEL (cm)
0
10
20
30
0
50
100
LIGHT INTENSITY (per cent daylight)

Table 53

The first record of zero light intensity at ground level in each density, and the depth of the dark zone approximately every 28 days thereafter. The corresponding L.A.I. values are shown, and also the lengths of the longest petioles at harvest. The Table indicates the leaves which were initiated within the dark zone.

Days from sowing	4 Plants per dm^2				16 Plants per dm^2				36 Plants per dm^2			
	L.A.I.	Depth of the dark layer (cm)	Longest petiole (cm)	Leaves subsequently initiated	L.A.I.	Depth of the dark layer (cm)	Longest petiole (cm)	Leaves subsequently initiated	L.A.I.	Depth of the dark layer (cm)	Longest petiole (cm)	Leaves subsequently initiated
41									2.8	0	5.0	
62					4.0	0	7.5	L 16–28	5.8	0 - 2	7.5	L 6 - 12
90	3.9	0- 0.5	8.0	L 41 onwards	6.2	0-5.5	10.5		8.2	0 - 8	13.5	L 13 onwards
118	7.0	0-6	16.0	L 64 onwards	8.0	0 - 9	17.5		8.5	0 - 9	15.5	

zone was 12-13 cm deep in all densities.

The petioles of leaves initiated in the dark were longer than their predecessors (Table 53), and this can be seen clearly in Fig. 43.

The petioles initiated after zero light at ground level was first recorded, were markedly longer than those which formed previously; e.g. L 41 onwards in the low density, L 18 onwards in the middle density and L 6 onwards in the high density (See Fig. 43). While the early elongation of petioles at high densities is undoubtedly due to etiolation, the long petioles in the low density cannot be attributed to this cause without some reservations. In the low density, and at the late harvests of the middle density, some leaves developed at the extremities of branches that were not located in the dark zone; yet these petioles were longer than necessary to carry the laminae vertically to full daylight, and the leaves rose above the level of the sward.

In the low density such leaves were carried higher and were larger, but occurred less frequently than in the middle density. Consequently the light profile was higher in the low density and differences in light interception near the top of the canopy can be distinguished between densities.

The light profiles were measured in an undisturbed portion of the sward, while the lamina heights were measured on an area that was frequently examined for labelling. As a result of regular handling there was some downward collapse of the sward, leading to discrepancies in height between the light readings and the measurements of position of the uppermost laminae. These discrepancies were greatest near the top of the leaf canopy, and do not apply to the depth of the dark zone, which was found to be consistent throughout each sward.

5.6.0. Discussion of the results of Experiment C.

5.6.1. Introduction.

The technique was successful in permitting the establishment of swards of similar yield and L.A.I. but composed of different plant and leaf populations.

The sward. The optimum L.A.I. at the high density was attained earlier, and was lower than, in the other two densities. The growth rate at optimum L.A.I. was less with rising density. This may also be deduced from Fig. 2 in Davidson and Donald's paper, by joining the values for densities rather than times, a point that is not discussed by these authors. As already shown, the magnitudes of other attributes also differed between densities, namely the rate of L.A.I. formation and the total number of expanded leaves that formed.

The plant. The experiment began with uniform plants. At 34 days there were differences in weight between the high and low density and these widened as the experiment progressed. At the end of the experiment each plant at the low, middle, and high densities had produced a mean of 66, 30, and 16 expanded leaves per plant respectively, while the maxima of expanded green leaves at any one time were 30, 13 and 7.

The leaf. The relationship of leaf growth to sward growth is examined at length in the discussion that follows.

5.6.2. The dynamic processes.

(a) Periodicity.

Firstly, low density plants, by virtue of their greater branching, produced more leaves per plant at any one time than did high density plants. Secondly, there was a time interval between the formation of successive groups of leaves, especially at the low density. Now if all the plants within a density produce the same sequence of leaves simultaneously, these plants may be described as being in phase. If however, the corresponding leaves develop on different plants, then new leaves form continuously, and the plants may be considered to be out of phase. During most of the experimental period, plants at the low density remained in phase, resulting in a strong periodicity of leaf formation. In the high density some plants moved out of phase, when they were not able to launch their new leaves out of the dark zone as readily as their neighbours. This difference between plants became more noticeable as the dark zone deepened. Where a large number of leaves formed simultaneously the periodicity was strong and where leaves developed singly and continuously it was weak.

Briefly recapitulating: As plants moved out of phase in their development, so the periodicity of leaf formation of the sward became weaker and this was one of the manifestations of competition within a sward. In this experiment the low density sustained a strong periodicity almost to the end, but at the high density it weakened very rapidly when leaves were being initiated in the dark.

(b) Competition

i. Three stages of sward growth.

Indirect references have already been made to the three phases of sward growth which may be distinguished in this experiment.

At 20 days all plants in the experiment were identical; analyses of the weights of cotyledons, the unifoliate leaf, the first trifoliate leaf, the roots, and the remainder, showed no significant differences.

In the second stage, differences between densities in individual root weight were rapidly followed by differences in individual top weights. A significant point is that these differences extended even to leaves which were still folded and only beginning to increase in weight. These differences in plant weight led to greater variability in the high than in the low density swards. During this phase, the leaf number per dm^2 ceased to be a function of the number of plants per unit area. The differences in the light gradient in the three swards were distinctive at this stage.

A third stage can be recognised from 90 days onwards when the variability increased, especially at 36 plants per dm^2. At the high density and to a slight degree in the middle density, the weight of the suppressed plants began to fall, leading to eventual death. At the same time, periodicity at the low density was strengthening and at the high density it was weakening. Beginning with the third stage, the character of the leaves being initiated also changed. The petioles were longer, the laminae were larger and the leaves were carried higher. This development modified the light microclimate within the swards. During this phase, the yield and L.A.I. of the swards attained similar values, but the individual plant differences became more marked.

ii. Underground competition?

It is questionable whether the early differences in root weight (at 34 days) can be attributed wholly to competition for light. Each plant at the low, middle and high density had 25, 6 and < 3 cm^2 of surface soil available to it. There are good reasons to suppose that the concentration gradient from soil to vascular bundle would decrease with increasing density and that nutrient uptake would therefore be less at the high density. The second stage possibly began with an interaction of competition for light and competition for nutrients until eventually light became the most important limiting factor. However, the data permit no firm conclusions on these points.

iii. Competition for light.

In the traditional view the loss of yield occasioned by the death of suppressed plants is compensated by the increased weight of the survivors. This is substantially true when the percentage of plants lost is small or when plants die over an extended period of time, but if the plant stand falls rapidly at an advanced stage of growth there may be a permanent effect on the sward.

When the leaves and meristems of an individual plant are in darkness, leaf losses exceed leaf gains and the plant dies. The space thus vacated in the sward does not necessarily bring about any improvement in the light gradient of the neighbouring plant, which may also be heavily shaded by the same taller plants and so die. In the high density swards the leaves and meristems of many plants were in darkness for a prolonged period, and the wholesale death of plants followed. This resulted in an irreversible loss in yield within the period of the experiment. In the low density, the dark zone did not develop until the sward matured. In the middle density the meristems were more favourably located than at the high one and the loss of stand was limited to a few retarded plants.

Thus the depth and duration of the dark zone and the location of the meristems in respect to it have a profound influence on the regeneration of leaves and continued growth of the sward. Suppression and dominance were clearly demonstrated in the middle and the high density swards.

(c) Leaf growth.

A brief description of leaf growth is necessary before discussing the development of L.A.I. in subterranean clover swards. In published descriptions of sward growth at high densities (Black 1958, Donald and Black 1958, Donald 1960) it has been assumed that leaves were initiated near ground level and that the leaves did not begin to decline in dry weight until they were shaded. This picture is true of very high density swards during the early stages of growth, and the evidence in this experiment suggests that these generalisations do not apply universally.

When a leaf bud has formed, leaf growth begins with a slow increase in lamina weight and petiole extension. As the petiole elongates the lamina opens and the leaf expands until it reaches its maximum lamina area and weight, and within a day or so its maximum petiole length also. These maxima are attained when the lamina first reaches the top of the leaf canopy, but later on, in dense swards, they occur before the laminae reach the top. As soon as the maximum petiole length has been attained the leaf begins to lose weight. There are no visual symptoms heralding the decline in lamina weight. Simultaneously with the decline in weight the leaves are overtopped and recede into the body of the sward as the angle of the petiole from the vertical increases. Colour changes accompany further weight losses and the leaf eventually dies. In a sparse sward the sequence is similar, but lamina weight may fall even while the leaf is favourably located in respect to the incident light. For example in the density 4 plants per dm^2, L 2-3 were at the top of the sward from about 50 to 70 days, but started to decline in weight at 60 days.

5.6.3. The L.A.I. and individual leaves.

It is now possible to consider the course of L.A.I. development in swards of subterranean clover in terms of leaf initiation, leaf development, longevity, senescence, and death (see pages 78-79).

Initiation at first depended on the primordia present in the embryo and the number of embryos per dm^2. Subsequently the gross environmental factors determined the number of new leaves initiated, and finally leaf formation depended on the location of meristems in the sward.

The density of stand may have an overriding influence. For example, at 118 days when L.A.I. was similar, each plant at the low density had formed four times the number of leaves of the high density plants, yet the low density sward produced only one third and carried only one half the number of leaves per dm^2 of the high density swards.

The rate of leaf initiation at first increased with rising density, and at about optimum L.A.I. it gradually changed. It was then 50 per cent. higher in the middle density than in the other two. All the rates fell and were approximately equal, at about ceiling L.A.I. It was as though the middle density had effected a successful compromise between plant stand and branching. In this density the dark zone did not form until the leaves were actively growing from branches, or were able to develop longer petioles to launch their leaves out of the dark zone.

The sites at which new leaves were formed should be considered. At higher densities new leaves originated in the crown of plants and were formed mostly in the dark zone of the sward. At lower densities, most leaves developed at the extremities of branches and thus were initiated in a more favourable light environment.

Leaf development. The similar growth patterns of contemporaneous leaf groups in the three densities and the approximately constant longevity of individual leaves (at about 6 weeks) suggests ontogenetic development. Single leaves failed to develop when they received insufficient light - and this may be classed as abortion rather than senescence. Petiole lengths have to be evaluated in relation to the stage of growth, and the parts of the plant from which they grew. The differences in petiole length between densities cannot be attributed invariably to light competition. Especially at the low density, long petioles were not necessarily vertical or etiolated.

Senescence began even while leaves enjoyed optimum light conditions. Senescence could first be detected by eye when the laminae had lost over 25 per cent. of their maximum weight. When the laminae weight had begun to decline, senescence was greatly accelerated if the leaf was shaded. This is well illustrated by L 3 and L 4 in Fig. 45.

Death rapidly followed senescence and this may have been accelerated by unfavourable circumstances.

The L.A.I. thus generates its own environment, and the manner in which it develops and continues to grow, not only depends on the light gradients, the petiole lengths and the manner in which the leaves were held, but also on the sites at which leaves are initiated.

6.0.0. Some comparisons between experiments A, B and C.

Before proceeding with the final discussion, a number of comparisons between the results of the three experiments will be made.

6.1.0. Experiments A and B.

In both experiments the grass with high nitrogen suppressed clover from the swards. In Experiment B the competition between species was for light and light alone, since underground competition was eliminated in the design of the experiment. It was possible to determine the radiation levels at which clover began to lose weight, i.e. when respiration exceeded photosynthesis. This was the compensation point of the clover stand. In the N 4 treatments of Experiment A it was of the order of 75 g cals cm^{-2} per day and in Experiment B it was 60 g cals cm^{-2} per day. In both experiments clover stand fell rapidly when the radiation received by the clover fell below these values; yields are considered in the following comparison:

The weight of clover when the radiation fell below 70 g cal cm^{-2} per day

	Experiment A		Experiment B			
	N 4		Mixed sward			
Days from sowing	99	113	65	79	93	107
Weight of clover, g per dm^2 of mixed sward	1.8	0.8	1.8	1.6	1.2	0.1

The recovery of clover from partial suppression was similar in both experiments. The clover of N 3 in Experiment A was similar to that of transfers 5 and 6 in Experiment B, and this may be seen by comparing them in Figs. 16 and 28. The weak recovery of clover in N 4 is equivalent to the poor recovery of transfer 8 (see Figs. 26 b and 34 a). It is noteworthy that these patterns of behaviour were recorded in two different seasons and at different times of the year.

The fall in radiation to below the compensation point at the clover surface effectively reduced stand, i.e. in plant numbers as well as plant weight. The recovery of clover from partial shade was the result of renewed leaf development, and this is discussed in 6.2.0.

6.2.0. Experiments B and C.

It is worth recalling that both these experiments were planted at the same time of the year to obviate gross temperature differences, and photoperiodic effects between seasons. The density in Experiment B was intermediate between the middle and high densities of Experiment C.

The results of the individual leaf studies may be applied to the transfer studies to explain the spectacular recoveries of transfers 5 and 6. The agreement between the data from the pure clover sward in Experiment B, and the middle and high densities in Experiment C, is good enough to warrant such a procedure. Two comparisons are given.

The peak leaf number of Experiment B was mid-way between the peak leaf numbers of the middle and high densities of Experiment C, and it occurred at about the same time.

Pure clover swards	Days from sowing	Number of fully expanded leaves per dm^2
B. 26 plants per dm^2	79	230
C. 16 plants per dm^2	83	208
36 plants per dm^2	83	248

The trend in the mean area of expanded green leaves is similar in both experiments, except that the value of 8.6 for 114 days in Experiment B is higher than the corresponding values in Experiment C.

	Days from sowing	Mean area of expanded green leaves (cm^2)	Days from sowing	Mean area of expanded green leaves (cm^2)
B. Pure clover	79	3.6	114	8.6
C. 16 plants per dm^2	76	3.8	118	6.1
36 plants per dm^2	76	3.1	118	5.5

In both experiments larger leaves were being initiated from about 90 days onwards, and the manner in which these leaves developed in pure clover stands is shown in Fig. 42. Transfers 5 and 6 were made at 85 and 93 days respectively. Before transfers 5 and 6, the yield of clover per dm^2 was declining and this means that the leaves were losing weight when the clover was transferred. It is unlikely that the senescence of individual leaves was arrested when these plants were transferred to a more favourable light environment, and it might be expected that the decline in weight of the attached leaves continued until they died. Observations in Experiment B confirm that this was the case. Meanwhile the primordia which had formed before transfer, but had failed to develop, were now able, after transfer, to grow into young leaves. The gains by these leaves balanced the losses of the senescent pre-transfer leaves. During the first 3 weeks after transfers 5 and 6 the net gain in leaf number and yield was nil (Table 42). There was a large increase in leaf number and yield during the second 3 weeks after transfer (Table 42 and Fig. 30). It was shown in Experiment C that the average life of a leaf is 5 to 6 weeks and that for half this time it is increasing in weight and for the other half it is losing weight. Therefore the new leaves which formed between 3 and 6 weeks after transfer, were close to their maximum weight, and were larger than any leaves which had previously formed on the plants.

Before clover was transferred from the mixed swards in transfers 7 and 8 the leaf losses were exceeding the leaf gains. Undoubtedly young clover leaves were aborting because of the severe shading by the grass.

	Transfer number	5	6	7	8
	Days from sowing	85	93	100	107
Leaf number per plant	in mixed sward at transfer	6	5	3	1
	in control sward at the corresponding harvest	-	6	-	5

These clover plants were thus in a similar situation to the suppressed plants in the high density swards of Experiment C. The number of expanded green leaves on the plants with the "lowest plant weight", and the "highest plant weight", depicted for density 36 plants per dm^2 in Fig. 40, is given for comparison:

	Days from sowing	83	90	104	118
Leaf number per plant	"Lowest plant weight"	6	5	2	0
	"Highest plant weight"	9	9	9	8

The rising variability of clover plants when competition for light increased in the high density swards of Experiment C, was also noted in clover in the mixed swards of Experiment B.

Thus, periodicity of leaf formation in clover was weakened by heavy competition, whether it was shaded by grass or by other clover plants. The degree of mutual shading within a sward is expressed by the form of the light profile. This will be discussed in section 6.3.0.

6.3.0. Experiments A and C.

In Experiment A differences in light profiles were demonstrated in swards of different botanical composition. The greater vertical dispersion of the foliage in grass was associated with a more gradual pattern of light penetration than in clover. This was clearly demonstrated in Experiment A. This will also apply, where for similar values of L.A.I., the foliage is dispersed over a greater vertical interval - a trend that is evident with decreasing density in Experiment C (Fig. 47).

The greater L.A.I. at which complete light interception first occurred in the low and the middle densities of Experiment C (L.A.I. 4) may be explained partly by the greater vertical dispersion of the foliage in these swards and partly by the higher level of radiation (and the altitude of the sun) at the time that these levels of L.A.I. were attained.

Seasonal differences in light interception may also be considered. In N 1 and N 2 of Experiment A, zero light at ground level first occurred at the end of September when the general level of radiation was 470 g cal cm^{-2} per day. At this time, the L.A.I. of the swards was about 5 and at these low levels of nitrogen the influence of grass on light interception was negligible. In the high density swards of Experiment C (the only treatment of comparable density) zero light at ground level first occurred at the end of June, when the level of radiation was about 220 g cal cm^{-2} per day; the L.A.I. of the sward was about 3. The mid-day altitude of the sun at Adelaide in September is 54^o and in June it is 32^o. Differences in light interception in different seasons were discussed on pages 62-64 and 97, and the differences between the two experiments which are outlined, are in accord with the findings of other workers.

7.0.0. General Discussion and Conclusion.

Some new concepts were introduced in the literature review and some of these were discussed when the results were examined. In summing up, a number of points are reconsidered bearing in mind that pastures may be managed for light if their growth patterns are known, and if the inter-relationship between light, L.A.I. and growth are understood.

The inter-relationship of light, L.A.I. and growth.

The radiation at the clover surface determines the ceiling yield of clover. The reduction in clover yield and the eventual death of clover plants in the mixed swards of Experiment B was due to shading alone. Similarly, because of a reduction in the light supply in N 3 and N 4 in Experiment A, clover failed to reach the level of production achieved by the clover in N 1 and N 2 at the corresponding harvests. This occurred, even before there was a decline in plant numbers. The influence of nitrogen fertiliser on mixed pastures consisting of grass and clover has been known for a long time and has been attributed to shading of the clover by the grass (page 26). The conclusions reached by Blackman and his colleagues 20 years ago (see pages 26-28) were based on the indirect evidence derived from shading studies with muslin, in which the nitrogen level was varied in separate stands of pure grass and pure clover (Blackman, 1938). Shading clearly depressed the growth of grass and of clover respectively, but nitrogen did not. These conclusions still hold today, but Experiment A provides the first direct account of the way in which nitrogen promotes the leaf growth of "grass-above-clover" and diminishes the light supply to the companion clover to a degree which depresses clover, or even suppresses it completely where shading is severe.

The procedure in Experiment A was to harvest the swards in layers, and measure the light profiles simultaneously. This is a refinement of a method first used by Monsi and his colleagues in Japan who have described it as the "stratifying clip method" (page 77). This method is useful in detailed studies, but entails a great deal of work if done properly. In this connection the point quadrat method devised by Warren Wilson (1959) might play a useful role. The clipping technique was used to determine the vertical distribution of the foliage and dry matter of the botanical components of the swards, and in examining the way in which light was intercepted by the swards. There were some gross differences between clover and grass swards, both in foliage distribution and in light dispersion, and this is in accord with the findings of other workers (pages 48-51).

When the swards were densest it was found that the "leaf concentration" (cm^2 of leaf area per cm^3 of vegetation) was 0.86 for clover and 0.29 for grass. Leaf concentration takes no account of leaf transmissability, reflection and leaf angle of the foliage, which the coefficient of extinction does (pages 54 and 57). Nevertheless leaf concentration expresses the major difference that was found between the clovery and grassy swards at the high densities used in this experiment. In this regard it is worth comparing Fig. 7 (page 57) derived theoretically by Monsi and Saeki (1953) and Fig. 22 (page 179) which shows the relationship between L.A.I. and light intensity at two harvests in Experiment A. At 113 days when the swards were elongating, leaf concentration was less than at 99 days, resulting in a more gradual light interception. In comparing the light profile of grass and clover it was found that light was absorbed more rapidly by the upper leaves of the clover canopy, partly because of different leaf concentrations and partly because the leaves were disposed differently in the two species. It is evident that leaf dispersion is a potent factor influencing the pattern of light penetration, and that it changed with the age of the pasture.

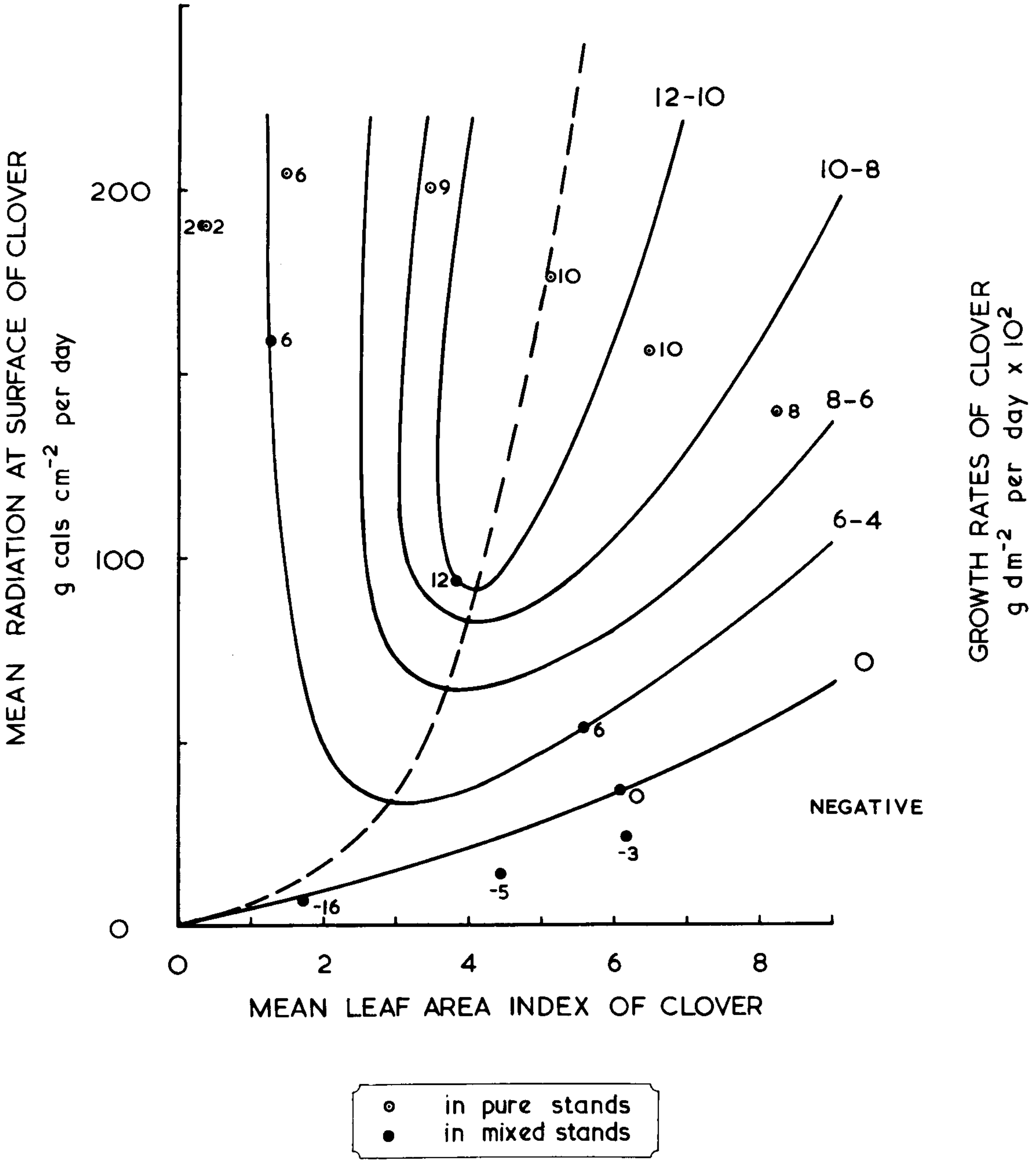
In these studies, the course of competition for light between the taller grass, and the shorter associate clover, was clearly demonstrated. While nitrogen was used to vary the extent of this competitive relationship, the concept established in Experiment A may be extended to any factor which promotes the differential growth of species grown in mixture, such as defoliation or growing pastures for hay. The possibilities were considered in some detail when the grass clover balance was discussed in the literature review.

The extreme sensitivity of the response of clover to variations in the light supply was first evident in the N 3 treatment of Experiment A. After a temporary set-back due to shading, clover resumed growth when the radiation increased at the clover surface. This was examined more closely in Experiment B, where the response of clover to varying periods of light stress was studied, and it was found that the response of clover to an improvement in the light supply was closely related to its ability to maintain or generate new leaves. This finding is of some significance in considering the management of pastures, because any cultural practice to improve the light supply to clover must be based on the premise that the clover stand can continue leaf production. Longer days and higher temperatures generally accompany higher radiation and since these modify the growth of clover, seasonal influences as well must be considered in applying these management practices.

In approaching the question of managing pastures for light it is useful to be able to consider simultaneously, light, L.A.I. and growth rates. These are brought together and expressed in a single diagram in Fig. 48. The results for Experiment B were used to construct this graph. Here the difference in clover growth in mixed and pure stands was due solely to the difference in the radiation received by the clover and the experiment provided a good range in radiation values for similar stages of growth. The L.A.I. is marked along the abscissa, and the mean radiation at the clover surface during the growth interval along the ordinate. The isopleths link growth rates of equal value. The highest values are in the centre and the zero line begins at the origin. On the left hand side the isopleths are nearly parallel to the ordinate, and on the right hand side they run parallel to the zero line. The zero line may be regarded as the compensation point of the sward and values below this are negative. As zero radiation is approached, the negative growth rates cease to be a function of radiation. The broken line on the diagram represents a condition of the sward at which the L.A.I. is optimal for any level of radiation.

Along this line the highest growth rates are attained, i.e. the sward makes the most efficient use of the incoming radiation. To state it in another way: for any given level of radiation the broken curve indicates that the leaf profile attains a state at which there is complete light absorption by the sward, and none of the leaves are in negative balance. At a single value of L.A.I. the optimum use of light

Fig. 48. - The inter-relationship of radiation, L.A.I. and growth rates in swards of subterranean clover.


MEAN RADIATION AT SURFACE OF CLOVER
g cals cm^{-2} per day
GROWTH RATES OF CLOVER
g dm^{-2} per day x 10^2
MEAN LEAF AREA INDEX OF CLOVER
200
100
O
O
2
4
6
8
12-10
10-8
8-6
6-4
O
NEGATIVE
2
2
6
9
10
10
8
6
12
6
O
-3
-5
-16
O
in pure stands
in mixed stands

in a sward may be obtained by adjusting the level of radiation; alternately, for a given level of radiation the optimum use of light may be obtained by adjusting the L.A.I. Between the ordinate and the dotted line only a part of the incident radiation is absorbed by the foliage, while to the right, between the dotted line and the abscissa all the incident radiation is absorbed by a part of the foliage; the remainder of the foliage is in negative balance. The diagram shows that the efficiency of production in the radiation range of 100 - 200 g cal cm^{-2} per day is greatest when the L.A.I. is 4-4.5. This is in accord with the experiments by Davidson and Donald (1958) and agrees with the views expressed by Ničiporovič (1956). An optimal relationship of the kind described, exists for any stand in any environment, and signifies maximal utilisation of the incoming radiation for photosynthesis.

These curves do not take into account temperature changes which may also influence the growth rate, and assume reasonably constant temperature conditions, such as were in fact experienced in the winter period from June-August, 1959. The shape of these curves can be expected to vary with different species or varieties of clover, depending on their nature of growth.

A distinction between plants of indeterminate and determinate habits of growth [1] must be made here. Plants with an indeterminate habit continue to increase in L.A.I. and dry weight, whereas determinate plants may

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[1] Indeterminate: Growth not limited or stopped by the development of a terminal inflloresence: indefinite prolongation and subdivision of an axis. e.g. subterranean clover.

Determinate: Axis terminates early with a flower bud. e.g. Wimmera ryegrass, wheat.

decline in L.A.I. and yet continue to increase in dry weight (Langer 1958). For each category, a curve may be drawn depicting the relationship between yield and L.A.I. and this is done in Fig. 49. Time is, in effect, a progression along the curve, beginning at the origin, and the relationship as depicted may be consummated slowly or rapidly depending on the response of the species to other environmental factors such as temperature, nutrients, etc. In some cases swards may reach maturity without attaining the end point of the curves.

Figure 49 was derived from experimental data and represents an average situation. In practice the position of the curves shown may be modified by such factors as density, nitrogen treatment, photoperiod, etc. It is therefore envisaged that for a species in any given environment, there is an optimum arrangement of stand and foliage at which maximal growth rates are sustained after optimum L.A.I. is reached.

In Experiment C, the optimum L.A.I. occurred, when zero light at ground level was first recorded. Thereafter growth rates fell. Also, maximum growth rates were less with rising density. Consequently, to maintain maximal growth rates of clover in pasture, it is not only necessary to provide an adequate light supply at the surface of the clover, but also to prevent excess foliage in the clover stand. Any management practices directed to this end, such as defoliation, or pasture renovation to bring about thinning of the stand, may prove advantageous in terms of the light supply and utilisation.

More needs to be known of the interdependence of light, L.A.I. and the growth rate of determinate pasture plants. The interrelationships are undoubtedly different from those outlined for clover. If the differences are very great, then other concepts may have to be

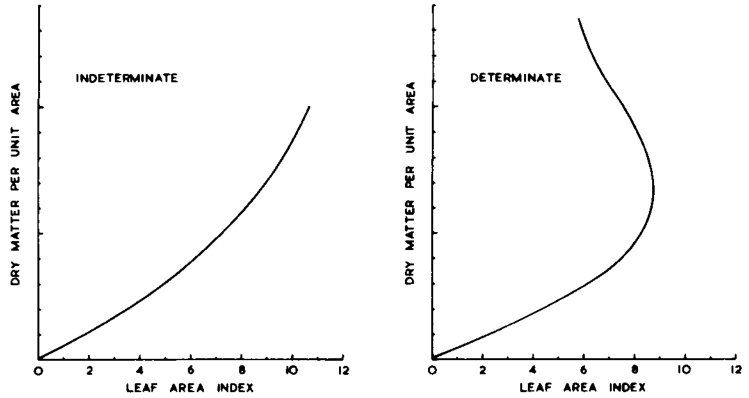

Fig. 49. - The relation between L.A.I. and yield for stands of

(a) indeterminate plants (clover).
(b) determinate plants (grasses).

Time is in effect represented by a continuous progression along the curve, beginning at the origin.

developed to manage for light, pastures consisting entirely of grasses.

With this background it becomes possible to consider more closely the inconsistencies that have been found in the relationship between L.A.I. and growth rate after optimum L.A.I. is reached. Growth rate was reported to be constant when complete light interception occurred (Brougham 1956), to decline (Davidson and Donald 1958) or even to become negative (Table 71). It seems that two factors ought to be considered. One is the botanical composition of the sward and the other is the nature of the growth habits of the botanical components. In Brougham's study, the sward consisted of over 70 per cent. ryegrass which is a plant of determinate habit; the reason for the sustained growth rate, even though complete light interception occurred and the L.A.I. of the entire sward continued to rise, might be explained on the basis that the grass component continued to increase in weight (Brougham 1956) while the L.A.I. was declining: the increasing L.A.I. of the clover component was responsible for the continued increase of the total L.A.I. of the sward. (Brougham 1958a, Table 1). To support this argument a curve of the shape in Fig. 49b may be drawn through the values for the sward defoliated to 5 ins. in Brougham's (1956) Fig. 3. In commenting on the growth rates of the two species, Brougham (1956 page 385) states that "in all treatments the rate of clover diminished markedly towards the end of the first phase of growth" and that this "was due to <u>interspecies</u> competition for light ...". This is in contrast to the decline in the growth rates obtained by Davidson and Donald (1958) after optimum L.A.I. was reached in pure swards of subterranean clover. Here the decline in growth rate was due to <u>intraspecies</u> competition for light resulting in a decline in the rate of new leaf formation (a declining $\frac{dLAI}{dt}$) and an increase in the respiration of the non-photosynthetic tissues, in a sward that retained an indeterminate habit. This decline in growth rate continues after ceiling L.A.I., until ceiling yields are attained (Donald 1960).

The cycling in Experiment C, where growth rates rose and fell through positive and negative values at about a steady value near ceiling L.A.I. was allied to the periodicity (page 259) in leaf development in pure stands of clover. This may be expected where the sward continues to form new leaves after ceiling L.A.I. is reached, and where there is only a moderate increase in the level of radiation.

Some relevant points concerning leaf growth and sward growth in clover. One of the important findings in the individual leaf studies was that all leaves began to lose weight soon after they were fully expanded. This loss in weight has been attributed to shading by the upper part of the canopy (Davidson and Philip 1956, Davidson and Donald 1958, Black 1958 b, Brougham 1958 b, Donald and Black 1958) without acknowledging the changing character of a leaf (Richards 1934, Goodall 1946). Whilst the description of sward growth given by Donald and Black (1958, on the middle of page 4) is substantially true, it must be qualified by the fact that mature leaves may lose weight while they are receiving sufficient light to carry on full photosynthesis and that immature leaves may lose weight when they receive inadequate light and are no longer able to draw on the reserves of the parent plant. Thus the young leaves which go on forming in spite of an inadequate light supply, are in fact the ones which become partially parasitic on the sward.

A leaf lamina that is not inhibited in its development, rises to maximum weight and then declines. It is suggested that this is ontogenetic development, and that the magnitude of the maxima vary according to species, temperature (Milthorpe 1960), the season of the year and the treatment. In the discussion of Experiment C (page 263) an example was given of how one group of leaves began to lose weight before it was overtopped by another group. Brougham (1958 b) observed that from the time that buds could be discerned until leaf death, 6 weeks elapsed regardless of the time of initiation or the ultimate size attained, and he went on to say that "lamina dimensions and petiole weight decreased after maximum values were reached" in almost all cases. The interval from leaf opening to visual senescence was 6 weeks in Experiment C.

The point was made in the discussion of Experiment C that a petiole reached its maximum length shortly after the lamina attained its maximum weight. In Brougham's study, leaves were harvested every second day and his data show this point more clearly than Experiment C, which was harvested weekly. In Brougham's study leaf age for maximum lamina weight was about 22 days and leaf age for maximum petiole length was about 26 days.

Light readings were made at short vertical intervals and the variations in light intensity at the top of the sward emphasised the irregularities in height among the surface leaves of the canopy.

The overtopping of one group of leaves by another is of considerable significance in determining the course of competition for light in swards of a single species. The manner in which groups of leaves overtopped each other was clearly demonstrated in Experiment C

(Fig. 44). As the experiment continued, and more leaves were packed into the canopy, the shading in the body of the sward became more severe and led to more rapid senescence of the older leaves. Ontogenetic development regulated the pattern in each leaf of a rise in weight to a maximum weight and a fall. Leaves may decline in weight, even though exposed to full daylight but overtopping usually occurs in swards above L.A.I. 3-4. There is no doubt that senescence and death were accelerated when the light reductions to the overtopped leaves was severe. The decline in the number of current expanded green leaves in Fig. 38 testifies this. The need for further studies of the effects of age and shading on the weight changes in clover leaves, is indicated from this work.

The suppression of individual plants in pure swards of clover consisting initially of uniform plants, began with small differences in root weight, and was rapidly followed by differences in the size of developing leaves. This led to divergences in total plant weight and resulted in an increasing variability between plants in the sward, and finally to suppression of the smaller members of the community.

In mixed swards, the variability between clover plants (due mainly to differential leaf growth) increased more rapidly as the radiation at the surface of the clover diminished to the compensation point. This was found to be 60 - 70 g cal cm^{-2} per day. When the radiation fell below this value the continued loss in leaf weight led to a loss of leaves from the sward and the eventual death of plants.

When the radiation to an individual clover plant - whether in pure stands or in mixture with grass - was insufficient to maintain photosynthesis over respiration the plant was doomed to suppression from the stand. It is probable that the mature tissues became disorganised when they lost weight (Williams 1955) and that the meristematic tissues also respired away if shading was prolonged.

The individual leaf studies showed that clover leaves do not actually achieve any steady state of mature weight. They are either increasing or decreasing in weight and are relatively short-lived. The rate of growth of a clover sward is sensitive to changes in radiation and this is shown in Fig. 48.

When considering the retention of clover in desirable proportion in mixed pasture, it is first necessary to think of the pasture in terms of the botanical components, and the growth habits of these components. It is also important to realise that clover is in a state of unstable equilibrium and is very sensitive to changes in the light supply. For example, where nitrogen is applied to mixed swards, it is necessary to resort to practices which maintain light to the clover. The extent of the response depends on the state of the clover at the time that the stres is removed. If the radiation at the surface of the clover, and the L.A.I. of the clover are known, it becomes possible to apply cultural practices which adjust the radiation at the clover surface so that the desired growth rates are obtained.

To manage pastures successfully, it is necessary to understand the complex of factors which influence the grass-clover balance (pages 3-37) and to think of the implications of any management practice in terms of its effect, amongst other things, on the light supply.

8.0.0. Summary.

Competition for light in pastures was studied and the literature has been reviewed; records and problems of light measurements were discussed. Three experiments have been conducted, and in each one the light intensity profile was measured.

In Experiment A, the composition of clover-grass swards was modified by varying the nitrogen level, and the way in which one species influenced the light regime of the other was examined. Swards were harvested in layers at vertical intervals of 3.5 cm, and it was established quantitatively that reduction in clover yield after nitrogen application, was due entirely to the shading by grass. At equivalent values of L.A.I. light was reduced more in clover-dominant, than in grass-dominant swards.

In Experiment B, clover-grass swards were grown where tops mingled and were therefore competing for light, but where roots were kept separate by growing the species in alternate narrow panels. Increasing light stress in clover firstly reduced leaf size, then leaf number, and finally plant density. To study the recovery of clover from varying periods of light stress, clover panels were transferred at intervals from the mixtures to pure clover swards. When radiation increased clover recovery depended on the formation of new leaves and was greatest before plant density fell. The growth rate of clover was related to radiation at the clover surface and to the L.A.I. of clover;

optimum L.A.I. increased with rising radiation.

In Experiment C, 16 harvests in 160 days permitted an examination of the initiation, development, expansion, senescence and death of individual leaves in swards of subterranean clover grown at 3 densities; from this study an integrated picture of leaf growth, individual plant development and sward growth was obtained. Plants were selected at random after emergence and leaves were labelled as they appeared. At each harvest, lamina height, area, weight, and petiole length were measured. In general, expanding leaves overtopped and shaded earlier leaves; on a single branch, each leaf was larger than its predecessor. The longevity of a leaf was about 6 weeks, and in that period lamina weight rose to a peak and declined shortly afterwards; a leaf showed no symptoms of senescence until it had lost 25 per cent. of its maximum weight. In comparisons between densities, differences in root weight per plant were detected before differences in top weight; and differences in lamina weight were apparent before leaves opened. Individual plants were more variable at the high density. In each sward complete light interception coincided with the attainment of an optimum L.A.I.

In the discussion, an account is given of the growth of a clover sward. The course of competition for light between grass and clover is traced; and finally the significance of these results in managing clover-grass pastures is considered.

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Appendix - Experiment A.

Table 54.

Weight of Dry Matter (Total of 3 quadrats - one harvested whole and 2 layered ones) GM per dm^2.

		September 14th / 67 days			October 1st / 84 days			October 16th / 99 days			October 30th / 113 days			November 19th / 133 days		
		Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total
N1	I	1.17	0.19	1.36	3.26	0.22	3.48	5.01	0.38	5.39	6.49	0.67	7.16	10.44	1.06	11.50
	II	1.19	0.19	1.38	2.83	0.57	3.40	5.39	0.44	5.83	6.75	0.52	7.27	13.64	1.09	14.73
	III	1.37	0.28	1.65	3.23	0.52	3.75	5.89	0.68	6.57	6.56	0.80	7.36	15.04	1.38	16.42
	IV	1.35	0.20	1.55	3.56	0.36	3.92	5.82	0.50	6.32	6.16	0.72	6.88	12.14	1.18	13.32
	Total	5.08	0.86	5.94	12.88	1.67	14.55	22.11	2.00	24.11	25.96	2.71	28.67	51.26	4.71	55.97
	Mean	1.27	0.21	1.49	3.22	0.42	3.64	5.53	0.50	6.03	6.49	0.68	7.17	12.81	1.18	13.99
N2	I	1.20	0.40	1.60	3.19	1.06	4.25	4.98	1.22	6.20	5.99	1.67	7.66	12.10	3.04	15.14
	II	1.45	0.40	1.85	3.19	0.69	3.88	5.39	0.92	6.31	5.37	1.79	7.16	13.00	2.50	15.50
	III	1.48	0.50	1.98	2.99	1.33	4.32	5.15	1.33	6.48	5.64	2.17	7.81	9.18	3.29	12.47
	IV	1.47	0.44	1.91	3.54	0.80	4.34	5.47	1.15	6.62	5.81	1.52	7.33	11.94	2.54	14.48
	Total	5.60	1.74	7.34	12.91	3.88	16.79	20.99	4.62	25.61	22.81	7.15	29.96	46.22	11.37	57.59
	Mean	1.40	0.43	1.83	3.23	0.97	4.20	5.25	1.15	6.40	5.70	1.79	7.49	11.55	2.84	14.40

Table 54 cont.

Weight of Dry Matter (Total of 3 quadrats - one harvested whole and 2 layered ones) GM per dm^2. (Cont.)

		September 14th / 67 days			October 1st / 84 days			October 16th / 99 days			October 30th / 113 days			November 19th / 133 days		
		Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total	Clover	Grass	Total
N3	I	1.43	0.78	2.21	3.06	1.69	4.75	4.29	2.48	6.77	4.13	3.64	7.77	8.57	4.84	13.41
	II	1.28	0.77	2.05	2.95	1.42	4.37	4.03	2.52	6.55	3.48	4.00	7.48	10.08	5.82	15.90
	III	1.32	0.86	2.18	2.63	2.06	4.69	3.79	2.82	6.61	3.39	4.62	8.01	7.36	5.11	12.47
	IV	1.47	0.44	1.91	2.87	1.86	4.73	3.89	2.59	6.48	4.14	3.63	7.77	6.63	5.51	12.14
	Total	5.50	2.85	8.35	11.51	7.03	18.54	16.00	10.41	26.41	15.14	15.89	31.03	32.64	21.28	53.92
	Mean	1.37	0.71	2.09	2.88	1.76	4.63	4.00	2.60	6.60	3.79	3.97	7.76	8.16	5.32	13.48
N4	I	1.40	0.93	2.33	2.63	2.81	5.44	2.05	4.93	6.98	1.02	8.98	10.00	1.28	13.35	14.63
	II	1.39	0.72	2.11	2.34	2.49	4.83	1.60	5.51	7.11	0.65	7.95	8.60	0.81	12.22	13.03
	III	1.53	1.06	2.59	2.76	3.01	5.77	1.50	5.13	6.63	0.87	9.31	10.18	0.51	13.05	13.56
	IV	1.42	0.61	2.03	2.58	1.87	4.45	1.96	4.89	6.85	0.67	7.00	7.67	0.70	12.83	13.53
	Total	5.74	3.32	9.06	10.31	10.18	20.49	7.11	20.46	27.57	3.21	33.24	36.5	3.30	51.45	54.75
	Mean	1.43	0.83	2.27	2.58	2.55	5.12	1.78	5.11	6.89	0.80	8.31	9.11	0.83	12.86	13.69

Total H_1

	I	II	III	IV	
N 1	1.36	1.38	1.65	1.55	5.94
2	1.60	1.85	1.98	1.91	7.34
3	2.21	2.05	2.18	1.91	8.35
4	2.33	2.11	2.59	2.03	9.06
	7.50	7.39	8.40	7.40	30.69

LSD bet	5%	1%	.1%
N Means	.243	.349	.513

Analysis of Variance

	DF	SS	MS	VR
Total	15	1.7598		
Blocks	3	.1782	.0594	2.58 NS
N	3	1.3740	.4580	19.86 ***
Res	9	.2076	.023067	

Total H_2

	I	II	III	IV	
N 1	3.48	3.40	3.75	3.92	14.55
2	4.25	3.88	4.32	4.34	16.79
3	4.75	4.37	4.69	4.73	18.54
4	5.44	4.83	5.77	4.45	20.49
	17.92	16.48	18.53	17.44	70.37
		.507	.728	1.072	

	DF	SS	MS	VR
Total	15	6.2644		
Reps	3	.5617	.1872	1.86 NS
N	3	4.7985	1.5995	15.92 ***
Res	9	.9042	.10047	

Total H_3

	I	II	III	IV	
N 1	5.39	5.83	6.57	6.32	24.11
2	6.20	6.31	6.48	6.62	25.61
3	6.77	6.55	6.61	6.48	26.41
4	6.98	7.11	6.63	6.85	27.57
	25.34	25.80	26.29	26.27	103.70
		.519	.746	1.097	

Analysis of Variance

	DF	SS	MS	VR
Total	15	2.6834		
Reps	3	.1525	.0508	-
N	3	1.5837	.5279	5.02^{*}
Res	9	.9472	.10524	

Total H_4

	I	II	III	IV	
N 1	7.16	7.27	7.36	6.88	28.67
2	7.66	7.16	7.81	7.33	29.96
3	7.77	7.48	8.01	7.77	31.03
4	10.00	8.60	10.18	7.67	36.45
	32.59	30.51	33.36	29.65	126.11
		.851	1.222	1.798	

	DF	SS	MS	VR
Total	15	13.5830		
Reps	3	2.2618	.7539	2.66 NS
N	3	8.7752	2.9251	10.34^{**}
Res	9	2.5460	.28289	

Total H_5

	L	II	III	IV	
N 1	11.50	14.73	16.42	13.32	55.97
2	15.14	15.50	12.47	14.48	57.59
3	13.41	15.90	12.47	12.14	53.92
4	14.63	13.03	13.56	13.53	54.75
	54.68	59.16	54.92	53.47	222.23
		2.612	3.753	5.521	

	DF	SS	MS	VR
Total	15	30.5377		
Reps	3	4.6280	1.5427	-
N	3	1.9087	.6362	-
Res	9	24.0010	2.6668	

Clover H_1

	I	II	III	IV	
N 1	1.17	1.19	1.37	1.35	5.08
2	1.20	1.45	1.48	1.47	5.60
3	1.43	1.28	1.32	1.47	5.50
4	1.40	1.39	1.53	1.42	5.74
	5.20	5.31	5.70	5.71	21.92
LSD		5%	1%	.1%	
N Means		.142	.204	.481	

Analysis of Variance

	DF	SS	MS	VR	
Total	15	0.1838			
Blocks	3	0.0521	.0174	2.20	NS
N	3	0.0606	.0202		NS
Res	9	0.0711	.0079000	2.56	

Clover H_2

	I	II	III	IV	
N 1	3.26	2.83	3.23	3.56	12.88
2	3.19	3.19	2.99	3.54	12.91
3	3.06	2.95	2.63	2.87	11.51
4	2.63	2.34	2.76	2.58	10.31
	12.14	11.31	11.61	12.55	47.61
		.333	.479	.704	

	DF	SS	MS	VR	
Total	15	1.7838			
Reps	3	.2281	.0760	1.75	NS
N	3	1.1652	.3884	8.95	**
Res	9	.3905	.043389		

Clover
H_3

	I	II	III	IV	
N 1	5.01	5.39	5.89	5.82	22.11
2	4.98	5.39	5.15	5.47	20.99
3	4.29	4.03	3.79	3.89	16.00
4	2.05	1.60	1.50	1.96	7.11
	16.33	16.41	16.33	17.14	66.21
		.505	.725	1.066	

Analysis of Variance

	DF	SS	MS	VR
Total	15	36.0226		
Reps	3	.1161	.0387	-
N	3	35.0108	11.6703	117.26 ***
Res	9	.8957	.099522	

Clover
H_4

	I	II	III	IV	
N 1	6.49	6.75	6.56	6.16	25.96
2	5.99	5.37	5.64	5.81	22.81
3	4.13	3.48	3.39	4.14	15.14
4	1.02	0.65	0.87	0.67	3.21
	17.63	16.25	16.46	16.78	67.12
		.446	.641	.943	

Total	15	77.8438		
Rep	3	.2765	.0922	1.18
N	3	76.8669	25.6223	329.24 ***
Res	9	.7004	.077822	

Clover
H_5

	I	II	III	IV	
N 1	10.44	13.64	15.04	12.14	51.26
2	12.10	13.00	9.18	11.94	46.22
3	8.57	10.08	7.36	6.63	32.64
4	1.28	0.81	0.51	0.70	3.30
	32.39	37.53	32.09	31.41	133.42
		2.450	3.521	5.179	

Total	15	374.5368		
Rep	3	5.9363	1.9788	-
N	3	347.4779	115.8260	49.35 ***
Res	9	21.1226	2.3470	

Grass H_1

	I	II	III	IV	
N 1	.19	.19	.28	.20	.86
2	.40	.40	.50	.44	1.74
3	.78	.77	.86	.44	2.85
4	.93	.72	1.06	.61	3.32
	2.30	2.08	2.70	1.69	8.77

	DF	SS	MS	VR
Total	15	1.1606		
Reps	3	.1335	.0445	3.77 NS
N	3	.9209	.3070	26.02 ***
Res	9	.1062	.011800	

LSD betw.	5%	1%	.1%
N Means	.174	.250	.367

Grass H_2

	I	II	III	IV	
N 1	.22	.57	.52	.36	1.67
2	1.06	.69	1.33	.80	3.88
3	1.69	1.42	2.06	1.86	7.03
4	2.81	2.49	3.01	1.87	10.18
	5.78	5.17	6.92	4.89	22.76

	DF	SS	MS	VR
Total	15	11.6347		
Reps	3	.6078	.2026	2.69 NS
N	3	10.3480	3.4493	45.73 ***
Res	9	.6789	.075433	

	.439	.631	.929

Grass H_3

	I	II	III	IV	
N 1	.38	.44	.68	.50	2.00
2	1.22	.92	1.33	1.15	4.62
3	2.48	2.52	2.82	2.59	10.41
4	4.93	5.51	5.13	4.89	20.46
	9.01	9.39	9.96	9.13	37.49
		.300	.431	.634	

Analysis of Variance

	DF	SS	MS	VR
Total	15	50.6881		
Reps	3	.1339	.0446	1.27 NS
N	3	50.2372	16.7457	475.43 ***
Res	9	.3170	.035222	

Grass H_4

	I	II	III	IV	
N 1	.57	.52	.80	.72	2.71
2	1.67	1.79	2.17	1.52	7.15
3	3.64	4.00	4.62	3.63	15.89
4	8.98	7.95	9.31	7.00	33.24
	14.96	14.26	16.90	12.87	58.99
		.774	1.112	1.635	

	DF	SS	MS	VR
Total	15	140.6911		
Reps	3	2.1102	.7034	3.01 NS
N	3	136.4753	45.4918	194.44 ***
Res	9	2.1056	.23396	

Grass H_5

	I	II	III	IV	
N 1	1.06	1.09	1.38	1.18	4.71
2	3.04	2.50	3.29	2.54	11.37
3	4.84	5.82	5.11	5.51	21.28
4	13.35	12.22	13.05	12.83	51.45
	22.29	21.63	22.83	22.06	88.81
		.668	.960	1.412	

	DF	SS	MS	VR
Total	15	321.6573		
Reps	3	.1874	.0625	-
N	3	319.8995	106.6332	611.11 ***
Res	9	1.5704	.17449	.17449

Table 55.

The Density of clover in N1, N2, N3 and N4 at 5 harvests.

		September 14th / 67 days	October 1st / 84 days	October 16th / 99 days	October 30th / 113 days	November 19th / 133 days	Total
N 1	I	26.3	33.3	38.0	30.3	26.5	154.4
	II	28.0	30.3	30.8	28.0	25.5	142.6
	III	28.5	31.7	28.5	28.7	29.2	146.6
	IV	29.7	30.8	31.8	31.0	26.3	149.6
	Total	112.5	126.1	129.1	118.0	107.5	593.2
N 2	I	26.0	31.2	32.8	30.7	25.5	146.2
	II	28.5	31.2	32.2	30.3	28.5	150.7
	III	29.7	26.0	32.8	28.2	24.2	140.9
	IV	26.5	30.0	31.5	28.8	30.5	147.3
	Total	110.7	118.4	129.3	118.0	108.7	585.1
N 3	I	25.0	30.2	32.5	25.7	20.0	133.4
	II	25.0	27.7	33.0	25.2	26.3	137.2
	III	24.5	29.0	27.3	24.0	22.7	127.5
	IV	28.3	29.0	29.8	23.7	22.5	133.3
	Total	102.8	115.9	122.6	98.6	91.5	531.4
N 4	I	23.7	30.3	26.2	11.3	7.0	98.5
	II	24.3	31.3	22.3	6.2	8.3	92.4
	III	26.5	26.3	30.3	13.2	3.2	99.5
	IV	27.3	27.2	24.7	10.3	5.0	94.5
	Total	101.8	115.1	103.5	41.0	23.5	384.9
Total		427.8	475.5	484.5	375.6	331.2	2094.6

Analysis of Variance.

Clover

	DF	SS	MS	VR
Total	79	3726.34		
Reps	3	8.19	2.730	- NS
Nit	3	1396.25	465.42	127.41 ***
N x R (Main Res)	9	32.88	3.6533	
Harv	4	1072.02	268.01	51.96 ***
H x N	12	969.40	80.78	15.66 ***
Split Plot Res.	48	247.60	5.1583	

L.S.D. Between harvest Means at any one nitrogen level

$$= \sqrt{\frac{5.1583}{4} \times 2} \times t_{48} = \sqrt{2.5791} \times t_{48} = 1.6059 \times t_{48}$$

5% 3.23
1% 4.30
0.1% 5.64

L.S.D. between nitrogen Means at any one harvest and any harvest

i.e. diagonal comparisons

= S.E. of diff x t_x =
= 1.5584 x t_x

5% 3.19
1% 4.31
0.1% 5.77

$$\text{S.E. of diff} = \sqrt{\frac{2\left[4(5.1583) + 3.6533\right]}{5 \times 4}} = \sqrt{2.4287} = 1.5584$$

$$t_x \; 5\% = \frac{4(5.1583)2.010 + 3.6533 \times 2.262}{4(5.1583) + 3.6533} = \frac{49.7365}{24.2865} = 2.048$$

$$t_x \; 1\% = \frac{4(5.1583)2.678 + 3.6533 \times 3.250}{24.2865} = \frac{67.1289}{24.2865} = 2.764$$

$$t_x \; 0.1\% = \frac{4(5.1583)3.509 + 3.6533 \times 4.781}{24.2865} = \frac{89.8683}{24.2865} = 3.700$$

Table 56.
The Density of grass in N1, N2, N3 and N4 at 5 harvests.

		September 14th / 67 days	October 1st / 84 days	October 16th / 99 days	October 30th / 113 days	November 19th / 133 days	Total
N 1	I	25.3	19.3	15.8	14.7	13.0	88.1
	II	26.3	28.5	22.2	16.2	10.5	103.7
	III	33.3	23.2	32.7	24.2	14.0	127.4
	IV	39.0	34.2	24.8	17.8	11.2	127.0
	Total	123.9	105.2	95.5	72.9	48.7	446.2
N 2	I	24.5	32.5	34.2	31.0	26.7	148.9
	II	25.7	27.3	24.0	27.5	28.5	133.0
	III	31.7	33.8	36.5	37.7	36.2	175.9
	IV	36.3	28.5	27.5	33.8	30.7	156.8
	Total	118.2	122.1	122.2	130.0	122.1	614.6
N 3	I	26.7	31.8	32.8	28.8	40.5	160.6
	II	26.5	29.8	34.3	37.0	43.0	170.6
	III	25.5	36.2	35.8	37.7	34.7	169.9
	IV	38.7	28.3	36.2	32.2	35.3	170.7
	Total	117.4	126.1	139.1	135.7	153.5	671.8
N 4	I	25.5	30.2	31.0	29.0	33.0	148.7
	II	21.7	27.7	32.2	28.8	28.0	138.4
	III	26.5	36.5	34.2	38.5	50.5	186.2
	IV	26.5	25.2	31.7	31.8	31.5	146.7
	Total	100.2	119.6	129.1	128.1	143.0	620.0
Total		459.7	473.0	485.9	466.7	467.3	2352.6

Analysis of Variance.

Grass

	DF	SS	MS	VR	
Total	79	4249.62			
Reps	3	440.02	146.67	5.14	*
Nit	3	1443.06	481.02	16.84	***
N x R (Main Plot Res.)	9	257.06	28.562		
Harv.	4	24.05	6.013	-	NS
H x N	12	1279.97	106.66	6.36	***
Split Plot Res.	48	805.46	16.7804		

L.S.D. between Harvest Means at any one nitrogen level

$$= \sqrt{16.7804 \times 2} \times t_{48} \quad = \sqrt{8.3902} \times t_{48} \quad = 2.8965 \times t_{48}$$

5%	5.82
1%	7.76
0.1%	10.16

L.S.D. between Nitrogen Means at any one harvest level or between any harvest levels, i.e. diagonal comparisons.

$$= \text{S.E. of diff} \times t_x = \begin{array}{ll} 5\% & 6.45 \\ 1\% & 8.81 \end{array}$$

$$\times t_x \quad 0.1\% \quad 12.03$$

$$\text{S.E. of diff} = \sqrt{\frac{2\boxed{4(16.7804) + 28.562}}{4.5}} = \sqrt{9.5684} = 3.0933$$

$$t_x \quad 5\% = \frac{4(16.7804)2.010 + 28.562 \times 2.262}{4(16.7804) + 28.562} = \frac{199.5216}{95.6836} = 2.085$$

$$t_x \quad 1\% = \frac{4(16.7804)2.678 + 28.562 \times 3.250}{95.6836} = \frac{272.5781}{95.6836} = 2.849$$

$$t_x \quad 0.1\% = \frac{4(16.7804)3509 + 28.562 \times 4.781}{95.6836} = \frac{372.0846}{95.6836} = 3.889$$

11.2.0.

Appendix - Experiment B.

Table 57.

Number of plants per dm^2, for transfer 1-6

	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6				
Weeks	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	Totals	
Rep. 1	28.3	31.7	26.7	25.0	26.7	26.7	30.0	26.7	26.7	28.3	26.7	25.0	28.3	26.7	25.0	28.3	20.0	16.7	Rep. 1	473.5
Rep. 2	28.3	26.7	23.3	28.3	23.3	26.7	28.3	26.7	25.0	28.3	28.3	25.0	28.3	26.7	25.0	26.7	25.0	21.7	Rep. 2	471.6
Rep. 3	28.3	26.7	28.3	30.0	28.3	25.0	26.7	26.7	25.0	28.3	26.7	28.3	25.0	21.7	25.0	21.7	20.0	23.3	Rep. 3	465.0
Total	84.9	85.1	78.3	83.3	78.3	78.4	85.0	80.1	76.7	84.9	81.7	78.3	81.6	75.1	75.0	76.7	65.0	61.7		
Mean	28.3	28.4	26.1	27.8	26.1	26.1	28.3	26.7	25.6	28.3	27.2	26.1	27.2	25.0	25.0	25.6	21.7	20.6	0 : 3 :	496.4 465.3
Total: 0+3+6	248.3			240.0			241.8			244.9			231.7			203.4			6 :	448.4

Grand Total 1410.1

Number of plants per dm^2, for transfers 7-8

	Transfer 7			Transfer 8		
Weeks	0	+3	+6	0	+3	+6
Rep. 1	16.7	8.3	11.7	5.0	0	1.7
Rep. 2	13.3	10.0	10.0	1.7	3.3	3.3
Rep. 3	11.7	10.0	6.7	1.7	15.0	1.7
Total	41.7	28.3	28.4	8.4	18.3	6.7
Mean	13.9	9.4	9.5	2.8	6.1	2.2

Analysis of Variance of transfers 1-6.

	df	S.S.	M.S.	V.R.
Total	53	397.82		
Reps.	2	2.21	1.11	
Trans.	5	150.62	30.12	6.70 xxx
Times	2	65.87	32.93	7.32 xx
Tr x Times	10	19.38	1.94	
Error	34	159.74	4.6982	
Error + Rep.	36	161.95	4.4986	

L.S.D.

Between transfers

$$\sqrt{\frac{4.4986}{9} \times 2} = 0.99985 \times t_{36}$$

Between times

$$\sqrt{\frac{4.4986}{18} \times 2} \times t_{36} = 0.707\, t_{36}$$

	Between transfers	Between times
At $P < 0.05$	2.02	1.43
< 0.01	2.72	1.92
< 0.001	3.58	2.53

The analyses of the post-transfer data in Experiment B.

1. Introductory remarks.

(1) The analyses of clover yield per dm^2, of L.A.I. of clover and the number of unfolded green leaves per dm^2 are presented as a group. These were complex analyses and the steps are outlined in the first analysis of the group. The number of plants per unit area is also presented and this is a straight-forward analysis of variance.

(2) The overall analyses of variance of the original data of dry weight, L.A.I. and the number of unfolded green leaves per dm^2 and the number of plants per unit area, showed no replicate differences. It was decided not to calculate the S.S. of replication in subsequent analyses.

(3) Analyses on the differences between times (i.e. at 0, 3 & 6 weeks) at each transfer showed significant trends and indicated that these trends were significant in all attributes (i.e. weight, L.A.I. and leaf number).

(4) Because of the nature of the variations and because the major differences were in the relative effects between transfers, the analyses were made on the log transformed data.

(5) The relative effects in transfers 7 and 8 were similar to those in transfers 5 and 6. The absolute differences between Tr. (5 and 6) and (7 and 8) were sufficiently large to render statistical analysis unnecessary, and it was obvious that the omission of transfers 7 and 8 would enhance the accuracy of the tests applied to transfers 1-6.

(6) The procedure for the analysis which was finally adopted is set out in detail for the weight data. The analyses of L.A.I. and leaf number are set out in the same way, but the explanatory details are omitted in their presentation.

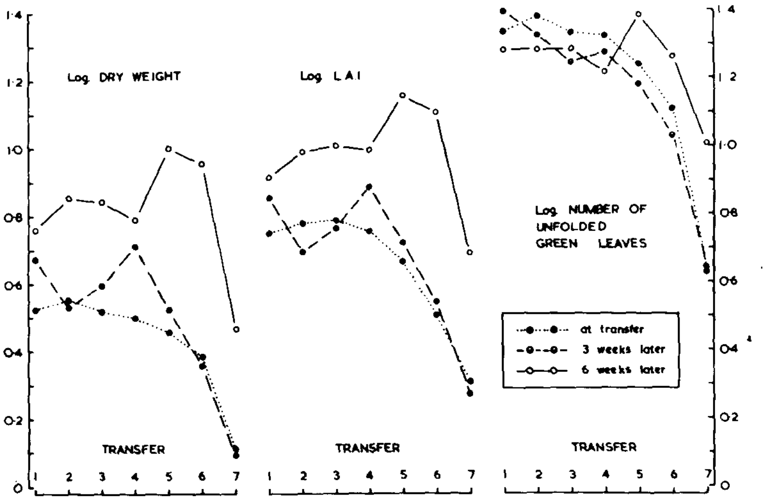

Fig. 50. - The log transformations of the growth attributes that were analysed in Experiment B:

(a) dry weight per unit area,
(b) L.A.I.,
(c) Leaf number per unit area,

are shown for each transfer, and at 3 and 6 weeks after transfer.

2. Analysis of the weight data.

Table 58.

A. Tabular Data.

The weight of clover ($g\ dm^{-2}$) at transfer, and at 3 and 6 weeks after transfer.

Weeks	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			Transfer 7			Transfer 8		
	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6
Rep. 1	3.17	5.87	6.75	2.87	4.13	8.07	2.73	3.53	7.48	2.78	4.20	8.18	2.61	3.70	11.90	2.40	2.13	8.33	1.47	1.27	4.05	0.55	0.00	0.00
Rep. 2	3.50	4.58	4.60	4.12	2.22	6.85	3.75	4.50	5.88	3.03	6.33	3.18	2.95	3.43	13.52	2.85	2.77	7.45	1.42	1.10	5.70	0.00	0.13	0.27
Rep. 3	3.40	3.87	6.08	3.80	4.25	6.60	3.50	3.85	7.58	3.73	5.07	9.00	3.02	2.93	6.17	2.08	1.98	11.55	1.03	1.37	1.10	0.00	1.22	0.15
Mean	3.36	4.77	5.81	3.60	3.53	7.17	3.33	3.96	6.98	3.18	5.20	6.79	2.86	3.35	10.53	2.44	2.29	9.11	1.31	1.25	3.62	0.18	0.45	0.14

Log transformation of the weight of clover, transfer 1-6 inclusive.

Weeks	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			
	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	
Rep. 1	0.501	0.769	0.829	0.458	0.616	0.907	0.436	0.548	0.874	0.444	0.623	0.913	0.417	0.568	1.076	0.380	0.328	0.921	Rep. 1: 11.608
Rep. 2	0.544	0.661	0.663	0.615	0.346	0.836	0.574	0.653	0.769	0.481	0.801	0.502	0.470	0.535	1.131	0.455	0.442	0.872	Rep. 2: 11.350
Rep. 3	0.531	0.588	0.784	0.580	0.628	0.820	0.544	0.585	0.880	0.572	0.705	0.954	0.480	0.467	0.790	0.318	0.297	1.063	Rep. 3: 11.586
Total	1.576	2.018	2.276	1.653	1.590	2.563	1.554	1.786	2.523	1.497	2.129	2.369	1.367	1.570	2.997	1.153	1.067	2.856	
Totals 0 + 3	3.594			3.243			3.340			3.626			2.937			2.220			0 + 3: 18.960
0 + 3 + 6		5.870			5.806			5.863			5.995			5.934			5.076		

Tr(1-4) (0 : 6.280
(+3: 7.523
(+6: 9.731

Total 23.534

Tr(5-6) (0: 2.520
(+3: 2.637
(+6: 5.853

Total 11.010

0: 8.800
+3: 10.160
+6: 15.584

Grand Total: 34.544

B. The analysis of variance of the log data.

1. (a) On all occasions.

	df	S.S.	M.S.	V.R.	
Total	53	2.246027			
Trans.	5	0.064237	0.012847	1.19	N.S.
Times	2	1.431334	0.715667	66.07	xxx
Tr x Times	10	0.360517	0.36052	3.33	xx
Error	36	0.389939	0.010832		

This analysis showed a significant Tr x Times interaction and further analyses were made at each time, i.e. at 0, and 3 and 6 weeks.

(b) At 0 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.099992			
Trans.	5	0.054514	0.010903	2.88	N.S.
Error	12	0.045478	0.0037898		

(c) At 3 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.346614			
Trans.	5	0.240661	0.048132	5.45	xx
Error	12	0.105953	0.0088294		

(d) At 6 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.368087			
Trans.	5	0.129579	0.025916	1.30	N.S.
Error	12	0.238508	0.019876-S_q^2		

(e) There was heterogeneity between the error variances in the 3 analyses as shown by the following tests.

Tests of homogeneity of E.M.S. 0, & 3 $\frac{0.0088294}{0.0037898} = 2.33$ N.S.

0, & 6 $\frac{0.019876}{0.037898} = 5.24$ xx

3, & 6 $\frac{0.019876}{0.0088294} = 2.25$ N.S.

(f) Because 0 & 3 were homogeneous the results of 0 & 3 were pooled and an analysis of variance follows:

	df	S.S.	M.S.	V.R.	
Total	35	0.497984			
Trans.	5	0.229688	0.045934	7.28	xxx
Times	1	0.051378	0.051378	8.14	xxx
Tr x Times	5	0.065487	0.013097	2.08	N.S.
Error	24	0.151431	0.0063096-S_p^2		

This test showed that the significant Tr x Times interaction which was present in the overall analysis, is absent in this grouping. This means that it occurs at 6 weeks.

(g) The pooled error variance of (0 & 3) was found to differ significantly from the error variance from 6 weeks.

$$(0, \& 3),6 \quad \frac{0.019876}{0.0063096} = 3.15^{x}$$

(h) In order to make comparisons of (0 & 3) and 6 weeks a weighted analysis was necessary.

2\. (a) An inspection of the graphs of the means of the log-transformed data, indicated that 6 weeks after transfer the response in transfers 5 and 6 was markedly better than the response in transfers (1-4). It was therefore decided to group the transfer data in order to isolate and test this response.

(b) The data were now reduced to the following table of totals.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6
0 & 3	3.594	3.243	3.340	3.626	2.937	2.220
6	2.276	2.563	2.523	2.369	2.997	2.856

	Tr(1-4)	Tr(5-6)
(0 & 3)	13.803	5.157
6	9.731	5.853

3. (a) The basis for the weighting procedure was to convert all the data to units of their respective standard deviations. Thus, the factors by which the data were weighed were:

$$W_{0+3} = \frac{1}{\sqrt{S_p^2}} \qquad W_6 = \frac{1}{\sqrt{S_q^2}}$$

(b) The marginal totals in the table incorporate the weighted factors.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6	
(0 & 3)	3.594	3.243	3.340	3.626	2.937	2.220	3004.97
6	2.276	2.563	2.523	2.369	2.997	2.856	784.06
	684.12	642.93	656.30	693.87	616.28	495.54	3789.03

	Tr(1-4)	Tr(5-6)
(0 & 3)	13.803	5.157
6	9.731	5.853
	2677.2	1111.81

(a) Analysis of variance of the grouped and weighed data.

(i)

	df	S.S.	M.S.	V.R.	
Times	1	89.8799	89.8799	89.8799	xxx
Transfers	5	23.7177	4.7435	4.7435	xxx
Tr x Times	5	19.2050	3.8410	3.8410	xx
Error	∞	∞	1		

(ii)

	df	S.S.	M.S.	V.R.	
Transfers	5	23.7177			
Between Groups (1-4) & (5-6)	1	15.5608	15.5608	15.5608	xxx
Within Groups (1-4) & (5-6)	4	8.1569	2.0392	2.0392	N.S.

(iii)

	df	S.S.	M.S.	V.R.	
Tr x Times	5	19.2050			
Between Groups (1-4) & (5-6)	1	16.6867	16.6867	16.6867	xxx
Within Groups (1-4) & (5-6)	4	2.5183	0.6296	0.6296	N.S.

a.a. The overall analysis (i) showed that Times, (0 & 3) and 6, were significantly different, and that there were significant differences between the transfers.

b.b. Analysis (i) showed a significant Tr x Times interaction. Consequently the following comparisons were made

(ii) between times and within transfers

and (iii) between transfers and within times

c.c. Analysis (ii) showed a highly significant difference between Transfers (1-4) and (5-6), but no differences between individual transfers in either group.

d.d. Analysis (iii) showed that there was a highly significant Tr x Times interaction between the groups. The estimate of error from "the within-groups S.S." is not significantly different from the error mean square in analysis (i). Hence the grouping was valid.

C. Comparison of Means.

1. A table of means summarising the essentials of the log transformed data is presented.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6
(0 & 3)	0.599	0.541	0.557	0.604	0.489	0.370
6	0.759	0.854	0.841	0.790	0.999	0.952

2.

	Tr(1-4)	Tr(5-6)
(0 & 3)	0.575	0.430
6	0.811	0.976

L.S.D. at P 0.05	0.01	0.001
0.058	0.078	0.105^{xxx} ←
0.154^{x} →	0.215	0.304

A comparison was made between transfer groups (Tr(1-4) and Tr(5-6)), within times ((0 & 3) and 6). This is shown with the two-way table above. The nature of the interaction is obvious.

3. A comparison was made between times (0 & 3) and 6) within transfer groups (Tr(1-4) and (5-6)).

(i) Within Tr (1-4) $^{0\ \&\ 3}$ = 0.236

S.E. of = 0.04381

t = 5.387^{xxx}

(ii) Within Tr(5-6) $\begin{matrix} 0\ \&\ 3 \\ 6 \end{matrix} = 0.545$

S.E. of $= 0.061956$

$t = 8.797^{xxx}$

(At $P < 0.001$ $\quad t^{12}_{24} = \begin{matrix} 4.32 \\ \text{to} \\ 3.74 \end{matrix}$)

A weighted t test was considered but in view of the high significance shown above it was deemed unnecessary.

3. Analysis of the L.A.I. data.

Table 59.

A. Tabular Data.

The L.A.I. of clover, at transfer, and at 3 & 6 weeks after transfer.

	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			Transfer 7			Transfer 8		
Weeks	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6
Rep. 1	5.17	8.72	9.80	4.77	6.31	11.09	5.32	5.34	10.29	4.93	6.91	12.56	4.07	6.11	15.55	2.93	3.55	12.13	1.55	2.12	5.86	0.20	0.00	0.00
Rep. 2	5.90	7.05	5.50	7.27	3.02	9.32	6.31	6.43	8.38	5.78	8.62	5.21	4.98	5.40	18.03	3.94	3.97	9.52	1.96	1.50	10.07	0.00	0.23	0.50
Rep. 3	5.78	5.75	10.02	6.21	6.28	8.94	6.86	5.69	12.03	6.37	7.60	14.43	4.84	4.35	10.14	2.84	3.07	17.60	1.40	2.08	1.98	0.00	2.20	0.27
Mean	5.62	7.17	8.44	6.08	5.20	9.78	6.16	5.82	10.23	5.69	7.71	10.73	4.63	5.29	14.91	3.24	3.53	13.08	1.64	1.90	5.97	0.07	0.81	0.77

Log transformation of the L.A.I., transfer 1-6 inclusive.

	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			Totals	
Weeks	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6		
Rep. 1	0.713	0.941	0.991	0.679	0.800	1.045	0.726	0.728	1.012	0.693	0.839	1.099	0.610	0.786	1.192	0.467	0.550	1.085	Rep. 1	14.956
Rep. 2	0.771	0.848	0.740	0.862	0.480	0.969	0.800	0.808	0.923	0.762	0.936	0.717	0.697	0.732	1.256	0.596	0.599	0.979	Rep. 2	14.475
Rep. 3	0.762	0.760	1.001	0.793	0.798	0.951	0.836	0.755	1.080	0.804	0.881	1.159	0.685	0.638	1.006	0.453	0.487	1.246	Rep. 3	15.095
Total	2.246	2.549	2.732	2.334	2.078	2.965	2.362	2.291	3.015	2.259	2.656	2.975	1.992	2.156	3.454	1.516	1.636	3.310		
Totals 0+3 0+3+6	4.795	7.527		4.412	7.377		4.653	7.668		4.915	7.890		4.148	7.602		3.152	6.462		0 + 3:	26.075
	Tr(1-4) (0: 9.201 (+3: 9.574 (+6: 11.687 Total 30.462												Tr(5&6) (0: 3.508 (+3: 3.792 (+6: 6.764 TotaL 14.064						0: +3: +6:	12.709 13.366 18.451

Grand Total 44.526

B. 1. (a) On all occasions

	df	S.S.	M.S.	V.R.	
Total	53	2.012061			
Trans.	5	0.138509	0.027702	2.47	N.S.
Times	2	1.097397	0.546899	48.86	xxx
Tr x Times	10	0.371922	0.037192	3.31	xx
Error	36	0.404233	0.011229		

(b) At 0 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.222057			
Trans.	5	0.173579	0.034716	8.59	xx
Error	12	0.048478	0.0040398		

(c) At 3 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.332576			
Trans.	5	0.222780	0.044556	4.84	x
Error	12	0.109796	0.0091996		

(d) At 6 weeks

	df	S.S.	M.S.	V.R.	
Total	17	0.360031			
Trans.	5	0.114072	0.022814	1.11	N.S.
Error	12	0.245959	0.020497-S_q^2		

(e) Tests of homogeneity of E.M.S. 0, & 3 $\frac{0.0091996}{0.0040398}$ = 2.28 N.S.

0, & 6 $\frac{0.020497}{0.004398}$ = 5.07 xx

3, & 6 $\frac{0.020497}{0.0091996}$ = 2.23 N.S.

(f) 0 & 3 weeks pooled

	df	S.S.	M.S.	V.R.	
Total	35	0.566624			
Trans.	5	0.348135	0.069627	10.56	xxx
Times	1	0.011991	0.011991	1.82	N.S.
Tr x Times	5	0.048224	0.009645	1.46	N.S.
Error	24	0.158274	0.006595-S_p^2		

B. 1. (g) $(0 \& 3), 6 \quad \frac{0.020497}{0.006595} = 3.11^{x}$

2 & 3. Table of Totals. The marginal totals include the weighted factors.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6	
(0 & 3)	4.795	4.412	4.653	4.915	4.148	3.152	3953.935
6	2.732	2.965	3.015	2.975	3.454	3.310	900.187
	860.388	813.679	852.663	890.440	797.504	639.448	4854.122

The weights applied were $W_{0+3} = \sqrt{\frac{1}{S_p^2}}$

$$W_6 = \sqrt{\frac{1}{S_q^2}}$$

	Tr(1-4)	Tr(5-6)
0 & 3	18.775	7.300
6	11.687	6.764
	3417.170	1436.952

4. (a) Analysis of Variance of grouped and weighted data.

(i)

	df	S.S.	M.S.	V.R.
Times	1	68.4264	68.4264	68.43 xxx
Trans.	5	37.9509	7.5902	7.59 xxx
Tr x Times	5	20.3476	4.0695	4.07 xx
Error	∞	∞	1	

(ii)

	df	S.S.	M.S.	V.R.
Transfers	5	37.9509		
Between Groups (1-4) & (5-6)	1	23.2880	23.2880	23.29 xxx
Within Groups (1-4) & (5-6)	4	14.6629	3.6657	3.67 xx

(iii)

	df	S.S.	M.S.	V.R.
Transfers	5	20.3476		
Between Groups (1-4) & (5-6)	1	18.0154	18.0154	18.02 xxx
Within Groups (1-4) & (5-6)	4	2.3322	0.58305	0.58 N.S.

C. Comparison of Means

1. Summary Table

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6
(0 & 3)	0.799	0.735	0.775	0.819	0.691	0.525
6	0.911	0.988	1.005	0.992	1.151	1.103

2. Between means of groups within times

	Tr(1-4)	Tr(5-6)
0 & 3	0.782	0.608
6	0.974	1.127

L.S.D. at P		
0.05	0.01	0.001
0.059	0.080	0.108 ^{xxx} ←
0.156	0.219	0.309

3. Between times within groups

(i) Within Tr(1-4) $\Delta^{0\ \&\ 3}_{6}$ = 0.192

S.E. of Δ = 0.037464

t = 5.12 ^{xxx}

(ii) Within Tr(5-6) $\Delta^{0\ \&\ 3}_{6}$ = 0.519

S.E. of Δ = 0.052984

= 9.795 ^{xxx}

(At $P < 0.001$ t^{12}_{24} = 4.32 to 3.74)

4. Analysis of Leaf Numbers.

Table 60.

A. Tabular Data.

The mean number of unfolded green leaves per dm^2

	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			Transfer 7			Transfer 8		
Weeks	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6
Rep. 1	206.8	253.3	240.0	200.0	232.0	240.0	210.0	154.7	240.0	235.2	178.7	182.5	181.3	168.0	247.5	107.7	128.0	195.0	45.0	51.7	143.5	8.5	0	6.7
Rep. 2	221.0	248.0	147.0	263.5	163.3	216.0	218.2	184.0	167.5	198.3	184.2	100.0	184.2	170.7	285.0	154.7	110.0	158.2	40.0	44.0	190.0	0.5	13.3	23.3
Rep. 3	226.7	248.0	206.8	270.0	255.0	140.0	221.3	194.7	182.5	198.3	205.3	246.5	160.0	123.5	205.0	119.2	88.0	203.0	43.2	38.0	38.7	3.5	69.0	6.7
Mean	218.1	249.7	197.9	244.5	216.7	198.6	216.5	177.8	196.6	210.6	189.4	176.3	175.1	154.1	245.8	127.2	108.6	185.4	42.7	44.6	124.0	4.2	27.4	12.2

Log transformations of the mean number of unfolded green leaves per dm^2,
transfers 1-6 inclusive.

	Transfer 1			Transfer 2			Transfer 3			Transfer 4			Transfer 5			Transfer 6			Totals	
Weeks	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6	0	+3	+6		
Rep. 1	1.316	1.403	1.380	1.301	1.365	1.380	1.322	1.190	1.380	1.371	1.253	1.262	1.258	1.225	1.393	1.033	1.107	1.290	Rep. 1	23.229
Rep. 2	1.344	1.394	1.167	1.420	1.212	1.334	1.338	1.265	1.223	1.297	1.265	1.000	1.265	1.233	1.455	1.190	1.041	1.199	Rep. 2	22.642
Rep. 3	1.356	1.394	1.316	1.431	1.406	1.146	1.344	1.290	1.262	1.297	1.312	1.393	1.204	1.090	1.312	1.076	0.944	1.308	Rep. 3	22.881
Total	4.016	4.191	3.863	4.152	3.983	3.860	4.004	3.745	3.865	3.965	3.830	3.655	3.727	3.548	4.160	3.299	3.092	3.797		
Totals 0 + 3	8.207			8.135			7.749			7.795			7.275			6.391			0 + 3	45.552
0 + 3 + 6		12.070			11.995			11.614			11.450			11.435			10.188			
	Tr(1-4) (0: (+3: (+6:	16.137 15.749 15.243											Tr(5-6) (0: (+3: (+6:	7.026 6.640 7.957					0: +3: +6:	23.163 22.389 23.200
	Total	47.129											Total	21.623						

Grand Total: 68.752

B. 1. (a) On all occasions

	df	S.S.	M.S.	V.R.
Total	53	0.719190		
Trans.	5	0.255638	0.051128	7.35 xxx
Times	2	0.023299	0.011649	1.67 N.S.
Tr x Times	10	0.189842	0.018984	2.73 x
Error	36	0.250411	0.006956	

(b) At 0 weeks

	df	S.S.	M.S.	V.R.
Total	17	0.188462		
Trans.	5	0.157923	0.031585	12.41 xxx
Error	12	0.030539	0.002545	

(c) At 3 weeks

	df	S.S.	M.S.	V.R.
Total	17	0.296984		
Trans.	5	0.242303	0.048461	10.64 xxx
Error	12	0.054681	0.004557	

(d) At 6 weeks

	df	S.S.	M.S.	V.R.
Total	17	0.210444		
Trans.	5	0.045254	0.009051	
Error	12	0.165190	$0.013766 - S_q^2$	

(e) Text of homogeneity of E.M.S. 0, & 3 $= \frac{0.004557}{0.002545} = 1.79$ N.S.

0, & 6 $= \frac{0.013766}{0.002545} = 5.41$ xx

3, & 6 $= \frac{0.013766}{0.004557} = 3.02$ x

(f) 0 & 3 weeks pooled

	df	S.S.	M.S.	V.R.
Total	35	0.0502088		
Trans.	5	0.380304	0.076061	21.42 xxx
Times	1	0.016641	0.016641	4.69 x
Tr x Times	5	0.019922	0.003984	1.12 N.S.
Error	24	0.085221	$0.003551 - S_p^2$	

B. 1. (g) $$(0 \& 3),\ 6 = \frac{0.013766}{0.035509} = 3.88^{xx}$$

2. & 3. Table of Totals. The marginal totals include the weighted factors.

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6	
(0 & 3)	8.207	8.135	7.749	7.795	7.275	6.391	12828.308
6	3.863	3.860	3.865	3.656	4.160	3.797	1685.318
	2591.86	2571.373	2463.031	2460.730	2350.973	2075.653	14513.626

The weights applied were $W_{0\&3} = \sqrt{\frac{1}{S_p^2}}$

$$W_6 = \sqrt{\frac{1}{S_q^2}}$$

	Tr(1-4)	Tr(5-6)
0 & 3	31.886	13.666
6	15.243	7.957
	10087.001	4426.626

4. (a) Analysis of Variance of the grouped and weighted data.

(i)

	df	S.S.	M.S.	V.R.	
Times	1	0.6321	0.6321	0.63	N.S.
Trans.	5	93.9639	18.7928	18.79	xxx
Tr x Times	5	16.4263	3.2853	3.29	xx
Error	∞	∞	1		

(ii)

	df	S.S.	M.S.	V.R.	
Transfers	5	93.9639			
Between Groups (1-4) & (5-6)	1	66.4920	66.4920	66.49	xxx
Within Groups (1-4) & (5-6)	4	27.4719	6.8680	6.87	xxx

(iii)

	df	S.S.	M.S.	V.R.	
Tr x Times	5	16.4263			
Between Groups (1-4) & (5-6)	1	15.5370	15.5370	15.54	xxx
Within Groups (1-4) & (5-6)	4	0.8893	0.2223	0.22	N.S.

C. Comparison of means.

1. Summary Table

	Tr1	Tr2	Tr3	Tr4	Tr5	Tr6
(0 & 3)	1.368	1.356	1.291	1.299	1.213	1.065
6	1.288	1.267.	1.288	1.218	1.387	1.266

2. Between means of groups within times.

			L.S.D. at P		
	Tr(1-4)	Tr(5-6)	0.05	0.01	0.001
0 & 3	1.329	1.139	0.043	0.059	0.079 xxx ←
6	1.270	1.326	0.128	0.179	0.253 ~~N.S.~~ N.S.

3. Between times within groups.

(i) Within Tr(1-4) $\Delta^{0\&3}_{6} = 0.0583$

S.E. of $\Delta = 0.035989$

$t = 1.620$ N.S.

(ii) Within Tr(5-6) $\Delta^{0\&3}_{6} = 0.1874$

S.E. of $\Delta = 0.050894$

$t = 3.682^{xx}$

(At $P < 0.05$ $t^{12}_{24} = \begin{matrix}2.18\\2.06\end{matrix}$

< 0.01 $t^{12}_{24} = \begin{matrix}3.06\\2.80\end{matrix}$

< 0.001 $t^{12}_{24} = \begin{matrix}4.32\\3.74\end{matrix}$)

11.3.0.

Appendix - Experiment C.

Table 61.

Dry weight of individual plant parts (mg) at 20 days.

Sample No.	4 plants per dm^2							16 plants per dm^2							36 plants per dm^2						
	C	U	L1	L2	rm	Rt	Total	C	U	L1	L2	rm	Rt	Total	C	U	L1	L2	rm	Rt	Total
1	4.7	3.2	3.9	-	4.9	7.7	24.4	5.1	2.4	3.2	-	4.4	10.8	25.9	3.7	2.3	1.5	-	3.1	9.2	19.8
2	4.5	2.5	3.0	-	4.7	6.4	21.1	4.0	2.7	3.6	-	4.2	6.5	21.0	3.8	2.8	2.8	-	3.9	5.8	19.1
3	4.1	2.7	2.9	-	3.9	7.1	20.7	3.8	2.4	2.7	-	4.1	7.9	20.9	3.7	2.3	2.9	-	4.1	5.8	18.8
4	4.6	2.6	3.1	-	4.3	4.8	19.4	4.5	2.5	3.1	-	3.9	6.0	20.0	4.0	2.6	2.5	-	3.8	5.5	18.4
5	4.9	2.9	2.3	-	3.7	5.5	19.3	3.8	2.8	2.3	-	3.7	7.0	19.6	4.2	2.0	1.6	-	2.9	7.1	17.8
6	3.6	2.5	2.7	-	3.7	6.2	18.7	3.8	2.9	2.6	-	3.7	6.1	19.1	3.6	2.4	2.5	-	3.3	6.0	17.8
7	5.0	2.3	2.5	-	3.9	4.9	18.6	3.2	2.1	2.2	-	3.2	7.9	18.6	3.5	2.7	2.7	-	3.8	5.0	17.7
8	3.5	2.7	2.7	-	4.0	5.3	18.2	3.5	1.9	1.9	-	3.2	6.7	17.2	3.0	2.4	1.5	-	2.7	3.9	13.5
9	3.7	2.7	2.5	-	3.4	5.7	18.0	3.3	2.5	2.3	-	3.3	5.2	16.6	3.3	2.6	1.9	-	3.5	5.8	17.1
10	3.8	1.3	-	-	2.4	4.2	11.7	3.4	1.9	1.5	-	3.1	6.3	16.2	4.4	1.8	-	-	3.7	6.7	16.6
11	2.7	2.1	-	-	3.7	3.1	11.6	2.6	1.6	1.3	-	2.0	6.0	13.5	3.5	2.2	1.3	-	2.7	5.1	14.8
12	2.2	1.0	-	-	2.1	1.6	6.9	3.3	1.6	1.1	-	2.5	3.3	11.8	3.5	1.7	-	-	3.7	5.7	14.6
			(25.6)							(27.8)							(21.2)				
Mean	3.9	2.4	2.8	-	3.7	5.21	17.4	3.7	2.3	2.3	-	3.4	6.6	18.4	3.7	2.3	2.1	-	3.4	6.0	17.2

C = cotyledons   U = unifoliate leaf   L1 = 1st trifoliate leaf   rm = remainder of top   Rt = root

Analysis of Variance of Total

	d.f.	S.S.	M.S.	V.R.
Total	35	464.29		
Tr.	2	9.82	4.91	-
Res.	33	454.47	13.772	

Analysis of Variance of Tops

	d.f.	S.S.	M.S.	V.R.
Total	35	216.80		
Tr.	2	5.71	2.855	-
Res.	33	211.09	6.3967	

Analysis of Variance of Roots

	d.f.	S.S.	M.S.	V.R.
Total	35	97.31		
Tr.	2	12.34	6.17	2.40 N.S.
Res.	33	84.97	2.5748	

Analysis of Variance of Ll.

	d.f.	S.S.	M.S.	V.R.
Total	30	14.52		
Tr.	2	2.65	1.33	3.14 N.S.
Res.	28	11.87	.4239	

Table 62(a)

Analysis of the early differences in dry weight of individual plants.

(1) Harvest 2 - 27 days from sowing.

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	44.2	42.0	35.4
	39.1	40.7	34.6
	38.2	37.5	33.0
	35.8	37.2	32.3
	34.4	33.7	28.4
	33.0	30.3	28.1
	28.0	29.4	27.9
	26.5	26.9	26.3
	24.3	24.8	25.9
	20.7	24.0	24.7
	33.9	22.8	24.5
	26.4	18.2	17.9
Total	384.5	367.5	339.0

Grand Total 1091.0

	df	S.S.	M.S.	V.R.	
Total	35	1528.62			
Tr.	2	88.10	44.05	1.01	N.S.
Res.	33	1440.52	43.652		

Table 62(a)

(ii) Harvest 3 - 34 days from sowing

Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
66.8	58.7	60.3
60.6	52.7	53.6
58.6	52.6	50.9
58.5	50.6	47.3
58.1	49.3	43.2
55.2	47.7	43.0
51.9*	46.3	40.3
51.7	45.7	37.2
49.9	42.9	34.7
41.6	40.6	33.8
35.9	39.0	36.7
33.6	31.4	22.6
Total 622.4	557.5	503.6

Grand Total 1683.5

	df	S.S.	M.S.	V.R.
Total	34	3439.58		
Tr.	2	589.74	294.87	3.31^{x}
Res.	32	2849.84	89.057	

Weighted L.S.D. on total data

4 v 16 $= \sqrt{\frac{113.65}{11} + \frac{53.028}{11}} \times t_{10} = \sqrt{10.332 + 4.821} \times t_{10} = \sqrt{15.153} \times t_{10}$

$= 3.8927 \times 2.228 = 8.67$
$\times 3.169 = 12.34$
$\times 4.587 = 17.86$

4 v 36 $= \sqrt{\frac{113.65}{11} + \frac{102.74}{11}} \times t_{10} = \sqrt{10.332 + 9.340} \times t_{10} = \sqrt{19.672} \times t_{10}$

$= 4.4353 \times 2.228 = 9.88$
$\times 3.169 = 14.06$
$\times 4.587 = 20.34$

16 x 36 $= \sqrt{\frac{53.028}{11} + \frac{102.74}{11}} \times t_{10} = \sqrt{4.821 + 9.340} \times t_{10} = \sqrt{14.161} \times t_{10}$

$= 3.7630 \times 2.228 = 8.38$
$\times 3.169 = 11.92$
$\times 4.587 = 17.26$

* estimated value (mean)

Table 62(a)

(iii) Harvest 4 - 41 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	98.8	107.8	73.0
	98.4	99.1	71.8
	98.2	95.0	64.9
	97.9	90.2	63.8
	96.7	81.9	60.4
	95.4	76.7	60.1
	93.7	74.9	56.5
	87.0	71.1	52.6
	82.7	62.6	52.6
	81.2	54.4	52.0
	71.1	53.9	50.2
	67.3	43.0	45.2
Total	1068.4	910.6	703.1

Grand Total 2682.1

	df	S.S.	M.S.	V.R.
Total	35	12176.17		
Tr.	2	5594.48	2797.24	14.02^{xxx}
Res.	33	6581.69	199.45	

Weighted L.S.D. on total data

$$4 \text{ v } 16 = \sqrt{\frac{124.22}{12} + \frac{399.22}{12}} \times t_{11} = \sqrt{10.352 + 33.268} \times t_{11} = \sqrt{43.620} \times t_{11}$$

$$= 6.6045 \times 2.201 = 14.54$$
$$\times 3.106 = 20.51$$
$$\times 4.437 = 29.30$$

$$4 \text{ v } 36 = \sqrt{\frac{124.22}{12} + \frac{74.901}{12}} \times t_{11} = \sqrt{10.352 + 6.242} \times t_{11} = \sqrt{16.594} \times t_{11}$$

$$= 4.0736 \times 2.201 = 8.97$$
$$\times 3.106 = 12.65$$
$$\times 4.437 = 18.07$$

$$16 \text{ v } 36 = \sqrt{\frac{399.22}{12} + \frac{74.901}{12}} \times t_{11} = \sqrt{33.268 + 6.242} \times t_{11} = \sqrt{39.510} \times t_{11}$$

$$= 6.2857 \times 2.201 = 13.83$$
$$\times 3.106 = 19.52$$
$$\times 4.437 = 27.89$$

Table 62(b)

(i) Harvest 2 - 27 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	29.1	27.0	25.3
	26.5	27.6	24.0
	24.7	24.6	22.2
	24.5	23.9	21.6
	23.1	23.7	19.1
	21.6	20.7	20.0
	22.7	21.4	19.4
	18.9	19.0	19.0
	22.2	17.3	18.5
	18.8	15.7	17.5
	17.2	17.9	16.9
	14.9	12.5	12.7
Total	264.2	251.3	236.2

	df	S.S.	M.S.	V.R.
Total	35	572.06		
Tr.	2	32.74	16.37	1.00 N.S.
Error	33	539.32	16.343	

Table 62(b)

(ii) Harvest 3 - 34 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	41.9	41.9	42.7
	40.4	37.2	36.5
	37.1	38.9	37.4
	37.5	37.1	34.7
	42.5	34.3	31.9
	37.8	33.9	32.0
	35.4	31.9	30.2
	38.0	32.1	27.7
	34.7	28.5	26.1
	28.4	27.1	26.0
	26.1	26.7	24.7
	24.7	21.9	17.9
Total	424.5	391.5	367.8

	df	S.S.	M.S.	V.R.
Total	34	1386.33		
Tr	2	135.16	67.58	1.73 N.S.
Error	32	1251.17	39.099	

Table 62(b)

(iii) Harvest 4 - 41 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	75.1	82.0	57.3
	67.6	74.2	51.5
	71.0	71.5	49.8
	68.2	67.5	50.1
	69.3	59.8	45.0
	66.5	58.3	46.2
	66.7	53.9	40.6
	60.2	52.6	40.1
	61.3	44.6	38.7
	58.7	42.3	38.7
	52.2	41.6	38.4
	47.7	32.9	31.8
Total	764.5	681.2	528.2

	df	S.S.	M.S.	V.R.
Total	35	6132.20		
Tr	2	2394.05	1197.03	10.57^{xxx}
Error	33	3738.15	113.28	

Weighted L.S.D. between treatments.

$$4 \text{ v } 16 = \sqrt{\frac{63.470}{12} + \frac{224.27}{12}} \times t_{11} = \sqrt{5.2892 + 18.6892} \times t_{11} = \sqrt{23.9784} \times t_{11}$$

$= 4.8968 \times t_{11}$

$4.8968 \times 2.201 = 10.78$ 5%

$\times 3.106 = 15.21$ 1%

$\times 4.437 = 21.73$ .1%

$$4 \text{ v } 36 = \sqrt{\frac{63.470}{12} + \frac{52.089}{12}} \times t_{11} = \sqrt{5.2892 + 4.3407} \times t_{11} = \sqrt{9.6299} \times t_{11}$$

$= 3.1031 \times 2.201 = 6.83$

$\times 3.106 = 9.64$

$\times 4.437 = 13.77$

$$36 \text{ v } 16 = \sqrt{\frac{224.27}{12} + \frac{52.089}{12}} \times t_{11} = \sqrt{18.6892 + 4.3407} \times t_{11} = \sqrt{23.0299} \times t_{11}$$

$= 4.7989 \times 2.201 = 10.56$

$\times 3.106 = 14.91$

$\times 4.437 = 21.29$

Table 62(c)

(i) Harvest 2 - 27 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	15.1	15.0	10.1
	12.6	13.1	10.6
	13.5	12.9	10.8
	11.3	13.3	10.7
	11.3	10.0	9.3
	12.3	9.6	8.1
	10.3	8.0	8.5
	9.1	7.9	7.3
	4.3	7.5	7.4
	7.6	8.3	7.2
	7.1	4.9	7.6
	5.8	5.7	5.2
Total	120.3	116.2	102.8

	df	S.S.	M.S.	V.R.	
Total	35	281.65			
Tr.	2	13.96	6.98	-	N.S.
Error	33	267.69	8.1118		

Table 62(c)

(ii) Harvest 3 - 34 days from sowing

Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
24.9	16.8	17.6
20.2	15.5	17.1
21.5	13.7	13.5
21.0	13.5	12.6
15.6	15.0	11.3
17.4	13.8	11.0
16.5	14.4	10.1
13.7	13.6	9.5
15.2	14.4	10.6
13.2	13.5	8.7
9.8	12.3	9.1
8.9	9.5	4.7
Total 197.9	166.0	135.8

	df	S.S.	M.S.	V.R.
Total	34	590.20		
Tr.	2	160.73	80.37	5.99^{xx}
Error	32	429.47	13.421	

Weighted L.S.D. between treatments.

4 v 16 = $\sqrt{\frac{25.42}{11} + \frac{3.183}{11}} \times t_{10} = \sqrt{2.311 + .289} \times t_{10} = \sqrt{2.600} \times t_{10}$

= 1.613 x 2.228 = 3.59
x 3.169 = 5.11
x 4.587 = 7.40

4 v 36 = $\sqrt{\frac{25.42}{11} + \frac{12.753}{11}} \times t_{10} = \sqrt{2.311 + 1.159} \times t_{10} = \sqrt{3.470} \times t_{10}$

= 1.863 x 2.228 = 4.15
3.169 = 5.90
4.587 = 8.55

16 v 36 = $\sqrt{\frac{3.183}{11} + \frac{12.753}{11}} \times t_{10} = \sqrt{.2894 + 1.1594} \times t_{10} = \sqrt{1.4488} \times t_{10}$

= 1.2036 x 2.228 = 2.68
x 3.169 = 3.81
x 4.587 = 5.52

Table 62(c)

(iii) Harvest 4 - 41 days from sowing

	Density 4 plants per dm^2	Density 16 plants per dm^2	Density 36 plants per dm^2
	23.7	25.8	15.7
	30.8	24.9	20.3
	27.2	23.5	15.1
	29.7	22.7	13.7
	27.4	22.1	15.4
	28.9	18.4	13.9
	27.0	21.0	15.9
	26.8	18.5	12.5
	21.4	18.0	13.9
	22.5	12.1	13.3
	18.9	12.3	11.8
	19.6	10.1	13.4
Total	303.9	229.4	174.9

	df	S.S.	M.S.	V.R.
Total	35	1228.91		
Tr.	2	698.93	349.47	21.76^{xxx}
Error	33	529.98	16.060	

Weighted L.S.D. between treatments.

4 v 16 $= \sqrt{\frac{15.889}{12} + \frac{27.433}{12}} \times t_{11} = \sqrt{1.3241 + 2.2861} \times t_{11} = \sqrt{3.6102} \times t_{11}$

$= 1.9001 \times 2.201 = 4.18$
$\times 3.106 = 5.90$
$\times 4.437 = 8.43$

4 v 36 $= \sqrt{\frac{15.889}{12} + \frac{4.858}{12}} \times t_{11} = \sqrt{1.3241 + .4048} \times t_{11} = \sqrt{1.7289} \times t_{11}$

$= 1.3148 \times 2.201 = 2.89$
$\times 3.106 = 4.08$
$\times 4.437 = 5.83$

16 v 36 $= \sqrt{\frac{27.433}{12} + \frac{4.858}{12}} \times t_{11} = \sqrt{2.2861 + .4048} \times t_{11} = \sqrt{2.6909} \times t_{11}$

$= 1.6404 \times 2.201 = 3.61$
$\times 3.106 = 5.10$
$\times 4.437 = 7.28$

Table 62(d)

Dry Weight of Leaf 1 (mg) at 27 days

Sample No.	4 plants per dm^2	16 plants per dm^2	36 plants per dm^2
1	5.7	4.4	4.1
2	5.8	5.0	4.7
3	4.5	3.1	4.4
4	4.3	4.8	5.3
5	4.9	5.7	4.8
6	6.6	5.7	5.0
7	5.3	5.0	4.8
8	4.9	6.5	5.9
9	5.7	3.6	5.1
10	5.5	3.9	2.9
11	3.1	6.6	5.0
12	6.3	5.9	6.0
Total	62.6	60.2	58.0
Mean	5.22	5.02	4.83

Analysis of Variance

	df	SS	MS	VR
Total	35	32.00		
Tr	2	.88	.440	-
Res.	33	31.12	.9430	-

Table 63(a)

Density 4 plants per dm^2
Weight of dry matter of entire plants including roots (mg per plant).

Days from sowing	20	27	34	41	48	55	62	69	76
	24.4	44.2	66.8	98.8	178.6	229.2	334.0	473.6	495.9
	21.1	39.1	60.6	98.4	166.9	219.1	282.5	443.8	484.1
	20.7	38.2	58.6	98.2	162.9	218.3	270.7	406.3	402.0
	19.4	35.8	58.5	97.9	148.8	217.9	253.6	373.5	367.1
	19.3	34.4	58.1	96.7	146.7	216.5	252.8	328.6	362.5
	18.7	33.9	55.2	95.4	144.4	207.6	183.9	305.7	322.0
	18.6	33.0	51.9	93.7	143.4	200.7			
	18.2	28.0	51.7	87.0	141.4	192.5			
	18.0	26.5	49.9	82.7	138.1	190.8			
	11.7	26.4	41.6	81.2	136.5	159.0			
	11.6	24.3	35.9	71.1	131.2	150.2			
	6.9	20.7	33.6	67.3	128.9	106.8			
Total	208.6	384.5	622.4	1068.4	1767.8	2308.6	1577.5	2331.5	2433.6
Mean	17.4	32.0	51.9	89.0	147.3	192.4	262.9	388.6	405.6
U.S.S.	3887.86	12847.09	33418.30	96489.62	262893.70	458631.42	426680.75	927267.79	1011726.28
C.F.	3626.16	12320.02	32281.81	95123.21	260426.40	444136.16	414751.04	905982.04	987068.60
S.S.	261.70	527.07	1136.49	1366.41	2467.30	14495.26	11929.71	21285.75	24657.68
Variance	23.791	47.915	113.65	124.22	224.30	1317.75	2385.94	4257.15	4931.54
S.D.	4.8777	6.9221	10.660	11.146	14.976	36.299	48.846	65.247	70.225
Coefficient of variation	0.280	0.216	0.205	0.125	0.102	0.189	0.186	0.168	0.173

Days from sowing	83	90	104	118	132	146	160
	639.7	901.5	1306.5	1874.6	2658.1	2903.5	2995.6
	626.8	827.3	1171.8	1625.1	2284.7	2640.7	2695.3
	548.0	711.2	1154.0	1512.1	2209.3	2581.4	2439.3
	522.8	709.4	1075.2	1385.4	2134.1	2293.7	1617.1
	496.3	602.0	973.5	1287.8	1943.7	2221.1	1613.5
	476.6	475.4	858.6	1217.1	1689.8	1957.3	1316.4
Total	3310.2	4226.8	6539.6	8902.1	12919.7	14597.7	12677.2
Mean	551.7	704.5	1089.9	1483.7	2153.3	2432.9	2112.9
U.S.S.	1849179.42	3094590.50	7252724.74	13500615.99	28354132.73	36092602.89	29139749.56
C.F.	1826237.34	2977639.71	7127728.03	13207897.40	27819774.68	35515474.21	26785233.31
S.S.	22942.08	116950.79	124996.71	292718.59	534358.05	577128.68	2354516.25
Variance	4588.42	23390.16	24999.34	58543.72	106871.61	115425.74	470903.25
S.D.	67.738	152.93	158.11	241.96	326.92	339.75	686.23
Coefficient of variation	0.123	0.217	0.145	0.163	0.152	0.140	0.323

Table 63(b)

Density 16 plants per dm^2
Weight of dry matter of entire plants including roots (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	25.9	42.0	58.7	107.8	134.8	191.8	199.2	279.9
	21.0	40.7	52.7	99.1	124.6	172.2	194.2	270.8
	20.9	37.5	52.6	95.0	118.7	154.6	189.3	260.1
	20.0	37.2	50.6	90.2	118.4	154.3	170.5	244.5
	19.6	33.7	49.3	81.9	111.5	146.3	117.0	185.6
	19.1	30.3	47.7	76.7	110.5	140.6	102.4	179.6
	18.6	29.4	46.3	74.9	106.6	136.0		
	17.2	26.9	45.7	71.1	105.6	134.7		
	16.6	24.8	42.9	62.6	99.7	132.2		
	16.2	24.0	40.6	54.4	97.6	128.3		
	13.5	22.8	39.0	53.9	95.6	106.4		
	11.8	18.2	31.4	43.0	75.4	102.4		
Total	220.4	367.5	557.5	910.6	1299.0	1699.8	972.6	1419.9
Mean	18.4	30.6	46.5	75.9	108.3	141.7	162.1	236.7
U.S.S.	4198.88	11894.45	26483.79	73490.74	143252.24	247706.32	166473.78	345590.07
C.F.	4048.01	11254.69	25900.52	69099.36	140616.75	240776.67	157658.46	336019.33
S.S.	150.87	639.76	583.27	4391.38	2635.49	6929.65	8815.32	9570.74
Variance	13.715	58.160	53.025	399.22	239.50	629.97	1763.06	1914.15
S.D.	3.7035	7.6262	7.2818	19.981	15.476	25.099	41.989	43.750
Coefficient of variation	0.201	0.249	0.157	0.263	0.143	0.177	0.259	0.185

Days from sowing	76	83	90	104	118	132	146	160
	308.7	327.9	351.1	402.5	590.7	564.5	936.7	1402.3
	306.6	297.4	304.7	392.0	433.8	561.2	913.5	844.4
	296.4	289.1	282.7	291.1	402.5	459.3	889.7	680.5
	272.0	278.8	265.7	269.3	329.9	408.7	882.3	465.4
	205.5	262.3	238.7	192.4	321.0	218.3	865.5	71.1
	189.0	240.3	200.0	127.4	198.7	150.7	407.8	0
Total	1578.2	1695.8	1642.9	1674.7	2276.6	2362.7	4895.5	3463.7
Mean	263.0	282.6	273.8	279.1	379.4	393.8	815.9	577.3
U.S.S.	429087.46	483818.80	463606.77	526180.47	950471.88	1081963.25	4197299.61	3364189.27
C.F.	415119.21	479289.61	449853.40	467436.68	863817.93	930391.88	3994320.04	1999536.28
S.S.	13968.25	4529.19	13753.37	58743.79	86653.95	151571.37	202979.57	1364652.99
Variance	2793.65	905.84	2750.67	11748.76	17330.79	30314.27	40595.91	399907.26
S.D.	52.856	30.097	52.447	108.40	131.64	174.11	201.48	632.39
Coefficient of variation	0.201	0.107	0.192	0.388	0.347	0.442	0.247	1.095

Table 63(c)

Density 36 plants per dm^2
Weight of dry matter of entire plants including roots (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	19.8	35.4	60.3	73.0	99.6	105.8	111.8	156.6
	19.1	34.6	53.6	71.8	94.3	104.4	103.2	130.7
	18.8	33.0	50.9	64.9	85.5	103.1	93.3	123.5
	18.4	32.3	47.3	63.8	84.5	94.6	85.4	123.3
	17.8	28.4	43.2	60.4	82.7	93.1	66.2	106.7
	17.8	28.1	43.0	60.1	80.9	88.7	65.5	85.7
	17.7	27.9	40.3	56.5	80.3	84.0		
	17.1	26.3	37.2	52.6	79.2	78.4		
	16.6	25.9	36.7	52.6	79.1	78.2		
	14.8	24.7	34.7	52.0	78.5	77.2		
	14.6	24.5	33.8	50.2	64.8	60.9		
	13.5	17.9	22.6	45.2	44.0	57.6		
Total	206.0	339.0	503.6	703.1	953.4	1026.0	525.4	726.5
Mean	17.2	28.3	42.0	58.6	79.5	85.5	87.6	121.1
U.S.S.	3578.24	9850.44	22264.50	42019.71	77922.08	90511.28	47820.22	90790.57
C.F.	3536.33	9576.75	21134.41	41195.80	75747.63	87723.00	46007.53	87967.04
S.S.	41.91	273.69	1130.09	823.91	2174.45	2788.28	1812.69	2823.53
Variance	3.810	24.881	102.74	74.901	434.89	557.66	362.54	564.71
S.D.	1.952	49.882	10.136	8.6546	20.854	23.615	19.040	23.764
Coefficient of variation	0.113	0.176	0.241	0.148	0.262	0.276	0.217	0.196

Days from sowing	76	83	90	104	118	132	146	160
	126.5	197.7	197.0	234.0	363.4	339.5	283.8	218.0
	123.7	192.1	182.3	215.6	288.3	274.1	161.1	151.5
	99.1	180.4	179.4	203.0	163.2	267.5	102.8	104.5
	79.5	150.9	172.8	133.6	142.0	130.9	71.4	56.8
	77.0	145.0	135.1	131.0	114.6	110.5	59.4	28.0
	68.2	92.1	115.1	81.2	64.2	62.4	30.0	21.1
Total	574.0	958.2	981.7	998.4	1135.7	1184.9	708.5	579.9
Mean	95.7	159.7	163.6	166.4	189.3	197.5	118.1	96.7
U.S.S.	58025.24	160810.08	165586.51	184051.76	279229.49	295186.13	126589.81	85851.95
C.F.	54912.67	153024.54	160622.48	166133.76	214969.08	233998.00	83662.04	56047.33
S.S.	3112.57	7785.54	4964.03	17918.00	64260.41	61188.13	42927.77	29804.62
Variance	622.51	1557.11	992.81	3583.60	12852.08	12237.63	8585.55	5960.92
S.D.	24.950	39.460	31.509	59.863	113.37	110.62	92.658	77.207
Coefficient of variation	0.261	0.247	0.193	0.360	0.599	0.560	0.785	0.798

Table 64(a)

Density 4 plants per dm^2
Weight of dry matter of tops (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	16.7	29.1	41.9	75.1	122.3	163.2	238.6	319.0
	14.7	26.5	40.4	67.6	114.2	151.4	179.0	291.7
	13.6	24.7	37.1	71.0	107.5	156.0	191.9	290.2
	14.6	24.5	37.5	68.2	99.8	155.2	171.2	260.8
	13.8	23.1	42.5	69.3	95.9	156.0	183.2	218.6
	12.5	22.7★	37.8 ★	66.5	96.1	149.7	129.5	206.9
	13.7	18.9	38.0	66.7	94.3	132.7		
	12.9	22.2	34.7	60.2	92.9	142.7		
	12.3	18.8	28.4	61.3	91.3	143.8		
	7.5	17.2	26.1	58.7	92.3	111.8		
	8.5	14.9★	24.7★	52.2	90.7	106.0		
	5.3	21.6	35.4	47.7	86.5	74.9		
Total	146.1	264.2	424.5	764.5	1183.8	1643.4	1093.4	1587.2
Mean	12.2	22.02	35.4	63.7	98.7	136.9	182.2	264.5
U.S.S.	1901.77	5996.20	15404.63	49403.19	118033.86	232721.60	205438.50	429676.14
C.F.	1778.76	5816.80	15016.69	48705.02	116781.87	225063.63	199253.93	419867.31
S.S.	123.01	179.40	387.94	698.17	1251.99	7657.97	6184.57	9808.83
Variance	11.183	16.309	38.79	63.470	113.82	696.18	1236.91	1961.77
S.D.	3.344	4.038	6.228	7.967	10.668	26.385	35.169	44.292
Coefficient of variation	0.274	0.183	0.176	0.090	0.108	0.193	0.193	0.167

★ missing plant

Days from sowing	76	83	90	104	118	132	146	160
	370.9	498.0	729.7	1105.5	1631.0	2294.2	2572.0	2661.5
	362.3	495.1	664.4	987.6	1407.5	1957.4	2330.5	2382.1
	293.9	422.5	574.7	952.9	1302.1	1841.7	2345.8	2196.0
	273.9	409.5	575.5	905.7	1207.9	1863.0	2001.2	1416.2
	269.2	386.7	482.0	818.5	1109.4	1655.9	1990.5	1413.3
	247.3	367.9	390.9	718.6	1039.3	1457.6	1759.0	1166.6
Total	1817.5	2579.7	3417.2	5488.8	7697.2	11069.8	12999.0	11235.7
Mean	302.9	429.9	569.5	914.8	1282.9	1845.0	2166.5	1872.6
U.S.S.	563852.45	1124211.81	2020496.60	5112123.12	10106616.92	20823998.86	28610164.58	22944393.55
C.F.	550551.04	1109142.01	1946209.31	5021154.24	9874481.31	20423412.01	28162333.50	21040159.08
S.S.	13301.41	15069.80	74287.29	90968.88	232135.61	400586.85	447831.08	1904234.47
Variance	2660.28	3013.96	14857.46	18193.78	46427.12	80117.37	89566.22	380846.89
S.D.	51.578	54.899	121.90	134.88	215.48	283.05	299.28	617.13
Coefficient of variation	0.170	0.128	0.214	0.147	0.168	0.153	0.138	0.330

Table 64(b)

Density 16 plants per dm^2
Weight of dry matter of tops (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	15.1	27.0	41.9	82.0	95.6	130.7	161.5	227.7
	14.5	27.6	37.2	74.2	87.4	131.3	150.1	228.9
	13.0	24.6	38.9	71.5	82.2	121.8	147.3	211.3
	14.0	23.9	37.1	67.5	86.7	121.4	135.5	201.0
	12.6	23.7	34.3	59.8	82.8	113.8	86.5	157.5
	13.0	20.7	33.9	58.3	84.4	105.3	75.2	152.7
	10.7	21.4	31.9	53.9	79.0	107.4		
	10.5	19.0	32.1	52.6	79.0	105.8		
	11.4	17.3	28.5	44.6	77.0	100.2		
	9.9	15.7	27.1	42.3	72.1	98.7		
	7.5	17.9	26.7	41.6	74.9	83.6		
	8.5	12.5	21.9	32.9	57.2	78.8		
Total	140.7	251.3	391.5	681.2	958.3	1298.8	756.1	1179.1
Mean	11.7	20.9	32.6	56.8	79.9	108.2	126.0	196.5
U.S.S.	1712.23	5498.71	13141.95	41136.46	77522.31	143642.44	101807.09	237414.73
C.F.	1649.71	5262.64	12772.69	38669.45	76528.24	140573.45	95281.20	231712.80
S.S.	62.52	236.07	369.26	2467.01	994.07	3068.99	6525.89	5701.93
Variance	5.684	21.461	33.569	224.27	90.370	279.00	1305.18	1140.39
S.D.	2.384	4.633	5.794	14.975	9.506	16.703	36.127	33.770
Coefficient of variation	0.204	0.222	0.178	0.264	0.119	0.154	0.287	0.172

Days from sowing	76	83	90	104	118	132	146	160
	253.8	283.7	306.0	353.0	518.1	490.0	828.6	1245.7
	257.4	256.7	258.8	336.1	377.0	478.8	808.8	770.0
	251.1	242.9	238.0	240.2	346.7	399.4	793.0	606.2
	233.3	229.6	226.4	226.8	283.9	356.4	774.0	404.9
	161.2	221.5	202.4	160.5	281.5	184.4	764.4	48.2
	165.0	200.4	168.2	108.1	170.0	124.2	363.3	0
Total	1321.8	1434.8	1399.8	1424.7	1977.2	2033.2	4332.1	3075.0
Mean	220.3	239.1	233.3	237.5	329.5	338.9	722.0	512.5
U.S.S.	301359.74	347319.56	337771.40	384152.35	719498.96	805319.76	3284954.65	2678414.18
C.F.	291192.54	343108.51	326573.34	338295.01	651553.31	688983.71	3127848.40	1575937.50
S.S.	10167.20	04211.05	11198.06	45857.34	62945.65	116336.05	157106.25	1102476.68
Variance	2033.44	842.21	2239.61	9171.47	13589.13	23267.21	31421.23	220495.34
S.D.	45.093	29.020	47.324	95.768	116.57	152.54	177.26	469.57
Coefficient of variation	0.205	0.121	0.203	0.403	0.354	0.450	0.246	0.916

Table 64(c)

Density 36 plants per cm^2
Weight of dry matter of tops (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	10.6	25.3	42.7	57.3	79.9	87.1	89.0	126.3
	13.3	24.0	36.5	51.5	72.8	86.5	83.7	111.1
	13.0	22.2	37.4	49.8	65.1	82.6	75.8	105.1
	12.9	21.6	34.7	50.1	66.4	77.5	68.4	105.2
	10.7	19.1	31.9	45.0	64.3	77.3	51.2	91.4
	11.8	20.0	32.0	46.2	64.4	72.1	52.4	69.3
	12.7	19.4	30.2	40.6	62.3	70.5		
	11.3	19.0	27.7	40.1	63.6	63.5		
	9.9	18.5	26.1	38.7	64.6	65.3		
	9.7	17.5	26.0	38.7	62.8	62.9		
	8.9	16.9	24.7	38.4	50.9	49.9		
	9.6	12.7	17.9	31.8	34.3	47.9		
Total	134.4	236.2	367.8	528.2	751.4	843.1	420.5	608.4
Mean	11.2	19.7	30.7	44.0	62.6	70.3	70.1	101.4
U.S.S.	1530.84	4773.06	11767.04	23822.58	48423.22	61078.79	30718.09	63564.40
C.F.	1505.28	4649.20	11273.07	23249.60	47050.16	59234.80	29470.04	61691.76
S.S.	25.56	123.86	493.97	572.98	1373.06	1843.99	1248.05	1872.64
Variance	2.324	11.260	44.906	52.089	124.82	167.64	249.61	374.53
S.D.	1.525	3.355	6.701	7.217	11.173	12.948	15.799	19.353
Coefficient of variation	0.136	0.170	0.218	0.164	0.178	0.184	0.225	0.191

Days from sowing	76	83	90	104	118	132	146	160
	106.5	171.9	167.7	203.7	323.6	284.4	243.2	218.0
	107.2	166.5	159.6	186.9	250.9	243.7	130.9	137.1
	85.8	153.2	157.0	185.0	144.7	230.5	93.4	94.5
	68.0	128.7	145.0	114.5	120.2	111.4	51.3	56.7
	61.9	129.6	116.1	115.0	97.4	92.1	50.8	28.9
	57.2	77.0	100.4	65.0	51.4	46.4	22.8	21.1
Total	486.6	826.9	845.8	870.1	988.2	1008.5	592.4	556.3
Mean	81.1	137.8	141.0	145.0	164.7	168.1	98.7	92.7
U.S.S.	41923.18	120030.95	122828.82	141210.55	215182.62	216448.63	90736.78	79745.97
C.F.	39463.26	113960.60	119229.60	126179.00	162756.54	169512.04	58489.63	51578.28
S.S.	2459.92	6070.35	3599.22	15031.55	52426.08	46936.59	32247.15	28167.69
Variance	491.98	1214.07	719.84	3006.31	10485.22	9387.32	6449.43	5633.54
S.D.	22.181	34.843	26.830	54.830	102.39	96.888	80.309	75.056
Coefficient of variation	0.274	0.253	0.190	0.378	0.622	0.576	0.814	0.810

Table 65(a)

Density 4 plants per dm^2
Weight of dry matter of roots (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	7.7	15.1	24.9	23.7	56.3	66.0	95.4	154.6
	6.4	12.6	20.2	30.8	52.7	67.7	103.5	152.1
	7.1	13.5	21.5	27.2	55.4	62.3	78.8	116.1
	4.8	11.3	21.0	29.7	49.0	62.7	82.4	112.7
	5.5	11.3	15.6	27.4	50.8	60.5	69.6	110.0
	6.2	12.3	17.4	28.9	48.3	57.9	54.4	98.8
	4.9	10.3	16.5	27.0	49.1	68.0		
	5.3	9.1	13.7	26.8	48.5	49.8		
	5.7	4.3	15.2	21.4	46.8	47.0		
	4.2	7.6	13.2	22.5	44.2	47.2		
	3.1	7.1	9.8	18.9	40.5	44.2		
	1.6	5.8	8.9	19.6	42.4	31.9		
Total	62.5	120.3	197.9	303.9	584.0	665.2	484.1	744.3
Mean	5.21	10.3	16.5	25.3	48.7	55.4	80.7	124.1
U.S.S.	356.79	1324.89	3517.89	7871.05	28675.62	38276.66	40616.13	95077.51
C.F.	325.52	1206.01	3263.70	7696.27	28421.33	36874.25	39058.80	92330.41
S.S.	31.27	118.88	254.19	174.78	254.29	1402.41	1557.33	2747.10
Variance	2.843	10.807	25.42	15.889	23.117	127.49	311.47	549.42
S.D.	1.686	3.287	5.042	3.986	4.808	11.291	17.648	23.430
Coefficient of variation	0.324	0.328	0.306	0.158	0.099	0.204	0.219	0.189

Days from sowing	76	83	90	104	118	132	146	160
	125.0	141.7	171.8	201.0	243.6	363.9	331.5	334.1
	121.8	131.7	162.9	184.2	217.6	327.3	310.2	313.2
	108.1	125.5	136.5	201.1	210.0	367.6	235.6	243.3
	93.2	113.3	133.9	169.5	177.5	271.1	292.5	200.9
	93.3	109.6	120.0	155.0	178.4	287.8	230.6	200.2
	74.7	108.7	84.5	140.0	177.8	232.2	198.3	149.8
Total	616.1	730.5	809.6	1050.8	1204.9	1849.9	1598.7	1441.5
Mean	102.7	121.7	134.9	175.1	200.8	308.3	266.5	240.3
U.S.S	65117.07	89838.77	114153.36	187127.10	245736.37	584919.15	439679.15	371792.83
C.F.	63263.20	88938.37	109242.03	184030.11	241964.00	570355.00	425973.61	346320.37
S.S.	1853.87	900.40	4911.33	3096.99	3772.37	14564.15	13705.54	25472.46
Variance	370.77	180.08	982.27	619.40	754.47	2912.83	2741.11	5094.49
S.D.	19.255	13.419	31.341	24.888	27.467	55.969	52.356	71.375
Coefficient of variation	0.187	0.110	0.232	0.142	0.137	0.175	0.196	0.297

Table 65(b)

Density 16 plants per dm^2
Weight of dry matter of roots (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	10.8	15.0	16.8	25.8	39.2	61.1	37.7	52.2
	6.5	13.1	15.5	24.9	37.2	40.9	44.1	41.9
	7.9	12.9	13.7	23.5	36.5	32.8	42.0	48.8
	6.0	13.3	13.5	22.7	31.7	32.9	35.0	43.5
	7.0	10.0	15.0	22.1	28.7	32.5	30.5	26.9
	6.1	9.6	13.8	18.4	26.1	35.3	27.2	27.5
	7.9	8.0	14.4	21.0	27.6	28.6		
	6.7	7.9	13.6	18.5	26.6	28.9		
	5.2	7.5	14.4	18.0	22.7	32.0		
	6.3	8.3	13.5	12.1	25.5	29.6		
	6.0	4.9	12.3	12.3	20.7	22.8		
	3.3	5.7	9.5	10.1	18.2	23.6		
Total	79.7	116.2	166.0	229.4	340.7	401.0	216.5	240.8
Mean	6.6	9.7	13.8	19.1	28.4	33.4	36.1	40.1
U.S.S.	564.43	1240.12	2331.34	4687.12	10157.11	14496.74	8025.19	10234.00
C.F.	529.34	1125.20	2296.33	4385.36	9673.04	13400.08	7812.04	9664.11
S.S.	35.09	114.92	35.01	301.76	484.07	1096.66	213.15	569.89
Variance	3.190	10.447	3.183	27.433	44.006	99.696	42.630	113.98
S.D.	1.786	3.232	1.784	5.238	6.634	9.985	6.529	10.676
Coefficient of variation	0.271	0.333	0.129	0.274	0.234	0.299	0.181	0.266

Days from sowing	76	83	90	104	118	132	146	160
	54.9	44.2	45.1	49.5	72.6	74.5	108.1	156.6
	49.2	40.7	45.9	55.9	56.8	82.4	104.7	74.4
	45.3	46.2	44.7	50.9	55.8	59.9	96.7	74.3
	38.7	49.2	39.3	42.5	46.0	52.3	108.3	60.5
	44.3	40.8	36.3	31.9	39.5	33.9	101.1	22.9
	24.0	39.9	31.8	19.3	28.7	26.5	44.5	0
Total	256.4	261.0	243.1	250.0	299.4	329.5	563.4	388.7
Mean	42.7	43.5	40.5	41.7	49.9	54.9	93.9	64.8
U.S.S.	11522.92	11421.86	10012.33	11362.22	16110.58	20514.77	55928.94	39764.07
C.F.	10956.83	11353.50	9849.60	10416.67	14940.06	18095.04	52903.26	25181.28
S.S.	566.09	068.36	162.73	945.55	1170.52	2419.73	3025.68	14582.79
Variance	113.22	13.672	32.546	189.11	234.10	483.95	605.14	2916.56
S.D.	10.640	3.698	5.705	13.752	15.300	21.998	24.600	54.004
Coefficient of variation	0.249	0.085	0.141	0.330	0.307	0.401	0.262	0.833

Table 65(c)

Density 36 plants per dm^2
Weight of dry matter of roots (mg per plant)

Days from sowing	20	27	34	41	48	55	62	69
	9.2	10.1	17.6	15.7	19.7	18.7	22.8	30.3
	5.8	10.6	17.1	20.3	21.5	17.9	19.5	19.6
	5.8	10.8	13.5	15.1	20.4	20.5	17.5	18.4
	5.5	10.7	12.6	13.7	18.1	17.1	17.0	18.1
	7.1	9.3	11.3	15.4	18.4	15.8	15.0	15.3
	6.0	8.1	11.0	13.9	16.5	16.6	13.1	16.4
	5.0	8.5	10.1	15.9	18.0	13.5		
	5.8	7.3	9.5	12.5	15.6	14.9		
	6.7	7.4	10.6	13.9	14.5	12.9		
	5.1	7.2	8.7	13.3	15.7	14.3		
	5.7	7.6	9.1	11.8	13.9	11.0		
	3.9	5.2	4.7	13.4	9.7	9.7		
Total	71.6	102.8	135.8	174.9	202.0	182.9	104.9	118.1
Mean	6.0	8.6	11.3	14.6	16.8	15.2	17.5	19.7
U.S.S.	445.82	914.54	1677.08	2602.61	3516.32	2898.21	1891.95	2471.47
C.F.	427.21	880.65	1536.80	2549.17	3400.33	2787.70	1834.00	2324.60
S.S.	18.61	33.89	140.28	53.44	115.99	110.51	57.95	146.87
Variance	1.692	3.081	12.753	4.858	10.545	10.046	11.590	29.374
S.D.	1.301	1.755	3.571	2.204	3.247	3.169	3.405	5.420
Coefficient of variation	0.217	0.204	0.316	0.151	0.193	0.208	0.195	0.275

Days from sowing	76	83	90	104	118	132	146	160
	20.0	25.8	29.3	30.3	39.8	55.1	40.6	-
	16.5	25.6	22.7	28.7	37.4	30.4	30.2	18.4
	13.3	27.2	22.4	18.0	18.5	37.0	18.2	14.4
	11.5	22.2	27.8	19.1	21.8	19.5	20.1	-
	15.1	15.4	19.0	16.0	17.2	18.4	17.1	-
	11.0	15.1	14.7	16.2	12.8	16.0	14.3	-
Total	87.4	131.3	135.9	128.3	147.5	176.4	140.5	32.8
Mean	14.6	21.9	22.7	21.4	24.6	29.4	23.4	5.5
U.S.S.	1330.40	3018.85	3225.47	2949.03	4259.97	6303.98	3792.55	545.92
C.F.	1273.13	2873.28	3078.13	2743.48	3626.04	5186.16	3290.04	179.31
S.S.	57.27	145.57	147.34	205.55	633.93	1117.82	502.51	366.61
Variance	11.454	29.114	29.468	41.110	126.79	223.56	100.50	73.322
S.D.	3.384	5.396	5.428	6.412	11.260	14.952	10.024	8.563
Coefficient of variation	0.232	0.246	0.239	0.300	0.458	0.509	0.428	1.557

Table 66(a)

4 Plants per dm^2.

Dry Weight of Leaf Laminae (mg per lamina)
(The number of observations is shown in brackets)

DAYS FROM SOWING

Leaf Grouping	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	3.8 (12)	4.4 (12)	4.0 (11)	4.3 (12)	4.7 (12)	3.9 (12)	3.3 (6)	2.6 (6)	1.3 (4)	2.2 (4)						
U	2.4 (12)	3.4 (12)	3.7 (11)	4.4 (12)	5.1 (12)	4.5 (12)	4.6 (5)	3.5 (6)	2.6 (5)	2.7 (5)	2.2 (2)					
L1	2.8 (9)	5.2 (12)	7.6 (11)	10.3 (12)	11.9 (12)	11.9 (12)	11.8 (6)	10.9 (6)	7.9 (6)	6.6 (6)	4.3 (5)					
L2-3		3.1 (8)	4.1 (22)	8.8 (24)	11.7 (24)	14.5 (24)	13.7 (12)	15.5 (12)	12.3 (12)	11.4 (11)	9.1 (12)	6.4 (10)	4.9 (7)			
L4-8				2.8 (24)	3.9 (60)	6.3 (60)	8.3 (20)	9.2 (30)	8.8 (30)	8.3 (30)	6.8 (30)	4.7 (25)	4.2 (13)	3.8 (2)		
L9-16					1.7 (8)	2.3 (40)	4.0 (38)	5.1 (48)	6.7 (48)	7.3 (48)	7.2 (48)	7.1 (46)	5.8 (20)	4.6 (3)		
L17-29							1.9 (2)	2.6 (40)	3.6 (71)	6.3 (78)	7.4 (78)	9.5 (76)	8.9 (64)	10.5 (13)		
L30-35									1.4 (8)	3.8 (33)	8.2 (36)	14.9 (36)	19.7 (33)	13.9 (20)	17.1 (8)	
L36-44										1.9 (11)	4.8 (45)	12.0 (54)	22.8 (52)	23.4 (46)	24.5 (37)	
L45-57											2.6 (6)	8.1 (38)	12.3 (59)	31.4 (76)	40.3 (72)	25.9 (37)
L58-70													3.6 (3)	4.7 (56)	11.1 (78)	-

Table 66(b)

16 Plants per dm^2

Dry Weight of Leaf Laminae (mg per lamina)
(The number of observations is shown in brackets)

DAYS FROM SOWING

Leaf Grouping	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	3.7 (12)	3.9 (12)	3.8 (12)	3.4 (12)	3.2 (12)	2.2 (12)	1.6 (5)	1.6 (1)								
U	2.2 (12)	3.1 (12)	3.7 (12)	3.9 (11)	3.6 (12)	3.1 (12)	2.5 (6)	1.9 (5)	1.7 (6)	1.9 (2)						
L1-2	2.3 (12)	3.8 (23)	5.8 (24)	8.6 (24)	9.7 (24)	9.7 (24)	8.7 (12)	8.8 (12)	6.3 (14)	5.3 (9)	4.7 (3)					
L3-5			2.8 (12)	4.3 (33)	6.6 (36)	8.2 (36)	8.2 (18)	10.5 (18)	9.2 (21)	7.1 (17)	5.0 (13)	2.3 (2)				
L6-8				2.1 (2)	2.1 (34)	4.2 (36)	5.1 (18)	7.6 (18)	7.5 (21)	6.9 (18)	5.5 (17)	4.1 (11)				
L9-15					0.4 (1)	1.7 (44)	2.5 (35)	4.5 (49)	5.4 (47)	6.8 (42)	6.3 (41)	5.7 (29)	6.5 (23)			
L16-19							0.3 (1)	2.3 (8)	2.8 (19)	4.4 (24)	6.1 (22)	8.3 (21)	11.6 (23)	8.5 (10)		
L20-28									2.2 (6)	2.4 (9)	3.4 (26)	5.7 (31)	10.6 (39)	16.2 (37)	22.7 (25)	25.5 (31)
L29-39												3.8 (2)	1.4 (4)	4.1 (14)	15.5 (53)	10.9 (53)

Table 66(c)

36 Plants per dm^2

Dry Weight of Leaf Laminae (mg per lamina)
(The number of observations is shown in brackets).

DAYS FROM SOWING

Leaf Grouping	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	3.7 (12)	3.6 (12)	3.3 (12)	3.1 (12)	2.4 (12)	1.8 (12)	1.4 (6)	1.3 (6)								
U	2.3 (12)	3.1 (12)	3.2 (12)	3.3 (12)	3.0 (12)	2.5 (12)	2.0 (6)	1.2 (2)								
L1	2.1 (10)	4.8 (12)	6.5 (12)	7.4 (12)	8.3 (12)	7.0 (11)	6.0 (6)	6.0 (8)	3.8 (6)							
L2		2.2 (11)	5.1 (12)	6.9 (12)	9.2 (12)	8.7 (12)	7.4 (6)	8.1 (8)	4.7 (7)	4.1 (4)						
L3			2.7 (9)	5.3 (12)	7.6 (12)	9.1 (12)	8.4 (6)	10.0 (8)	8.2 (7)	6.3 (6)	5.5 (3)					
L4-6				1.8 (14)	2.9 (32)	4.0 (36)	4.4 (18)	6.5 (23)	5.8 (21)	6.7 (20)	4.9 (18)	4.3 (9)	3.8 (2)			
L7-10					0.8 (2)	1.3 (15)	1.5 (13)	3.0 (25)	2.9 (26)	5.0 (28)	5.6 (24)	6.3 (20)	6.8 (14)	5.0 (2)		
L11-12									1.4 (3)	2.8 (10)	5.6 (12)	6.8 (12)	7.6 (11)	9.1 (6)	4.1 (1)	
L13-16										2.0 (9)	3.2 (16)	5.5 (18)	12.2 (14)	9.4 (9)	5.4 (4)	
L17-24												3.4 (6)	6.4 (11)	7.3 (4)	5.4 (3)	3.1 (11)

Table 67(a)

Density 4 plants per dm^2 - Mean lamina area (cm^2 per lamina)

(The number of observations is shown in brackets)

Leaf Grouping	DAYS FROM SOWING															
	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
L1	1.17 (7)	2.13 (12)	3.27 (11)	3.64 (12)	3.82 (12)	4.14 (11)	3.72 (6)	4.05 (6)	3.73 (6)	3.64 (1)						
L2&3		0.84 (8)	1.29 (20)	3.01 (24)	3.89 (24)	4.57 (22)	4.19 (12)	4.82 (12)	4.27 (12)	4.56 (11)	4.04 (6)					
L4-8				0.90 (22)	1.10 (58)	2.47 (55)	2.98 (30)	3.31 (30)	3.54 (30)	3.31 (30)	3.55 (30)	3.31 (7)	2.78 (1)			
L9-16					0.45 (6)	0.70 (40)	1.12 (38)	2.22 (48)	4.43 (48)	3.19 (48)	3.55 (48)	2.99 (44)	4.52 (5)			
L17-29							0.64 (2)	0.84 (40)	1.49 (72)	3.08 (78)	3.69 (78)	4.16 (77)	4.73 (56)	5.98 (4)	3.50 (1)	-
L30-35									0.56 (8)	1.58 (33)	4.00 (36)	6.49 (36)	8.68 (33)	7.25 (19)	10.42 (6)	-
L36-44										0.73 (11)	2.34 (44)	6.29 (54)	9.50 (53)	11.16 (42)	12.19 (35)	13.75 (2)
L45-57											1.15 (6)	3.67 (37)	4.65 (59)	13.09 (77)	17.64 (81)	18.08 (25)
L58-70													1.36 (3)	2.13 (65)	5.48 (87)	

Table 67(b)

Density 16 plants per dm^2 - Mean lamina area (cm^2 per lamina)

(The number of observations is shown in brackets).

Leaf Grouping	DAYS FROM SOWING															
	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
L1 & 2	0.98 (11)	1.51 (23)	2.87 (24)	3.72 (24)	3.73 (24)	3.76 (24)	4.25 (12)	4.65 (12)	3.78 (10)	-	-	-				
L3 - 5			0.96 (10)	1.75 (30)	2.72 (36)	3.27 (36)	3.62 (18)	4.86 (18)	4.81 (21)	4.26 (15)	2.87 (5)	-				
L6 - 8				0.71 (1)	0.71 (31)	1.55 (36)	2.05 (18)	3.98 (18)	3.80 (21)	3.58 (18)	3.61 (16)	3.02 (9)				
L9 - 15						0.61 (44)	0.85 (42)	1.92 (42)	2.85 (46)	3.00 (42)	3.27 (40)	3.42 (32)	3.77 (15)			
L16-19							0.39 (1)	0.72 (10)	1.26 (19)	2.21 (24)	3.21 (22)	4.61 (21)	5.48 (23)	5.09 (6)		
L20-28									0.88 (6)	0.93 (9)	1.85 (22)	2.66 (31)	3.33 (39)	7.98 (37)	11.25 (21)	13.36 (31)
L29-39													0.47 (4)	1.43 (14)	7.27 (52)	5.42 (53)
L40-43															0.45 (3)	0.71 (4)

Table 67(c)

Density 36 plants per dm^2 - Mean lamina area (cm^2 per lamina)

(The number of observations is shown in brackets)

Leaf Grouping		DAYS FROM SOWING														
	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
L1	1.28 (7)	2.28 (12)	3.51 (12)	3.69 (12)	3.78 (12)	3.49 (11)	3.38 (6)	4.45 (7)	2.92 (1)							
L2		0.72 (11)	2.20 (12)	2.98 (12)	4.10 (12)	3.85 (12)	3.56 (6)	4.73 (7)	3.15 (5)	4.10 (1)						
L3			0.84 (8)	2.00 (12)	3.85 (12)	4.01 (12)	3.62 (6)	4.78 (7)	4.51 (7)	4.31 (4)	4.48 (2)					
L4-6				0.82 (5)	1.13 (32)	1.81 (36)	1.97 (18)	3.16 (21)	3.24 (21)	3.65 (20)	3.31 (17)	3.86 (6)	2.93 (2)			
L7-10					0.43 (2)	0.62 (14)	0.59 (13)	1.33 (24)	1.50 (26)	2.81 (28)	3.40 (24)	3.29 (17)	3.75 (14)	4.51 (1)		
L11-12								0.79 (2)	0.65 (3)	1.64 (10)	3.17 (12)	3.64 (12)	4.01 (11)	4.72 (6)	3.80 (1)	
L13-16										0.93 (9)	1.31 (14)	2.69 (19)	6.17 (14)	5.07 (9)	4.52 (4)	6.49 (3)
L17-24												2.03 (6)	3.63 (11)	4.27 (4)	4.37 (3)	5.21 (4)

Table 68(a)

4 Plants per dm^2. Mean Length of Petioles (cm per petiole)
(The number of observations is shown in brackets)

Leaf Grouping	DAYS FROM SOWING															
	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	0.90 (12)	0.97 (12)	0.99 (11)	1.03 (12)	1.11 (12)	1.02 (11)	1.04 (6)	1.13 (6)								
U	0.98 (12)	1.40 (11)	2.18 (11)	2.41 (12)	2.77 (11)	2.67 (12)	2.66 (5)	2.64 (6)	2.57 (4)							
L1	0.39 (6)	1.15 (12)	2.77 (11)	4.10 (12)	4.67 (11)	4.94 (12)	4.65 (6)	4.80 (6)	4.37 (6)	4.40 (1)						
L2		0.20 (7)	1.13 (11)	3.21 (12)	3.97 (11)	4.77 (12)	5.27 (6)	5.30 (6)	5.00 (6)	4.27 (3)						
L3				1.80 (12)	2.52 (11)	4.56 (12)	5.31 (6)	5.85 (6)	5.71 (6)	5.92 (4)	5.53 (4)					
L4				0.26 (11)	1.16 (11)	2.84 (12)	4.35 (6)	5.31 (6)	6.19 (6)	5.84 (4)	5.41 (4)					
L6					0.26 (8)	1.50 (12)	2.55 (6)	4.43 (6)	6.00 (6)	6.02 (4)	6.40 (4)					
L9						0.67 (7)	1.22 (6)	2.95 (6)	5.64 (6)	6.62 (4)	6.40 (4)	6.38 (6)				
L12							0.50 (6)	2.46 (6)	5.86 (6)	7.42 (4)	6.18 (4)	5.32 (5)				
L18								0.65 (4)	3.01 (6)	8.00 (4)	7.98 (4)	8.10 (6)	9.45 (4)			
L24									0.73 (5)	3.42 (4)	8.35 (4)	10.32 (6)	11.63 (3)			
L29-31 (L30 ± 1)										1.67 (12)	6.56 (12)	12.98 (18)	15.16 (16)	14.16 (8)	20.07 (3)	
L41-43 (L42 ± 1)											0.61 (4)	5.12 (18)	11.33 (17)	19.16 (17)	23.66 (11)	
L52-56 (L54 ± 2)													3.07 (9)	9.71 (30)	19.84 (31)	21.02 (12)
L64-68 (L64 ± 2)														0.47 (8)	3.10 (25)	15.57 (27)

Table 68(b)

16 Plants per dm^2.

Mean Length of Petioles (cm per petiole)
(The number of observations is shown in brackets)

		DAYS FROM SOWING														
Leaf Grouping	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	0.98 (12)	1.02 (12)	1.10 (12)	1.12 (12)	1.07 (12)	1.06 (12)	1.15 (5)	1.07 (2)								
U	1.18 (12)	1.70 (12)	2.70 (12)	2.96 (11)	2.74 (12)	2.84 (12)	2.63 (6)	2.84 (4)								
L1	0.46 (11)	1.51 (12)	3.30 (12)	4.58 (12)	4.81 (11)	5.16 (12)	4.98 (6)	5.89 (6)								
L2			1.47 (12)	3.73 (12)	4.85 (12)	5.21 (12)	6.02 (6)	7.53 (6)	7.31 (7)							
L3			0.21 (5)	1.84 (12)	3.65 (12)	5.50 (12)	6.45 (6)	9.13 (6)	8.97 (7)							
L4				0.51 (6)	1.78 (12)	3.75 (12)	4.86 (6)	8.21 (6)	9.04 (7)	8.40 (3)	7.47 (3)					
L6					0.17 (8)	1.67 (12)	3.31 (6)	7.48 (6)	9.66 (7)	8.73 (3)	8.57 (6)	8.6 (1)				
L9						0.77 (7)	1.81 (6)	5.40 (6)	8.49 (7)	9.73 (3)	9.88 (6)	9.66 (5)	9.20 (1)			
L12							0.69 (3)	2.62 (6)	6.67 (7)	9.25 (2)	9.08 (6)	11.86 (5)	12.87 (4)			
L15							0.20 (1)	0.81 (3)	4.79 (5)	10.40 (3)	10.58 (5)	13.22 (4)	18.97 (3)			
L18								0.10 (1)	2.68 (4)	6.19 (3)	8.75 (6)	15.20 (4)	16.92 (5)	18.93 (3)		
L21									0.22 (2)	1.18 (2)	7.62 (4)	9.04 (5)	16.20 (5)	21.00 (2)	19.10 (1)	
L22-31											2.82 (9)	6.96 (16)	9.75 (21)	14.17 (36)	21.69 (36)	22.45 (42)

Table 68(c)

36 Plants per dm^2.

Mean Length of Petioles (cm per petiole)
(The number of observations is shown in brackets)

Leaf Grouping	DAYS FROM SOWING															
	20	27	34	41	48	55	62	69	76	83	90	104	118	132	146	160
C	1.11 (12)	0.98 (12)	1.04 (12)	1.09 (12)	1.10 (12)	1.06 (12)	1.07 (6)									
U	1.45 (12)	2.04 (12)	2.90 (12)	3.12 (12)	3.37 (12)	3.13 (12)	2.79 (6)	2.65 (2)								
L1	0.44 (7)	1.83 (12)	3.42 (12)	4.95 (12)	6.37 (12)	6.41 (11)	5.51 (5)	6.85 (7)								
L2			1.66 (12)	3.88 (12)	6.32 (12)	7.30 (12)	6.34 (6)	8.05 (8)	7.83 (3)							
L3				1.39 (12)	4.09 (12)	6.27 (12)	6.68 (6)	9.14 (8)	8.67 (7)	9.55 (2)						
L4				0.15 (3)	1.21 (11)	3.53 (12)	4.53 (6)	7.90 (8)	8.00 (7)	9.57 (3)	10.78 (4)					
L6						0.70 (12)	1.75 (6)	5.64 (7)	8.63 (7)	10.60 (4)	11.88 (6)	10.38 (5)	12.00 (2)			
L9								1.92 (5)	3.59 (6)	8.78 (4)	13.93 (6)	13.97 (6)	14.62 (4)			
L12										5.05 (2)	10.98 (6)	11.03 (6)	15.72 (5)	16.52 (4)		
L14-20 (L17 ± 3)										4.90 (3)	6.67 (9)	8.59 (18)	11.12 (21)	13.14 (11)	11.54 (5)	16.12 (6)

Table 69(a)

Density 4 plants per dm^2 - Mean height at which laminae are held (cm)

(The number of observations is shown in brackets).

Leaf Grouping	DAYS FROM SOWING													
	20	27	34	41	48	55	62	69	76	83	90	104	118	132
L1		0.7 (12)	1.2 (12)	1.1 (12)	1.5 (12)	1.4 (12)	-	0.7 (6)						
L2-3			0.7 (12)	0.7 (24)	1.7 (24)	1.8 (24)	-	2.0 (14)	1.8 (14)	-	1.1 (2)	1.6 (1)		
L4-8				0.6 (12)	0.5 (57)	1.0 (58)	-	1.5 (35)	3.1 (40)	-	2.5 (19)	1.3 (5)		
L9-16						0.7 (13)	-	0.6 (49)	3.4 (64)	-	4.1 (32)	2.8 (17)		
L17-29								0.1 (3)	1.4 (57)	-	5.6 (49)	4.9 (26)	5.3 (15)	
L30-35											3.0 (21)	7.6 (12)	8.1 (11)	6.1 (1)
L36-44											1.7 (12)	5.7 (18)	9.4 (18)	10.2 (9)
L45-53												2.7 (12)	7.6 (14)	14.4 (9)
L54-62													3.6 (4)	8.3 (4)

Table 69(b)

Density 16 plants per dm^2 - Mean height at which laminae are held (cm)

(The number of observations is shown in brackets)

Leaf Grouping	DAYS FROM SOWING													
	20	27	34	41	48	55	62	69	76	83	90	104	118	132
L1-2		1.3 (12)	2.0 (24)	2.4 (24)	2.6 (24)	2.4 (24)	-	2.2 (12)	2.3 (12)					
L3-5				1.5 (23)	1.8 (35)	2.7 (36)	-	5.2 (17)	4.6 (18)	-	3.3 (4)			
L6-8					0.5 (13)	1.4 (34)	-	5.8 (18)	7.0 (18)	-	5.7 (8)	6.9 (9)		
L9-15						0.8 (21)	-	3.4 (18)	5.9 (37)	-	9.0 (21)	6.8 (18)	8.4 (11)	
L16-19									2.0 (14)	-	9.2 (10)	11.0 (11)	9.3 (11)	9.8 (6)
L20-28									1.3 (3)	-	4.2 (9)	8.2 (18)	9.8 (23)	13.8 (36)

Table 69(c)

Density 36 plants per dm^2 - Mean height at which laminae are held (cm)

(The number of observations is shown in brackets)

Leaf Grouping	DAYS FROM SOWING													
	20	27	34	41	48	55	62	69	76	83	90	104	118	132
L1		1.9 (12)	3.2 (12)	3.9 (12)	2.9 (12)	1.8 (11)	-	2.1 (6)	1.2 (6)	-				
L2			1.7 (12)	3.5 (12)	3.5 (12)	4.0 (12)	-	3.8 (5)	2.2 (5)	-				
L3				2.1 (12)	3.4 (12)	4.0 (12)	-	5.2 (6)	4.2 (6)	-	3.9 (3)			
L4-6					1.2 (15)	2.2 (36)	-	5.6 (15)	6.1 (18)	-	6.7 (12)	2.8 (2)		
L7-10						1.0 (5)	-	3.7 (15)	4.5 (20)	-	11.1 (16)	7.0 (8)	11.0 (11)	7.3 (1)
L11-12									0.7 (1)	-	12.5 (6)	9.7 (6)	7.6 (7)	10.8 (7)
L13-16											5.6 (7)	7.3 (9)	9.7 (8)	13.6 (10)

Table 70.

A comparison of the lamina weight changes and the visual criteria of senescence in representative leaves at each density.

A comparison of lamina weight, lamina colour and leaf condition.

Density 4 plants per dm^2

Leaf number	Days from sowing	Lamina weight (mg)	Percentage of maximum weight	Leaf condition and colour criterion
L 3	34	2.5	15.2	All laminae folded
	41	7.8	47.3	All laminae open
	48	11.0	66.7	All laminae 1
	55	14.8	89.7	" "
	62	14.6	88.5	" "
	69	16.5	100.0	" "
	76	14.7	89.1	" "
	83	13.2	80.0	All laminae 1B
	90	10.7	64.8	2, 2, 3, 2, 2, 3, 2
	104	6.2	37.6	5, 5, 5, 5, 5, 5, 5
	118	5.0	30.3	
L 4	41	4.0	28.4	All laminae folded
	48	7.7	54.6	All laminae open
	55	10.8	76.6	All laminae 1
	62	12.0	85.1	" " 1
	69	14.1	100.0	" " 1
	76	13.4	95.0	" " 1
	83	11.4	80.8	" " 1
	90	8.6	61.0	1, 2, 4, 2, 2, 2
	104	5.7	40.4	5, 5, 5, 5, 5, +
	118	4.8	34.0	5, 5, 5, + + +
L 6	48	3.7	33.0	All laminae folded
	55	6.4	57.0	60 per cent. of lamina open
	62	8.9	79.5	All laminae open
	69	11.0	98.2	All laminae 1
	76	9.9	88.4	" " 1
	83	11.2	100.0	" " 1
	90	8.5	75.9	1, 2, 1, 1, 2, 1
	104	4.8	42.9	5, 5, 2, 5, 5, +
	118	4.4	39.3	
L 30	76	1.4	6.0	All laminae folded
	83	2.8	11.9	Half the laminae are open
	90	7.4	31.5	All laminae 1
	104	12.8	54.5	" " 1
	118	23.5	100.0	1, 1, 1B, 1, 1, +
	132	15.5	66.0	2, + + + + +
	146	12.3	52.3	

Density 4 plants per dm^2 cont.

Leaf number	Days from sowing	Lamina weight (mg)	Percentage of maximum weight	Leaf condition and colour criterion
L 34	76	1.9	9.6	
	83	3.6	18.3	All laminae folded
	90	7.5	38.1	One lamina open
	104	7.3	37.1	All laminae 1
	118	19.7	100.0	" " 1
	132	14.9	75.6	1, 2, 2, 1B, + +
	146	-	-	+ + + + + +

A comparison of lamina weight, lamina colour and leaf condition.

Density 16 plants per dm^2

Leaf number	Days from sowing	Lamina weight (mg)	Percentage of maximum weight	Leaf condition and colour criterion
L 3	34	2.8	20.6	All laminae folded
	41	6.9	50.7	All laminae folded
	48	9.7	71.3	Laminae open
	55	11.4	83.8	All laminae 1
	62	11.0	80.9	" " 1
	69	13.6	100.0	" " 1
	76	11.4	83.8	1, 2, 1, 1, 1, 1
	83	7.5	55.1	5, 2, 3, 4, 2, 3
	90	6.5	47.8	5, +, +, +, +, 5
L 4	41	3.5	30.4	All laminae folded
	48	6.7	58.3	All laminae open
	55	8.5	73.9	All laminae 1
	62	8.9	77.4	" " 1
	69	11.5	100.0	" " 1
	76	10.6	92.2	" " 1
	83	8.8	76.5	1, 2, 2, 2, 2, 1
	90	6.0	52.2	5, 5, 5, 5, 3, 5
L 6	41	2.1	21.0	All laminae folded
	48	3.2	32.0	" " "
	55	5.9	59.0	All laminae open
	62	6.6	66.0	All laminae 1
	69	10.0	100.0	" " 1
	76	9.8	98.0	" " 1
	83	8.5	85.0	" " 1
	90	7.3	73.0	1, 1, 2, 2, 1, 1
	104	4.6	46.0	5, 5, 5, 2, + +
L 18	69	2.0	13.2	Laminae folded
	76	3.2	21.2	" "
	83	3.5	23.2	Laminae half-open
	90	5.6	37.1	All laminae 1
	104	9.4	62.3	" " 1
	118	15.1	100.0	1, 1, 1, 1, 1, +
	132	9.7	64.2	5, 2, 5, 5, 2, 1B

A comparison of lamina weight, lamina colour and leaf condition.

Density 36 plants per dm^2

Leaf number	Days from sowing	Lamina weight (mg)	Percentage of maximum weight	Leaf condition and colour criterion
L 3	34	2.7	27.0	All laminae folded
	41	5.3	53.0	Half the laminae open
	48	7.6	76.0	All laminae open
	55	9.1	91.0	All laminae 1
	62	8.4	84.0	" " 1
	69	10.0	100.0	" " 1
	76	8.2	82.0	3, 1, 1, 1, 1, 1
	83	6.4	64.0	2, 2, 2, 2, 5, +
	90	5.6	56.0	2, 5, 5, 5, + +
L 4	41	1.9	21.3	Laminae folded
	48	4.6	51.7	Laminae folded
	55	6.4	71.9	All laminae unfolded
	62	6.5	73.9	All laminae 1
	69	8.9	100.0	" " 1
	76	7.9	88.8	" " 1
	83	8.4	94.4	" " 1
	90	5.5	61.8	5, 4, 2, 1, 3, 5
	104	3.6	40.4	5, 5, 3, + + +
L 6	48	1.7	20.5	All laminae folded
	55	3.0	36.1	All laminae folded
	62	3.7	44.6	60 per cent. laminae open
	69	6.3	75.9	All laminae 1
	76	6.4	77.1	" " 1
	83	8.3	100.0	" " 1
	90	6.9	83.1	" " 1
	104	5.5	66.3	5, 2, 4, 2, 2, 2
	118	3.5	42.2	2, 4, + + + +
L 11	76	1.3	17.8	
	83	2.9	39.7	Half the laminae open
	90	6.7	91.8	Laminae open
	104	7.3	100.0	All laminae 1
	118	5.8	79.5	1, 2, 1, 1, 1, 1
	132	5.3	72.6	1, 1, 1, 2, 3, +
	146	-	-	+ + + + + +

Density 36 plants per dm^2 cont.

Leaf number	Days from sowing	Lamina weight (mg)	Percentage of maximum weight	Leaf condition and colour criterion
L 12	76	1.7	15.4	Laminae folded
	83	2.7	24.5	Laminae folded
	90	4.5	40.9	Half laminae open
	104	6.2	56.4	Laminae 1
	118	9.6	87.3	" 1
	132	11.0	100.0	2, 1, 1, 2, 2, 1B
	146	4.1	37.3	1, 1, 1, 2, +, +
L 13	83	2.1	22.1	All laminae folded
	90	3.9	41.1	50 per cent. laminae open
	104	6.9	72.6	60 per cent. laminae open
	118	9.4	98.9	All laminae open
	132	9.5	100.0	1, 1, 1, 1, 1, 1
	146	-	-	1, 1, + + + +

Table 71.

L.A.I., Growth rates of tops, leaves, and roots.

Days from sowing	4 Plants per dm^2				16 Plants per dm^2				36 Plants per dm^2			
	L.A.I.	Crop growth rate-tops only $\frac{dw}{dt}$ gdm^{-2}/day	Rate of leaf formation $\frac{dL.A.I.}{dt}$ L.A.I./day	Rate of root growth $\frac{dw}{dt}$ gdm^{-2}/day	L.A.I.	Crop growth rate-tops only $\frac{dw}{dt}$ gdm^{-2}/day	Rate of leaf formation $\frac{dL.A.I.}{dt}$ L.A.I./day	Rate of root growth $\frac{dw}{dt}$ gdm^{-2}/day	L.A.I.	Crop growth rate-tops only $\frac{dw}{dt}$ gdm^{-2}/day	Rate of leaf formation $\frac{dL.A.I.}{dt}$ L.A.I./day	Rate of root growth $\frac{dw}{dt}$ gdm^{-2}/day
28	0.07	0.008	0.011	0.003	0.42	0.027	0.054	0.008	1.00	0.048	0.154	0.013
32	0.15	0.012	0.018	0.004	0.75	0.037	0.081	0.011	1.72	0.060	0.150	0.015
36	0.25	0.017	0.026	0.005	1.12	0.044	0.092	0.012	2.29	0.069	0.133	0.016
40	0.35	0.017	0.028	0.008	1.50	0.052	0.100	0.016	2.69	0.079	0.137	0.014
44	0.47	0.022	0.030	0.011	1.90	0.054	0.097	0.017	3.32	0.071	0.154	0.009
48	0.60	0.023	0.030	0.011	2.30	0.060	0.096	0.017	4.10	0.058	0.162	0.005
52	0.73	0.024	0.034	0.010	2.66	0.058	0.103	0.012	4.62	0.036	0.132	0.004+
56	0.85	0.021	0.042	0.010	3.07	0.050	0.123	0.009	5.12	0.023	0.116	0.003+
60	1.05	0.029	0.064	0.013	3.77	0.083	0.194	0.007	5.52	0.044	0.142	0.004+
64	1.34	0.037	0.074	0.013	4.55	0.108	0.233	0.007	5.91★	0.072★	0.093★	0.005★
68	1.71	0.039	0.071	0.008	5.80	0.106	0.190	0.005	6.27★	0.099★	0.090★	0.006★
72	1.93	0.037	0.071	0.004	6.20	0.067	0.096	0.003	6.64★	0.098★	0.087★	0.006★
76	2.10	0.047	0.088	0.004	6.32	0.050	0.017	0.004	7.00★	0.098★	0.091★	0.005★
80	2.64	0.065	0.113	0.008	6.35	0.042	0.001	0.003	7.36★	0.082★	0.091★	0.005★
84	3.13	0.121	0.122	0.008	6.32	0.021	-0.014	0.000	7.72★	0.058★	0.086★	0.005★
88	3.60	0.127	0.132	0.012	6.22	0.000	-0.033	-0.003	8.05	0.033	0.032	0.004
92	4.15	0.135	0.144	0.017	5.95	0.000	-0.045	-0.002	8.00	0.027	-0.038	0.004
96	4.80	0.097	0.158	0.022	5.84	0.006	-0.056	0.001	7.61	0.029	-0.096	0.003
100	5.43	0.100	0.141	0.018	5.61	0.021	-0.012	0.003	7.22	0.035	-0.062	0.003
104	6.05	0.100	0.112	0.010	5.40	0.056	0.067	0.006	6.95	0.042	0.016	0.004
108	6.30	0.102	0.079	0.001	6.15	0.090	0.146	0.008	7.30	0.048	0.079	0.005
112	6.58	0.106	0.068	-0.004	6.88	0.035	0.183	0.009	7.75	0.050	0.121	0.005
116	6.85	0.125	0.087	0.008	7.62	0.033	0.105	0.008	8.25	-0.008	0.044	0.000
120	7.25	0.090	0.112	0.009	7.89	0.004	0.029	0.005	8.26	-0.067	-0.025	-0.006
124	7.78	0.161	0.130	0.031	7.70	0.003	-0.049	0.014	7.90	-0.127	-0.100	-0.012
128	8.30	0.150	0.117	0.024	7.50	0.003	0.030	0.031	7.50	-0.114	-0.135	-0.009
132	8.82	0.127	0.084	0.009	7.32	0.092	0.179	0.090	7.01	-0.096	-0.242	-0.002
136	8.95	0.106	0.052	-0.006	8.95	0.180	0.328	0.056	5.05	-0.075	-0.333	0.004
140	9.11	0.096	0.036	-0.013	10.55	0.177	0.387	0.029	4.02	-0.067	-0.392	0.008
144	9.25	0.129	0.017	-0.011	12.12	0.171	0.200	-0.041	2.58	-0.060	-0.171	0.004
148	9.30	0.001	0.001	-0.008	12.45	-0.065	0.017	-0.027	2.10	-0.054	-	0.001
152	9.24	-0.102	-0.015	-0.006	11.85	-0.060	-0.162	-	3.02	-0.050	-	-0.003

★ Harvests 8 & 10 joined directly)
\+ Harvests 5 & 7 joined directly)

The following pages have been missed and do not appear in the thesis.

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