

Copyright is owned by the Author of the thesis. Permission is given for a copy to be downloaded by an individual for the purpose of research and private study only. The thesis may not be reproduced elsewhere without the permission of the Author.

**A STUDY OF THE RELATIONSHIPS BETWEEN LEAF AREA INDEX,
CHLOROPHYLL CONTENT PER UNIT OF GROUND AREA
AND RATE OF DRY MATTER INCREASE IN A
PERENNIAL RYEGRASS SWARD**

A thesis presented at Massey College in part
fulfillment of the requirements for the
Degree of Master of Agricultural Science
in
Victoria University of Wellington,
New Zealand

L. A. HUNT

1962

ACKNOWLEDGEMENTS

The study reported in this thesis was prompted by Mr R. W. Brougham of Grasslands Division, Department of Scientific and Industrial Research, to whom the author is indebted for guidance and encouragement.

Thanks are also due to Mr A. C. Glenday, of the Applied Mathematics Laboratory, Department of Scientific and Industrial Research, to Mr W. A. Jacques of the Field Husbandry Department, Massey College and to the staff of Massey College Library.

TABLE OF CONTENTS

Chapter		Page
	Introduction.	1
1.	Review of Literature.	
	A. The Relationships between Leaf Area Index and Rate of Dry Matter Increase.	4
	B. The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.	8
	C. The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.	11
2.	Materials and Methods.	
	First Experiment.	13
	Second Experiment.	15
	Determination of the 95% Light Interception Level.	15
	Determination of the Chlorophyll Content per Unit of Ground Area.	16
	Determination of the Leaf Weight/Area Ratio.	20
	Determination of the Percentage of Stem in the Living Matter, the Leaf Area Index and the Dead Matter Yield.	20
	Determination of the Dry Matter Yield.	21
	Statistical Procedure.	22
3.	Results.	
	Dry Matter Yield Measurements.	23
	Rates of Dry Matter Increase.	24

Dead Matter Yield Measurements.	25
The Percentage of Stem in the Living Matter.	26
Leaf Area Index Measurements.	27
Leaf Weight/Area Measurements.	28
Chlorophyll Content per Unit of Ground Area Measurements.	29
The Relationships between Leaf Area Index and Rate of Dry Matter Increase.	30
The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.	30
The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.	31
4. Discussion.	
A. The Relationships between Leaf Area Index and Rate of Dry Matter Increase.	32
B. The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.	42
C. The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.	43
Summary.	47
References.	49
Appendices.	

LIST OF TABLES

Table		Page
1.	Comparison of Dry Matter Yields Measured by Cutting to Ground Level with those Measured by Cutting to 1" from Ground Level.	23
2.	Rates of Dry Matter Increase at Various Stages of Growth.	24
3.	Dead Matter Yields at Various Stages of Growth.	25
4.	Percentage of Stem in the Living Matter Harvested at Various Stages of Growth.	26
5.	Leaf Area Index above the Level at which 95% of the Noon Light was Intercepted at Various Stages of Growth.	27
6.	Leaf Weight/Area Ratios at Various Stages of Growth.	28
7.	Chlorophyll Content per Unit of Ground Area above the Level at which 95% of the Noon Light was Intercepted at Various Stages of Growth.	29
8.	Average Amount of Solar Radiation Received on a Horizontal Surface in Palmerston North, 1955-1956.	38
9.	Net Assimilation Rate and Rate of Dry Matter Increase per Unit of Chlorophyll at two Leaf Area Indices.	45

LIST OF FIGURES

Figure		Facing page
1.	Leaf efficiency index at various stages of growth (Brougham, 1956).	4
2.	Dry matter yields at various stages of growth.	23
3.	Leaf Area Indices at Various Stages of Growth.	27
4.	Chlorophyll Content per Unit of Ground Area at Various Stages of Growth.	29
5.	The Relationships between Leaf Area Index and Rate of Dry Matter Increase.	30
6.	The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.	30
7.	The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.	31

INTRODUCTION

Many factors are operative in determining the overall productivity of any system of farming. In most cases these can be placed into distinct groups, and where animal production from pasture is concerned three such groups can be distinguished:-

- (a) Factors affecting the amount of dry matter which is produced by the pasture.
- (b) Factors affecting the proportion of this which is harvested.
- (c) Factors affecting the efficiency with which harvested dry matter is converted into animal products.

While all of these factors affect the ultimate level of production only those concerned with pasture dry matter production are considered in this thesis.

Many studies have been carried out in an attempt to improve the understanding of those factors which affect the amount of dry matter produced by the pasture. Some of these have been concerned with the roles of intensity and frequency of defoliation, and in general, they demonstrate an inverse relationship between the yield of pasture dry matter and both the severity and frequency of defoliation. In the light of such information many farmers have attempted to increase the overall output from their grassland by adopting grazing systems in which, ideally, grazing and spelling alternate at intervals appropriate to the climatic

and edaphic environments and to the specific pasture type.

In recent years several systems of grazing management have been tested on a farm scale (McMeekan, 1960). These studies show that the amount of animal material produced from management systems based on the results of pasture studies is little, if any, greater than that from systems previously employed. In order to explain such results, and to facilitate the development of better grazing methods, a more precise understanding of pasture growth has become necessary.

Many recent attempts to obtain a more detailed understanding of pasture growth have involved an intensive study of relationships between the rate of dry matter increase and various characteristics of the photosynthetic system. Leaf area has been widely used as a measure of the size of the photosynthetic system despite the fact that many photosynthetically active cells occur in the stalks, sheaths and petioles. Chlorophyll is essential for photosynthesis and Brougham (1960) found that there was a better correlation between maximum rate of dry matter increase and the chlorophyll content per unit of ground area above the level at which 95% of the noon light was intercepted than between maximum rate of dry matter increase and leaf area index^(*) above a similar measurement level. As a logical extension of such work this thesis involves a study of the relationships

(*) The term leaf area index is used to refer to the ratio of leaf area to ground area occupied (Watson, 1947).

between rate of dry matter increase, leaf area index and chlorophyll content per unit of ground area during the growth of a pasture.

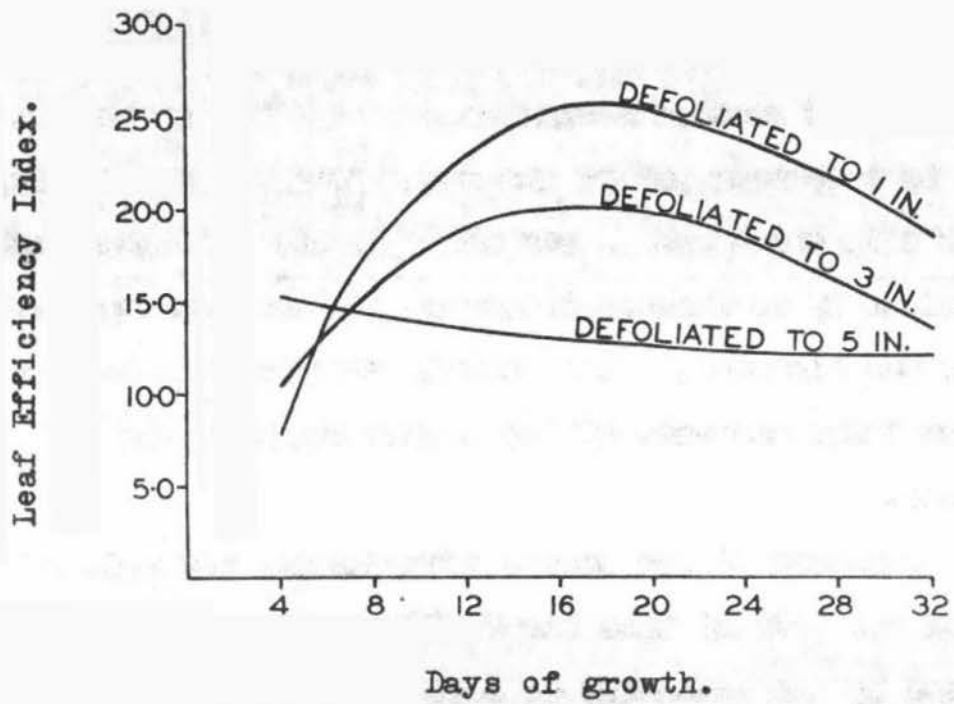


Fig. 1. Leaf Efficiency Index at various stages of growth.

(Brougham, 1956).

CHAPTER 1

REVIEW OF LITERATURE

A. The Relationships between Leaf Area Index and Rate of Dry Matter Increase.

Brougham (1956) defoliated swards of short rotation ryegrass - white clover - red clover to three different levels and found that in all cases the rate of aerial dry matter increase reached a maximum when sufficient leaf was present to intercept 95% of the noon light. The leaf area index at this point was 5, and although the leaf area index increased to 9, no further change in the rate of dry matter increase was recorded. The overall relationship between leaf area index and rate of dry matter increase was thus asymptotic.

The quantity of dry matter accumulating per unit of leaf area per unit of time (leaf efficiency index) was influenced by the intensity of defoliation, as is shown in Fig. 1. The low value following defoliation to 1" from ground level was explained on the assumption that these swards would expend a larger proportion of their synthesised carbohydrate in respiration, and the higher maximum value was attributed to the bulk of the leaves being at the optimum age for photosynthesis. In the later stages of growth the rate of dry matter increase per unit of leaf area declined and it was suggested that this was due to mutual shading, although leaf age was considered as a possible factor.

In a further study Brougham (1958a) showed that different species intercepted different amounts of light with the same measured leaf area. The amount of leaf necessary to bring about maximum rate of dry matter increase at any particular light receipt thus varies between species. This has been substantiated by further studies (Watson, 1958; Watson and French, 1958; Davidson and Donald, 1958) of the relationships between leaf area index and rate of dry matter increase.

Watson (1958) obtained stands of sugar beet and kale with different leaf area indices, and avoided the complications experienced when plants are differentially defoliated, by thinning them to different densities. He measured the total dry matter increase during the subsequent ten days and found that in kale the rate of dry matter increase was at a maximum when the leaf area index was between 3.0 and 4.0 and was slightly lower when this was between 5.0 and 5.5. The relationship between leaf area index and rate of dry matter increase was thus quadratic. This contrasted with the relationship established in the stands of sugar-beet, the rate of dry matter accumulation of which increased up to the maximum leaf area index value investigated (6.3). A similar relationship to this was established by Watson and French (1958) in stands of barley, the maximum leaf area index investigated in this case being 9.0. In all cases the rate of dry matter increase per unit of leaf area (net assimilation rate) was inversely related to the leaf area index. An increase of one leaf

area index unit did, however, have a much greater effect on the net assimilation rate in kale than in barley or sugar-beet.

The relationship between rate of dry matter increase and leaf area index established in kale by Watson (loc cit.) was similar to that found by Davidson and Donald (1958) in stands of subterranean clover. In these stands the rate of dry matter increase was at a maximum at a leaf area index of between 4 and 5. At the highest leaf area index reached (8.7) the rate of dry matter increase was 30% below the maximum.

Monsi and Saeki (1953) applied theoretical considerations to the relationship between leaf area index and rate of dry matter increase. They pointed out that within a plant community competition for light or carbon dioxide would limit the assimilation possible by individual leaves. Although this would become more severe at higher leaf area index values, the rate at which dry matter accumulated in the community would increase as long as the carbon dioxide fixation in each unit of leaf tissue was sufficient to offset its loss of carbohydrate in respiration. Up to this point, therefore, the relationship between leaf area index and rate of dry matter increase would take the form of a diminishing response curve.

The authors pointed out that the amount of leaf necessary to bring about the maximum rate of dry matter increase depended largely on the amount of light received and on the optical properties of the foliage. Theoretical

considerations suggest that the light absorption properties of the foliage vary according to the arrangement, dispersion and orientation of the leaves (Mitchell and Calder, 1958; Saeki, 1960; Warren Wilson, 1960a), but much experimentation is required before the exact relationships between such factors and the ability to intercept light is fully understood.

Davidson and Philip (1958) and Davidson and Donald (1958) extended the thesis of Monsi and Saeki (loc cit) and suggested that the rate of dry matter increase would be reduced at leaf area indices above a certain optimum value. They considered that leaves would survive and become semi-parasitic, so drawing on internal plant carbohydrate until the dry matter loss in respiration of a whole stand equalled its gross dry matter gain in photosynthesis, at which stage the rate of dry matter loss would be zero.

This hypothesis was, however, considered invalid by Black (1958) and Saeki (1960). They both pointed out that there was very little evidence to suggest that a plant maintains mature leaves in a position unfavourable for photosynthesis. Further support for their argument was provided by Kursanov (1961). In a review of the transport of organic substances in plants he pointed out that several workers had been unable to bring about a flow of carbohydrate to a mature leaf, even by prolonged shading. Most of the experimentation had been carried out with soya-beans and other annual plants and the author concluded that in annual plants there is very little exchange of carbohydrate between mature leaves at different levels.

In an extension of the argument Saeki (1960) pointed out that the relationship between leaf area index and rate of dry matter increase would depend on the rate at which leaves decayed when their loss of carbohydrate in respiration exceeded their gain from photosynthesis. Few studies of the rate of decay of plant material have been reported, but Brougham (1958b) found that white clover leaves passed through their life cycle and decayed completely in thirty days.

B. The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.

(a) Overall Relationships.

In a study of the growth of several pure stands of crop and pasture species Brougham (1960) measured the amount of chlorophyll contained in the herbage above the 95% light interception level and compared this with the critical leaf area index. For perennial ryegrass 35 mg. of chlorophyll per square foot of leaf area was recorded in February, whereas for red clover and white clover the values ranged between 42 and 47 mg. per square foot. These values depended on both the relationship between chlorophyll contained in the leaves and in other parts of the plant and on the relationship between chlorophyll content and leaf area in individual leaves. For this reason it is necessary to consider these relationships separately.

(b) Relationships between Chlorophyll Contained in the Leaves and in other Parts of the Plant.

Brougham (loc cit) reported that the chlorophyll in the

stems accounted for 15% of the total chlorophyll contained in a stand of red clover with a leaf area index of between 4 and 5 in February. In grasses the green leaf sheath may make up a considerable proportion of the total assimilating surface (Blackman and Black, 1959) and at certain times assimilation in the ear of cereals is known to be appreciable (Watson and Norman, 1939; Porter et al., 1950; Thorne, 1960). Chlorophyll found in organs other than leaf may thus contribute a considerable amount to the measured chlorophyll content per unit of ground area, particularly at certain times of the year and stages of growth.

(c) Relationships between Chlorophyll Content and Leaf Area in Individual Leaves.

The chlorophyll content of individual leaves of a large number of species varies between 36 and 76 mg. per square foot of leaf area (Seybold and Egle, 1940; Rabinowitch, 1945). Part of this variation is caused by a characteristic change throughout the life history of the leaf. The chlorophyll content increases until a maximum is attained about the time that the leaf reaches full size, it then remains relatively constant through maturity and finally decreases as the leaf senesces (Skene, 1948).

Nutritional and genetic factors also influence the chlorophyll content per unit of leaf area. Bonner and Galston (1952) pointed out that the production of chlorophyll is controlled by a great number of different genes, and that mutation or loss of any of these will result in plants which

have a different amount of chlorophyll per unit of leaf area. A deficiency of either magnesium or nitrogen, essential components of the chlorophyll molecule, will also have an effect, and any leaves produced will be yellow and of low chlorophyll content (Rabinowitch, 1945). A similar effect is noted when iron, zinc or copper are deficient. These are not themselves constituents of the chlorophyll molecule but they are required for its synthesis (Rabinowitch, loc cit).

When nutrients are in adequate supply, the chlorophyll content per unit of leaf area in plants of one particular genotype is controlled by the light and temperature conditions under which the leaves develop (Smith and Young, 1956). Shirley (1929) reported that in a number of broad leaved plants a five-fold reduction in light intensity increased the chlorophyll content per unit of green weight but had an inconsistent effect on the chlorophyll content per unit of leaf area. Friend (1960; 1961a) found that the rate of formation and the maximum quantity of chlorophyll in the first three leaves of Marquis wheat is controlled by light and temperature, but is not affected by photoperiod. At temperatures between 20°C and 30°C the chlorophyll content per unit of dry weight increased as the light intensity was increased from 200 to 1,000 foot candles. At higher light intensities there was an interaction between the effects of light and temperature, and under optimum temperatures the chlorophyll content increased until light intensities of 2,500 foot candles were reached. At temperatures lower than 20°C the chlorophyll content decreased as the light intensity

was increased. This effect was explained in terms of two opposing reactions, pigment production from the precursor protochlorophyll and pigment destruction, both under the influence of light. At low temperatures the rate of production of protochlorophyll was retarded whereas the light-activated pigment breakdown continued unhampered. In a further study Friend (1961) reported that there was a strong correlation between chlorophyll content and leaf thickness. Thus, under conditions which favoured an increase in the thickness of the leaves the chlorophyll content per unit leaf area was increased.

The relationship between leaf area and chlorophyll content may change throughout the day. Doubt as to the existence of diurnal changes does however exist, Bukatsch (1930) working with Rumex alpinus and Adenostyles albifrons and Bavrina (1959) working with red perilla, Japanese millet and rudbeckia, have both reported the existence of such changes whereas Wilsatter and Stoll (1918) reported that chlorophyll content remained relatively constant.

C. The Relationships between Chlorophyll Content per unit of Ground Area and Rate of Dry Matter Increase.

Several studies of the relationship between chlorophyll content per unit area of water surface and the rate of dry matter increase in aquatic communities have been reported (Manning and Juday, 1941; Ichimura, 1954; Odum, 1959). In these communities the chlorophyll content per square foot of water surface area varied between 5 and 300 mg. The rate of assimilation per unit of chlorophyll appeared to be very

similar in the different communities and this led Odum (1959) to suggest that the chlorophyll content of a community could be used as an index of potential productivity.

Bray (1960) investigated the relationships between chlorophyll content per unit of ground area and the productivity of some native and managed plant communities in Central Minnesota. He found that there was a highly significant relationship between the maximum weight attained by the aerial parts of annual herbaceous stands and the chlorophyll content per unit of ground area. This is supported by a recent investigation which established a highly significant correlation ($r = + 0.912$) between the maximum rate of dry matter increase and the amount of chlorophyll per unit of ground area above the 95% light interception level (Brougham, 1960). Pure stands of perennial ryegrass, short rotation ryegrass, white clover and several other pasture and crop plants were used in the investigation carried out by Brougham (loc. cit.).

CHAPTER 2

MATERIALS AND METHODS

Pure swards of certified New Zealand perennial ryegrass (Lolium perenne L.) in their third year from sowing were used. These were growing on an open, level terrace in fertile Manawatu silt loam on part of the field plot experimental area at the Palmerston North station of the Grasslands Division, Department of Scientific and Industrial Research (Latitude $40^{\circ} 30' S.$). In 1959 and 1960 the swards had been used for a study of pasture growth involving daily cutting and in 1961 they had been grazed regularly with sheep.

Two experiments were carried out, preparation for the first beginning in early March, 1961.

First Experiment.

On 4th March the herbage was cut to a height of 1 in. from ground level and the clippings removed. The swards were then allowed to grow for a week before being cut to the same level again. Subsequently, they were allowed to grow unchecked and dressings of sulphate of ammonia were applied on 15th and 21st March. In total the equivalent of 100 lbs. of nitrogen per acre was used in order to ensure that continuous growth was maintained throughout the first experimental period of 41 days and to reduce any unevenness of growth caused by sheep excrement.

When the swards reached a height of approximately 3 in. four replications, each 40 ft. by 20 ft., were measured out and marked off with wooden pegs. The surrounds were mown

back to be used as access areas. Previous experiments conducted at Grasslands Division suggested that four replications would be sufficient (Brougham, pers. comm.). Each replicate was divided into two plots, each 40 ft. by 10 ft., and on the 28th March one of these was cut to a height of 1 in. from ground level and the other to 2½ in. from ground level. The allocation of the defoliation treatments was made at random.

In order to ease the sampling procedure 10 sub-plots of approximately 10 ft. by 2 ft. 6 in. were selected in each plot at the beginning of the experiment. Areas which included apparent weak spots were excluded. A sub-plot at the end of each plot was selected at random and the first samples were cut on this area. On the second sampling date the adjacent sub-plot was used; this process was repeated throughout the course of the experiment so that each sub-plot was sampled once only. A strip of grass at least 6 in. wide was discarded between the sub-plots. This was necessary to overcome edge effects (Black, 1961).

On each sub-plot samples for the determination of chlorophyll content per unit of ground area and dry matter yield were taken. A half square foot quadrat was cut to ground level for the chlorophyll determination and on the following day a 2 ft. by 7 - 10 ft. area was cut to 1 in. from ground level for the dry matter yield determination. On the plots which had been cut to 1 in. from ground level this process was repeated every four days until 95% of the noon light was intercepted by the herbage above one half inch from ground level, and from then on at intervals of eight days. The plots which had been cut to 2½ in. at the commencement of the

experiment were not sampled until sufficient herbage had been formed to intercept approximately 90% of the noon light. The first day on which samples were cut on these swards coincided with the day on which the swards cut to 1 in. from ground level were sampled. In order to ease the pressure of work the second sample for chlorophyll determination was cut seven days later. After this an interval of eight days passed between samplings. An eight day interval between dry matter yield samplings was adhered to throughout so that two days elapsed between chlorophyll and dry matter yield samplings on all but the first sampling on the swards cut to $2\frac{1}{2}$ in.

Second experiment.

After completion of the first experiment, the areas were grazed by sheep and then maintained by mowing to 1 in. from ground level at frequent intervals. Dressings of 60 lb per acre of nitrogen in the form of sulphate of ammonia were applied in June and September. In early November, the swards were irrigated and prepared as for the first experiment. The swards at this time were reasonably uniform and there was no evidence of a carry-over effect from the first experiment.

The experiment, which differed from the first only in the timing of some of the samplings for chlorophyll content per unit of ground area was started on November 22nd. In order to maintain continuous growth, the swards were irrigated on several occasions during the course of the experiment.

Determination of the 95% Light Interception Level.

The percentage of light that penetrated into the sward

was measured by using a small (1.8 x 1.1 cm.) barrier-layer selenium photocell connected to a sensitive galvanometer. The apparatus has been described by Barrowman (1956). A check recording was taken with the photocell exposed to full light, and after pushing the recording head carefully into the sward a second reading was made. At least six such determinations in each plot were used to calculate the percentage interception. All measurements were taken during bright sunlight about local noon, when fluctuation in the intensity of light was relatively small (Brougham 1958a).

The percentage penetration was measured at various heights above and below the level to which only 5% of the noon light penetrated. The 95% light interception level was determined by linear interpolation between the two points enclosing the 95% point.

Determination of the Chlorophyll Content per Unit of Ground Area.

Bray (1960) pointed out that chlorophyll in detached herbage degrades quite rapidly when it is exposed to light at normal room temperatures, but in a refrigerator the rate of degradation is reduced though not halted completely. In view of this, it was considered essential to place harvested herbage in a refrigerator as quickly as possible and to complete all chlorophyll extractions within a few hours of harvesting. Preliminary investigations showed that one person could harvest the material from four quadrats of one half square foot each, could subsample these and extract the chlorophyll from two subsamples from each quadrat in between 6 and 7 hours. In the light of this information, the following procedure was adopted

as the one which made full use of the available time:-

(a) Field sampling procedure.

Two randomly sited one half square foot quadrats were cut to ground level on each sub-plot. One quadrat in each sub-plot was cut between 6.30 and 8.0 a.m. and the other between 1.00 and 2.30 p.m. In this way it was hoped that any possible error caused by diurnal variation in chlorophyll content (Bulatsch, 1930; Bavrina, 1959) would be minimised. The herbage was clipped with a pair of surgical scissors with 3 in. curved blades. During clipping the herbage immediately on either side of the edge of the quadrats was carefully separated. The material collected from the quadrats was placed in a plastic bag, and was placed in the refrigerator as soon as the full complement of samples had been collected.

After the 95% light interception level was reached the material above the 95% point was harvested separately from the material below the point. The material above the 95% level was first collected using a pair of shears with 6 in. blades and welded sides, and then the remaining material was cut to ground level using curved scissors.

(b) Laboratory sub-sampling procedure.

In the laboratory herbage from each quadrat was weighed and a subsample of between 1 and 2 gm. weight was taken for chlorophyll extraction. At the same time two similar subsamples were taken for dry matter percentage determination.

These samples were obtained by thoroughly mixing the herbage on the dissection table and then dividing, by hand, the whole pile of herbage into 2, 4 and so on until the requisite size of sample was obtained. In this way, the separation of small particles from the bulk was avoided and a representative sample of the herbage obtained. The resulting subsamples were weighed accurately on a Mettler air-damped balance, and then placed in a small aluminium container. One of the subsamples was stored in the refrigerator until required for chlorophyll determination. The other two were placed in an oven and dried for 24 hours at between 160 and 180°F. The herbage remaining was placed in a plastic bag and stored in the refrigerator until required for further subsampling for leaf weight/area ratio, dead matter, percentage of stem and leaf area index determinations. After further subsampling the remainder was dried and the total dry matter yield of the quadrat determined by adding the weight of the remainder to the dry weight of the subsamples.

(c) Determination of the chlorophyll content of the subsamples.

The subsamples were extracted in a 4:1 (by volume) mixture of acetone and ethyl alcohol (Mackinney, 1941; Zscheile and Comar, 1941; Arnon, 1949; Bruinsma, 1961). In order to prevent breakdown of chlorophyll only one sample at a time was processed. The material was ground up in the acetone-alcohol mixture using a pestle and mortar, and the resulting solution decanted into a 100 ml. measuring cylinder. This was stored in the dark. A further extraction was made and this process was repeated until

~~was thought that~~ the material was completely extracted. The lack of any green colour in the remaining plant material and the lack of colour in the acetone-alcohol following extraction were the criteria used in this judgment.

When extraction was complete the solution in the measuring cylinder was immediately made up to 100 ml. with the acetone-alcohol mixture, and after thorough stirring an aliquot of the crude extract was centrifuged for about five minutes in a Griffin and George autopoise centrifuge run at approximately 2,500 r.p.m. Five minutes was in all cases sufficient to clear the supernatant. A pipette was then used to transfer 1 ml. of the chlorophyll solution into a 10 ml. measuring cylinder. This was made up to 10 ml. with the acetone-alcohol mixture and well shaken. A small cuvette was filled with the solution and the optical density determined at wave-lengths of 645 and 663 mμ in a Unicam SP 600 spectrophotometer.

The amount of chlorophyll in the extract was calculated using the equations of Arnon (1949):-

$$\text{Chlorophyll a} = (0.0127D_{663} - 0.00269D_{645}) \text{ gms. per litre.}$$

$$\text{Chlorophyll b} = (0.0229D_{645} - 0.00468D_{663}) \text{ gms. per litre.}$$

(Where D is the optical density at the particular wavelength shown in subscript).

The reliability of the acetone spectrophotometer method has been found to decrease when either chlorophyll 'a' or 'b' becomes 3-5 times more concentrated than the other (van Norman, 1957). The ratio of chlorophyll a: chlorophyll b rarely increased above 4 in the present investigation and this was not considered to be an important source of error.

(d) Calculation of the Chlorophyll Content per Unit of Ground Area.

In order to overcome some of the complications associated with extraneous water and diurnal variation in the plants' dry matter percentage the dry weight basis was used in this calculation. The dry weight of the chlorophyll subsamples was calculated from the mean of three dry matter percentage determinations, small subsamples weighed out at the same time as the subsample for chlorophyll extraction providing two of the determinations, the third being determined on a quadrat basis by relating the total dry weight of the harvested material to its fresh weight. The chlorophyll content per unit of ground area was calculated by relating the chlorophyll content and calculated dry weight of the subsample to the total dry weight of the material harvested from the quadrat.

Determination of Leaf Weight/Area Ratio.

The herbage remaining after subsampling for the chlorophyll determinations was used. From each sample a variable number of leaf laminae with a total surface area of between 30 and 50 square centimetres was taken. The area of these was determined by using an air-flow planimeter similar to the one described by Jenkins (1959), they were then dried and weighed, and the leaf weight/area ratio calculated.

Determination of the Percentage of Stem in the Living Matter, the Leaf Area Index and the Dead Matter Yield.

From the material remaining after subsampling for chlorophyll and leaf area/weight determinations a subsample

of between 5 and 10 gm. fresh weight was taken. This size was chosen in order to obtain at least 0.2 gm. of dried dead matter after separation. The remainder of the material taken from the quadrat was dried at a temperature between 160 and 180°F.

The subsample was separated into leaf, stem and dead matter. Only the laminae were classed as leaf, the leaf sheath being included in the stem fraction. An arbitrary demarcation between the living and dead matter was adopted. The yellow leaves were included along with the completely brown dead ones and classed as dead matter. The various fractions were dried and the total weight of dead matter, stem and leaf in the quadrat sample calculated. From these figures an estimate of the total dead matter yield and of the percentage of stem in the living matter was obtained. The area of leaf taken from the quadrat was found by relating the leaf weight to the leaf weight/area ratio. When the area of leaf taken from the quadrat is divided by the ground area of the quadrat it is, by definition, leaf area index (Watson, 1947).

Determination of the Dry Matter Yield.

A 2 ft. wide strip was cut to 1 in. from ground level along the length of the sub-plots. A Dennis rotating drum mower was used for this purpose. The area mown varied in length between 7 ft. and 10 ft. and included the areas harvested for chlorophyll content per unit of ground area determinations. In view of this the area mown was measured in each case. The herbage was carried to the

oven room in a jute sac and all the harvested material dried at a temperature between 180 and 200°F. for 24 hours. It was then weighed and the dry matter yield calculated.

Statistical Procedure.

Regression equations and standard errors of the means were calculated according to methods described by Snedecor (1956). Where two samples per plot had been taken replication effects were removed by calculating the standard error of the mean in the following manner:-

$$\text{Standard error of the mean} = \sqrt{\frac{\text{Total Sums of Squares} - \frac{\text{Rep. Sums of Squares}}{(n) (n - r)}}{(n) (n - r)}}$$

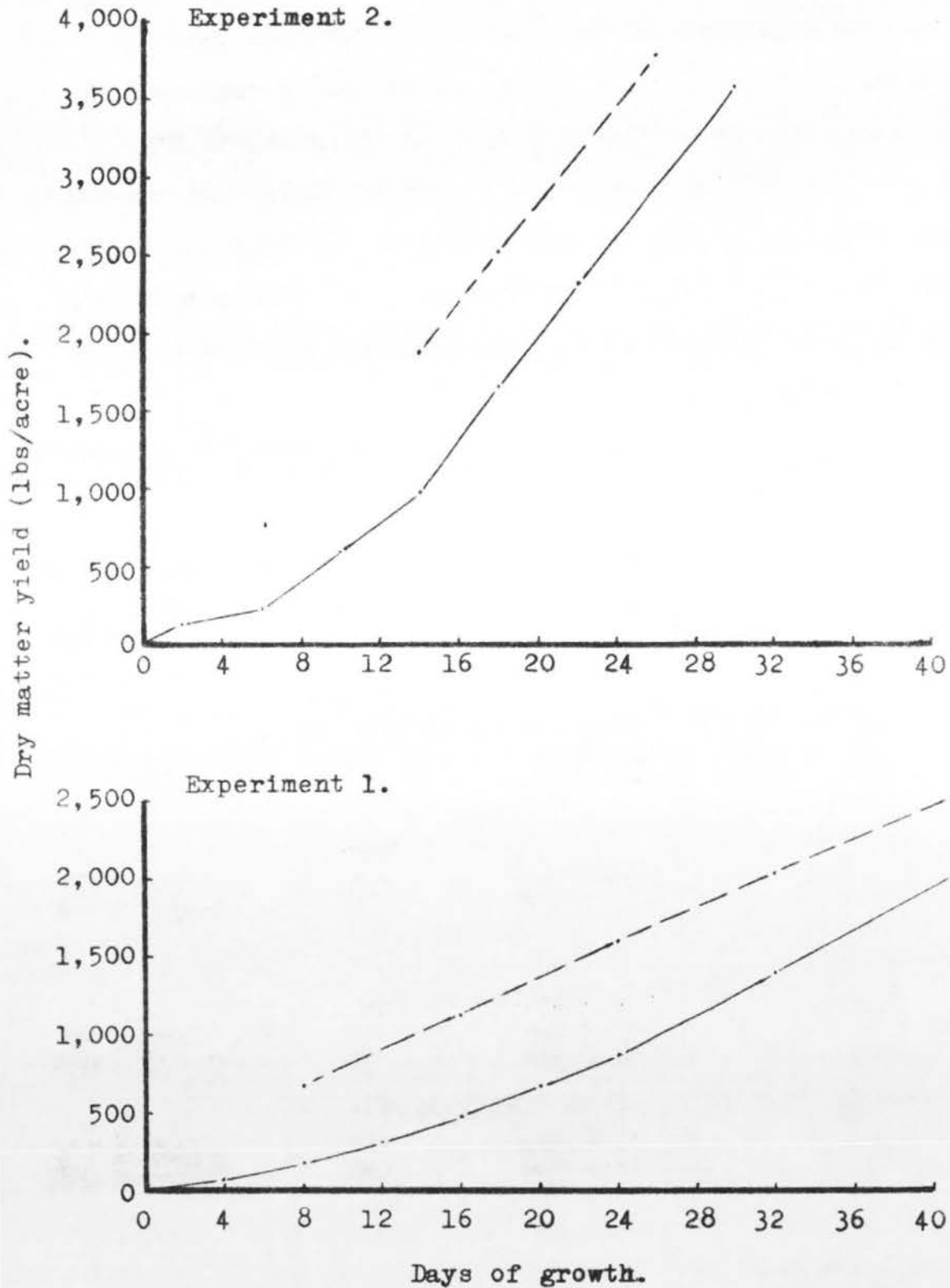
Where n is the number of observations and r is the number of replications. The standard error of the rate of dry matter increase was calculated according to the following formula:-

$$\sqrt{\frac{SE_1^2 + SE_2^2}{t_2 - t_1}}$$

Where SE_1^2 and SE_2^2 are the standard errors of the dry weight determinations at times t_1 and t_2 respectively.

Fig. 2. Dry matter yields at various stages of growth.

— Swards cut to 1" from ground level.
- - - Swards cut to 2½" from ground level.



CHAPTER 3

RESULTS

Dry Matter Yield Measurements.

The dry weight of the material harvested above 1" from ground level increased with time in both experiments. This is illustrated in Fig. 2. (Experimental data are presented in Appendix 1). Dry matter yields measured by cutting half square foot quadrats to ground level were approximately 1,000 lbs. per acre greater than when yields were measured by cutting to 1" from ground level. The data from the first and last samplings in both experiments are shown in Table 1. Complete data are presented in Appendices 1 and 2.

Table 1. Comparison of dry matter yields measured by cutting to ground level with those measured by cutting to 1" from ground level.

Cut to ground level		Cut to 1" from ground level	
Days of growth	Mean yield (lbs/acre)	Days of growth	Mean yield (lbs/acre)
Experiment 1.			
Swards cut to 1" from ground level.			
3	1,126 \pm 59	4	77 \pm 5
40	3,011 \pm 149	41	2,026 \pm 112
Swards cut to 2½" from ground level.			
7	1,732 \pm 80	8	790 \pm 43
39	3,463 \pm 230	41	2,515 \pm 121
Experiment 2.			
Swards cut to 1" from ground level.			
1	1,527 \pm 121	2	140 \pm 10
29	4,660 \pm 231	30	3,585 \pm 204
Swards cut to 2½" from ground level.			
16	3,774 \pm 212	14	1,881 \pm 113
24	4,712 \pm 231	26	3,790 \pm 212

Rates of Dry Matter Increase.

The rates at which dry matter accumulated were calculated from the measurements of dry matter yield made by cutting to 1" from ground level. These calculations show that the rate of dry matter increase on the swards cut to 1" from ground level in the first experiment increased from 19 lbs. per acre per day on the third day of growth to 65 lbs. per acre per day on the thirty-first day of growth. In the second experiment the rate of dry matter increase on the swards cut to 1" from ground level was 70 lbs. per acre per day during the first few days of growth and a maximum of 170 lbs. per acre per day on the seventeenth day of growth. The rates at which dry matter accumulated and their standard errors are shown in Table 2.

Table 2. Rates of dry matter increase at various stages of growth.

Experiment 1		Experiment 2	
Days of growth	Rate of dry matter increase (lbs./acre/day)	Days of growth	Rate of dry matter increase (lbs./acre/day)
Swards cut to 1" from ground level.			
3	19 ± 1	1	70 ± 5
7	29 ± 3	5	50 ± 2
11	32 ± 6	9	90 ± 4
15	41 ± 10	13	95 ± 6
19	47 ± 12	17	170 ± 15
23	51 ± 11	21	170 ± 21
31	65 ± 11	29	156 ± 29
40	70 ± 17		
Swards cut to 2½" from ground level.			
14	43 ± 13	16	160 ± 23
22	57 ± 17	24	160 ± 32
30	56 ± 18		
39	59 ± 20		

Dead Matter Yield Measurements

The amount of dead matter fluctuated considerably. A maximum quantity of 1,234 lbs. per acre was measured after sixteen days of growth on the swards cut to 2½" from ground level in the second experiment. The minimum amount (211 lbs. per acre) was recorded nineteen days after cutting to 1" from ground level in the first experiment. The dead matter yields and their standard errors are presented in Table 3.

Table 3. Dead matter yields at various stages of growth.

Experiment 1.		Experiment 2.	
Days of growth	Dead matter yield (lbs. of dry matter/acre)	Days of growth	Dead matter yield (lbs. of dry matter/acre)
Swards cut to 1" from ground level.			
3	352 ± 26	1	913 ± 81
7	362 ± 34	5	610 ± 61
11	345 ± 50	9	696 ± 51
15	262 ± 49	13	427 ± 47
19	211 ± 55	17	444 ± 43
23	240 ± 45	21	460 ± 50
31	440 ± 42	29	1,004 ± 99
40	492 ± 51		
Swards cut to 2½" from ground level.			
7	371 ± 52	16	1,234 ± 111
14	240 ± 60	24	782 ± 81
22	428 ± 46		
30	534 ± 33		
39	686 ± 44		

The Percentage of Stem in the Living Matter.

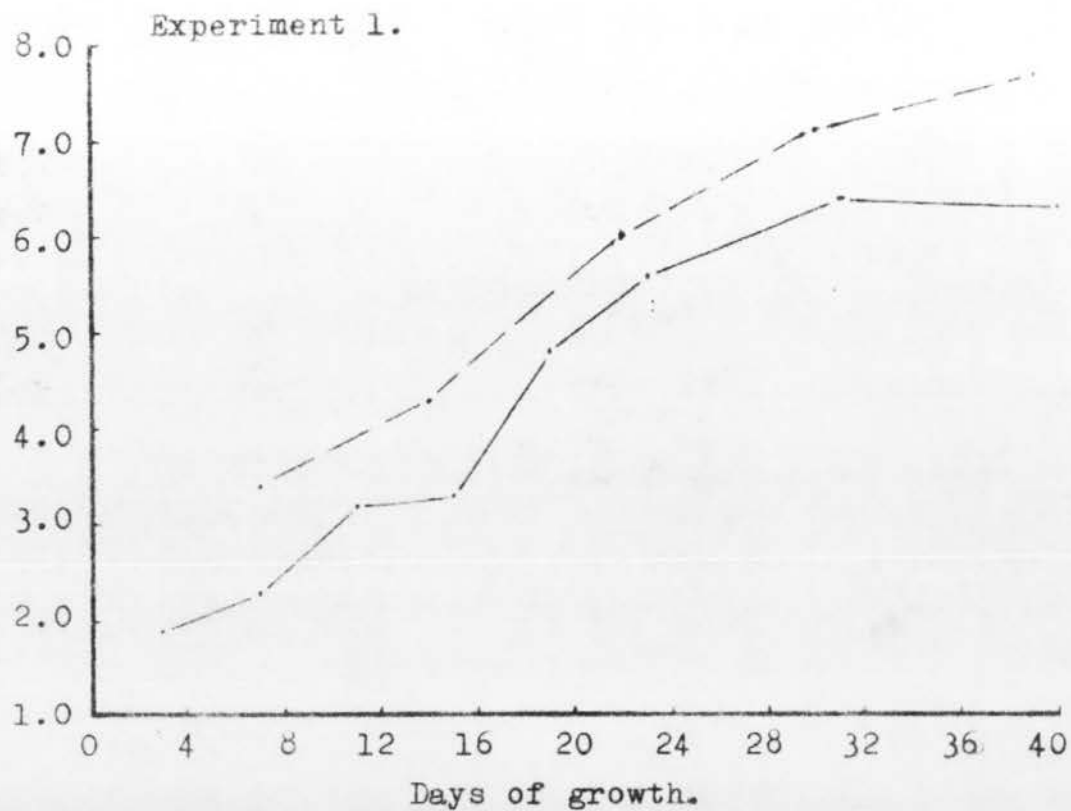
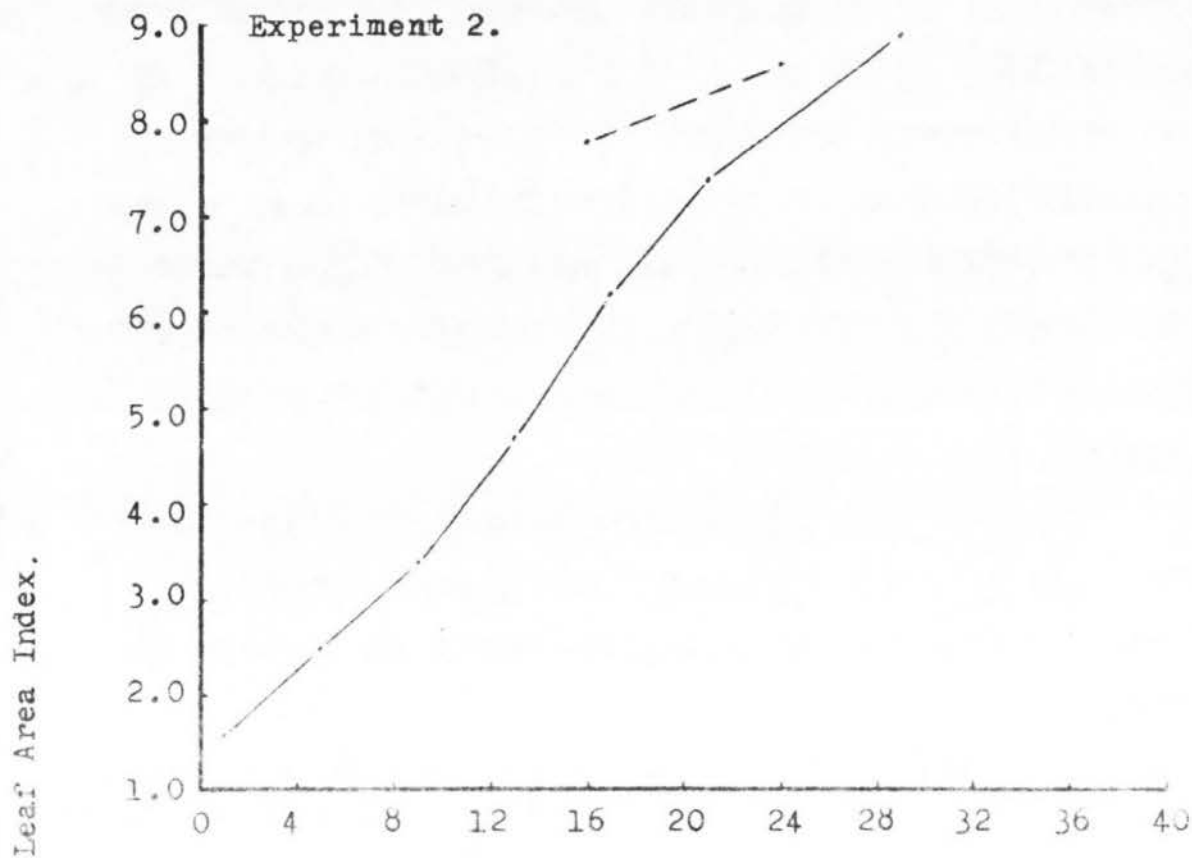
The percentage of stem in the living matter varied between 4.2 and 38.3. In the first experiment (April) the range was from 7.2 to 16.8 in material taken from the swards cut to 1" from ground level, and from 4.2 to 13.5 in material taken from the swards cut to 2½" from ground level. In the second experiment (December) the percentage of stem was higher and varied between 24.0 and 38.3. This is shown in Table 4,

Table 4. Percentage of stem in the living matter harvested at various stages of growth.

Experiment 1		Experiment 2	
Days of growth	Percentage of stem in the living matter	Days of growth	Percentage of stem in the living matter
Swards cut to 1" from ground level.			
3	14.8 ± 1.1	1	38.3 ± 2.1
7	15.8 ± 2.1	5	34.4 ± 2.3
11	16.8 ± 1.1	9	30.5 ± 1.9
15	12.1 ± 1.0	13	24.3 ± 2.7
19	12.6 ± 1.1	17	24.0 ± 2.9
23	12.1 ± 1.2	21	19.4 ± 2.6
31	7.2 ± 0.7	29	30.6 ± 2.7
40	16.4 ± 1.2		
Swards cut to 2½" from ground level.			
7	13.5 ± 0.6	16	30.2 ± 2.8
14	7.4 ± 0.8	24	32.7 ± 3.2
22	4.2 ± 0.4		
30	5.1 ± 0.9		
39	12.8 ± 0.9		

Fig. 3. Leaf Area Indices at various stages of growth.

— Swards cut to 1" from ground level.
- - - Swards cut to 2½" from ground level.



Leaf Area Index Measurements.

In the first experiment the leaf area index increased from 1.1 to 6.4 in the swards cut to 1" from ground level, and from 3.3 to 7.7 in the swards cut down to 2½". In the second experiment higher values were reached and the increase was from 1.6 to 8.9 in the swards cut to 1" from ground level, and from 7.8 to 8.6 in the swards cut to 2½". The values increased rapidly in the early stages of growth and this is illustrated in Fig. 3. Data are presented in Appendix 3.

The leaf area index above the level at which 95% of the noon light was intercepted was greater during the second experiment than during the first, as is shown in Table 5.

Table 5. Leaf Area Index above the level at which 95% of the noon light was intercepted at various stages of growth.

Experiment 1		Experiment 2	
Days of growth	Leaf area index	Days of growth	Leaf area index
Swards cut to 1" from ground level.			
31	5.4 ± 0.5	17	6.2 ± 0.3
40	5.3 ± 0.3	29	6.3 ± 0.4
Swards cut to 2½" from ground level.			
14	3.9 ± 0.1	16	6.9 ± 0.4
22	4.5 ± 0.5	24	6.5 ± 0.4
30	5.1 ± 0.5		
39	5.1 ± 0.1		

Leaf Weight/Area Measurements.

The leaf weight/area ratios are shown in Table 6.

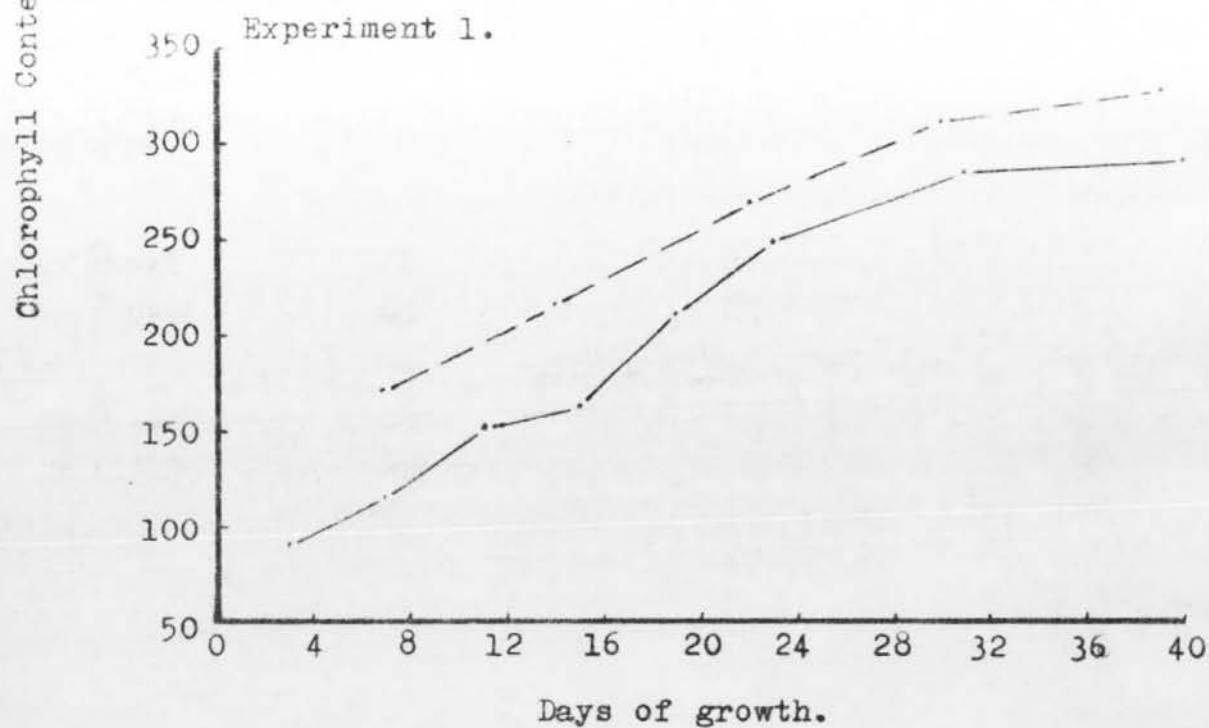
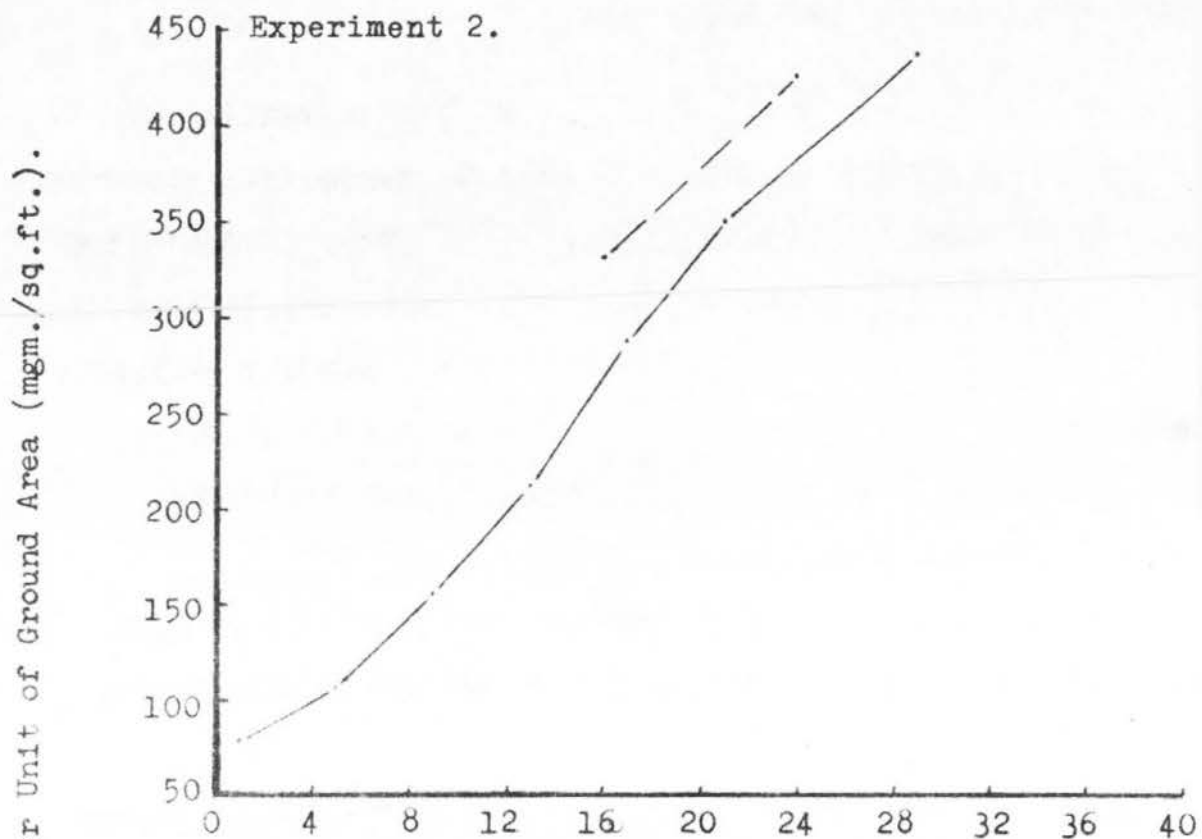
Table 6. Leaf weight/area ratios at various stages of growth.

Experiment 1		Experiment 2	
Days of growth	Leaf weight/area ratio mg./cm.	Days of growth	Leaf weight/area ratio mg./cm.
Swards cut to 1" from ground level.			
3	4.11 \pm 0.18	1	4.00 \pm 0.21
7	4.15 \pm 0.18	5	4.02 \pm 0.17
11	3.49 \pm 0.11	9	3.97 \pm 0.16
15	3.76 \pm 0.12	13	3.61 \pm 0.17
19	3.08 \pm 0.12	17	2.65 \pm 0.12
23	3.45 \pm 0.09	21	2.99 \pm 0.12
31	3.15 \pm 0.14	29	2.92 \pm 0.13
40	3.69 \pm 0.10		
Swards cut to 2½" from ground level.			
7	3.90 \pm 0.20	16	2.93 \pm 0.14
14	3.72 \pm 0.08	24	3.01 \pm 0.16
22	3.48 \pm 0.09		
30	3.42 \pm 0.13		
39	3.64 \pm 0.07		

In the swards cut to 1" from ground level the leaf weight/area ratio decreased throughout the growing period, and regressions for leaf weight/area ratio on time were calculated for both experiments. In the second experiment the regression was significantly linear at the 5% level, but this was not the case in the first. The regression analyses are shown in Appendix 4. The regression coefficients and their standard errors were -0.017 ± 0.011 mgm. per cm² per day for experiment one and -0.051 ± 0.015 mgm. per cm² per day for experiment two. The regressions did not differ significantly

Fig. 4. Chlorophyll Content per Unit of Ground Area at various stages of Growth.

- Swards cut to 1" from ground level.
- - - Swards cut to 2½" from ground level.



and the data were combined to give an overall regression equation (Appendix 4). The regression coefficient so obtained was -0.026 ± 0.010 mgm. per cm^2 per day. This was significant at the 5% level.

Chlorophyll Content per Unit of Ground Area Measurements.

The chlorophyll content per unit of ground area increased rapidly following defoliation to 1" from ground level in both experiments. The rate at which chlorophyll accumulated declined in the later stages of growth and corresponded more closely with that measured on the swards cut to 2½" from ground level. This is shown in Fig. 4, the data being presented in Appendix 5.

The chlorophyll content per unit of ground area above the level at which 95% of the noon light was intercepted is shown in Table 7.

Table 7. Chlorophyll Content per Unit of Ground Area above the level at which 95% of the noon light was intercepted at various stages of growth.

Experiment 1		Experiment 2	
Days of growth	Chlorophyll content per unit of ground area mgm./sq.ft.	Days of growth	Chlorophyll content per unit of ground area mgm./sq.ft.
Swards cut to 1" from ground level.			
31	242 \pm 18	17	290 \pm 11
40	238 \pm 20	29	298 \pm 17
Swards cut to 2½" from ground level.			
14	192 \pm 20	16	311 \pm 17
22	215 \pm 20	24	313 \pm 17
30	229 \pm 18		
39	221 \pm 19		

Fig. 5. The Relationships between Leaf Area Index and Rate of Dry Matter Increase.

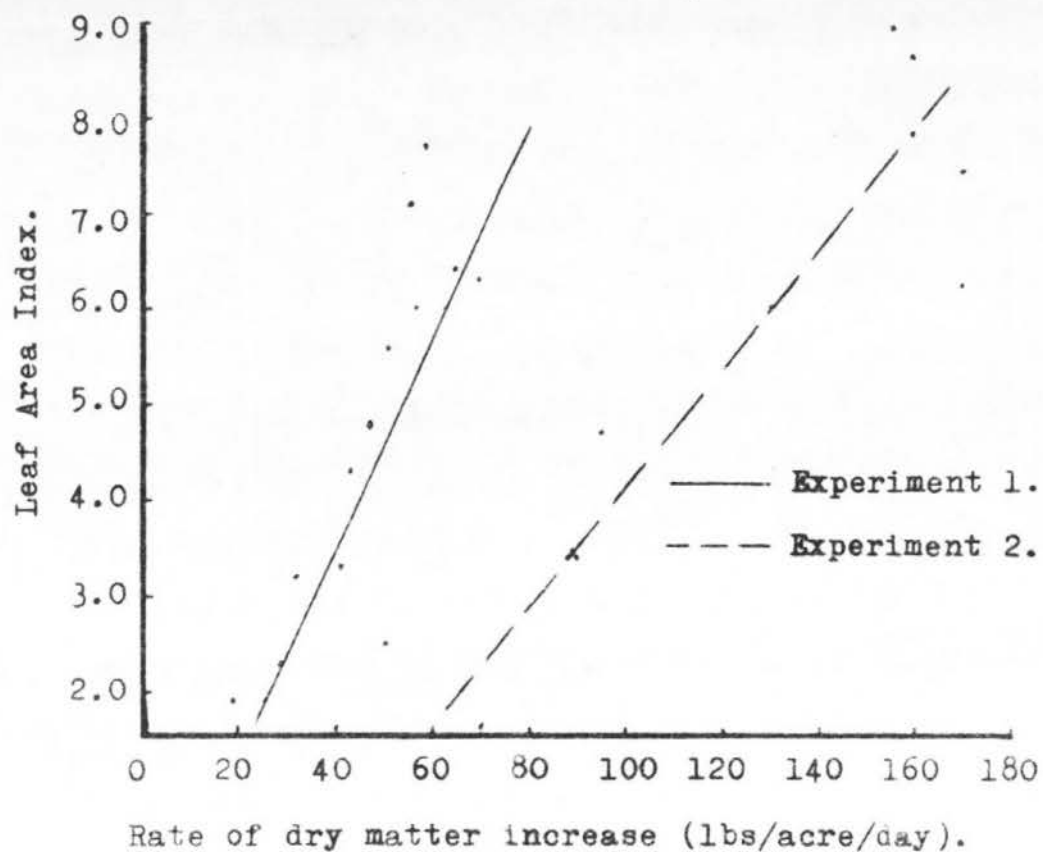
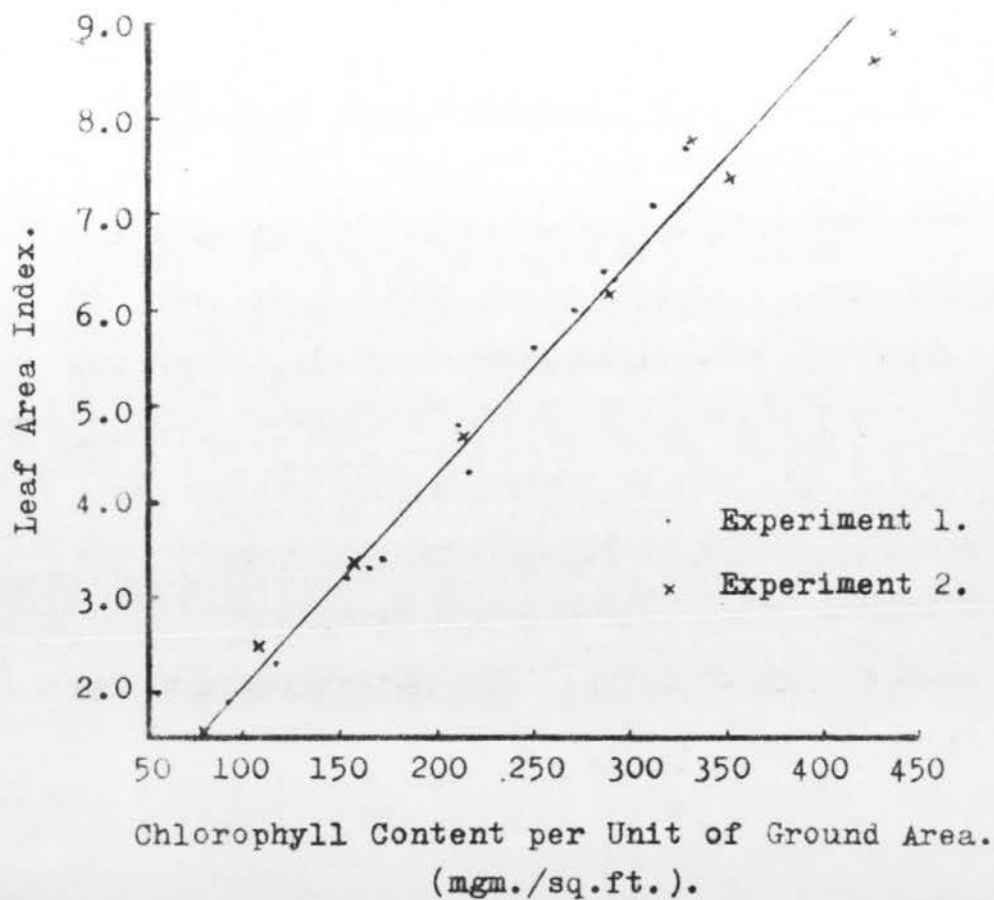


Fig. 6 The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.



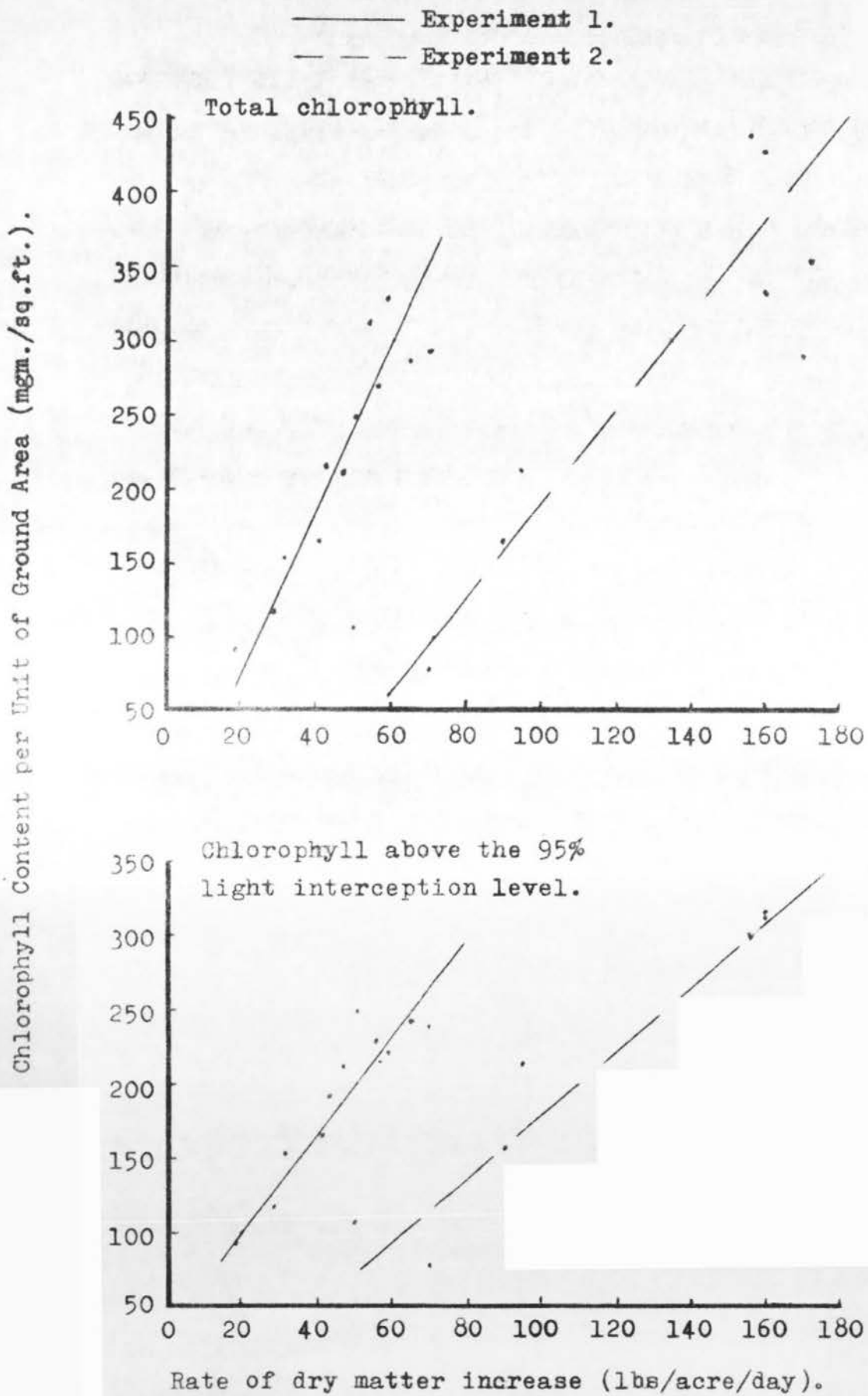
The Relationships between Leaf Area Index and Rate of Dry Matter Increase.

The regression lines for rate of dry matter increase on leaf area index in the two experiments are shown in Fig. 5. Data obtained from the swards cut to 1" and 2½" from ground level are used in the calculation of these regressions, and the regression analyses are shown in Appendix 6. The regression coefficients and their standard errors were 7.3 ± 1.0 for experiment one and 15.8 ± 2.8 for experiment two, i.e., an increase of 1 square foot of leaf area was accompanied by an increase in the rate at which dry matter accumulated of 7.3 lbs. per acre per day in experiment one and 15.8 lbs. per acre per day in experiment two. The linear equations were highly significantly different from zero, but the improvement due to fitting a quadratic was only significant at the 10% level in the first experiment and not significant in the second.

The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.

Highly significant linear regressions of chlorophyll content per unit of ground area on leaf area index were obtained. The regression coefficients were 40.5 ± 1.4 for the first experiment and 48.7 ± 2.2 for the second (Appendix 7). There was a highly significant difference between the regressions but the data were combined and a highly significant linear regression with a coefficient of 45.5 ± 1.5 obtained (Appendix 7). The regression line for the combined data is shown in Fig. 6.

Fig. 7. The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.



The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.

The regression lines for rate of dry matter increase on chlorophyll content per unit of ground area are shown in Fig. 7. Data from both treatments were used in the calculation of the regressions, and the analyses are shown in Appendix 8. The regression coefficients and their standard errors were 0.183 ± 0.067 for experiment one and 0.319 ± 0.060 for experiment two. The linear equations were highly significantly different from zero, but the improvement due to fitting a quadratic was not significant in either case (Appendix 8).

When the chlorophyll which was below the 95% light interception level was excluded from the analyses highly significant linear regressions with coefficients of 0.304 ± 0.030 for the first experiment and 0.471 ± 0.059 for the second were obtained. The regression analyses are shown in Appendix 8 and the regression lines in Fig. 7.

CHAPTER 4

DISCUSSION

A. The Relationships between Leaf Area Index and Rate of Dry Matter Increase.

In both experiments a significant linear regression of rate of dry matter increase on leaf area index was obtained (Appendix 6). Approximately constant maximum rates of dry matter increase were, however, maintained when sufficient foliage had been formed to intercept 95% of the noon light. This latter finding corresponded with that of Brougham (1956) and suggested that asymptotic relationships would have been obtained in the present study if a greater number of replicates had been used. This is supported by the fact that a quadratic relationship, significant at the 10% level, was obtained in the first experiment.

Influence of dead matter build-up and decay.

Watson (1958) and Davidson and Donald (1958) recorded a maximum rate of dry matter increase at one particular leaf area index in stands of kale and subterranean clover. In the present investigation maximum rates of dry matter increase were maintained over a range of leaf area index values. It was observed, however, that when the rate of dry matter increase was constant the quantity of dead matter present in the sward increased at a rate corresponding with the rate of increase in total aerial dry matter. No information is available on the amount of dead matter that was present in the stands studied by Watson (loc. cit.) and Davidson and Donald (loc. cit.). Brougham (1958b) has however reported

that the rate of decay of white clover leaves in undisturbed stands is very rapid, and Frame (1957) has reported that leaf shedding began shortly after a stand of marrow stem kale completely covered the ground surface. It may well be that the reduction in the rate of dry matter accumulation recorded in the studies of Watson (loc. cit.) and Davidson and Donald (loc. cit.) was due to a rapid destruction of dead plant material and was not due to a growth response in the plant itself. Further work is however, necessary before a complete understanding of the significance of dead matter build up and decay in pastures and crops is obtained. In view of the saprophytic mode of nutrition of the facial eczema fungus Pithomyces chartarum (Brook, 1961) this is of special significance in New Zealand.

Importance of the 95% light interception level.

Studies reported by Warren Wilson (1960a) on the relationship between light intensity and dry matter accumulation in individual leaves support the contention that the relationship between leaf area index and rate of dry matter increase is curvilinear. These show that the individual leaves of many crop plants can build up sufficient dry matter to compensate for their losses of dry matter in respiration when exposed continuously to a light intensity of 100 foot candles. At Palmerston North the light intensity on a horizontal surface at noon in midsummer is approximately 10,000 foot candles (Brougham, 1958a). Leaf tissue receiving 5% of the noon light would be exposed to 500 foot candles for a short time in the middle of the day,

but would receive very little light in the morning and afternoon. Over the 24 hours of the day such a leaf may well receive light of an average intensity of less than 100 foot candles. If grass leaves require 100 foot candles before their dry matter gain through photosynthesis exceeds losses through respiration such a leaf would be unable to make a contribution to the dry matter accumulation of the community. Photosynthetic tissue below the level at which 95% of the noon light is intercepted is thus of little value and studies of the effective photosynthetic system can be restricted to the tissue situated above the 95% light interception level.

Leaf area indices above the 95% light interception level.

The leaf area index above the 95% light interception level was termed the 'critical leaf area index' by Brougham (1958a) and the mean value of this was 4.9 ± 0.3 in April and 6.5 ± 0.4 in December (Table 5).

In the first experiment however, a critical leaf area index of 3.9 ± 0.1 was measured on April 11th. The critical leaf area index increased subsequently and on 27th April had reached a figure of 5.1 ± 0.3 . A similar phenomenon in a subterranean clover sward was noted by Black (1958a). He explained a change of from 4 to 7 in the critical leaf area index as being due to an increase in the amount of light transmitted through each leaf. The maximum difference in the amount of light so transmitted would appear to be about 13% (Geiger, 1950; Moss and Loomis, 1952), so that changes in leaf transmissibility would not fully account for the measured difference in

critical leaf area index. A change in the form of the photosynthetic canopy may have been involved, as appeared to be the case in the first experiment of the present investigation. The change of form in this case involved a certain amount of flagging (a tendency for the tips of the leaves to bend towards the horizontal) following a period of rainy weather. A change in form of this type would reduce the extent to which light penetrated into the sward (Mitchell and Calder, 1957) and so lower the critical leaf area index. Further growth in the sward resulted in the re-establishment of the normal habit of growth, this would change the light absorbing properties of the foliage and so increase the amount of tissue needed to intercept 95% of the noon light.

In December the critical leaf area index of perennial ryegrass swards has been measured as 7.1 ± 0.9 (Brougham 1958a). This does not differ significantly from the mean figure of 6.5 ± 0.4 measured in experiment two. The mean critical leaf area index at this time of year is higher than in April, and this difference is explained by a higher maximum elevation of the sun and dependent upon this, a higher noon light intensity. These factors would act independently and both would increase the extent to which light penetrated into the sward (Brougham, 1958a) and hence, the leaf area index necessary to intercept 95% of the incoming light at noon.

Net assimilation rate calculations.

The relationship between leaf area index and rate of dry matter increase at any one time can be expressed in

one figure as the 'net assimilation rate' (Watson 1952).

The term 'net assimilation rate' is generally used to refer to the figure calculated by dividing the rate of increase of total dry weight by the leaf area, rather than the one calculated using aerial dry weight data only (Watson, loc. cit.). The term can, however, be used more widely and without confusion if it is qualified by reference to the material used in the calculation of the rate of dry matter increase. In the present experiments this is restricted to all material above 1 in. from ground level and net assimilation rate calculated in this way corresponds to the 'leaf efficiency index' referred to by Brougham (1956).

In this investigation the net assimilation rate can be calculated by inserting appropriate values in the regression equation of rate of dry matter increase on leaf area index (Appendix 7) and then dividing the rate of dry matter increase by the leaf area index. In the first experiment (April) the net assimilation rate at the mean critical leaf area index (4.9) was approximately $9.7 \pm 0.4^{(*)}$ lbs. of dry matter per acre of leaf tissue per day. In the second experiment (December) the rate

(*) The standard error of an estimated net assimilation rate at a given leaf area index is the same as the standard error of the estimated rate of dry matter increase. In all cases where a particular value (\bar{y}), which is in this case rate of dry matter increase, is calculated from a regression equation the standard error is given by:-

$$\sqrt{s^2 \frac{1}{n} + \frac{(\bar{x} - x_1)^2}{S.S.x.}}$$

Where s^2 is the residual variance from the regression analysis, \bar{x} is the mean of the concomitant variable, n is the number of observations and $S.S.x.$ is the corrected S.S. for \bar{x} .

of dry matter increase was approaching the maximum attainable and the net assimilation rate at the mean critical leaf area index (6.5) was 21.2 ± 1.2 lbs. of dry matter per acre of leaf tissue per day. A similar figure to that obtained in the second experiment can be calculated when the rate of dry matter increase measured in midsummer (156 lbs. of dry matter per acre per day) by Brougham (1960) is related to the critical leaf area index of 7.1 measured in another experiment carried out at the same time of year (Brougham 1958a). The net assimilation rate calculated from these data is 21.9 lbs. of dry matter per acre of leaf per day.

The net assimilation rate at the critical leaf area index, when converted to gm. per square metre per week, was approximately 5.2 in the first experiment and 11.7 in the second. These figures contrast with the figure of approximately 55 gm. per square metre which Heath and Gregory (1938) accepted as the net assimilation rate for all species and environments. Subsequent work has shown that the net assimilation rate can vary according to the environment (Blackman and Wilson, 1951; Warren Wilson, 1960b) the leaf area index (Watson, 1958; Watson and Witts, 1959) and the species (Watson, 1947). The difference between the figures obtained in the present study and the figure of Heath and Gregory (loc. cit.) may be explainable in these terms. On the other hand, no account was taken of root growth in the present investigation, so that the low values may have been due to a higher proportion of the dry matter produced being accumulated in underground organs.

Seasonal variation in net assimilation rates.

The difference in the net assimilation rates calculated for critical leaf area index values in April and December is attributed to seasonal change in climatic factors. It is difficult to distinguish which factors are responsible, however, for those which are likely to affect net assimilation rate, viz. temperature, length of day and maximum light intensity are highly correlated. The mean air temperatures (59.7°F. in April and 64.1°F. in December) measured at an official climatological station sited approximately 400 yards from the experimental site were, however, within the range considered optimum for the growth of perennial ryegrass by Mitchell (1956). In view of this, the difference in net assimilation rates can be attributed to a difference in the amount of light received each day. In December the mid-day light intensity and the daylength are both approaching the maximum values, and the amount of light energy received each day is in consequence higher than in the autumn. This is shown in the following table which is taken from data published by Brougham (1959).

Table 8. Average amount of solar radiation received on a horizontal surface in Palmerston North, 1955-1956.

Month	Nov.	Dec.	Jan.	Feb.	March	April	May
Radiation received per day.	450	500	475	400	350	250	150
(g.cal.per cm^2 .)							

Species variation in net assimilation rates.

Watson (1947) used the dry matter increases of both above and below ground organs in the calculation of net assimilation rate and showed that the net assimilation rate of sugar-beet was nearly twice that of wheat. A similar difference between sugar-beet and barley was reported by Thorne (1960) and it would appear that the net assimilation rate of cereal crops is lower than that of dicotyledonous root crops.

A true comparison of the differences in net assimilation rates of different species can, however, only be made when the species are grown in environments where the same amount of light is intercepted. No data are available for dicotyledonous species where both the rate of dry matter increase and the critical leaf area index were recorded at the same time. Watson (1956) however measured a net assimilation rate of approximately 30 gm. per square metre for a stand of kale growing at its maximum rate at a leaf area index of 3.0 and of approximately 45 gm. per square metre for a stand of sugar-beet at a leaf area index of 5.5. The leaf area index when stands reach their maximum rate of dry matter increase may well correspond with the critical leaf area index. If this is so the figures obtained by Watson (loc. cit.) can be compared with those obtained in the present study. Such a comparison shows that the net assimilation rate in both experiments carried out with ryegrass swards was much lower than in the dicotyledonous stands, despite the fact that the second experiment was carried out when conditions for growth were very good.

Deficiencies of nitrogen, phosphorous and potassium can all affect the net assimilation rate (Watson, 1952) but as adequate nitrogen had been applied to the swards and as there were no indications that potassium or phosphorus were deficient, it is unlikely that the low values were caused by mineral deficiency. It would thus appear that the net assimilation of perennial ryegrass and possibly other graminaceous species is inherently lower than that of dicotyledonous root crops. A much more intensive study of the photosynthetic system of different species and of the direction in which dry matter is distributed among different plant organs is, however, essential before firm conclusions can be made.

Effect of increasing leaf area index on net assimilation rate.

In the first experiment the net assimilation rate declined from 19.0 ± 4.3 lbs. per acre of leaf tissue per day (10.4 gm./m²/week) to 9.0 ± 0.4 lbs. per acre of leaf per day (4.9 gm./m²/week) as the leaf area index increased from one to seven. Change in the leaf area index had a great effect on net assimilation rate in experiment two and the decrease over the same leaf area index range was from 50.7 ± 14.7 lbs. per acre of leaf per day (27.78 gm./m²/week) to 20.8 ± 1.4 lbs. per acre of leaf per day (11.4 gm./m²/week). In both experiments the standard error of the estimated net assimilation rate was much greater at the lower leaf area index value. This is explainable because the lower leaf area index was further away from the mean of the leaf area index measurements (4.8 in experiment one and 5.7 in experiment two).

A fall in the net assimilation rate as the leaf area index increased was also reported by Watson (1956; 1958). Such a reduction could be due to competition for carbon dioxide, a change in the photosynthetic ability of the leaves, or competition for light.

Major reductions below normal atmospheric carbon dioxide concentration have not been reported, although several studies of the atmosphere within the canopy of crops and pastures have been carried out (Fuller, 1948; Lemon, 1960; Tamm and Krzysch, 1961). Mitchell (1960) however, considered that competition for carbon dioxide would adversely affect pasture growth when leaves flagged and formed a horizontal thatch across the top of the canopy. In the present investigation flagging of leaves was relatively unimportant and only assumed significance for a short period during the first experiment. It would thus appear that competition for carbon dioxide was not the main factor in determining the reduction in net assimilation rate. Watson (1958) came to a similar conclusion in his study of the relationships between leaf area index and rate of dry matter increase in stands of sugar beet and kale.

The ageing of leaves and chloroplasts may have been partially responsible for the reduction in net assimilation rate (Singh and Lal, 1935; Clendinning and Gorham, 1958). In the study carried out by Watson (1958) however, a decline in net assimilation rate was recorded even though the leaves and chloroplasts were of comparable age. It would thus appear that the main factor responsible for a decline in net assimilation rate as the leaf area index increases is mutual

shading of leaves.

Changes in the leaf weight/area ratio.

Variation in the light intensity under which leaves develop is normally linked with a change in the leaf weight to leaf area ratio (Blackman, Black and Kemp, 1955; Mitchell, 1955; Blackman, 1956), and in both of the present experiments the leaf weight/area ratio declined throughout the growing period. A similar phenomenon was noted during the growth of a subterranean clover sward by Davidson and Donald (1958). Thus, the reduction in net assimilation rate could also be associated with a reduction in leaf weight/area ratio.

3. The Relationships between Leaf Area Index and Chlorophyll Content per Unit of Ground Area.

Friend (1961) reported that a reduction in the leaf weight/area ratio was associated with a reduction in the chlorophyll content per unit of leaf area. In the first of the present experiments the regression equation of chlorophyll content per unit of ground area on leaf area index was $y = 40.461 x + 27.03$. (Where y is the chlorophyll content per unit of ground area in mgm./sq.ft. and x the leaf area index. Appendix 8). Inserting the appropriate values for the leaf area index it can be calculated that there was a significant change in the chlorophyll content per unit area of leaf as the leaf area increased from one to seven. At a leaf area index of one the chlorophyll content was 67.5 ± 5.8 mgm. per square foot of leaf area and at a leaf area index of seven it was 44.3 ± 0.6 mgm. per square foot. In experiment two,

however, there was no significant change in the calculated chlorophyll content. At a leaf area index of one this was 38.9 ± 11.5 mgm. per square foot of leaf area and at a leaf area index of seven 47.3 ± 0.9 mgm. per square foot.

The difference between the two experiments can be explained in terms of the physiological state of the majority of tillers. In the first experiment no heads were formed, whereas in the second many tillers were in the floral stage and the mean percentage of stem in the living matter was much greater (11.6 ± 1.0 in the first experiment and 29.4 ± 2.6 in the second). The failure to measure any change in the chlorophyll content per unit of leaf area may thus have been due to chlorophyll contained in the stem and ear.

The chlorophyll content calculated for the mean critical leaf area index was 46.0 ± 0.5 mgm. per square foot in the first experiment and 47.2 ± 0.9 mgm. per square foot in the second. These figures are higher than the figure of 35 ± 3 mgm. per square foot measured by Brougham (1960). Yellow leaves were included along with the living ones in the investigation carried out by Brougham (pers. comm.) and this would reduce the chlorophyll content per unit dry weight. When converted to chlorophyll content per 100 square centimetres the values were 4.9 and 5.1 mgm. for the first and second experiments respectively. These are very similar to the figures obtained by Seybold and Egle (1940) for a number of species.

C. The Relationships between Chlorophyll Content per Unit of Ground Area and Rate of Dry Matter Increase.

The relationships between chlorophyll content per unit of

ground area and rate of dry matter increase are similar in form to the relationships between leaf area index and rate of dry matter increase (Appendices 6 and 8). Examination of the variance of estimate for the two experiments shows that there are no significant differences in the efficiency of estimating rate of dry matter increase from leaf area index or chlorophyll content per unit of ground area.

In the discussion of the relationships between chlorophyll content per unit of ground area and leaf area index it was, however, pointed out that the chlorophyll content per unit of ground area was reduced significantly as the leaf area index increased from one to seven in the first experiment. In this range of leaf area index values the reduction in rate of dry matter increase per unit of leaf area (net assimilation rate) would thus be significantly greater than the reduction in rate of dry matter increase per unit of chlorophyll. In the second experiment there was no significant change in the chlorophyll content per unit of leaf area as the leaf area index increased from one to seven. The reduction in net assimilation rate would thus not differ significantly from the reduction in rate of dry matter increase per unit of chlorophyll. The percentage reductions in net assimilation rate and in rate of dry matter increase per unit of chlorophyll are shown in Table 9.

Table 9. Net Assimilation Rate and Rate of Dry Matter Increase per Unit of Chlorophyll at two Leaf Area Indices.

	Net Assimilation Rate	Rate of Dry Matter Increase per Unit of Chlorophyll
Experiment 1.		
Leaf area index of 1	19	$\frac{19}{67.5} = 0.28$
Leaf area index of 7	9	$\frac{9}{44.3} = 0.20$
<hr/> Percentage reduction	<hr/> 53	<hr/> 28
Experiment 2.		
Leaf area index of 1	51	$\frac{51}{38.9} = 1.31$
Leaf area index of 7	21	$\frac{21}{47.3} = 0.44$
<hr/> Percentage reduction	<hr/> 59	<hr/> 66

In the light of the above discussion it can be suggested that leaf area is related to rate of dry matter increase only insofar as it is related to chlorophyll content. In the discussion of the relationships between leaf area index and rate of dry matter increase it was, however, stated that photosynthetic tissue below the 95% light interception level is unable to make a contribution to the dry matter accumulation of the community. The regressions of rate of dry matter increase on chlorophyll content above the 95% light interception level were highly significantly linear (Appendix 8) and it would appear that the above suggestion should be restricted to chlorophyll above the 95% light interception level.

The chlorophyll content per unit of ground area above the 95% light interception was different in the two experiments. In the first experiment the mean value was 223 ± 19 $\mu\text{gm.}$ per square foot, a figure not significantly different from the one of 209 ± 19 $\mu\text{gm.}$ per square foot measured by Brougham (1960)

in similar swards in February. In December the figure was 303 ± 16 mgm. per square foot. The higher figure at this time of year is explainable in view of the increase in the elevation of the sun and in the noon light intensity between April and December.

In conclusion it is suggested that chlorophyll determinations can play a valuable part in further analytical studies of crop and pasture growth. The use of chlorophyll will obviate the arbitrary division of leaf tissue into sheath and lamina, or into living, senescing and dead fractions, and will impart a little more precision into growth studies. This will be of ~~great~~ value in suggesting reasons for these more elusive changes in net assimilation rates and in leaf efficiency indices which now remain unexplained.

SUMMARY

Two experiments were carried out to study the relationships between leaf area index, chlorophyll content per unit of ground area and rate of dry matter increase. An established perennial ryegrass sward was used and at the commencement of the experiments areas of this were cut to 1 in. and 2½ in. from ground level. Measurements were taken at varying intervals over a period of 41 days in the autumn and 30 days in the spring of herbage dry matter yield, dead matter yield, percentage of stem in the living matter, leaf weight/area ratio, leaf area index above and below the 95% light interception level and chlorophyll content per unit of ground area above and below the 95% light interception level.

The rate at which dry matter accumulated increased until sufficient foliage had been formed to intercept 95% of the noon light and thereafter almost constant maximum rates were sustained.

The leaf area index increased rapidly in the early stages of growth but after sufficient herbage was formed to intercept 95% of the noon light the rate of increase declined. The maximum leaf area index measured in experiment one was 7.7 ± 0.4 and in experiment two 8.9 ± 0.4 . In the former the mean leaf area index above the level at which 95% of the noon light was intercepted was 4.9 ± 0.3 and in the latter, 6.5 ± 0.4 .

The changes in chlorophyll content per unit of ground area were similar to the changes in leaf area index, the

maximum chlorophyll content per unit of ground area in experiment one being 328 ± 18 mgm./sq.ft. and in experiment two 437 ± 18 mgm./sq.ft. The mean chlorophyll content per unit of ground area above the level at which 95% of the noon light was intercepted was 223 ± 19 in the first experiment and 303 ± 16 in the second.

Significant linear regressions were obtained for rate of dry matter increase on leaf area index, chlorophyll content per unit of ground area on leaf area index and rate of dry matter increase on chlorophyll content per unit of ground area. In each case the regressions calculated for experiment one differed significantly from those for experiment two.

The suggestion was made that leaf area is related to rate of dry matter increase only insofar as it is related to the chlorophyll content of the community and in particular to the chlorophyll above the 95% light interception level. It was concluded that chlorophyll determinations can play a valuable part in further analytical studies of crop growth.

REFERENCES

- Arnon, D.I. 1949: Copper enzymes in isolated chloroplasts. Polyphenoloxidase in Beta vulgaris. Plant Physiol. 24: 1-15.
- Barrowman, J.M. 1956: A simple portable instrument for measuring the light transmission of pastures. Dom. Phys. Lab. (N.Z.) Rep. R259.
- Bavrina, T.V. 1959: Diurnal dynamics of chlorophyll content in plant leaves. Fiziol. Rastenii. 6: 221-5. Transl. Amer. Inst. Biol. Sci.
- Black, J.N. 1958: Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterranean L.) with particular reference to the light microclimate. Aust. J. agric. Res. 9: 299-318.
- Black, J.N. 1961: Border and orientation effects and their elimination in experimental swards of subterranean clover (Trifolium subterranean L.) Aust. J. agric. Res. 12: 203-11.
- Blackman, G.E. 1956: Influence of light and temperature on leaf growth. In The Growth of Leaves. London: Butterworths.
- Blackman, G.E. and Black, J.N. 1959: Physiological and ecological studies in the analysis of plant environment. XI. A further assessment of the influence of shading on the growth of different species in the vegetative phase. Ann. Bot. Lond. N.S.23: 51-63.

- Blackman, G.E., Black, J.N. and Kemp, A.W. 1955:
Physiological and ecological studies in the analysis
of plant environment. X. An analysis of the effects
of seasonal variation in daylight and temperature on
the growth of Helianthus annuus in the vegetative phase.
Ann. Bot. Lond. N.S.19: 527-48.
- Blackman, G.E. and Wilson, G.L. 1951: Physiological and
ecological studies in the analysis of plant environment.
VI. The constancy for different species of a
logarithmic relationship between Net Assimilation
Rate and light intensity and its ecological significance.
Ann. Bot. Lond. N.S.15: 373-408.
- Bonner, J. and Galston, A.W. 1952: In Principles of Plant
Physiology. San Francisco: Freeman.
- Bray, J.R. 1960: The chlorophyll content of some native
and managed plant communities in central Minnesota.
Canad. J. Bot. 38: 313-33.
- Brook, P.T. 1961: The fungus Pithomyces chartarum and
facial eczema. In Sheepfarming Annual. Massey agric.
Coll.
- Brougham, R.W. 1956: Effect of intensity of defoliation
on regrowth of pastures. Aust. J. agric. Res. 7:
377-87.
- Brougham, R.W. 1958a: Interception of light by the foliage
of pure and mixed stands of pasture plants. Aust. J.
agric. Res. 9: 39-52.
- Brougham, R.W. 1958b: Leaf development in swards of white
clover. N.Z. J. agric. Res. 1: 707-18.

- Brougham, R.W. 1959: The effects of season and weather on the growth rate of a ryegrass and clover pasture. N.Z. J. agric. Res. 2: 283-96.
- Brougham, R.W. 1960: The relationship between the critical leaf area, total chlorophyll content, and maximum growth rate of some pasture and crop plants. Ann. Bot. Lond. N.S.24: 463-74.
- Bruinsma, J. 1961: A comment on the spectrophotometric determination of chlorophyll. Biochem. Biophys. Acta. 52: 576-8.
- Bukatsch, F. 1959: The variation of the content of the green pigment in the leaves of Alpine plants during the course of the day. Z. ges. Naturwiss 5: 263-72. (Seen only in Chem. Abstr. 34: 4416. 1940).
- Clendinning, K.A. and Gorham, P.R. 1950: Photochemical activity of isolated chloroplasts in relation to their source and previous history. Canad. J. Res. C28: 114-39.
- Davidson, J.L. and Donald, C.M. 1958: Light and pasture growth. In Climatology and Microclimatology. Proc. Canberra Symp. p.181. Paris. Unesco.
- Frame, J. 1957: A study of the effect of thinning on the yield, composition, palatability and digestibility of Narrow-stem Kale. M. Agr. Sc. Thesis, Massey Agric. Coll.

- Friend, D.J.C. 1960: The control of chlorophyll accumulation in leaves of Marquis wheat by temperature and light intensity. I. The rate of chlorophyll accumulation and maximal absolute chlorophyll contents. Physiol. Plant. 13: 776-85.
- Friend, D.J.C. 1961: The control of chlorophyll accumulation in leaves of Marquis wheat by temperature and light intensity. II. Chlorophyll contents relative to leaf area and thickness. Physiol. Plant. 14: 28-39.
- Fuller, J.H. 1948: Carbon dioxide concentration of the atmosphere above Illinois forest and grassland. Amer. Midland Naturalist. 39: 247-9.
- Geiger, R. 1957: In The climate near the ground. 2nd Ed., revised by M.M. Stewart. Cambridge: Harvard.
- Heath, O.V.S. and Gregory, F.G. 1938: The constancy of the mean Net Assimilation Rate and its ecological importance. Ann. Bot. Lond. N.S.2: 811-8.
- Ichimura, Shun-Ei, 1954: Ecological studies on the plankton in paddy fields. I. Seasonal fluctuations in the standing crop and productivity of plankton. Jap. J. Bot. 14: 269-79.
- Jenkins, H.V. 1959: An airflow planimeter for measuring the area of detached leaves. Plant. Physiol. 34: 805-18.
- Kursanov, A.L. 1961: The transport of organic substances in plants. Endeavour. 20: 19-25.

- Lemon, E.R. 1960: Photosynthesis under field conditions. II. An aerodynamic method for determining the turbulent carbon dioxide exchange between the atmosphere and a corn field. Agron. J. 52: 697-703.
- Mackinnay, G. 1941: Absorption of light by chlorophyll solutions. J. Biol. Chem. 140: 315-22.
- Manning, W.M. and Juday, R.E. 1941: The chlorophyll contents and productivity of some lakes in North East Wisconsin. Trans. Wisc. Acad. Sc. Arts, Lett. 33: 363-93.
- McMeekan, G.P. 1960: Grazing management. Proc. 8th Int. Grassl. Cong. 21-6.
- Mitchell, K.J. 1955: Growth of Pasture species. 2. Perennial ryegrass (Lolium perenne), cocksfoot (Dactylis glomerata), and Paspalum (Paspalum dilatatum). N.Z. J. Sc. Tech. A37: 8-26.
- Mitchell, K.J. 1956: Influence of light and temperature on the growth of pasture species. Proc. 7th Int. Grassl. Congr. 58-69.
- Mitchell, K.J. 1960: The structure of pasture in relation to production potential. Proc. N.Z. Soc. Anim. Prod. 82-92.
- Mitchell, K.J. and Calder, D.M. 1958: The light regime within pastures. N.Z. J. agric. Res. 1: 61-8.
- Monsi, M. and Saeki, T. 1953: Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. Jap. J. Bot. 14: 22-52.

- Moss, R.A. and Loemis, W.E. 1952: Absorption spectra of leaves. 1. The visible spectrum. Plant Physiol. 27: 370-381.
- Norman, R.W. van. 1957: Errors in spectrophotometric analyses of chlorophyll mixtures. Utah Acad. Sc. Proc. 34: 39-44.
- Odum, E.P. 1959: In Fundamentals of Ecology. Philadelphia: Saunders.
- Porter, H.K., Pal, N. and Martin, R.V. 1950: Physiological studies in plant nutrition. XV. Assimilation of carbon by the ear of barley and its relation to the accumulation of dry matter in grain. Ann. Bot. Lond. N.S.14: 55-68.
- Rabinowitch, E.I. 1945: In Photosynthesis. Vol. 1. New York: Interscience.
- Saeki, T. 1960: Interrelationships between leaf amount, light distribution and total photosynthesis in a plant community. Bot. Mag., Tokyo. 73: 55-63.
- Seybold, A. and Egle, K. 1940: Leaf pigments in alpine plants. Botan. Arch. 40: 560-70. (Seen only in Chem. Abstr.) 36: 6204. 1942).
- Shirley, J.L. 1929: The influence of light intensity and light quality upon the growth of plants. Amer. J. Bot. 16: 354-90.
- Singh, B.H. and Lal, K.N. 1935: Investigations of the effect of age on assimilation of leaves. Ann. Bot. Lond. 49: 291-307.

- Skene, M. 1948: In The biology of flowering plants.
London: Sidgwick and Jackson.
- Smith, J.H.C. and Young, V.M.K. 1956: Chlorophyll
Formation and Accumulation in Plants. In Radiation
Biology III. New York: McGraw-Hill.
- Snedecor, G W. 1956: In Statistical Methods. Ames:
Iowa State Coll.
- Tamm, E. and Kraysch, G. 1961: Zum Verlauf des CO₂ -
Gehaltes der Luft im Bereich landwirtschaftlicher
Kulturpflanzenbestände III Beitrag. (CO₂ content
of air surrounding agricultural crops III). Z. Acker.
u. Pflanzenbau. 112: 253-78.
- Thorne, G.N. 1960: Variations with age in Net
Assimilation Rate and other growth attributes of
sugar-beet, potato and barley in a controlled
environment. Ann. Bot. Lond. N.S.24: 356-71.
- Warren Wilson, J 1960a: Influence of spatial arrangement
of foliage area on light interception and pasture
growth. Proc. 8th int. Grassl. Cong. 275-9.
- Warren Wilson, J 1960b: Observations on Net Assimilation
Rates in arctic environments. Ann. Bot. Lond. N.S.24:
372-81.
- Watson, D.J. 1947: Comparative physiological studies on
the growth of field crops. I. Variation in Net
Assimilation Rate and leaf area between species and
varieties and within and between years. Ann. Bot. Lond.
N.S.11: 41-76.

- Watson, D.J. 1952: The physiological basis of variation in yield. Adv. Agron. 4: 101-45.
- Watson, D.J. 1956: Leaf growth in relation to crop yields. In The growth of leaves. London: Butterworths.
- Watson, D.J. 1958: The dependence of Net Assimilation Rate on Leaf Area Index. Ann. Bot. Lond. N.S.22: 37-54.
- Watson, D.J. and French, S.A.W. 1958: Dependence of Net Assimilation Rate of barley on Leaf Area Index. Rep. Rothamsted exp. Sta. 1957. 90-1.
- Watson, D.J. and Norman, A.G. 1939: Photosynthesis in the ear of barley and movement of nitrogen into the ear. J. agric. Sci. 29: 321-45.
- Watson, D.J. and Witts, J.J. 1959: The Net Assimilation Rates of wild and cultivated beets. Ann. Bot. Lond. N.S.23: 431-9.
- Willstater, B. and Stoll, A. 1918: In Untersuchungen über die Assimilation der Kohlensäure. Berlin: Springer.
- Zscheile, F.P. and Comar, C.L. 1941: Influence of preparative procedure on the purity of chlorophyll components as shown by absorption spectra. Botan. Gaz. 102: 463-81.

APPENDICES.

LIST OF APPENDICES

- I. Dry matter yield measurements. (Above 1" from ground level).
- II. Dry matter yield measurements. (Above ground level).
- III. Leaf area index measurements.
- IV. Analyses of regressions of leaf weight/area ratio on time.
- V. Chlorophyll content per unit of ground area measurements.
- VI. Analyses of regressions of rate of dry matter increase on leaf area index.
- VII. Analyses of regressions of chlorophyll content per unit of ground area on leaf area index.
- VIII. Analyses of regressions of rate of dry matter increase on chlorophyll content per unit of ground area.

APPENDIX I

Dry matter yield measurements
(Above 1" from ground level)

Days of growth	Mean yield (lbs of dry matter per acre)	Standard Error of mean (n = 4)
----------------	---	--------------------------------------

Experiment 1. Swards cut to 1" from ground level.

4	77	5
8	194	10
12	324	20
16	486	36
20	673	35
24	877	24
32	1,398	83
41	2,026	112

Swards cut to 2½" from ground level.

8	790	43
16	1,136	96
24	1,592	101
32	2,042	99
41	2,515	121

Experiment 2. Swards cut to 1" from ground level.

2	140	10
6	240	13
10	600	32
14	980	36
18	1,660	110
22	2,339	124
30	3,585	204

Swards cut to 2½" from ground level.

14	1,881	113
18	2,520	140
26	3,790	212

APPENDIX II

Dry matter yield measurements (Above ground level)

Days of growth	Mean yield (lbs of dry matter per acre)	Standard Error of mean (n = 8)
Experiment 1. Swards cut to 1" from ground level.		
3	1,126	59
7	1,401	83
11	1,536	164
15	1,446	111
19	1,631	79
23	2,157	91
31	2,610	121
40	3,011	149
Swards cut to 2½" from ground level.		
7	1,732	80
14	1,905	115
22	2,561	131
30	3,102	150
39	3,463	230
Experiment 2. Swards cut to 1" from ground level.		
5	1,989	132
9	2,258	112
13	2,416	171
17	2,804	168
21	3,434	193
29	4,660	231
Swards cut to 2½" from ground level.		
16	3,774	212
24	4,712	231

APPENDIX III

Leaf area index measurements

Days of growth	Mean leaf area index	Standard Error of mean (n = 8)
Experiment 1. Swards cut to 1" from ground level.		
3	1.90	0.03
7	2.33	0.10
11	3.23	0.22
15	3.25	0.23
19	4.77	0.17
23	5.58	0.23
31	6.36	0.28
40	6.29	
Swards cut to 2½" from ground level.		
7	3.36	0.14
14	4.32	0.16
22	5.95	0.30
30	7.10	0.33
39	7.74	0.39
Experiment 2. Swards cut to 1" from ground level.		
1	1.57	0.08
5	2.51	0.14
9	3.37	0.27
13	4.67	0.17
17	6.15	0.31
21	7.40	0.38
29	8.90	0.44
Swards cut to 2½" from ground level.		
16	7.75	0.41
24	8.57	0.47

APPENDIX IV

Analyses of regressions of leaf weight/area ratio on time

Data presented in Table 6

y is leaf weight/area ratio (mg/cm^2)

X is time measured in days from start of experiment

Experiment 1: Swards cut to 1" from ground level.

$$\begin{aligned} S_y &= 28.88 & S_x &= 149 & n &= 8 \\ SS_y &= 1.1030 & SS_x &= 1079.87 & SP_{xy} &= 18.60 \end{aligned}$$

$$y - \bar{y} = b(x - \bar{x})$$

$$b = \frac{SP_{xy}}{SS_x} = \frac{-18.60}{1079.87} = -0.0172$$

$$y = -0.0172x + 3.9304$$

$$SS \text{ due to regression of } y \text{ on } x = b (SP_{xy}) = 0.3199$$

Test for significance of linear regression.

Source of Variation	S.S.	d.f.	M.S.	E	Result
Regression	0.3199	1	0.3199	2.45	N.S.
Error	0.7831	6	0.1305		
Total	1.1030	7			

$$s_b = \pm \sqrt{\frac{MSE}{SS_x}} = \pm \sqrt{\frac{0.1305}{1079.87}}$$

$$= \pm 0.0110$$

Experiment 2: Swords cut to 1" from ground level.

$$y = -0.0513x + 4.14$$

Test for significance of linear regression.

Source	S.S.	d.f.	M.S.	F.	Result
Regression	1.4677	1	1.4677	12.48	*
Error	0.5882	5	0.1176		
Total	2.0559	6			

$$s_b = \pm 0.0145$$

Test for difference between regressions.

Source	d.f.	SSx	SPxy	SSy	SSy ¹	d.f. ¹
Exp. 1	7	1079.87	-18.60	1.1030	0.7827	6
Exp. 2	6	557.71	-28.61	2.0559	0.5883	5
					1.3710	11
Total	13	1637.58	-47.21	3.1589	1.7979	12

Source	S.S.	d.f.	M.S.	F.	Result
Difference between Regressions	0.4269	1	0.4269	2.62	N.S.
Residual	1.3710	11	0.1246		
Total	1.7979	12			

Combining data from both experiments.

$$y = -0.0255x + 3.94$$

Test for significance of linear regression.

Source	S.S.	d.f.	M.S.	F.	Result
Regression	1.1274	1	1.1274	6.89	*
Error	2.1254	13	0.1634		
Total	3.2528	14			

$$s_b = \pm 0.0097$$

APPENDIX V

Chlorophyll content per unit of ground
area measurements

Days of growth	Mean chlorophyll content per unit of ground area mgm/sq.ft.	Standard Error of mean (n = 8)
Experiment 1. Swards cut to 1" from ground level.		
3	92.8	3.4
7	116.5	2.7
11	154.4	2.5
15	164.6	2.6
19	212.1	7.0
23	249	14
31	286	17
40	293	18
Swards cut to 2½" from ground level.		
7	172.1	4.1
14	216	11
22	270	13
30	312	10
39	328	18
Experiment 2. Swards cut to 1" from ground level.		
1	77.6	3.0
5	106.6	2.8
9	155.6	2.7
13	214.0	6.1
17	289	11
21	352	17
29	437	18
Swards cut to 2½" from ground level.		
16	332	17
24	426	18

APPENDIX VI

Analyses of regressions of rate of dry matter increase on leaf area index

Data presented in Tables 1 and 5 and Appendix 3

y is rate of dry matter increase (lbs/acre/day).

x is leaf area index.

Experiment 1:

$$y - \bar{y} = b (x - \bar{x}).$$

$$b = + \frac{292.626}{40.0038} = +7.315$$

$$y = +7.315x + 11.667$$

$$SS \text{ due to regression of } y \text{ on } x = b \text{ } SP_{xy} = 2140.59$$

Test for significance of linear regression.

Source	S.S.	d.f.	M.S.	F.	Result
Regression	2140.59	1	2140.59	51.1	**
Error	419.17	10	41.92		
Total	2559.76	11			

$$s_b = \pm \sqrt{\frac{41.92}{40.0038}} = \pm 1.023.$$

Curvilinear regression.

$$y - \bar{y} = b_1 (x - \bar{x}) + b_2 (x^2 - \bar{x}^2).$$

$$b_1 = \frac{(SP_{xy})(SSx^2) - (SPx^2y)(SP_{xx}^2)}{(SSx)(SSx^2) - (SP_{xx}^2)^2}$$

$$b_2 = \frac{(SSx)(SPx^2y) - (SP_{xx}^2)(SP_{xy})}{(SSx)(SSx^2) - (SP_{xx}^2)^2}$$

$$SSxb_1 + SPxx^2b_2 = SPxy$$

$$SPxx^2b_1 + SSx^2b_2 = SPyx^2$$

$$b_1 = +18.2172$$

$$b_2 = -1.149$$

$$y = +18.22x + (-1.15)x^2 - 10.35$$

$$SS \text{ due to curvilinear regression of } y \text{ on } x = b_1(SPxy) + b_2(SPxx^2y)$$

$$= 2274.60$$

Test for significance of curvilinear regression

Source of variation	S.S.	d.f.	M.S.	F.	Result
Quadratic regression	2274.60	2			
Linear regression	2140.59	1			
Quadratic increment	134.01	1	134.01	4.23	*
Error	285.16	9	31.68		
Total	2559.76	11			

$$s_{b_1} = \pm \sqrt{\frac{EMS (SSx^2x^2)}{(SSx^2x^2)(SSxx) - (SSxx^2)^2}}$$

$$= \pm 5.398$$

$$s_{b_2} = \pm \sqrt{\frac{EMS (SSxx)}{(SSx^2x^2)(SSxx) - (SSxx^2)^2}}$$

$$= \pm 0.56$$

Experiment 2.

Linear $y = +15.837x + 34.86$
 $S_b = \pm 2.768$

Quadratic $b_1 = +32.576$ $b_2 = -1.570$

Source	S.S.	d.f.	M.S.	F.	Result
Linear regression	14916.9	1	14916.9	32.7	*
Error	3188.5	7	455.5		
Quadratic	15405.4	2			
Quadratic increment	485.5	1	485.5	1.09	N.S.
Error	2700.0	6	450.0		
Total	18105.4	8			

Test for difference between regressions.

Source	S.S.	d.f.	M.S.	F.	Result
Difference between regressions	1683.02	1	1683.02	10.68	**
Residual	2836.54	18	157.59		
Total	4519.56	19			

Combining data from both experiments.

$$y = +45.54 x + 4.94$$

Test for significance of linear regression.

Source	S.S.	d.f.	M.S.	F.	Result
Regression	219237.76	1	219237.76	938.0	
Error	4674.15	20	233.71		
Total	223911.91	21			

$$s_b = \pm 1.49$$

APPENDIX VII

Analyses of regressions of chlorophyll content per unit
ground area on leaf area index

Data presented in appendices 3 and 6

y is chlorophyll content per unit of ground area (mgm/sq.ft.).

x is leaf area index.

Experiment 1:

$$y = +40.461 x + 27.03$$

Test for significance of linear regression

Source	S.S.	d.f.	M.S.	F.	Result
Regression	69082.30	1	69082.30	898.9	**
Error	845.32	11	76.85		
Total	69927.62	12			

$$s_b = \pm 0.1349$$

Experiment 2:

$$y = +48.72 x - 9.81$$

Test for significance of linear regression

Source	S.S.	d.f.	M.S.	F	Result
Regression	141173.02	1	141173.02	499.8	**
Error	1977.23	7	282.46		
Total	143150.25	8			

$$s_b = \pm 2.179$$

APPENDIX VIII

Analyses of regressions of rate of dry matter increase on
chlorophyll content per unit ground area

Data presented in Tables 1 and 7 and Appendix 6

y is rate of dry matter increase (lbs per acre per day).

x is chlorophyll content per unit of ground area (mgm./sq.ft.).

A. Total chlorophyll

Experiment 1:

$$\text{Linear } y = +0.1832 x + 6.3801$$

$$S_b = \pm 0.0665$$

$$\text{Quadratic } y = +0.3556 x - 0.0406x^2 - 7.5103$$

$$S_{b_1} = \pm 0.1383$$

$$S_{b_2} = \pm 0.0322$$

Test for significance of regressions

Source	S.S.	d.f.	M.S.	F.	Result
Linear regression	2262.15	1	2262.15	76.0	**
Error	297.61	10	29.761		
Quadratic regression	2307.08	2			
Quadratic increment	44.93	1	44.93	1.60	N.S.
Error	252.68	9	23.08		
Total	2559.76	11			

Experiment 2:

$$\text{Linear } y = +0.3189 x + 39.63$$

$$s_b = \pm 0.0595$$

$$\text{Quadratic } y = +0.8269 x - 0.0982x^2 - 10.40$$

$$s_{b_1} = \pm 0.2773 \quad s_{b_2} = \pm 0.0527$$

Test for significance of regressions

Source	S.S.	d.f.	M.S.	F.	Result
Linear regression	14559	1	14559	28.7	**
Error	3546	7	507.6		
Quadratic regression	15859	2			
Quadratic increment	1300	1	1000	3.47	N.S.
Error	2246	6	374.3		
Total	18105	8			

B. Chlorophyll above the 95% light interception level

Experiment 1:

$$y = +0.3043 x - 10.2518$$

Source	S.S.	d.f.	M.S.	F.	Results
Regression	2344.33	1	2344.33	104.7	**
Error	201.49	9	22.39		
Total	2545.82	10			

$$s_b = \pm 0.0297$$

Experiment 2:

$$y = +0.4706 x + 14.85$$

Source	S.S.	d.f.	M.S.	F.	Results
Regression	14417	1	14417	63.37	**
Error	1365	6	2275		
Total	15782	7			

$$s_b = \pm 0.0591$$