FREQUENCY AND INTENSITY OF DEFOILATION, DRY MATTER PRODUCTION
AND NET PHOTOSYNTHESIS IN GRASS AND LEGUME FORAGES

by

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The investigations reported in the thesis were designed to discover the importance of leaf area remaining after defoliation for subsequent forage regrowth. In field trials with a wide range of temperate grasses the effects of differing frequencies and intensities of defoliation on dry matter production were examined. The results of these experiments showed that lenient defoliations at 3 inches (designed to leave photosynthetic leaf area after defoliation) did not in fact result in increased forage production compared with defoliations at 1 inch. The low production with defoliation at 3 inches was accompanied by a depression of the clover content in the stand.

For more detailed investigations of the light use, leaf area index (LAI) and net photosynthesis relationships, orchardgrass (*Dactylis glomerata* L.) and white clover (*Trifolium repens* L.) were chosen. Growth and net photosynthesis, of the two selected species, were measured under a number of temperature regimes with other major environmental factors at nearly constant and optimal levels. Both species grew optimally at 25°C; while net photosynthesis was maximal at or below 15°C in orchardgrass and maximal at 20°C in white clover.

The two species were established in pure and mixed stands in the field and subjected to defoliation managements, similar to those in the original experiments.

The yields again confirmed the earlier result that defoliations at 3 inches, compared with 1 inch, resulted in lower yields and reduction in the clover content of the stands.
Samples of the forage stands and attached soil were removed to the laboratory for the determination of net photosynthesis at a number of light energy (400-700 nm) levels. The LAI and dry matter of these forage stands and their components were then determined. From these data net photosynthesis at varying LAIs was compared between stands of contrasting managements and botanical composition.

The results of these laboratory investigations showed that there were differences in the net photosynthesis-LAI response between the defoliation managements only in the pure orchardgrass stands. With orchardgrass stands defoliated at 1 inch the relationship between net photosynthesis and LAI was linear up to an LAI of 17. However, with orchardgrass stands defoliated at 3 inches the response was curvilinear and the optimum LAI was about 12. In the pure white clover stands there were no clearly defined optimum LAIs or difference in response between the stands with differing managements. The grass-clover forage stands showed an optimum LAI of 10 and the presence of some clover may have nullified an effect from the defoliation managements.

The data show that the light interception-LAI theory was applicable to grass stands under lenient defoliation. The lower leaves, left after a defoliation, did not contribute greatly to the stands ability to assimilate carbon dioxide and finally they became "parasitic" resulting in the stand having an optimum LAI of about 12. When the defoliation was heavy there was no evidence of leaves becoming "parasitic". Frequency of defoliation at 1 inch had little influence on yield despite differences in the increase in net photosynthesis for a unit increase in LAI.
Carbon dioxide fixation efficiency was calculated from the light energy response data. The efficiencies were similar to those published for similar material and showed furthermore only slight differences in light energy use between the forage stands of pure grass, pure clover and their mixture. The differences between the dry matter productivity of the forage stands caused by the management treatments appeared to be a result of an inability of the clover to produce a sufficiently high LAI to compete under the lenient defoliation.
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---

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1. **INTRODUCTION**

The adjustment of defoliation in managing forage swards to achieve maximum production, is a well recognised objective. However, in a broad sense published results show no consensus in the optimal defoliation system. Undoubtedly the reason for the lack of consensus is the complex nature of the problem as it encompasses an entire ecosystem which, within itself, shows many interactions.

During the past 30 years a number of hypotheses have been put forward to account for the regrowth response of forage swards following different defoliation treatments. The hypothesis of leaf area and light interception regulating photosynthesis, and hence dry matter production, is a comparatively recent contribution (Kasmaga and Monsi, 1954). The research reported in this thesis has been designed to test this hypothesis in both the field and controlled environments.

The first section of research work completed in Australia, was a field scale defoliation management trial on grass-legume forage swards using sheep for the defoliations. The trial was designed to test the "leaf area-light interception-photosynthesis hypothesis" by comparing the yields from defoliation managements which varied both in the frequency and intensity of defoliation. The results from the above experiment did not agree well with the hypothesis.
Investigations, in Canada, were undertaken to clarify the situation. Two of the species used in the Australian research viz. orchardgrass *Dactylis glomerata* L. and white clover *Trifolium repens* L. were used and their growth and net photosynthesis was examined under controlled conditions. The two species were grown alone and together in forage swards which were subjected to the same defoliation frequencies and intensities as in the initial experiment in Australia. The objectives were three a) to compare the dry matter yield response to the management treatments in an environment differing substantially from the Australian one, b) to provide material from known defoliation treatments so that the progress of leaf area, dry matter and net photosynthesis could be followed between defoliations and c) to follow the changes in the net photosynthesis-light response curve as the swards regrew after defoliation. This approach allowed further testing and examination of the "leaf area-light interception-photosynthesis hypothesis" and provided possible reasons for the differences in the performance of the defoliation treatments.
2 REVIEW OF LITERATURE

2.1 Frequency and Intensity of Defoliation and the Regrowth Yield of Forage Stands

Regrowth of forage stands is influenced by the frequency and intensity of previous defoliations (Brougham, 1955, 1956). However, unlike environmental factors which also influence regrowth rates, frequency and intensity of defoliation cannot easily be described in terms of optimal levels. Undoubtedly this is a reflection of the interactions of frequency and intensity of defoliation with environment, and their influence regrowth rates. The extensive literature on this topic can be divided into two major areas of concern a) the efficiency with which the leaf area of the plant community intercepts light energy for regrowth and b) the carbohydrate reserve status of the plants.

2.1.1 Leaf Area and Light Energy Interception

The relationship between leaf area, light interception and subsequent growth in plant communities has been based on the fact that the primary synthesis of dry matter in most ecosystems results from the photosynthetic activities of the plant's leaves in utilizing light energy to fix carbon dioxide. The efficiency of this process must depend, to a
large degree, on the size, shape, position and structure of the photosynthetic organs.

In 1947 Watson suggested that a useful index of the photosynthetic capacity of a plant community would be the Leaf Area Index (LAI); i.e. the ratio of the leaf area of the community to the area of land associated with that community. The index has been used extensively since 1947 especially in studies of light interception in developing communities. Brougham (1955, 1956) examining growth in a forage stand of short rotation ryegrass, \((\text{Lolium perenne L.} \times \text{L. multiflorum Lam.})\), red and white clover \((\text{Trifolium pratense L.} \text{ and } T. \text{ repens L.})\), observed an initial phase where, as the LAI increased, growth rate increased until 95% of all incident light was intercepted; he attributed the rise in growth rate simply to the fact that with a greater LAI the community was able to "trap" more light energy for photosynthesis. A second phase followed where the growth rate became constant regardless of further increases in the LAI, and a third and final phase where an increase in the LAI caused a decline in growth rate.

The models, describing light interception by a plant community (Monsi and Saeki, 1953) and related net photosynthesis (Ksanga and Monsi, 1954) agreed well with the steady and declining phases of growth reported by Brougham (1955). The Monsi and Saeki (1953) model for light attenuation by a plant community was based on Beer's Law so that:

\[ I = I_o \exp (-kF) \]

where

- \( I = \) light intensity beneath an LAI of \( F \).
- \( I_o = \) light intensity at the crop surface.
- \( k = \) the extinction coefficient of the community.
- \( F = \) Leaf area index above the observation point.
With this relationship in mind Kasanga and Monsi (1954) proposed that, as plants both respire and photosynthesize there should be an optimal LAI at which illumination of the lowest leaves in the community would be just above their light compensation point. They also stated that, at this LAI, there was maximum use of light for photosynthesis by the community for fixing carbon dioxide. The concept of "marginal compensation area" as proposed by Davidson and Philip (1958) also considers this situation and is analogous to the concept of optimum LAI.

Donald (1961) has reported that increases in LAI above the optimum placed the lower leaves of the community below their light compensation point so that they effect a net loss in carbon dioxide fixation.

Donald stated that these lower leaves continued to respire until the plant reached a point where the lower leaf death rate equalled the rate of unfolding of new leaves. This point he called the ceiling LAI and, in the case of forage communities, this was also the ceiling agricultural yield, where the agricultural yield consisted of photosynthetic parts. However, at the ceiling LAI assimilation was still positive as not all the light energy assimilated was required for continuing leaf expansion. The surplus energy was used to increase the size of non-photosynthetic organs until respiration balanced assimilation.

In 1961, Donald, reviewing the above sequence, observed that there were only two published accounts of an optimal LAI under field conditions, one by Watson (1956) using artificially thinned stands of kale (*Brassica oleracea* var. *acephala*) and another by Davidson and Donald (1958) using subterranean clover (*Trifolium subterraneum* L.). Some workers have been unable to demonstrate an optimal LAI. Brougham (1956), for example, examined the growth rate of a ryegrass-clover forage...
stand and found that its growth rate rose to an asymptote at LAI 5 which was maintained to LAI 10. Brougham also measured light interception and found that 95% was intercepted when the LAI reached 5. To agree with the concept of the optimum LAI there should have been a decline in growth rate between LAI 5 and 10.

Later Watson and French (1962) attempted to stabilise the LAI of a kale crop at an optimum by repeated thinning. However, a maximum growth rate was not obtained due to errors in estimation of the optimum LAI; it appeared that the optimum varied through the growing season. Seasonal variation in optimal LAI may well have been the reason for the unexpected results of Brougham (1956). Clearly over a specific growth period some crops may reach an optimum LAI whereas others may not because a particular combination of environmental factors has shifted the optimum LAI and maximum yield to a level far above that which the plant community is capable of supporting.

If the concept of an optimum LAI is assumed to be valid, control of LAI at an optimum is probably most practical in monospecific forage stands when subject to light and frequent defoliations. However, such defoliations have rarely produced maximum growth rates, probably because both animal and mechanical defoliators tend to remove the younger leaves, as they are invariably at the top of the canopy. Begg and Wright (1964) have shown that these young leaves are the most efficient in promoting further shoot growth. Consequently grazing management studies, such as those of Brougham (1959) and Bryant and Blaser (1961) have shown lenient defoliations do not produce growth rates as high as heavy defoliations.
The maintenance of an optimal LAI also appears difficult for several other reasons. Brougham (1958) has shown a diurnal variation in optimal LAI, and Stern and Donald (1961) have shown that the optimum varied with the amount of solar radiation received. The latter observation may have in part caused the seasonal changes in optimal LAI suggested by the results of Watson and French (1961). When multispecific forage stands are considered the optimal LAI will vary with the species composition. For example, Brougham (1960) has shown that, at LAI 3, the light interception of a white clover sward was 92\% and of a short-rotation ryegrass sward 75\% and of a mixture of the two 80\%. These results are similar to those of Stern and Donald (1962) for Wimera ryegrass (*Lolium rigidum* Gaud.) grown alone and with subterranean clover. In these forage stands the inclination and position of the leaves is complex and influences the LAI required to produce 95\% interception of the incident light ("Critical LAI" is the term used by Brougham (1958) to describe this particular LAI). Brougham (1958) reported that the Critical LAI for the white clover swards was 3.5, while for the short-rotation ryegrass sward it was 7.1 and for the mixture of the two 4.8. Warren Wilson (1965) has shown the importance of these variations in foliage inclination in influencing the light attenuation of forage stands. Further, Pearce *et al.* (1967) have shown that these differences in foliage inclination do in fact result in differences in net photosynthesis of the forage stands.

The theoretical studies on light penetration in foliage by Anderson (1964) and Monteith (1965) have shown that an additional reason for failure of the optimum LAI light interception concept was the use of the analogy with Beer's law. Beer's law accounts for attenuation of
a parallel beam of monochromatic light passing through a uniform solution and, as neither of these conditions are found in a plant community, the analogy with Beer's law is not justified. Monteith (1965) has therefore proposed the use of a binomial expression to express light attenuation by foliage; thus for a given stratum:

\[ I = I_0 (S + (1 - S) T) \] \hspace{1cm} (1.2)

where \( S \) is the fraction of the total incident light energy not intercepted by the forage stratum and \( T \) is the transmission coefficient of the leaves in that stratum. Verhagen et al. (1963) have shown that the objections of Anderson (1964) and Monteith (1965) to equation (1.1) can be overcome by modifying it so that \( k \) varies with LAI and with depth into the foliage stand. However, further modification appears necessary as Anderson (1966) has demonstrated that \( k \) will differ in diffuse and direct light.

Notwithstanding these difficulties with light attenuation models, it is clear, as shown by Smith et al. (1964), that the LAI is the most important single variable accounting for variation in the dry matter yield of forage swards. However, not all forage stands show an optimum LAI; some show an asymptotic growth rate at high LAIs. Much research since 1961 has been concerned with the investigation of those two categories. Black (1963) has confirmed the optimum LAI for subterranean clover, but has shown that it varied between 4 and 7 depending on the level of solar radiation. Similarly Harper (1963) has shown that the optimum LAI for a crop of potatoes (Solanum tuberosum L.) varied with harvest date from 2.5 to 4.0. However, Rees (1963) working with oil palm (Elaeis guineensis, Jacq.) plantations found an optimal
LAI of 3 from a number of samplings over a 54 day period. For graminaceous species the optimal LAI is frequently higher than those previously quoted. For example Pearce et al. (1965) found that the optimum LAI in an orchardgrass sward was 5.5 while Cooper (1966) found the optimum LAI in a forage sward of Italian ryegrass (*Lolium multiflorum* Lam.) was 7. Murtagh and Gross (1966) have published a number of optimum LAIs for stands of tall fescue (*Festuca arundinacea* Schreb.) and rice (*Oryza sativa* L.). In the rice communities the optimum LAIs declined with planting density suggesting that at high plant densities the rice stem became photosynthetically important to the plant. If allowance for this stem effect is made the optimum LAI for both tall fescue and the rice stands was about 11.

Schibles and Weber (1965) found no depression in the growth rate of a crop of soybeans (*Glycine max* (L.) Merr.) between LAI 3 and 6, while Williams et al. (1965) observed that the growth rate of a crop of corn (*Zea mays* L.) rarely became asymptotic. However, they observed that the magnitude of the increase in rate was substantially reduced between LAIs of 5 and 16. Wilfong et al. (1967) have examined forage swards of alfalfa (*Medicago sativa* L.) and Ladino white clover and found that the optimum LAI occurred over a broad, rather than a narrow range. In both species an increase in the LAI above 3 caused only slight changes in the crop growth rate. Finally Anslow (1967) was unable to find a relationship between the mid summer growth rate of a sward of perennial ryegrass (*Lolium perenne* L.) and LAI.

Despite the fact that some forage swards appear to have an optimum LAI while others do not, the association between LAI, light interception and photosynthesis is well established. Further support comes from the
work of Brougham (1960) and of Hunt and Cooper (1967) who have both shown very high correlations between chlorophyll content per unit area and crop growth rate with a wide range of species and genera. Additional discussion of the relationship between crop growth rates, LAI and net photosynthesis is given in section 2.2.2.

2.1.2 Carbohydrate Reserve Status after Defoliation

One of the more controversial topics of forage agronomy is the question of the importance of carbohydrate reserves for regrowth following defoliation. Although this topic does not constitute part of the experimental section of the thesis, a review of the carbohydrate reserve literature is necessary because of its close association with leaf area, light interception and photosynthesis. The aim of this review is to delineate those situations where carbohydrate reserves are important in forage regrowth as distinct from those situations where light interception and leaf area are important.

It is first necessary to define the terms, reserve and carbohydrate. Reserve compounds are organic compounds which are elaborated by the plant, stored, either passively or actively, and utilized by the plant at some later date for maintenance and/or growth. In forage plants the most important reserve carbohydrates are sugars, fructosans and starches. However, Davidson and Milthorpe (1965) have pointed out that these reserve carbohydrates are in equilibrium with a pool of labile structural and nitrogenous compounds. Inclusion of these nitrogenous compounds agrees with the original concept for reserve compounds proposed by Graber et al. (1927).
Numerous investigations, such as those of Sullivan and Sprague (1943), Alberda (1960) and del Poso (1963), have shown following defoliation of forage plants, there is always an associated decrease in the carbohydrate reserves of the plants. These observations have lead to the general belief that a large proportion of the reserves are incorporated into new regrowth tissue of the plant. Therefore a high concentration of the 'reserve' carbohydrate should be a prerequisite for high regrowth rates. This hypothesis that reserves were mainly carbohydrate was first advanced by Graber et al. (1927) from an extensive review of literature, and more recently has been supported in a review by Weinmann (1952).

In 1958 May and Davidson obtained results from a defoliation experiment which suggested that the drop in carbohydrates was a consequence of continued respiration and that they had little or no effect in initiating regrowth. May (1960) reviewed the literature and concluded that "It seems somewhat premature, therefore, to attribute special significance to a correlation between root carbohydrate levels and the behaviour of the tops after defoliation ...".

Concurrent with May's review re-assessment of the carbohydrate reserve problem occurred. This research has, to a large extent, clarified the problem from an agronomic standpoint, and, has suggested a possible role of a labile pool of reserves. The exact nature of the pool is unclear but it appears to include proteinaceous material, non-structural and structural carbohydrate.

An early contribution to the recent research came from Ward and Blaser (1961) who found that the regrowth of orchardgrass plants depended both on the leaf area remaining after defoliation, as well as the
carbohydrate reserve level. Other workers, Baker and Garwood (1961), found that these two factors were, however, important at different times of the year. Eastin et al. (1964) has confirmed the action of a growth regulator acting with the carbohydrate reserves to control the rate of re-growth. They found the level of a growth regulator in the apex of brome grass (Bromus inermis Leyss.) appeared to suppress tillering. Once the apical dominance was established, usually at internode elongation, further tillering and regrowth did not occur even if the carbohydrate reserves were sufficient.

In orchardgrass research indicates that the stubble fructosans are the principal reserve compounds (Sullivan and Sprague 1953, Ward and Blaser 1961, Baker and Garwood 1961). Other authors, Reynolds and Smith (1962) and Smith (1962), have included some root and or rhizome portions in the carbohydrate reserve structures of other forage plants. Notwithstanding these differences in the reserve structures, and the interplay of other factors such as leaf area, all the above mentioned authors have shown a common pattern for the carbohydrate reserve concentration in plants following defoliation. Initially after defoliation the reserve concentration declined and this continued for at least 10 days. Following the decline phase the concentration of carbohydrate reserves increased with the rate of increase back to the original level being slowest under the most severely defoliated treatments. In many forage plants re-growth comes from established structures as well as crown or tiller buds. Thus in white clover Sasaki and Fukuju (1964) have shown that root carbohydrate reserves were used mainly to initiate re-growth from the crown, while the stolon reserves were used for further re-growth from the stolon buds. They found that the most active phase of
use of all reserves was up to the 10th day following defoliation. This has been confirmed by Hoshino and Oizumi (1968).

Brown and Blaser (1964) have shown that the length of the phase before new carbohydrate reserves began to regenerate depended on the growth activity of the plants, in that environmental conditions predisposed to high growth rates tended to keep the carbohydrate reserve level low. Thus, in orchardgrass and Kentucky 31 fescue they found that the carbohydrate reserves could begin to rise as early as 10 days after defoliation, but if nitrogen were applied, and or rainfall were near optimal the reserve carbohydrate level would not begin to rise for 40 days. The rise in reserve carbohydrate was generally accompanied by a slowing of the growth rate together with maturity of the plants, lower air temperatures and reduced nitrogen supply. Under these conditions there was an energy surplus in the plants which was conserved as reserve carbohydrates.

Davidson and Milthorpe (1965, 1966) examined the relation between defoliation, the carbohydrate reserve level and the carbon balance of orchardgrass plants. By measuring continuously photosynthesis and respiration of the plant leaves together with root respiration and concurrently sampling for the carbohydrate levels and the dry matter production they were able to construct a carbon balance sheet for the plants as they regrew from a defoliation. With severe defoliation they found that the photosynthesis of the new leaves was insufficient to balance the respiration of the plant and up to the 4th day the plants drew on stored reserves. However, from their measurements of the carbohydrate levels they were unable to account for all the carbon used and therefore they suggested that other substances, probably proteins,
were being utilized. By varying the carbohydrate reserve level of the plants they were able to show that, during the first two days of regrowth, if the reserves were high they accounted for 80% of growth and respiration. On the other hand if the reserves were low they were hardly used and other substances made up the carbon deficit. They therefore questioned the universal role of carbohydrate reserves, especially as the environmental conditions which produce high levels of reserve carbohydrate (see Brown and Blaser 1964; Vengris et al. 1966; and Smith and Jewiss 1966) are those which restrict regrowth per se. This type of situation may well have been the reason for the poor correlation found between carbohydrate reserves and regrowth rates found in experiments such as those of Davies (1966) with perennial ryegrass. Davidson and Milthorpe (1966) concluded from their study that carbohydrate reserves were important in controlling regrowth rates of forage in that they were part of a labile energy pool.

Notwithstanding the above evidence some workers, for example Alberda (1966) insist that non structural carbohydrates per se are of very great importance in determining regrowth rates of forage swards. Clearly more analyses are necessary to describe the labile pool proposed by Davidson and Milthorpe (1965). The evidence of both Ward and Blaser (1961) and Davidson and Milthorpe (1966) is in agreement in that reserve compounds are utilized during the first week of regrowth of orchardgrass and that later regrowth is dependant on leaf area and photosynthesis. Tropical graminaceous forages also show this dual dependance; Humphreys and Robinson (1966) using green panic (Panicum maximum var. trichoglume (K.Schum) Eyles) and buffel grass (Conchorus ciliaris L.) found that regrowth in both these species was dependent on both carbohydrate reserves
and leaf area left after defoliation. Humphreys also suggested that the two factors may interact.

Despite the general pattern described above there may be differences in the agronomic response to carbohydrate reserves with a particular cultivar, strain or environment. Eagles (1967) has shown that high latitude populations of orchardgrass accumulate carbohydrate in response to low temperatures while populations from lower latitudes do not. Colby et al. (1966) have shown that high carbohydrate reserves are necessary for orchardgrass to withstand both high and low temperature stress conditions.

Finally from an agronomic point of view it is necessary to consider the influence of the carbohydrate reserves on ruminant growth and nutrition. As pointed out by Blaser et al. (1966) many forages are low in utilizable energy, and fertilizer nitrogen applied to increase the yield results in additional lowering of utilizable energy. On the other hand imposition of grazing managements to produce high carbohydrate reserves and good ruminant nutrition can cause reduced dry matter yield. Thus improved animal nutrition may have to be balanced against reduced output per acre. In this context the exact nature of the reserves is of smaller significance.

2.1.3 Observations of Dry Matter Production by Forage Stands

The early work on the effects of frequency and intensity of defoliation on herbage production by forage stands has been reviewed by Brougham (1959); he observed that these reports showed differing yields with similar managements. In his experiments Brougham showed that intensive grazing and long spelling maximized production from a short
rotation ryegrass sward. Frequent intensive grazings, however severely reduced yield while frequent and lax grazings gave an intermediate yield. Bryant and Blaser (1961, 1968) conducted similar grazing experiments with orchardgrass-ladino clover and orchardgrass-alfalfa swards. Again the least frequent and most intensive treatment produced the highest yield under grazing conditions but in this experiment the frequent and lax treatment gave the poorest yields. The purpose of this review section therefore is to point out such differences in this recent literature and examine them to see if there is any consistent pattern.

The production of some species may be depressed by close cutting even with infrequent defoliation. Cerro-Costas and Vicente-Chandler (1961) cut a number of species of tropical forage grasses every 2 months at 3 and at 10 inches. Over a two year period yields of molasses grass (*Melinis minutiflora* Beauv.) were severely reduced by cutting at 3 inches. By contrast guinea grass (*Panicum maximum* Jacq.) yields were not influenced by cutting height. However, with three other grasses tested, pangola grass (*Digitaria decumbens* Stent.), para grass (*Panicum purpurascens*) and napier grass (*Pennisetum purpureum* Schum.) close cutting always outyielded the 10 inch cut. Vicente-Chandler et al. (1959 a, b and c, 1961) investigating the effect of frequency of cutting on napier, guinea, para and pangola grasses, found that the least frequent cuttings (every 90 days for the first three and every 60 days for the latter) produced the highest annual yields. Oyenuga (1959 a and b) also found cutting every 90 days optimal for napier grass, but with gamba grass (*Andropogon tectorum* Schum.) he found cutting every 50 days gave greater yields than every 90 or 20 days. It appears from
this work that the tropical forage grasses napier, para, guinea and pangola behave in much the same way as the temperate grasses in that they give their maximum yield under intensive but infrequent defoliation. Other species such as molasses and gamba grasses do not behave in this manner as the former produces the greatest dry matter yield with lax defoliation while the latter appears to have an optimum defoliation frequency of every 7 weeks.

Research on forage plants from temperate climates can be conveniently considered in three categories viz. a) grass swards, b) legume swards and c) mixed grass-legume swards. Some of the studies were purely practical while others are aimed at elaboration of the concept or the evaluation of differences between herbage measurement techniques. Because of these differences in aim, it is necessary to take them into account when comparing the various studies. Studies aimed at practical verification of LAI concepts were made by Lambert (1962, 1964). By taking concurrent LAIs and dry matter yields of pure swards of timothy (Phleum pratense L.) and meadow fescue (Festuca pratensis L.), Lambert found that frequent cutting, every 4 weeks, reduced yields compared with a hay aftermath management where cuts were at 10 week intervals. The leaf area followed the same pattern so that the hay cut swards had a higher integrated leaf area than the 4 week cut swards. Dewey (1961) used similar defoliation treatments plus an intermediate frequency and found that with orchardgrass swards the most intensive frequency gave the lowest yield in all three years of the trial. Again the hay management produced the greatest yield except in one year when it was equal to the intermediate frequency.
However, increased cutting frequency is not necessarily associated with reduced yields; Robards and Leigh (1967) examined barley grass (Hordeum leporinum Link.) pastures and found that cutting once a month gave a greater accumulated yield than cutting every 6 months while intermediate frequencies gave intermediate yields. Clipping height too, can influence the outcome of the clipping frequency trials. Holt and Lancaster (1968) examined the effects of both frequency and intensity of defoliation on the production of coastal bermudagrass (Cynodon dactylon (L.) Pres.). They found that with cutting at 13 cm there were no differences in yield between the three clipping frequencies. However, when clipped at 5 cm the usual pattern appeared and the least frequent clippings gave the highest yield. Clipping height per se influenced yield and the close clipping at 5 cm gave the highest yield.

With intermediate wheatgrass (Agropyron intermedium Host.) and pubescent wheatgrass (A. spicatum var. pubescons Elmer.) Baker and Hunt (1961) found plants clipped at 2 inches produced significantly more herbage than did plants clipped at 4 inches. Unlike clipping frequency, clipping height shows no general pattern. Davis (1960) working with reed canarygrass (Phalaris arundinacea L.) found that a 5 inch clipping height gave greater yields than a 1 inch clipping height. Other workers (Drake et al. 1963) found that orchardgrass swards clipped at 3 inches consistently outyielded swards clipped at 1.5 inches, no matter what the date of the first cut or the nitrogen level. Matches (1966) also found similar trends with Kentucky 31 tall fescue where 4 inch clipping outyielded 1 inch clippings.

Clearly many factors influence the outcome of the clipping height experiments. Scott (1956) has stressed the importance of the position
of the basal tiller buds with reference to defoliation height and management. However, stage of growth at which defoliation takes place will also influence the outcome of defoliation experiments. Sheard and Winch (1966) examined swards of timothy, brome grass and orchard-grass all clipped to a height of 2.5 inches with the clippings re-initiated every 2, 4 or 6 weeks, when there was 80% or 95% light interception and at pre or post elongation. They found that for these species there were no harvest criteria which consistently produced the maximum yield. Thus, although morphological features and phenological events play a part in determining the outcome of defoliation practice they do not always show consistent trends.

When the defoliation is by animal grazing, the selective nature of the animals, especially at moderate stocking pressures, frequently negates the potential extra gains available from surplus herbage and moderate stocking. Roe et al. (1959) subjected Bothrichloa ambigua S.T. Blake pastures to three stocking rates with rotational or continuous grazing and were unable to detect any consistently significant difference between the grazing treatments in their effect on the pasture or on the live weight gain of the sheep.

With leguminous forages wide differences between results of defoliation experiments exist. Davies et al. (1960) found that Grimm and Du Puits alfalfa cut 3 times a season gave greater yields than when cut only twice. Ridgman (1960) working with Provence alfalfa, found cutting at ground level severely reduced yield potential while cutting at any other stubble height between 2 and 6 inches produced no differences in yield. Opposite trends were obtained with Ladino clover by Gervais (1960); he found that cuttings at 1\(\frac{1}{2}\) inches produced a
greater cumulative dry matter yield than did cuttings at 3 inches and 2 cuts per season gave a greater total yield than four cuts per season which in turn was greater than 6 cuts per season. Rossiter (1961) has reported a similar trend with subterranean clover where one cut gave a greater total yield than 3 cuts.

Legumes, however, are frequently grown in association with forage grasses and it is in these forage mixtures that the influence of frequency and intensity of defoliation shows its maximum complexity. The complexity arises when, as is almost always the case, the reaction of the grass and legume to defoliation differs. In such associations a particular defoliation management can often give one or the other species a competitive advantage so that in time it dominates the sward. The net result is that the managements often result in comparisons of the productive capacity of individual species rather than of the mixed swards. Thus, when comparing defoliation managements with mixed swards it is necessary, as well as comparing yields, to compare the changes in the botanical composition.

Gervais (1960) examined the effects of both cutting height and frequency on the yield of ladino clover-timothy and ladino clover-bromegrass swards. Cutting frequency influenced composition of swards in the experiments in that they yielded more clover, but less grass and total production when cut 4 or 6 times than when cut twice. However, they found that cutting height did not influence the botanical composition of the swards. Thus in this instance species reacted as in pure swards and the clover cuts at 1.5 inches outyielded the cuts at 3 inches. Similar results have also been reported by Reid (1966, 1968) who found close cutting of perennial ryegrass-white clover and
orchardgrass-white clover, produced the maximum yield in both swards. In both the forage stands examined by Corvais (1960) the infrequent clipping tended to produce grass dominance presumably due to competition for light as outlined by Donald (1961) and by Blake et al. (1966).

The competitive ability of some cultivars differs too. Davies et al. (1960) was able to show that Du Puits alfalfa was able to produce and survive in association with timothy, perennial ryegrass or meadow fescue even with only 2 defoliations per season, however, Grimm alfalfa was not able to survive in these associations with 2 defoliations per season. They also found that if S123 red clover was grown with either grass its ability to produce was not influenced by the defoliation frequency. In general all the swards examined by Davies et al. (1960) showed slightly greater yields when the legume was present compared to the pure grass swards. They also found that three defoliations per season usually gave a greater cumulative yield than 2 defoliations per season. By contrast Ward et al. (1968) found greater yield and persistence of alfalfa, in association with orchardgrass, under four cuts per season compared with 6 cuts per season.

The legume, however, is not always the suppressed species; Wolf and Smith (1964) examined alfalfa growing with bromegrass, orchardgrass or timothy. They found, with 400 lb./acre nitrogen applied and a 3 cut per season management, that the alfalfa dominated both the timothy and bromegrass. However, with a 5 cut per season management a 50:50 grass: clover balance was obtained. Orchardgrass on the other hand was better able to compete with the alfalfa and showed a 50:50 grass-legume ratio at 3 cuts per season while at 5 cuts per season there was a grass dominance. In general all three swards gave a greater cumulative yield
with 3 cuts per season than with 5. Holliday and Wilman (1965) also have found the greatest annual yield at the lowest cutting frequency on timothy-meadow fescue-white clover swards.

Under some conditions deviation occurs from the pattern of "highest yield with the lowest frequency". Reid (1966, 1968) used two cutting frequencies, cutting swards of perennial ryegrass-orchardgrass-white clover when 8 or 10 inches high. With swards defoliated at 2.5 inches, there was no depression in yield even though the 8 inch swards were harvested an extra two times. Deviation from the 'highest yield with lowest frequency" pattern can also occur where tissue senescence in the stand is high. Hunt (1965) has shown with infrequent cutting tissue decay can occur within the sward, often without any accompanying new growth. It seems likely that this occurred in the alfalfa-grass swards of Davies et al. (1960) where two cuts per season yielded less than the three cuts per season treatments.

As a result of the diversity of results from clipping experiments and the ultimate necessity, in many instances, to relate defoliation practice to animal production, many workers have turned to measurement of forage production in terms of animal production. Although it is not the purpose of this review to cover this topic it is necessary to emphasise some of the difficulties in relating clipping studies to agricultural systems using grazing animals. Plot clipping techniques can be made to closely approximate practical harvesting of hay or silage and there is no problem in relating plot management to commercial farm management practice. With animal defoliation the problem is complex because clipping studies cannot easily be made to approximate animal defoliation; missing from simulated pasture in plots are animal
selectivity, animal treading and the return of dung and urine.

Broadbent (1964) designed a grazing experiment to bridge the gap between clipping and commercial grazing. By comparing rotational grazing systems where the sheep were moved to a new paddock when the LAI had been reduced to either 1 or 2 he found that lambs and ewes had significantly higher live weight gains when an LAI of 2 was left in each paddock. However, when this latter treatment was compared with a set stocked system there was no difference in the live weights. Other workers (Ruane and Raftery 1964) found a 20 paddock rotation superior to a 2 paddock one in terms of utilizable starch equivalent produced, and of hay conserved but not in milk production.

To improve the relation between clipping and grazing experiments a number of workers have used simple grazing management systems which closely approximate clipping systems. However, even with such systems there still appear to be differences; for example Frame (1966) found, with perennial ryegrass-white clover swards that sheep grazings out-yielded cuttings in both accumulated dry matter as well as digestible organic matter. Bryant and Blaser (1961, 1968) on the other hand found that clipping consistently out-yielded cattle grazing of both white clover-and alfalfa-orchardgrass forage swards. In the experiment of Frame the difference appeared to be a consequence of interactions between the grass-legume ratio and the excretal-, clover- and fertilizer-nitrogen. Thus as Bryant and Blaser removed the manure from their plots, part of the difference in result between the experiments could have been a consequence of differences in technique. Matches (1968) has compared clipping with grazing by sheep, and with grazing by cattle. The yields from swards of tall fescue-ladino clover,
smooth bromegrass-alfalfa and Kentucky bluegrass-birdsfoot trefoil were not influenced by the method of defoliation. Swards of orchardgrass-ladino clover, however, yielded more dry matter with animal defoliation than with clipping but there was no difference between the yields with sheep or cattle.

Clearly the above experiments support the general conclusion that the results of clipping and animal defoliation experiments are both necessary as stages in grassland evaluation. However, because of the great variability in result between apparently similar experiments the results are best fitted to optimizing forage production in the region of the experiment rather than to theoretical considerations of optimizing forage regrowth in general.

2.2 Net Photosynthesis and Light Energy Conversion in Forage Stands

2.2.1 Factors Influencing Net Photosynthesis of Leaves within Forage Stands

Net photosynthesis, LAI and light energy interception by forage stands has already been discussed (2.1.1). It is the purpose of this section to briefly outline the other factors which influence net photosynthesis in forage stands.

The influence of temperature on net photosynthesis is well known and the response of a number of forage species has been documented by Beinhart (1962), Murata and Iyama (1963), El-Sharkway and Hesketh (1964) and Hesketh (1967). In these reports the species with the higher rates of photosynthesis are those with a tropical origin and a higher optimum temperature for photosynthesis. This difference between
species of tropical and temperate origin is genetical and appears to be a consequence of the plants with the higher optimum temperatures having virtually no photorespiration whereas in those plants with the lower optimum temperatures photorespiration and photosynthesis may be simultaneously active. In the temperate species the optimum temperature observed for net photosynthesis is the integral of the temperature response curves of the two processes. Results presented for these species suggest that the photorespiration process increases sharply with temperatures around 15 - 20°C.

Temperature has also been shown to affect photosynthesis in plants in other ways; McWilliam and Naylor (1967) have shown that in maize temperatures of 16°C result in prolongation of a photosensitive stage in chlorophyll synthesis while temperatures of 28°C do not. In wheat (Triticum aestivum L.) however, there is no prolongation at 16°C so that at this temperature the maize plants generally have a lower chlorophyll content than the wheat. They suggest that this may account for the fundamental difference between the species in adaption to differing temperature zones of the world.

Among other temperature effects on photosynthesis Hesketh (1967) has observed that the season influences the maximum net photosynthesis measured; the maximum is less in winter than in summer. Diurnal changes in net photosynthesis are influenced by temperature in two ways. Gates (1966) has demonstrated that the diurnal cycle of leaf temperature can cause a mid-day depression of photosynthesis. Other authors (Iyama et al. 1964) have shown a clear diurnal rhythm in photosynthesis under constant conditions. They have further shown that some forage species, for example Dallis grass (Paspalum dilatatum Poir.) and sudan grass
Sorghum sudanense (Piper) Staph.) showed almost no diurnal rhythm in net photosynthesis at the optimum temperatures for this process but when kept at a constant temperature below their optimum they showed a strong diurnal rhythm.

It is well known that net photosynthesis in plants is dependent on the CO₂ concentration of the surrounding atmosphere. The phenomenon has been well reported in research work such as that of Decker (1959), in which he found a curvilinear decrease in net photosynthesis with decreasing CO₂ concentration. This response line passed to the right of the origin at a CO₂ concentration where photosynthesis and respiration were in equilibrium (the CO₂ compensation point). Moss, et al. (1961) were the first to report that maize plants could assimilate CO₂ from air with very low levels of CO₂ with a CO₂ compensation point of almost zero. This indicated that the leaves of this plant produced very little CO₂ themselves in the light. Later Forrester et al. (1966 a and b) found that CO₂ assimilation in soybean was enhanced in an O₂ free atmosphere whereas in maize there was no effect. In the O₂ free atmosphere the soybean behaved like maize and was able to assimilate CO₂ at very low concentrations. These results led to the conclusion that some plants possessed a photorespiration mechanism concurrent with photosynthesis (e.g. soybean) while other plants possessed only photosynthesis in the light (e.g. maize).

In the Gramineae, Downton and Tregunna (1967) have shown that the tropical genera do not possess photorespiration and exhibit optimum temperatures of about 35°C for net photosynthesis while the temperate genera have lower optimum temperatures for net photosynthesis and show photorespiration. The absence of a photorespiration system appeared
also to be correlated with the 4-carbon photosynthetic pathway of Kortschak et al. (1965) and Hatch and Slack (1966), whereas the temperate members of Gramineae appeared to show Calvin cycle photosynthesis. Leaf anatomy too is correlated with the absence of photorespiration. El-Sharkway and Hesketh (1965) suggested that the construction and structure of the bundle sheath was such that the sites of respiration in the bundle were protected and the CO₂ released was therefore recycled. This agrees well with the analogue model of Lake (1966) for leaf respiration. However, Hatch et al. (1967) have found high concentrations of phosphoenolpyruvate carboxidase in tropical grasses; the enzyme necessary for the 4-carbon photosynthetic path. Photorespiration may likewise be absent for biochemical rather than structural reasons. Despite these areas of doubt it is clear that the absence of a photorespiration system in the tropical grasses and other plants confers on the plants a superior ability to fix CO₂ compared with those plants possessing photorespiration.

Recent studies to determine the point at which water deficit in plants reduces their photosynthetic capacity were made by El-Sharkway and Hesketh (1964). In intense light, with sorghum (Sorghum vulgare L.) stomatal area limited the maximum net photosynthesis so that closure of the stomata with increased water deficit decreased photosynthesis before visible wilting. Moss et al. (1961) however, found only slight reductions in photosynthesis of maize subject to a moisture tension of -16.0 bars. Murata et al. (1966) studied a number of forage plants and also found an abrupt decrease in net photosynthesis generally, with a soil moisture tension of about -1.0 bars; following the decrease in net photosynthesis there was a decrease in the moisture content of the
leaves. These workers also found that dark respiration was depressed by moisture stress so that energy conservation took place. After watering, recovery to the original rate of net photosynthesis took between 1 and 12 hours. Red clover and alfalfa were among the species most resistant to moisture stress while Italian ryegrass, orchardgrass and maize were among the most susceptible species.

Mineral nutrition is also known to affect the photosynthetic performance of plants. For example Murata (1961) found positive correlations of net photosynthesis with nitrogen, phosphorus and potassium levels as well as chlorophyll content in rice. Clearly mineral deficiencies which reduce chlorophyll content must also reduce net photosynthesis. However, the relation between net photosynthesis and chlorophyll content is by no means simple; Šesták (1966) has shown that in young leaves grown under high light intensities there is often greater net photosynthesis than would be predicted from a normal linear relation with chlorophyll content. The relationship between net photosynthesis and the mineral content of the leaves is also non-linear. Peaslee and Moss (1965) and Moss and Peaslee (1966) have found a curvilinear relationship between net photosynthesis and leaf magnesium and potassium levels in maize; above a critical level of the element there was no further increase in CO₂ assimilation.

The findings of Tsuno and Fujise (1965 a and b) viz. that photosynthesis was a function of the rate of photosynthate removal taken together with the observations of Hart et al. (1965) viz. that translocation rates of sugar from leaves were depressed when any one of the elements N, K, P, or Fe were deficient, suggests a mechanism by which low mineral nutrition depresses net photosynthesis. Similar
depressions of net photosynthesis with high sugar levels have also been reported in barren maize plants by Moss (1962).

High levels of minerals can depress net photosynthesis; Schroder (1966) has shown that 9,000 ppm NaCl severely reduced net photosynthesis in both pangola and bahia grasses (Paspalum notatum Flugge). However, in St. Augustine grass (Stenotaphrum secundatum (Walt.) Kuntze) and coastal bermuda grass there was greater resistance to salinity with the latter species showing no appreciable depression in net photosynthesis until a level of 1,800 ppm NaCl was reached in the soil.

Increasing leaf age has been shown to be accompanied by reduced net photosynthesis. For example, Jewiss and Woledge (1967) using the 5th leaf of a tall fescue tiller found a progressive decline in CO₂ assimilation with increased age. Begg and Wright (1964) examined the efficiency of top and basal leaves of reed canarygrass and, although they did not measure CO₂ uptake, in terms of dry weight they found the older leaves showed a depressed weight gain. Recently Brown et al. (1966) have measured CO₂ assimilation in upper and lower leaves of white clover and alfalfa plants. At saturating light energy levels, in a four week old stand, leaves at the bottom of alfalfa plants were about half as efficient in fixing CO₂ as those at the top. With white clover there was a progressive decline in CO₂ assimilation with age. Defoliation studies by the same authors showed that after leaves reached two weeks of age they contributed very little to further regrowth. In fact with reed canarygrass lower leaves appeared to be "parasitic" in that they respired more carbon than they fixed.

Within a particular plant species populations of differing genetic origin, particularly from climatically differing areas, often show
differences in photosynthetic capacity. For example, Bjorkman and Holmgren (1963) found plants from shaded and exposed habitats showed their greatest photosynthetic efficiency when growing in light conditions approximating those of their habitats. Similarly Milner and Hiesey (1964) found in climatic races of *Mimulus cardinalis* Dougl. overall rates of photosynthesis were proportional to the length of growing season in their original environment. More recently Eagles (1967) has shown that Danish populations of perennial ryegrass had a lower optimum temperature for net photosynthesis than populations from Algeria.

The capacity of the CO\(_2\) diffusion process limits photosynthesis, not only by diffusion resistances inside and at the leaf surface but also by the resistance to CO\(_2\) transport from the air above the crop to the crop surface. Taking all these resistances into account Gaastra (1962) has estimated that photosynthesis of closed crop surfaces is limited by diffusion on most mid-summer days. On such days the light energy wasted due to diffusion limiting photosynthesis is about 40% of that available for CO\(_2\) fixation.

Recently Sweet and Wareing (1966) have presented evidence which suggests that growth itself can limit photosynthesis. However, their results did not show conclusively whether it was a consequence of a metabolic sink effect or an auxin level effect on photosynthesis.

2.2.2 Methods of Measuring Net Photosynthesis in Forage Stands

Measurements of net photosynthesis in forage stands has usually been accomplished by measurement of the CO\(_2\) exchange rate. The most convenient method for measuring the CO\(_2\) concentration changes and hence
the exchange rates, is by infrared absorption. Alternatively $^{14}\text{CO}_2$ radioactive tracer techniques may be used to estimate $\text{CO}_2$ concentrations in the air and its incorporation into plants. The use of these two techniques will be discussed separately. In addition, for completeness, it is convenient to discuss the mathematical models for estimating net photosynthesis in this section.

The use of infrared gas analysers (IRGA) to measure $\text{CO}_2$ concentration in the air came into prominence in the early 1950s; it is now well known and needs no further elaboration. However, the systems for sampling the $\text{CO}_2$ concentration of the air surrounding the plants needs discussion as there have been considerable changes and refinements. The aim of all these has been to devise a system giving an authentic estimate of $\text{CO}_2$ exchange. At present there is still debate on the most convenient and accurate system.

The early systems were generally only suitable for the measurements of exchange rates of plant parts. For example, Parker (1953) enclosed a small twig and leaves of *Picea excelsa* in a plastic tube and drew air over the twig and leaves and then through an IRGA. He calculated the $\text{CO}_2$ exchange from the difference in concentration between the inlet and outlet of the plastic tube. By contrast Decker (1954) enclosed the above ground portion of scotch pine (*Pinus sylvestris*) seedlings in a sealed chamber system and from the monitored rate of $\text{CO}_2$ depletion between 270 and 330 ppm $\text{CO}_2$ he calculated the $\text{CO}_2$ exchange. Orchard and Heath (1963) have described an apparatus which can easily be modified to either a closed or open system. The design of chambers for small plant parts has been shown to be critical by the work of Avery (1966), Hardwick *et al.* (1966) and Etherington (1967). However,
these chambers are generally too bulky for use on leaves in their natural field condition.

For field studies of whole plants and groups of plants larger and more complex chambers are necessary so that whole plants can be enclosed in their field state. The systems cover the whole range from the closed circuit of Decker (1954) to the open circuit of Parker (1953). In the closed circuit category Koller and Samish (1964) designed a null point compensating system where additions or removals of CO₂, keeping a constant concentration, were measured. The system uses a polythene bag of suitable size to enclose the plants which although somewhat permeable to CO₂ does not influence the results if the null point is kept at ambient levels of CO₂ and if a slight positive pressure is maintained within the bag.

A semiclosed system was described by Musgrave and Moss (1961); this has been used, and in some cases slightly modified by Moss et al. (1961), Baker and Musgrave (1964) and Baker (1965). Essentially the system was kept closed and the rate of CO₂ depletion measured; however, they periodically metered in measured quantities of CO₂ so that the concentration was kept at ambient ± 50 ppm CO₂. Initially CO₂ assimilation was calculated from the rates of CO₂ depletion. This was later modified so that the CO₂ additions would maintain a smaller range and in this case the rates of CO₂ uptake were calculated from the CO₂ additions.

The open circuit system has been used by a number of workers, Hesketh and Musgrave (1962), Hesketh and Moss (1963), Baker and Musgrave (1964), Pearce et al. (1965) and McCree and Troughton (1966). In this system, as CO₂ uptake is the product of flow rate and the CO₂ differ-
ential between the inlet and outlet, the flow rate is usually adjusted for a CO$_2$ differential of not more than ambient ± 25 ppm CO$_2$. With a larger differential the influence of the CO$_2$ level on net photosynthesis must be taken into account. McCree and Troughton (1966) corrected for the CO$_2$ differential by a linear relation, but a curvilinear one would be necessary if the differential were great. If the chamber volume is kept large, compared to the foliage volume, a small differential can be achieved without high flow rates, which cause unnatural wind conditions. Low flow rates, as shown by Takakura (1966), can result in errors and under estimation of CO$_2$ exchange due to diffusion problems. Takakura has shown that if the chamber volume to foliage volume ratio is large, moderate flow rates give maximum CO$_2$ exchange but if the ratio is small, maximum exchange may never be observed even at extreme flow rates.

All the systems described, apart from their own difficulties, have errors associated with the infrared analyses. These analytical errors have been stressed by Brown and Rosenberg (1968). As an alternative to infrared analyses $^{14}$CO$_2$ may be introduced into closed chamber systems and its rate of depletion monitored with a Geiger tube. Lister et al. (1961) have described such a system which also uses an IRGA so that levels of both $^{14}$CO$_2$ and $^{12}$CO$_2$ may be followed.

More recently Austin and Longden (1967) have described a small chamber which can be clamped to leaves in the field for short term $^{14}$CO$_2$ exposure. Here the CO$_2$ assimilation rates are calculated by counting the $^{14}$C activity in the leaves. Wolf (1967) has described a system for exposing whole plants in the field to CO$_2$. However, here problems of quantity of isotope and contamination of the soil become
Infrared gas analysers can also be used to measure the CO₂ gradient above a crop. The CO₂ moved into the area by the wind is estimated from the relative changes in the CO₂ and wind profiles and together with an estimate of the CO₂ liberated from the soil is used to estimate the CO₂ assimilation. This system, because it is completely chamberless, imposes no artificial environment on the crop. The technique has been used by Inoue et al. (1958), Lemon (1960) and Monteith and Szeicz (1960). However, as pointed out by Monteith (1962) there is difficulty in maintaining accurate records of the CO₂ gradients over long periods. He has also shown that there is uncertainty about the relationship between gradient and flux in the presence of temperature gradients. These two reasons and a combination of them can, on occasions, produce absurd flux values. With care and with appreciation of the limitations of the method worthwhile results can be obtained and often in situations which cannot be explored by the chamber methods. For example, Wright and Lemon (1966) have used this method to examine the vertical distribution of photosynthesis within a corn crop.

Four mathematical models have recently been published to predict net photosynthesis in field crops; these are by Monteith (1965), de Wit (1965), Duncan et al. (1967) and Idso and Baker (1967). The model by Monteith (1965) is based on his binomial expansion for light passing through a unit leaf layer, combined with two parameters describing the light response curve of single leaves and assumes that solar radiation varies sinusoidally. Net photosynthesis was then estimated for any day length and solar radiation level. He has shown that
the model's estimates are close to actual data from published growth rate experiments. However, it requires a knowledge of the radiation profile, leaf transmission and LAI for the light attenuation expression.

The model by de Wit was more complex; he used a light attenuation expression but then included factors for the distribution of leaves at various angles, the LAI, the amount of diffuse and direct light, the height of the sun and the resistance to CO₂ movement from the air to the canopy. Most of these factors represented geometric problems and these have been solved by programming the model for an electronic computer. This model too, gave results which closely approximate those of field observations. Its overall accuracy depends on the suitability of the light response curve expression and a knowledge of the overall leaf area and leaf angle distribution in the sward. Duncan et al. (1967) used a larger computer and thus were able to include a greater number of factors in their model. They allowed for the plant variables of leaf area, angle, position, reflectivity, transmissivity and the variations in the photosynthetic light response curve of the leaves. The environment variables allowed for were sun elevation, solar brightness and sky light brightness. The model has been shown to give extremely good estimates of actual data.

The model of Idso and Baker (1967) used the light and temperature response curves of plants. It is of note that these authors are the only workers who have included temperature as a factor in photosynthetic prediction models. The environment was analysed by energy flow analyses based on meteorological parameters. The allowance for leaf geometry was made by classifying leaves on the plant for position and then ascertaining the energy regime for each class. The model has been
used on hypothetical crops to predict changes in productivity due to differences in leaf geometry.

2.2.3 Measurements of Net Photosynthesis and Production from Forage Stands

Experiments where both dry matter production and net photosynthesis have been measured for forage stands are few; due largely to difficulties in measurement of net photosynthesis. In 1962 Stanhill used de Wit's model for calculating potential photosynthesis (see Section 2.2.2) and compared these results with the measured dry matter production from an alfalfa field. The general seasonal trend of measured and predicted values was very similar, however, measured production was consistently lower than the potential. Measurements of the light interception showed for a yearly average only 33% of the light intercepted. This indicated that inefficient light interception was a major reason for the failure of dry matter production to reach the potential predicted from the photosynthetic model.

The first direct measurements of net photosynthesis in a forage stand were made by Alexander and McCcloud (1962). They used an IRGA in a closed circuit with a chamber containing a sod of bermudagrass to measure the CO₂ exchange under a range of light intensities. Swards cut daily to 8 inches required 5,000 ft·c. to produce a saturation level of net photosynthesis of 2.4g CO₂/m²/hr, while swards cut to 1 and 2 inches were not light saturated at 7,000 ft·c. This difference in response appeared to be a consequence of differences in LAI and angular distribution of the leaves, with the 1 and 2 inch swards showing more erect leaves. The light response curves of bermudagrass

1 All CO₂ assimilation rates in this section are per unit area of land.
swards at LAI's between 14 and 25 were also determined. Swards at LAI 14 were light saturated at 5,000 ft-c. and fixed 2.4g CO\textsubscript{2}/m\textsuperscript{2}/hr. while those at an LAI of 25 were light saturated at 7,000 ft-c. and fixed 1.2g CO\textsubscript{2}/m\textsuperscript{2}/hr. The photosynthetic capacity of an 8 inch stubble was nil when the LAI before cutting was 20, but where the LAI was 14, before the stubble was cut, the stubble fixed 1.2g CO\textsubscript{2}/m\textsuperscript{2}/hr. at a light saturation level of 4,000 ft-c. The stubble below 2 inches was not capable of fixing CO\textsubscript{2}.

Billings et al. (1966) measured the CO\textsubscript{2} assimilation of alpine turf by covering a section of it with a chamber in an open circuit system with an IRGA. At a light intensity of 3,700 ft-c. they found 2.1g CO\textsubscript{2}/m\textsuperscript{2}/hr. fixed. However, as the plants are specialized this rate cannot be evaluated in terms of LAI or other plant production measures.

The most extensive investigations of net photosynthesis in forage stands accompanied by LAI measurements have been made by Pearce et al. (1965, 1967), Brown et al. (1966) and Wilfong et al. (1967). They used an open circuit chamber system with an IRGA to measure the CO\textsubscript{2} concentration differential. The chamber temperature was controlled by refrigeration and the light intensity varied either by cloth screens or by using reflector flood lamps. With orchardgrass stands Pearce et al. (1965) found the saturation light level was 4,500 ft-c. for LAIs between 3 and 8. The regrowth weight of herbage increased linearly from 8 to 30 days after cutting with 95% light interception after 15 days and at a LAI of 5. At a LAI of 5 the swards fixed 2.5g CO\textsubscript{2}/m\textsuperscript{2}/hr., however there was no clearly defined optimal LAI as CO\textsubscript{2} uptake was
almost the same over the LAI range of 3 to 8. Light interception and regrowth of dry matter also indicated a similar wide range in optimal LAI between 3 and 8. From studies of net photosynthesis before and after cutting they found that leaves below 4 inches in the sward were incapable of utilizing the high light energies.

Pearce et al. (1967) examined the influence of leaf angle and LAI on the net photosynthesis of a barley stand. The differences in leaf angle were obtained by growing the plants in flats of soil kept at various slopes and then returning the flats to the horizontal position for measurement. Above an LAI of 2 they found differences in net photosynthesis due to the leaf angle. Leaves at 90° required an LAI of 11 to intercept 95% of the incident light while those at 53° required an LAI of 7 and those at 18° required only an LAI of 4.5. At an LAI of 11 the stand fixed 8g CO₂/m²/hr. The data from these experiments was compared with net photosynthesis as predicted by the light attenuation model of Saeki (1960) and a close relation was found between the predicted and the experimental results.

Wilfong et al. (1967) examined the net photosynthesis and LAI relationships in alfalfa and Ladino clover swards. With stands of these species they found a curvilinear decrease in net assimilation rate as LAI increased. Net photosynthesis in Ladino clover swards was light saturated at about 4,500 ft-c. while in alfalfa swards light saturation was reached between 5,000 and 7,000 ft-c. At these saturating light levels the Ladino clover sward fixed 3.0g CO₂/m²/hr. while the alfalfa sward fixed 7.0g CO₂/m²/hr. The data indicated that the optimum LAI for these swards occurred over a broad rather than narrow range viz. LAI 2 – 5 for Ladino clover and LAI 2 – 8 for alfalfa.
In further work, the same group (Brown et al. 1966) confirmed the above trends for swards of orchardgrass, Ladino clover and alfalfa, although at saturating light levels, slightly higher rates of net photosynthesis were reported. They also examined bermudagrass swards; with an LAI of 4.5 there was no light saturation of net photosynthesis even at 12,000 ft-c. At 12,000 ft-c. the swards fixed 14g CO$_2$/m$^2$/hr., a much higher rate than previously observed with other species. This agrees well with the evidence of Downton and Tregunna (1967) that members of the Chlorideae, such as bermudagrass, have little or no photorespiration. The earlier work, by Alexander and McCloud (1962), on bermudagrass indicated a lower CO$_2$ fixation rate. This may have been a low estimate as it appears that they did not correct for CO$_2$ evolution from the soil. Monteith et al. (1965) have shown that CO$_2$ from the soil can make up 20% of the carbon budget of actively growing grass swards.

Net photosynthesis in artificial forage stands has been studied by King and Evans (1967); they grew stands of wheat, alfalfa and subterranean clover in phytotron cabinets and determined their CO$_2$ uptake with an open circuit IRGA system. These swards all showed a rise in CO$_2$ uptake with increases in LAI and then a plateau maximum. The LAI at which the maximum was reached increased with increasing intensity of illumination. At the highest light intensity (3,300 ft-c.) wheat fixed a maximum of 5g CO$_2$/m$^2$/hr. at an LAI of 5. While with alfalfa stands the same rate as wheat was observed at an LAI of 10, however, the response of these stands at 3,300 ft-c. indicated that maximum and plateau were outside the range of the experiment. Subterranean clover behaved in the same manner as alfalfa and showed no
plateau at LAI 5 and 3,300 ft-c.; here 3.2g CO₂/m²/hr. were fixed. Leaf area indices above 10 in alfalfa and 5 in clovers rarely occur as the plants appear to self prune by senescence of the lower leaves. Speculation as to the behaviour of legume stands above these LAIs is therefore of dubious value.

In all of the experiments described so far in this section there was no clear evidence of a decline in net photosynthesis above an "optimal" LAI. The results of Alexander and McCloud (1962) vaguely suggest such a behaviour above an LAI of 20 in bermudagrass and the results of King and Evans (1967) similarly suggest that this may happen about LAI 5 in subterranean clover given a very low level of light energy. Most of the evidence points to the wide rather than the narrow "optimum" LAI. This would indicate that living lower leaves are not often "parasitic" and often have a positive net assimilation rate. The evidence that the lowermost leaves have no net CO₂ assimilation does not conflict with the above as it is only necessary for them to show zero net assimilation.

Recently Hunt et al. (1967) have described a wind tunnel technique to measure net photosynthesis from profiles of CO₂, water vapour and wind velocity. From these preliminary studies they observed a maximum CO₂ fixation of 7.1g CO₂/m²/hr. for an alfalfa sward and 3.9g CO₂/m²/hr. in orchardgrass both at a light energy level 42cal/cm²/hr.; a level which should have light saturated the swards. It is of note that the CO₂ fixation levels from this method compare well with those reported for these species by Brown et al. (1966) and Wilfong (1967) using the open circuit chamber technique.
2.2.4 The Efficiency of Light Energy Conversion by Forage Stands

As has been previously shown in this review many factors limit net photosynthesis and growth in forage stands. Factors such as moisture, nutrients, disease and insects are all subject to some measure of control by agriculturalists. When such controls are successful the growth of the plants, suitably adapted to the particular climate, depends on light interception and CO$_2$ assimilation by the sward. As discussed in Section 2.2.1 the LAI of the sward must be sufficient to intercept all the light if high growth rates are to be achieved. Assuming therefore all other factors are optimal and that the LAI is close to optimal what then is the potential productivity or capacity of a forage sward to fix CO$_2$? The purpose of this section is to explore this question, in other words, how much CO$_2$ can be fixed and with what efficiency of light energy use? The answers of these questions are of value as they allow the comparison of swards of different plant species as well as providing a scale on which the extent of a growth limitation by a particular factor may be judged.

In 1956 Nišiporović put forward a general figure of 15% for the efficiency of light energy use by agricultural crops in fixing CO$_2$. At this efficiency he estimated that these crops could fix 100g CO$_2$/m$^2$/day. More recently Gastra (1958) and Blackman and Black (1959) found that during the most active growth phase of sugar beet its efficiency of light energy use was 9%, while with barley, Kamel (1959) found an efficiency of 14% which was very close to Nišiporović's estimate. However, lower efficiencies have been reported too. Rees (1962) working with oil palm plantations found the efficiency of light energy use was 1.2% while Cooper (1966) with perennial ryegrass pastures found only a
2% efficiency. Both these workers found higher efficiencies but these were only for the seedling year of the communities. Bonner (1962) has pointed out that efficiencies as high as 20% are possible with algal cultures subject to low light energy levels, but as the light energy level increases the efficiency declines to about 5% due to shading between the cells. The same occurs with forage associations where the decline in efficiency is a consequence of intra- and inter-leaf shading as well as mutual shading between the cells and chloroplasts. It is clear therefore that the lower efficiencies for established stands are realistic, especially if they are subject to high mid-summer radiation levels for a large proportion of their growing period.

Loomis and Williams (1963) have estimated the upper limit of crop productivity by evaluating the absorption and utilization of solar radiation on a quantum basis. They estimated that with a light energy input of 222 cal/cm²/day and 8.64 μEinstineis/cal. the CO₂ fixation could reach 104g CO₂/m²/day which corresponded to an efficiency of light energy use of 12%, including an allowance for respiration. Correcting for the inorganic nutrient content their figure for potential productivity was 77g organic material/m²/day i.e. 690 lb/acre/day. This estimate is surprisingly close to the earlier estimate by Nišiporović (1956). Williams and Loomis (1963) reported that the highest producer they could find was sudan-grass with a dry matter productivity of 51g/m²/day and a light energy conversion efficiency of 6.7%. More recently Begg (1965) reported a similar dry matter production with Bulrush millet (Pennisetum typhoides) of 54g/m²/day with a light energy conversion efficiency of 9.5%. It is of note that Downton and Tregunna (1968) suggest that both these plants would have no photorespiration.
Using the assumption that a maize stand was as efficient as Chlorella on a quantum basis Yocum, et al. (1964) estimated a maximum efficiency of light energy use of 12%. However, from their field studies of CO₂ exchange they found that the efficiency was only 5.1%. Uncertainty as to the magnitude of dark and photorespiration makes estimation of the potential maximum CO₂ uptake rate difficult, however, taking the overall figure of a 33½% loss for total respiration used by Loomis and Williams (1963) and their productivity estimate, the average CO₂ uptake would be 12.8 g CO₂/m²/hr. The average rate quoted by Yocum et al. (1964) for the maize with the 5.1% efficiency was 9.0 g CO₂/m²/hr. indicating a considerable margin available for increased efficiency and uptake for this crop as well as the forage crops mentioned in Section 2.2.3.

Black (1964) used a different approach. With a knowledge of the growth responses of subterranean clover to radiation and using a mean seasonal radiation level and an average calorific value of 4,000 cal/gram he found a maximum efficiency of light energy use of 4.2%. For the environment of Adelaide, South Australia he calculated a seasonal dry matter production of 65 metric tons/hectare (m.tons/ha) was possible compared with an actual average of 8 m.tons/ha. He demonstrated that the actual production was reduced by 32 m.tons/ha with summer drought and by 2 m.tons/ha with sub-optimal LAI and by 16 m.tons/ha with a super-optimal LAI. With none of these factors limiting the maximum daily rate of production would be 23 g/m²/day and the minimum 10g/m²/day with a seasonal average efficiency of light use of 2.9%.

Recently Hunt and Cooper (1967) have compared the efficiency of
light energy conversion by a number of forage stands as they regrew from 50% light interception. Rough-stalk meadowgrass (*Poa trivialis*) with a growth rate of 7 g dry matter/m²/day showed an efficiency of 3.3% while tall fescue with a growth rate of 12 g/m²/day showed an efficiency of 7.2%. From their measurements of CO₂ uptake under growth chamber conditions King and Evans (1967) found that the efficiencies of light energy use for swards of wheat, lucerne and subterranean clover were 12.8, 13.5 and 9.8 at growth rates of 30, 39 and 20 g/m²/day respectively. These authors found that the growth rates were depressed by a relatively high rate of dark respiration, often between 40 and 50% of gross photosynthesis. The high efficiencies of light energy use, based on gross CO₂ uptake, therefore reflect the optimum CO₂ diffusion conditions and are therefore in line with the lower field estimates where CO₂ availability could be limiting its uptake.
3. **FIELD EXPERIMENT WITH DEFOlation BY ANIMALS**

The experiment reported in this section is the first in the series of three mentioned in the introduction. The problems which became evident from this experiment are then investigated in the two later experiments.

3.1 **Materials and Methods**

The experimental area was located on the Laureldale Research Station at the University of New England, New South Wales, Australia. Climatically, the area is characterised by summer rain with high variability and a mean annual rainfall of 28.9 inches. Winters are cool with a July mean maximum of 53.1°F, and mean minimum of 32.7°F and summers are warm with temperatures of 80.0°F and 90.0°F occurring commonly to give a January mean maximum 80.0°F and mean minimum 55.1°F, (Roe, 1948). The soil type in the experimental area is a "normal chocolate", as described by Hallsworth et al. (1952), with some Wisenboden/Black earth (Stephens, 1953).

In February 1962 grass-legume pasture stands were established. Each stand had the same clover mixture and one of the following grasses:- New Zealand Perennial ryegrass (*Lolium perenne* L.), Grass-
lands Ariki ryegrass (*L. perenne* x *L. multiflorum* x *L. perenne*), Grasslands Cocksfoot (*Dactylis glomerata* L.), S143 Cocksfoot, S26 Cocksfoot, Alta Fescue (*Festuca arundinacea* Schreb.) and S170 Tall Fescue. The seeding rates were 10 lb. per acre for ryegrass and fescues, and 8 lb. per acre for cocksfoot. Each of the above pasture grasses were drillsown together with 2 cwt. per acre of superphosphate, 2 lb. per acre of New Zealand white clover (*Trifolium repens* L.), 1 1/2 lb. per acre of Montgomery red clover (*Trifolium pratense* L.) and 1 1/4 lb. per acre Broad red clover. The field design was a randomised block – split plot. Each of three blocks were divided into seven plots and within each block the seven grass-legume stands were randomly allocated to the blocks. Each plot was split into 3 sub-plots for three grazing managements in which sheep were used as defoliators. Allocation of the three grazing managements to those sub-plots was random. The grazing managements were:

1. The herbage grew to 3-4 in. and then was grazed to a height of 1 in., henceforth designated as management (3-1).
2. The herbage grew to 9-10 in. and then was grazed to a height of 1 in. viz. management (9-1).
3. The herbage grew to 9-10 in. and then was grazed to a height of 3 in. viz. management (9-3).

Each of the 63 sub plots measured 39 ft. x 63 ft.

By April, 1962, the pastures were well established and received a common grazing with sheep. From that date until the experiment began in February, 1963, the pastures continued to receive a common grazing

---

1 The individual grass-legume stands will be referred to by the standard common name of their sown grass.
management designed to keep them between 1 and 6 inches in height. During this period the area was fenced into the appropriate paddocks.

The grazing managements were first applied in February, 1963 and from this date yields of herbage and botanical composition at the time of grazing were recorded. From August, 1963, leaf area index (LAI) at grazing was also recorded. Records of rainfall at the experimental site also commenced in August, 1963. The procedure for the grazing managements was as follows: when the average height of the herbage, between the three blocks of a particular pasture and grazing management was judged to have reached the grazing height, as estimated by measurement with a staff, samples of herbage were cut to determine the plot yield. The sample consisted of four random 6 ft. x 1 ft. quadrats cut from each plot at a height appropriate to the particular grazing management. Each sub-plot sample was mixed, weighed and sub-sampled for dry matter determination (200 g) and botanical analysis (50 g). Botanical analyses were by hand separation of the herbage into three categories viz; green grass, green clover and "dead material" consisting of senescent and dead grass and clover. After botanical analysis and before drying, the leaf areas of the green grass and clover components of the pasture were determined with an air-flow planimeter (Jenkins, 1959). All drying of herbage was done in a forced-draught oven at 90°C. The yield of herbage on each sub-plot was then used to estimate the number of sheep required to graze the herbage to treatment height in three days. The estimate was based on mean live weight of the sheep, as experience had shown that they would consume dry matter equivalent to approximately 2% of their body weight each day. The appropriate number of sheep were then placed on the plots. Usually
grazing commenced the day after the herbage samples were taken. To ensure that fertility transfer was minimal, the sheep were always removed after three days even if small patches of herbage were not consumed. The sheep were also pregrazed on pastures similar to those of the experimental plots to further reduce fertility transfer errors. The herbage left after grazing was topped with a rotary mower to the grazing management height and the clippings distributed over the plot.

Every six months (July 31st and February 1st) cuts of herbage present on all plots were taken to allow assessment of the yields for two growth periods per year. Each autumn the experimental area received 2 cwt per acre superphosphate and 0.5 cwt per acre muriate of potash.

3.2 Results

3.2.1 Production of Individual Pastures

Production of herbage in the second year was considerably less than in the first (Table 3.I). The rainfall records (Table 3.II) also show a marked reduction in precipitation in the second year of the trial. However, the productivity rank of the sown grass components pastures was essentially similar in both years. S170 tall fescue was the most productive pasture grass and perennial ryegrass the least productive while the remaining grasses showed intermediate production. In 1964, the yield of the clovers growing with the tall fescue and cocksfoot was significantly lower than that growing with the ryegrasses (P < 0.001). Dead foliage also showed differences in 1964, with greatest senescence in the S143 and S26 cocksfoot and least senescence in the S170 tall fescue swards.

The pasture types did not show similar total production in the two
### Table 3.1
Mean yields of seven pasture stands in lb./acre/annum of dry matter

<table>
<thead>
<tr>
<th>Pasture Component</th>
<th>Perennial</th>
<th>Ariki</th>
<th>Grasslands</th>
<th>S143</th>
<th>S26</th>
<th>Alta Fescue</th>
<th>S170 Tall Fescue</th>
<th>S.E. of Means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ryegrass</td>
<td>Ryegrass</td>
<td>Cocksfoot</td>
<td>Cocksfoot</td>
<td>Cocksfoot</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>1227</td>
<td>1705</td>
<td>2005</td>
<td>1741</td>
<td>1962</td>
<td>1813</td>
<td>2179</td>
<td>136</td>
</tr>
<tr>
<td>Clover</td>
<td>929</td>
<td>829</td>
<td>977</td>
<td>1205</td>
<td>1037</td>
<td>819</td>
<td>754</td>
<td>99</td>
</tr>
<tr>
<td>Dead Foliage</td>
<td>341</td>
<td>464</td>
<td>386</td>
<td>470</td>
<td>382</td>
<td>473</td>
<td>397</td>
<td>55</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>232</td>
<td>315</td>
<td>334</td>
<td>338</td>
<td>390</td>
<td>515</td>
<td>744</td>
<td>50</td>
</tr>
<tr>
<td>Clover</td>
<td>472</td>
<td>526</td>
<td>245</td>
<td>401</td>
<td>254</td>
<td>175</td>
<td>213</td>
<td>44</td>
</tr>
<tr>
<td>Dead Foliage</td>
<td>276</td>
<td>235</td>
<td>220</td>
<td>460</td>
<td>386</td>
<td>220</td>
<td>121</td>
<td>33</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Year</td>
<td>Total Production</td>
<td>(grass + clover)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1963</td>
<td>2156</td>
<td>2553</td>
<td>2982</td>
<td>2946</td>
<td>2998</td>
<td>2632</td>
<td>2933</td>
<td>142</td>
</tr>
<tr>
<td>1964</td>
<td>704</td>
<td>841</td>
<td>579</td>
<td>740</td>
<td>645</td>
<td>960</td>
<td>957</td>
<td>58</td>
</tr>
</tbody>
</table>
years. In 1963 the perennial ryegrass pastures showed significantly less total production \( (P<0.01) \) than the rest, while in 1964, the Grasslands cocksfoot pastures showed significantly lower total production than the other pastures \( (P<0.01) \). Further in 1964 the S170 tall fescue pastures showed significantly greater total production than the other pastures \( (P<0.01) \). The production of the pastures was also examined with the year divided into two growth seasons, one from February to July (Autumn - Winter) and the other from August to January (Spring - Summer). Production from the sown grasses was significantly different in the two growth seasons \( (P<0.05 \text{ in } 1963, \text{ and } P.< 0.01 \text{ in } 1964 \text{ see Table 3.III}) \). In 1963, this interaction with

Table 3.II Rainfall, monthly totals in inches.

<table>
<thead>
<tr>
<th>Season</th>
<th>Feb.</th>
<th>Mar.</th>
<th>Apr.</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1963</td>
<td>1.25</td>
<td>5.46</td>
<td>1.96</td>
<td>7.78</td>
<td>1.68</td>
<td>1.13</td>
<td>19.26</td>
</tr>
<tr>
<td>1964</td>
<td>0.68</td>
<td>5.12</td>
<td>2.25</td>
<td>0.52</td>
<td>1.16</td>
<td>3.31</td>
<td>13.04</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1963/4</td>
<td>1.98</td>
<td>0.10</td>
<td>1.94</td>
<td>2.76</td>
<td>1.78</td>
<td>6.84</td>
</tr>
<tr>
<td>1964/5</td>
<td>1.04</td>
<td>1.95</td>
<td>2.04</td>
<td>3.15</td>
<td>1.16</td>
<td>1.47</td>
</tr>
</tbody>
</table>

Total for Feb. 1963 to Jan. 1964 34.66 in.

1 The data for Feb. to July 1963 is from Armidale P.O. 2\( \frac{1}{2} \) miles distant from the experimental site.
Table 3.III

Seasonal interactions with sown grass production, mean yields given in lb./acre of dry matter.

<table>
<thead>
<tr>
<th>Growth Season</th>
<th>Perennial Ryegrass</th>
<th>Ariki Ryegrass</th>
<th>Grasslands Cocksfoot</th>
<th>S143 Cocksfoot</th>
<th>S26 Cocksfoot</th>
<th>Alta Fescue</th>
<th>Tall Fescue</th>
<th>S.E. of Means +</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass 1963</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn-Winter</td>
<td>1054</td>
<td>1344</td>
<td>1721</td>
<td>1422</td>
<td>1531</td>
<td>1399</td>
<td>1494</td>
<td></td>
</tr>
<tr>
<td>Spring-Summer</td>
<td>1394</td>
<td>2065</td>
<td>2288</td>
<td>2060</td>
<td>2393</td>
<td>2227</td>
<td>2865</td>
<td>146</td>
</tr>
<tr>
<td>Grass 1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn-Winter</td>
<td>354</td>
<td>366</td>
<td>180</td>
<td>336</td>
<td>291</td>
<td>331</td>
<td>561</td>
<td></td>
</tr>
<tr>
<td>Spring-Summer</td>
<td>110</td>
<td>264</td>
<td>488</td>
<td>340</td>
<td>488</td>
<td>699</td>
<td>927</td>
<td>90</td>
</tr>
<tr>
<td>Dead Material 1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Autumn-Winter</td>
<td>270</td>
<td>300</td>
<td>327</td>
<td>302</td>
<td>428</td>
<td>256</td>
<td>293</td>
<td></td>
</tr>
<tr>
<td>Spring-Summer</td>
<td>283</td>
<td>169</td>
<td>113</td>
<td>617</td>
<td>343</td>
<td>184</td>
<td>1</td>
<td>67</td>
</tr>
</tbody>
</table>
season occurred because of high production by the S170 tall fescue pastures in the spring - summer while in the autumn - winter period tall fescue production was similar to that of the other grasses. In 1964, the interaction with season was a consequence of low autumn - winter production by the Grasslands cocksfoot and low spring - summer production by the perennial ryegrass. Dead foliage too, showed a highly significant interaction with season in 1964 (P<0.001), herbage senescence was uniform during the autumn - winter period; in the spring - summer S170 tall fescue showed little senescence and the S143 cocksfoot much senescence.

3.2.2 Management Effects on Dry Matter Production

The effect of grazing management on dry matter yield was similar in both years (Table 3. IV). The (9-1) management gave the greatest total herbage production, the (3-1) intermediate and the (9-3) least (P<0.001). The pasture components also followed this pattern except for grass production in 1964 where the (3-1) management gave slightly more grass dry matter than the (9-1).

Table 3. IV The influence of grazing management on pasture production, given in lb./acre/annum of dry matter.

<table>
<thead>
<tr>
<th>Pasture Component</th>
<th>Grazing Management</th>
<th>S.E. of Means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3-1</td>
<td>9-1</td>
</tr>
<tr>
<td>Grass 1963</td>
<td>1921</td>
<td>2423</td>
</tr>
<tr>
<td>Clover 1963</td>
<td>992</td>
<td>1155</td>
</tr>
<tr>
<td>Dead foliage 1963</td>
<td>501</td>
<td>546</td>
</tr>
<tr>
<td>Grass 1964</td>
<td>601</td>
<td>530</td>
</tr>
<tr>
<td>Clover 1964</td>
<td>315</td>
<td>529</td>
</tr>
<tr>
<td>Dead foliage 1964</td>
<td>176</td>
<td>517</td>
</tr>
</tbody>
</table>
The season of growth also influenced the relative differences between the grazing managements (Table 3.V). Between the (9-1) and the (3-1) managements, the difference in production of grass, clover and dead material was least in the autumn and greatest in the spring, however between the two intensive grazing managements and the (9-3) management, the differences were greatest in the autumn and least in the spring. The interaction was highly significant (P<0.001) in 1964, with negligible production from the (9-3) treatments in the autumn.

With dead foliage the interaction in 1963 was a result of low autumn senescence in the (9-3). However, in 1964, it was a result of very low senescence in the (3-1) management in the spring (Table 3.V).

Table 3.V  The influence of season and grazing management on pasture production, given in lb./acre of dry matter.

<table>
<thead>
<tr>
<th>Growth Season</th>
<th>Grazing Management</th>
<th>Autumn - Winter</th>
<th>Spring - Summer</th>
<th>S.E. of Means</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3-1</td>
<td>9-1</td>
<td>9-3</td>
<td>3-1</td>
</tr>
<tr>
<td>Pasture</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Component</td>
<td>1963</td>
<td>1964</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grass</td>
<td>1643</td>
<td>738</td>
<td>1</td>
<td>650</td>
</tr>
<tr>
<td>Clover</td>
<td>303</td>
<td>270</td>
<td>1</td>
<td>183</td>
</tr>
<tr>
<td>Dead foliage</td>
<td>232</td>
<td>340</td>
<td>146</td>
<td>60</td>
</tr>
</tbody>
</table>
3.2.3 **Species and Grazing Management Interactions**

The species x management interactions which were statistically significant are shown in Table 3.VI. In 1964, the (3-1) management showed the greatest grass production from the perennial ryegrass; Grasslands cocksfoot and SL43 cocksfoot pastures whereas the (9-1) management favoured grass production from both strains of tall fescue \((P<0.01)\). The (3-1) management gave similar grass and clover production in both ryegrass pastures, while the clover production was lower than the grass production in the cocksfoot and tall fescue pastures. However, the cocksfoot and tall fescue pastures subject to (9-1) grazing management showed a wide range of grass:clover ratios. The grazing managements resulted in differing senescence in the pastures in both years \((P<0.01 \text{ and } P<0.001)\).

3.2.4 **Dry Matter and Leaf Area Index Relationships**

To examine the relationship between the total dry matter yield and the LAI the data were reduced into six groups, 'the ryegrasses', 'the cocksfoots' and 'the fescues' and the three grazing managements. To the data in these groups quartic polynomial regressions were fitted with total dry matter as the dependant variable and LAI as the independant variable. The significance of fitting terms higher than linear were tested by analysis of variance. In three groups of data a quadratic term produced a significant reduction in the error variance. These groups were cocksfoot \((P<0.001)\), (9-1) \((P<0.05)\), (9-3) \((P<0.05)\).

The regressions for the six groups were all highly significant \((P<0.001, \text{ Table 3.VII})\). The regressions show that at high LAIs there was a reduction in the increment of dry matter for each unit LAI in the
Table 3. VI

The interactions of pasture stands and grazing management on dry matter yield, in lb./acre/annum.

<table>
<thead>
<tr>
<th>Management</th>
<th>Perennial Ryegrass</th>
<th>Ariki Ryegrass</th>
<th>Grasslands Cocksfoot</th>
<th>S143 Cocksfoot</th>
<th>S26 Cocksfoot</th>
<th>Alta Fescue</th>
<th>Tall Fescue</th>
<th>S.E. of Means +</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grass 1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>526</td>
<td>468</td>
<td>717</td>
<td>548</td>
<td>571</td>
<td>599</td>
<td>777</td>
<td></td>
</tr>
<tr>
<td>9-1</td>
<td>133</td>
<td>420</td>
<td>301</td>
<td>392</td>
<td>566</td>
<td>707</td>
<td>1195</td>
<td>85</td>
</tr>
<tr>
<td>9-3</td>
<td>38</td>
<td>57</td>
<td>1</td>
<td>72</td>
<td>33</td>
<td>240</td>
<td>261</td>
<td></td>
</tr>
<tr>
<td>Clover 1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>603</td>
<td>445</td>
<td>179</td>
<td>386</td>
<td>268</td>
<td>173</td>
<td>149</td>
<td></td>
</tr>
<tr>
<td>9-1</td>
<td>604</td>
<td>874</td>
<td>396</td>
<td>771</td>
<td>478</td>
<td>251</td>
<td>327</td>
<td>79</td>
</tr>
<tr>
<td>9-3</td>
<td>209</td>
<td>258</td>
<td>160</td>
<td>477</td>
<td>17</td>
<td>102</td>
<td>160</td>
<td></td>
</tr>
<tr>
<td>Dead Material 1963</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>475</td>
<td>601</td>
<td>435</td>
<td>594</td>
<td>616</td>
<td>461</td>
<td>323</td>
<td></td>
</tr>
<tr>
<td>9-1</td>
<td>436</td>
<td>620</td>
<td>465</td>
<td>553</td>
<td>347</td>
<td>772</td>
<td>631</td>
<td>67</td>
</tr>
<tr>
<td>9-3</td>
<td>114</td>
<td>171</td>
<td>258</td>
<td>263</td>
<td>183</td>
<td>185</td>
<td>238</td>
<td></td>
</tr>
<tr>
<td>Dead Material 1964</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3-1</td>
<td>165</td>
<td>193</td>
<td>167</td>
<td>246</td>
<td>285</td>
<td>106</td>
<td>69</td>
<td></td>
</tr>
<tr>
<td>9-1</td>
<td>605</td>
<td>426</td>
<td>321</td>
<td>855</td>
<td>685</td>
<td>481</td>
<td>247</td>
<td>67</td>
</tr>
<tr>
<td>9-3</td>
<td>60</td>
<td>85</td>
<td>172</td>
<td>279</td>
<td>188</td>
<td>73</td>
<td>48</td>
<td></td>
</tr>
</tbody>
</table>
Table 3. VII  Mean dry matter yield per grazing in lb.acre and LAI at grazing for data from August 1963 to January 1965 together with coefficients for regression equations relating dry matter yield to LAI in the form \( Y = a + b \cdot \text{LAI} + c \cdot \text{LAI}^2 \)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>LAI</th>
<th>Yield/ grazing</th>
<th>Regression coefficients</th>
<th>Correlation Coefficients</th>
<th>No. of Observation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>a</td>
<td>b</td>
<td>c</td>
</tr>
<tr>
<td>Ryegrass</td>
<td>1.24</td>
<td>1105</td>
<td>206.5</td>
<td>727.2</td>
<td>NS</td>
</tr>
<tr>
<td>Cocksfoot</td>
<td>2.23</td>
<td>1133</td>
<td>11.2</td>
<td>618.0</td>
<td>-35.8</td>
</tr>
<tr>
<td>Tall Fescue</td>
<td>1.45</td>
<td>1109</td>
<td>305.9</td>
<td>555.0</td>
<td>NS</td>
</tr>
<tr>
<td>3-1</td>
<td>1.42</td>
<td>837</td>
<td>281.6</td>
<td>390.8</td>
<td>NS</td>
</tr>
<tr>
<td>9-1</td>
<td>2.52</td>
<td>1804</td>
<td>691.3</td>
<td>604.2</td>
<td>-48.1</td>
</tr>
<tr>
<td>9-3</td>
<td>1.51</td>
<td>951</td>
<td>109.5</td>
<td>721.9</td>
<td>-64.1</td>
</tr>
</tbody>
</table>

NS indicates non significant regression coefficient.
two grazing managements which were defoliated when the pasture height was 9 inches. Further this effect only occurred in the pastures with cocksfoot as the grass component. As the relationship between dry matter and LAI in the cocksfoot pastures was curvilinear these pastures had a higher LAI at grazing than the ryegrass or tall fescue pastures. Although the "b" coefficient for the cocksfoot pastures was greater than that of the tall fescue pastures it did not result in greater yields per grazing because of the curvilinearity in the dry matter LAI response. The ryegrass pastures showed the largest "b" coefficient but this did not result in a higher mean yield per grazing compared with cocksfoot and tall fescue pastures. Thus despite the differences between the regressions the three pasture types all produced approximately the same mean dry matter yield per grazing.

With the management regressions there were differences in the regression coefficients which reflected the differing yields per grazing. The slopes and curvilinearity of the (9-1) and the (9-3) regressions were similar and the differing yields of dry matter per grazing was a consequence of the differing amounts of leaf area removed with each grazing (cf. the "a" coefficients). The (3-1) grazing management showed a substantially lower dry matter increment per unit LAI ("b" coefficient) compared with the other managements.

3.3 Discussion

The experiment reported in Section 3 showed that ranks of the pasture types in response to the three grazing managements were the same, regardless of the absolute seasonal yield from the pastures. The results of the second year constituted very low seasonal yields
and it has been noted that the low rainfall in this year contributed to these yields; the heavy clay soil was probably an additional factor.

Consistently the (9-1) grazing management showed the highest total and component yields of herbage except for grass herbage in 1964 when it was similar to the (3-1) management in yield. The (9-3) management always showed the lowest herbage yields. These results agree with those published by Castle and Reid (1958), for perennial ryegrass in a clipping experiment and those of Bryant and Blaser (1961), for cocksfoot in a clipping and grazing experiment. However, Brougham (1959) in a grazing experiment with short-rotation ryegrass found that a (7-3) grazing management gave herbage production equal to that from a (9-1) management. There was a great difference between the experiment reported here and that of Brougham, for in his experiment the number of grazings were considerably higher. Consequently there was probably less loss of herbage, by tissue decay below 3 in., in Brougham's experiment. In Brougham's experiment the (7-3) management permitted a greater number of grazings than the (9-1), and as a result they showed equal yields despite the fact that the herbage growing below 3 in., was never harvested. However, in the experiment reported here the re-growth was slow and tissue decay occurred below 3 in. in the (9-3) management. As a result the herbage for each subsequent grazing consisted mainly of new re-growth and not of continued growth from the herbage left after grazing.

From considerations of LAI and light interception as published by Brougham (1956), Davidson and Donald (1958) and Donald (1961), the (9-3) grazing management should have been advantageous to pasture production because the re-growth would have to replace less LAI to reach
the optimum and maximum re-growth rate. The herbage left below 3 in. was approximately 1000 lb./acre dry matter and should have provided a reasonable leaf area index for re-growth. However, obviously the data reported here did not support this theory. There are a number of reasons which could account for the poor re-growth. Firstly re-growth could have occurred up to the ceiling LAI without reaching the treatment height. From the LAI figures this was unlikely unless there was an unusual arrangement of the grass leaves. Secondly, the tissue left after grazing may have been unable to assimilate carbon dioxide even when placed in a favourable light regime as found by Alexander and McCloud (1962). Thirdly the tillers of the (9-3) management may have undergone some jointing which could have permitted an apical dominance to suppressed pasture re-growth as found by Eastin et al. (1964). Fourthly, intraplant competition for soil moisture between the remaining herbage of the (9-3) management and new growth may have limited production. Of these reasons the second was probably the one responsible for the poor performance with the (9-3) management.

Generally the results did not show a low grass to clover ratio on plots subjected to the (3-1) management as suggested by the work of Blackman (1939) and Willoughby (1954), but the ratios were similar to those observed by Brougham (1959) and Wolf and Smith (1964) for similar species and managements. Donald (1956) has pointed out the ultimate grass to clover ratio will be a consequence of the interaction of fertility level, rate of nitrogen fixation, grazing management and rate of cycling of nutrients through the plants, animals and soil. Hence in this grazing situation where the clover could dominate the grass, this result could be balanced by high nitrogen availability, thus
maintaining an equal grass-clover balance.

The most productive species was S170 tall fescue and the least productive, perennial ryegrass; however, this order is of little significance except for the environment and soil type on which it was obtained. The order of productivity agrees with the findings of Hilder (1963) for another area in the same region. Production from the clover showed greatest yield in association with ryegrasses, intermediate with cocksfoots and least with the tall fescues. From this rank and considering the reverse rank order of production from the grass components, it seems unlikely that nitrogen was limiting grass growth in the less productive ryegrass pastures. Further the high clover yields in the ryegrass pastures appeared to be a result of the poor grass growth and colonization of bare spaces in the pastures by the edaphically adjusted clovers. From the grass-clover figures it seems unlikely that clover suppression occurred in the cocksfoot and tall fescue pastures. The relatively slow decline in autumn productivity of the ryegrasses as noted by Brougham (1956) was also observed in this experiment.

Considering species x management interactions for grass production, the (3-1) management favoured all species except S170 tall fescue which showed its best performance under the (9-1) management. From the LAI and dry matter regressions it was hoped that information would be obtained on species x management interactions by showing changes in the regression as a consequence of the grazing management treatments. However, as the interaction was only significant in 1964, when production was least, it is unrealistic to expect such differences because light would not be limiting except for very short periods. These management regressions were not significantly different.
In summary the results from the experiment do not support the LAI - light interception and pasture re-growth rate hypothesis. This agrees with the results of Anslow (1965) for midsummer re-growth of perennial ryegrass pastures and thus the hypothesis for LAI - light interception may need modification for grass-clover pastures in some environments.
4. THE PRODUCTIVITY AND NET PHOTOSYNTHESIS OF ORCHARDGRASS 
AND WHITE CLOVER UNDER CONTROLLED ENVIRONMENTS

The experiment reported in this section is the second, in the 
series of three, mentioned in the introduction. In this experiment two 
of the species used in the first experiment were chosen and their growth 
and net photosynthesis was examined under controlled environment 
conditions. The species were Dactylis glomerata L. (orchardgrass) and 
Trifolium repens L. (Ladino white clover). There are two parts in 
this section. In the first the effect of temperature on above ground 
growth was studied and in the second the influence of temperature and 
relative humidity on net photosynthesis was examined.

4.1 Materials and Methods

4.1.1 General

In both the above experiments the source of the experimental plants 
was the same. The orchardgrass was obtained by vegetative propagation 
of tillers taken from a productive clonal selection made by R.H. Turley 
at the Canada Department of Agriculture Research Station, Saanichton, 
British Columbia. The white clover obtained by vegetative propagation 
of stolon selections which were taken from a high producing clone of
commercial Ladino white clover growing on the campus plots at the University of British Columbia.

Propagules of these species were collected from the field in October 1965 and established in pots of fertile glasshouse soil. Four propagules were planted in each pot together with the moist soil equivalent to 125 g of air dry soil. Five hundred pots of each species were prepared and placed in a heated glasshouse. The pots were watered and allowed free drainage three times a week. When the plants were growing actively, groups of pots were selected for uniformity and used in the experiments. As all experiments were not run simultaneously the remaining groups of pots were held in the glasshouse. When the herbage height in these pots exceeded 20 cm. the herbage was trimmed to 1 cm. above the soil surface, and the pots fertilized with a 20:20:20 complete liquid fertilizer.

On completion of each experiment the herbage was removed from each pot by cutting just above the soil surface. The leaf area of each sample was then determined. Two measurements were taken on orchardgrass leaves, and the area determined by the method of Kemp (1960); Leaf Area = 0.905 x Length x Breadth mid-way along the length. For white clover, the leaf area was determined by the use of the scoring standards of Williams et al. (1964). A computer programme was written to compute area and leaf count number directly from leaf scores or measurements. After measurement of the leaf area the herbage samples were dried in a forced air oven at 60°C for 72 hours. The dry weight was then determined. On the day following the harvest the pots were examined and the number of tillers in each orchardgrass pot recorded, while in the white clover pots the number of rooted stolon nodes was
recorded.

4.1.2 Growth Measurement at Four Temperatures Regimes

To provide different temperature regimes two Percival P.G.C.No.78 growth chambers, designated A and B, were used. As it was desired to use four temperature regimes the experiment was split into three runs with the lowest regime included in each run together with one of the others. The temperature regimes for each run are shown in Table 4.1.

Table 4.1 Temperatures in °C of experimental runs.

<table>
<thead>
<tr>
<th>Growth Chamber</th>
<th>A</th>
<th>B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Run Number</td>
<td>Day</td>
<td>Night</td>
</tr>
<tr>
<td>I</td>
<td>22</td>
<td>12</td>
</tr>
<tr>
<td>II</td>
<td>22</td>
<td>12</td>
</tr>
<tr>
<td>III</td>
<td>22</td>
<td>12</td>
</tr>
</tbody>
</table>

The plant bench of each chamber was divided into four rows and four columns. Each cell was twice as wide in the row direction as in the column direction and, within each of these 16 cells, one pot of orchardgrass and one of white clover was placed. The first pot in each row was alternated between the two species so that a uniform arrangement of each species existed within the chambers. Each run started with pots from which the herbage had been removed to 1 cm. above the soil surface. After 30 days the run was terminated by cutting the plants close to the soil surface. Leaf area were then measured and then the herbage was dried and weighed.

The following environmental and cultural conditions were maintained during each run.

a) Day and night temperatures maintained for 12 hours each.
b) Day length of 16 hours composed of 16 hours of incandescent light, 14 hours with half the fluorescent light on and 12 hours with all the fluorescent lights on. The daily switching cycle was: 4 AM incandescent lights on, 5 AM half fluorescent lights on, 6 AM remaining fluorescent lights on and change to day temperature, 6 PM half fluorescent lights off and change to night temperature, 7 PM remaining fluorescent lights off, 8 PM incandescent lamps off.

c) Before the start of each run the light intensity at the plant bench with all the lights on was measured with a "Weston 756" illuminometer. The average light intensity varied little between all runs and the chambers as aged fluorescent tubes were used. The grand mean light intensity for all runs, all chambers and all positions within each chamber was 1800 ft candles.

d) All pots were watered three times per week with distilled water and then allowed free drainage. The watering for the 10th day of each run was replaced by a nutrient solution which supplied each pot with fertilizer equivalent to 100 lb./acre nitrogen, 80 lb./acre phosphorus pentoxide and 60 lb./acre potassium oxide.

The data from the three runs were pooled for statistical analysis, and as the growth at the lowest temperature regime differed between the runs it was necessary to use analysis of covariance to adjust the growth at the other temperatures for the differences between runs. The variance due to rows and columns was removed as part of the analysis to help eliminate the effects of gradients within the growth chambers.
4.1.3 Net Photosynthesis Measurement

Two pots of orchardgrass and two pots of white clover were selected from the material described in Section 4.1.1. Within each species the selection was made to obtain two pots with similar leaf areas, few senescent leaves and a reasonably high leaf area. Each of the pots of plants was then subject to all combinations of four temperatures and four relative humidities. The four temperatures were 15°C, 20°C, 25°C and 30°C, while the four relative humidities were 40%, 60%, 80% and 90%. These environmental conditions were achieved by sealing the pots in a Blue M Vapor-Temp Controlled Relative Humidity Chamber as modified by Ormrod and Woolley, (1966). The plants in the chamber were continuously illuminated with 2,000 ft. candles of fluorescent light as measured by a "Weston" 756 illuminometer.

While the plants were subject to a particular combination of temperature and relative humidity a small sample of air was circulated through a closed system using a "Beckman" model 15A infrared gas analyser to determine the CO₂ concentration in the manner described by Decker (1954). The CO₂ concentration of the system was adjusted to about 400 ppm by small additions of CO₂ and then the rate of removal, by the plant, measured between 340 and 260 ppm CO₂. This process was repeated to give three estimates of the rate of CO₂ uptake by the plant before a new combination of temperature and relative humidity was established. Readings were never taken until the chamber had maintained the particular environment for 10 minutes, and, to ensure adjustment of the plants to the new environment, only the second and third readings were used for calculation.

When readings at all combinations of the above temperatures and
relative humidities were complete the pot of plants was removed from the chamber and the plants harvested by cutting close to the soil surface, and leaf area and dry weight determined. The pot of soil and roots was re-sealed into the chamber and the rate of $\text{CO}_2$ evolution between 260 and 340 ppm determined at each of the four temperatures, with the relative humidity maintained at 60%. For these measurements the $\text{CO}_2$ level was first lowered to 250 ppm $\text{CO}_2$ by scrubbing the air in the system through an "Ascarite" bypass. Care was taken to ensure that the soil mass had come into thermal equilibrium at each temperature before any measurements were taken. Two measurements of the $\text{CO}_2$ evolution rate were made at each temperature and the mean calculated. The measured $\text{CO}_2$ uptake rates by the plant were then corrected for the appropriate rate of $\text{CO}_2$ evolution from the soil. The rate of net photosynthesis by the plants was related to leaf area and leaf weight. As the measurements took over 16 hours per pot, the four pots were measured on four consecutive days. During this period unmeasured plants were kept in the glasshouse.

4.2 Results
4.2.1 The Influence of Temperature on the production of a Vegetative Unit

Mitchell (1956) has shown that data from controlled environment studies of forage plants, when expressed as growth of a vegetative unit, give a good indication of the plant's field performance. Results in this section are therefore expressed in this manner. For orchardgrass the vegetative unit was a tiller while for white clover the unit was a rooted node.
The adjusted mean weights of a vegetative unit for plants grown at 22, 24, 29 and 34°C differed considerably (Fig. 4.2.1). In both species the weight of a vegetative unit was maximal at 29°C. However, the magnitude of response at 29°C was much greater in orchardgrass than white clover. Area responded in the same manner as weight (Fig. 4.2.2) with the maximum area obtained at 29°C in both species and the response greater in orchardgrass than in white clover.

The adjusted mean number of leaves on a vegetative unit followed similar trends to leaf weight (Fig. 4.2.3). With orchardgrass, the only significant change in leaf number was an increase between 22 and 24°C (P = 0.06). Above 24°C the leaf number of a tiller was unaffected. In contrast white clover showed a distinct optimum temperature for the maximum number of leaves on a rooted node. As with area and weight the optimum temperature for the maximum number of leaves on a rooted node was 29°C. The adjusted mean number of leaves on a rooted node at 24°C was not significantly different from the number at 22°C.

The influence of temperature on the adjusted mean weight and area per leaf in orchardgrass was different from that in white clover (Fig. 4.2.4 and 4.2.5). Weight per leaf in orchardgrass was maximal at 29°C. However, in white clover the weight per leaf was not significantly different between 22°C and 29°C while above 29°C the weight was significantly depressed (P < 0.05). In each species the response to temperature of area per leaf were similar to those of:

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1 All figures in this section use the following abbreviations:
D.N.S. Differences necessary for significance between means, within each species adjusted means with the same letter do not differ significantly.
O.G. Orchardgrass.
W.C. White Clover.
Fig. 4.2.1 Adjusted mean weight of orchardgrass tillers and white clover nodes as influenced by temperature. D.N.S. at $P < 0.01$ are for orchardgrass, 73.1, and for white clover, 12.6

Fig. 4.2.2 Adjusted mean area of orchardgrass tillers and white clover nodes as influenced by temperature. D.N.S. at $P < 0.01$ are for orchardgrass, 10.85, and for white clover, 2.11
Fig. 4.2.3 Adjusted mean number of leaves on orchardgrass tillers and white clover rooted nodes as influenced by temperature. D.N.S. are for orchardgrass, 0.64, \((P < 0.01)\) and for white clover, 0.49, \((P < 0.05)\).

Fig. 4.2.4 Adjusted mean weight of orchardgrass and white clover leaves as influenced by temperature. D.N.S. are for orchardgrass, 13.26, \((P < 0.01)\), and for white clover, 7.18, \((P < 0.05)\).
weight. In orchardgrass area per leaf was optimal at 29°C, and in white clover the area was not significantly different between 22°C and 29°C but depressed above 29°C.

The weight:area ratio of the orchardgrass and white clover leaves responded to temperature (Fig. 4.2.6). The maximum weight per unit area in orchardgrass occurred between 24°C and 29°C whereas in white clover the weight per unit area increased over the range 24 to 34°C. This increase in the white clover weight:area ratio between 24°C and 34°C was a consequence of increasing numbers of flowers between 24°C and 34°C. The flower stems were included as part of the leaf weight, but as their area was not measured the weight:area ratio at 34°C was artificially high where flowering was greatest.

4.2.2 The Influence of Temperature and Relative Humidity on net Photosynthesis

Net photosynthesis in both orchardgrass and white clover was influenced by temperatures between 15 and 30°C (Fig. 4.2.7, and Table 4.II). The regression equations describing these associations are polynomials of the form: \( Y = a + bx + cx^2 + dx^3 \) where \( Y = \) net photosynthesis and \( X = \) temperature °C.
Fig. 4.2.5 Adjusted mean area of orchardgrass and white clover leaves as influenced by temperature. D.N.S. at $P < 0.01$ are for orchardgrass, 1.83, and for white clover, 1.32.

Fig. 4.2.6 Adjusted mean weight: area ratio of orchardgrass and white clover leaves as influenced by temperature. D.N.S. at $P < 0.01$ are for orchardgrass, 0.49, and for white clover, 1.08.
The response to temperature of net photosynthesis in orchardgrass was significantly linear \((P<0.001)\) on both a leaf area and leaf weight basis. The slopes of the regressions \((b\) values\) indicate that the reduction in net photosynthesis, for each degree centigrade rise in temperature, was slightly more on a leaf weight than on a leaf area basis. For white clover the optimum temperature for net photosynthesis was within the range of the experiment, \(\text{Fig. 4.2.2}\). Net photosynthesis on a leaf area basis showed a significant cubic response \((P<0.001)\) to temperature and the optimum temperature was approximately 23\(^\circ\)C. However, differences in net photosynthesis between 15 and 25\(^\circ\)C were slight and the treatment means did not differ significantly. By contrast, a 30\(^\circ\)C temperature resulted in a highly significant depression in net photosynthesis \((P<0.001)\). Between 15 and 30\(^\circ\)C, net photosynthesis, on a leaf weight basis, showed a quadratic response; the optimum temperature was 20\(^\circ\)C. The response of net photosynthesis

<table>
<thead>
<tr>
<th>Units</th>
<th>Species</th>
<th>Regression coefficients</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>(a)</td>
<td>(b)</td>
</tr>
<tr>
<td>mgCO(_2)/dm (\frac{hr}{w})</td>
<td>w. clover</td>
<td>47.531</td>
<td>-5.505</td>
</tr>
<tr>
<td>o. grass</td>
<td>9.539</td>
<td>-0.120</td>
<td>NS</td>
</tr>
<tr>
<td>mgCO(_2)/g (\frac{hr}{w})</td>
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<td>-2.253</td>
<td>3.923</td>
</tr>
<tr>
<td>o. grass</td>
<td>34.747</td>
<td>-0.442</td>
<td>NS</td>
</tr>
</tbody>
</table>

NS - coefficient not significant; i.e. "t" for this coefficient is less than 2.5.
The relationship between temperature and net photosynthesis in orchardgrass (•——•) and in white clover (x- - - x). Points are treatment means.

A) Unit leaf area S.E. 0.22mg CO₂/dm²/hr. B) Unit leaf weight S.E. 0.78mg CO₂/g/hr.

Fig. 4.2.7
to temperature on a leaf weight basis was in reality similar to that on a leaf area basis and in both cases highly significant depressions in net photosynthesis were recorded at 30°C.

The mean rates of net photosynthesis in orchardgrass and white clover showed slight changes with changes in the level of relative humidity (Table 4.III). Net photosynthesis in white clover did not differ significantly at any of the four levels of relative humidity on a leaf area or leaf weight basis. With orchardgrass, net photosynthesis at 40% RH was significantly greater than at 90% RH. (P<0.05) both on a leaf area and leaf weight basis. There were no significant interactions of temperature with relative humidity.

Since relative humidity is not in itself a simple measure of the drying power of the air, this was examined by determining the vapour pressure deficit for each temperature and relative humidity combination.

Table 4.III The net photosynthesis of orchardgrass and white clover as influenced by relative humidity.

<table>
<thead>
<tr>
<th>Units</th>
<th>Species</th>
<th>Relative humidity</th>
<th>S.E.†</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>40%</td>
<td>60%</td>
</tr>
<tr>
<td>mg CO₂ dm⁻² hr⁻¹</td>
<td>w.clover</td>
<td>12.02</td>
<td>11.91</td>
</tr>
<tr>
<td></td>
<td>o.grass</td>
<td>7.25</td>
<td>6.97</td>
</tr>
<tr>
<td>mg CO₂ g⁻¹ hr⁻¹</td>
<td>w.clover</td>
<td>34.18</td>
<td>33.97</td>
</tr>
<tr>
<td></td>
<td>o.grass</td>
<td>26.33</td>
<td>25.27</td>
</tr>
</tbody>
</table>
using the chart of Hughes (1961). The data were examined by multiple regression analyses because the intervals between the vapour pressure deficits were not equal at each temperature. In analysing the data, orchardgrass and white clover were treated separately to allow for the previously described curvilinear response to temperature of white clover. In all analyses coefficients for the interaction of temperature and vapour pressure deficit were calculated.

The results of the multiple regression analysis showed significant responses of net photosynthesis to vapour pressure deficit at each treatment temperature (Table 4. IV, Figs. 4.2.8 and 4.2.9). In all analyses the coefficients for the interaction of temperature and vapour pressure deficit were not significant; they are therefore omitted from the regressions.

Table 4. IV Multiple regressions of temperature \( (X_1) \) and vapour pressure deficit \( (X_2) \) on net photosynthesis \( (Y) \) in orchardgrass and in white clover. Regression form: \( Y = a + bX_1 + cX_1^2 + dX_1^3 + eX_2 \)

<table>
<thead>
<tr>
<th>Units</th>
<th>Species</th>
<th>Regression coefficients</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>mgCO₂ dm⁻² hr⁻¹</td>
<td>w.clover</td>
<td>47.797</td>
<td>-5.554</td>
</tr>
<tr>
<td></td>
<td>o.grass</td>
<td>9.644</td>
<td>-0.143</td>
</tr>
<tr>
<td>mgCO₂ g⁻¹ hr⁻¹</td>
<td>w.clover</td>
<td>-1.759</td>
<td>3.827</td>
</tr>
<tr>
<td></td>
<td>o.grass</td>
<td>35.142</td>
<td>-0.531</td>
</tr>
</tbody>
</table>

NA coefficient not applicable.
Fig. 4.2.8 The influence of vapour pressure deficit and temperature on net photosynthesis of unit leaf area in white clover, and in orchardgrass. (●) 15°C, (○) 20°C, (x) 25°C and (■) 30°C.
Fig. 4.2.9 The influence of vapour pressure deficit and temperature on net photosynthesis of unit leaf weight in white clover, and in orchardgrass. (●) 15°C, (○) 20°C, (x) 25°C and (■) 30°C.
In white clover the regression coefficients for the vapour pressure
deficit were significant at \( P < 0.05 \) on a leaf area basis and \( P < 0.1 \) on a leaf weight basis. The comparable regression coefficients in orchardgrass were significant at \( P < 0.01 \) and \( P < 0.001 \). By comparing the regression coefficients in Tables 4.II and 4.IV it can be seen that the inclusion of vapour pressure deficit in the regression of net photosynthesis and temperature caused only slight changes in the coefficients for temperature. In all cases the correlation was improved by the inclusion of the terms for vapour pressure deficit. On the average, the 100 \( R^2 \) value rose by 5.0 units with the inclusion of the vapour pressure deficit coefficient. The regression coefficients "e" indicate that the slopes of the vapour pressure deficit, net photosynthesis response lines were similar in orchardgrass and in white clover on both a leaf weight and on a leaf area basis. In white clover the response of net photosynthesis to changes in vapour pressure deficit was not significantly influenced by temperatures between 15 and 25°C but at 30°C the regression line was significantly lower than those for 15 to 20°C. In orchardgrass there were significantly different net photosynthesis, vapour pressure deficit regression lines at each of the treatment temperatures (Fig. 4.2.8 and 4.2.9).

4.3 Discussion

4.3.1 Dry Matter Production

The optimum temperature regime of 29°C day and 19°C night found in this experiment for growth of orchardgrass, agrees quite well with the optimum temperatures found by Sprague (1943) (27°C day and 13°C night). In both studies the daylength was 16 hours; Rosenquist and
Gates (1961) using a 13 hour day length found a similar optimum of 30°C day and 21°C night. However, exact comparisons are not possible because of the difference in light energy levels between the experiments.

Other workers have used constant temperatures and in these instances the optimum was lower. For example, Mitchell (1956), Eagles (1967) and Baker and Jung (1968) have found the optimum temperature for orchardgrass growth to be approximately 20°C. In Mitchell's study the daylength was 12 hours while Eagles used 16 hours and Baker and Jung 15 hours. Davidson and Milthorpe (1967) also used 16 hours but found that the constant temperature giving optimum growth of S 37 orchardgrass was 25°C. Although genotype differed in each of these experiments the evidence of Cooper (1964) suggests that the 5°C difference in optimum temperature was likely to be a consequence of these genotype differences. Cooper examined three races of orchardgrass from climatically different regions (Israel, Anglesey and Norway) and found that, although the races differed in their dry matter productions at temperature extremes, all races showed an optimum temperature regime of 25°C day and 12°C night under a 16 hour daylength. Eagles (1967) also examined geographic races of orchardgrass from Portugal and Norway, and found that the optimum was not influenced by the geographic origin. From these studies it appears that optimum temperature may interact with a number of environmental factors. None of the present studies are sufficiently comprehensive to clarify these interactions, although Alberda (1966) has reported an increase in the optimum temperature as daylength is extended.

The optimum temperature for growth of white clover in the present study varied with the parameter examined. Leaf area and weight were
 maximal between 24 and 29°C day which was similar to the constant 24°C optimum temperature for growth of white clover reported by Mitchell (1956). Weight, area and leaf number of a rooted node were all maximal under a regime of 29°C day and 19°C night in the present experiment. However, this experiment and that of Mitchell indicated a general insensitivity of white clover growth to temperatures between 20 and 30°C.

Beinhart (1962, 1963, 1964) examined the growth of white clover under a number of day and night temperature and light intensity regimes. In general any day and night temperature combination within the range 17 to 23°C gave optimum growth. In these experiments the daylength was 14.5 hours and the optimum temperature range was not influenced by increase in light intensity from 600 to 2000 ft. candles. By contrast, Takeda and Agata (1966) have concluded that the optimum temperature for the growth of white clover (c.v. Ladino) was 20°C.

Published evidence suggests that day length per se has little influence on the optimum temperature for growth of white clover; Mitchell (1956) used 12 hours compared with 14.5 hours in Beinhart's experiments. However, in the present experiment, where the optimum temperature was higher than those published the optimum temperature may have been influenced by the daylength of 16 hours.

4.3.2 Net Photosynthesis

Murata and Iyama (1963) in a comprehensive study of net photosynthesis in forage crops found that, for both orchardgrass and white clover "... photosynthesis was substantially constant between 5 and 20°C". However, examination of their data indicates that the optimum temperature for net photosynthesis in orchardgrass was approximately
$10^\circ C$ and in white clover approximately $15^\circ C$.

The $10^\circ C$ optimum for orchardgrass agrees with the data of the present experiment which indicated that the optimum temperature was $15^\circ C$ or less. For white clover, however, the present experiment shows a higher optimum temperature for net photosynthesis in the region of $20-25^\circ C$, that is $10^\circ C$ higher than Murata and Iyama (1963). Beinhart (1962) reported that CO$_2$ uptake in white clover leaves was greater at $30^\circ C$ than at $20^\circ C$, supporting the contention of the present experiment that the optimum is above $20^\circ C$. Murata and Iyama (1963) have reported that the growing environment may influence the optimum observed, so that winter grown plants may have a lower optimum temperature than summer grown plants. This may account for the differences between the experiments in the optimum temperature observed for net photosynthesis.

Definition of the growing environment prior to observations of the optimum temperature are undoubtedly necessary for such experiments. However, even such definition of the growing environment is unlikely to provide an exact optimum temperature for net photosynthesis as both orchardgrass and white clover appear to have wide optimum temperature ranges.

The stimulating effect on net photosynthesis of increased vapour pressure deficits between 0 and 20 mm of Hg has not been reported previously. Bierhuizen and Slatyer (1964) and Baker (1965) have examined the influence of some vapour pressure deficits on CO$_2$ uptake of cotton (*Gossypium hirsutum* L.) and found that above 10-20 mm of Hg, there was a decline in CO$_2$ uptake. The results of the two experiments considered together with the present one suggest that there may be an optimum vapour pressure deficit for maximum net photosynthesis.
5. **FIELD DEFOILIATION MANAGEMENT EXPERIMENT WITH CONCURRENT MEASUREMENT OF NET PHOTOSYNTHESIS**

The experiment reported in this section is the third, in the series of three. The two forage species used in the previous experiments, orchardgrass and white clover, were established alone and together as forage swards. They were subjected to the same defoliation managements of section one, and their seasonal yields measured. Concurrent with these field measurements, the net photosynthesis - light energy response was determined for the swards at various stages of regrowth.

5.1 **Materials and Methods**

This section is divided into two parts; the first contains the design and techniques of the field experiment and the second the techniques used to determine the net photosynthesis, light energy responses of the forage swards.

5.1.1 **Field technique and experimental design**

The experimental area was within the Division of Plant Science research fields on the University of British Columbia campus, Vancouver, B.C. The general climate of the area has been described as cool and moist in winter and mild and dry in summer by Kendrew and Kerr, (1955).
Actual weather data was obtained from an intensive meteorological station located some 500 ft. south of the experimental area. The soil of the experimental area was derived from glacial till and outwash parent material and is classified as a Nicholson acid brown-wooded sandy loam soil.

During the period from February 1966 to May 1966 the experimental area was ploughed and disc harrowed, treated with farmyard manure at 1,000 lb. per acre and fertilized with 8 : 10 : 6 N:P:K fertilizer at 500 lb. per acre. In May 1966 the area was divided into four blocks with each block divided into 24 plots. Each plot measured 5 ft. x 8 ft. and each of the 24 treatments, were randomly allocated to one of the plots within each block. The 24 treatments were made up of eight forage swards x three defoliation managements. The seeding composition of the forage swards is given in Table 5.1. The orchardgrass (*Dactylis glomerata* L.) was S143 strain while the white clover (*Trifolium repens* L.) was the cultivar Ladino. The white clover seed was

Table 5.1.  Seeding densities of grass and clover for the eight forage swards in lb./acre of 100% viable seed.

<table>
<thead>
<tr>
<th>Sward</th>
<th>Orchardgrass</th>
<th>White Clover</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>B</td>
<td>25</td>
<td>0</td>
</tr>
<tr>
<td>C</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>D</td>
<td>0</td>
<td>9</td>
</tr>
<tr>
<td>E</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>F</td>
<td>25</td>
<td>9</td>
</tr>
<tr>
<td>G</td>
<td>5</td>
<td>9</td>
</tr>
<tr>
<td>H</td>
<td>25</td>
<td>3</td>
</tr>
</tbody>
</table>
inoculated with Rhizobium AB peat culture at double the recommended rate. A 10% w/v maltose gum arabic solution was used as a carrier. All seeds were broadcast early in May 1966 and the area lightly raked and rolled.

The defoliation managements were as follows:

(1) The herbage grew to 3-4 in. and then was defoliated at a height of 1 in. viz. management (3-1).

(2) The herbage grew to 9-10 in. and then was defoliated at a height of 1 in. viz. management (9-1).

(3) The herbage grew to 9-10 in. and then was defoliated at a height of 3 in. viz. management (9-3).

Although the defoliation management treatments were allocated to the plots at the time of sowing they were not applied until 6 months later. During the establishment phase when the average height of herbage in all plots reached 14 in. the plants were defoliated to a height of 4 in. All defoliations were made with an 18 in. rotary mower and after each defoliation the plots were raked clean of mown herbage.

By July 1966 the swards were well established and received a further 500 lb. per acre of 8 : 10 : 6 N:P:K fertilizer. The final defoliation of the first growing season, in October 1966, was at the treatment height. This minimised bias in material carried over into the 1967 season when the regular defoliations commenced. In the 1967 growing season the decision to defoliate a particular treatment was made on the average height of the swards. The heights of the swards were determined weekly with a graduated staff on 10 sites per plot.

In May 1967 the plots received 550 lb. per acre of 4 : 10 : 10 N:P:K fertilizer and on July 9 the pure grass plots (Treatments A and B)
received further fertilizer as sulphate of ammonia at a rate of 200 lb. per acre. To maintain adequate soil moisture during the 1967 growing season the experimental site was given water by sprinkler irrigation approximately every 3 weeks. When rain occurred after an irrigation the next irrigation was delayed in proportion to the amount of rain received.

Yields were taken from quadrats during September 1967 at the same time as the normal defoliation treatments. The quadrats consisted of a mown strip taken from the centre of each plot with the same mower used for defoliation treatments. The quadrat strips were 18 in. wide by 8 ft. long. The species composition of each plot was estimated twice (July and October) using the Grasslands Research Institute, Hurley, (1961) procedure. On each occasion two operators made the estimates. Seasonal yields of the species were determined from quadrat yields, number of defoliations, and the mean percentage for each component.

5.1.2 Pasture Sampling and the Measurement of Photosynthesis

The response of net photosynthesis in the forage swards to changes in the light energy level were examined by removing herbage-soil cores from the plots. For sampling, the forage swards were grouped into three types viz. pure grass (A + B)\(^1\), pure clover (C + D) and grass clover mixtures (E + F + G + H). These three forage sward types were sampled from each of the three defoliation managements making 9 treatments in all. Each of these 9 treatments were sampled on 10 occasions.

---

1 Letters refer to the sward types as described in Table 5.1.
spread over the regrowth periods. To ensure that all treatments were sampled uniformly over the growing season the treatments were sampled randomly. However, the sampling occasions were adjusted so that each treatment was represented by as wide as possible a range of LAIs.

The herbage-soil cores measuring approximately $20 \times 20 \times 15$ cm were removed from the plots with a spade. The soil blocks were then trimmed to $16 \times 16$ cm by $10$ cm deep and placed in a plexiglass box (A). All herbage-soil cores were collected in the early morning when the radiation on the plants was low and immediately taken to the laboratory. The time taken from the removal at the plots to arrival in the laboratory was less than 15 minutes.

In the laboratory the soil cores were watered to field capacity and then sealed in a plexiglass chamber for CO$_2$ assimilation measurement (B). The plants were allowed 2 hours to adjust to the chamber conditions before CO$_2$ assimilation measurements commenced. The CO$_2$ assimilation chamber measured $22$ by $22$ cm by $41$ cm high with the sides surrounded by a $6.5$ cm thick water jacket. The plexiglass base of the chamber was mounted on $\frac{1}{2}$ in. plywood. The upper portion of the chamber was in the form of a hinged lid (C) to admit the herbage-soil sample. The lid was sealed to the chamber with a silicone rubber gasket to make a gas tight joint. Two gas sampling ports (D) allowed gas to be drawn off to measure the CO$_2$ concentration. These ports were also used to flush the chamber with laboratory air, when the sample was first placed in the chamber and whenever CO$_2$ assimilation measurements were not in progress.

1 Letters refer to items marked in Figure 5.1.1.
Fig. 5.1.1 Chamber and apparatus to measure CO₂ uptake and release rates of herbage-soil cores. For explanation of letters see text.
Carbon dioxide assimilation of the herbage growing on the soil core was measured by connecting the gas sampling ports to an infrared gas analyser (Beckman No.215) (E) to form a closed circuit system (Decker, 1954). The gas lines were "Tygon" tubing (F), and the gas was drawn from the bottom of the chamber through a flow meter (G), through the measuring cell of the analyser and then pumped back into the top of the chamber with a Thunberg pump (H). The gas flow rate was 28.3 litres per hour with a total system volume of 17.1 litres.

At the start of each measurement of CO₂ assimilation the concentration was adjusted to about 400 ppm CO₂ and then the time for a 340 to 260 ppm CO₂ concentration change was recorded on the chart recorder (I). The volume of CO₂ used by the plant was corrected for temperature prior to calculation of the CO₂ uptake rate.

During the measurements of CO₂ assimilation the pasture sward samples were illuminated with light from a 300 watt narrow spot "cool beam" incandescent lamp (J) as described by Beesley, et al. (1963). The lamp was suspended over the chamber and shone through the water jacket of the chamber lid. To eliminate the radiant heating effect of the lamp, tap water was circulated through the jacket. The lamp suspension system (K) was arranged so that the distance between the lamp and the chamber could be varied and to provide a range of light intensities. The air temperature and vapour pressure deficit within the chamber were measured by wet and dry thermocouples (L) connected to a potentiometer (M). These temperature measurements were taken at the commencement of each CO₂ assimilation measurement.

Each herbage-soil core was subject to 10 light intensities, usually values of approximately 10,000, 8,000, 6,000, 4,000, 3,000,
2,000, 1,000, 800, 400 and 100 ft. candles, and the CO₂ assimilation measured at each. Duplicate measurements were made at each light intensity with the order of all measurements being random. The light intensities refer to light incident on the upper leaves of the herbage as measured with a Weston 756 illuminometer placed just below the lid of the chamber. Subsequently the light intensities were evaluated, as energy between 400 and 700 nm, by determining their spectral energy distribution with an "ISCO" spectral radiometer. To ensure that the upper leaves of each sample of herbage received comparable doses of incident light a small laboratory jack (N) was used to position the soil box so that the upper leaves of the herbage were within a few mm of the chamber lid. At low light intensities, because of the low CO₂ assimilation, the soil respiration often caused a net increase in the CO₂ concentration of the system. In this instance the previously described measurement procedure was reversed and the CO₂ concentration was lowered to 250 ppm CO₂ with a bypass "ascarite" scrubbing tower and pump (O), and then the time for the concentration to increase from 260 to 340 ppm CO₂ recorded.

On the completion of measurements of CO₂ assimilation the chamber was opened and the sample removed. The herbage was then severed from the roots at the soil surface and the soil block replaced in the chamber. Duplicate measurements were made of the CO₂ evolution from the soil block. All measurements of CO₂ exchange in the light by the herbage-soil core were corrected for the mean rate of CO₂ evolution from the soil core to give a measurement of CO₂ assimilation by the plant.

The herbage removed from the core was separated into grass, clover
leaves, clover petioles and dead material (grass and clover). The area of the grass leaves was calculated with the equation of Kemp (1961) for length and mid point breadth measurements, while the area of the clover leaves was estimated with the aid of the scoring standards of Williams et al. (1964). The area of the clover petioles was estimated by considering the structure as a cylinder and taking length and width measurements. To maintain comparability with the other leaf areas which were for one side only, half the cylinder's surface area was used. After the area measurements, all herbage fractions were dried in a forced draft oven at 90°C for 48 hours and the dry weight of each determined.

5.2 Results
5.2.1 Results of Field Investigations

The above ground production for each pasture forage sward in the 1967 growing season differed significantly (Table 5.II). The total production between swards differed significantly (P<0.01) with swards C and H having significantly greater production than the others. In the two major components, grass and clover, the swards differed significantly at the P<0.001 level. The major difference in grass and clover production was a consequence of seedings in the swards where no clover was sown in treatments A and B and no grass in treatments C and D. However, as can be seen from Table 5.II there was some grass invasion into treatments C and D and some clover invasion into treatments A and B.
The 1967 above ground production of orchardgrass and white clover swards with differing seeding compositions in lb./acre dry matter. Letters refer to sward as in Table 5.I.

<table>
<thead>
<tr>
<th>Sward Composition</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>6470</td>
<td>6080</td>
<td>6030</td>
<td>5901</td>
<td>6948</td>
<td>7095</td>
<td>8402</td>
<td>9056</td>
<td>656</td>
</tr>
<tr>
<td>Grass</td>
<td>5736</td>
<td>5956</td>
<td>814</td>
<td>927</td>
<td>4753</td>
<td>5102</td>
<td>5369</td>
<td>6933</td>
<td>549</td>
</tr>
<tr>
<td>Clover</td>
<td>359</td>
<td>73</td>
<td>4520</td>
<td>4294</td>
<td>1856</td>
<td>1920</td>
<td>2654</td>
<td>2000</td>
<td>327</td>
</tr>
</tbody>
</table>

1 SE Standard error of treatment means, ±.

The three defoliation managements differed significantly in above ground production ($P<0.01$) with the (9-3) treatment significantly lower than the rest (Table 5.III). The defoliation managements however, did not significantly influence the grass production and hence the effect was almost entirely a consequence of the significantly lower clover production under the (9-3) management ($P<0.001$).

It can be seen (Table 5.III) that the similar seasonal total for the (3-1) and (9-1) defoliation were a consequence of compensatory changes in defoliation frequency and in amount of material removed with each defoliation. The dry matter yield per defoliation from the (3-1) and (9-3) treatments did not differ significantly. Under the (9-1) the amount removed was significantly greater than that removed under the (3-1) and (9-3) managements ($P<0.001$). Thus, even though the (9-1) plots were defoliated least frequently, their greater yield compensated for their infrequent defoliation. The (9-3) defoliation
management permitted only 8 defoliations, and this together with the lowest yield per defoliation, caused the (9-3) management to be least productive.

<table>
<thead>
<tr>
<th>Management</th>
<th>3 - 1</th>
<th>9 - 1</th>
<th>9 - 3</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total</td>
<td>7687</td>
<td>7475</td>
<td>5831</td>
<td>401</td>
</tr>
<tr>
<td>Grass</td>
<td>4198</td>
<td>4629</td>
<td>4519</td>
<td>336</td>
</tr>
<tr>
<td>Clover</td>
<td>2902</td>
<td>2627</td>
<td>1081</td>
<td>201</td>
</tr>
<tr>
<td>Yield per defoliation</td>
<td>783</td>
<td>1289</td>
<td>740</td>
<td>57</td>
</tr>
<tr>
<td>Mean number of defoliations</td>
<td>10</td>
<td>6</td>
<td>8</td>
<td>-</td>
</tr>
</tbody>
</table>

The defoliation managements interacted with the forage swards (Table 5. IV), in total production (P<0.001), grass production (P<0.05) and clover production (P<0.05). The most striking feature of these interactions was the significantly low clover content (P<0.05) of swards E, F, G and H under the (9-3) defoliation management compared with the (3-1) and (9-1) treatments. Further it can be seen that the most productive management for the swards sown only with white clover (C and D) was the (3-1) or (9-1) treatment whereas the (9-1) treatment was most productive in the swards sown only with orchardgrass (A and B). Taken together, these results, with the results of the managements
per se. indicate that the poor re-growth rate of the swards subject to the (9-3) management was largely a consequence of slow re-growth of clover in swards with the (9-3) management.

Table 5. IV  The interaction of defoliation management with the pasture swards in total production, grass production and clover production in lb./acre dry matter. Standard error of treatment means ± 1136 for Total production, ± 951 for Grass production and ± 567 for Clover production.

<table>
<thead>
<tr>
<th>Management</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>Pasture Sward</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Total production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 - 1</td>
<td>5742</td>
<td>4225</td>
<td>8457</td>
<td>6623</td>
<td>7905</td>
<td>7367</td>
<td>10,010</td>
<td>11,171</td>
<td></td>
</tr>
<tr>
<td>9 - 1</td>
<td>7201</td>
<td>8954</td>
<td>6472</td>
<td>5794</td>
<td>6163</td>
<td>9943</td>
<td>6691</td>
<td>8582</td>
<td></td>
</tr>
<tr>
<td>9 - 3</td>
<td>6465</td>
<td>5061</td>
<td>3160</td>
<td>5285</td>
<td>6776</td>
<td>3975</td>
<td>8506</td>
<td>7416</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Grass production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 - 1</td>
<td>4759</td>
<td>4047</td>
<td>1400</td>
<td>575</td>
<td>4508</td>
<td>5350</td>
<td>5011</td>
<td>7937</td>
<td></td>
</tr>
<tr>
<td>9 - 1</td>
<td>6487</td>
<td>8764</td>
<td>446</td>
<td>424</td>
<td>4458</td>
<td>6443</td>
<td>3918</td>
<td>6092</td>
<td></td>
</tr>
<tr>
<td>9 - 3</td>
<td>5960</td>
<td>5057</td>
<td>601</td>
<td>1784</td>
<td>5290</td>
<td>3513</td>
<td>7177</td>
<td>6769</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Clover production</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3 - 1</td>
<td>222</td>
<td>94</td>
<td>5950</td>
<td>5268</td>
<td>2753</td>
<td>1840</td>
<td>4240</td>
<td>2848</td>
<td></td>
</tr>
<tr>
<td>9 - 1</td>
<td>543</td>
<td>119</td>
<td>5455</td>
<td>4899</td>
<td>1572</td>
<td>3500</td>
<td>2532</td>
<td>2393</td>
<td></td>
</tr>
<tr>
<td>9 - 3</td>
<td>310</td>
<td>5</td>
<td>2155</td>
<td>2714</td>
<td>1243</td>
<td>423</td>
<td>1189</td>
<td>608</td>
<td></td>
</tr>
</tbody>
</table>

The meteorological data for the growing season (Table 5.V), when examined with reference to the data from the controlled environment studies (Section 4.2.1) provided evidence of near optimum growing.
conditions during the growing season. However, low temperatures may have limited pasture growth in April and May. Evaporation exceeded precipitation in all months except April, but this deficit was, to a reasonable extent, made good by irrigation.

Table 5.5 Meteorological data during the 1967 growing season. Figures are monthly means for screen temperatures and radiation and totals for rainfall, class A pan evaporation and irrigation.

<table>
<thead>
<tr>
<th>Month</th>
<th>April</th>
<th>May</th>
<th>June</th>
<th>July</th>
<th>Aug.</th>
<th>Sept.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainfall in.</td>
<td>2.62</td>
<td>1.64</td>
<td>0.54</td>
<td>1.18</td>
<td>0.18</td>
<td>2.73</td>
</tr>
<tr>
<td>Max. Temp. °C</td>
<td>10.2</td>
<td>14.9</td>
<td>20.1</td>
<td>21.1</td>
<td>24.2</td>
<td>19.4</td>
</tr>
<tr>
<td>Min. Temp. °C</td>
<td>3.9</td>
<td>8.8</td>
<td>12.8</td>
<td>13.3</td>
<td>14.3</td>
<td>12.2</td>
</tr>
<tr>
<td>Radiation langleys / day</td>
<td>356</td>
<td>430</td>
<td>565</td>
<td>583</td>
<td>524</td>
<td>341</td>
</tr>
<tr>
<td>Evaporation in.</td>
<td>2.32</td>
<td>4.15</td>
<td>6.64</td>
<td>6.76</td>
<td>7.01</td>
<td>3.33</td>
</tr>
<tr>
<td>Irrigation in.</td>
<td>0.0</td>
<td>0.0</td>
<td>2.0</td>
<td>3.5</td>
<td>5.0</td>
<td>0.0</td>
</tr>
</tbody>
</table>

Data on the soil environment of the experimental area may be found in Appendix 8.1. This also indicated favourable conditions for plant growth.

5.2.2 Light Energy Response of Net Photosynthesis in the Forage Stands

Rabinowitch (1951) suggested that the relation between net photosynthesis (Pn) of individual leaves and light intensity (I) could be described by a rectangular hyperbola so that:

\[ Pn = \frac{A (I - Io)}{1 + B (I - Io)} \]  \hspace{1cm} (5.1)

where Io is the light compensation point and where A and B are
parameters which characterize the shape and position of the response curve. The validity of this equation for maize (*Zea mays*) and tobacco (*Nicotiana tabacum* L.) leaves was confirmed by Hesketh and Moss (1963). Pearce *et al.* (1967) neglected the light compensation value and found that the equation:

\[ P_n = \frac{A I}{1 + B I} \quad \text{(5.2)} \]

gave a good description of the net photosynthesis/light intensity response of barley (*Hordeum vulgare* L.) leaves. van den Driessche and Waring (1966) have further shown that the monomolecular growth equation (Richards, 1959) gave a good fit for net photosynthesis/light intensity data from seedlings of *Pinus* spp. Thus:

\[ P_n = A - B \exp^{-I} \quad \text{(5.3)} \]

For the decay phase of the monomolecular growth equation Brody (1945) gives the following:

\[ P_n = A - B \exp^{-CI} \quad \text{(5.4)} \]

which is more convenient than equation (5.3) as the parameter *C* characterizes the shape of the response curve.

Equations (5.1) and (5.2) have been used by a number of workers in models of photosynthesis in plant communities; de Wit (1965), Duncan *et al.* (1967) and Idso and Baker (1967). All these models calculate net photosynthesis of individual leaves and then extrapolate to a layer of leaves with the same illumination and finally to the community as a whole. However, very little attention has been given to a general light response equation for a plant community as a whole, although Baker and Musgrave (1964) state that equation (5.1) gave a good fit with a maize community.
In deciding which of the above four equations would be most suited for the present community data equation (5.1) was eliminated as the light compensation values were not known in advance, while equation (5.3) was also eliminated as it was a less convenient form of equation (5.4). The choice therefore, was between equations (5.2) and (5.4). Equation (5.2) will give a good fit if a plot of $1/P_n$ vs $1/I$ is linear and Paauw (1952) states that equation (5.4) will give a good fit if a plot of $\log_e P_n$ vs $1/I$ is linear.

The correlation coefficients for linear regressions of the data with the above two transformations were calculated and compared for the 90 sets of data to decide which was the most suitable equation. In all data sets the transformation for equation (5.4) gave a highly significant correlation ($P < 0.001$) while the transformation for equation (5.2) gave non significant correlations, at the $P < 0.001$ level, with 15 data sets. With 80 data sets the correlation coefficients for equation (5.4) transformation exceeded those for equation (5.2) transformation. Therefore because of the good fit with the equation (5.4) transformation in almost all data sets and the generally higher correlation coefficients it was decided to use this equation to compare the net photosynthesis/light energy response curves.

In equation (5.4) the parameter $A$ (the asymptote) is an estimate of maximum net carbon dioxide fixed at saturating light. The parameter $B$ is an estimate of true photosynthesis assuming that the net carbon dioxide evolved at zero light energy is an estimate of photorespiration; the difference between $A$ and $B$ is an estimate of photorespiration. The $C$ parameter is a measure of the relative curvilinearity of the response line and the larger the $C$ value the more
acutely curved will be the response line. The three parameters A, B and C were estimated using an iterative least squares method similar to that suggested by Glass (1967). From these parameters two other I values were calculated; the light energy at which net photosynthesis is zero i.e. the "light compensation" point and the light energy to give 50% of the A value. The initial slope of the regression was measured by calculating the carbon dioxide uptake at the light compensation point plus 2.0 cal./cm²/hr. The equation parameters and regression lines for two typical data sets treated in the above manner are presented in Fig. 5.2.1.

The relationship between the equation (5.4) parameters, the calculated values and the sward characteristics were then examined by multiple regression analyses for all data. The sward characters were regrowth days, LAI and weight per unit area of land and these were generally regarded as the independent variables. As it had been found previously, (Section 4.2.2), that orchardgrass and white clover had differing optimum temperatures for net photosynthesis, the data were treated in three separate groups. Those groups were pure orchardgrass swards, pure white clover and swards which contained both species. Within each of the sward groups homogeneity of the regressions for each of the three managements was tested.

5.2.2.1 Pure Grass Swards

The relationship between LAI and days of regrowth with the orchardgrass swards was linear (Fig. 5.2.2). This relationship was highly significant (P<0.001) and there were no significant differences between the slopes of the regressions for the individual managements.
The influence of light energy on net photosynthesis per metre$^2$ land. Lines fitted to equations in the form $Y = A - Be^{cX}$. Data (X) a mixed orchardgrass-white clover sward 25 days after defoliation, and (o) an orchardgrass sward 9 days after defoliation.
As can be seen from Figure 5.2.3 there was considerable variability about the regression. This variability was largely a consequence of the non-uniform distribution of plants in the field so that a sward sample taken just prior to a defoliation would not necessarily have the same LAI as the average LAI of the sward.

In the orchardgrass swards the relationship between LAI and weight of herbage from unit land area, was highly significant (P<0.001), (Figure 5.2.3). The slopes of the regressions for the individual managements did not differ significantly.

In the CO₂ uptake comparisons which follow, the mean temperature of measurement was 22.0 ± 1.1°C and the mean vapour pressure deficit was 2.9 ± 1.12 mm Hg.

In the relationships between LAI and net photosynthesis in the orchardgrass swards, at saturating light energies, the three managements showed differing responses (Figs. 5.2.4 A and B and 5.2.5); swards with the (3-1) and (9-1) managements showed significant and positive linear responses but the slopes differed significantly (P<0.001). The data from the swards with the (3-1) and (9-1) managements did not show evidence of an optimum LAI. The swards subjected to the (9-3) management showed a significantly quadratic response (P<0.01) and an optimum LAI of about 12.

Examination of the data from the orchardgrass swards indicated that the differences between managements were partly a consequence of the particular LAIs sampled with each management. Therefore the data were combined to give a general regression for the grass swards (Table 5.VI). The quadratic regression was significant (P<0.001) and the optimum LAI was 14.5. The regressions between net photosynthesis
Fig. 5.2.2 The relationship between LAI and days of regrowth since the last mowing for pure orchardgrass swards.

Fig. 5.2.3 The relationship between LAI and weight of herbage from unit area of land for pure orchardgrass swards.
Fig. 5.2.4 The relationship between net photosynthesis per metre$^2$ land and LAI in orchardgrass swards at saturating light energy levels: A) subject to (3-1) defoliation management and B) subject to (9-1) defoliation management.
Fig. 5.2.5 The relationship between net photosynthesis per metre$^2$ land and LAI in orchardgrass swards at saturating light energy levels subject to a (9-3) defoliation management.

\[ Y = -1.013 + 0.711X - 0.027X^2 \]

\[ R = 0.845 \]
and LAI were also calculated at four light energy levels, (Fig. 5.2.6 and Table 5.VI). It can be seen that the optimum LAI increases with increasing light energy levels. At 3.0cal./cm²/hr. the optimum LAI was 11 and at 12.0 cal./cm²/hr. the optimum was 14. However, once LAI 14 was reached there was very little change in the optimum between 12.0 cal./cm²/hr. and saturating light levels. Saturating light energies were usually reached at a maximum of 30 cal./cm²/hr.

Table 5.VI  
The regression coefficients relating net photosynthesis (Y) to LAI (X) in orchardgrass swards at saturating and four other light energy levels. Regressions in the form Y = a + bX + cX² n = 30, coefficients in g CO₂/m²/hr.

<table>
<thead>
<tr>
<th>Light energy cal/cm²/hr.</th>
<th>Coefficients</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>Saturating</td>
<td>0.746</td>
<td>0.437</td>
</tr>
<tr>
<td>24.0</td>
<td>0.663</td>
<td>0.406</td>
</tr>
<tr>
<td>12.0</td>
<td>0.453</td>
<td>0.338</td>
</tr>
<tr>
<td>6.0</td>
<td>0.220</td>
<td>0.242</td>
</tr>
<tr>
<td>3.0</td>
<td>0.057</td>
<td>0.154</td>
</tr>
</tbody>
</table>

From the curves in Fig. 5.2.6 it was possible to calculate the efficiency of light use, in the uptake of CO₂, by the orchardgrass swards. For these calculations the CO₂ uptake at the optimum LAI for each light energy level was taken and converted to calories with the calorific equivalent for CO₂ (2,700cal./g CO₂) used by Yocum, et al. (1964). When the efficiencies of light energy use together with the optimum LAI and CO₂ uptake for the four light energy levels are compared (Table 5.VII) it can be seen that maximum efficiency of light energy use
The relationship between net photosynthesis per metre² land and LAI in orchardgrass swards at four levels of incident light energy. The regression equations for the four lines are given in Table 5.VI.
Table 5.VII The efficiency of light energy use in CO₂ uptake in orchardgrass swards at four light energy levels together with their CO₂ uptake and optimum LAI at these energy levels.

<table>
<thead>
<tr>
<th>Light energy cal/cm²/hr.</th>
<th>CO₂ Uptake g CO₂/m²/hr.</th>
<th>Optimum LAI</th>
<th>Efficiency %</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>0.93</td>
<td>11.0</td>
<td>8.35</td>
</tr>
<tr>
<td>6.0</td>
<td>1.81</td>
<td>13.0</td>
<td>8.15</td>
</tr>
<tr>
<td>12.0</td>
<td>2.79</td>
<td>14.0</td>
<td>6.29</td>
</tr>
<tr>
<td>24.0</td>
<td>3.49</td>
<td>14.2</td>
<td>3.93</td>
</tr>
</tbody>
</table>

occurred in the region of 3 to 6cal/cm²/hr. This, compared with the mean light energy required to produce 50% of the maximum CO₂ uptake rate (6.8 ± 1.9cal/cm²/hr.), indicated a relatively efficient light energy use by the swards when at the optimum LAI. Calculation of efficiencies below 3.0cal./cm²/hr. were not made as the light compensation for some of the swards occurred within this region. A value 2.3cal./cm²/hr. was the highest light compensation point recorded.

The initial slope of the light response curves, calculated from the net photosynthesis at the light compensation point plus 2.0cal./cm²/hr., was related to LAI (Fig. 5.2.7). In this instance the intercepts of regressions for the three managements differed significantly (P<0.001); however, the slopes of the three management regressions were not significantly different. The regression coefficients for these three regressions (Table 5.VIII) and (Fig. 5.2.7) show that the (9-1) and (9-3) swards both showed an optimum LAI which in both instances was close to 14. The intercept of the (9-3)
Fig. 5.2.7 The relationship between the initial slope, of the light energy response curves of orchardgrass swards, and LAI of the swards under three defoliation managements. The regression equations for the three managements are given in Table 5.VIII.
Table 5.VIII  The regression coefficients relating the initial slope (Y) of the light response curves in orchardgrass swards to their LAI (X). Regressions in the form 
Y = a + bX + cX^2  units of coefficients g CO₂/m²/hr.

<table>
<thead>
<tr>
<th>Management</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>n</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>(3-1)</td>
<td>0.0059</td>
<td>0.150</td>
<td>-0.0040</td>
<td>11</td>
<td>0.818</td>
</tr>
<tr>
<td>(9-1)</td>
<td>-0.0656</td>
<td>0.153</td>
<td>-0.0056</td>
<td>9</td>
<td>0.911</td>
</tr>
<tr>
<td>(9-3)</td>
<td>-0.3442</td>
<td>0.160</td>
<td>-0.0057</td>
<td>10</td>
<td>0.847</td>
</tr>
</tbody>
</table>

Management was significantly different from the other two managements, and it reflected the 3 inch cutting height in that the material left resulted in a lower rate of CO₂ fixation for the (9-3) management than for the (3-1) and (9-1) managements. This strongly suggests that, under field conditions of moderate light energy levels, the 3 inches of herbage left was in fact a drain on the swards CO₂ fixing ability of the stand compared with those stands with managements where the cutting height was 1 inch.

Weight of dry tissue influenced the net photosynthesis of the orchardgrass swards with no significant differences between the managements. When weight was combined in a multiple regression with LAI the 100 R² increased from 39% to 60% (P<0.001). This regression equation was:

Y = 1.645 + 0.427X₁ - 0.642X₂  R = 0.778

where Y = net photosynthesis in g CO₂/m²/hr., and X₁ = LAI and X₂ = herbage weight g/dm² land.

This reflected increasing photorespiration with increased herbage weight and this agreed with the relation found between estimated
photorespiration, parameters A - B, and LAI (P<0.001). This relation was not significantly different for the three managements and was:

\[ Y = 0.089 - 0.101X \quad r = -0.671 \]

where \( Y \) = photorespiration (A - B) in g CO₂/m²/hr. and \( X \) = herbage weight g/dm² land.

The decline in leaf efficiency with increasing LAI at saturating light energies is shown by a linear decrease in net assimilation rate (NAR) with increasing LAI, (P<0.001). The managements showed no significant differences in this relationship. On average there was only a slight positive NAR at an LAI of 17 which suggests in all probability some of the lower leaves had a negative NAR (Fig. 5.2.8). This is consistent with the concept of an optimum LAI and the linear decrease in NAR to LAI 17 is also consistent with the optimum concept.

As stated earlier the C value of the light response exponential regressions gives a measure of the relative curvature of this line. Thus swards with a large C value have more prostrate leaves, and they become light saturated more rapidly (per unit of light energy) than swards with a lower C value. These differences in leaf inclination were transmitted into differences in the amount of light energy required to produce 50% of the maximum rate of net photosynthesis. In this relation there were no significant differences between managements (Fig. 5.2.9). The relation was significantly quadratic and negative (P<0.001) indicating that beyond a particular leaf inclination (C = 0.18) there was little gain in the efficiency of light use with leaves closer to the horizontal.
Fig. 5.2.8 The relationship between net assimilation rate (NAR) of leaves in orchardgrass swards and LAI.

\[ Y = 774 - 0.325X \]

\[ r = 0.702 \]
The relationship between the light energy required to produce 50% of the maximum rate of net photosynthesis in orchardgrass swards and C value of the exponential equations fitted to the light energy response curves.
Figure 5.2.10 shows the relationship between LAI and days of regrowth with the white clover swards. This relationship was highly significant ($P < 0.001$) and there were no significant differences between the slopes of the regressions for the individual managements. With these swards as with the orchardgrass swards, the variability about this regression reflected the sampled variability in sward clover plant density.

In the white clover swards the relationship between LAI and weight of herbage from a unit land area, was highly significant ($P < 0.001$), (Fig. 5.2.11). The slopes of the regressions for the individual managements did not differ significantly.

In the $CO_2$ uptake comparisons which follow the mean temperature of measurement was $22.1 \pm 1.2^{\circ}C$ and the mean vapour pressure deficit was $3.1 \pm 0.9$ mm of Hg.

In the relationship between LAI and net photosynthesis in the white clover swards, at saturating light energies, (Fig. 5.2.12 A), there were no significant differences between the managements and the overall regression was significantly linear ($P < 0.001$). For comparability with the orchardgrass data, the regressions at the four light energy levels were calculated as quadratics even though the $X^2$ coefficients were barely significant, ($P < 0.2$), (Fig. 5.2.12 B and Table 5. IX). By comparing Figures 5.2.12 A and B it can be seen that the optimum LAIs were all outside the range of experimental data except those determined at $3.0$ cal./cm$^2$/hr. It is of note that the estimated optimum LAIs behave in the same manner as those for the pure grass swards, i.e., the optimum increased with increasing light energy levels.
Fig. 5.2.10 The relationship between LAI and days of regrowth since the last mowing for pure white clover swards.

Fig. 5.2.11 The relationship between LAI and weight of herbage from unit area of land for pure white clover swards.
Fig. 5.2.12: The relationship between net photosynthesis per metre $^2$ land and LAI in white clover swards, A) at saturating light energy levels and B) at the light energy levels as shown. The regression equations for B are given in Table 5.1X

$Y = 1.478 + 0.297X \quad r = 0.807$
to 12 cal./cm²/hr. after which it showed no further increase. The quadratic $x^2$ coefficient for the 3.0 cal./cm²/hr. level was significant at $P < 0.1$ and as the optimum LAI of 5 was within the data, reasonable confidence can be placed in this figure.

Table 5. IX The regression coefficients relating net photosynthesis ($Y$) to LAI ($X$) in white clover swards at four light energy levels. Regressions in the form $Y = a + bX + cX^2$

<table>
<thead>
<tr>
<th>Light energy cal./cm²/hr.</th>
<th>a</th>
<th>b</th>
<th>c</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td>24.0</td>
<td>0.863</td>
<td>0.630</td>
<td>-0.0443</td>
<td>0.817</td>
</tr>
<tr>
<td>12.0</td>
<td>0.645</td>
<td>0.589</td>
<td>-0.0442</td>
<td>0.783</td>
</tr>
<tr>
<td>6.0</td>
<td>0.253</td>
<td>0.504</td>
<td>-0.0438</td>
<td>0.691</td>
</tr>
<tr>
<td>3.0</td>
<td>-0.142</td>
<td>0.419</td>
<td>-0.0445</td>
<td>0.533</td>
</tr>
</tbody>
</table>

From the curves in Fig. 5.2.12 B it has been possible to calculate the efficiency of light energy use, in CO₂ uptake, by the white clover swards. These calculations used the same method and calorific value as in Section 5.2.2.1, and when the results are compared with the appropriate light energy levels, CO₂ uptake and optimum LAI (Table 5.X) it can be seen the maximum efficiency of light energy use occurred with approximately 6.0 cal./cm²/hr. This level of light energy is close to that required to produce 50% of the maximum rate of net photosynthesis ($5.3 \pm 0.9$ cal./cm²/hr.) and indicated a relatively efficient light energy use by the swards when at their optimum LAI. As with the grass swards, calculations of the efficiency of light use were not made below 3.0 cal./cm²/hr. as light compensation values as high as 2.1 cal./cm²/hr.
had been recorded with these clover swards. The maximum efficiency of light use was within the range of the data and occurred at about 6.0 cal./cm²/hr. (Table 5.X).

The initial slope of the light response curve calculated from the net photosynthesis at the light compensation point plus 2.0 cal./cm²/hr., was related linearly to LAI (P < 0.001) (Fig. 5.2.13). There were no significant differences between the regressions for the three managements. Considerable variability was evident and indicated variability in the light compensation. There was no evidence of an optimum LAI here.

Table 5.X The efficiency of light energy use in CO₂ uptake in white clover swards at four light energy levels together with their CO₂ uptake and optimum LAI at these energy levels.

<table>
<thead>
<tr>
<th>Light energy cal./cm²/hr.</th>
<th>CO₂ Uptake g CO₂/m²/hr.</th>
<th>Optimum LAI</th>
<th>Efficiency %</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>0.841</td>
<td>5.0</td>
<td>7.57</td>
</tr>
<tr>
<td>6.0</td>
<td>1.700</td>
<td>6.0</td>
<td>7.65</td>
</tr>
<tr>
<td>12.0</td>
<td>2.598</td>
<td>6.8</td>
<td>5.85</td>
</tr>
<tr>
<td>24.0</td>
<td>3.102</td>
<td>7.0</td>
<td>3.45</td>
</tr>
</tbody>
</table>

The weight of dry tissue influenced net photosynthesis in that the estimated photorespiration, parameters A - B, was linearly related to tissue weight (P < 0.02). The relation was similar over all the managements as there were no significant differences between the regressions for them; this was:

\[ Y = -0.043 - 0.236 X, \quad r = -0.442 \]

where \( Y \) = photorespiration (A - B) in g CO₂/m²/hr. and \( X \) = herbage
Fig. 5.2.13 The relationship between the initial slope of the light energy response curves of white clover swards and their LAI.

\[ Y = 0.395 + 0.089X \]

\[ r = 0.633 \]
Net assimilation rate declined curvilinearly with increasing LAI (P<0.001), (Fig. 5.2.14). There were no significant differences between the regressions for the three managements. All the swards showed a positive average NAR even at LAIs of almost 6 indicating that there were few leaves in the lower strata with negative NARs. The shape of the response curve suggested for these swards that minimum assimilation per unit leaf area or maximum per unit area of land occurred at about LAI 6. However, there was no evidence to suggest that there would necessarily be a decline in CO₂ assimilation above LAI 6. Therefore this data could not clearly define an optimum LAI.

As the leaf angle of the clover swards was more horizontal than the grass swards (mean C 0.17 clover and 0.12 grass) the amount of light energy required to produce 50% of the maximum rate of net photosynthesis was less (Fig. 5.2.15). There was no significant difference between the regressions for the three managements and a linear regression fitted the data best (P<0.001).

5.2.2.3 Mixed Grass - Clover Swards

The relationship between LAI and days of regrowth with the grass-clover swards was linear (Fig. 5.2.16). The regression was highly significant (P<0.001) and there were no significant differences between the regressions for the individual managements. With these mixed swards, as with the pure swards, the variability about this regression reflected sampled variability in the plant density.

In the swards containing both orchardgrass and white clover the relationship between LAI and weight of herbage from a unit land area
The relationship between net assimilation rate (NAR) of leaves and petioles in white clover swards and LAI.

\[ Y = 16.262 - 3.631X + 0.306X^2 \]

\[ R = 0.874 \]

Fig. 5.2.14 The relationship between net assimilation rate (NAR) of leaves and petioles in white clover swards and LAI.
Fig. 5.2.15 The relationship between light energy required to produce 50% of the maximum rate of net photosynthesis in white clover swards and the C value of the exponential equations fitted to the light energy response curves.
was highly significant \((P<0.001)\); (Fig. 5.2.17). The slopes of the
regressions for the individual managements did not differ significantly.

In the \(\text{CO}_2\) uptake comparisons which follow the mean temperature of
measurement was \(22.9 \pm 1.5^\circ\text{C}\) and the vapour pressure deficit was
\(2.2 \pm 1.3\text{mm of Hg}\).

In the relationship between LAI and net photosynthesis at
saturating light energies, the mixed orchardgrass-white clover swards
showed no significant differences between the managements (Fig.
5.2.18); the overall regression was significantly quadratic \((P<0.001)\).
There was an optimum LAI in these swards of about 10; however, as can
be seen, there was some variability about this. The regressions for
the four light energy levels were calculated as Section 5.2.2.1 (Fig.
5.2.19 and Table 5.XI). All the \(X\) coefficients and \(X^2\) coefficients
were significant \((P<0.001)\) except for \(X^2\) at \(3.0\text{cal.}/\text{cm}^2/\text{hr}\). which was
significant at \(P<0.05\). The optimum LAIs behaved in the same manner
as previously and increased with increasing light energy from 8.0 at
\(3.0\text{cal.}/\text{cm}^2/\text{hr}\) to 9.0 at \(12\text{cal.}/\text{cm}^2/\text{hr}\). However, by contrast to the
pure swards, above \(12\text{cal.}/\text{cm}^2/\text{hr}\). there was a significant increase in
the optimum LAI to 10.0 at \(24\text{cal.}/\text{cm}^2/\text{hr}\).

From the above data it has been possible to calculate the effici­
cy of light energy use in \(\text{CO}_2\) uptake by these mixed forage swards.
These calculations used the same method and calorific value as in
Section 5.2.2.1 and the results are presented, together with the
appropriate light energy levels, \(\text{CO}_2\) uptake and optimum LAI (Table 5.XII).
As can be seen the maximal light energy use occurred with
approximately \(6.0\text{cal.}/\text{cm}^2/\text{hr}\). This level of light energy was close to
that required to produce \(50\%\) of the maximum rate of net photosynthesis
Fig. 5.2.16 The relationship between LAI and days of regrowth since the last mowing for mixed orchardgrass-white clover swards.

Fig. 5.2.17 The relationship between LAI and weight of herbage from unit area of land for mixed orchardgrass-white clover swards.
Fig. 5.2.18 The relationship between net photosynthesis per metre$^2$ land and LAI in mixed orchardgrass-white clover swards at saturating light energy levels.
Fig. 5.2.19 The relationship between net photosynthesis per metre² land and LAI in mixed orchardgrass-white clover swards at four levels of incident light energy. The regression equations for the four lines are given in Table 5.XI.
Table 5.XI  The regression coefficients relating net photosynthesis (Y) to LAI (X) in mixed orchardgrass-white clover swards at four light energy levels. Regressions in the form \( Y = a + bX + cX^2 \) \( n = 30 \), coefficients in g CO\(_2\)/m\(^2\)/hr.

<table>
<thead>
<tr>
<th>Light energy cal./cm(^2)/hr.</th>
<th>Coefficients</th>
<th>R</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>24.0</td>
<td>0.728</td>
<td>0.518</td>
</tr>
<tr>
<td>12.0</td>
<td>0.503</td>
<td>0.477</td>
</tr>
<tr>
<td>6.0</td>
<td>0.281</td>
<td>0.345</td>
</tr>
<tr>
<td>3.0</td>
<td>0.188</td>
<td>0.164</td>
</tr>
</tbody>
</table>

Table 5.XII  The efficiency of light energy use in CO\(_2\) uptake in mixed forage stands containing orchardgrass and white clover, at four light energy levels together with their CO\(_2\) uptake and optimum LAI at these light energy levels.

<table>
<thead>
<tr>
<th>Light energy cal./cm(^2)/hr.</th>
<th>CO(_2) Uptake g CO(_2)/m(^2)/hr.</th>
<th>Optimum LAI</th>
<th>Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0</td>
<td>0.815</td>
<td>8.0</td>
<td>7.34</td>
</tr>
<tr>
<td>6.0</td>
<td>1.742</td>
<td>8.5</td>
<td>7.84</td>
</tr>
<tr>
<td>12.0</td>
<td>2.666</td>
<td>9.0</td>
<td>6.00</td>
</tr>
<tr>
<td>24.0</td>
<td>3.188</td>
<td>10.0</td>
<td>3.59</td>
</tr>
</tbody>
</table>

(5.9 ± 1.7 cal./cm\(^2\)/hr.) and indicated a relatively efficient use of light energy by these swards when at their optimum LAI. As with the grass, and clover swards calculation of the efficiency of light use were not made below 3.0 cal./cm\(^2\)/hr., as light compensation values up to 2.2 cal./cm\(^2\)/hr. had been recorded.
The initial slope of the light response curve, calculated from the net photosynthesis at the light compensation point plus 2.0cal./cm\(^2\)/hr., was curvilinearly related to LAI (P<0.001) see Fig. 5.2.20. There were no significant differences between the regressions for the three managements and there was considerable variability about the general regression. However, the response line indicated that the optimum LAI was about 9 which agrees with the optimum calculated from the response curve at 12.0cal./cm\(^2\)/hr.

Weight of dry tissue influenced net photosynthesis. When included in a multiple regression with LAI the coefficient for tissue weight was negative indicating increased photorespiration with increased tissue weight. The 100 \(R^2\) with LAI only, was 68.2% and with the inclusion of tissue weight this increased to 73.4%. The regression was significant (P<0.001) and was:

\[ Y = 1.638 + 0.384 X_1 - 0.449 X_2 \quad R = 0.857 \]

where \(Y\) = net photosynthesis in g CO\(_2\)/m\(^2\)/hr. and \(X_1\) = LAI and \(X_2\) = herbage weight g/dm\(^2\) land.

The effect of tissue weight on photorespiration was confirmed by the regression of estimated photorespiration, parameters \(A - B\), on tissue weight. In this regression photorespiration increased with the higher tissue weights in a curvilinear manner, and there was no significant difference between the regressions for the three managements. The regression was significant (P<0.001), and was:

\[ Y = 0.272 - 0.439 X + 0.040 X^2 \quad R = 0.754 \]

where \(Y\) = photorespiration (\(A - B\)) in g CO\(_2\)/m\(^2\)/hr. and \(X\) = herbage weight g/dm\(^2\) land.
Fig. 5.2.20 The relationship between initial slope of the light energy response curves of mixed orchardgrass-white clover swards and their LAI.

\[ Y = 0.069 + 0.197x - 0.011x^2 \]

\[ R = 0.790 \]
The curvilinear nature of the above regression indicated that past a particular leaf weight, there was very little increase in photorespiration, presumably a point where the canopy had reached an equilibrium and where further increases in leaf weight represented only an increased quantity of senescent material.

Net assimilation rate declined curvilinearly with increasing LAI ($P<0.001$), (Fig. 5.2.21). There were no significant differences between the regressions for the three managements. All of the swards showed a positive average NAR, however, at LAIs around 12 it was so low that in all probability some leaves in the lower strata had negative NARs. The shape of the response curve suggested for these swards that minimum assimilation per unit leaf area, or maximum per unit area of land occurred at about LAI 12. However, there was no evidence to suggest that there would necessarily be a decline in $\text{CO}_2$ assimilation above LAI 12. Therefore this data does not establish an optimum LAI.

The leaf angle influenced the amount of light energy required to produce 50% of the maximum rate of net photosynthesis (Fig. 5.2.22). There was no significant difference between the regressions for the three managements on these mixed orchardgrass-white clover swards. As with the pure grass there was a curvilinear decrease in the amount of light energy required to produce 50% of the maximum rate of net photosynthesis ($P<0.001$). The response line showed a rise above a C value of 0.24; however, as this covers a region with only one observation it is of little significance. Thus, in general, as the leaves became more horizontal there was a decrease in the amount of light energy required to produce 50% of the maximum rate of net photosynthesis.
Fig. 5.2.21. The relationship between net assimilation rate (NAR) of leaves and petioles in mixed orchardgrass-white clover swards and LAI.
The relationship between the light energy required to produce 50% of the maximum rate of net photosynthesis in mixed orchardgrass-white clover swards and the C values of the exponential equations fitted to the light energy response curves.
5.3 Discussion

Although this is primarily a discussion of the results from Section 5 it is useful to include in the discussion, some of the results from Sections 3 and 4 as the experiments in these sections were studies which lead to the Section 5 experiments.

5.3.1 The Influence of the Growing Season Environment on Net Photosynthesis and Production

The moisture regimes of the Australian and Canadian\(^1\) trials (Tables 3.II and 5.V) show that for the spring-summer growing season the rainfall and irrigation in the Canadian trial exceeded that in the Australian trial by 5 to 8 inches. However, when the differences in soil physical conditions between the two trials are taken into account, the Australian trial with a heavy cracking clay probably had considerably less available moisture than the Canadian trial with a sandy loam. This difference in available moisture between the two trials was accentuated by the irregular and, at times, heavy rain in the Australian trial which often resulted in poor infiltration into the rooting zone. The lower level of available moisture in the Australian trial was undoubtedly a major cause of the lower yields.

The summer temperatures in the Australian trial ranged from 12 to 26° C. It seems therefore that differences in temperature would not have been a major factor in the yield differences between the two trials. Viewed in the light of the controlled environment studies for orchardgrass and white clover the field diurnal range was similar to:

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\(^1\) For purposes of convenience the defoliation experiments will be referred to by the country in which they were run viz. Section 3, Australia, Section 5 Canada.
that used in the growth cabinets. The optimum temperatures found for these two species indicated that with the prevailing summer temperatures growth was probably near optimal in both trials. However, temperatures during April and May in the Canadian trial probably limited growth while winter temperatures (0-12°C) in the Australian trial most likely limited growth. The net photosynthesis and growth studies (Section 4) indicate that CO₂ fixation occurred over a greater length of time than for top growth in the swards.

Using the tables published by de Wit (1965) and the actual solar radiation levels (Table 5.V) the potential production for the growing season of the Canadian trial was calculated. To use these tables, to estimate production, it was assumed that stand geometry was optimal and that radiation between 400 and 700nm was 44% of the total solar radiation and further that, gross respiration was 33% of photosynthesis, the latter two figures being those of Loomis and Williams (1963). Under the environmental conditions of the Canadian trial potential photosynthesis would be 42,650 lb. (CH₂O)/acre and by allowing for respiration potential production could be 28,580 lb. (CH₂O)/acre. This estimate, compared with the highest actual production (Table 5.II) of about 11,200 lb. dry matter/acre indicates only 38% of the potential production was achieved. The situation appears similar to that described by Stanhill (1962) who concluded that the discrepancy was due to light energy wastage. In the present trial, the defoliation height of 9 inches did not permit a high enough average LAI to utilize all the light energy available. This, however, is not completely consistent with the results, as the highest production was achieved from the (3-1) management. In the grass swards it was shown that the (9-1) managed
pastures had a higher rate of net photosynthesis at cutting height (Fig. 5.2.4 A) than those cut at 9 inches. This probably compensated for any extra light wastage by the (3-1) managed swards and from field observations appeared to be a consequence of more horizontal leaves and less light wastage.

5.3.2 Dry Matter Production and the Influence of Frequency and Intensity of Defoliation

The dry matter production of the two defoliation management experiments differed greatly. As can be seen by comparing Table 3.IV and 5.II the yield in the trial in Canada was 3 times that of the trial in Australia. However, despite this great difference in yield the order of yields from the three managements was essentially the same in both trials. Differences between the (3-1) and (9-1) managements were slight while the (9-3) management showed a significantly lower total production. Thus these results agree well with those of Brougham (1959) and Bryant and Blaser (1968) in that leaving 3 in. of herbage generally results in lower yields than a closer defoliation. They also confirm the trends shown by Bryant and Blaser (1968), that with managements of this type both clipping and grazing give the same yield order. The results also support the data of Matches (1968) that in such trials the yield rank will be the same with clipping, or grazing by sheep or cattle.

In the trials in Australia the (9-3) management depressed both grass as well as clover production while in the Canadian trial only clover production was depressed. In the Australian trial the poor grass production could have arisen from the low clover content of the sward
and hence low levels of fixed nitrogen as demonstrated by Herriott and Wells (1960) and Cowling (1961 and 1962). Alternatively the use of animals as defoliators could have caused selective defoliation of the grass component. In the Canadian trial soil nitrogen was apparently adequate as the (9-3) managed plots had the same yield of grass herbage as the plots with the (3-1) or (9-1) managements despite the lower clover content in the (9-3). In this trial then, the lower clover yield, under the (9-3) management, appears to have been caused by competition for light as described by Donald (1961). The evidence of Wilkinson and Gross (1964) has shown that reduction in light competition is a necessary prerequisite to re-establishing Ladino white clover into orchardgrass swards. Thus in the Canadian experiment the 3 inch mowing level allowed the orchardgrass to shade the white clover and depress its yield. This however, does not agree with the evidence of Trautner and Gibson (1966) who found greatest branching and flowering in white clover under moderate shade. Other workers, for example, Blake et al. (1966) have found white clover shade intolerant. They also found disease and insects reduced the persistence of this plant.

The total seasonal yields in the Canadian trial were about 2,000 lb./acre lower than those reported by Gardner et al. (1960) for orchardgrass-perennial ryegrass-white clover pastures grown on Vancouver Is. some 35 miles distant from the present experiment. These workers found that without potassium fertilization their pastures showed a lower clover content than those receiving potassium. However, in the present experiment this is unlikely as all the managements received the same potassium fertilizer applications while the lower clover percentage only occurred under the (9-3) management. The (3-1) management
had 38% clover, the (9-1) 31% clover while the (9-3) had only 14% clover.

In the pure orchardgrass swards the highest yielding management was the (9-1) while in the pure white clover swards both the (3-1) and (9-1) managements gave the best production (Table 5.31). The observation that a 3 inch cutting height gave a lower yield than a 1 inch cut in the pure white clover swards agrees with the results of Gervais (1960) who used similar cutting heights. With pure orchardgrass swards Drake et al. (1963) found greater yields from swards cut at 3 inches than from those cut at 1 inch while Blake et al. (1966) found cutting height, between $\frac{3}{4}$ and 2 inches had little influence on the orchardgrass yields. Thus the superiority of yields from the 1 inch cut, in the Canadian experiment, was by no means unique. Of the swards cut to 1 inch those with cutting initiated at 3 inches (3-1) yielded less than those with cutting initiated at 9 inches (9-1). This agrees well with the findings of Dewey (1961) who found that orchardgrass plants clipped when 3 inches tall gave a lower seasonal yield than plants clipped when 10 inches tall. Wolf and Smith (1964) have also found high cutting frequencies (5 times) gave lower yields in orchardgrass-white clover swards than only 3 cuts per season.

In the mixed swards in the Australian trial the (3-1) management favoured orchardgrass while the (9-1) favoured clover production. In the Canadian trial the (3-1) management favoured clover production while swards cut when 9 inches high were the better grass producers. As the differences between the managements in grass and clover yields were comparatively small, there is little significance in a particular management showing superior grass or clover production. However, with
the Canadian trial the trends were similar to those reported by Ward et al. (1966) and by Reid (1968) for orchardgrass-white clover swards.

Apart from these considerations of component yield, the value of leaving some LAI after defoliation by the use of the (9-3) management must be considered with response to total yield. In the Australian trial, the yields were low, therefore when considering LAI and light interception it seems unlikely that the material left with the 3 inch grazing height conferred any advantage in the form of light interception. In the Canadian trial, the yields and LAIs were higher (Table 5.II and Figs. 5.2.2, 5.2.10 and 5.2.16). As the frequency of defoliation with the (9-3) management was lower than with the (3-1) and the quantity of material removed per defoliation was similar (Table 5.II) the 3 inch stubble clearly depressed the growth rate of the clover. This result is contrary to that found by Brougham (1956) who found the regrowth rate of swards defoliated to 3 inches was greater than those defoliated to 1 inch. If an effect such as that described by Brougham (1956) occurred it was of very short duration and had no influence on the average regrowth rate. In other words, the lag phase before a high level of light energy interception was not shortened in the swards defoliated at 3 inches compared with those defoliated at 1 inch. This agrees well with the findings of Begg and Wright (1964) and Mittara and Wright (1966) who found that the basal leaf blades, in a reed canarygrass sward, were less efficient in supporting regrowth than the upper leaf blades.

The poor regrowth from the (9-3) management treatments could also have been a consequence of high rates of tissue senescence as
suggested by Brougham (1962), Hunt (1965) and Hunt and Brougham (1966). They found that during active growth the accumulation of dry matter in grass or clover swards was dependant on the rate of tissue senescence. Hunt (1965) suggested therefore that defoliation managements with close cutting initiated at maximal light interception would minimise tissue senescence. In the present trials therefore, the (9-3) management would be expected to have greater senescence than the (9-1) and hence a lower yield.

From Figures 5.2.3, 11 and 17 it is evident that both the grass and grass-clover swards under the (9-1) and (9-3) defoliation managements attained LAIs between 10 and 17 together with up to 8,000 lb./acre dry matter. Thus sward LAIs were often above the optimum LAI for tall fescue swards estimated by Murtagh and Gross (1966). However it is quite likely that these high LAIs had little effect on the pasture growth rate as a whole; especially in view of the findings of Anslow (1965) that midsummer growth is not necessarily related to LAI and that high LAI does not always exert a depressing effect on growth. Discussion of the presence of an optimum LAI in these swards is given in Sections 5.2.3 and 4 where it is considered with reference to the rate of CO₂ assimilation.

Apart from the factors discussed above, the outcome of the management treatments may also have been influenced by differences in the reserve carbohydrate level. Ward and Blaser (1961) have shown that carbohydrate reserves and leaf area can also interact so that the whole situation is complex. In the Australian trials where year-round yields were taken, examination of the season x management interaction could have provided evidence of different carbohydrate reserves in
response to the defoliation treatments (Table 3.V). However, as environmental conditions were such that the yield potential was low it seems unlikely that the reserves would have been important as regrowth was so small. In the Canadian trial where the environment dictated a shorter growing season any effect of extra reserve carbohydrate from the (9-3) management would have occurred in the late fall. However, during this period no growth occurred on any of the treatments. Thus in general even if active growth and defoliation at 1 inch resulted in lowering of carbohydrate levels in the (3-1) and (9-1) managements, the environment of both trials probably prevented these managements showing any disadvantage compared with the (9-3).

5.3.3 The Influence of Frequency and Intensity of Defoliation on Net Photosynthesis in Forage Stands

The defoliation management treatments caused significant changes in the relationship between net photosynthesis and LAI in the orchardgrass swards. However, in the white clover and mixed orchardgrass-white clover sward there were no differences between the managements in the above relationship. In the pure orchardgrass swards (Figs. 5.2.4 A and B, 5.2.5 and 5.2.7) the increase in net photosynthesis per unit LAI was much greater in (3-1) managed swards than in the (9-1) or (9-3) managements despite the greater frequency of defoliation with the (3-1). The (9-1) managed swards with a linear relation between net photosynthesis permitted the yield to continue to increase with time and LAI even with the most infrequent defoliation.

The only sward to show an optimum LAI at saturating light levels was the sward with the (9-3) defoliation management which indicated that
the 3 inch stubble left acted as "parasitic" material as described by Donald (1961) and particularly in the latter phases of the LAI increase. It was not expected that the swards with the (3-1) management would show an optimum LAI. However, the fact that there was no optimum LAI with the (9-1) management even up to LAI 17 gives confidence to the findings of Anslow (1966) that midsummer growth rates in grass swards was not related to, or dependant on LAI. At lower light intensities the (9-1) managed swards did show an optimum LAI for maximum net photosynthesis. This was consistent with the "optimum LAI theory" as at saturating light levels there was no optimum LAI while at lower light levels there was an optimum LAI where the lower leaves could be below the light compensation point. The effect of an optimum LAI appearing at low light energy levels is in agreement with, and further confirms the findings of Brougham (1958) that there is a diurnal change in the optimum LAI.

The initial slope of the light response curve vs. LAI for the (9-3) managed swards shows that these swards as well as having an optimum LAI at all light levels gained absolutely no extra net photosynthesis from the 3 inches of stubble left. Thus the initial slope vs. LAI curve also provides further evidence that these lower leaves were in fact "parasitic". These (9-3) managed orchardgrass swards were therefore similar to the reed canarygrass swards of Begg and Wright (1964) and Brown et al. (1966) which were shown to have the lower leaves "parasitic".

The fact that the white clover swards did not show an optimum LAI except at very low levels coupled with the fact that there were no differences between the managements is evidence of differences in the
behaviour of these swards compared with the pure grass swards. In these clover swards LAIs above 6 were not obtained, and observations indicated that the canopy became stable and was maintained at this level by new growth and leaf senescence. The 3 inch stubble left with the (9-3) management consisted of almost entirely petiole stumps which senesced rapidly as new regrowth occurred. This behaviour strongly contrasted to the grass swards where the LAIs continued to increase to 17 and where senescence in the 3 inch stubble was much slower. The lower yield of clover with the (9-3) management appeared to be a consequence of competition with other species which invaded these plots in this management rather than differences in net photosynthesis.

The fact that the mixed orchardgrass-white clover swards showed no differences between the managements in the net photosynthesis-LAI relationship was, however, not entirely a consequence of the above behaviour by the clover in the (9-3) swards compared with the (3-1) and (9-1) the (9-3) swards contained the least clover. The reason for this lack of difference between the managements in essentially grass dominant swards was not apparent. The results clearly indicated an overall optimum LAI at saturating light levels for all swards so that the evidence of "parasitic" leaves was not confined to the (9-3) managed swards.

5.3.4 The Influence of Botanical Composition on Net Photosynthesis of the Forage Stand

The net photosynthesis-LAI response of the mixed orchardgrass-white clover swards showed that the optimum LAI was intermediate between the LAIs from swards where the species were grown alone. At
24.0 cal./cm²/hr the orchardgrass swards showed an optimum LAI of 14.2 and the white clover swards an optimum LAI of 7.0, while the optimum for mixtures of the two species was 10.0. A slightly higher optimum might have been expected for the mixture as the mean clover content was only 33% on a dry matter basis. However, it was observed that in the mixed swards the white clover petioles which were able to survive were longer than those of the clover in pure swards. Hence the clover leaves in the mixed swards were located at the top of the canopy in a favourable position for carbon dioxide assimilation. Thus, even though the clover proportion was only 1/3 by weight the positioning of the clover leaves resulted in an optimum LAI closer to that of the pure clover swards than the pure grass.

In the pure orchardgrass and white clover forage stands, a light energy level of 24.0 cal./cm²/hr, in swards with an optimal LAI, resulted in net photosynthesis levels of between 3.0 and 3.5 g CO₂/m²/hr. The mixed sward of these two species did not, as expected, show any difference in net photosynthesis from the above range; (Figs. 5.2.6, 5.2.12 B and 5.2.19). Little literature is available on the effect on net photosynthesis of mixing a grass and legume species in a sward. Brougham (1958) found that mixed swards of short-rotation ryegrass and white clover had intermediate light interception properties compared with pure swards of the same species. Pearce et al. (1967) have shown that the optimum LAI of a pure stand of barley decreased as the leaves became horizontal. The data from the present experiment was consistent with both these observations in that mixed swards had an intermediate optimum LAI for carbon dioxide assimilation; presumably they had an intermediate mean leaf angle and light interception compared
with the swards where the species were grown alone. The net photosynthesis values for orchardgrass and white clover when grown alone were similar to those obtained by Pearce et al. (1965) and Wilfong et al. (1967) for these species.

5.3.5 An Assessment of the Efficiency of Light Energy Use by the Forage Associations

The highest efficiencies of light energy use recorded for orchardgrass and white clover in pure and mixed stands were 8.35%, 7.65% and 7.84% respectively; with optimum LAIs of 13.0, 6.0 and 8.0. In all cases the light energy level which gave these efficiencies was comparatively low, viz. 6.0 cal./cm²/hr. Brougham (1958) has shown that with similar light and LAI levels, white clover swards were more efficient "interceptors of light" than short-rotation ryegrass swards. The data presented in this thesis clearly supports Brougham's findings as the optimum LAI was lowest in the pure white clover swards. However, when the orchardgrass swards reached their optimum they, in terms of net photosynthesis, did make more efficient use of the light energy available; the efficiency of light energy use was 0.7% greater than that in the white clover swards. The more vertical distribution of the leaves in the orchardgrass swards was most likely the factor responsible for the increase in efficiency. However, other factors such as leaf age which affects the level of net photosynthesis (See Brown et al. 1966) undoubtedly influenced the overall response.

The efficiencies of light use compare favourably with those reported by other workers. The efficiency of 8.35% for orchardgrass is higher than that reported by Yocum et al. (1954) for a maize crop.
which was 5.1%. However, their efficiency was estimated over an "average" day so that no doubt during the lower light intensity periods of the day the efficiency would have been higher. Allowing for a loss of carbon dioxide by night respiration of 33% the 8.35% efficiency for net photosynthesis becomes 5.57% efficiency for net daily carbon dioxide assimilation in the orchardgrass swards. This figure of 5.57% is lower than that of 7.9% reported by Bray (1961) for dry matter production in a Picea omorika plantation. In their estimate of maximum crop productivity Loomis and Williams (1963) suggested an overall efficiency for dry matter production of 12.0%. The efficiencies reported in this thesis do not approach this figure. However, they are in the same region as those of other workers using forage swards. Hunt and Cooper (1967) found a 6.0% efficiency of net assimilation in tall fescue swards kept at 90% light interception.

Allowing for a 33% night respiration loss the figure light energy use for white clover in the present experiment would be 5.32%. Black (1964) found a maximal seasonal net assimilation efficiency of 4.2% in subterranean clover. King and Evans (1967) have calculated efficiencies of light use for subterranean clover from carbon dioxide exchange data, and making an allowance of 33% for night respiration, their efficiency light use in CO₂ net assimilation was 6.5% for subterranean clover. Clearly the data of this and other published experiments indicate that there is considerable room for increased efficiency of light use in forage stands.

Taking a figure of 4.0 gCO₂/m²/hr, at 40 cal./cm²/hr. of 400-700nm radiation, as the mean maximum measured net photosynthesis for the orchardgrass, white clover and mixed swards at their optimum LAI, a
comparison can be made of this value with estimates of potential photosynthesis for the Vancouver region from the tables of de Wit (1965). The daily mean net photosynthesis for Vancouver, at approximately latitude 50, read off from de Wit's tables for a clear day, with 405 cal./cm²/day of 400-700nm radiation, would be 6.1gCO₂/m²/hr. As the mid-day rates could be double the daily mean, the measured level of 4.0gCO₂/m²/hr confirms the earlier suggestion that there is a wide margin for improvement in carbon dioxide assimilation.
6. SUMMARY AND CONCLUSIONS

6.1 The Field Experiment with Defoliation by Animals

An experiment is reported in which the effects of three grazing managements, differing in frequency and intensity, on the productivity of seven grass-clover pasture swards were examined. The grass-clover swards studied contained one of the following forage grasses as their major grass component: perennial ryegrass, Ariki ryegrass, Grasslands Cocksfoot, Sl43 Cocksfoot, S26 Cocksfoot, Alta Tall fescue and Sl70 Tall fescue. Herbage, botanical composition, LAI and dry matter yield were measured at grazing. The relationship between dry matter yield and LAI was examined by regression analysis.

The Festuca arundinacea pastures showed the greatest annual herbage production. In the two years of this experiment moisture stress appeared to be a prime limiting factor for pasture growth. Under these conditions grazing managements which involved intensive grazing to ground level (3-1) and (9-1) showed greater herbage production than those which left some herbage (9-3). This effect applied to all the grass-clover mixtures examined.

The results showed that, under conditions of low rainfall, the LAI of the pasture did not exceed 4.0 and hence light interception did
limit plant growth. The possible reasons why the (9-3) grazing management did not show superior production to those managements based on total herbage consumption are discussed.

The regressions of LAI and dry matter showed significant differences between the grass species in the weight:area ratio but no differences as a consequence of the particular grazing managements.

6.2 Controlled Environment Studies

In Section 4 of the thesis the influence of differing day temperatures was studied on the growth and net photosynthesis of orchardgrass and Ladino white clover. Growth was studied from 22°C to 34°C, with the night temperatures 10°C lower; while net photosynthesis was measured from 15 to 30°C at a number of vapour pressure deficits.

Light, moisture and nutrients were kept at a constant and high level.

Growth in orchardgrass as measured by tiller weight or area, reached a maximum at a 29°C day temperature; weight per leaf and area per leaf were also maximal at this temperature. Weight per unit area of leaf was maximal between 24 and 29°C with no clear optimum temperature, however, above or below these temperatures the leaves were lighter per unit area. The number of leaves per tiller was unaffected between 24 and 34°C but at 22°C the number was significantly reduced.

The optimum temperature for net photosynthesis in orchardgrass was outside the range of the experiment (15-30°C) with net carbon dioxide uptake greatest at 15°C and declining linearly above this temperature. Increasing vapour pressure deficit from 5 to 20 mm Hg increased net photosynthesis in orchardgrass, however, the increase was slight and
variable.

In Ladino white clover the influence of day temperatures, between 22 and 34°C, on vegetative growth was slight. However, plants grown at 29°C had significantly greater weights and areas. The number of leaves per rooted node was maximal at 29°C. Weight and area per leaf were greatest with day temperatures between 24 to 29°C. The weight per unit leaf area was unaffected by day temperatures from 22 to 29°C.

For Ladino white clover optimum temperature for net photosynthesis occurred within the range of the experiment and it was maximal at approximately 20°C. However, there was not a sharp optimum temperature and there were only slight differences in net carbon dioxide assimilation between 15 and 25°C. Increased vapour pressure deficit also appeared to increase carbon dioxide assimilation in white clover over the range 5 to 20 mm Hg, however, as with orchardgrass variability was high.

6.3 Net Photosynthesis and Dry Matter Production in the Field

The experimental work for this phase of the thesis is in two parts; first a field trial with measurement of forage yield under a number of defoliation treatments, and second, concurrent laboratory determination of net photosynthesis in material from the field trial.

In the field trial orchardgrass, white clover and orchardgrass-white clover forage stands were subjected to three defoliation managements which differed both in frequency and intensity of defoliation. Over a complete growing season the managements with defoliation to within 1 inch of the ground gave the greatest yield of herbage dry matter. The frequency with which these forage stands were
defoliated had little influence on the herbage yield.

The defoliation management with the least intensive defoliation (at 3 inches) showed the lowest yield with the effect being mainly on the clover component. The yields of the orchardgrass and white clover when growing as pure stands also confirmed the above contention that defoliation at 3 inches had a depressive effect through the clover component.

With the laboratory measurements of net photosynthesis of material taken from the field trial it was possible to examine the relationship between LAI and carbon dioxide uptake by the forage stands at a number of light energy levels.

Within the orchardgrass pastures there were differences in the net photosynthesis-LAI response due to the defoliation managements. The orchardgrass swards defoliated to within 1 inch of the ground showed a linear relation between net photosynthesis and LAI when at saturating light energy levels. This linear relationship was found as high as LAI 17 with no evidence of an optimum LAI. The frequency with which these swards were defoliated influenced the slope of the net photosynthesis-LAI response so that the most frequently defoliated swards at LAI 6 fixed as much carbon dioxide as the less frequently defoliated swards at LAI 17. Failure to show yield differences between these two managements was, therefore, a true reflection of the photosynthesis capacities of the swards.

In the orchardgrass swards, defoliated at 3 inches and allowed to regrow to 9 inches, there was clear evidence of an optimum LAI at about 12. This suggested that the management practice of lenient defoliation left herbage which became "parasitic" as far as the overall
carbon dioxide uptakes of the sward was concerned. Over the initial portions of the light response curves there were differences between the managements in the net photosynthesis-LAI responses of the orchardgrass swards. At these lower light energy levels the least frequent and intensive defoliation (9 inches defoliated to 1 inch) also showed an optimum LAI close to that of the management with the 3 inch defoliation height; in this case the optimum LAIs were about 14. The curve for the 3 inch defoliation treatments was displaced to the right and lower than that for the 1 inch defoliation giving further evidence that some of the leaves in the 3 inch defoliated plants were "parasitic."

At the optimum LAI the efficiency of light energy use by the orchardgrass swards varied from 3.2% at near saturation light energy levels to 8.4% at low light energy levels.

The optimum LAI for the Ladino white clover swards was not clearly defined by the experiments but appeared to be in the region of 4-6. In this region the efficiency of light energy use ranged from 3.5% at near saturating light energy levels to 7.5% at low light energy levels.

There were not any detectable differences between the responses of net photosynthesis-LAI under the differing defoliation managements.

In the swards consisting of a mixture of orchardgrass and white clover the optimum LAI was clearly defined and was intermediate between those of the swards of the species alone. With the optimum LAI of about 10 the efficiencies of light energy use were similar to those for the white clover swards being 7.3% at low levels of light energy and 3.6% at near saturating light energy levels. As with the white clover swards there were not any detectable differences between the net photosynthesis-LAI responses of the different defoliation managements.
7. LITERATURE CITED


Davies, Alison, 1966. The regrowth of swards of S24 perennial ryegrass subjected to different pre-treatments. J. Agr. Sci., 67:139-144.


8. APPENDIXES

8.1 Soil Physical and Chemical Data Canadian Experiments

8.1.1 Methods

At the conclusion of mowing in 1967 the soil was sampled by taking 1 in. cores from 0 to 6 in. and 6 to 12 in. The plots sampled were pastures A, B, C, D, E and G for each of the three defoliation managements. Within each management samples from all A and B plots were pooled (i.e. pure grass), C and D were pooled (i.e. pure clover) and E and G (i.e. mixed grass clover). Plots F and H were omitted as the high seeding rates of orchardgrass had resulted in grass dominance in many of these plots. Five cores were taken from each plot and block so that 9 treatments (3 pastures x 3 managements) were each represented by a 40 core composite at each depth. These samples were air dried, mixed and passed through a 2 mm sieve. The following analyses were then made: a) pH with a 2:5 soil water ratio (Soil Reaction Committee of the International Society of Soil Science, 1930), b) organic carbon by the method of Walkley and Black (1934) and c) cation exchange:

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1 See Section 7. Literature Cited, for references in this appendix.
capacity by ammonium replacement and distillation with magnesium oxide. All determinations were made in duplicate.

Two soil profiles, located at either end of the experimental site were examined to delineate the extremes of soil conditions in the experimental area. Full field descriptions were made of these profiles and laboratory analysis of each horizon for the following were made: a) pH, b) organic matter, c) cation exchange capacity, d) moisture tension and e) mechanical analysis by the method of Bouyoucos (1962). From the profile sites 3 in. diameter cores were taken to determine bulk density and moisture tension relations by tension table drainage. The cores were 3 in. high and therefore the profiles were only sampled as surface and subsoil zones. Six cores were taken from each site and zone. Disturbed samples were also taken from the core zones, these were air dried, passed through a 2 mm sieve and drained at 0.3, 0.9, 4.0 and 15.0 bars on pressure plates as described by Richards (1948).

8.1.2 Results

As assessment of the soil environment of the experimental area is given by the analyses on the 40 core composite samples (Table 8.I). Each figure is presented as a mean of the two sampling depths as there were no significant differences between them. The profiles showed some trends with depth (Tables 8.II and 8.III). The moisture tension relationships for the two profile sites showed some gradient over the experimental area (Fig. 8.1.1).

From the soil data it appears that limits to plant growth due to differences between the soils of particular treatments were unlikely.
In all parameters except organic carbon the differences between pastures or defoliation managements were not significant (Table 8.1). The lower level of organic carbon in the grass clover pastures, though significant \((P < 0.01)\) represents only a small difference from a biological standpoint. The data from the profile sites (Fig. 8.1.1, Tables 8.II and 8.III) indicate that the slight gradient across the experimental site largely due to the lower silt content of Site 1 compared with Site 2.

Table 8.I  Analyses of 40 core soil composites; values are expressed on an oven dry soil basis and each is the mean of the 0-6 in. and 6-12 in. determinations.

<table>
<thead>
<tr>
<th>Pasture</th>
<th>O.grass</th>
<th>W.clover</th>
<th>grass/clover</th>
<th>S.E. ±</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>6.14</td>
<td>6.06</td>
<td>6.14</td>
<td>0.043</td>
</tr>
<tr>
<td>Organic carbon %</td>
<td>3.40</td>
<td>3.52</td>
<td>3.12</td>
<td>0.078</td>
</tr>
<tr>
<td>Cation exchange Capacity m.e. %</td>
<td>11.19</td>
<td>11.32</td>
<td>11.80</td>
<td>0.436</td>
</tr>
<tr>
<td>Management</td>
<td>3-1</td>
<td>9-1</td>
<td>9-3</td>
<td>S.E. ±</td>
</tr>
<tr>
<td>pH</td>
<td>6.08</td>
<td>6.14</td>
<td>6.13</td>
<td>0.043</td>
</tr>
<tr>
<td>Organic carbon %</td>
<td>3.42</td>
<td>3.42</td>
<td>3.21</td>
<td>0.078</td>
</tr>
<tr>
<td>Cation exchange Capacity m.e. %</td>
<td>11.32</td>
<td>11.73</td>
<td>11.26</td>
<td>0.436</td>
</tr>
</tbody>
</table>
Table 8.11 Field description of profile sites;  
+ = present, ++ = moderate, +++ = heavy, ++++ = very heavy. Colours are measured with the Mansel System. SABL = subangular blocky structure.

<table>
<thead>
<tr>
<th>Site 1</th>
<th>Horizon</th>
<th>Depth in.</th>
<th>Colour</th>
<th>Texture and Structure</th>
<th>pH</th>
<th>Roots</th>
<th>Concretions</th>
<th>Stones</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ap</td>
<td>0-8</td>
<td>10YR 3/2</td>
<td>S.Loam SABL</td>
<td>6.5</td>
<td>+++</td>
<td>-</td>
<td>++ 1/8&quot;</td>
</tr>
<tr>
<td></td>
<td>A/B</td>
<td>8-10</td>
<td>2.5Y 6/4</td>
<td>CS.Loam</td>
<td>6.5</td>
<td>-</td>
<td>+++ Fe</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>10-20</td>
<td>2.5Y 6/4</td>
<td>CS.Loam</td>
<td>6.5</td>
<td>-</td>
<td>++ Fe</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Water</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Site 2</th>
<th>Horizon</th>
<th>Depth in.</th>
<th>Colour</th>
<th>Texture and Structure</th>
<th>pH</th>
<th>Roots</th>
<th>Concretions</th>
<th>Stones</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ap1</td>
<td>0-4</td>
<td>10YR 2/2</td>
<td>S.Cl.Loam SABL</td>
<td>6.5</td>
<td>+++</td>
<td>-</td>
<td>++ 3/8&quot;</td>
</tr>
<tr>
<td></td>
<td>Ap2</td>
<td>4-10</td>
<td>10YR 2/2</td>
<td>S.Cl.Loam SABL</td>
<td>6.5</td>
<td>++</td>
<td>-</td>
<td>++ 1/4&quot;</td>
</tr>
<tr>
<td></td>
<td>A/B</td>
<td>10-14</td>
<td>10YR 5/4</td>
<td>S.Loam</td>
<td>6.5</td>
<td>-</td>
<td>+ Fe</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>14-23</td>
<td>10YR 6/6</td>
<td>S.Loam</td>
<td>6.5</td>
<td>-</td>
<td>++</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Water</td>
<td>23</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
### Table 8.11
Laboratory analyses for profile sites, values are expressed on an oven dry soil basis.

#### Site 1

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Organic Carbon %</th>
<th>Cation Ex. Capacity m.e. %</th>
<th>pH</th>
<th>Available water</th>
<th>Mechanical Analysis</th>
<th>Bulk Density g/cc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ap</td>
<td>2.339</td>
<td>10.415</td>
<td>6.43</td>
<td>7.066</td>
<td>76.15 14.83 9.02</td>
<td>1.239</td>
</tr>
<tr>
<td>A/B</td>
<td>0.412</td>
<td>1.901</td>
<td>6.35</td>
<td>1.535</td>
<td>93.01 5.08 1.27</td>
<td>-</td>
</tr>
<tr>
<td>B</td>
<td>0.253</td>
<td>1.942</td>
<td>6.27</td>
<td>1.569</td>
<td>96.19 2.54 1.27</td>
<td>1.428</td>
</tr>
</tbody>
</table>

#### Site 2

<table>
<thead>
<tr>
<th>Horizon</th>
<th>Organic Carbon %</th>
<th>Cation Ex. Capacity m.e. %</th>
<th>pH</th>
<th>Available water</th>
<th>Mechanical Analysis</th>
<th>Bulk Density g/cc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ap1</td>
<td>3.649</td>
<td>12.893</td>
<td>6.05</td>
<td>18.003</td>
<td>62.90 27.99 9.11</td>
<td>-</td>
</tr>
<tr>
<td>Ap2</td>
<td>3.787</td>
<td>12.872</td>
<td>6.10</td>
<td>11.209</td>
<td>68.78 20.16 11.06 1.137</td>
<td></td>
</tr>
<tr>
<td>A/B</td>
<td>1.082</td>
<td>5.448</td>
<td>5.95</td>
<td>4.369</td>
<td>80.22 13.40 6.38</td>
<td>-</td>
</tr>
<tr>
<td>B</td>
<td>0.427</td>
<td>2.371</td>
<td>6.00</td>
<td>2.332</td>
<td>88.60 7.60 3.80</td>
<td>1.418</td>
</tr>
</tbody>
</table>

1 Moisture content between 0.333 and 15.0 - bars.
2 U.S. size fractions.

#### 8.2 Glossary of Major Terms

**Defoliation:** Removal of herbage from a forage stand; clipping and grazing are particular forms of defoliation relating to herbage removal by mechanical and animal means respectively.

**Dry matter yield (.... production):** Aerial plant biomass incorporated into the herbage of a forage stand of unit area in a specific time period.

**Forage stand (.... sward):** A community of herbage plants grown or utilized to provide food for animal consumption.
Fig. 8.1.1 Moisture tension relationships for surface and subsoils in the two profile sites. Points are means of three replicates, the lines have been fitted by hand.
Frequency of defoliation: The number of occasions on which defoliation takes place in a specific time period.

Gross photosynthesis: Synthesis of carbohydrate from carbon dioxide and water using light energy.

Herbage: Above ground plant material produced by plants with one or more stems which die back each year; as distinct from shrubs and trees. The term refers to all above ground plant material; leaf, stem, seed and associated organs.

Intensity of defoliation: The degree of removal of herbage from a forage stand. Often this is indicative of the height above the ground at which defoliation has taken place.

Leaf area index (LAI): The ratio of the leaf area of a community to the area of land associated with that community.

Light energy: Electromagnetic radiation between 400 and 700 nm.

Net assimilation rate: Rate of increase in aerial plant dry weight in relation to unit leaf area. In this thesis rate of increase in dry weight has been replaced by rate of net carbon dioxide assimilation.

Net photosynthesis: Gross photosynthesis less the quantity of organic compounds respired by the photosynthetic organs during the time of synthesis; as measured by the net carbon dioxide assimilation of the aerial plant parts.

Pasture stand (.... sward): Synonymous with forage stand; used mainly in the Australian section of the thesis.