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## Photosynthesis and solar energy conversion

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The primary objectives have been to evaluate for different climatic conditions the role played by solar radiation in determining the accumulation of dry matter by terrestrial species and the manner in which the resulting photosynthetic products are utilized for the physiological and metabolic processes concerned with growth and development.

The interacting effects of different levels of radiation and temperature on the components of growth of whole plants have been examined for a range of species from both tropical and temperate environments. These studies have been extended to include the interrelationships of density and the leaf area index on the productivity of populations of selected species. In some of these investigations the concepts of growth analysis have been combined with techniques which now permit the CO<sub>2</sub> fluxes within the canopy to be continuously recorded over long periods and so allow the diurnal changes in the levels of photosynthesis and respiration in the field to be directly assessed. This approach, coupled with others where similar measurements are made in a closed system, has provided much new information on the balance between gross and net photosynthetic activity.

Differences in photosynthetic potential between species have been further interpreted in terms of (i) the pattern of light interception by canopies of differing structure, (ii) the component processes of photosynthesis at varying stages of development and (iii) the factors which are involved in the distribution and use of assimilates within the plant or population.

### 1. INTRODUCTION

At the first General Assembly it was resolved that of the nine working groups to be set up, one would consider a broad programme concerned with the *Productivity of Terrestrial Communities* (P.T.) and the other *Production Processes* (P.P.) relating to the primary productivity of terrestrial communities. It was concluded that the two most crucial aspects of Production Processes were (i) *Photosynthetic Activity and Solar Energy Conversion* and (ii) the *Biological Fixation of Nitrogen* and its circulation in living matter. Because of the diversity and complexity of the interrelationships it was decided that the planning of the two programmes (P.P.-P and P.P.-N) should be undertaken by separate sub-groups.

In the following year under the auspices of U.N.E.S.C.O. a symposium was held at Copenhagen on *Functioning of terrestrial ecosystems at the primary production level* 'where the accent should be placed more on methods for solving the problems of the functioning, not of isolated living beings, but of the ecosystem as a basic unit of modern ecology'. During the discussion of how some of these objectives could best be met it was emphasized that the programme of the P.T. Sectional Committee with its integrated studies of primary and secondary production would inevitably overlap with aspects relating to the functioning of the photosynthetic system, but that an appraisal of the consequences of secondary production would largely be within the framework of the P.T. programme.

It was concluded that the starting points for comparative studies of photosynthetic potential

should be best concerned with relatively simple plant communities rather than complex ecosystems. In such investigations the base lines would be (i) the quantitative responses of either individuals or populations to solar radiation and other climatic factors of importance in different regions; (ii) the distribution of the radiation intercepted by canopies of different age, size and structure, and the characteristics of the patterns of photosynthetic response; (iii) the efficiency with which the energy reaching the green tissues of different species is utilized for the production of those assimilatory products on which growth and development are dependent.

From the outset it was recognized that when Phase II was initiated in 1967 it would be neither feasible nor practicable for all aspects of the programme to be undertaken by each participating country. It was also apparent that while some aspects would require complex apparatus and special laboratory facilities, for others the demands would be relatively modest. Against this background, in 1966 the United Kingdom put forward a cooperative scheme for Level I experiments in which the performances of either widely spaced plants or plant populations could be measured by standardized procedures and the relationships with solar radiation, temperature and other climatic variables evaluated by multiple regression analyses.

It was also apparent from the discussions at Copenhagen that since there is in the open a high degree of correlation between radiation and temperature there is a requirement for parallel experiments under controlled conditions. Moreover, important advances were being made in micro-meteorological methods for the evaluation in the field of the exchange of carbon dioxide between the biomass, the soil and the atmosphere during the day and night periods.

It is against this background that the British contribution in this field will be discussed.

## 2. CONCEPTS OF GROWTH ANALYSIS

Between 1919–1921, Blackman & Gregory at Imperial College and Briggs, Kidd & West at Cambridge were the first to consider how the assessment of plant productivity under field conditions could be put on logical and quantitative bases. There was a common emphasis that growth of an individual plant involves continuous accumulatory processes and that in consequence valid comparisons of performance between species or ecological conditions must rest on recording quantitatively the dynamic changes in the growth of whole plants and their component parts in terms of mass and the surface areas of green tissue. Since it was already well established for a wide range of herbs that the contents of nitrogen and inorganic constituents remain relatively unchanged at about 10–15% of the dry matter, it followed that the gain in dry mass of the whole plant is directly linked with the proportions of assimilatory products either synthesized into new tissues or utilized to supply energy for respiration and other metabolic processes. Thus the diurnal rate of gain in dry mass of the whole plant – the relative growth rate ( $G_m$ ) – is determined by the net efficiency of assimilation per unit of assimilatory surface – net assimilation rate ( $E_m$ ) – and the ratio of the total assimilatory surface to total plant mass, normally expressed as the leaf area ratio ( $L_p$ ). Extending this approach it was shown that this ratio ( $L_p$ ) is the product of the ratio of leaf mass to plant mass ( $\omega_1$ ) and the ratio of leaf area to leaf mass or specific leaf area ( $L_1$ ). Since then experience and time have established that the methodology of sequential sampling and the mathematical derivation of some components of growth have required modification, see Radford (1967), but the principles have not changed.

Subsequently Watson (1947) extended these concepts to include the growth components of

a population. Here the equivalent to the relative growth rate is the population growth rate ( $A_{gB}$ ) expressed as the average rate of change in biomass per unit area of ground surface in a stated interval. The leaf area ratio is replaced by the leaf area index ( $L$ ), which is the ratio of total leaf surface to ground surface and the definition of the net assimilation rate remains unchanged. In other words the population growth rate is dependent on  $L$  and  $E_m$ , which themselves interact.

### 3. THE GROWTH OF INDIVIDUAL PLANTS

#### (a) *Level I experiment: seasonal changes in the growth of selected species*

These procedures of growth analysis were chosen for the conduct of the Level I experiment since they required a minimum of experimental resources to record the essential changes in mass and leaf area of samples taken at intervals in the field. To eliminate site differences in the availability of water and mineral nutrients the plants were raised in boxes in a standardized system, while at the times of the initial samplings plants of a standard size in the early vegetative phase were selected. Lastly, it was recommended that at each participating centre some of the experiments would be undertaken with species known to grow in a wide range of environments, namely *Helianthus annuus* L., *Phaseolus vulgaris* L., and *Zea mays* L.

In the U.K. programme between 1965 and 1970 investigations with these three species were undertaken at Oxford and the Scottish Horticultural Research Institute, Invergowrie. It is proposed only to summarize the main findings since the results at Invergowrie have already been reported by Hegarty (1973) and those for *Z. mays* at Oxford by Voldeng & Blackman (1973*a*).

For the main components of growth, multiple regression on the environmental factors of solar radiation and temperature over nine experiments accounted for on average 63 % of the total variation, while one third of the regressions accounted for 70–88 %. It is therefore clear that the seasonal changes were largely determined by the interactions of solar radiation and temperature.

For each species the relative growth rate ( $G_m$ ) and net assimilation rate ( $E_m$ ) are positively correlated with both light and temperature. In contrast, the final leaf area ratio ( $L_{p,t}$ ) is negatively dependent on light, and its response to the mean diurnal temperature may be positive or negative or replaced in *Z. mays* by a combination of negative and positive effects of day and night temperature.

At both sites over three years the conditions were less favourable for the growth of *P. vulgaris*, particularly at Invergowrie. As an example, figure 1 shows that over the whole season of 1969 the values of the principal components of the growth of *H. annuus* are consistently higher than those of *P. vulgaris*. As a further indication of the goodness of fit of each regression, comparisons have been included of the observed and calculated weekly figures for each component. The close agreements are very evident.

With a grant from the Royal Society for the provision of meteorological equipment and assistance in the computation of the field data, the seasonal changes in these two species were also followed by weekly experiments over 10 months at the University of Sierra Leone. The results reported by Eze (1973) established for both species that  $G_m$  is directly linked with solar radiation and the mean diurnal temperature. But while radiation enhances assimilation the effect of temperature (range 22–26 °C) is positive for *H. annuus* and negative for *P. vulgaris*.

Neither light nor temperature significantly influenced the leaf area ratios. There was some suggestion that a high humidity which is associated with the rainy season was detrimental, but undoubtedly the seasonal patterns of the growth of both species were dominated by the great differences in the levels of incoming radiation.

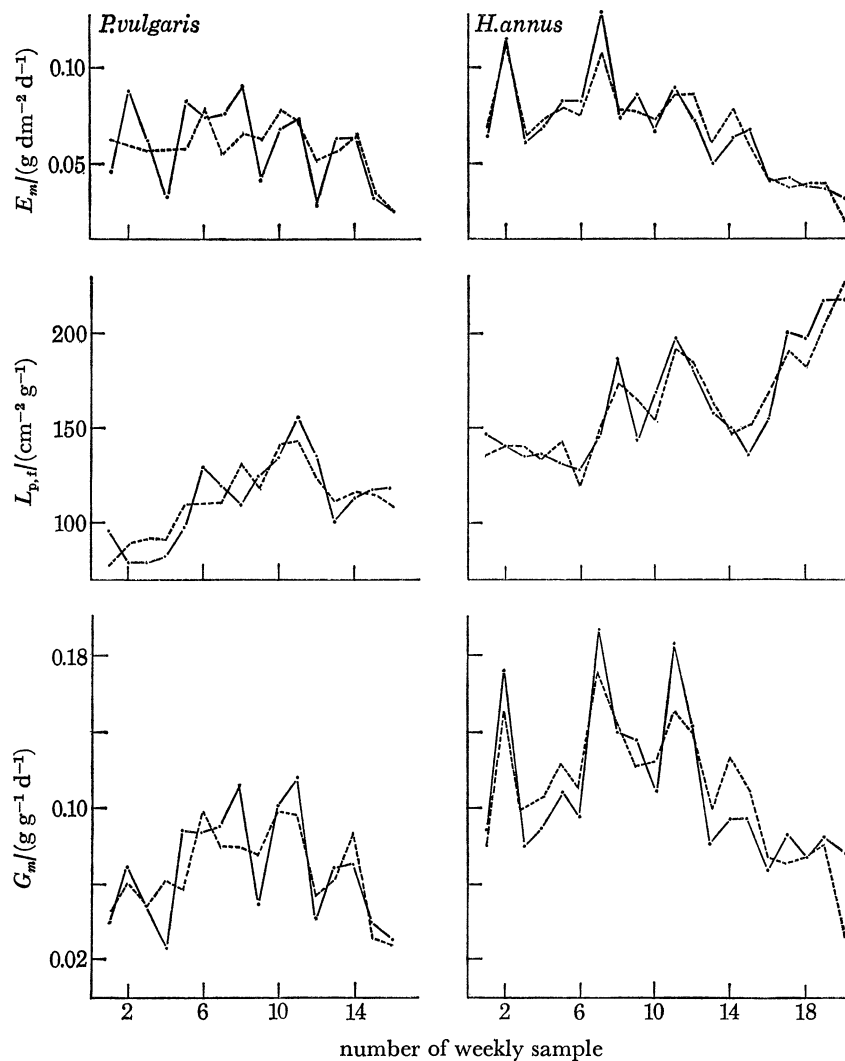


FIGURE 1. Comparisons between observed (—) and estimated (---) values of the weekly changes in the net assimilation rate ( $E_m$ ), the final leaf area ratio ( $L_{p,l}$ ) and the relative growth rate ( $G_m$ ) of *P. vulgaris* and *H. annuus* recorded in the summer of 1969 at Invergowrie. The estimated values of the individual components were based on the fitted regressions on the weekly changes in solar radiation and mean diurnal temperature.

(b) *Growth of conifers in the early vegetative phase*

The course of development in an unheated greenhouse of *Pinus radiata* D. Don, *P. contorta* Douglas ex Loudon and *Larix kaempferi* (Lamb.) Carrière (*L. leptolepis*) was followed in their second year by Sweet & Wareing (1968*a*). Between March and November, when the deciduous *L. kaempferi* shed all its leaves, it gained mass and height faster than the other two species because the higher levels of assimilation more than offset the lower leaf mass ratios. Whereas over the late summer the rate of growth of the two evergreen species and their leaf mass ratios

were of the same order, between October and February *P. radiata* continued to grow at a diminished rate, but faster than *P. contorta*.

An allied study was made by Sweet & Wareing (1968*b*) of the initial year of growth of four populations (provenances) of *P. contorta* from the west coast of America. The experiments were conducted either in the open or in a glasshouse heated to a minimum temperature of 13 °C and receiving supplementary illumination and a photoperiod of 18 h. In the first two experiments intact 'seedlings', raised in the greenhouse for 12 or 19 weeks, were subjected to a range of light intensities (0–358 W m<sup>-2</sup>) and a constant temperature (20 °C) and the photosynthetic activity measured by an infrared gas analyser in an open circuit system. All the provenances reached an asymptotic level of activity at the highest intensity when the maximum differences between provenances were *ca.* 20%. In contrast, the influence of light had an opposing effect on the leaf mass ratio ( $\omega_1$ ), since the ratio was least for the provenance with the highest photosynthetic activity. As a consequence other experiments conducted at the same time failed to produce any significant differences in  $G_m$ .

For plants grown in water culture in the open it was confirmed that there were no statistically significant differences between provenances in their growth rates.

(c) *The growth potential of Lolium populations*

Investigations at the Welsh Plant Breeding Station had indicated that the procedures of growth analysis could be profitably employed for the comparison and selection of forage grasses (Cooper 1966; Cooper & Tainton 1968). Based on these criteria the relative performances of some 18 populations of *Lolium perenne* L., 8 of *L. multiflorum* Lam. and two hybrid cultivars, collected from a wide variety of climatic and agronomic sources, were examined (Wilson & Cooper 1969*a*). In one series of experiments evenly spaced seedlings were planted in the autumn in a heated greenhouse without supplementary lighting and sampled in December. In a later series the plants were subjected for 9 h to a minimum daily illumination of  $27 \times 10^3$  lx, which experience had shown was not 'light limiting'. There were 4 series of experiments between January and March.

At the low light intensity mean differences in the growth of the two groups of populations were dependent on the component. The populations had similar values of  $G_m$  because the advantage of a greater  $E_m$  by *L. perenne* was offset by the larger leaf area ratio ( $L_p$ ) of *L. multiflorum*. Likewise the *L. perenne* grouping had a greater leaf mass ( $m_1$ ) and the leaves contained more chlorophyll, but the ratios of shoot to root in the two groups were the same. When the data were combined  $G_m$  was highly correlated only with  $E_m$ , and  $L_p$  with  $m_1$ . The remaining less significant correlations were (i) negative and positive linkages of  $L_p$  with the shoot to root ratio and  $E_m$  respectively and (ii) a positive dependence of  $m_1$  on the shoot to root ratio.

Changing to a high light intensity alters the pattern of correlation. The faster growth of the *L. multiflorum* populations can be ascribed to a greater  $L_p$  since the  $E_m$  values are now equal. At both intensities  $m_1$  and chlorophyll content of *L. perenne* are higher, but in contrast the shoot to root ratio is lower. Nevertheless within *L. perenne* the assimilation rate is the main characteristic determining the growth rate.

This initial survey established the existence of significant variation in the growth components of these *Lolium* populations, but it was also apparent that the sampling errors were high. Nevertheless, it was possible to select a number of contrasting populations for more intensive studies of the photosynthetic rate and its regulation by genetic and physiological mechanisms.

*(d) Climatic variation in populations of Dactylis glomerata*

MacColl & Cooper (1967) obtained evidence that within Europe there was considerable variation in the responses of regional populations of *Dactylis glomerata* L. to climatic factors. More recently the studies have been extended to cover changes induced by altering the length of the photoperiod and the levels of light and temperature on disparate natural populations from Norway and Portugal. Most of the experiments were conducted under controlled conditions on young single plants raised in pots.

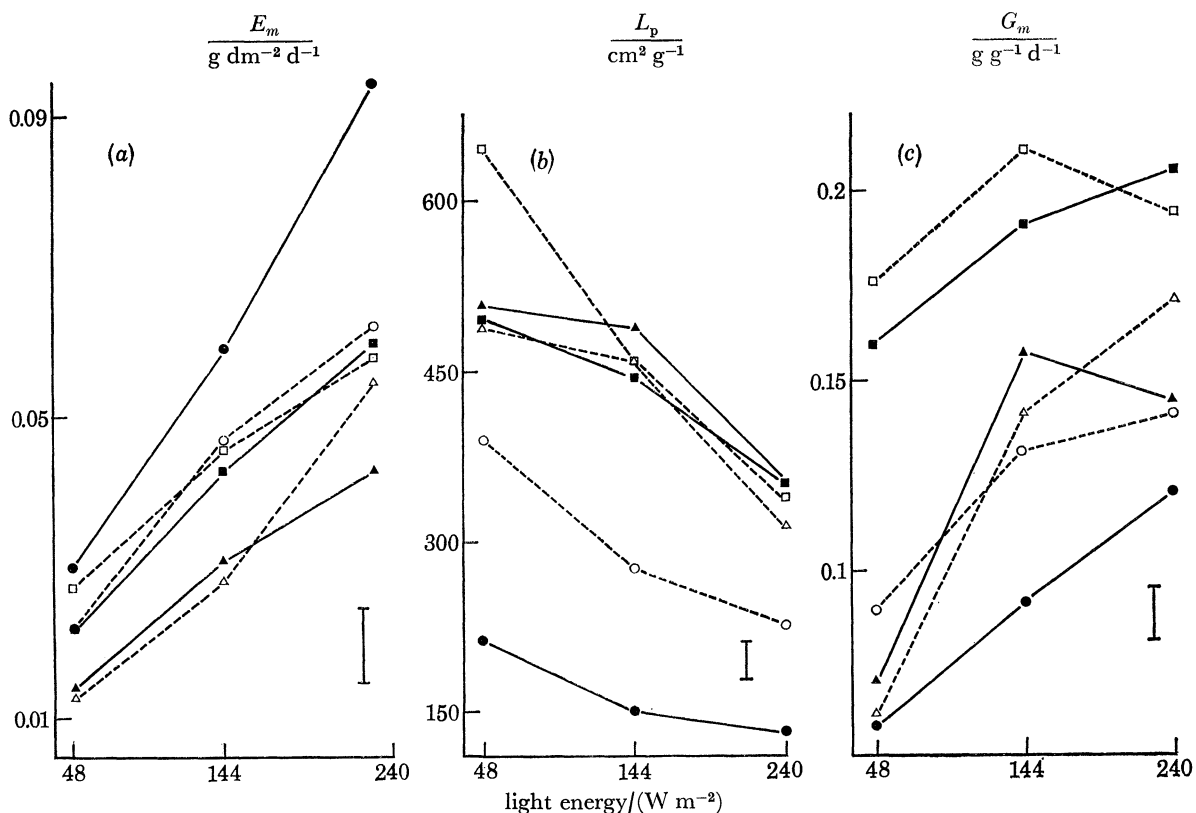


FIGURE 2. The interacting effects of variations in light (48, 144 and 240 W m<sup>-2</sup> for 8 h per day) and constant temperatures of 7 °C(○), 20 °C(□) and 30 °C(△) on (a) the net assimilation rate ( $E_m$ ), (b) the leaf area ratio ( $L_p$ ) and (c) the relative growth rate ( $G_m$ ) of individual plants from a Norwegian (—) and a Portuguese (---) population of *D. glomerata*. I, l.s.d.  $P = 0.05$ .

Initially Eagles & Østgård (1971) and Eagles (1971) examined the interrelationships between population, photoperiod and temperature, but later when a Norwegian and a Portuguese population with contrasting characteristics were compared (Eagles 1973) the design was extended to include three constant temperatures (7, 20 and 30 °C) and two photoperiods during which the plants received 48, 144 or 240 W m<sup>-2</sup> (wavelength interval 400–700 nm) for 8 h with or without supplementation by weak light (2 W m<sup>-2</sup>) for a further 8 h. Since a wide range of components was measured, in aggregate the volume of data collected was very large and perforce citations must be highly selective. Figure 2a establishes that for the short day there are major positive increases in  $E_m$  brought about by both light energy and temperature. It is ecologically significant that the highest rates result from a combination of the highest light

and the lowest temperature and that the superior photosynthetic activity of the Norwegian population is maximal at the lowest temperature. It should be added that under long days the rate for the Norwegian population reached a plateau under a combination of 20 °C and 144 W m<sup>-2</sup>, whereas for the Portuguese population 240 W m<sup>-2</sup> caused a further substantial rise.

The major effects of light and temperature on  $L_p$  are apparent in figure 2*b*. As the level of light is reduced there are progressive increases in the ratio, but on the other hand the ratio is positively linked with temperature. It is also apparent that the resultant balance between these opposing effects varies with the population. At 48 W m<sup>-2</sup> there are major differences between the two populations at temperatures of 7 and 20 °C and none at 30 °C, but at 240 W m<sup>-2</sup> a significantly greater value for the Portuguese population is only observed at the lowest temperature. For long days it was found that whereas at 7 °C the Portuguese population at each intensity had a lower ratio, the position at 30 °C, save for the lowest intensity, was reversed.

Inspection of figure 2*c* shows that for 48 and 144 W m<sup>-2</sup> all the increases in the growth rate are significant whereas at 240 W m<sup>-2</sup> the only significant gain is for the Norwegian population. Over both populations there is a sharp rise in the rate between 7 and 20 °C at each intensity, followed by a considerable decline at 30 °C. At 7 and 20 °C differences between the two populations are maximal at 48 and 144 W m<sup>-2</sup>, but the differences are not significant at the highest intensity.

When the populations were exposed to long days there were some differences in the response to light. For the Norwegian population maintained at 20 °C and both populations at 30 °C the growth rates were increased over the whole range of the light treatments.

(*e*) Responses of disparate species to light and temperature

Since in terrestrial environments radiation and air temperature are interrelated, it was evident that the interpretation of the Level I results – see §3*a* – would be enhanced if the independent regulation of radiation and temperature could be extended to high levels. Because in 1966 this need could not be met by available commercial equipment, the lighting systems of Sax Air control cabinets were redesigned to allow a maximum illumination of  $5.4 \times 10^4$  lx, and the ‘balance’ of fluorescent and tungsten lamps so adjusted that growth and development were normal. These procedures have been reported by Rajan, Betteridge & Blackman (1971).

Employing the modified cabinets plants of each of three species in the United Kingdom experiments, plus *Gossypium hirsutum* L., were subjected in the early vegetative phase to six constant air temperatures (10–35 °C) combined multifactorially with five levels of radiation (1.08 to  $5.4 \times 10^4$  lx), with a common photoperiod of 14 h. Routine measurements of lx were made with a Megatron meter but on occasion the spectral composition of the energy between 400 and 900 nm was recorded at  $4.32 \times 10^4$  lx and the integrated energy between these limits was *ca.* 90 W m<sup>-2</sup>. Rajan, Betteridge & Blackman (1973) concluded that the complex patterns of interacting factors could best be illustrated by three dimensional diagrams, but because of limitations of space the results have been further summarized. Table 1*a* shows that the differences in assimilation between the highest and lowest intensities range from 2.4 to 4.8 times according to the species. It is also evident that there are interactions between species, temperature and light. At  $1.08 \times 10^4$  lx the optimal temperature for *Phaseolus* and *Helianthus* is 15 °C and for *Gossypium* 35 °C while for *Zea* there is no change between 25 and 35 °C. When the illumination is raised the optima for *Phaseolus* and *Helianthus* are now 25 °C, but there is no corresponding shift for the other two species.



The dominant role of light in regulating  $L_p$  is very clear from table 1*b*. On average the reduction in light nearly doubles the ratio for each species. By comparison the effects of temperature are relatively small and most evident between 15 and 20 °C.

Since the relative growth rate is the resultant of the combined effects of light and temperature, the pattern of variation set out in table 1*c* can be interpreted in terms of the data presented in tables 1*a* and *b*. Considering first the higher level of radiation, at each temperature *Helianthus* grows fastest and *Phaseolus* makes the least growth because the advantages of much higher values of  $E_m$  in *Helianthus* outstrip the disadvantages of a somewhat smaller  $L_p$ . Similarly, the intermediate growth rates of *Zea* and *Gossypium* at 25 and 35 °C are largely determined by the levels of assimilation, but at 15 °C reductions in the ratio and assimilation rate both contribute to the depressions. It is also of interest that raising the temperature to 35 °C is inimical to *Phaseolus* but favourable to *Gossypium*. When illumination is reduced there are sharp falls in the growth rate because the depressions in  $E_m$  markedly outweigh the increases in  $L_p$ .

TABLE 1. SPECIFIC DIFFERENCES IN THE RESPONSES TO TEMPERATURE AND LIGHT  
(PHOTOPERIOD 14 h)

light/lx ...	...	$1.08 \times 10^4$			$5.4 \times 10^4$			l.s.d. ( $P = 0.05$ )
		15	25	35	15	25	35	
temperature/°C ...	...	(a) net assimilation rate/(g dm <sup>-2</sup> week <sup>-1</sup> )						
<i>Phaseolus</i>		0.37	0.26	0.19	0.57	0.76	0.68	0.03
<i>Zea</i>		0.16	0.40	0.38	1.23	1.55	1.58	0.04
<i>Helianthus</i>		0.48	0.40	0.37	1.97	2.10	1.97	0.04
<i>Gossypium</i>		0.23	0.27	0.34	0.55	1.11	1.48	0.02
		(b) leaf area ratio/(cm <sup>2</sup> g <sup>-1</sup> )						
<i>Phaseolus</i>		195	243	273	114	155	141	18
<i>Zea</i>		142	214	210	85	102	102	21
<i>Helianthus</i>		199	290	283	109	131	129	19
<i>Gossypium</i>		143	283	252	90	130	118	12
		(c) relative growth rate/(g g <sup>-1</sup> d <sup>-1</sup> )						
<i>Phaseolus</i>		0.10	0.13	0.07	0.09	0.16	0.13	0.01
<i>Zea</i>		0.03	0.13	0.12	0.16	0.23	0.23	0.01
<i>Helianthus</i>		0.14	0.17	0.16	0.24	0.27	0.27	0.01
<i>Gossypium</i>		0.04	0.11	0.12	0.07	0.19	0.19	0.01

Went (1944, 1945) in his original investigations of controlled environments concluded that for some species growth is superior when a constant temperature is replaced by appropriate variations in the day and night temperatures. Subsequently many like papers have been published, but the levels of light have been much below optimal. Therefore the existing programme on the four species has been extended (Rajan & Blackman 1975). The plants were subjected to medium and high intensities of 2.16 and  $4.32 \times 10^4$  lx while the temperature regimes consisted of 20 and 25 °C during the day and night temperatures of either 20, 15 and 10 °C or 25, 20 and 15 °C, respectively.

These results could be combined with those when plants received constant diurnal temperatures ranging from 10 to 25 °C (Rajan *et al.* 1973).

For these species none of the growth components are favoured by cool nights. Rather such reductions in night temperature retard growth to a variable degree according to the species. In

general, significant changes do not take place unless there is a fall at night of 10 °C and the reductions are most evident for the relative growth rates in mass and leaf area at the lower level of light. Indeed doubling the intensity removes or damps down these depressions.

When comparisons are made between changes in diurnal temperature *vis-à-vis* changes restricted to the night, it can be concluded that the day temperatures play a dominant role in regulating the growth processes which result in variations in the growth rates for plant weight and leaf area. There are also interactions with the level of radiation since the importance of the day temperature is accentuated at  $2.16 \times 10^4$  lx.

In concluding this section, the relative performances of *Helianthus* and *Zea* under conditions of high light and high temperature are of interest. Rajan *et al.* (1973) have already commented that the net assimilation rate of *Helianthus* achieved a maximum of  $2.1 \text{ g dm}^{-2} \text{ week}^{-1}$  which is the highest ever recorded for any plant and much greater than that for *Zea* – see table 1*a*. These specific differences are not in keeping with the suggestions of Hatch, Slack & Johnson (1967), that high rates of photosynthesis as in the tropical grasses, including *Zea*, are invariably associated with the  $C_4$  pathway of photosynthesis. This aspect will be further discussed in a later section.

#### 4. THE PRIMARY PRODUCTION OF PLANT POPULATIONS

##### (a) *Interrelationships between density and the productivity of Zea mays*

Following Watson's original investigations (1947) at Rothamsted, the principles of growth analysis were first applied in England to evaluate the roles played by the site, the soil and the season in determining the productive capacity and genotypic variation within arable crops. Blackman (1962), discussing recent investigations of the interrelationships between the population growth rate, the leaf area index and light interception, commented that the  $_{AGB}$  is dependent not only on the amount of light intercepted but also on the pattern of light gradients within the canopies of different species. Under conditions where the individual leaves are likely to approach light saturation in full daylight then, when  $L$  is high, an open canopy, associated with a low light gradient, will allow the light energy to be spread over a larger photosynthetic area and so decrease the average amount of radiation received per leaf but increase the efficiency of conversion. It was further reported at the Unesco symposium in 1965 that populations with either vertical leaves or narrow leaves widely dispersed on erect stems had a high potential for dry matter production. Against this background, Eddowes at Harper Adams Agricultural College and Blackman and others at Oxford initiated studies of the influence of density on the growth and development of *Z. mays* with its upright habit.

Eddowes (1969*a, c*) employing a range of 4.6–23 plants per square metre found that dry matter accumulation was maximal at the highest density when the final yield reached 9–13 t ha<sup>-1</sup>. Sequential sampling between July and September allowed  $_{AGB}$  together, with  $L$  and  $E_m$  to be determined. In the two years recorded the maximal values of  $_{AGB}$  were 21 and 18 g m<sup>-2</sup> d<sup>-1</sup> while at the time  $L$  was *ca.* 4. In one year when  $E_m$  was evaluated between mid July and the end of August the rate fell with time and density. Additional nitrogen enhanced  $_{AGB}$  most at the highest density.

In the field investigations at Oxford, Voldeng (1971) and Voldeng & Blackman (1973*b*, 1974, 1975) followed seasonal changes of production over three years, and confirmed that the final shoot yield is optimal at the highest density when it ranged from 14.0 to 17.4 t ha<sup>-1</sup>.

In 1965 and 1966 from June onwards sampling was at weekly or fortnightly intervals. At each density, after conversion to logarithmic scales of the leaf area or plant mass, the dependence on days from emergence was determined by regression analysis up to the time when there was no further increase in leaf area. Analysis of variance of the pooled regressions in each experiment established that the percentage of the 'within density' sums of squares due to regression ranged from 98.2 to 99.6%. Thus it was feasible to calculate the main components of growth at 5 to 10 day intervals up to the cessation of leaf expansion.

In 1965 between 33 and 90 days from emergence over the three populations (7.2, 14.4 and 21.5 plants per square metre) there was a close inverse curvilinear relation between  $E_m$  and  $L$  when  $E_m$  fell from nearly 8 to 2 g m<sup>-2</sup> d<sup>-1</sup> and  $L$  ranged from initially below 0.5 to finally above 11. This relation again held in 1966 up to about 80 days, when the differences in  $L$ , this time over six densities (3.6–32.3 plants per square metre), were of the same order as in 1965. But the decline in  $E_m$  was somewhat steeper (12 to 2 g m<sup>-2</sup> d<sup>-1</sup>). Turning to the population growth rates, in 1965 there were peaks of 18, 22 and 24 g m<sup>-2</sup> d<sup>-1</sup> at 80–90 days, when the  $L$  values were 4.7, 7.8 and 10.7 at the three densities. In the following year the maximal  $_{AGB}$  values were attained at about 70–75 days from emergence and at the lowest middle and top densities the rates were 15.5, 22.7 and 24.6 m<sup>-2</sup> d<sup>-1</sup> with equivalent  $L$  values of 2.8, 5.7 and 10.7. During this period the levels of light reaching the soil surface were recorded by selenium cells and the order of interception (42–90%) reflected the variations in  $L$  between densities.

Following pollination one of the most striking features, which was also observed by Eddowes (1969*b*), was that the optimal density for ear development was quite different from that of the whole shoot. Since the two hybrids employed matured too late to produce ripe grain, further experiments were undertaken employing eight genotypes with a wide range of maturity and the comparisons involved 15 densities from 5 to 30 plants per square metre. Because the variance for shoot mass was density-dependent the mathematical treatment was complex, but the general conclusion was that for two genotypes plant mass was little affected by density, but for the remaining six there were variable incremental gains in mass up to the highest density. On the other hand the optimum densities for grain production were widely disparate and for the three most productive genotypes ranged from 6.2 to 10.8 plants per square metre.

Examining the interactions between genotype and density on the components of grain production within the ear, it was observed that between the lowest and highest densities in all genotypes the number of rows was unaffected, but the reduction in grains per row ranged from 0 to 80% and the mass per grain from 8 to 40% depending on the genotype.

Moss (1962) has recorded reduction in the photosynthetic activity of individual leaves if pollination is prevented by placing bags over the ears before the silks are extruded, and postulated that at high densities the supply of photosynthates is restricted by the absence of adequate physiological sinks. When this 'bagging' was repeated in the field at low and high densities at Oxford it was found, particularly at the high density, that the heights, masses and leaf areas were the same as those of the fertile plants, but that the husks and stems were markedly heavier. This suggests that at a high density it is the distribution rather than the supply of carbon substrates which is limiting, since in other experiments progressive thinning in July resulted in greater grain production per plant in the residual populations.

Finally by combining the present investigations with those reported in previous sections, it can be concluded that up to the time when leaf expansion is completed, radiation and temperature are the principal environmental factors which operate in determining the accumulation of

dry matter at each density through their effects on the total leaf surface, the level of light interception and the efficiency of energy conversion. There is cumulative evidence that changes in the depth and structure of the fully green canopy must also be considered. During the phase of the rapid extension of the stem internodes and the consequent separation of the terminal whorl of leaves, the changing pattern of light interception results in an over-all rise in  $E_m$ .

(b) *Relationships between canopy structure and crop growth rate ( $A_{gB}$ ) in forage grasses*

The bearing of variation in canopy structure or in the photosynthetic activity of individual leaves on the  $A_{gB}$  have been examined by Sheehy & Cooper (1973) using six forage grass varieties of contrasting growth habit. Following an initial cutting back of the foliage and re-growth to complete light interception of populations raised in boxes and out of doors, the growth rates in June ranged from 21.9 g m<sup>-2</sup> d<sup>-1</sup> for *Phleum pratense* L. (S. 352) to 43.6 g m<sup>-2</sup> d<sup>-1</sup> for *Festuca arundinacea* Schreb. (S. 170), corresponding to a 2.6–7.8 % conversion of incoming light energy into chemical energy. These differences were closely correlated with canopy structure, as measured by the angular distribution of the leaves, the gradient of light interception, or the ‘critical’  $L$ , i.e. the value at which 95 % of the incoming visible radiation is intercepted. When these species and varieties were examined at 20 °C and intensities up to 185 W m<sup>-2</sup> there were no significant differences between these varieties in the maximum rates of photosynthesis of the individual leaves. The measured crop growth rates are in reasonable agreement with those predicted from the models of Monteith (1965), de Wit (1965) and Verhagen, Wilson & Britten (1963).

Genetic variation in canopy structure in the ryegrasses (*Lolium perenne* and *L. multiflorum*) and its effects on  $A_{gB}$  have also been studied. An initial survey of light profiles, leaf arrangement and  $A_{gB}$  in varieties differing in growth habit, showed that the more erect forms had a greater ‘critical’  $L$  and in consequence a higher maximum  $A_{gB}$  than the more prostrate varieties when comparisons were made at complete light interception (Rhodes 1968, 1969*a*). More detailed studies (Rhodes 1971*a*) on the development of leaf area and light interception in one erect (Ba 6280) and one prostrate (S. 23) variety of *L. perenne* showed that 14 days after cutting back the foliage the more prostrate variety, with an interception of 63 %, had a higher  $A_{gB}$  (16.1 g m<sup>-2</sup> d<sup>-1</sup>) than the erect variety (11.7 g m<sup>-2</sup> d<sup>-1</sup>) with an interception of only 42 %. After 28 days, however, when for both canopies interception was complete, the erect form with a critical  $L$  of 10 had a considerably higher crop growth rate than the prostrate variety with a critical  $L$  of 7.

The plant characteristics which determine canopy structure, such as leaf length, leaf rigidity and tiller angle, proved to be under genetic control, and contrasting selection lines could readily be developed, even from within a single variety (Rhodes 1969*b*, 1971*b*, 1972). In these selection lines, as in the varietal comparisons, the most productive material under infrequent cutting, i.e. when allowed to reach complete interception, had a tall canopy characterized by a low light gradient and a high critical  $L$ . On the other hand, under a frequent cutting regime short-leaved, prostrate plants, which attain complete light interception earlier, were more productive (Rhodes 1973).

(c) *Environmental factors and the productivity of barley*

At the University of Nottingham, Monteith and his co-workers have combined for the first time micro-meteorological techniques and the procedures of growth analysis in a detailed study of the growth and production of a population of barley from the early vegetative phase to

maturity. The basic approaches of experimentation and methodology have been given in two papers. In the first, Biscoe *et al.* (1975*a*) described the instrumentation with its attendant sensitivity, accuracy and reliability for continuous recording, together with the advantages of a multipoint profile combined with the Bowen ratio and aerodynamic methods for calculating the exchanges of CO<sub>2</sub> and water vapour between the population and the atmosphere. In the second paper by Gregson & Biscoe (1975) the requirements for computer analysis are discussed in terms of the methods of data capture, the checking of the paper tape input from a data-logger and the need for a simple standard programme with accessibility to the averages on an hourly basis of the selected criteria.

Biscoe, Scott & Monteith (1975) have evaluated the physical and physiological factors which operate in determining the accumulation of dry matter and the net assimilation of CO<sub>2</sub> in relation to (i) the importance of the atmosphere and soil as sources of CO<sub>2</sub>; (ii) the diurnal course of photosynthesis by the canopy and its relationships to changing environmental factors; (iii) seasonal variations in the balance of photosynthesis and respiration in the populations; (iv) the comparability of estimates of carbon accumulation derived either by integrating the net diurnal uptakes of CO<sub>2</sub> by the crop or by recording the gains in dry matter by sequential sampling, and (v) the progression of photosynthetic efficiency.

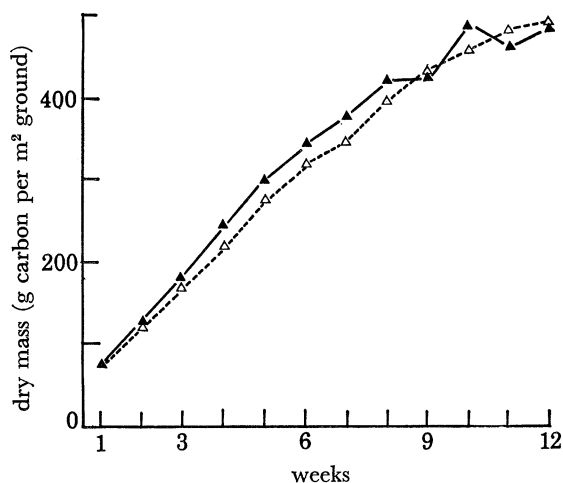


FIGURE 3. Comparison of the accumulation of carbon by a barley crop as measured by growth analysis (▲) or calculated from CO<sub>2</sub> fluxes (△).

By direct measurement of the CO<sub>2</sub> released by the soil surface and the amount of root respiration, interpolated from temporal changes in the activity and mass of the roots, it was concluded that the roots were responsible for half the output of CO<sub>2</sub>, which is recycled within the system. On the other hand, decomposition of the organic matter by soil organisms provides an additional supply of CO<sub>2</sub> for photosynthesis.

In following the diurnal changes in net CO<sub>2</sub> fixation it was found that there were advantages in using the Bowen ratio method during the day and the aerodynamic method at night.

By selecting adjacent days with marked fluctuations in solar radiation it was demonstrated that in mid-July, when  $L$  was *ca.* 5.8, the net CO<sub>2</sub> fixation exhibited a linear response up to 500 W m<sup>-2</sup>. Similar diurnal records were made weekly between 28 June and 26 July. In the first week the photosynthetic rate was still rising at 600 W m<sup>-2</sup>. But 3 weeks later there was seemingly light saturation at 400 W m<sup>-2</sup> and the maximum rate was halved. In the final week

when much of the foliage was yellow the maximum rate recorded was at  $200 \text{ W m}^{-2}$  and was only 15% of that observed in the first week. Measurements of the water potential of the flag leaf suggested that below  $-3 \text{ MPa}$  ( $-30 \text{ bars}$ ) photosynthesis was depressed.

Given that the 'gross' photosynthesis is compounded of the daily net uptake of  $\text{CO}_2$  from the atmosphere and the 'dark' respiration during the day, Biscoe *et al.* (1975) concluded that this respiration could be estimated from the known respiration at night adjusted for the diurnal differences in tissue temperature and an assumed common  $Q_{10}$  of 2. On these bases the ratios of the total respiration to gross photosynthesis were calculated for the 11 weekly intervals. In the initial phase of rapid growth the loss of assimilates due to respiration was some 40%, but reached nearly 90% when much of the tissue was no longer green.

The onset of senescence is also reflected in the changing efficiency of the conversion of light energy into chemical energy. In terms of gross photosynthesis the efficiency for the first 6 weeks was some 5.5%, reached a peak after ear emergence and then fell progressively. A maximum of 10% was recorded on some dull days.

Sequential sampling included the determination of the carbon content of the dry matter, so that the accumulation of carbon over the whole season could be directly compared with that evaluated from the  $\text{CO}_2$  fluxes. Figure 3 reveals a remarkably good agreement which reinforces both the validity of the procedures and the basic assumptions that the turbulent transfer coefficients of carbon dioxide, water vapour and heat are equal.

Although these studies provided much information on the seasonal pattern of net photosynthesis by the crop it was clear that further analysis was required to follow the internal balance of photosynthetic and respiratory activities within the component parts at different stages of development. To achieve these objectives Biscoe *et al.* (1975*b*) constructed, for use in the field, a sensitive infrared gas analyser with a high flow rate and a temperature controlled chamber made of polypropylene film which is impermeable to  $\text{CO}_2$ .

From records of (i) solar radiation at different levels within the crop; (ii) the measured photosynthetic responses to light of the various organs contained within the chamber, and (iii) the distribution of active assimilatory tissues within the canopy the photosynthesis of the whole canopy could be estimated. Comparisons of these estimates with micrometeorological records of  $\text{CO}_2$  exchange by using the aerodynamic methods indicated that at low rates of photosynthesis the leaf chamber estimates were substantially higher than those of the micrometeorological records, but above a rate of about  $10 \text{ mg CO}_2 \text{ dm}^{-2} \text{ h}^{-1}$  the discrepancy was comparatively small and above  $30 \text{ mg dm}^{-2} \text{ h}^{-1}$  some of the chamber estimates were smaller than those of the aerodynamic fluxes.

These methods were also used to assess the course of net photosynthesis of each organ and its contribution to canopy photosynthesis and the filling of the grain. The time course of net carbon production after anthesis was determined mainly by the gradual decline in photosynthetic activity and area of its constituent organs. The ear contributed little to the pool of photosynthates, except for a short period during mid-July, but an outstanding contribution was made by the flag leaf sheath, as a result of its longevity, its favourable exposure to light and its sustained level of high photosynthetic activity. During the ripening period between anthesis and the end of July 1972, however, the estimated total dry mass assimilated amounted to about  $300 \text{ g m}^{-2}$  while the measured dry mass of grain reached  $442 \text{ g m}^{-2}$ . Such differences suggest that the grain is partly filled by previously formed assimilates translocated from other parts of the plant, a suggestion strongly supported by a corresponding decrease in stem mass. The contribution to

the grain from different organs thus appeared to be leaf number 7, 6%; leaf number 8, 19%; flag leaf lamina, 9%; flag leaf sheath, 25%; ear, 13%; translocated from elsewhere, 28%.

These estimates of translocation to the grain of about 30% of its dry mass were obtained in 1972, a comparatively favourable year. In 1970, a dry year, corresponding estimates suggested that up to 70% of the dry matter in the grain might have been translocated from other parts. In this variety of barley, Proctor, a stable mean grain mass appears to be maintained by translocating a variable amount of assimilate from the stem to the grain (Gallagher, Biscoe & Scott 1975).

(d)  $CO_2$  exchange in grassland swards

Eckardt (1970) has discussed the comparative problems involved in interpreting the diurnal changes in the growth of plant populations when they are raised in the open or in a relatively large closed system, and emphasized the need for minimal disturbance of the environmental conditions within the enclosure.

In studies of the seasonal growth of *L. perenne* swards in the field, Leafe (1972) has developed an enclosed system where a small internal air pressure excludes the entry of  $CO_2$  arising from soil and root respiration and allows the course of net photosynthesis and dark respiration of the shoot during the day to be recorded by an infrared gas analyser.

For a ryegrass sward, complete light interception during the summer was achieved about 20 days after an initial cutting. At the peak period of growth, maximum net photosynthetic rates of up to  $1.4 \text{ mg } CO_2 \text{ min}^{-1} \text{ dm}^{-2}$  ground surface were achieved with light saturation at about  $700 \text{ W m}^{-2}$  of total radiation, but growth rates and photosynthetic activity of the canopy declined after 40–50 days. The total crop assimilation, estimated as net photosynthesis less dark respiration of the shoot, was greater than the increase in dry matter, but it has already been noted that this estimate does not take account of root respiration.

A rough carbon balance in the field suggests that of a net photosynthesis of about  $25 \text{ g m}^{-2} \text{ d}^{-1}$ , more than 50% was utilized in dark respiration and root respiration. The decline in crop growth rate of the older swards appeared to be due to a decline in net photosynthesis rather than an increase in dark respiration.

The same enclosure technique has been employed to study the carbon budget of simulated swards of *L. perenne* grown in a controlled environment ( $85 \text{ W m}^{-2}$  for 16 h:  $22.5^\circ \text{C}$  day and  $12.5^\circ \text{C}$  night) for about 12 weeks from germination (Robson 1973*a, b*). The rate of dry matter increase was exponential for the first 6 weeks, by which time complete light interception had been achieved when *L* was 10. A steady  $A_{gB}$  of about  $20 \text{ g m}^{-2} \text{ d}^{-1}$  was then maintained for a further 6 weeks. By then *L* had increased to 23–24, resulting in a final yield of  $10 \text{ t ha}^{-1}$  dry matter. During the early stages of growth, canopy photosynthesis increased with *L*, but after complete light interception it remained steady for several weeks, with a maximum net photosynthetic rate of  $24 \text{ mg } CO_2 \text{ dm}^{-2} \text{ h}^{-1}$  which was in accord with that found in the field under similar light intensities. Although the individual leaves became light-saturated at about  $130 \text{ W m}^{-2}$ , the photosynthetic rate for the whole canopy continued to increase up to almost  $400 \text{ W m}^{-2}$ . After about 10–12 weeks from germination, crop photosynthesis began to decline, and this decline was associated with a marked reduction in the maximal photosynthetic rates of the individual leaves. Dark respiration increased with dry mass, though not proportionally, and losses due to 'maintenance' respiration and to 'growth' respiration appeared to be about equal.

The estimates of total assimilation by the canopy based on gas analysis records agreed well with those of measured dry matter production up to the 8th week, but thereafter the estimates derived from the gas analysis records were lower than the measured dry matter increase.

In these grass swards, it appears that 30–50 % of the daily assimilates is needed to meet the over-all requirements of transport and respiration, and that of the remainder only about half is incorporated into tissues which can be harvested by cutting or grazing.

#### 5. SOME ASPECTS OF CO<sub>2</sub> EXCHANGE IN INDIVIDUAL LEAVES

The findings of Hatch *et al.* (1967) that in certain tropical grasses, including *Z. mays*, the high photosynthetic rates resulting from high levels of temperature and radiation are associated with the formation of C<sub>4</sub> compounds as the first products of photosynthesis led to further examinations in other species of the role of the traditional Calvin cycle which involves the initial formation of C<sub>3</sub> compounds.

The light and temperature responses in the photosynthetic activity of individual leaves of a range of grasses have been examined in the programmes of the Grassland Research Institute and the Welsh Plant Breeding Station while, in addition, some of the biochemical implications have been studied at Aberystwyth.

##### (a) *Interacting effects of light and temperature*

In the temperate grasses (*L. perenne* and *L. multiflorum*, *D. glomerata* and *F. arundinacea*), as in many other C<sub>3</sub> species, net photosynthesis reached light saturation at about 100–150 W m<sup>-2</sup>, with maximum values of about 20–30 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup> (Treharne & Eagles 1970; Charles-Edwards, Charles-Edwards & Cooper 1971; Woledge 1971). The photosynthetic activity of the leaf, including its stomatal and mesophyll resistances, remains relatively constant for 1–2 weeks after complete expansion, but then declines steadily (Woledge 1971; Treharne & Eagles 1970). In the C<sub>4</sub> grass *Cenchrus ciliaris*, however, photosynthetic rates of over 50 mg CO<sub>2</sub> dm<sup>-2</sup> h<sup>-1</sup> have been obtained, with no indication of light saturation at over 200 W m<sup>-2</sup> (Treharne, Pritchard & Cooper 1971).

These temperate grasses also show similar temperature responses for net photosynthesis to those of many other C<sub>3</sub> species, with a broad optimum about 20–25 °C and rapid declines either towards 5 or 35 °C (Woledge & Jewiss 1969; Charles-Edwards *et al.* 1971). This contrasts with the optimum temperature of 35–40 °C recorded for the C<sub>4</sub> species *Cenchrus ciliaris* L. (Treharne, Pritchard & Cooper 1971).

Responses to light and temperature are markedly affected by the environment in which the leaf develops. The influence of the conditions during leaf expansion on the photosynthetic activity of ten temperate grass varieties raised in combinations of 25 °C and 72 W m<sup>-2</sup>, 25 °C and 180 W m<sup>-2</sup>, and 15 °C and 72 W m<sup>-2</sup> has been studied by Charles-Edwards *et al.* (1971). In all this material, growing plants at the higher temperature increased the optimum temperature for photosynthesis from a mean of 16.9 to one of 19.7 °C. When the plants were grown at the lower light intensity or at the higher temperature the maximum CO<sub>2</sub> exchange rate at light saturation was decreased. In general, these maximum CO<sub>2</sub> exchange rates were correlated with the leaf resistances ( $r_a + r_1$ ) derived from transpiration measurements, suggesting that differences in stomatal resistances were involved.



Similarly, Woledge (1972, 1973) found that in *Lolium*, leaves which developed in lower light intensities had lower maximum photosynthetic rates and so did leaves from plants grown at high densities in the field, and subjected to intense mutual shading.

The comparative studies on the growth and assimilation of Norwegian and Portuguese populations of *D. glomerata* (see §3*d*) have been extended to include measurements of CO<sub>2</sub> exchange and of the activity of several photosynthetic enzyme systems in material grown under different light and temperature regimes (Eagles & Treharne 1969; Treharne & Eagles 1970). Changing the irradiance from 48 to 240 W m<sup>-2</sup> during growth had little effect on the maximum photosynthetic rate which could be achieved in the Norwegian material, but markedly increased maximum photosynthetic activity in the Portuguese population.

Similar population differences in the effects of irradiance on the CO<sub>2</sub> assimilated were reflected in the activity of the main carboxylating enzyme, RUDPcase, but not by the Hill reaction or by photophosphorylation. When the two populations during growth were subjected to 5, 15 and 25 °C and the photosynthetic activities expressed on a unit area basis there were no differences in the maximum rate when grown at 25 °C, but when grown at the lower temperatures, and in particular at 5 °C, the assimilation of the Norwegian population was greatly enhanced while only a slight increase was observed in the Portuguese population. These differences were paralleled by those in transpiration and RUDPcase activity suggesting that stomatal and biochemical resistances are involved.

In further biochemical studies (Treharne 1972), populations of *Lolium* known to differ in maximum photosynthetic rate at light saturation were examined for variation in the activity of certain component biochemical processes. Isolated chloroplasts showed a wide range in activity of the Hill reaction and photo-phosphorylation, but these bore little or no relationship to variation in photosynthetic rate. Differences in RUDPcase activity were, however, closely correlated with those in leaf photosynthesis.

#### (b) *Genotypic differences in Lolium*

Although care is needed in interpreting the results of manometric techniques using detached leaves or leaf pieces, Wilson, Treharne, Eagle & de Jager (1969) have developed a technique of this type, the results of which correlate well with those obtained from infrared gas analysis of attached leaves, and which has proved of value in comparative studies on genetic variation in photosynthetic activity in *Lolium* (Wilson & Cooper 1969*b*). Considerable variation in light-saturated photosynthesis was found between contrasting genotypes of *Lolium perenne* and a diallel cross indicated a high degree of genetic control for this character. In the parental genotypes and in the diallel progenies, the maximum photosynthetic rate at light saturation was inversely correlated with mesophyll cell size, such that a high photosynthetic rate per unit area of leaf was associated with a large number of mesophyll cells contained beneath that leaf area. These differences in individual leaf photosynthesis, however, bore no relation to dry matter production. Further results (Wilson 1975) suggested that growth in these *Lolium* genotypes and selection lines was limited not so much by the initial rate of synthesis as by the subsequent fate of assimilates in the plant and, in particular, by the level of maintenance respiration.

## 6. CONCLUSIONS

It is now a decade since the symposium at Copenhagen concluded that an understanding of the functioning of terrestrial ecosystems demanded the development of new methods and concepts. Since then the U.K.P.P.-P. programme has aimed at identifying and quantifying the nature of the principal physical, physiological and biochemical factors which contribute to the production and use of assimilates in different environmental conditions for a range of selected species grown either as individuals or as populations. This comprehensive appraisal has involved a diversity of experimental procedures which allow studies in the field to be integrated with others in the laboratory.

Much new information is now available on the roles played by different components of growth which participate in regulating the growth rate of plants exposed to contrasting light and temperature regimes. It is evident that response to these contrasting conditions can vary greatly between and within species at both the physiological and biochemical levels.

The perfection of techniques which has allowed the continuous recording of CO<sub>2</sub> fluxes to be combined with the procedures of growth analysis calls for the reappraisal of some accepted views. For example, the proportions of the CO<sub>2</sub> taken up by the barley canopy which accumulates in the tissues as carbon products were very much less than those anticipated. Other experiments on grassland swards within a closed system have affirmed these high respiratory losses. It is clear that further investigations of other species are required, including improved methods for studying root respiration and a further examination of the concepts of 'growth' and 'maintenance' respiration.

The importance of the leaf area index and canopy structure in determining the level of interception of the incoming radiation have been confirmed, together with their resultant effects on the population growth rate. But further studies are required of the extent to which changes in light interception at different stages of development can influence the growth of the reproductive parts or the transfer of assimilates from other potential sources.

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