

# PHOTOSYNTHESIS IN ARTIFICIAL COMMUNITIES OF WHEAT, LUCERNE, AND SUBTERRANEAN CLOVER PLANTS

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## *Summary*

The relation between leaf area index (L.A.I.) and rates of net photosynthesis at three light intensities, and of dark respiration, was examined throughout the course of growth of artificial communities of wheat and lucerne at 20°C, and of subterranean clover at 25°/20°C.

For all three species, net photosynthesis rose rapidly with increase in L.A.I. to values of 3–4, and with wheat and lucerne continued to rise, slowly, up to the highest L.A.I. values attained, above 10. With the subterranean clover communities there was a slight fall in net photosynthesis at the highest L.A.I. reached, 5. At a light intensity of 3300 foot candles, the highest rates of net photosynthesis were 48·5, 44·5, and 31·5 mg CO<sub>2</sub>/dm<sup>2</sup> ground surface/hr for wheat, lucerne, and subterranean clover respectively.

Dark respiration increased asymptotically with increase in L.A.I. of the communities. With wheat and lucerne, leaf respiration rate fell progressively with depth in the community. The highest respiration rates reached were 14·5, 21·5, and 16·5 mg CO<sub>2</sub>/dm<sup>2</sup> ground surface/hr for the wheat, lucerne, and subterranean clover communities respectively.

Gross photosynthesis accounted for 12·8, 13·5, and 9·8% of the visible light absorbed by the wheat, lucerne, and clover communities respectively. Their highest crop growth rates were 30 g/m<sup>2</sup>/day for wheat, 39 g/m<sup>2</sup>/day for lucerne (excluding root growth), and 20 g/m<sup>2</sup>/day for subterranean clover.

The dependence of transpiration rate of the plant communities on their L.A.I. and the energy balance of the communities within the artificially lit cabinets are also considered.

## I. INTRODUCTION

The relation between photosynthetic rate and leaf area index (L.A.I.) of plant communities has recently been examined with several species. The earlier work was reviewed in a previous paper (Ludwig, Saeki, and Evans 1965), and it appeared that while some species, such as subterranean clover and kale, may show a fairly pronounced optimum L.A.I., others, such as wheat and sunflower, show no fall in net photosynthesis at high L.A.I. values. Subsequent work with communities of corn (Williams, Loomis, and Lepley 1965), soybean (Shibles and Weber 1965), and lucerne (Wilfong, Brown, and Blaser 1967) plants showed no decline in net photosynthesis or crop growth rate at high L.A.I. values.

This finding is in agreement with our earlier work (Ludwig, Saeki, and Evans 1965) with communities of mature cotton and sunflower plants. In these it was shown that the lack of a decline in net photosynthesis by the communities at high

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L.A.I. values was associated with progressively lower respiration rates in the lower leaves of the canopy, with the result that the lower leaves were at compensation point even in the low light intensities at the bottom of the canopy.

However, species with a greater proportion of actively respiring, young tissue below the canopy, which could act as a sink for assimilates translocated from upper leaves, might be expected to show a more pronounced optimum L.A.I. On the other hand, communities in which light penetrates to a greater extent to the base of the leaf canopy might be expected to show a progressive increase in photosynthesis up to high L.A.I. values, rather than the plateau relation found with cotton and sunflower plants.

Of the species used in the present study, subterranean clover was chosen as likely to represent one extreme, with a high proportion of meristematic tissue below the canopy, and poor light penetration. Wheat was chosen to represent the other extreme, with little meristematic tissue at the base of the canopy, and good light penetration. Lucerne was chosen as likely to have intermediate light penetration and few young basal shoots but a large, actively respiring, root and crown.

The way of varying L.A.I. may also have a marked influence on the relation between L.A.I. and net photosynthesis, as well as the species used. With communities of *Dactylis glomerata*, Pearce, Brown, and Blaser (1965) found that photosynthesis was maximal at an L.A.I. of about 5 when L.A.I. was varied by varying the period of regrowth, but increased progressively with increase in L.A.I. up to high values when L.A.I. was varied by cutting the sward to various heights. In the present study the relation between L.A.I., net photosynthesis, respiration, and transpiration, in the three species was examined by following the course of growth in communities of normal density under controlled environmental conditions. Although more time consuming, this method has the advantage of avoiding the disruptions to adaptation by thinning, cutting, or defoliation techniques, and the atypical growth habits of plants at extremely high and low planting densities.

## II. MATERIALS AND METHODS

The plants used were wheat (*Triticum aestivum* cv. Gabo), lucerne (*Medicago sativa* cv. Hairy Peruvian), and subterranean clover (*Trifolium subterraneum* cv. Clare). All plants were grown singly in perlite in 13 cm pots and the planting density of all communities was 47.5 plants/m<sup>2</sup>. The wheat and subterranean clover communities were grown from seed, while the lucerne communities developed by regrowth from 2-year-old rootstocks which had been grown in glasshouse conditions at 21°/16°C and regularly cut back at flowering. Two experiments were carried out with each species.

The plant communities were grown in two artificially lit LB cabinets set to provide the same conditions of temperature, light, and air renewal. One cabinet was used as an assimilation chamber for the growing community, with the CO<sub>2</sub> and water vapour contents of the incoming and outgoing air and the rate of air renewal monitored to allow calculation of the rates of photosynthesis, dark respiration, and transpiration. The plant community in this cabinet remained undisturbed throughout the course of its growth. The community in the second cabinet was used for sampling

leaf areas and the distribution of dry weight at various stages during growth. The samples from the second cabinet were removed in blocks, to avoid interference with the structure of the plant community. To facilitate this, 6 in. high Perspex spacers were used to prevent intergrowing of the samples of the subterranean clover community, and wire grids to support and separate the lucerne samples. These were present in both cabinets. Removal of the sample blocks from the second cabinet probably changed the growing conditions to some extent, but this was minimized by replacing them with comparable border plants. Measurement of the leaf areas during the first half of each experiment showed close agreement between the two cabinets, while the leaf areas and dry weights at the end of the experiment were usually within 6% of each other.

The plants were given nutrient solution and water daily from a network of pipes which permitted uniform watering of the community without disturbance of its structure, and without the need to open the cabinets.

The methods used for the measurement of CO<sub>2</sub> and water vapour levels, air and leaf temperatures, and light intensities have been described in detail by Ludwig, Saeki, and Evans (1965). In the present experiments the fresh air supply to the cabinets was drawn directly from the atmosphere by way of a pipe of 15 cm diameter, in which the air flow was adjusted with a baffle. The air renewal rate was determined daily by measuring the profile of air velocity across the pipe with an Alnor thermo-anemometer. In the early stages of growth of each community, the fresh air renewal rate was restricted to about 650 litres/min, but this was increased to about 1300 litres/min when the L.A.I. approached 2. The CO<sub>2</sub> concentration of the incoming air varied around 0.03% (v/v), and the air renewal rate was such that the CO<sub>2</sub> content of the air in the cabinets was never more than 15% below the input level.

Incident radiation at the top of the community was measured with a Kipp solarimeter, and net radiation above and below the community using a miniature net radiometer (Funk 1962).

The communities were grown under a daily period of 12 hr light followed by 12 hr of darkness at 20°C from 6.30 p.m. to 6.30 a.m. The day temperature was 20°C for the wheat and lucerne experiments, and 25°C for subterranean clover. The light intensity during the day was kept at 3300 f.c. at plant height, except during the period each morning, beginning at 9 a.m., when the equilibrium rates of photosynthesis and transpiration at 3300, 2200, and 1100 f.c. and of dark respiration were determined. The reductions in light intensity were achieved by switching off fluorescent lamps only. At the highest intensity, the incandescent lamps accounted for only 50 f.c. of the 3300 f.c. total intensity, but contributed about 25% of the incident radiation. There was therefore a change in the spectral composition at the lower intensities, the incandescent lamps contributing almost half of the incident radiation at the lowest intensity.

The leaf areas of lucerne and subterranean clover plants were determined by comparing each leaf with a set of standards of known areas (Williams, Evans, and Ludwig 1964). For wheat plants, a linear regression of length by breadth was used, with periodic comparisons with areas determined by an airflow planimeter (Jenkins 1959). An arbitrary allowance for the leaf sheaths of wheat and the stems of lucerne

was made by including the length  $\times$  breadth of exposed sheaths and stems in the leaf area estimates. No allowance was made for the subterranean clover petioles, and the effective photosynthetic area of the clover communities will therefore be underestimated. For wheat, the proportion of the total leaf area contributed by the leaf sheath estimates rose from 5% at a L.A.I. of 0.5 to 9.6% at a L.A.I. of 10. For lucerne, the estimate of stem area comprised 17–20% of the total.

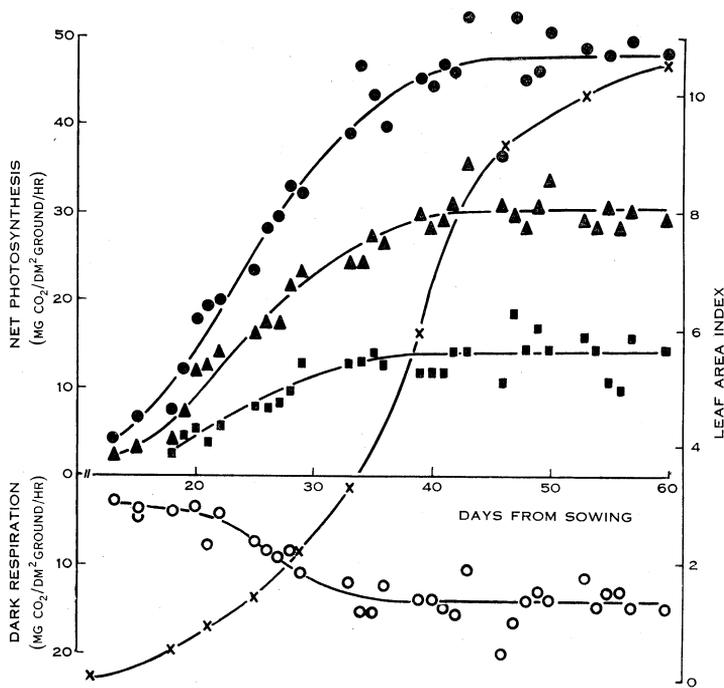


Fig. 1.—Changes in the rates of net photosynthesis at 3300 f.c. (●), 2200 f.c. (▲), and 1100 f.c. (■), and of dark respiration (○), during the course of growth of a community of wheat plants. The change in the cumulative L.A.I. is also indicated (×).

### III. RESULTS

#### (a) $CO_2$ Exchange

The changes in rates of net photosynthesis and dark respiration and in L.A.I. during the growth of one of the wheat communities are shown in Figure 1. Similar results were obtained in the other wheat experiment. L.A.I. increased in a smooth sigmoid manner, whereas net photosynthesis and respiration increased rather irregularly. Since the variations in net photosynthesis and respiration on any one day often showed discrepancies with one another, they were probably due largely to short-term variations in  $CO_2$  concentration and saturation deficit of the incoming air. The saturation deficit of the incoming air will be seen below to have had a marked effect on transpiration rates.

There was no obvious decline in net photosynthetic rate per unit ground surface at high L.A.I. values, even at the lowest light intensity. Nor did the dark respiration rate per unit ground surface of the community increase linearly with increase in L.A.I. but, rather, approached an asymptote at L.A.I. values above 5. This implies very low respiration rates in the lower, older leaves. The dark respiration rates of attached single leaves at various levels in the community were measured at the end of the experiment, before the final harvest. For leaves at the top of the canopy, the average respiration rate at 20°C was 1.24 mg CO<sub>2</sub>/dm<sup>2</sup>/hr, and for leaves at successively lower positions was 0.86, 0.72, 0.72, and 0.13 mg CO<sub>2</sub>/dm<sup>2</sup>/hr.

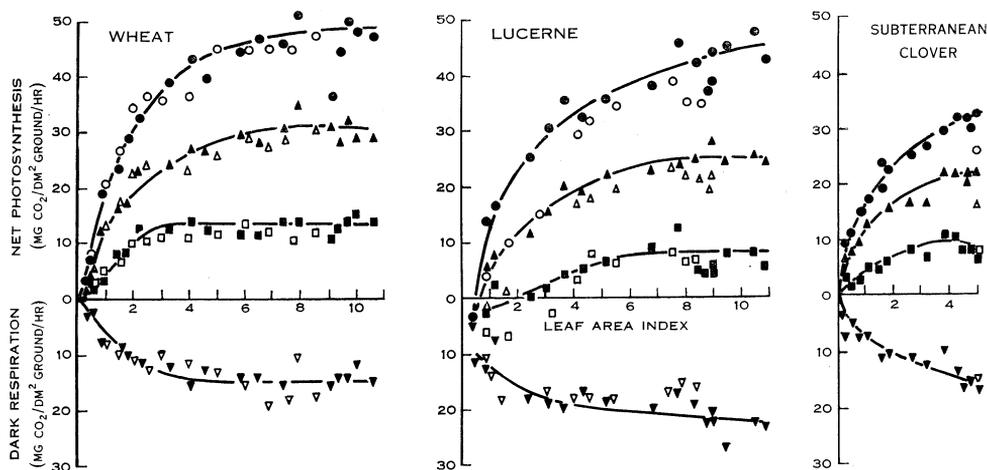


Fig. 2.—Relation between L.A.I. and net photosynthesis at 3300 f.c. (○, ●), 2200 f.c. (△, ▲), and 1100 f.c. (□, ■), and dark respiration (▽, ▼) per unit ground area, for communities of wheat, lucerne, and subterranean clover plants. Open symbols, first experiments; solid symbols, second experiments. Open symbols for subterranean clover indicate measurements at the end of the second experiment. The curves refer to data from the second experiments only.

The relation between net photosynthesis, respiration, and L.A.I. is presented in Figure 2. The results of both experiments with wheat and lucerne are presented, but only those of the second experiment with subterranean clover, since poor germination in the first one resulted in an uneven community. In the wheat communities net photosynthesis rose rapidly with increase in L.A.I. to about 4, and then slowly with further increase in L.A.I. to 10.6.

The results of the two lucerne experiments differed at low L.A.I. values, probably because of a difference in the method of cutting back prior to regrowth. This was much less severe in the first experiment, resulting in more rapid initial development of the canopy from a greater number of actively respiring shoots. Also, the plants for the first experiment had grown under higher light intensities before cutting back, and may therefore have had higher initial respiration rates, as found by Thomas and Hill (1949). Even in the second experiment, the high respiration rate of the crown and root tissue during early regrowth resulted in no net photosynthesis until the L.A.I. reached 0.5 at the highest light intensity, and 1.5 at the lowest.

Thereafter, net photosynthesis increased progressively with increase in L.A.I. up to 11, at the two higher intensities. As with wheat, the respiration rate per unit ground area did not increase linearly with increase in L.A.I. The rise in respiration rate beyond a L.A.I. of 9 may reflect the development of a number of shoots from the crowns following flowering of the early shoots. This may be seen in the L.A.I. and dry weight data presented in Figure 3, which indicate a renewal of leaf and stem

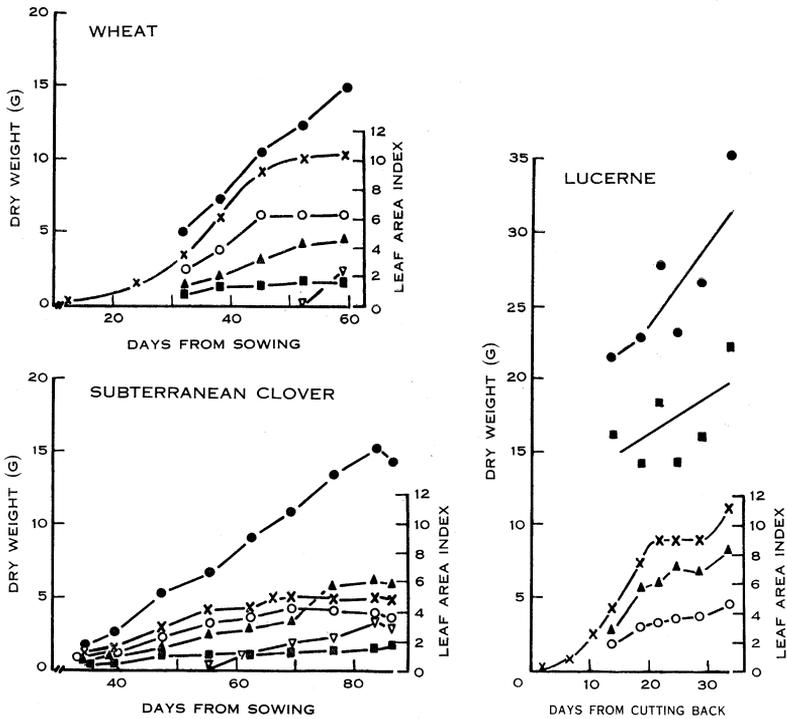


Fig. 3.—Changes in L.A.I. (x), in dry weight per plant (●), and in dry weight of leaves (○), stems (▲), roots (■), and dead leaves (▽), during the course of growth of communities of wheat, lucerne, and subterranean clover plants.

growth at the end of the experiment. Dark respiration rates at 20°C of leaves at various heights in the lucerne community were measured at the end of the experiment, and again showed a progressive fall with depth in the canopy. For leaves 55, 45, 35, 25, and 15 cm above pot level, the mean respiration rates were 1.17, 0.92, 0.78, 0.42, and 0.12 mg CO<sub>2</sub>/dm<sup>2</sup>/hr, a range of values closely comparable with that for the wheat leaves.

With the subterranean clover community, the high L.A.I. values reached by the wheat and lucerne communities could not be attained. As may be seen from Figure 3, lucerne reached a L.A.I. of 5 within 14 days, and wheat within 36 days, and went on to reach a L.A.I. of 10 in 32 and 50 days respectively. Subterranean clover, on the other hand, reached a L.A.I. of 5 only after 66 days, and showed no further increase in L.A.I. Stem and petiole weight per plant, and the weight of dead leaves, continued to increase beyond 66 days. Net photosynthesis and dark respiration

increased with increase in L.A.I. to about 4. Further increase in L.A.I. to 5 resulted in a slight fall in net photosynthesis, especially at the lower light intensities. Aging of the community at this ceiling L.A.I. during the last 3 weeks of the experiment resulted in a further decline in net photosynthesis, without any increase in respiration, presumably due to a fall in photosynthesis with increased leaf age.

The relation between photosynthesis and L.A.I. of the communities could have been expected to change with light intensity, in that an optimum L.A.I. might be more apparent at lower intensities. However, Figure 2 gives no evidence of such a change for the wheat and lucerne communities, but a slight change of this kind is evident in the results with subterranean clover. For all three species, gross photosynthesis by the communities increased hyperbolically with increase in light intensity, the more rapidly the higher the L.A.I.

No detailed comment need be made on the data from the growth analysis of each community. In the early stages of growth there was good agreement between the calculated net assimilation rates and those estimated from the daily measurements of photosynthesis and respiration. In the later stages, however, the net assimilation rates were consistently below the estimated rates. Presumably, the afternoon rates of photosynthesis were below those measured on the communities each morning. Because of the relatively high night temperature, the total respiration per day was a high proportion of daily gross photosynthesis. For our lucerne community at a L.A.I. of 3-5, this proportion was 68-70%, while for wheat and subterranean clover communities over the same L.A.I. range it was 48% and 60-66% respectively. In spite of these high respiratory losses, high crop growth rates were achieved by all the communities, reaching 30 g/m<sup>2</sup> ground surface/day for wheat, and 20 g/m<sup>2</sup>/day for subterranean clover. The great variability in the weight of the lucerne rootstocks, evident in Figure 3, preclude the estimation of a crop growth rate, but the growth rate of the tops alone reached 39 g/m<sup>2</sup>/day.

#### (b) *Evapotranspiration*

Evapotranspiration by all three plant communities showed extreme variation from day to day. It was independent of the light intensity, and also of L.A.I. at values above 3. It was influenced to some extent by the air renewal rate, and markedly by the vapour pressure deficit of the incoming air. Figure 4 presents the relation between evapotranspiration per unit ground surface and the vapour pressure deficit of the incoming air for the lucerne and wheat communities at the high air renewal rate, and at L.A.I. values above 3. The close dependence of evapotranspiration rate on the vapour pressure deficit of the incoming air, its independence of light intensity, and the similarity between the wheat and lucerne communities is clear. Figure 5 presents the relation between L.A.I. of the wheat and lucerne communities and their rate of evapotranspiration, corrected to a uniform vapour pressure deficit of 8 mmHg in the incoming air. The lucerne data at low L.A.I. values were obtained at an air renewal rate of only 650 litres/min, whereas all others were at an air renewal rate of about 1300 litres/min, and are likely to be relatively higher for this reason. The results suggest a sharp rise in evapotranspiration with increase in L.A.I. to 3 or so, and only a slight increase at higher L.A.I. values.

(c) *Energy Balance*

A striking feature of the rates of evapotranspiration by the wheat and lucerne communities is that the energy required for the high rates of evapotranspiration, on days when the vapour pressure deficit exceeds 8 mmHg, is greater than the net radiation absorbed by the plant communities. Since the energy balance of plants growing in controlled-environment cabinets has not previously been examined, we present below data for a wheat community on a day with high vapour pressure deficit in the incoming air. The data are from the second wheat experiment, 36 days after sowing, when the L.A.I. (see Fig. 1) was 4.5, net photosynthesis at 3300 f.c. was 39.9 mg CO<sub>2</sub>/dm<sup>2</sup> ground surface/hr, and evapotranspiration was 4.46 g H<sub>2</sub>O/dm<sup>2</sup> ground surface/hr.

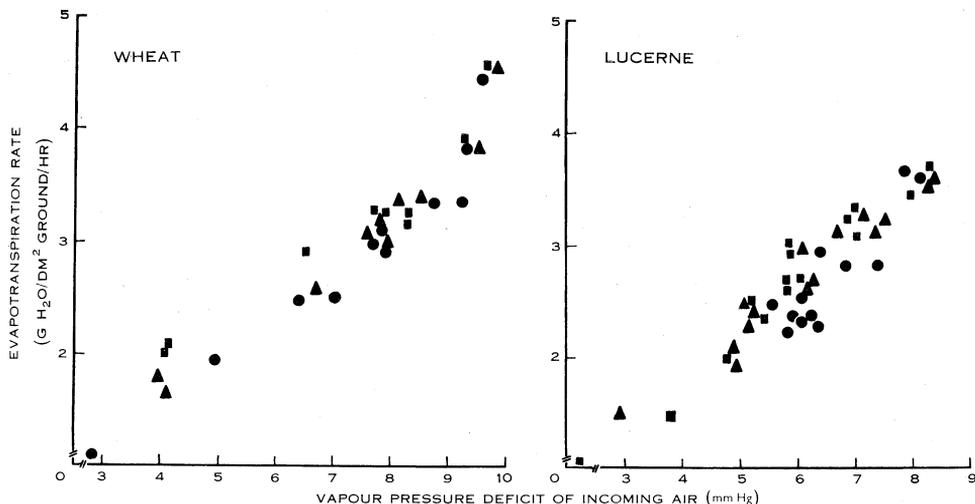


Fig. 4.—Relation between evapotranspiration per unit ground surface and vapour pressure deficit of the incoming air for wheat and lucerne communities. All data are for communities with L.A.I. > 3 and with an air renewal rate of about 1300 litres/min. ● 3300 f.c. ▲ 2200 f.c. ■ 1100 f.c.

The mean net radiation at the top of the canopy was 16.5 cal/cm<sup>2</sup>/hr, while that at the base of the canopy was less than 0.1 cal/cm<sup>2</sup>/hr. The incident radiation at the top of the canopy, measured with a Kipp solarimeter, was only 16.9 cal/cm<sup>2</sup>/hr. However, this underestimated the total incident radiation, and the albedo of the wheat community, because of its glass dome which excluded the long-wave radiation from the glass ceiling below the lamp canopy. This ceiling was at about 30°C, while the wheat leaves were about 20°C, and the net long-wave radiation from the ceiling, using Stefan's constant ( $8.13 \times 10^{-11}$  cal/cm<sup>2</sup>/min/°K<sup>4</sup>), was probably about 3 cal/cm<sup>2</sup>/hr. While this would be excluded by the glass dome of the Kipp solarimeter, it would have been passed by the polythene dome of the net radiometer. In fact, measurement with the net radiometer in the cabinet as soon as all lamps were switched off yielded a downward net radiation of close to 3 cal/cm<sup>2</sup>/hr. The data of Gates *et al.* (1965) indicate that leaves absorb such radiation, at wavelengths between 2.5 and 10  $\mu$ , almost completely. Total incident radiation was therefore 19.9 cal/cm<sup>2</sup>/hr, and the albedo of the community 17%. This value is reasonable

since most of the incoming radiation was in the visible region of the spectrum, and since there was no net back radiation by the foliage to the walls and ceiling of the cabinet, which were at the same temperature as the leaves, or warmer.

The energy balance of the community can be given as

$$R_n = E + H + P,$$

where  $R_n$  = the net radiant energy absorbed by the crop,  $E$  = the energy consumed in evapotranspiration,  $H$  = the energy exchanged by convection, and  $P$  = the energy used in photosynthesis. In the wheat community,  $R_n = 16.5$  cal/cm<sup>2</sup>/hr,  $E = 26.1$  cal/cm<sup>2</sup>/hr, and  $P = 1.02$  cal/cm<sup>2</sup>/hr.  $H$  must therefore have equalled  $-10.6$  cal/cm<sup>2</sup>/hr. Assuming heat transfer occurred equally on all leaf surfaces, the gain in heat by the leaves from the air would be 0.019 cal/cm<sup>2</sup> of leaf surface/min.

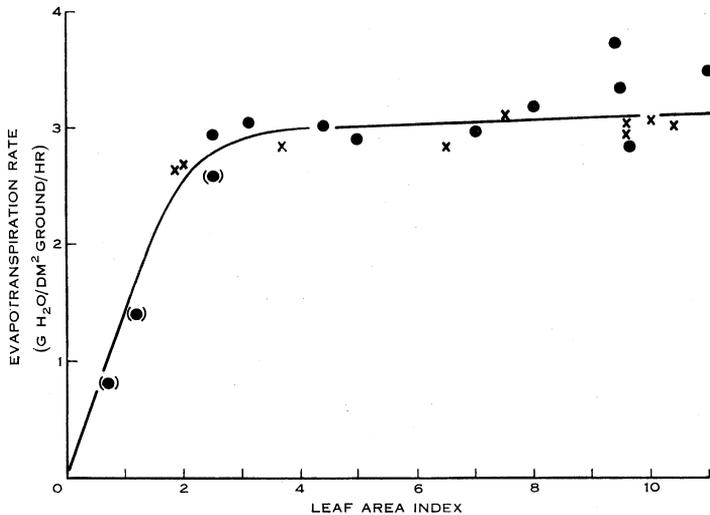


Fig. 5.—Relation between L.A.I. of wheat (x) and lucerne (●) communities and their evapotranspiration rate at 20°C, 3300 f.c., corrected to a vapour pressure deficit of 8 mmHg in the incoming air. Bracketed values are those obtained at an air renewal rate of 650 litres/min.

For leaves about 1 cm wide in a wind speed of 0.3 m/sec, the relevant conditions, Raschke (1956) gives a heat transfer coefficient of 0.04 cal/cm<sup>2</sup>/min/degC. On this basis, mean leaf temperature need be only about 0.5 degC below ambient air temperature for the plants to gain the additional heat required to maintain the high evapotranspiration rate. Measurements of leaf temperature were made, with thermocouples touching the lower surface of leaves at several levels in the canopy, and also with a Stoll-Hardy radiometer at the surface of the canopy. With both wheat and lucerne, leaf temperatures at the top of the canopy were usually very close to air temperature, or slightly below it. Leaves in the middle of the canopy were usually 0.7–1 degC below the air temperature, while those at the base of the canopy were close to air temperature or up to 0.8 degC below it. There is thus reasonable agreement between measured leaf temperatures and those expected from the energy balance and the assumed heat transfer coefficient.

## IV. DISCUSSION

*(a) Relation between Respiration, Photosynthesis, and L.A.I.*

The relation between L.A.I. and net photosynthesis of a plant community clearly varies with species and with light intensity, and also with temperature (Ludwig, Saeki, and Evans 1965). For the species with better light penetration to the base of the canopy, wheat and lucerne, the communities reached high L.A.I. values (above 10) without any decline in net photosynthesis, even at the lower light intensities. With lucerne this was so despite its relatively higher extinction coefficient (Wilfong, Brown, and Blaser 1967) and high root respiration, evident from the initial rates in Figure 2. Wang and Wei (1964) and Stoy (1965) also found no decline in net photosynthesis by wheat communities with increase in L.A.I. to 6.5 and 8 respectively. Similarly, Wilfong, Brown, and Blaser (1967) found no decline in net photosynthesis by lucerne communities with increase in L.A.I. values to 8.5.

As in the cotton communities (Ludwig, Saeki, and Evans 1965) the absence of an optimum L.A.I. for wheat and lucerne was associated with extremely low respiration rates in the lower, shaded leaves of the canopy, respiration rate falling progressively with depth in the canopy. Consequently, dark respiration rate did not increase in proportion to L.A.I., but asymptotically. With increase in L.A.I. of all communities there was a progressive fall in dry weight per unit area of leaf, as found by Williams, Loomis, and Lepley (1965) with corn. This change, which presumably reflects the loss of stored materials from older leaves, would cause a reduction in respiration rate per unit leaf area at high L.A.I. However, the maximum decrease in dry weight per unit leaf area was only about 28–37%, whereas the fall in respiration rate was far greater, about 90%, and must therefore reflect a fall in respiration rate per unit dry weight in the canopy, as well as per unit leaf area.

Respiration rates in the light may be higher than those in darkness, due to "photorespiration". However, if the increase in respiration is proportional to light intensity, this would accentuate further the gradient in respiration rates down the canopy. It would also allow a rapid adaptation of the photorespiration increment of the community to changes in light intensity. The similarity of the relation between net photosynthesis and L.A.I. at all light intensities, evident in Figure 2, suggests that this may occur.

Adaptation of the dark respiration rate to changing light intensities was shown to occur within a day in older cotton leaves (Ludwig, Saeki, and Evans 1965), and also in white clover plants (McCree and Troughton 1966). A similar adaptation of dark respiration of lucerne roots is suggested by the close relation found by Thomas and Hill (1949) between the rate of root respiration one day and the rate of net photosynthesis by lucerne communities on the preceding days. Root respiration in wheat seedlings has also been found to rise during each daily light period, and to fall during dark periods (Neales and Davies 1966).

The subterranean clover communities behaved rather differently, in that their L.A.I. did not increase beyond 5. The L.A.I. remained at this value over a period of

3 weeks, during which new leaves were added and old leaves died at a fairly constant rate. The respiration rate increased progressively with increase in L.A.I. up to 5, and then remained stable. Apparently, the lower leaves could not obtain assimilates from the upper leaves, which would have allowed the L.A.I. to increase still further, at the cost of a fall in net photosynthesis. These results are similar to those of Wilfong, Brown, and Blaser (1967) with white clover communities, in which the L.A.I. did not exceed 5. They differ from the results of Davidson and Donald (1958) and of Black (1963) with subterranean clover communities, in which they found clear optima in L.A.I. for crop growth rate, the optimum L.A.I. increasing with increase in radiation level. In Black's experiments L.A.I. values above our maximum of 5 were reached only with plant densities 100–200 times those in our communities. The smaller plants of such dense communities probably used a much higher proportion of their photosynthesis in respiration. Under these conditions they could be expected to show a clear optimum L.A.I.

Increased water stress at high L.A.I. values could contribute to an apparent optimum L.A.I. in field experiments. However, transpiration by the wheat and lucerne communities did not increase with increase in L.A.I. beyond 3 (Fig. 5). Thus greater transpiration at high L.A.I. values, inducing earlier water stress, and resulting in lowered photosynthesis, is unlikely to change the relation between L.A.I. and net photosynthesis in communities in the field. A more likely cause of difference is the continual fluctuation of conditions in the field. In the artificially lit cabinets the communities can approach equilibrium between their rates of photosynthesis and respiration. Continual changes in temperature and light intensity will preclude this in field communities since the adaptation of dark respiration rate appears to be slower than the rate at which environmental conditions may change.

#### *(b) Efficiency of Photosynthesis and Energy Balance Considerations*

From the energy balance measurements we know the amount of radiation absorbed by the plant communities. If we assume that respiration in the dark is equal to that in the light, we can then calculate the proportion of absorbed energy used in gross photosynthesis. Under fluorescent and incandescent light of 3300 f.c. intensity the proportion was 9.7% for wheat, 10.2% for lucerne, and 7.4% for subterranean clover communities of high L.A.I. Under fluorescent lamps alone, the proportion was 12.8% for wheat, 13.5% for lucerne, and 9.8% for subterranean clover. These latter values for wheat and lucerne correspond to 76–80% of the possible efficiency calculated by Gaastra (1963) for similar light sources, assuming a quantum requirement of 10. Neither water nor temperature was likely to be limiting for these communities, and the reduction below maximum efficiency was probably caused mainly by a limiting supply of CO<sub>2</sub>, or by light saturation of the upper leaves.

Daily net photosynthesis was greatly reduced by the relatively high rate of respiration in the communities. This ranged from 48% of gross daily photosynthesis in the wheat communities to 68–70% in the lucerne communities of high L.A.I. Because of the relatively high night temperature, these proportions are likely to be higher than in field communities. For lucerne crops in the field the proportion was

35–49% (Thomas and Hill 1949), and Monteith (1966) has estimated it at 44% for a sugar-beet crop. This proportion appears to be even higher for crops such as corn grown at higher temperatures. Respiration is often assumed to be 20–25% of crop photosynthesis. If it is more, say 40–50%, some of the highest growth rates recorded for field crops (e.g. Begg 1965) imply photosynthesis at close to maximum potential rates.

Our energy balance data for wheat may be compared with unpublished data of Dr. O. T. Denmead for a wheat crop in the field at Canberra, in early summer. A time was chosen when the rate of photosynthesis by the field crop, at noon, was the same as the rate at 3300 f.c. by our wheat community, 40 mg CO<sub>2</sub>/dm<sup>2</sup> ground surface/hr. Evapotranspiration rates by the two communities were also similar, equivalent to 26.1 cal/cm<sup>2</sup>/hr in the cabinet and 29.9 cal/cm<sup>2</sup>/hr in the field. However, the radiation loads on the two crops were very different. Incident radiation was 19.9 and 90 cal/cm<sup>2</sup>/hr in the cabinet and in the field respectively, while net radiation was 16.5 and 59 cal/cm<sup>2</sup>/hr, respectively. In the cabinets the energy required for evapotranspiration exceeded the radiant energy absorbed by the crop, and was made up by the advection of warmer air. Comparable occurrences in the field have been described, for example, by Lemon (1963), Begg *et al.* (1964), and Millar (1964). In the field wheat community, on the other hand, evapotranspiration accounted for only one-third of the incident energy, and one-half of the net radiation. In the cabinet 12.8% of the absorbed visible radiation was conserved by photosynthesis, whereas in the field crop only 6.4% of the visible radiation absorbed throughout the day was conserved. This difference indicates the extent to which photosynthesis in the field may be limited by factors other than CO<sub>2</sub> supply, since the field crop reduced the CO<sub>2</sub> concentration rather less than did the cabinet community.

#### V. ACKNOWLEDGMENTS

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#### VI. REFERENCES

- BEGG, J. E. (1965).—High photosynthetic efficiency in a low latitude environment. *Nature, Lond.* **205**, 1025–6.
- BEGG, J. E., BIERHUIZEN, J. F., LEMON, E. R., MISRA, D. K., SLATYER, R. O., and STERN, W. R. (1964).—Diurnal energy and water exchanges in bulrush millet in an area of high solar radiation. *Agric. Meteorol.* **1**, 294–312.
- BLACK, J. N. (1963).—The interrelationship of solar radiation and leaf area index in determining the rate of dry matter production of swards of subterranean clover (*Trifolium subterraneum* L.). *Aust. J. agric. Res.* **14**, 20–38.
- DAVIDSON, J. L., and DONALD, C. M. (1958).—The growth of swards of subterranean clover with particular reference to leaf area. *Aust. J. agric. Res.* **9**, 53–72.
- FUNK, J. P. (1962).—A net radiometer designed for optimum sensitivity and a ribbon thermopile used in a miniaturized version. *J. geophys. Res.* **67**, 2753.
- GAASTRA, P. (1963).—Climatic control of photosynthesis and respiration. In “Environmental Control of Plant Growth”. (Ed. L. T. Evans.) pp. 113–38. (Academic Press, Inc.: New York.)
- GATES, D. M., KEEGAN, H. J., SCHLETER, J. C., and WEIDNER, V. R. (1965).—Spectral properties of plants. *Appl. Optics* **4**, 11–20.

- JENKINS, H. V. (1959).—An airflow planimeter for measuring the area of detached leaves. *Pl. Physiol., Lancaster* **34**, 532–6.
- LEMON, E. R. (1963).—Energy and water balance of plant communities. In “Environmental Control of Plant Growth”. (Ed. L. T. Evans.) pp 55–77. (Academic Press, Inc.: New York.)
- LUDWIG, L. J., SAEKI, T., and EVANS, L. T. (1965).—Photosynthesis in artificial communities of cotton plants in relation to leaf area. I. Experiments with progressive defoliation of mature plants. *Aust. J. biol. Sci.* **18**, 1103–18.
- MCCREE, K. J., and TROUGHTON, J. M. (1966).—Prediction of growth rate at different light levels from measured photosynthesis and respiration rates. *Pl. Physiol., Lancaster* **41**, 559–66.
- MILLAR, B. D. (1964).—Effect of local advection on evaporation rate and plant water status. *Aust. J. agric. Res.* **15**, 85–90.
- MONTEITH, J. L. (1966).—The photosynthesis and transpiration of crops. *Expl Agric.* **2**, 1–14.
- NEALES, T. F., and DAVIES, J. A. (1966).—The effect of photoperiod duration upon the respiratory activity of the roots of wheat seedlings. *Aust. J. biol. Sci.* **19**, 471–80.
- PEARCE, R. B., BROWN, R. H., and BLASER, R. E. (1965).—Relationships between leaf area index, light interception, and net photosynthesis in orchard grass. *Crop Sci.* **5**, 553–6.
- RASCHKE, K. (1956).—Über die physikalischen Beziehungen zwischen Wärmeübergangszahl, Strahlungsaustausch, Temperatur und Transpiration eines Blattes. *Planta* **48**, 200–38.
- SHIBLES, R. M., and WEBER, C. R. (1965).—Leaf area, solar radiation interception and dry matter production by soybeans. *Crop Sci.* **5**, 575–7.
- STOY, V. (1965).—Photosynthesis, respiration, and carbohydrate accumulation in spring wheat in relation to yield. *Physiologia Pl. Suppl.* **IV**.
- THOMAS, M. D., and HILL, G. R. (1949).—Photosynthesis under field conditions. In “Photosynthesis in Plants”. (Eds. J. Franck and W. E. Loomis.) pp. 19–52. (Iowa State College Press: Ames, Iowa.)
- WANG, T. D., and WEI, J. (1964).—The CO<sub>2</sub> assimilation rate of plant communities as a function of leaf area index. *Acta Bot. Sinica* **12**, 154–8.
- WILFONG, R. T., BROWN, R. H., and BLASER, R. E. (1967).—Relationships between leaf area index and apparent photosynthesis in alfalfa (*Medicago sativa* L.) and Ladino clover (*Trifolium repens* L.). *Crop Sci.* **7**, 27–30.
- WILLIAMS, R. F., EVANS, L. T., and LUDWIG, L. J. (1964).—Estimation of leaf area for clover and lucerne. *Aust. J. agric. Res.* **15**, 231–3.
- WILLIAMS, W. A., LOOMIS, R. S., and LEFLEY, C. R. (1965).—Vegetative growth of corn as affected by population density. II. Components of growth, net assimilation rate and leaf area index. *Crop Sci.* **5**, 215–19.

