

# THE INTERACTION OF LIGHT AND TEMPERATURE IN DETERMINING THE GROWTH RATE OF SUBTERRANEAN CLOVER (*TRIFOLIUM SUBTERRANEUM* L.)

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An experiment is described in which the growth of subterranean clover (*Trifolium subterraneum* L.) in the early vegetative stage was measured over 52 consecutive weekly periods. To eliminate possible trends of growth rates with age, plants of comparable morphological stage were used for each period. The variety Bacchus Marsh was grown in pot culture in the open at the Waite Agricultural Research Institute, Adelaide, South Australia.

Determination of dry weights (including those of the root fraction) and leaf areas enabled growth to be analysed in terms of relative growth rate, net assimilation rate, and leaf area ratio. Records of total light energy and temperature (daily mean, daily mean maximum, and daily mean minimum) were kept.

Statistical analysis by the method of simultaneous solution of multiple linear regressions demonstrated significant positive effects of light and maximum temperature and a significant negative effect of minimum temperature on net assimilation rate. It was shown that the value of the leaf area ratio at the final harvest was affected positively by the initial value, which may be taken as summing the pre-experimental environmental conditions, and by temperature (positively) and by light (negatively) during the experimental period. Relative growth rate was shown to be independent of temperature but significantly correlated with the amount of light received.

## I. INTRODUCTION

The interaction of light and temperature in determining the rate of plant growth has been assessed for relatively few plant species. Gregory (1926), Goodall (1945), Watson (1947), and Blackman, Black, and Kemp (1955) have sought to relate variations in the relative growth rate, net assimilation rate, and leaf area ratio (or relative leaf growth rate) to fluctuations in total radiation and temperature, the plant species investigated being barley, tomatoes, potatoes and sugar-beet and wheat, and sunflowers respectively. The present investigation was undertaken to assess the influence of environmental factors on the growth of subterranean clover (*Trifolium subterraneum* L.), and forms part of a programme of research in progress at the Waite Agricultural Research Institute into the growth and development of this important pasture species.

The growth of a leguminous plant has not been studied in any of the previous investigations in which the effects of light and temperature have been independently determined. The special problems introduced by the presence of nitrogen-fixing bacteria in the root nodules were avoided as far as possible by

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inoculating the soil with an effective strain of *Rhizobium* and completing the experiments while the plants were still in the early vegetative phase. It was not thought possible to assess the separate effects of the environmental factors on the behaviour of the nitrogen-fixing bacteria and thus on the metabolism of the host plant, though regular examination of the nodules suggested that they were always well established and healthy. It must be borne in mind, therefore, that the effects of light and temperature on the growth of subterranean clover reported in this investigation may not in all cases be direct effects, but may contain elements of their effect upon the nodule bacteria.

In other ways, the use of subterranean clover as experimental material has much to commend it. The seed germinates regularly and quickly under optimal conditions. The species is self-pollinated, and a large number of easily recognizable strains have evolved, all of them breeding true for a number of characteristics, both morphological and physiological; as a result, the error introduced by variability of plant material is greatly reduced. The roots are strong and do not break up when washed out of the soil, and determination of leaf areas can readily be made, despite the small size of the early leaves.

## II. EXPERIMENTAL METHODS

### (a) General

In attempting to establish quantitative relationships between factors of the environment and the growth rate of plants, it is essential to separate fluctuations in growth rate caused by the changing environment from changes attributable to ontogenetic drifts. While it is never possible to eliminate entirely the effects of such drifts, the use of plants at a similar morphological stage for each determination of growth rate in the present experiment presupposed that growth rate was then influenced primarily by environmental conditions. Since the water and nutrient factors of the environment could be controlled, the growth rate measured over weekly periods was related to light energy and temperature, which, if they cannot be controlled, can at least be measured. Each determination of growth rate was based on two sampling occasions, both from plants sown at the same time, the first being taken when the plants had reached the second trifoliate leaf stage. Fifty-two consecutive measurements of growth rate over weekly periods were made, starting in October 1952, and finishing in October 1953.

### (b) Pot Culture Methods

Standard 8-in. porous flower pots, with a basal drain hole, were used throughout the experiment; the whole inner surface was coated with bituminous paint in order to reduce loss of water. All the experimental pots were kept under natural open air conditions in a plunge bed of moist sawdust and were watered daily. Although very high shade temperatures, often exceeding 100°F, were encountered, no plants were ever observed to wilt.

The pots were filled to within an inch of the top with a sandy soil, and 1 g of superphosphate was added to each. In view of the rapid drying out of

the surface soil in summer and the difficulty of germinating subterranean clover in temperatures exceeding 90°F (32°C), it was decided to germinate all the seed at 18°C in an incubator for 24 hr, after which it was sown on the surface of the soil and covered with sand to the level of the top of the pots. All pots were inoculated with a liquid culture of *Rhizobium trifolii*, and after emergence the number of seedlings in each was reduced, usually in three stages, to six. The Bacchus Marsh strain of subterranean clover was used throughout, all seed being drawn from the same sample. Sowing dates were so adjusted that, each week, one batch of plants reached the standard initial stage of development, with the second trifoliate leaf beginning to expand. It was not always possible to judge this time interval correctly, but it had previously been established that over a considerable portion of the period of early vegetative growth, the rate of growth in the same environmental conditions remains constant. In accordance with the results of a simple uniformity trial conducted before the main experiment was designed, it was anticipated that 12 pots, each with six plants, would be required for both initial and final harvests and, in fact, each sowing consisted of 28 pots, four of which were subsequently rejected. Pots were allocated at random to the two sampling occasions.

#### (c) Sampling Procedure

Every Wednesday morning, 12 pots from one sowing were withdrawn for determination of "initial" weight; the following week, the other 12 were used for a "final" weight determination. Thus each week 24 pots were sampled, 12 for an initial and 12, from the previous sowing, for a final weight.

The plants were cut off at ground level and leaves separated from stems, petioles being included in the stem fraction. Leaves of one sample plant selected at random from each pot were set aside for determination of leaf area. Roots were recovered by washing, first through a sieve which retained all root material, and secondly in a dish where roots were separated from organic and other contaminating matter. All plant material was dried in an oven at 100°C for 24 hr before weighing.

Estimates of leaf area were made by spreading out the leaves of the sample plant on blueprint paper and exposing them to the sun. The areas of these leaf prints were subsequently determined with a planimeter and the total leaf area per pot was calculated from the area-weight ratio of the leaves of the sample plant and the known total leaf weight for each pot. Apart from the isolation of the leaves of one plant for blueprinting, no separate data were taken on the individual plants of each pot.

#### (d) Measurement of Light and Temperature

Blackman, Black, and Martin (1953) described an integrating recorder for the measurement of daylight designed for use in a similar experimental analysis of the growth of sunflower. An instrument using the identical circuit and components, differing only in the absence of a filter to eliminate infra-red radiation, was constructed and placed in the meteorological station of the Waite Institute.

Under the climatic conditions to which this instrument was exposed, there was a drift of sensitivity with aging, but regular calibrations were made and appropriate conversion factors calculated.

Mean temperatures for each period were obtained with a planimeter from the charts of a thermograph kept in a standard Stevenson screen. Mean daily maximum and minimum temperatures, which were used as an index of "day" and "night" temperatures respectively, were obtained by use of maximum and minimum thermometers.

The choice of an area for the experiment was limited to some extent by the need for proximity to the laboratory and to a water supply, and the plunge beds were eventually built at a distance of about 100 yd from the meteorological instruments. During the winter months, plants at the eastern end of the plunge beds came under the shade of trees in the early morning only, but care was taken to see that pots were removed from this end as the initial sampling occasion approached.

### III. RESULTS

#### (a) *Techniques of Growth Analysis*

In a recent review, Watson (1952) has discussed the uses and limitations of the techniques of growth analysis, and a detailed elaboration of the methods will not be attempted here.

Net assimilation rate (Gregory 1917) was defined as the rate of increase in total plant weight per unit of assimilating material, i.e.

$$\text{Net assimilation rate} = \frac{1}{A} \times \frac{dW}{dt},$$

where  $W$  = plant weight,  $t$  = time, and  $A$  is a measure of the assimilating material. Between two sampling occasions ( $t_1$  and  $t_2$ ) the mean net assimilation rate can be calculated from the formula

$$\frac{W_2 - W_1}{A_2 - A_1} \times \frac{\log_e A_2 - \log_e A_1}{t_2 - t_1}.$$

At various times, different measures of "assimilating material" have been proposed; leaf area has been most generally used, but leaf weight (e.g. Goodall 1945) or leaf protein (e.g. Williams 1939) have been substituted. Watson (1952), in discussing the use of these various bases, has stressed the use of leaf area for the sake of uniformity, and it has accordingly been used in the present investigation.

Relative growth rate or efficiency index (Blackman 1919) was defined as the increase in plant weight per unit initial weight per day,

$$\frac{1}{W} \times \frac{dW}{dt},$$

and between two sampling occasions the mean value can be calculated from the formula

$$\frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}.$$

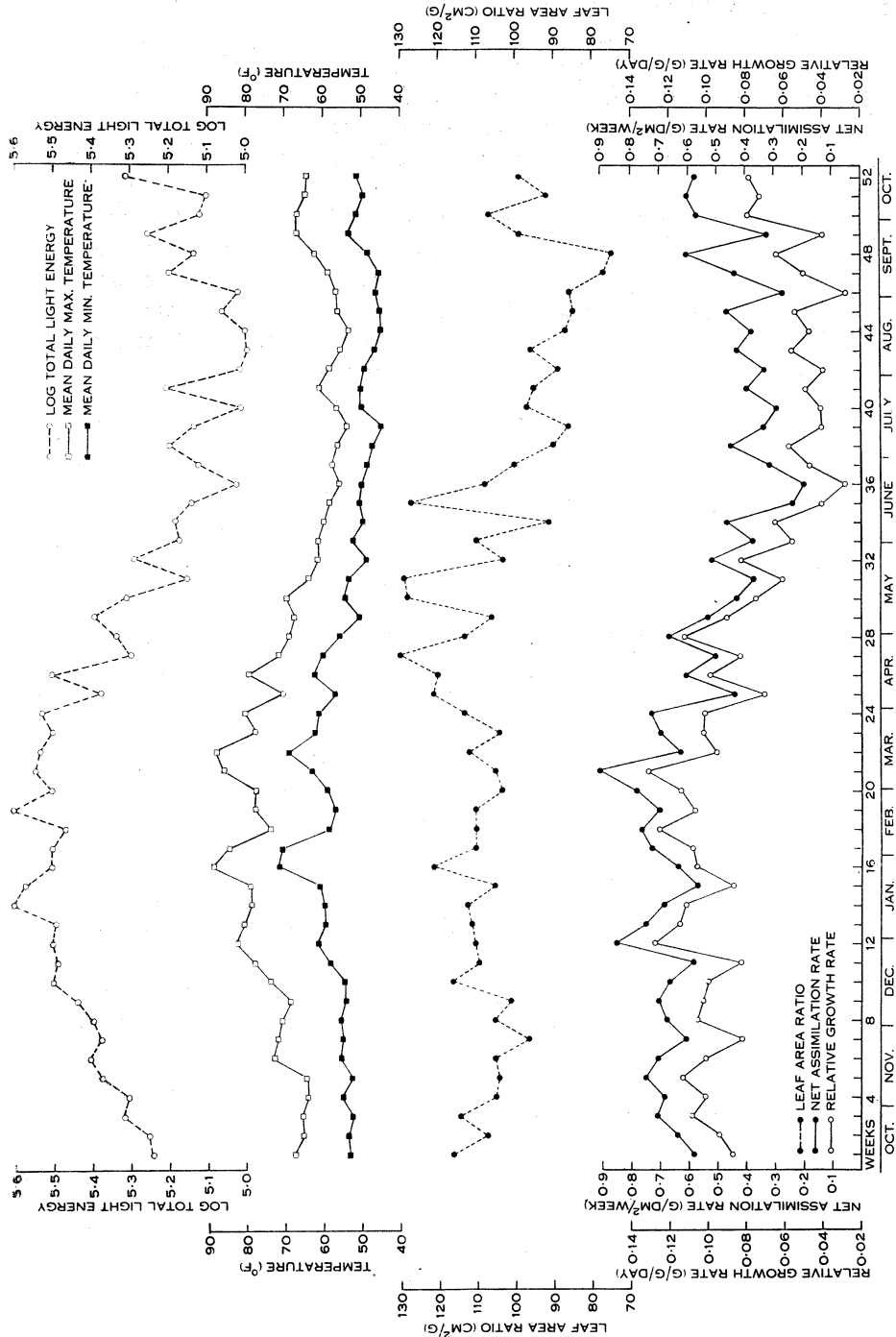


Fig. 1.—Seasonal trends in total light energy, mean daily maximum and minimum temperatures, net assimilation rate, leaf area ratio, and relative growth rate.

Briggs, Kidd, and West (1920) pointed out that relative growth rate is the product of net assimilation rate and the ratio of leaf area to plant weight, or the leaf area ratio, and these interrelationships have been further examined by Blackman and Wilson (1951*b*). It is apparent that environmental influences on relative growth rate must operate through net assimilation rate or leaf area ratio, or both.

Williams (1946) has stressed the fact that the integrated form of the net assimilation rate equation is approximate, as it assumes a linear relationship between plant weight and leaf area during the experimental period. However,

TABLE 1

REGRESSION CONSTANTS RELATING NET ASSIMILATION RATE, LEAF AREA RATIO, AND RELATIVE GROWTH RATE TO ENVIRONMENTAL FACTORS

$$(y = a + b_1x_1 + b_2x_2 + b_3x_3 + b_4x_4 + b_5x_5 + b_6x_6)^\dagger$$

Growth Index ( <i>y</i> )	Regression Constants						
	<i>a</i>	<i>b</i> <sub>1</sub>	<i>b</i> <sub>2</sub>	<i>b</i> <sub>3</sub>	<i>b</i> <sub>4</sub>	<i>b</i> <sub>5</sub>	<i>b</i> <sub>6</sub>
Net assimilation rate (g/dm <sup>2</sup> /week)	-1.803	0.407* ±0.183		0.0155* ±0.0062	-0.0158* ±0.0071		
or	-1.770	0.397** ±0.142				0.0155* ±0.0061	
Leaf area ratio (cm <sup>2</sup> /g)	165.10	-35.886* ±15.109	1.262*** ±0.327				0.543*** ±0.107
Relative growth rate (g/g/day)	-0.602	0.129*** ±0.012					

\* Significant at  $P < 0.05$ .

\*\* Significant at  $P < 0.01$ .

\*\*\* Significant at  $P < 0.001$ .

†  $x_1$  = logarithm of total light energy;  $x_2$  = mean temperature;  $x_3$  = mean max. temperature;  $x_4$  = mean min. temperature;  $x_5$  = mean daily range of temperature;  $x_6$  = initial leaf area ratio.

since the time intervals in the present investigation were short (7 days), serious departures from linearity would be unlikely and the net assimilation rate formula quoted above could be used with confidence.

It was accordingly possible to calculate relative growth rate, net assimilation rate, and leaf area ratio for each of the 52 consecutive weeks of the experiment. In Figure 1, the data are plotted graphically to show the seasonal trends in both environmental conditions and the measures of growth rate employed. The logarithm of the total light energy received is used since Blackman and Wilson (1951*b*) had shown that, for a number of species (including subterranean clover) the relationship between light intensity and both net assimila-

tion rate and leaf area ratio is logarithmic over a wide range of shading treatments.

The seasonal trends of relative growth rate and net assimilation rate are seen (Fig. 1) to correspond in general to the trends in light and temperature, but it is clearly impossible from this method of presentation to determine the separate effects of the two environmental factors on growth rates. The data were accordingly submitted to statistical analysis and the results will be considered separately for each measure of growth.

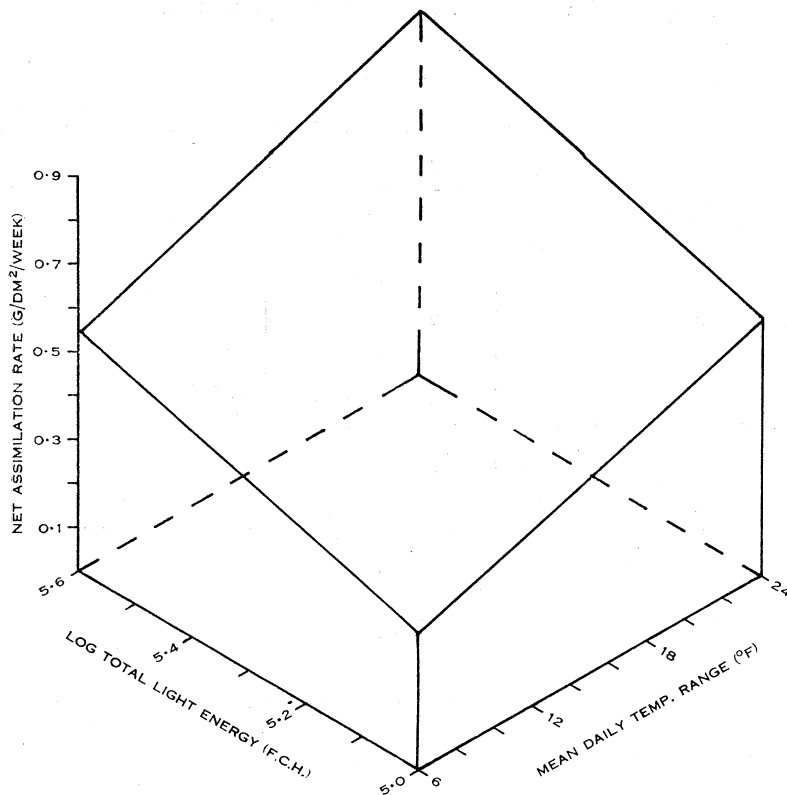


Fig. 2.—Interaction of total light energy (f.c.h.) and mean daily temperature range in determining net assimilation rate.

(b) *The Interaction of Light and Temperature in Determining Net Assimilation Rate*

The analysis of the net assimilation rate data by means of a multiple linear regression on the logarithm of the total light energy and temperature showed a significant positive effect of light ( $P < 0.05$ ), a significant positive effect of mean maximum temperature ( $P < 0.05$ ), and a significant negative effect of mean minimum temperature ( $P < 0.05$ ). The regression coefficients of the two temperature indices were almost equal in absolute value (a test of significance of the difference gave a probability of 90 per cent.). It was therefore possible

without loss of accuracy to replace the mean maximum and mean minimum temperatures in the regression equation by a single index, the mean daily range of temperature. It also followed that the mean daily temperature has no effect on net assimilation rate when the effect of light is eliminated. The effect of mean daily range of temperature is positive and significant ( $P < 0.05$ ). The appropriate regression coefficients are given in Table 1. The interaction of light and temperature in determining net assimilation rate is shown in Figure 2.

An alternative method of illustrating these data is based on the departure of the values of net assimilation rate calculated from the regression equation from the observed values: if the calculated values are plotted against the observed values, the fit of the calculated regression will be paralleled in the extent to which the data depart from the strict linear relationship. This procedure is illustrated in Figure 3.

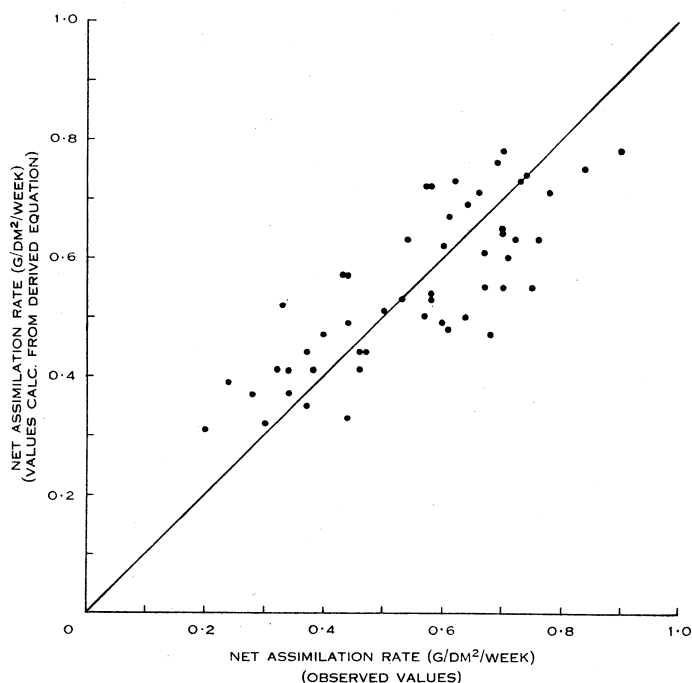


Fig. 3.—Agreement between observed and calculated values of net assimilation rate.

At this point it is necessary to observe that the use of regression analysis to determine the separate effects of several predicting variables may lead to some instability in the regression coefficients where the predicting variables are themselves intercorrelated. By continuing the experiment throughout the whole year it was hoped to obtain the greatest possible number of combinations of light and temperature conditions, but the limitations of the form of analysis performed must not be overlooked.



(c) *The Interaction of Light and Temperature in Determining Leaf Area Ratio*

In the analysis of net assimilation rate it was assumed that the measured rate could be attributed to the current environment and that a mean net assimilation rate could reasonably be related to mean — or total — values of light and temperature. This assumption cannot be made in the analysis of leaf area ratio, the value for which at any one time must to a certain extent reflect the whole

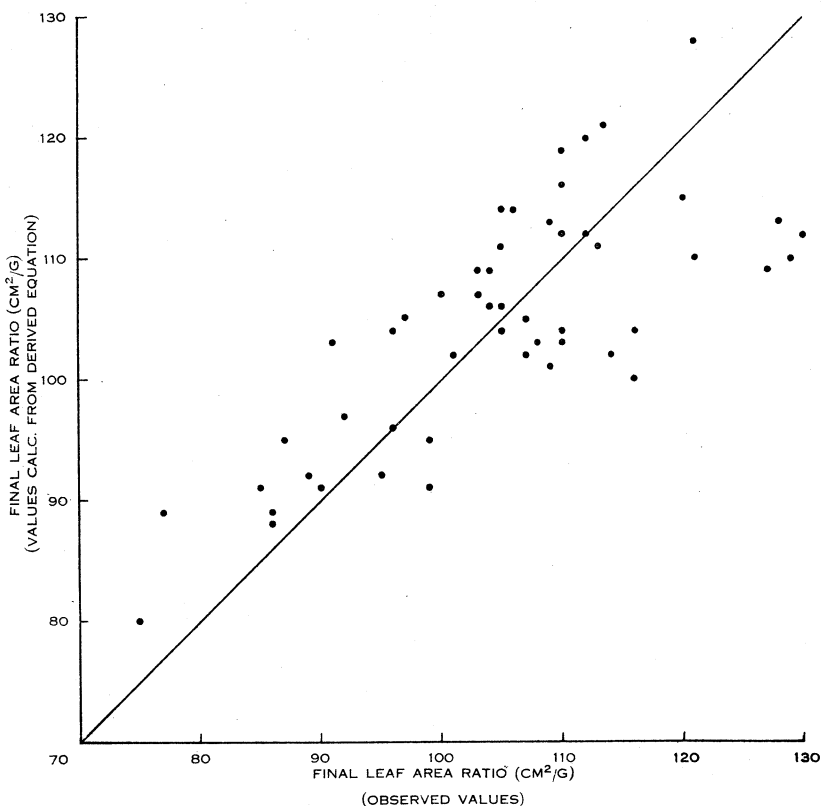


Fig. 4.—Agreement between observed and calculated values of leaf area ratio.

previous history of the plant; in particular, the use of the mean value — in this case the mean of the leaf area ratios at the initial harvest and the final harvest 7 days later — would be inappropriate in view of the evidence presented by Blackman and Wilson (1951*b*) that the response of this species to imposed shading is markedly slower than for other species investigated. Furthermore, Blackman, Black, and Kemp (1955) have shown that, for sunflower, there is a seasonal effect on leaf area ratio which is best interpreted as a residual effect of the previous environment. If the value of the leaf area ratio at the final harvest is taken as the dependent variable, and the initial value added to the environmental factors as a further independent variable, it should be possible

to determine whether in fact the conditions prior to the first harvest — as reflected in the initial value of the leaf area ratio — have any significant effect on final values, and also to what extent the final value is affected by the environmental conditions between harvest occasions when the initial value is held constant.

The analysis performed in this way demonstrated a significant ( $P < 0.001$ ) and positive effect of the initial value in determining the final value of leaf area ratio. The effect of total light energy was negative and was significant ( $P < 0.05$ ). Both mean maximum and mean minimum temperatures significantly affected final leaf area ratio, and as a result of the close correlation between them either could be used alone without affecting the goodness of fit of the regression; it was therefore decided to use the mean temperature. As an effect of temperature range had been noted in the analysis of net assimilation rate this too was tested, but no significant effect was demonstrated.

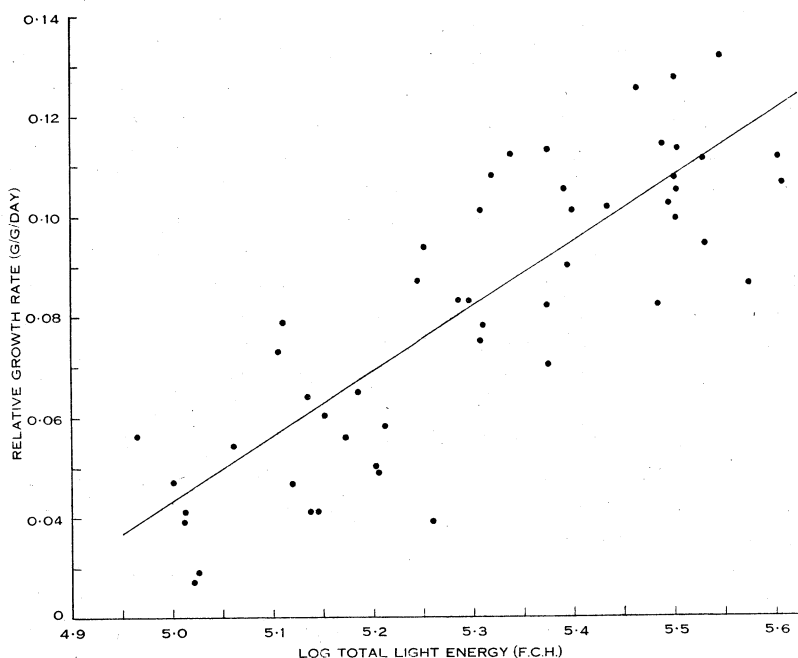


Fig. 5.—Effect of varying total light energy on relative growth rate.

The regression coefficients relating final leaf area ratio to initial value, to the total light energy, and to mean temperature are given in Table 1, and the correspondence between final values calculated from the regression equation and the observed values are illustrated in Figure 4.

(d) *The Interaction of Light and Temperature in Determining the Relative Growth Rate*

It is clear from Figure 1 that relative growth rate follows very closely the seasonal trend of net assimilation rate, and that since variation in leaf area

ratio had been minimized by the use of plants of comparable morphological condition, the factors affecting net assimilation rate are likely to be those determining relative growth rate. Analysis in terms of the logarithm of the total light energy and the various temperature indices demonstrated, however, a positive and significant ( $P < 0.001$ ) effect of light but no effect of temperature; the appropriate regression coefficients are to be found in Table 1. The relationship between relative growth rate and total light energy is shown in Figure 5.

#### IV. DISCUSSION

It is of considerable interest to compare the results obtained from the present investigation with others in which a quantitative relationship between growth and environmental factors has been attempted. These are fewer than might have been expected in view of the importance of climate in agricultural crop production, and only seven species have been examined in a comparable manner: maize (an analysis of Kreuzer's data by Briggs, Kidd, and West 1920), barley (Gregory 1926), tomatoes (Goodall 1945), wheat, sugar beet, and potatoes (Watson 1947), and sunflower (Blackman, Black, and Kemp 1955). For barley, tomato, sunflower, and subterranean clover there is a significant and positive effect of light on net assimilation rate, and for no species has a significant negative effect been demonstrated. This is in accord with the results of Blackman and Wilson (1951a), who demonstrated a linear relationship between net assimilation rate and the logarithm of light intensity relative to full daylight for 10 species. Unpublished data of Blackman and Black confirmed this relationship and extended its application to a number of graminaceous and leguminous species of agricultural importance.

The influence of temperature on the net assimilation rate of barley (Gregory 1926) and subterranean clover is similar, in that there is a positive effect of day (or maximum) temperature and a negative effect of night (or minimum) temperature; in both cases these effects, though opposite in sign, are equivalent in magnitude. Gregory (1926), in discussing the barley data, suggested that high night temperatures increase respiration rate, thus reducing net assimilation rate, and that high day temperatures increase photosynthesis, thus increasing net assimilation rate, and it is probable that the same explanation holds for subterranean clover. The opposite effects of day and night temperatures suggest that analysis in terms of mean temperature is unlikely to yield a significant relationship with net assimilation rate; in fact mean temperature is the least satisfactory index, the mean daily range being a far preferable single value index. Clearly the wider the range of temperature the greater the net assimilation rate. However, while the range has the numerical advantage of giving a single value determinant, it is possible that, if Gregory's explanation is correct, more accurate data would demonstrate that the positive effect of day temperature and the negative effect of night temperature are independent; in these circumstances the use of the diurnal range would be inappropriate.

The importance of the range of temperature has been stressed by Went (e.g. 1944), and the concept of thermoperiodicity has been developed to

cover the results of the series of experiments in which the growth of a number of plant species has been investigated in controlled conditions. Increases in stem height and not changes in dry weight have been the usual index of growth and the experiments have demonstrated temperature relationships similar to those reported here for net assimilation rate. It would appear that temperature range may be an environmental factor of greater importance than has been appreciated in the past. These opposing effects of day and night temperature were not, however, shown for maize, tomato, potato, wheat, sugar-beet, or sunflower.

The negative effect of light and the positive effect of mean temperature on final leaf area ratio, initial values being held constant, is in agreement with the findings of Blackman, Black, and Kemp (1955), the only comparable study in which leaf area ratio was examined. It is of interest to note that Blackman and Wilson (1951*b*) found that marked changes in the light environment of subterranean clover (shading to 0.50, 0.24, and 0.12 daylight) brought about only a small increase in leaf area ratio, but that when the plants were sampled after a further 9 days at the imposed shading conditions, a more marked increase in leaf area ratio was observed, this increase being greatest at low levels of light intensity, but still of only a small order at 0.50 daylight. It would seem, therefore, that the rate at which the leaf area ratio of subterranean clover becomes adapted to changes in the light environment is slow. It is considered that this lack of plasticity of response to changing environmental conditions is largely responsible for the importance of initial values in determining final values of leaf area ratio. While it was possible to put forward a tentative physiological explanation of the effect of temperature on net assimilation rate, it is not possible to do so for leaf area ratio, which, being a ratio rather than a rate, is much less capable of direct physiological explanation.

Both Gregory (1926) and Blackman and Wilson (1951*b*) have stressed that there exists in the species studied by them a mechanism whereby the growth rate is maintained approximately constant despite changes in radiation or light intensity; the contrasting effects of a decreasing net assimilation rate and increasing leaf area ratio with shading combine to protect the plant over a range of light conditions. While in the present experiment there are contrasting effects of light on net assimilation rate and leaf area ratio, analysis of relative growth rate shows that subterranean clover is not protected against changes in the light environment since the negative effect on leaf area ratio is more than offset by the positive effect on net assimilation rate. It is important to note that in the experiments of Blackman and Wilson the leaf area ratio used is the mean of initial and final values, whereas for the present analysis the final value was considered more appropriate; as a result it is not possible to analyse with the same precision the relative contributions of net assimilation rate and leaf area ratio to relative growth rate, and since there is an effect of pre-experimental environment on leaf area ratio, there must also be a similar effect on relative growth rate. However, such a pre-conditioning effect is unlikely to affect net assimilation rate (Blackman and Wilson 1954) and it is clear from Figure 1 that fluctuations in relative growth rate are attributable more to varia-

tions in net assimilation rate than to leaf area ratio. Blackman, Black, and Kemp (1955) were unable to demonstrate a seasonal effect on either net assimilation rate or relative growth rate although both that investigation and the present one have shown that leaf area ratio cannot adequately be analysed without taking into account the influence of the pre-experimental environment. It is accordingly clear that further detailed experimentation on the influence of residual environmental effects on net assimilation rate and relative growth rate, as well as on leaf area ratio, is now required before the influence of environmental factors on growth rate can be established with greater precision.

From the interaction of net assimilation rate and leaf area ratio Blackman and Wilson (1951*b*) calculated by extrapolation that the light intensity at which the growth rate of subterranean clover would be maximal was 1.87 Oxford summer daylight. The mean summer light energy per week received at Oxford (latitude 52°N) during 1950 and 1951 (May-August) was 214,460 f.c.h.; 1.87 of this is 401,040 f.c.h., a value which was exceeded only twice in Adelaide (latitude 35°S), where the most light energy received in any one 7-day experimental period was 405,710 f.c.h. Even at high values, no deviation from the logarithmic relationship between relative growth rate and total light energy could be demonstrated, and it is possible that the light intensity for maximal growth rate is even higher than the figure quoted.

On the basis of the data presented here, it would appear that the rate of growth of subterranean clover is independent of temperature, at least within the range of temperatures studied. There is presumably a minimum temperature below which growth does not proceed, but there is no evidence that temperatures of this order were experienced during the course of this experiment, in which the lowest weekly mean temperature was 47.6°F. There can be little doubt that growth is limited by low temperatures in some parts of southern Australia, and C. M. Donald (private communication) has suggested that they are a constant feature of the winter environment of Canberra, A.C.T. (mean temperature of coldest month, July, is 42°F). On the other hand, there is no evidence that growth is limited by high temperatures. It is clear that within the range of temperatures at Adelaide (weekly means during the course of the experiment from 46.7 to 77.3°F), the rate of growth of this species in the early vegetative stage is determined only by the amount of light energy received.

#### V. ACKNOWLEDGMENTS

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