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EXPANSION OF LEAF AREA PER PLANT IN FIELD BEAN (*VICIA FABIA* L.) AS RELATED TO DAILY MAXIMUM TEMPERATURE

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Differences from year to year in the rate of development of leaf area can influence final crop yields and, in particular, larger yields may be obtained if optimal leaf area index (L) is attained earlier in the season (Watson 1952). The leaf area at any time depends on the numbers and sizes of leaves, both of which are influenced by effects of environment on leaf initiation and rate of expansion.

Leaf initiation is regulated by the environment during the early growth of seedlings (Schwabe 1957; Humphries 1966) and is influenced both by temperature and by the supply of assimilates from upper leaves. Gregory (1956) concluded that the main effect of temperature on leaf growth was on the rate of leaf initiation and that it had little or no effect on expansion. However, Milthorpe (1959) demonstrated that the rate at which cucumber leaves expanded was influenced by temperature, and was greatest at about 25° C. Blackman, Black & Kemp (1955) suggested that in *Helianthus annuus* the direct effect of temperature on leaf expansion was less significant than the interaction between temperature and radiation receipt.

The decline in the rate of increase of the area of leaves was attributed to a light factor by Gregory (1956), but Blackman *et al.* (1955) and Milthorpe (1959) showed that rates of expansion were not affected when radiation receipt was increased above about 100 cal cm^{-2} day^{-1}. Newton (1963) found that cucumber leaves expanded most rapidly at 80 cal cm^{-2} day^{-1}; beyond this, up to 120 cal cm^{-2} day^{-1}, smaller rates of expansion were attributed to increased competition for available nutrients.

Leaf expansion can also be restricted if the soil is cold or insufficiently aerated because water is taken up more slowly and the water deficit in the leaves increases (Brouwer 1964). The rate of expansion of bean leaves increased with root temperature between 10 and 20° C but was almost constant when it was between 20 and 30° C.

Related to the influence of water deficit on leaf growth are the effects of wind and relative humidity on transpiration. Whitehead (1962) reported that winds up to 33 miles/h greatly retarded the expansion of leaves of *H. annuus* and *Zea mays* if the transpiration rate also increased. Thorne & Ford (1965) found that the leaf area of kale and wheat in growth rooms was unaffected by increasing the air temperature from 15 to 25° C if the water-vapour pressure remained constant but it was significantly increased when the water-vapour pressure was also increased so as to maintain a constant vapour-pressure deficit and hence a constant transpiration rate.

Obviously many factors influence the rate of leaf growth over long periods, but the most important will be those that influence day-to-day leaf expansion and consequently the time at which full leaf cover is attained. To determine the relative importance of the major environmental variables, the daily rates of increase of leaf area per plant were followed through a season in a crop of field beans.

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METHODS

Field beans (*Vicia faba* variety Maris Bead) were planted in north–south rows, 50 cm apart, over an area of 100×100 m in Rothamsted Great Field II. Seeds were drilled on 9 March 1966 at 200 lb/ac (*c.* thirty plants/m of row) together with 400 lb/ac of granular compound fertilizer (0 : 14 : 28). Plants began to emerge in early April and the positions of ten plants selected at random were marked. The total leaf area of each plant was measured at 08.00 hours GMT on 42 days between 28 April and 8 July. The use of marked plants lessened sampling variation and made it easier to detect daily changes in expansion rates. Subsidiary estimates, obtained from other randomly selected plants throughout the season, showed that the constant handling of marked plants did not influence the rates at which the leaf surface had expanded on them.

The total leaf area of a plant was estimated by summing the areas of individual leaflets of all leaves. Leaflet area (a) was calculated from leaflet length (l) and breadth (b) using the function $a = 0{\cdot}74\ l \times b$ derived from planimeter measurements on thirty-two leaves. All leaves with an area greater than $0{\cdot}5\ \mathrm{cm}^2$ were included in the comparison.

Relative rates of increase of leaf area per plant were calculated for individual plants by the function $\ln A_2/A_1$ (where A_1 and A_2 are the total leaf areas of an individual plant on successive days). The rates obtained from all ten plants were averaged each day and a standard error of the mean was calculated. Where more than 1 day had elapsed since the previous measurement a mean rate was estimated over the time interval involved.

Although the numbers of leaves on the selected plants were not identical the rates of leaf appearance were similar.

Metereorological data were obtained from a nearby meteorological enclosure. Total daily solar radiation was registered on a Kipp solarimeter some 300 yd away. Each week Mr I. F. Long monitored the soil moisture profiles with a neutron moisture meter, and the field was irrigated on the two occasions when the soil moisture deficit exceeded 1 in. (1 June and 17 July 1966).

RESULTS AND DISCUSSION

Analysis of current results

Daily relative rates of increase in leaf area per plant fluctuated greatly during the early growth of the bean plants. These fluctuations were apparently closely related to daily maximum temperatures until mid-June when the leaf area index (L) had reached about 3 and pods had begun to form (Fig. 1). Thereafter the relative rate of increase in leaf area per plant (R_L) steadily declined in a manner which was apparently unrelated to environmental factors. This decline was probably associated with competition for light between plants and the diversion of assimilates and other materials to the growing pods.

Comparison of the variations in certain environmental factors and those in the rate of increase in leaf area per plant up to mid-June showed that the closest correlation was with *maximum* temperature (Fig. 2, Table 1). The significant positive correlation of rate of increase in leaf area with saturation deficit is no doubt related to the positive association which is to be expected between temperature and saturation deficit. There is little correlation with *minimum* temperature, presumably because growth is slow when temperatures are low. For the same reason the correlation of relative rate of leaf area increase with the *mean* of maximum and minimum temperature is smaller than the correlation with maximum temperature alone.

From the regression line fitted to Fig. 2(a), i.e. $\log_{10} R_L = 0{\cdot}030T + \bar{2}{\cdot}357$ (where R_L is

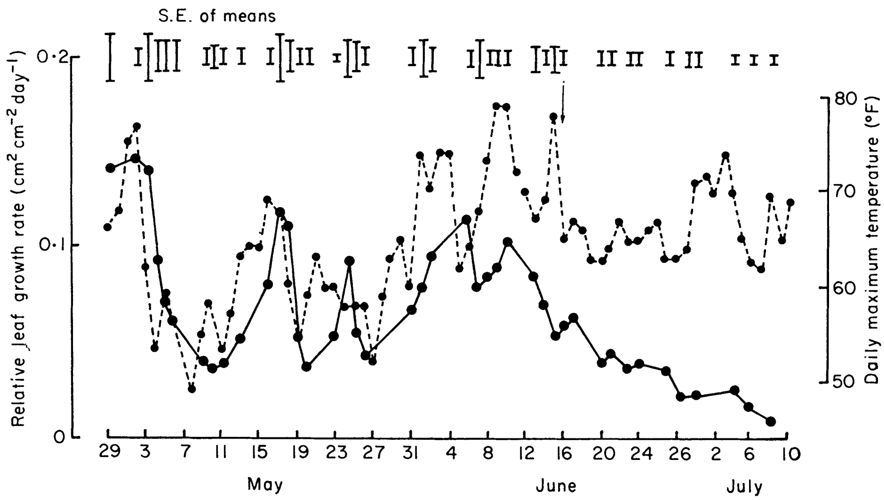

FIG. 1. Fluctuations in relative rate of increase in leaf area per plant (——) and in maximum temperature (- - -) throughout the season. The arrow indicates when pods were first seen.

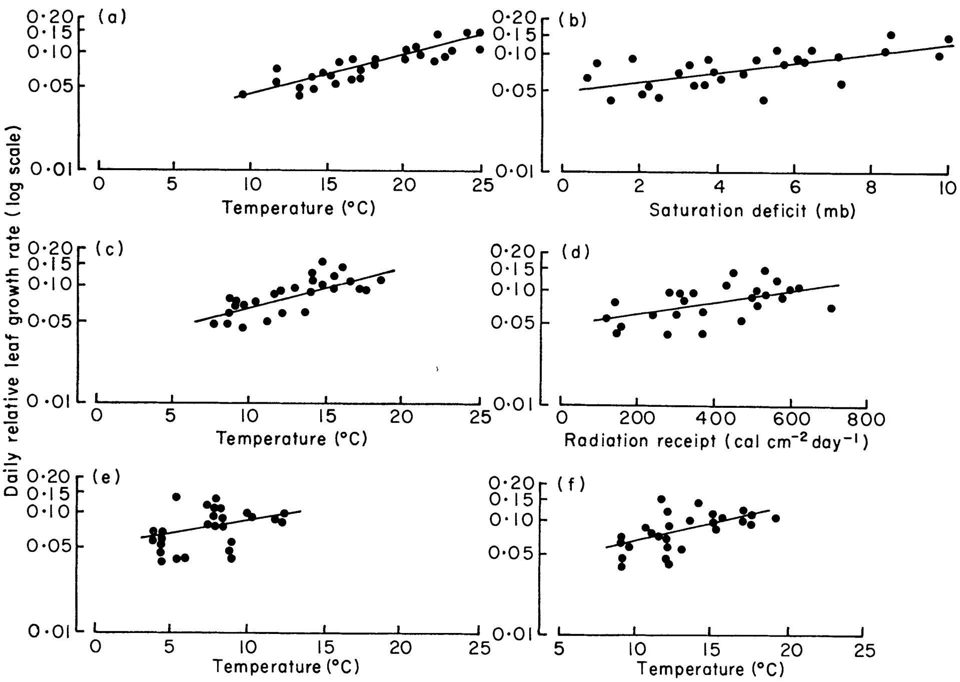

FIG. 2. Correlations up to mid-June between log relative rate of increase in leaf area per plant and (a) maximum temperature, (b) saturation deficit at 08.00 hours GMT, (c) mean temperature, (d) total daily solar radiation receipt, (e) minimum temperature, (f) soil temperature.

the relative rate of increase in leaf area per plant and T (°C) the daily maximum temperature) the temperature coefficient (Q_{10}) for leaf expansion is 2·0, which is similar to the Q_{10} of 2–3 found for leaf production by Watson & Baptiste (1938). Williams & Biddiscombe (1965) have reported a similar close correlation between the daily extension growth of tillers and the temperature of the soil surface.

When the data were averaged over weekly intervals (Table 1) the correlation ($r = 0{\cdot}84$) between relative rates of leaf area increase per plant and mean maximum temperature

Table 1. *Correlation coefficients between the relative rates of increase in leaf area per plant and various environmental factors, from* 28 *April to* 10 *June, expressed on a daily or mean weekly basis*

	Correlation coefficients Daily	Weekly
Maximum air temperature	0·85**	0·84**
Mean of maximum and minimum air temperatures	0·73**	0·41
Minimum air temperature	0·36	0·01
Soil temperature (at 08.00 hours GMT)	0·58*	0·06
Solar radiation receipt	0·58*	0·75*
Saturation deficit (at 08.00 hours GMT)	0·70**	0·86**
Wind speed	−0·27	−0·46

* Significant at 1·0%; ** Significant 0·1%.

Table 2. *Mean weekly values of relative rates of increase in leaf area and of leaf production per plant and of the environmental factors measured*

	Weeks from 27 April to 12 July 1966 1	2	3	4	5	6	7	8	9	10	11
Relative rate of increase of leaf area per plant (cm²/cm²/day × 10³)	150	56	82	64	62	96	88	65	30	28	10
Relative leaf production rate (leaves/leaf/day × 10³)	106	40	51	36	28	28	35	26	13	17	10
Maximum temperature (°F)	70	55	62	59	59	69	72	65	65	69	66
Minimum temperature (°F)	42	40	43	44	42	47	54	50	50	51	52
Mean temperature (°F)	56	48	53	52	51	58	63	58	58	60	59
Soil temperature (°F) at 4 in.	53	49	54	54	54	61	63	62	60	62	62
Solar radiation receipt (cal cm⁻² day⁻¹)	510	298	446	381	450	485	393	357	312	485	253
Saturation deficit (mb)	7·1	2·2	3·0	2·0	2·9	3·9	2·5	2·0	2·5	2·4	2·0
Wind speed (miles day⁻¹)	98	131	85	147	138	89	87	76	140	61	73

was similar to that obtained on a daily basis. The correlations with saturation deficit and solar radiation receipt were both considerably increased, and those with soil, mean and minimum temperatures were decreased. This suggests that sampling at weekly or longer intervals may obscure some short-term effects of environment on specific aspects of plant growth.

One of the components of the rate of increase in leaf area per plant is the rate of leaf appearance. The relationships between temperature and the weekly rate of leaf appearance and of increase in leaf area were similar, but the effects of temperature on the former were less pronounced (Table 2). As the rate of leaf appearance was generally less than 0·4 per day, no effect of daily variation in environmental factors could be detected, even though significant daily increases in leaf area could be measured. The daily rate of increase in leaf area per plant appears to have been governed mainly by the rate of leaf expansion of individual leaves, which, as water and assimilates were not limiting, was largely influenced by temperature.

Analysis of previous results

Fig. 3 gives the relationship between mean maximum air temperature and mean relative rate of increase of leaf area or leaf area index for some other temperate crops. As the relationship held with beans only until L attained about half its final value the same period was used in each case for this comparison. The regression line fitted to these results, i.e. $\log_{10} R_L = 0{\cdot}033T + \bar{2}{\cdot}316$ is very similar to that fitted for beans alone (Fig. 2); it represents a Q_{10} of 2·1 for increase in leaf area with a correlation coefficient of $r = 0{\cdot}81$ significant at the 0·1% level.

Some of the results from field experiments probably depart from the line because the values were obtained over long harvest intervals. Similarly the results from controlled environments may depart from the line because light intensities were small or because the plants became adapted to controlled environment conditions. The data for sugar beet, although consistent with the general trend for other crops, may be more conveniently fitted by a parallel regression line, indicating that Q_{10} is similar but the rate of increase of leaf area per plant is smaller. Cooper (1964) found that leaves of Mediterranean varieties

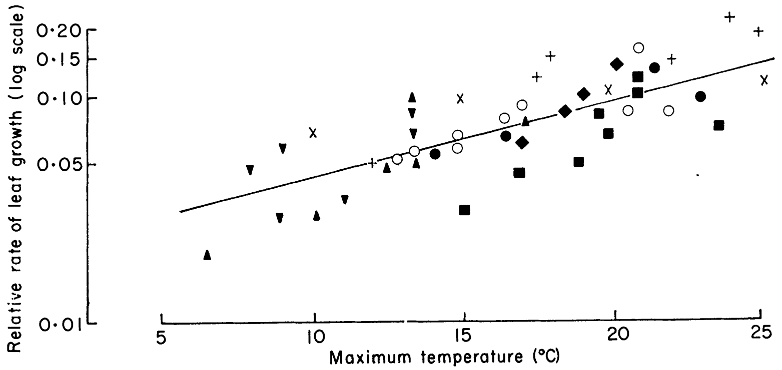

FIG. 3. General relationship between mean relative rate of increase in leaf area per plant and mean daily maximum temperature extracted from published work on various temperate crops grown at Rothamsted and in some controlled environment studies. Field crops at Rothamsted: ○, beans (1966); ●, barley (Watson, Thorne & French 1958; Monteith, unpublished); ▲, spring wheat (Watson *et al.* 1958); ▼, winter wheat (Watson 1947; Watson *et al.* 1958), ■, sugar beet (Watson 1947; Goodman, unpublished); ◆, potatoes (Watson 1947; Dyson 1965). Controlled environment studies: +, cucumbers (Gregory 1928; Milthorp 1959); ×, wheat (Friend, Helson & Fisher 1965).

of *Lolium* and *Dactylis* expand faster at low temperatures than those of indigenous British or adapted varieties. Perhaps the relationship indicated by Fig. 3 is restricted to improved varieties of temperate crop species.

Effect of temperature on rate of canopy development

Watson (1956) noted that the leaf area index in many crops was less than unity for between half and three quarters of the growth period, and pointed out the advantages of more rapid expansion of leaf area. The influence of daily maximum temperatures on the rate of increase in L can be computed using the equation of the regression line in Fig. 3.

Assuming an L of 0·1 on 28 April the daily increases in L were calculated from daily maximum temperature for the years 1959, 1963 and 1966 (Fig. 4). The calculated values for 1966 agreed closely with the measured increases in beans up to $L = 3$, after which the actual rate of expansion was significantly smaller. In May 1966 the mean maximum temperature was 15·7° C. By calculation from the individual daily maximum temperatures, a relatively warm month (e.g. May 1959, mean maximum 17·5° C) would be expected to decrease by about 2 days the time taken to reach $L = 2$. A relatively cool month (e.g. May 1963, mean maximum 15·0° C) would increase it by about 2 days. Thus the time

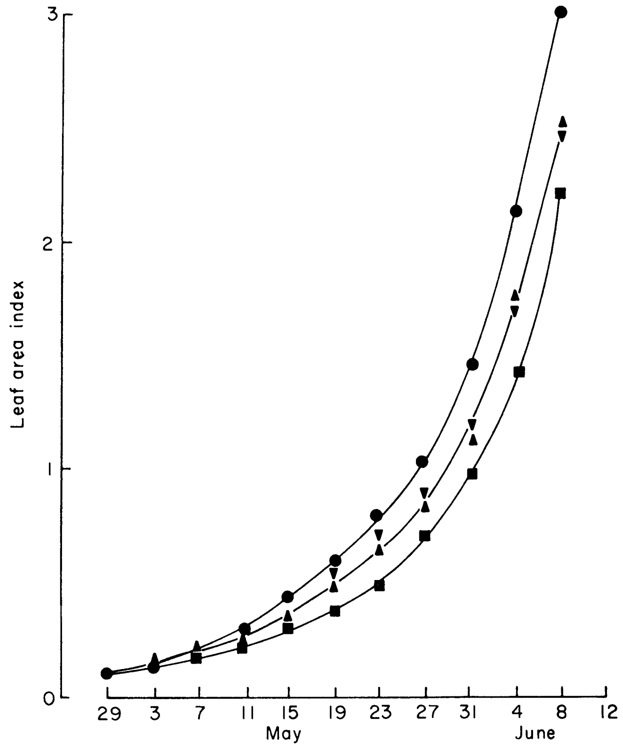

FIG. 4. Calculated changes in leaf area index (L) for the years 1959 (●), 1963 (■) and 1966 (▲) using daily maximum temperatures substituted in the equation of the regression line in Fig. 3. Actual measurements of L in beans during 1966 (▼) are also included.

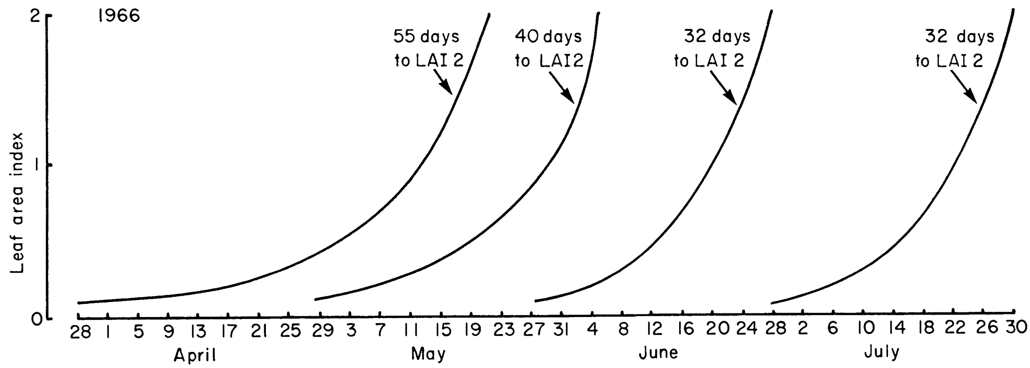

FIG. 5. Effects of different sowing dates on calculated time to reach a leaf area index (LAI) of 2 using maximum daily temperatures during 1966.

taken for L to expand from 0·1 to 2·0 decreases by about 2 days per °C increase of mean monthly maximum temperature. Obviously in a spring in which daily maximum temperatures are greater than the average the development of the leaf surface will be more rapid, but in practice the effect is small because temperatures do not differ greatly between years.

Similarly the possible effects of starting from $L = 0{\cdot}1$ in successive months can be estimated using the daily maximum temperatures for 1966 (Fig. 5). The estimated time taken to reach $L = 2$ fell from 55 days for a sowing at the end of March to 32 days for one at the end of June. The apparent advantages of later planting must be weighed against many other agronomic factors, particularly a shortage of water, but it is possible that delayed planting may give a more economic use of land under some circumstances.

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SUMMARY

The relative rate of increase of leaf area per plant was measured in field beans (*Vicia faba* L.) from May to August 1966. In the early stages of growth, until the leaf area index (L) reached about 3, the rate was closely related to daily maximum air temperature. Previous results from some other temperate crops suggests that this relation may be general up to the point at which L has about half its final value. Combining the present and previous results the relative rate of leaf area increase (R_L) and daily maximum temperature ($T°$ C) are related by $\log_{10} R_L = 0{\cdot}033T + \bar{2}{\cdot}316$ giving a $Q_{10} = 2{\cdot}1$ for the increase of leaf area per plant.

When the above expression and actual daily maximum temperatures were used to compare the effects of a warm or cool spring on the increase of leaf area per plant, the calculated time taken to reach $L = 2$ differed by about 4 days for a mean temperature difference of 2·5° C. Similarly it was shown that the greater temperatures associated with later plantings in the same year would shorten the time to achieve $L = 2$ by up to 23 days.

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