Climate and the Efficiency of Crop Production in Britain [and Discussion]

J. L. Monteith and C. J. Moss

Phil. Trans. R. Soc. Lond. B 1977 **281**, 277-294
doi: 10.1098/rstb.1977.0140

Phil. Trans. R. Soc. Lond. B. **281**, 277–294 (1977)
Printed in Great Britain

Climate and the efficiency of crop production in Britain

By J. L. Monteith, F.R.S.
University of Nottingham School of Agriculture,
Sutton Bonington, Loughborough, Leics.

The efficiency of crop production is defined in thermodynamic terms as the ratio of energy output (carbohydrate) to energy input (solar radiation). Temperature and water supply are the main climatic constraints on efficiency. Over most of Britain, the radiation and thermal climates are uniform and rainfall is the main discriminant of yield between regions.

Total production of dry matter by barley, potatoes, sugar beet, and apples is strongly correlated with intercepted radiation and these crops form carbohydrate at about 1.4 g per MJ solar energy, equivalent to 2.4 % efficiency. Crop growth in Britain may therefore be analysed in terms of (*a*) the amount of light intercepted during the growing season and (*b*) the efficiency with which intercepted light is used. The amount intercepted depends on the seasonal distribution of leaf area which, in turn, depends on temperature and soil water supply. These variables are discussed in terms of the rate and duration of development phases.

A factorial analysis of efficiency shows that the major arable crops in Britain intercept only about 40 % of annual solar radiation and their efficiency for supplying energy through economic yield is only about 0.3 %. Some of the factors responsible for this figure are well understood and some are immutable. More work is needed to identify the factors responsible for the large differences between average commercial and record yields.

Efficiency

In general reviews of husbandry and agricultural production, the word 'efficiency' is often used colloquially as a synonym of 'performance'. The thermodynamic definition of efficiency is more exact: it is the output of useful energy from a system expressed as a fraction of the energy input. Since this fraction cannot be less than zero or greater than unity, the definition incorporates a convenient numerical scale.

The thermodynamic definition of efficiency is directly applicable to crop production because the energy stored by photosynthesis in carbohydrates and other organic compounds is a useful output from a system which has solar energy as its primary input. (Other energy inputs from fertilizers, etc., have been considered by White (1977) and are not relevant in this context.) Simply expressing the growth of a crop in terms of relative energy rather than absolute mass is an academic exercise and deeper analysis is needed to make the procedure relevant to agricultural science. Such analysis has already been applied to primary production in the tropics (Monteith 1972). This paper contains a similar analysis for Britain, with special emphasis on climatic constraints such as temperature and water supply. The end-point of the analysis is an attempt to estimate the ultimate limit set by climate on the productivity of British farms, an appropriate conclusion for a meeting in which many other forms of constraint have been identified and analysed.

CLIMATE

Solar radiation

The amount of solar radiation reaching Britain, expressed as a mean daily value for the year, ranges from 10 MJ/m^2 in southern England to 8 MJ/m^2 in the north of Scotland (Collingbourne 1976). Over most agricultural parts of England the daily mean insolation is within ± 10 % of 9 MJ/m^2, corresponding to an annual total of 3.3 GJ/m^2. Insolation is even more uniform in summer months such as June when the daily mean over most of England is between 17 and 20 MJ/m^2. Significantly higher figures have been reported at coastal stations, however (e.g. Aberporth, Littlehampton), possibly because the air is cleaner, or because of reflexion from cloud building up a few miles inland (Monteith 1966; Rees 1968). In winter, insolation is much smaller (about 1.5 MJ/m^2 during December in the English Midlands) and is much less uniform, decreasing by a factor of about 2 between latitudes 50 and 60° N.

Water balances

Because annual solar radiation does not vary much over Britain, the net income of radiant energy follows a similar uniform pattern and so does the annual potential evaporation which is strongly correlated with net radiation. Regional differences in the annual excess of rainfall over evaporation are therefore determined almost entirely by the distribution of rain (and snow). In parts of Wales and the West Country, annual rainfall is of the order of 100 cm whereas potential evaporation is only 50 cm, leaving a surplus of 50 cm to be drained into rivers and aquifers. Even in summer, when the monthly evaporation may reach a maximum of 8 cm, the soil water deficit is very small when calculated as an average for a series of years. However, in any single year, an erratic distribution of rain may be responsible for small deficits of a few centimetres or for severe drought as in 1975 and 1976. In East Anglia and Essex on the other hand, and in a narrow but agriculturally very productive coastal strip east of Edinburgh, average rainfall in the range 40–50 cm is of the same order as the potential evaporation. The soil water budget therefore runs into substantial deficits in most summers. Much more detail is available in maps discussed by Ward (1976) and in the tables presented by Smith (1976).

Temperature

Mean annual temperature decreases by only 1 °C between the Midlands of England and the Moray Firth, but this almost isothermal state conceals an important winter difference: the southwest coasts of England and Wales are several degrees warmer than central and eastern areas at the same latitude, a point emphasized by Wareing & Allen (this volume). In summer, maritime effects are reversed and coastal stations are somewhat cooler than those inland.

RADIATION AND CROP PRODUCTION

Measurement and analysis

When the foliage of a plant community produces dry matter by photosynthesis, a small fraction of the absorbed radiant energy is stored in the chemical bonds of carbohydrate. This fraction can be regarded as the 'efficiency' of the photosynthetic system. The usefulness of efficiency figures in this context depends on the unit of area chosen for the calculation of productivity or insolation. A rate of dry matter production can be expressed per unit leaf area (the net assimilation rate) or per unit ground area (the crop growth rate or C). Radiation is usually expressed as a flux of energy per unit area of horizontal ground but it can also be measured (or estimated) as the amount of radiation intercepted by foliage per unit ground area.

Several field experiments during the 1960s showed that, at least during their vegetative growth, crops assimilated carbon and accumulated dry matter at rates which were proportional to intercepted radiation. (Warren Wilson 1967; Monteith 1972). Similar but more recent evidence has been reviewed by Biscoe & Gallagher (1977). Further analysis showed that the maximum amount of dry matter accumulated by a crop was strongly correlated with the amount of radiation which its foliage intercepted during growth and figure 1 shows several examples of such relations. The line for barley fits the maximum standing dry weight of Proctor harvested at Sutton Bonington between 1969 and 1972, and at Rothamsted in 1955 (Gallagher 1976). The line for potatoes was derived from unpublished results of trials at Sutton Bonington (Scott, in preparation) and the sugar beet line from an experiment in which Klein E was sown on five dates in 1971 (Scott, English, Wood & Unsworth 1973). Figures for orchards of Golden Delicious apples grown at 3 spacings were calculated from the work of Palmer (1976).

The relation between intercepted radiation and the annual production of dry matter is surprisingly similar for all four crops although the lines intersect the X-axis at different points. If a composite line were drawn through the origin, its slope would be approximately 1.4 g/MJ and taking a representative figure of 17.5 kJ/g for the heat of combustion of dry matter, this slope is equivalent to an efficiency of about 2.4 %. The individual figures for the arable crops are within about ± 15 % of these mean values.

Figure 1 is based on experiments in which the crops were well fertilized and the supply of water was adequate for good growth. Evidence is now accumulating that when crops are subject to water stress, the yield is less than predicted from the appropriate line on the figure, implying that the average photosynthetic efficiency is depressed. In the dry summers of 1975 and 1976, figures for sugar beet revealed a substantial loss of efficiency (R. K. Scott, personal communication).

The coherence of measurements in figure 1 provides a new basis for analysing the dry matter D accumulated by a crop in terms of the light intercepted by its foliage I and the efficiency e with which that light is used (proportional to D/I). In figure 2, the slope of the line AB represents the maximum value e^* which might be determined by well-managed field trials, and the abscissa of B is the maximum interception I^*. Since the total insolation during a growing season is usually within ± 10 % of the long term mean, the value of I for a particular crop depends mainly on the fraction of intercepted light which, in turn, is a function of the seasonal distribution of leaf area index L.

Suppose the total dry matter production and light interception of a crop were represented by a point Q. Because Q lies on AB, the crop used intercepted light with maximum efficiency but failed to achieve maximum yield because light interception was less than I^*. If the performance of a crop were represented by Q', the deficit in yield could be ascribed to a failure in efficiency (given by OQ') as well as poor light interception.

The analysis of crop growth in terms of an efficiency and a light interception factor has an obvious parallel in conventional growth analysis. Photosynthetic efficiency is equivalent to but is *not* proportional to net assimilation rate, and light interception is a function of leaf area

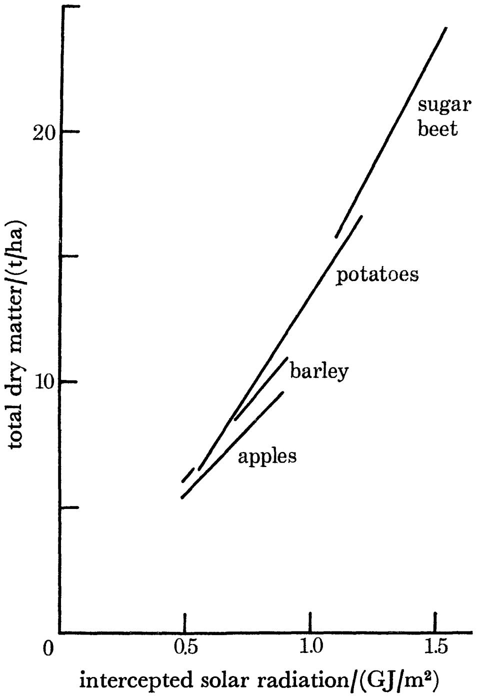

FIGURE 1. Relation between total dry matter at harvest and radiation intercepted by foliage throughout growing season: correlations from measurements discussed in text.

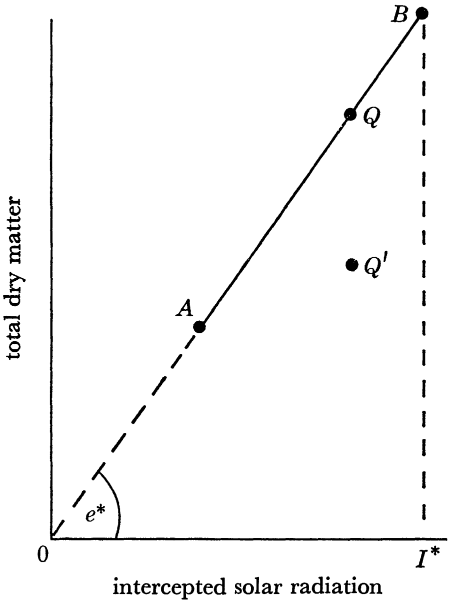

FIGURE 2. Graphical presentation of growth analysis in terms of the amount of radiant energy intercepted by a crop canopy and the efficiency with which it is used (details in text).

index – a measure of the size of the photosynthetic system. It can be shown, however, that because light interception is an exponential function of leaf area, net assimilation rate, relative growth rate and leaf area duration are appropriate indices of crop growth only when the leaf area index is small. When mutual shading of the leaves becomes significant, net assimilation rate and relative growth rate inevitably decrease with time, so that a mathematical artefact becomes inseparable from ontogenetic changes in the photosynthetic system.

Basis of a model for crop growth

The measurements summarized in the previous section are consistent with a simple model of crop growth developed for tropical crops (Monteith 1972). This model has recently been modified in several minor respects. In particular, the expression for light transmission has been replaced by a conventional Beer's law equation with a transmission coefficient K appropriate for visible light. The fraction of light transmitted by a leaf is assigned an arbitrary but representative value of 7 % and the same figure is used for reflected light.

To establish the (maximum) efficiency of photosynthesis in dim light, the (minimum) quantum requirement of the photosynthetic system is assumed to be 10 E/mol. This value must be increased to 20 E/mol to allow for the fact that only 50 % of the solar energy is in the appropriate waveband for photosynthesis. From figures tabulated by Zelitch (1975), the fraction of photosynthetic products lost by photorespiration is assumed to have a mean value of 0.3, and to allow for this loss, the quantum energy need is increased to 26 E/mol of carbohydrate, net of photorespiration. If the mean energy equivalent of dry matter is assumed to be 17.5 kJ/g, a figure of 26 E/mol corresponds to a storage of solar energy at an efficiency of 7 %. (For C_4 species without photorespiration, the efficiency is 10 %.)

Finally, it is necessary to assign values to

(i) the further fraction of assimilate which is used for 'dark' respiration;

(ii) the maximum rate of leaf photosynthesis in bright light P_m (taken as the sum of the maximum *net* rate of photosynthesis plus the contemporary rate of dark respiration expressed as a carbohydrate equivalent).

On the basis of field measurements for temperate crops, supported by recent laboratory work (Ryle, Cobby & Powell 1976), the ratio of dark respiration rate to photosynthesis rate (after allowing for photorespiration) was assumed to be 0.4. To select a representative value for P_m, the model was then used to predict the relation between crop growth and intercepted radiation for comparison with figure 1. Taking a round figure of 15 MJ/d for insolation during the growing season in Britain, the dry matter production and intercepted radiation were both calculated as functions of leaf area index. A time interval of 100 d was chosen for compatibility with figure 1. Figure 3 shows that the predicted dry matter C is nearly proportional to I, as observed, and figure 4 shows that the conversion rate of 1.4 g/MJ derived from figure 1 is consistent with the model when P_m is about 3 g (CH_2O) $m^{-2}\ h^{-1}$. As this value conforms with laboratory measurements on the leaves of temperate species, the model provides a simple but successful link between gas exchange measurements on single leaves and the production of dry matter by a crop canopy.

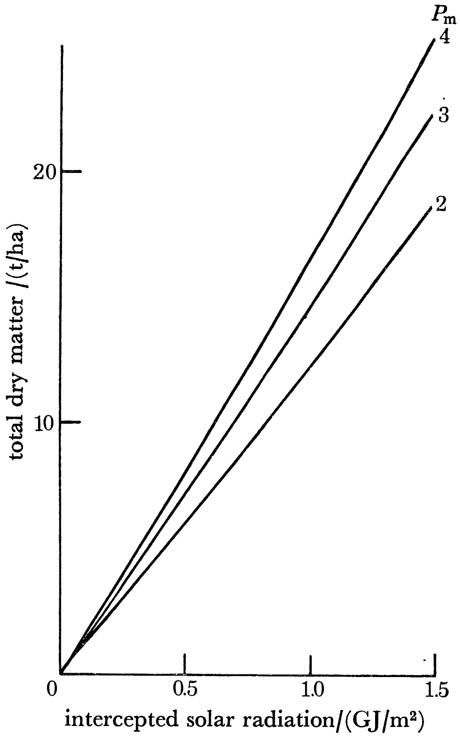

FIGURE 3. Theoretical relation between dry matter production and radiation intercepted by crop stands with a range of constant leaf area indexes. The maximum figure of 1.5 GJ/m² corresponds to complete light interception at a standard insolation of 15 MJ/m² continued for an arbitrary period of 100 days. P_m is the maximum rate of leaf photosynthesis in bright light expressed in g CH_2O m^{-2} h^{-1}.

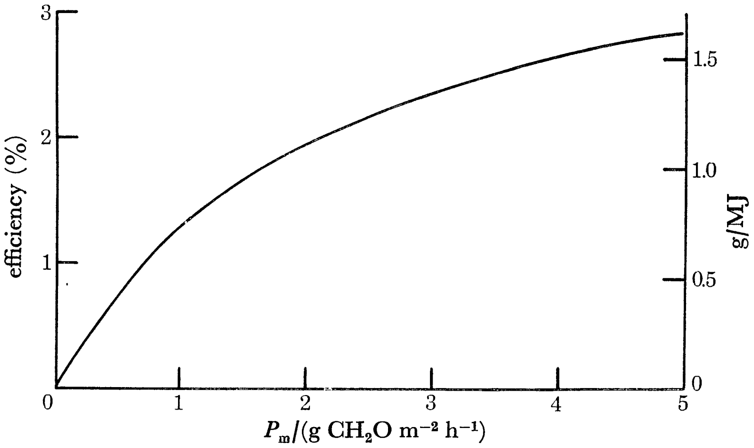

FIGURE 4. Relation between efficiency of dry matter production and maximum rate of leaf photosynthesis P_m (g CH_2O m^{-2} h^{-1}).

APPLICATION OF THE MODEL

The model was first used to calculate the potential rate of dry matter production at a number of British stations between latitudes 51 and 60° N, assuming that light interception was complete throughout the year and that P_m was independent of temperature. During the growing season from April to September, the range of insolation was about ±5 % but because of the effects of light saturation, the corresponding range of production was only ± 2 %. The radiation régime at Sutton Bonington (53° N) was therefore taken as representative for the whole country and figures 5–7 show how the seasonal change of growth rate predicted for this station was related to the parameters of the model.

First, figure 5 shows the dependence of C on P_{m}. For standard values of $P_{\mathrm{m}} = 3$ g m^{-2} h^{-1} and $K = 0.6$, C lies between 20 and 25 g m^{-2} day^{-1} for most of the summer, a range consistent with many field records in Britain, with the evidence from Dutch agriculture reviewed by Sibma (1968) and with estimates from the model of de Wit (1965). Dry matter production is not very sensitive to the value assumed for P_{m}: doubling P_{m} from 2 to 4 g m^{-2} h increases C by only 30 % during the summer. It may therefore be difficult to increase crop yields much by breeding for small increases of maximum photosynthesis rate.

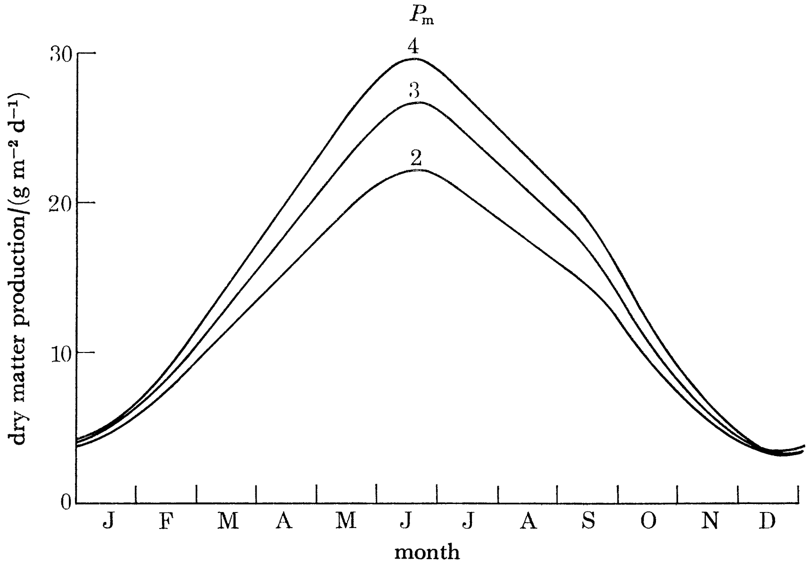

FIGURE 5. Seasonal change of rate of dry matter production as function of P_{m}, maximum rate of leaf photosynthesis (g CH$_2$O m^{-2} day^{-1}) ($K = 0.6$).

Secondly, figure 6 shows how C is expected to depend on the light transmission coefficient K, when L is large. A value of $K = 0.3$ corresponds to a stand with predominantly erect leaves and $K = 0.9$ to predominantly horizontal leaves, but the relation between crop growth rate and K changes with leaf area index. When L is small, horizontal foliage intercepts more light than vertical foliage with the same value of L and therefore grows faster if all other factors are the same. As L increases, a critical value is reached at which C is independent of K, and for greater values of L, erect canopies grow faster (Monteith 1965). The condition of complete light interception assumed for figure 6 therefore confers the maximum advantage on erectness.

Relations between crop growth rate and canopy architecture are difficult to establish in the field, partly because the dependence of C on K changes with time and partly because species or varieties with different arrangements of foliage may also differ in other characteristics which influence rates of photosynthesis. Nevertheless, Sheehy & Cooper (1973) were able to show that the growth rate of six forage grasses in simulated swards was strongly correlated with K and for a range of K from 0.9 to 0.3, C doubled, a somewhat larger response than figure 6 predicts. In real swards, however, erect leaves, as they extend, begin to bend under the combined action of gravity, wind and rain. The decrease in the growth rate of grass which occurs when a sward is approaching maturity is due at least in part to the transition from an erect to a prostrate habit (Sheehy & Peacock 1977).

Austin, Ford, Edrick & Hooper (1976) reported a comparison of photosynthesis rates for semi-dwarf wheat genotypes, one with mainly erect leaves and the other with a more lax habit. After anthesis, the canopy of the erect variety had a faster rate of photosynthesis and the leaves lasted longer. But the lax variety had a larger number of grains (faster photosynthesis when spikelets were initiated?) and appeared to fill them by drawing on a reserve of assimilates in the stem. Differences in yield were therefore marginal.

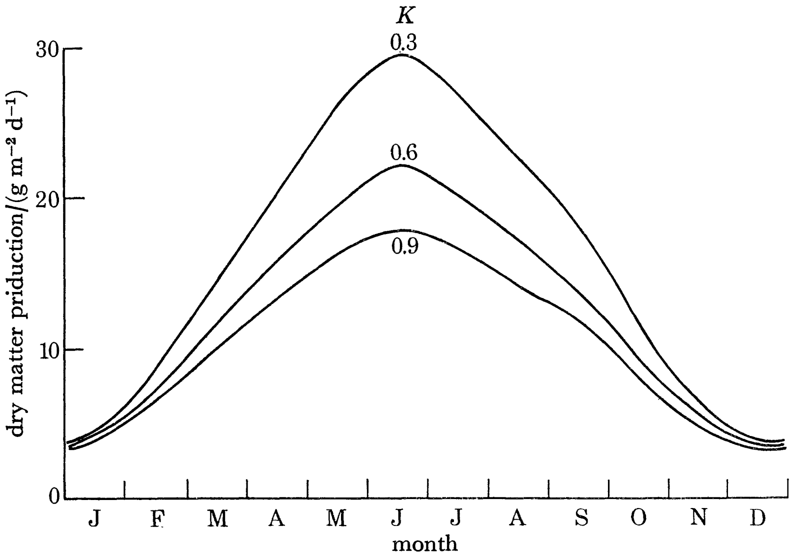

FIGURE 6. Seasonal change of rate of dry matter production as function of K, light transmission coefficient of canopy (P_m = 3 g m^{-2} h^{-1}).

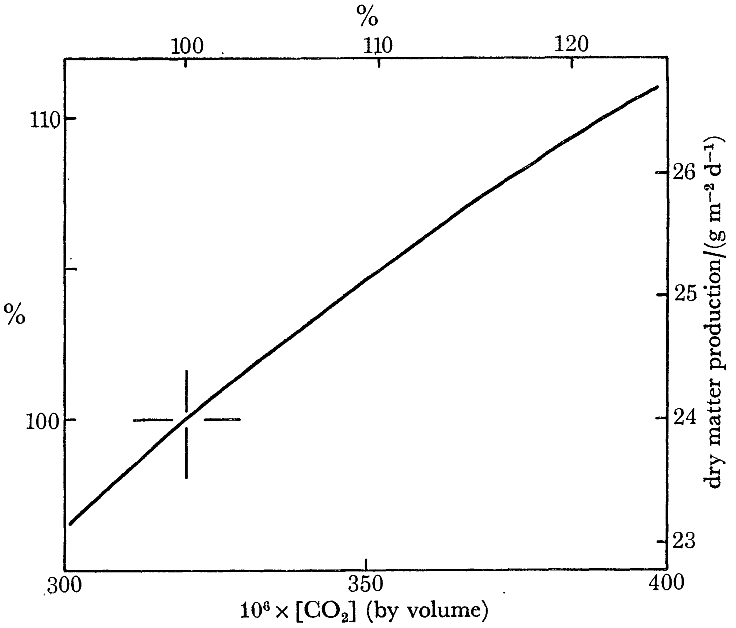

FIGURE 7. Estimated increase of daily dry matter production in response to increase of atmospheric CO_2 concentration. (Estimates based on insolation of 15 MJ/d, P_m = 3 g m^{-2} h^{-1} and K = 0.6.)

In general, it will be difficult to achieve consistently high yields of British crops by breeding for more erect leaves. The main advantages of erectness are likely to be expressed in less cloudy climates where light saturation has a more limiting influence on canopy photosynthesis (Trenbath & Angus 1975).

The mean global concentration of CO_2 is increasing at about $1/10^6$ (by volume) per year and the rate of increase may be even faster within and close to the industrial regions of Britain. At Rothamsted in the period 1960–5, the CO_2 concentration above a growing crop on sunny June days was often in the range $280–290/10^6$. At Sutton Bonington in the period 1970–5, the corresponding range was $315–325/10^6$. Further work is needed to discover whether this unexpectedly large difference is a result of errors in calibration, of a real difference between sites, or of a secular change much larger than the global average. Until this issue is settled, $400/10^6$ may be regarded as a conservative estimate of the CO_2 concentration in Britain at the end of the century. Figure 7, based on the model, predicts that the corresponding growth rate for a crop should then be 11 % higher than the rate achieved in 1976, assuming a current mean concentration of $320/10^6$ during the growing season. The increase of 4.6 % per decade is a substantial fraction of the observed increase in yields over the decade 1966–75 (see Conclusions). (By the turn of the century, this discussion may prove to be irrelevant if the increase of carbon dioxide is responsible for changes in climate, currently a topic for speculation rather than accurate prediction. The indirect effect of these changes on crop growth may prove to be larger than the *direct* effects of increasing CO_2 calculated here.)

Other climatic constraints

The response of leaf photosynthesis to light, systematically investigated in many laboratory studies, provides a basis for simple models of crop production in relation to insolation. The response of photosynthesis to temperature and water stress has also been examined, mainly in terms of stomatal behaviour, but because the physiological basis of these responses is not fully understood, photosynthesis models incorporating the temperature or water potential of leaf tissue rely heavily on empiricism and lack generality. Even less is known about the dependence of rates of growth and differentiation on temperature and water stress – a field of study central to crop ecology. In this section, a small fraction of the evidence for British crop plants will be reviewed very briefly but it will not be possible to extend the quantitative analysis presented in the previous section.

Temperature

Laboratory experiments on the relation between photosynthesis rate and temperature are difficult to extrapolate to the field because the response often depends on the environmental history of the material. Provided roots have access to adequate water, the leaves of many temperate crop plants assimilate CO_2 at a maximum rate when tissue temperature is between 20 and 30 °C; so summer midday temperatures in Britain must often be near the optimum. The maximum photosynthesis rate in bright light does not decrease much when temperature is lowered from 20 to about 10 °C but approaches zero when temperature is between 0 and 5 °C. For many tropical plants, including members of the C_4 group, the optimum temperature for photosynthesis is between 30 and 40 °C, but approaches zero between 10 and 15 °C. The climate of northern Britain is therefore unsuitable for crops such as maize and even in the south, the temperature in some summers is too low for good growth.

To give a broad indication of the extent to which crop productivity may depend on temperature through the photosynthesis rate, the value of P_m for a C_3 crop plant was assumed to increase linearly with temperature from zero at 0 °C to a maximum of 3 g m^{-2} h^{-1} at and above 10 °C. For a C_4 plant, P_m was taken as zero at 10 °C increasing to 6 g m^{-2} h^{-1} at and above 30 °C. Table 1 shows the annual dry matter production calculated for the climate of Sutton Bonington, making the additional assumption that the interception of sunlight was 40 % of the annual total, irrespective of plant type or temperature. The table implies that whereas the yield of C_3 crops is limited mainly by the availability of light, C_4 crop yields are limited by temperature as well as light.

TABLE 1. CALCULATED VALUES OF ANNUAL PRODUCTION FOR C_3 AND C_4 STANDS INTERCEPTING ALL AVAILABLE LIGHT†

	dry matter/(t/ha)	
	no temperature limit	temperature limited
C_3	22	20
C_4	32	14

† For other assumptions, see the text.

The calculations for table 1 were based on an arbitrary figure for annual light interception but as leaf expansion and leaf senescence both depend on temperature, seasonal light interception must also be related to temperature in a rather complex way. Like many processes of development, the rate at which leaves appear and grow increases almost linearly with temperature over a range of 15–20 °C. For many temperate crop species, the rate reaches a maximum at a temperature between 20 and 25 °C but the corresponding figure for tropical species is about 10 °C higher (Monteith 1977). Above the optimum temperature, development rate decreases sharply. The dependence of developmental rates on temperature can be interpreted in terms of the temperature dependence of cellular division and expansion but the biochemical basis of temperature control is obscure.

The relation between temperature and the growth of an organ can be analysed in terms of two variables which may or may not be independent: the rate of growth and the duration of the growth phase. When the size or number of organs is fixed genetically, an increase in growth rate may be offset by a proportional decrease in duration. The net effect of dry matter production on final yield may then be very small (Sofield, Evans & Wardlaw 1974). However, when a rate of growth is limited by some external constraint such as the supply of assimilate, an increase in growth rate when the temperature is raised may not fully compensate for the decrease in growth duration. In this case, the final size of the organ may decrease with increasing temperature (Ford, Pearman & Thorne 1976). The affect of increasing temperature is usually adverse when an organ is ageing because a faster rate of ageing implies a shorter useful life.

Combining these responses, the rate of dry matter production by a crop stand is expected to be positively correlated with temperature during the early stages of growth when foliage is expanding to form a complete canopy, but negatively correlated with temperature when the stand is mature. The statistical analysis used by Hooker (1921) showed that the correlation between cereal yields and temperature in eastern England changed during the season in a manner consistent with this prediction.

The relative importance of temperature early and late in the season may depend on whether vegetative or reproductive growth determines yield. A strong positive correlation between temperature and the growth of forage grasses was demonstrated by Peacock (1975), and Thomas (1975) found a consistent correlation between temperature and yield. On the other hand, in the growth room work reported by Thorne, Ford & Watson (1968) yields of spring wheat grown at 15 °C were larger than yields at 20 °C. A negative correlation of yield with temperature may be the main reason why cereal yields in northern England and in Scotland are consistently higher than in the warmer south and it is significant that the record yield for barley was obtained in Cumbria (see table 2).

Water

The effects of water stress on crop growth and yield can be discussed in the same terms as the effects of temperature but general quantitative relations are even more difficult to establish. Water stress can be induced in two ways: by a shortage of water supply to the root system (determined by the state of the soil), or by an excessive water demand from leaves (determined by the state of the atmosphere). In terms of climatic control, the availability of soil water depends on the balance of rainfall and evaporation whereas the potential rate of evaporation is set mainly by radiant energy and the saturation deficit of air.

To avoid the erratic effects of changing weather, the physiological responses of crop plants to a limited supply of water have often been measured in controlled environments. These studies show that rates of growth (e.g. leaf expansion or stem elongation) can be slowed or even stopped by a moderate water stress as measured at some point within the plant – say 0.2–0.5 MPa (2–5 bar) (Boyer 1970). Stress of this order can develop after a few days without rain during a British summer. If the rainless weather continued, further stress would tend to close stomata and reduce P_{m}, the maximum rate of photosynthesis in bright light (Sheehy, Green & Robson 1975). Other evidence suggests that crop plants established in the field are less affected by drought than plants raised in a growth room which are exposed to stress more abruptly. Diurnal and seasonal changes of osmotic potential may be partly responsible for this form of adaptation (Biscoe, Cohen & Wallace 1976; Hsiao, Acevedo, Fereres & Henderson 1976).

Evidence for the influence of water demand on crop growth is very scanty. Ford & Thorne (1974) found that the leaves of both sugar beet and kale grew faster in humid air than in dry air, presumably because less water stress was imposed on the leaves when transpiration was slowed. The rate of photosynthesis of sugar beet is slowed also when the humidity of the air is decreased (Milford & Lawlor 1975) and the adverse effect of dry air on photosynthesis rate observed in a number of species is probably a consequence of stomatal closure. Milford (1975) was able to increase the stomatal conductance and the photosynthesis of sugar beet plants in the field by exposing leaves to a fine mist. The wilting of sugar beet leaves on bright days, even when the soil is moderately wet, shows that this crop is particularly sensitive to water stress induced by rapid transpiration. Little evidence is available for other temperate crops which may respond to dry air in the same manner as sugar beet but to a lesser degree.

In the field, the effects of humidity and temperature will nearly always operate in opposite directions because hot air (accelerating growth) is usually dry air (retarding growth) and vice versa. Temperature is probably the dominant factor in early spring but the apparent loss of temperature response during the summer may be associated with the opposing effects of relative humidity.

Table 2. Factorial analysis of crop yields in England and Wales

production level	dry matter/(t/ha)			
(I) equivalent of annual radiation (3.3 GJ/m²)	1900			
(II) dry matter equivalent of theoretical ‘gross’ photosynthesis neglecting dark respiration and effects of light saturation	130			
(III) dry matter equivalent of theoretical *net* photosynthesis: 100 % light interception throughout year and $P_m = 3\ \mathrm{g\ m^{-2}\ h^{-1}}$ consistent with figure 1	54			
	wheat	barley	potatoes	sugar beet
(IV) record dry matter (estimated from V)	20.7	20.1	20.0	26.7
(V) record yield	10.7	10.4 (grain)	17.0 (tubers)	12.0 (sugar)
(VI) national average yield (1965–74)	4.2	3.7	5.3	5.5
(VII) efficiency, i.e. (VI) as % of (I) equivalent to product of factors (*a*) to (*e*)	0.22	0.19	0.28	0.29

loss of production	loss factor			
(*a*) spectral composition, quantum need photorespiration	0.07			
(*b*) light saturation dark respiration	0.7 0.6			
	wheat	barley	potatoes	sugar beet
(*c*) seasonal light interception from IV/III	0.38	0.37	0.37	0.49
(*d*) yield as fraction of dry matter (assumed)	0.52	0.52	0.85	0.45
(*e*) effects of bad weather, poor soil, poor husbandry (from VI/V)	0.39	0.35	0.31	0.46

The reduction of leaf growth by wind may also be a result of water stress. In addition to the more obvious signs of mechanical damage to stems and branches, the abrasion of cuticular wax caused by the rubbing of adjacent leaves can increase the conductance of the cuticle, so increasing the transpiration rate (Grace 1974) and possibly reducing the capacity for photosynthesis (Mackerron 1976).

Some crops are particularly sensitive to water stress during specific phases of development, in particular, cereals and other seed bearing crops during critical stages of reproduction. The experimental evidence for a wide range of agricultural and horticultural crops was reviewed by Salter & Goode (1967) but few attempts have been made to quantify the relation between stress and reproductive capacity for crops grown in Britain.

Irrigation

From the results of a long series of irrigation experiments at Woburn (continued at Rothamsted), Penman (1971) was able to relate the yield of grass, lucerne, clover, beans and potatoes to water supply during the growing season. The results for cereals were less conclusive, as expected for crops which yield well in the driest parts of the country. The rate of transpiration by each crop was estimated from the Penman formula for potential evaporation and the application of water was designed to maintain a range of soil water deficits. Analysis was based on the very simple assumption that growth stopped when the deficit reached a limiting value D_l characteristic of the crop, but continued at its previous rate whenever the soil was rewetted by rain or by irrigation. Measurements of yield and estimates of soil water deficit were manipulated to derive values of D_l which ranged from almost zero for early potatoes to about 10 cm for sugar beet. For clover, maincrop potatoes, grass, beans and cereals before anthesis, D_l was between 2.5 and 5 cm. The analysis also yielded the increase in growth expected per centimetre of applied water, a figure which ranged from about 0.2 t/ha of grain for cereals to 0.5 t/ha of tuber dry weight for potatoes.

The Woburn irrigation experiment included no systematic botanical measurements other than yield at harvest. It was not designed as an exercise in crop ecology but as a source of agronomic information useful to British agriculture. The success of the exercise can be gauged from the extent to which A.D.A.S. and the Meterological Office have extrapolated results from Woburn to other parts of the country, supplementing them by local studies where necessary. One such extrapolation (in the 1962 White Paper on irrigation in Great Britain) showed that the average increase of yield expected from irrigation in Britain ranged from 50% for early potatoes to 15% for spring cereals (Laverton 1964).

Rates and duration of growth

To link the discussion of temperature and water stress as discriminants of growth, the yield of a crop as estimated from Penman's model can be expressed in terms of a rate and a duration of growth. As the mean daily rate of evaporation in summer is about 3 mm, a limiting deficit of $D_l = 5$ cm implies that growth can continue for about 17 days without rain. When the deficit exceeds D_l, the rate of growth is assumed to be zero and the duration of zero growth is determined by the length of the rainless period.

Real rates of growth are slowed rather than stopped by water stress and some organs (e.g. grains) may continue to grow when the deficit is much larger than D_l. For crops growing in Britain, however, little systematic information is available about the relation between soil drying, the rate at which specific organs grow, and the duration of specific phases of development.

When high temperature and drought occur together, a common combination during anticyclonic weather, their effects on growth are difficult to separate. Gallagher, Biscoe & Hunter (1976) were fortunate to repeat measurements of grain growth in Maris Huntsman winter wheat in three consecutive but contrasting summers: 1974, 1975 and 1976. In 1975, the period of grain growth was hotter than in 1974 but there was little visible evidence of water stress. The rate at which grain filled was faster in the hotter season but as the duration of filling was shorter, final grain weight was almost the same in the two years. In 1976, the grain filling period was even hotter than in 1975 and, after anthesis, leaves aged very quickly in response to high temperature or drought or both. The rate of grain growth in 1976 was even faster than in 1975 but, presumably as a result of premature senescence of the leaves, the period of grain growth was curtailed so much that mean grain weight in 1976 was about 27 % less than the 1975 value. Evidence of this kind is difficult to collect from field studies because of the erratic nature of British weather but, when it comes, it provides clues about the interaction of climatic factors which rarely emerge from growth room experiments. Field enclosures within which crops can be grown at predetermined levels of temperature and water supply may prove to be the best experimental environment for studying and distinguishing the constraints which temperature and water supply impose on crop production in Britain.

Factorial analysis of efficiency

If the mean annual insolation over agricultural land in Britain is taken as 3.3 GJ/m^2 and the energy stored in vegetation is set at 17.5 kJ per g dry matter, the dry matter equivalent of radiant energy is $(3.3 \times 10^6/17.5)$ g/m^2 or 1890 t/ha. Using national averages, the amount of dry matter at harvest is between 5 and 6 t/ha from potatoes (as tubers) and from beet (as sugar); and is about 4 t/ha for cereals (as grain). The efficiency of production for the main agricultural crops is therefore about 5/1890 or 0.3 % as a round number. From the treatment of photosynthesis and radiation already described, it is possible to express the figure of 0.3 % as the product of a series of factors, each representing a discrete component of efficiency (Monteith 1972).

Table 2 contains the two sets of figures contained in such a calculation with dry matter on the left hand of the table and the components of efficiency on the right. The round figure of 1900 corresponding to 100 % efficiency is first multiplied by 0.07 to allow for factors already discussed: the spectral composition of sunlight, the quantum need of the photosynthetic cycle, and photorespiration. The dry matter equivalent of 'gross' photosynthesis defined in this way (130 t/ha, line II) is then multiplied by a factor of 0.6 to allow for dark respiration and by 0.7 to allow for the effects of light saturation. (This last factor depends on the level of irradiance as well as on the value chosen for P_m. When $P_m = 3$ g m^{-2} h, the light saturation term is close to unity for the period from October to March when 20 % of the annual radiation is received but is only 0.6 from April to September. The figure of 0.7 is an appropriate annual average implying a loss of 30 % of dry matter production as a result of light saturation.)

The figure of 54 t/ha so obtained (line III) may be regarded as the maximum production of dry matter that could be achieved by a (C_3) crop with a complete canopy throughout the year and with a photosynthesis rate which was not slowed either by low temperature in winter or by drought in summer.

Line (V) contains the record yields of four crops: wheat, var. Maris Huntsman (McWhirter & McWhirter 1975); barley, var. Clermont (McWhirter & McWhirter 1975); potatoes, var. Maris Piper (Dyke 1973) and sugar beet, var. Klein E (Scott *et al.* 1973). Corresponding estimates of maximum dry matter production (line IV) were derived by dividing these economic yields by the harvest indices shown in line (*d*). (This procedure may over-estimate total dry matter production if record yields are associated with unusually high values of harvest index.) Assuming that the maximum dry weights (20–27 t/ha) are achieved when growth is unrestricted by drought or by low temperature, the difference between these figures and the theoretical maximum of 54 t/ha can be ascribed to the failure of crop canopies to intercept solar radiation. For all four crops, the fraction of annual sunlight which foliage *does* intercept is close to 0.4 (line *c*). (Error in the assumed harvest index is incorporated in this figure.)

National yield figures at the bottom of the table were extracted from returns published by the Ministry of Agriculture. Expressed as a fraction of experimental maximum yields, the national averages are between 0.3 and 0.4 for cereals and potatoes but are higher for sugar beet (0.46) (line *e*). This set of ratios represents losses in commercial farming, some being unavoidable and some avoidable. The distinction is necessarily arbitrary because the decision to avoid or to minimize a loss of yield often depends on economic or social factors. In most years and on many farms, however, unavoidable factors will include bad weather, (particularly during establishment of the crop or at harvest), poor soil, the interaction of weather and soil factors, and attack by pests and diseases on an uncontrollable scale. Avoidable losses may include the inadequate application of fertilizer or pesticides, poor seedbed preparation or inefficient harvesting.

Conclusions

Whatever environmental or human factors are responsible for the figures displayed in line (*e*) of table 2, they are comparable with the ratios for light interception (line *c*) and for harvest index (line *d*). Improvement in crop production over the past 30 years can be ascribed to increases in all 3 ratios. Can similar progress be expected in the next 30 years?

Increasing the length of the growing season would allow crops to intercept more light (Watson 1947). Higher yields might be obtained if leaves were able to expand more rapidly in spring when growth is limited by low temperature but good early growth should be associated with frost hardiness (Cooper 1964). At the other end of the season, the yields of cereals and of potatoes could be increased if the ageing of leaves could be retarded, particularly during spells of hot, dry weather.

If the annual loss of light, even for a record crop, is about 60 % (line *c*) the loss for average commercial crops must be substantially larger, say 70 %. If this figure could be reduced even slightly, say from 70 to 67 %, corresponding to an increase of intercepted light from 30 to 33 % of annual insolation, dry matter production should increase proportionately (figure 1), i.e. by 10 % of its absolute value. Good returns may therefore be expected from any form of research, in genetics, physiology, or pathology, which enables farmers to grow crops intercepting more light.

Further increases of harvest index may be more difficult to achieve because the efficient growth of a reproductive or storage organ which is harvested implies the preceding growth of enough foliage to form a complete canopy. At a figure of 0.85, the index for potatoes cannot move much higher. The index for some short strawed cereals has already reached the range 0.5–0.6 (Bingham 1971), but if assimilate stored in the stem can be used as a reserve in seasons of poor growth (Gallagher, Biscoe & Scott 1975), breeding for shorter stems may have gone far enough.

Finally, the low ratio of national average to maximum yields underlines a continuing need for the effective application of knowledge derived from research. In most seasons, crop yields in some part of Britain are depressed by bad weather or by disease or both. To compare yields between seasons, between sites, between varieties, or between programmes of management, losses of yield should be analysed initially in terms of the seasonal distribution of leaf area and the photosynthetic efficiency of the foliage. At present, this type of analysis can be attempted only for a few experimental sites or field trials. To emphasize the importance of attempting similar analysis region by region maximum experimental yields (table 2, line V) may be related to national averages and to the rate at which they are increasing.

To avoid an unfavourable bias from poor yields after the dry summers of 1975 and1976, the following figures were calculated for the decade 1964–75. In England and Wales, the mean yield of wheat in this decade was 4.2 t/ha. The corresponding increase of yield, assumed linear and expressed as a fraction of the mean was $(+22 \pm 7)\ \%$ per decade where the large standard error indicates the uncertainty introduced by the variability of weather from season to season. It has already been shown that about one fifth of this increase can be ascribed to the increase of CO_2 in the atmosphere.

Even if the increase of yield is assumed to continue at a constant (absolute) rate, it would be 35 years before average yields were even half-way to the current record figure of 10.7 t/ha reported for Maris Huntsman. Corresponding figures for barley are 3.7 t/ha and $(+14 \pm 6)\ \%$ per decade. The half-way point to the record yield of 10.4 t/ha would not be reached till the year 2034. Sugar beet yields cannot be treated in this way because the mean figure of 35.4 t/ha decreased at a rate of $(22 \pm 14)\ \%$ per decade between 1965 and 1974.

Extrapolation of trends in yield is a notoriously dangerous exercise and the assumption of linear increases in yield may be over-optimistic. The analysis performed by Blaxter (1976) showed a statistically significant deceleration in the rate at which crop yields have increased since 1946. When the yield of cereals was assumed to be an exponential function of time, the limits predicted were only 5.5 t/ha for wheat and 4.3 t/ha for barley.

All these figures suggest that further increases of crop production in Britain will need more careful scrutiny, on a national scale, of the major environmental factors still limiting yield: rainfall, temperature, soil physical conditions, and disease.

Preparation of this paper was assisted by Dr R. K. Scott, source of much useful information besides figures for crop yields; and by Dr M. Dennet who calculated the linear time trends of national average yields.

References (Monteith)

Austin, R. B., Ford, M. A., Edrick, J. A. & Hooper, B. E. 1976 Some effects of leaf posture on photosynthesis and yield in wheat. *Ann. appl. Biol.* **83**, 425–446.

Bingham, J. 1971 Physiological objectives in breeding for grain yields in wheat. *Proceedings 6th Eucarpia Congress, Cambridge*, pp. 15–29.

Biscoe, P. V., Cohen, H. & Wallace, J. 1976 Daily and seasonal changes of water potential in cereals. *Phil. Trans. R. Soc. Lond.* B **273**, 565–580.

Biscoe, P. V. & Gallagher, J. N. G. 1977 Weather, dry matter production and yield. In *Environmental effects on crop physiology* (eds J. J. Landsberg & C. V. Cutting), pp. 75–100. London: Academic Press.

Blaxter, K. L. 1976 The use of resources. *Anim. Prod.* **23**, 267–279.

Boyer, J. S. 1970 Leaf enlargement and metabolic rates. *Plant Physiol.* **46**, 233–235.

Collingbourne, R. H. 1976 Radiation and sunshine. In *The climate of the British Isles* (eds T. C. Chandler & S. Gregory), pp. 74–95. London: Longmans.

Cooper, J. P. 1964 Climatic variation in forage grasses. *J. appl. Ecol.* **1**, 45–62.

Dyke, G. V. 1973 *Rothamsted exp. Stn, Rep. for* 1972, part I, pp. 246–259.

Ford, M. A. & Thorne, G. N. 1967 Effect of CO_2 concentration on growth of sugar beet, barley, kale and maize. *Ann. Bot.* **31**, 629–644.

Ford, M. A. & Thorne, G. N. 1974 Effect of atmospheric humidity on plant growth. *Ann. Bot.* **38**, 441–452.

Ford, M. A., Pearman, I. & Thorne, G. N. 1976 Effects of variation in ear temperature on growth and yield of spring wheat. *Ann. appl. Biol.* **82**, 317–333.

Gaastra, P. 1959 Photosynthesis of crop plants. *Meded. LandbHoogesch. Wageningen* **59** (13).

Gallagher, J. N. 1976 The growth of cereals in relation to weather. Ph.D thesis, University of Nottingham.

Gallagher, J. N. G., Biscoe, P. V. & Hunter, B. 1976 Effects of drought on grain growth. *Nature, Lond.* **264**, 541–542.

Gallagher, J. N., Biscoe, P. V. & Scott, R. K. 1975 Barley and its environment. V. Stability of grain weight. *J. appl. Ecol.* **12**, 319–336.

Grace, J. 1974 The effect of wind on grasses. *J. exp. Bot.* **25**, 542–551.

Hooker, R. H. 1921 The weather and the crops in E. England 1885–1921. *Q. Jl R. met. Soc.* **48**, 115–138.

Hsiao, P. C., Acevedo, E., Fereres, E. & Henderson, D. W. 1976 Water stress, growth and osmotic adjustment. *Phil. Trans. R. Soc. Lond.* B **273**, 479–500.

Laverton, S. 1964 *Irrigation.* Oxford University Press.

Mackerron, D. K. L. 1976 Wind damage to the surface of strawberry leaves. *Ann. Bot.* **40**, 351–354.

McWhirter, N. & McWhirter, R. 1975 *Guinness book of records.* London: Guinness Superlatives Ltd.

Milford, G. F. J. 1975 Effect of mist irrigation on the physiology of sugar beet. *Ann. appl. Biol.* **20**, 247–250.

Milford, G. F. J. & Lawlor, D. W. 1975 Effects of varying air and soil moisture on the water relations and growth of sugar beet. *Ann. appl. Biol.* **80**, 93–102.

Monteith, J. L. 1966 Local differences in the attenuation of solar radiation over Britain. *Q. Jl R. met. Soc.* **88**, 508–521.

Monteith, J. L. 1972 Solar radiation and productivity in tropical ecosystems. *J. appl. Ecol.* **9**, 747–766.

Monteith, J. L. 1975 Light distribution and photosynthesis. *Ann. Bot.* **29**, 17–37.

Monteith, J. L. 1977 Climate. In *Ecophysiology of tropical crops* (eds P. T. Alvim & T. Kozlowski). New York: Academic Press.

Palmer, J. 1976 Interception and utilisation of light by apple orchards. Ph.D. thesis, University of Nottingham.

Peacock, J. 1975 Temperature and leaf growth in *Lolium perenne. J. appl. Ecol.* **12**, 99–114.

Penman, H. L. 1971 *Rothamsted exp. Stn, Rep. for* 1970, part 2, pp. 147–170.

Rees, A. R. 1968 Solar radiation on the south coast of England. *Q. Jl R. met. Soc.* **94**, 397–401.

Ryle, G. J. A., Cobby, J. M. & Powell, C. E. 1976 Synthetic and maintenance respiratory losses of $^{14}CO_2$ in uniculm barley and maize. *Ann. Bot.* **40**, 571–586.

Salter, P. J. & Goode, J. E. 1967 *Crop reponses to water at different stages of growth.* Farnham Royal: Commonwealth Agricultural Bureaux.

Scott, R. K., English, S. D., Wood, D. W. & Unsworth, M. H. 1973 The yield of sugar beet in relation to weather and the length of the growing season. *J. agric. Sci., Camb.* **81**, 339–347.

Skeehy, J. E. & Cooper, J. 1973 Light interception and photosynthesis in grass crops. *J. appl. Ecol.* **10**, 239–250.

Sheehy, J., Green, R. & Robson, M. 1975 The influence of water stress on the photosynthesis of a simulated sward of perennial ryegrass. *Ann. Bot.* **39**, 387–401.

Sheehy, J. & Peacock, J. 1977 Canopy structure and growth in three contrasting temperate forage grasses. *Ann. Bot.* (In the press.)

Sibma, L. 1968 Growth of closed green crop surfaces in The Netherlands. *Neth. J. agric. Sci.* **16**, 211–216.

Smith, L. P. 1976 *The agricultural climate of England and Wales.* M.A.F.F. Tech. Bull. no. **35**. London: H.M.S.O.

Sofield, I., Evans, L. T. & Wardlaw, I. F. 1974 The effects of temperature and light on grain filling in wheat. In *mechanisms of regulation of plant growth* (eds R. L. Bieleski, A. R. Ferguson & M. M. Cresswell), pp. 909–915. Bull. 12, R. Soc. New Zealand. Wellington, N.Z.

Thomas, H. 1975 The growth responses to weather of a single genotype of *Lolium perenne. J. agric. Sci., Camb.* **84**, 333–343.

Thorne, G. N., Ford, M. A. & Watson, D. J. 1968 Growth, development, and yield of spring wheat in artificial climates. *Ann. Bot.* **32**, 425–446.

Trenbath, B. R. & Angus, J. F. 1975 Leaf inclination and crop production. *Fld Crop Abstr.* **28**, 231–244.

Ward, R. C. 1976 Evaporation, humidity and the water balance. In *The climate of the British Isles* (eds T. J. Chandler & S. Gregory), pp. 183–198. London: Longman.

Warren Wilson, J. 1967 Ecological data on dry-matter production. In *The collection and processing of field data* (eds E. F. Bradley & O. T. Denmead), pp. 77–123. New York: Interscience Publishers.

Watson, D. J. 1947 Comparative physiological studies on the growth of field crops. *Ann. Bot.* **11**, 41–76.

White, D. J. 1977 Prospects for greater efficiency in the use of different energy sources. *Phil. Trans. R. Soc. Lond.* B **281**, 261–275. (This volume.)

de Wit, C. T. 1965 Photosynthesis of leaf canopies. *Agric. Res. Reports*, no. 663. Wageningen: Centre for Agricultural Publications and Documentation.

Zelitch, I. 1975 Environmental and biological control of photosynthesis. In *Environmental and Biological control of photosynthesis* (ed. R. Marcelle), pp. 251–262. The Hague: W. Junk.

Discussion

C. J. Moss (*National Institute of Agricultural Engineering, Wrest Park, Silsoe, Beds. MK*45 4*HS*). I should like to know if the difference between the average outputs of crops grown in the U.K. and the best yield was, in part at least, explained by the inability of the farmer to do his work at the proper time. It was one of the most important aspects of the work of the engineer in agriculture to try to provide equipment which made it possible for the farmer to do his work at the optimum time. I have heard it said often that if more winter wheat could be sown then improvements of output of the order of $\frac{1}{2}-1$ t/ha could be achieved compared with spring wheat. If this is true then the improved methods of cultivation, e.g. the rotary digger developed by N.I.A.E., should make it possible for the farmer to cultivate a greater percentage of his farmland before the end of the year, and thus to grow more winter wheat. If this is possible then it would follow that bigger outputs before the end of the century may be achieved than has been predicted by Dr Blaxter and Professor Monteith.

It may well be that a similar argument applies to the developing countries. In many parts of Asia the climate and soil and the availability of labour would make it possible to grow two crops of rice per year rather than one. At present it is difficult for peasants to do all the work of harvesting one crop and to prepare the land and transplant rice paddy in time to get a second crop, but it should be possible to provide them with suitable tools which would enable them to do their harvesting, soil preparation, transplanting etc. more quickly so as to make it possible to get two crops. If this is true, then it may become practicable for much more rice to be grown in suitable areas of Asia. I know that this is already being done on a relatively small area of farmland in Thailand, but I wonder if it is not practicable for similar progress to be made much more extensively.

J. L. Monteith. The difference between yields of winter and spring wheat varies from season to season because it depends on the sequence of weather, particularly at sensitive stages of growth such as spikelet initiation and flowering. Generalizations are dangerous but at least part of the difference between average and best yields must be the result of restrictions which the weather imposes on cultivation or harvesting – and if Mr Moss is unable to provide average figures, I doubt whether anyone else can! In our present state of knowledge, all we can safely say is that more light interception per year should mean a bigger annual harvest, whether we are talking about cereals in Britain or rice in Southeast Asia. It remains to be seen whether the relation between light interception and yield is generally as linear as my figure 1 suggests.