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PHYSICAL LIMITATIONS TO CROP GROWTH

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Studies of Crops and Weather

In May, 1922 the Fellows of the Royal Meteorological Society and some distinguished guests met to discuss two papers on the statistical analysis of crop yields and weather. The first paper was a Presidential Address by R. H. Hooker who showed how the partial correlations of yield with rainfall and temperature changed systematically throughout the year in southern England. In his conclusion, Hooker welcomed the recruitment of a mathematician to the staff of Rothamsted—'Mr. R. A. Fisher who has developed a line of attack that promises to be fertile in results'. In a second paper, A. E. Geddes[1] presented a similar analysis for north-east Scotland. A long discussion followed, published in the Society's Journal as seven pages of small type with contributions from Sir Daniel Hall, Chief Scientific Adviser to the Ministry of Agriculture and formerly Director of Rothamsted; Sir Napier Shaw, Professor of Meteorology at the Royal College of Science, formerly Director of the Meteorological Office; and Sir Thomas Middleton then holding office as Commissioner under the Development and Road Improvement Fund Acts. This unusual concentration of scientific and administrative talent suggests that the study of agricultural meteorology may have enjoyed more prestige then than it does now!

Middleton spent several years managing the Ross-shire farm where he spent his boyhood, and he knew as well as anyone at that meeting how the well-being and security of a farming community depends on getting the right weather at the right time for cultivating the soil and growing crops. Though he welcomed the attempts that Hooker and Geddes made to express farming experience in graphs and formulae, he made gentle fun of their purely statistical approach to the problem. 'We must agree that in spite of errors, there was an amazing similarity between most of Mr. Hooker's forecasts and the actual yields. One felt that Mr. Hooker had hit a system. It was the sort of system that if applied at Monte Carlo would make Mr. Hooker a rich man. But it was a system that in the 35 years (of the analysis) made misses enough to cause misgivings to the prudent agriculturist. The prudent agriculturist in the person of Sir Daniel Hall had already urged a closer study of the effects of weather on crops and co-operation between the meteorologist and the plant physiologist'.

Statistical papers on weather and crop yield are still being written, some facilitated, some apparently stimulated, by the availability of electronic computers. For example, in the most recent analysis of the Broadbalk experiment at Rothamsted, Buck[2] calculated multiple regressions for the yield of wheat from 6 plots with 17 variates in 67 years. Rainfall was the only weather parameter significantly correlated with yield—a result first suggested by Lawes and Gilbert[3] in 1880 and confirmed by Fisher[4] over 40 years ago. Watson[5] commented on this lack of progress: 'The fundamental defect of this approach is that the dependence of yield on climatic factors is usually far too complex to be described adequately by linear regressions on a few gross measurements of climatic variation, except perhaps when one factor, most likely rainfall or lack of it, dominates over all others. At best, any correlations so established are empirical, difficult to interpret reliably in terms of known effects of climatic factors on plant growth, and do not necessarily describe a direct influence of weather on the plants'.

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Statistics is the wrong tool for exploring crop-weather relationships because it tries to bypass the search for fundamental mechanisms and causes. In most of the early papers in this subject, the effects of soil conditions on cultivation or of weather on germination were considered very briefly, but the environmental control of other important physiological processes was often completely ignored. This seems strange because, from about 1900 onwards, plant physiologists were measuring the exchange of carbon dioxide by leaves and plants growing under controlled conditions in the laboratory. At first, they may have been wary of extrapolating their results to the field, but in 1920 the foundations of modern growth analysis were laid by the publication of two classic papers in which Briggs, Kidd and West[6] established the concept of a unit leaf rate. This is commonly referred to now as a net assimilation rate, the net production of dry matter by a stand of plants per unit leaf area per unit time. Briggs and his colleagues showed that the unit leaf rate of maize was more closely correlated with temperature than with hours of sunshine or other environmental factors; they were among the first to compare rates of photosynthesis in the field and in the laboratory; and their attempt to describe the seasonal change of photosynthesis and respiration separately is still unique.

Within the last 40 years, plant physiologists, ecologists and micrometeorologists have all made major advances along their own lines of research, but because they have often chosen to work independently, our knowledge of the relation between crop growth and weather is still primitive. The main reason for this lack of co-operation is the division of physical and biological sciences in schools and universities. How many ecologists have attended a course in physical meteorology? How many physicists realise there are challenging problems in plant physiology they might help to solve? On the level of the molecule, many of the old barriers between the sciences have already come down and there are signs of similar progress in research that looks at whole plants and whole animals in relation to their environment. There are now several universities in Britain where students of agriculture and forestry are encouraged to take courses in the physics of micro-climate and the water relations of plants. In the USA, Australia and elsewhere, workers from several disciplines co-operate in field experiments that exploit the principles and techniques of modern ecology to study the growth of crops, and similar teams are forming here.

Because I believe that Middleton would have warmly approved all these attempts to foster the interchange of ideas between biology and meteorology, I shall try this afternoon to illustrate this theme from the results of recent research on the physical factors that limit crop growth. This account may not satisfy the 'prudent agriculturists' in the audience, but I hope it may show how physical principles and models can help ecologists to interpret the responses of plants to their complex and ever-changing environment.

Efficiency in Agriculture

When the leaves of a plant assimilate carbon dioxide from the air around them, energy for running the photosynthetic machine is supplied by quanta of visible radiation absorbed by chloroplasts in leaves. Only a fraction of this absorbed energy is stored chemically in the final products of photosynthesis. In ideal conditions, the maximum storage of energy is equivalent to about one-fifth of visible radiation in the waveband from 0.4 to 0.7μ, constituting about half the total energy in the solar spectrum at the earth's surface. In terms of total incident radiation as measured with a conventional solarimeter, the maximum possible efficiency of photosynthesis is about 8 per cent. Because this figure represents an upper limit set by the nature of the photosynthetic process, it holds for all species that synthesise carbohydrate in daylight. The amount of energy from solar radiation is the ultimate physical factor limiting crop growth when all other restrictions are removed.

Assuming an efficiency of 8 per cent, I calculated the fastest mean rates at which three crops could produce dry matter in three climates: sugar beet in England; sugar cane in Hawaii; maize in California. Giving each of these rates the value 100, Table I shows the relative rates at which the accumulation of dry matter has been recorded at research stations or on commercial farms. The differences between lines (i), (ii) and (iii) provide a basis for discussing the whole complex relationship between the growth of crops and their environment.

TABLE I

THE CONVERSION OF RADIANT ENERGY TO CARBOHYDRATE

Crop	Sugar beet[7]	Sugar cane[8]	Maize[9]
Length of growing season (months)	6	18	4
Mean solar radiation in growing season (cal cm^{-2} day^{-1})	260	500	620
Carbohydrate production at 8 per cent energy conversion (g m^{-2} day^{-1})	60 (100)	104 (100)	140 (100)
Relative dry matter production (per cent)			
(i) maximum for experimental plot	52	41	37
(ii) seasonal mean for experimental plot	30	22	22
(iii) seasonal mean for commercial farming	15	10	7

Under experimental conditions, dry matter is produced fastest when there are enough leaves to intercept all the incident sunlight and when roots have access to enough water and nutrients in the soil. Even when these conditions are met, the fastest rates of production on experimental plots are only 40 to 50 per cent of the possible potential rates calculated from the income of radiation. The loss of 60 to 50 per cent can be attributed to two factors: light saturation and respiration. When the leaves of any crop are exposed to sunshine, the efficiency of photosynthesis is always less than 8 per cent and decreases when the intensity of radiation increases. The leaves behave as if they were saturated with light because their chloroplasts are starved of carbon dioxide: the supply of CO_2 molecules from the external air is too slow for the chloroplasts to exploit all the light energy they absorb. Thus the concentration of carbon dioxide in the earth's atmosphere can be regarded as a second physical factor limiting the growth of crops.

The oxidation of carbohydrate by respiration provides living organisms with the energy they need for metabolism and growth. From 20 to 50 per cent of the carbohydrate synthesised by crop plants is later lost by respiration[10], the exact proportion depending on species, stage of development and temperature. Because plants respire, the *net* storage of solar energy in carbohydrate can never exceed about 6 per cent.

Line (ii) of the Table shows that the *mean* rate at which carbohydrate was produced during the growing season was only about 60 per cent of the *maximum* rate for the same crop. At least three factors are responsible for this difference: (a) in the early stages of growth when there are too few leaves to form a complete canopy, crops are inefficient because they fail to intercept all the light reaching the fields where they are growing; (b) as

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leaves get older, they assimilate carbon dioxide more slowly in bright light, possibly because younger leaves compete for nutrients needed to maintain the performance of enzyme systems; (c) towards the end of the growing season, rates of respiration by fruits and other bulky organs of mature plants may approach or even exceed the rate of gross photosynthesis, so that dry matter accumulates much more slowly than during the main period of growth.

Finally, from lines (ii) and (iii), average yields of dry matter obtained commercially are about a half to one third of the yields from the experimental plots. Factors contributing to this large fractional loss include the lack of water or fertilisers, attack by pests and diseases, and waste during harvesting, particularly in bad weather. For world agriculture as a whole, losses attributable to poor husbandry or to extremes of climate are much larger than those represented by the figures in line (iii), imposing a human limit to the production of food in addition to the physical and physiological factors that restrict growth. But whatever the standard of agriculture, Table I implies that at least three quarters of the maximum theoretical yield are lost by the plants themselves because their leaves develop too slowly, die too quickly, and receive too little carbon dioxide to exploit available radiation. We shall now explore more closely the relation between these biological losses and the physical nature of the plant environment.

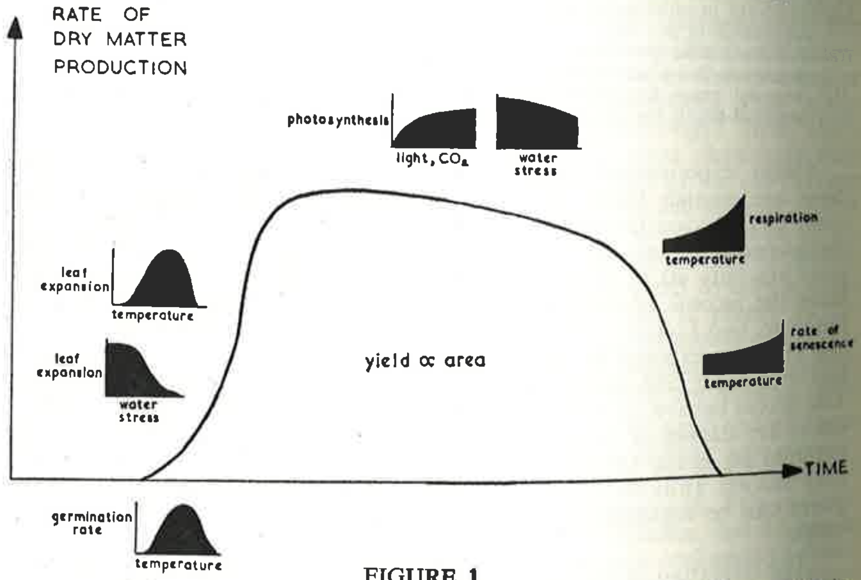

FIGURE 1

Seasonal trend of the rate at which dry matter might be produced by a crop to illustrate the dependence of physiological processes on physical conditions in the environment.

The Growing Season

Figure 1 shows how the rate at which dry matter is produced by a hypothetical crop might change during the growing season with changes in the size and development of the photosynthetic system and with changes in the environment. For many crops, the yield of roots, shoots, or fruits at harvest is approximately proportional to the accumulated dry matter, but this proportionality can fail when a crop is seriously short of water or nutrients[11]. In Figure 1, the total dry matter at harvest is given by the area

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w the curve and is increased either by extending the growing season or
raising the mean rate of production.
The left-hand portion of the curve represents a juvenile phase during
ich the ability to produce dry matter increases rapidly as the leaves
and to intercept more and more light. In a second, mature phase, when
re are enough leaves to absorb all the available light the rate of pro-
tion may stay nearly constant, or may decrease slightly because the rate
photosynthesis by a sunlit leaf gets slower as the leaf ages. In a third,
escent phase, production declines rapidly as the leaves die. Yield is in-
ased by any factor that accelerates the rate at which leaves expand
ovided later development is not also accelerated), and by any factor that
eases photosynthesis or retards senescence.

The relative importance of the three phases in determining the final
ld will depend on their relative duration. For example, cereals such as
eat and barley maintain their largest area of leaves for a relatively short
iod of a week or two in the middle of the growing season, so that the
ape of the production curve is determined mainly by the rates at which
ves expand and wither. Then, as Watson[12] and others have shown, the
ld of grain is closely correlated with mean leaf area during part of the
wing season—though *which* part is still being argued[13]! This interpreta-
n oversimplifies the relation between cereal production and leaf area
cause it ignores an important contribution to photosynthesis by the
rs[14].

rmination

Starting at the lower left-hand of Figure 1, the rate seeds germinate
er sowing depends on temperature, and is usually fastest between about
and 25°C depending on the species[15]. During spring in a temperate
mate, soil temperatures are usually well below the optimum, but ger-
nation often continues at lower temperatures and the minimum for
eals is about 3°C. In some climates, germination is inhibited in soil that
too hot. During summer, in parts of Israel where vegetables are grown,
mean soil temperature consistently exceeds the mean maximum for
mination, about 33°C. By covering the soil with commercial magnesium
bonate in the form of a white powder that reflects radiation, Stanhill[16]
reased the temperature at 2 cm depth by 5 to 10°C for a period of
eral weeks. This difference would probably be large enough to make
me seeds germinate much faster and the economic possibilities of the
thod are now being studied more closely.

There is evidence that germination is promoted when the diurnal range
temperature increases, and other recent measurements show that the
ce exerted by seedlings as they break through the soil may also depend
temperature. The force was strongest at 20°C for clover seedlings and
C for lucerne[17].

af expansion

After shoots emerge from the soil, the rate of photosynthesis per unit
a of field increases rapidly as the leaves unfold and expand. The rate
which the leaf area increases depends on a sequence of physiological
cesses each governed by conditions in the environment. Milthorpe[18]
nd that the new leaves on cucumber plants formed and unfolded faster
their illumination and temperature increased, at least up to 30°C. The
es at which leaves form and unfold are likely to depend on the supply
assimilates from older leaves, which depends on the intensity of light
y receive. Temperature may govern the rate at which the assimilates

move to new leaves and are used to form new cells. After unfolding, the leaves expanded at a rate that was independent of light intensity, apparently because they could assimilate fast enough for their own immediate needs even in weak light equivalent to the average intensity of natural radiation on a very cloudy summer day. In contrast, the rate they expanded increased rapidly as the temperature of the growth rooms increased from 5 to 24°C, but decreased rapidly at temperatures above 24°C. Changes in expansion of the leaf as a whole were associated more with changes in the size of individual cells than in the rate at which the cells divided.

The dependence of leaf expansion on temperature rather than illumination was demonstrated for several species by G. E. Blackman[19] and others but the physiological basis of this dependence is still being sought. In Wageningen, Brouwer showed that the development of seedlings depends on the temperature of the soil or solution in which the roots are growing rather than on air temperature. The rate of development was also sensitive to changes in the osmotic pressure of the root medium and on aeration. In short, any physical factor that inhibited the uptake of water by roots seemed to slow the leaf expansion of seedlings.

In a recent anatomical study of the root system of bean seedlings, Brouwer[20] found that the unsuberised and relatively permeable endodermis behind root tips was longer at 20°C than at higher or lower temperatures and, if this behaviour is common to other crop plants, it may explain why leaves usually grow fastest when their roots are between 20 and 25°C. Other measurements[21] suggest that individual root cells become more permeable as temperature increases, but it is difficult to explain the existence of an *optimum* temperature solely on the basis of changes in the permeability of cell walls or protoplasm.

If Brouwer's hypothesis is correct, the effect of water uptake on leaf expansion is likely to be mediated to leaves by their turgor or water stress. Any atmospheric factor increasing this stress would be expected to retard the expansion of leaves, a deduction that is supported by measurements of growth at different rates of transpiration. For example, members of the Botany Department at Rothamsted[22] found that leaves of kale, sugar beet, and wheat plants expanded more slowly as the relative humidity decreased. Transpiration was presumably faster in drier air and, for a given resistance to water flow through the plants, water stress in the leaves would increase as transpiration increased. Elsewhere, Whitehead[23] showed that the expansion of sunflower leaves was strongly dependent on wind speed in conditions where the transpiration rate increased with wind speed. In one experiment, seedlings grown in an air-flow of 1 mile per hour developed a total leaf area of 330 cm² whereas similar seedlings grown at 33 mph grew only to 20 cm² in the same time.

To summarise, investigations in growth rooms and laboratories show that the rate at which leaves of a field crop expand depends in a complex way on the temperature and water content of the soil and on the atmospheric factors governing transpiration. More evidence is needed to construct models that can be used to predict how the growth of a crop will change with conditions in the environment during the first phase of growth. Meanwhile, one of the few relations that can be expressed quantitatively is the dependence of rates of leaf expansion on temperature. The rate of expansion is described by a relative growth rate, the increase of leaf area per unit leaf area per unit time. During the first few weeks of growth, this relative rate is often nearly constant so that the area of leaves increases by the law of compound interest. At a temperature of about 20°C, measurements of the relative growth rate range from 0.15 or 13 per cent per day for sunflowers to 45 per cent per day for potatoes[24]. The relative rate is strongly dependent on temperature, usually decreasing by two to three times when temperature decreases from 20 to 10°C.

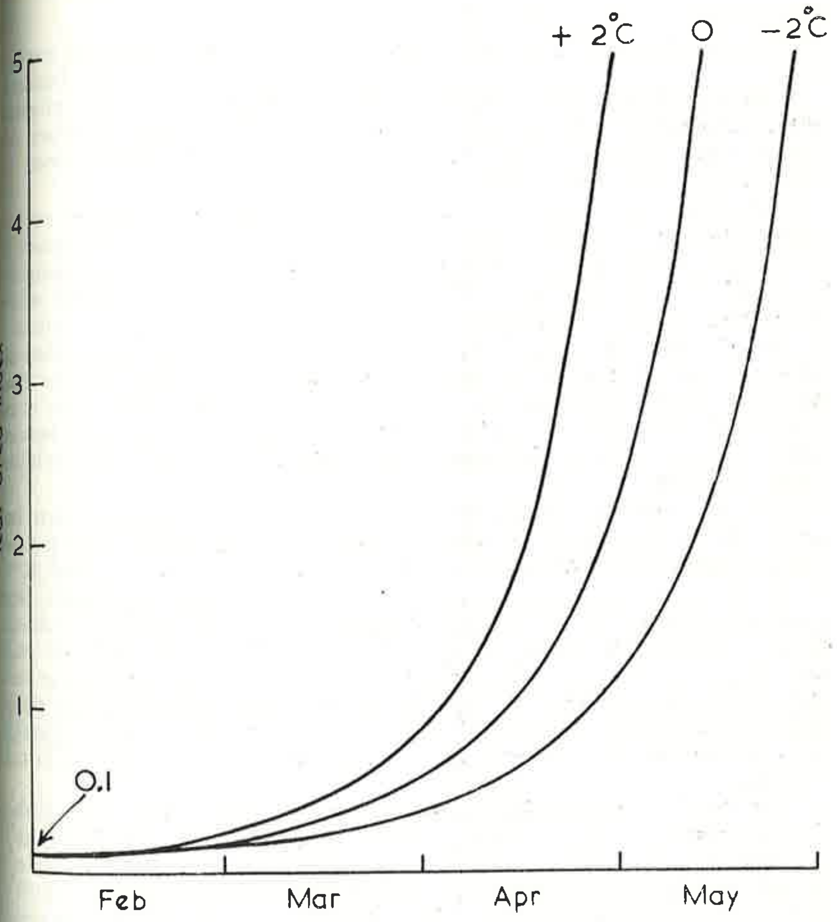

FIGURE 2

The increase of leaf area index L for a crop with L=0.1 at the beginning of February, assuming average weather (0°C) and temperatures 2°C above and below average. The relative leaf growth rate (1/L dL/dt) is 0.2 at 20°C and has a Q_{10} of 3.

To illustrate how the expansion of leaves by a field crop might change with differences of temperature in the same season from year to year, Figure 2 shows the behaviour of a hypothetical crop (e.g. winter wheat) with a leaf area index of 0.1 at the beginning of April. (The leaf area index, introduced by Watson, is the ratio of leaf area counting one surface only, to the area of underlying ground). I assumed that the relative growth rate was 0.2 per day at 20°C, decreasing to a third or 0.07 at 10°C, and pro rata, and calculated the rate week by week for three seasons: (i) an average spring at Rothamsted with temperature increasing by 3°C per month; (ii) a cold spring with temperatures 2°C *below* average throughout; (iii) a warm spring with temperatures 2°C *above* average throughout. When the leaf area index is more than 2, the temperature range of ±2°C accelerates or retards growth by about a fortnight, an effect that is consistent with year-to-year differences in the growth of cereals, grass, and other crops that have stood in the ground over winter.

Photosynthesis

Once the leaves of a field crop have expanded to form a closed canopy intercepting all the available light, the gross rate of photosynthesis becomes independent of leaf area and is therefore independent of the physical factors governing leaf area *per se*. The rate at which plants produce dry matter then depends on the balance between carbohydrate formed by photosynthesis and destroyed by respiration.

Laboratory experiments show that the rate leaves assimilate carbon dioxide depends mainly on their illumination and on the concentration of carbon dioxide in the surrounding air. Photosynthesis is much less sensitive to water stress than the rate of leaf expansion. In one experiment where clover was grown in drying soil, the plants absorbed carbon dioxide at a steady rate until the leaves began to wilt[25]. Other work has shown that the critical water stress at which leaves stop expanding is much smaller than the stress needed to induce wilting. During a period of intermediate stress when leaves can produce carbohydrate but cannot expand, they become tough and thick: hence the unpalatable texture of lettuce grown without proper watering.

Similarly, the rate of photosynthesis is much less sensitive than leaf expansion to changes of temperature, and in many species is relatively constant between 10 and 30°C[10, 26]. At temperatures between 30 and 40°C, the inactivation of enzymes prevents the photochemical machinery from working properly, and below 10°C the supply of carbon dioxide to chloroplasts is seriously restricted by the slowing of diffusion through cell walls and cytoplasm. Very recently, Kuiper[27] showed that photosynthesis at temperatures between 0 and 10°C can be greatly increased by treating plants with a chemical that makes leaf cells more permeable to carbon dioxide, and this technique may have important implications for agriculture in cold climates.

The relation between photosynthesis and the concentration of carbon dioxide depends on light intensity. When leaves are very brightly lit, as in full sunshine, the rate at which they can assimilate carbon dioxide is limited by its rate of diffusion from the external atmosphere to the sites of photosynthesis within cells. This means that the assimilation rate increases almost linearly with the external concentration of carbon dioxide, an effect exploited by growers who add carbon dioxide to the air in their glasshouses to increase crop growth. Figure 3 demonstrates a general rule that the departure from linearity is greater in species with faster rates of photosynthesis. The supply of carbon dioxide for field crops is not an important discriminant in their photosynthesis because diurnal changes of concentration are usually small. The thickened parts of the two curves in Figure 3 show the average range of concentration during daylight measured by Tamm and Krzysch[28] within the canopies of sugar beet and maize crops. The amount of carbon dioxide absorbed per day by a vigorously growing crop is equivalent to *all* the CO_2 in a layer of atmosphere 30 to 40 metres thick, but because the atmosphere is so thoroughly stirred and mixed by turbulence, this demand is met by a relatively trivial decrease in the mean concentration through a height of 1000 metres or more.

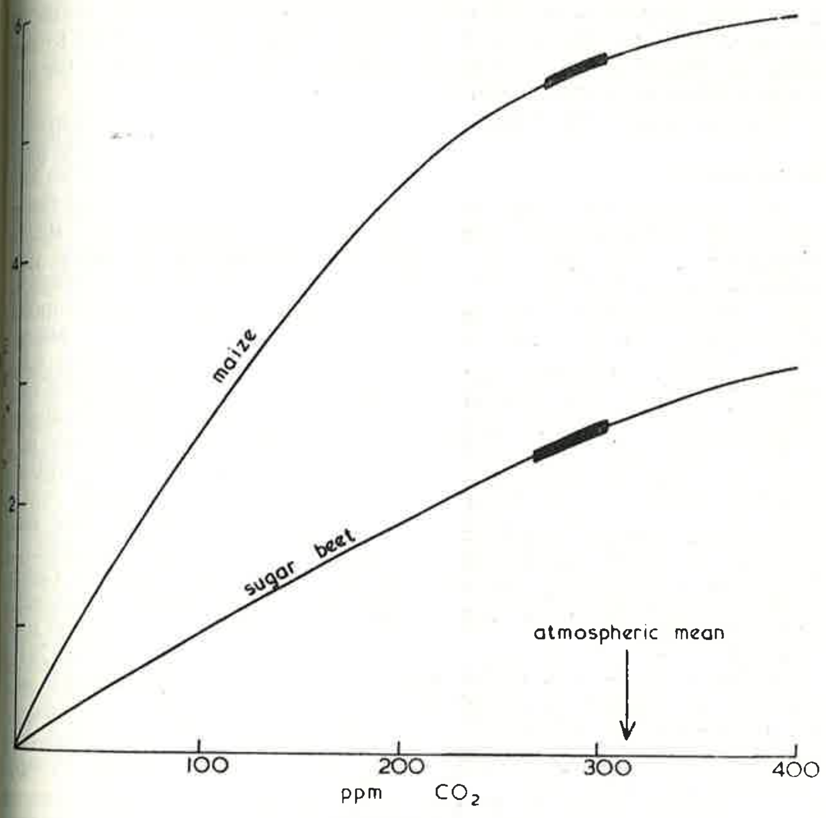

FIGURE 3

easured gross photosynthesis of the leaves of maize (Hesketh[38]) and of sugar beet aastra[39]) as a function of carbon dioxide concentration in the external air. The ck lines show the range of concentration in the canopies of field crops (Tamm and Krzysch[28]).

Although *diurnal* changes of carbon dioxide can be dismissed from a scussion of the physical factors that limit growth, long-term changes can t, because any general increase of carbon dioxide in the earth's atmosere will increase rates of photosynthesis and the yield of crops. There is idence that the carbon dioxide released by the burning of fossil fuels s increased the mean concentration from about 280 parts per million the middle of the 19th century to about 314 ppm in the early nineteenties[29]. Unless future needs for fuel are met largely by the development nuclear power, the growing consumption of coal, gas, and oil may inease atmospheric carbon dioxide to almost 400 ppm by the year 2000. y itself, this change might be expected to increase crop yields by 10 to 20 r cent, but it is difficult to predict whether changes in the absorption of diation by carbon dioxide will lead to changes in the earth's climate rge enough to be welcomed or deplored by farmers[30].

At the concentration of carbon dioxide prevailing in the atmosphere, e dependence of photosynthesis on light intensity follows a law of diminning returns. In weak light the photosynthesis of all crop plants increases early with light intensity, but as the light gets stronger, the efficiency photosynthesis decreases, and in full sunlight many species behave as if they were saturated with light. However, some species, notably maize, sunflower, cotton and several tropical grasses, seem better adapted to sunny climates, because their leaves are not saturated with light even at the maximum intensity of tropical sunshine[31].

Because light is the main external factor governing the photosynthesis of a mature crop canopy, several workers have developed simple models of crop structure that allow the intensity of light on leaves at a given height within a canopy to be related to the area and distribution of the leaves above them. Then, knowing the relation between photosynthesis and light intensity for a single leaf, it is possible to estimate rates of gross photosynthesis for a complete canopy and to show how these rates change with the income of radiation and with leaf area index. From one such model[32], I calculated gross photosynthesis as a function of leaf area index assuming mean values for radiation and day length throughout the growing season, and Figure 4 shows the relation for sugar beet and for maize. The curves also show seasonal changes of leaf area index for crops of sugar beet grown at Rothamsted and maize grown at Davis, California[9]. The leaves of the sugar beet expanded relatively slowly so that the complete interception of radiation needed for the maximum efficiency of photosynthesis was not achieved till nearly four months after sowing. The waste of solar energy during this first phase of growth was equivalent to about 40 per cent of all the energy available during the growing season from April to October. In the much sunnier and warmer climate of California, maize leaves expanded so rapidly that maximum rates of photosynthesis were reached in just over one month after sowing. An exceptionally dense sowing of 283,000 plants per acre accounts for the remarkable leaf area index of this stand. At the end of July, it produced dry matter at a rate of 52 g m^{-2} day^{-1} or 29 cwt per acre per week, the fastest rate on record for *Zea mays*. Comparison of the two curves in Figure 4 emphasises the importance of rapidly panding leaves in the early weeks of growth to achieve maximum rates photosynthesis as early as possible.

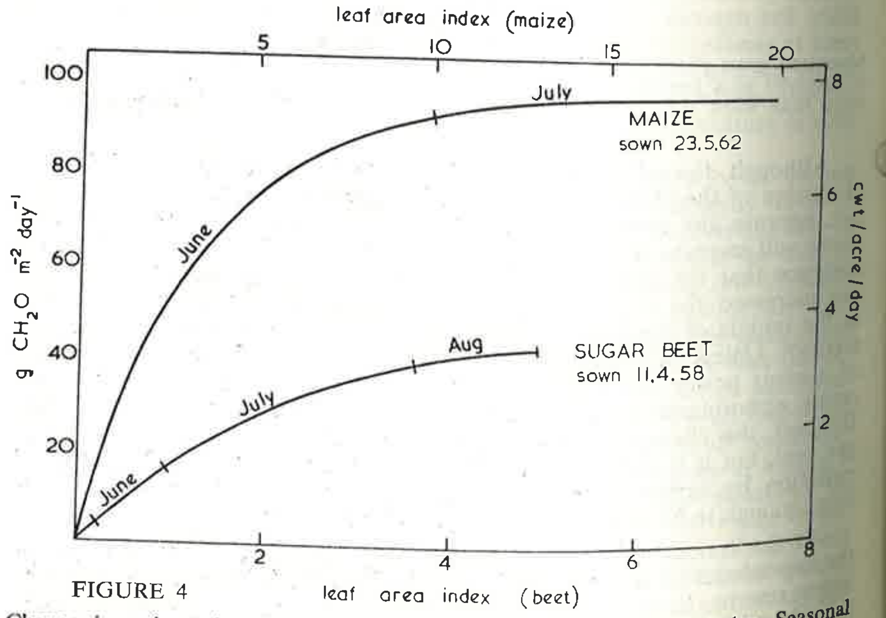

FIGURE 4

Change in estimated rates of gross photosynthesis with leaf area index. Seasonal increases of leaf area index shown for sugar beet at Rothamsted and for maize in California (Williams *et al*[9]).

The fraction of light intercepted by a canopy of given leaf area depends the angle of the leaves with respect to the source of light. To intercept per cent of incident light, crops like clover and kale with relatively rizontal leaves need a leaf area three to four times the area of the field low them, whereas cereals and grasses with leaves hanging more vertically ed a leaf area index of 8 or 9. Figure 5 shows how the estimated gross otosynthesis by stands of sugar beet and maize changes with the income radiation, assumed to be completely intercepted by the canopy. The same aph shows the range of mean radiation recorded over a period of several ars for each month of the growing season. During the growth of sugar et in south-east England, the mean rate of photosynthesis in a given onth will change very little, even if the weather is unusually cloudy or usually sunny. Small changes of photosynthesis that might be attribu- ble to differences in radiation will often be obscured by changes in other rrelated weather parameters such as rainfall. For maize growing in Israel, otosynthesis changes more rapidly with radiation, but because there is most no cloud in summer, the income of radiation in a given month is most constant from year to year[33].

Thus, although the uptake of carbon dioxide by field crops must ulti- ately be governed by the light they absorb, changes in the standing dry eight of plant communities can seldom be correlated with *natural* changes radiation. To increase the range of light intensity, several workers have own plants beneath screens and have shown that the production of dry atter is correlated with the amount of radiation received below the reen. Results from these experiments need cautious interpretation be- use plants cannot be screened from radiation without changing other portant features of the microclimate such as temperature, humidity and ind. These secondary changes can affect the rates leaves expand, trans- re and respire, so that changes in the production of dry matter cannot be scribed to changes of gross photosynthesis alone.

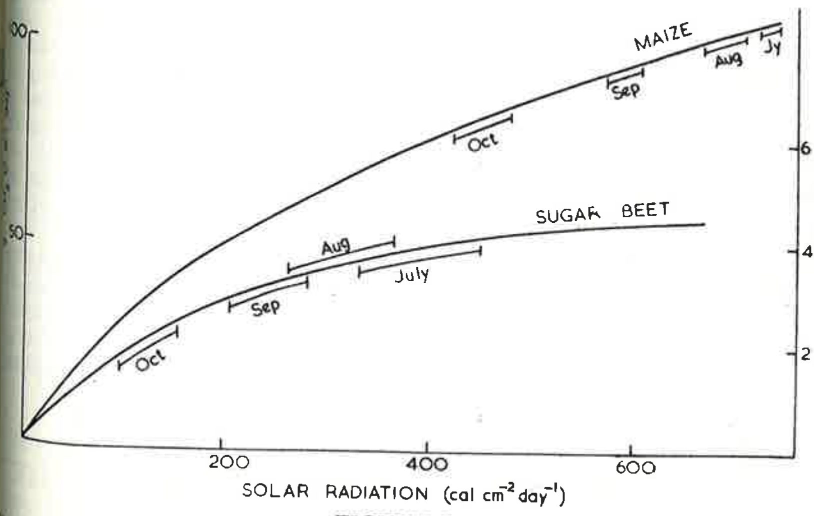

FIGURE 5

nge in estimated rates of gross photosynthesis with mean daily radiation. The ge of radiation for each month of the growing season is shown for the climates of south-east England (sugar beet) and of central Israel[32] (maize).

Respiration

All plant organs respire carbon dioxide while they are growing, and any increase in the rate of respiration decreases the amount of dry matter remaining at harvest. The main physical factor governing the rate of respiration is temperature, and for any plant at a given stage of development an increase of temperature by 10°C is expected to double the respiration rate. The biochemistry of respiration has been studied in great detail at the level of individual cells, but comparatively little is known about the respiration of whole plants and still less about the respiration of crops in the field. The available evidence suggests that, on the basis of dry weight, plants respire less in the dark as they age, and in the light, respiration may be correlated with the gross rate of photosynthesis[34].

By shading young plants in growth rooms, Watson and Hayashi[35] found that sugar beet and barley respired at about the same rate per unit leaf area. Because the photosynthesis of barley was slower, it lost 18 per cent of its assimilated carbon by respiration whereas sugar beet lost only 12 per cent. These percentage losses are smaller than others reported,

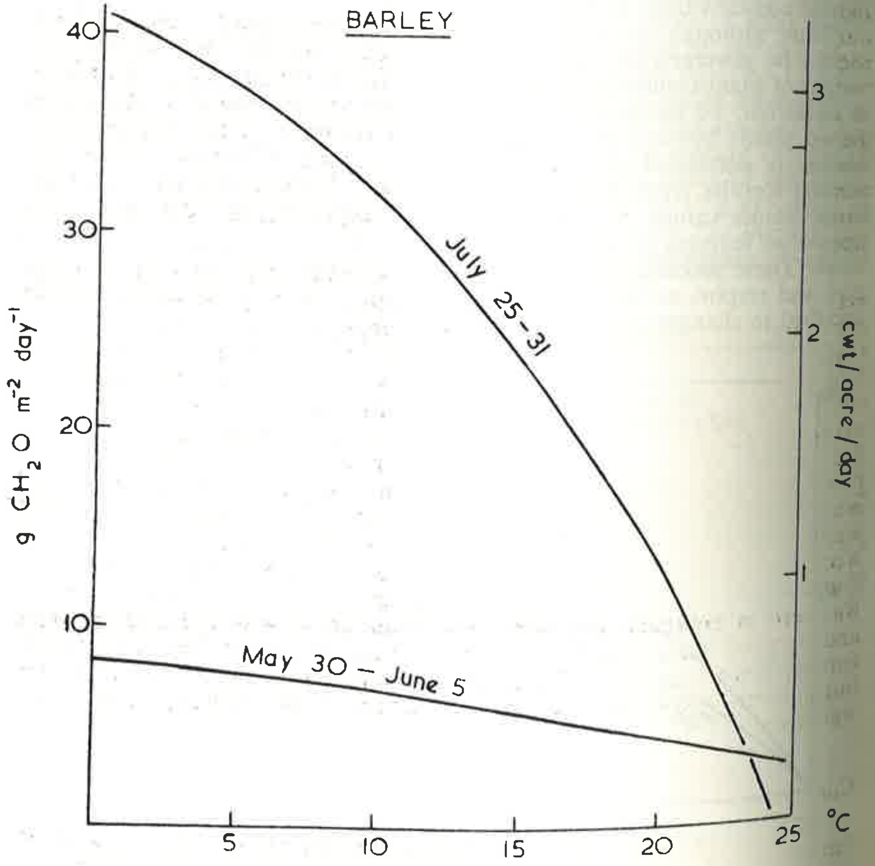

FIGURE 6

Estimated change of dry matter production with temperature for a field of barley at Rothamsted.

sibly because the plants were only a few weeks old. With the growth of rge root (beet) or a seed head (barley), the weight of respiring tissue reases in relation to the area of the photosynthetic surface, so the frac- al loss of carbohydrate by respiration is likely to increase as plants ture. This increase was demonstrated at Rothamsted in 1963 when the bon dioxide of a field of barley was measured throughout the growing son by combining meteorological estimates of the CO_2 flux with labora- y measurements of photosynthesis and respiration. From unpublished alysis, the respiration of the whole crop increased from 34 per cent of ss photosynthesis at the end of June to 45 per cent at the end of July en the crop was ripe. Assuming that photosynthesis was independent of perature and that respiration doubled for an increase of 10°C, Figure 6 ows a hypothetical change of *net* photosynthesis or dry matter production th temperature. During the earlier part of the season, an increase of tem- ature from 0 to 25°C would be needed to halve production. In the ture crop, production is much more sensitive to changes of temperature d would be zero at 25°C because the rate of respiration estimated at this mperature equals the estimated photosynthesis.

In one of the earliest studies of the effects of temperature on the yield d quality of peas, Boswell[36] showed that the plants developed faster in rm than cool summers, flowered when they were smaller and set fewer ds. The adverse effect of higher temperature on yield can be split into o components. First, there was less time for flowering and the formation f seeds, so that in terms of Figure 1, growth was decreased by shortening e growing season. Second, as respiration increased, there was probably ss carbohydrate left to fill the pods. Again in terms of Figure 1, increasing mperature would slow the maximum rate of production and the right nd leg of the production curve would approach the time axis more eeply.

Looking at the whole growing season, it seems that the yield of crops ay be positively correlated with temperature during the period of leaf xpansion and negatively correlated with temperature after flowering. When looker[37] examined the partial correlation of yield with temperature, he und a systematic change from a positive to a negative correlation co- fficient in the spring for cereals, beans and turnips. The yield of peas, angolds and hay was negatively correlated with temperature throughout e summer. He concluded that 'a cool summer means a good quantity of roduce. Coolness is much more important than rainfall though the latter ust obviously not fall below a certain minimum'. In a much more detailed alysis, Buck[2] calculated the effect of an additional degree Fahrenheit in eekly mean air temperature on the yield of winter wheat from the heavily unged plot on Broadbalk, eliminating the effects of rainfall. The effect as zero in February, increased to a maximum of 4 lb per acre in April, nd dropped sharply to *minus* 8 lb per acre in August. This variation is ntirely consistent with the analysis of temperature effects discussed here, ut in terms of cold statistics, the correlation of yield on temperature is not gnificant!

Conclusion

This account of the relationship between crop growth and physical en ironment is far from complete. It contains no reference to the significance f different day and night temperatures or to the effects of changing day ngth on plant development: these are discussed in detail elsewhere. Get-

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ting the right weather for a few days or even a few hours at some critical stage of plant development may be very important, but little is known about this.

I have concentrated on the main effects of weather on the size and efficiency of the photosynthetic system, trying to show how the results of physiologists working in the laboratory and ecologists in the field can be related by basic physical principles. At each stage of this work, the physicist has an important part to play. First, his help is needed in the design and proper exposure of instruments for measuring weather and for estimating the exchange of heat, water vapour and carbon dioxide between plant communities and their environment. When records from these instruments have been analysed and interpreted, his next task is to develop simple but realistic models that can be used to predict the behaviour of different species in various environments. Finally, he can co-operate in the practical applications of crop ecology to grow more food: by irrigation and drainage; by spraying plants with chemicals that close stomata and save water; by supplying extra carbon dioxide in glasshouses; by changing the thermal properties of soils to speed germination; by sheltering crops behind wind breaks. Techniques such as these cannot be fully exploited for agriculture until their physical and physiological bases are fully understood. It is in response to this urgent challenge that work in several disciplines and in many countries is now being co-ordinated by the International Biological Programme.

Finally, this address was based on what I have learnt from colleagues in the Physics and Botany Departments at Rothamsted, at the School of Agriculture, Sutton Bonington, and at research institutes in Wageningen. I hope they will not feel their ideas have been misrepresented.

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