Response of Crops to Environmental Change Conditions: Consequences for World Food Production

Research · April 2015

DOI: 10.13140/RG.2.1.3098.5769

David W. Lawlor
Formerly Rothamsted Research
164 PUBLICATIONS **10,707** CITATIONS

J. Agric. Meteorol. 52 (5) 769−778, 1997

Response of Crops to Environmental Change Conditions: Consequences for World Food Production

David W. Lawlor
(Biochemistry and Physiology Department, IACR-Rothamsted,
Harpenden, Herts., AL5 2JQ, UK)

Abstract

Numbers of people and their fossil fuel consumption are increasing, also land use is changing, contributing to increasing atmospheric carbon dioxide (CO_2) concentrations and probably increasing global temperatures: by 2100 AD these may reach 700 µmol/mol and 4°C respectively. The consequences for growth and production of the main foods - the cereals wheat and rice (with C3 photosynthesis) and maize, sorghum and millet (with C4 photosynthesis) - and the mainly C3 root and pulse crops will be considerable for food production on local and global scales. To assess the effects on agricultural production, experiments which analyse the effects of CO_2 concentration and air temperature and their interaction, and the effects of altered rainfall on crops, are assessed. Studies at IACR-Rothamsted on wheat and sugar beet are specifically discussed. Plants with C3 photosynthesis will respond positively to elevated CO_2; C4 crops less so. Wheat and rice respond with ca. 25% increase in yield with CO_2 doubling, equivalent to an increase of ca. +2.5% per decade over the next century. Root crops respond with larger increases. Adequate water and nutrition are essential for increased production to be expressed. Increasing temperatures will probably decrease production of most crops except where they are currently limited by cool conditions. Wheat and rice yields decrease about 25% for a 4°C increase and sugar beet about 8% (-2.5 and -1% per decade respectively). Production will increase most with good nutrition, water, etc, and least in poor growth conditions. Effects of changing environment on photosynthetic acclimation and production are considered. Acclimation is related to assimilate production and the "sink strength" of growing organs for assimilates, and to the feedback mechanisms between carbohydrate accumulation and development of the photosynthetic system. Complex source-sink and plant-environment interactions may explain variability of acclimation in crops. Use of experimental results to assess food production over large areas suggests a beneficial effect of elevated CO_2 where water and nutrients are adequate but as in much of world agriculture this is not so, gains will be modest and possibly offset by negative effects of elevated CO_2 under resource limitation. The needs for plant breeding and genetic manipulation in order for staple foods to be more efficiently produced under global environmental change conditions are considered.

Key words: climate change, crop production, carbon dioxide, temperature, water supply, photosynthesis.

1. Introduction

Composition of the global atmosphere is changing: carbon dioxide, methane, nitrogen oxide and ground level ozone concentrations are increasing (Rozema et al, 1993). This is caused by increasing use of fossil fuels by a rapidly growing human population and to destruction of forests and grasslands causing loss of fixed carbon. The rate of increase of CO_2 is substantial, currently some 1.5 µmol/mol per annum and likely to continue for a considerable period. Few ecosystems or indeed agriculture will be spared the effects. Carbon dioxide is a major determinant of biomass and yield as it is the substrate for photosynthesis and thus directly affects plants (Lawlor, 1993). However, the changing concentrations of other gases will have considerable long term effects, e.g. decreasing stratospheric ozone is increasing the UV-B incident on parts of the globe (Krupka and Kickert, 1993).

A major consequence of increasing CO_2 and other gases which absorb infra-red radiation, is global warming. Although fragmentary, there is now much direct and indirect evidence that global temperature has indeed increased (International Panel on Climate Change) (see also Rosenzweig and Parry, 1994). Since the start of the industrial revolution temperatures have increased by approximately 0.6°C and five of the hottest years on record have occurred in the last 20 years: currently warming is about 0.1°C per decade. Predictions from global climate models are that temperature will increase most at high latitudes, and probably more in winter than summer. Additional expected changes include altered cloud cover and rainfall and snowfall amounts and patterns. Extreme events may increase, globally and locally. Evidence for such trends is poor but even slight changes will have direct and potentially damaging effects on crops and human well-being. What will the effects of altered atmospheric composition, temperature and precipitation be for crops and what will the consequences be for man and other organisms dependent upon them? There is large literature examining these topics and much scientific activity is directed to analysing and assessing the problem. Ultimately to be able to assess or forecast the effects of environmental changes requires detailed and accurate forecasts of the potential climate changes. However, it is necessary to assess and quantitatively model the likely effects of a range of future environmental conditions on plants and crops. One approach to obtaining the necessary information is to subject crops to a range of conditions experimentally (Lawlor, 1996), including extremes and interactions between variables, and measure responses. The aim should be to obtain information to explain mechanisms and control/regulation of responses as well as to obtain empirical relationships from which the effects on crops caused by future environments may be forecast. Ultimately the goal must be to formulate robust, quantitative models which are as mechanistic as possible and necessary for the task (Mitchell et al, 1995). They should reflect the responses of crops over a wide range of conditions, including the most likely future scenarios: they should be tested. Successful models can be used for economic assessments (Carter et al, 1992), to judge costs and benefits of potential remedial measures for minimizing the possible damage resulting from environmental change. Also they aid in optimizing resources. This article addresses specifically the problem for crop production and the consequences for global food supplies and assess how progress has been made in understanding the responses of crops to specific conditions and their interactions.

2. Experimental methods of assessing crop responses

Many experimental studies of different crop responses to environmental change have been done under a range of conditions with many techniques. Ideally, the crop's response to a range of CO_2 concentrations, temperatures, water supplies etc, would be analyzed singly and in interaction, whilst maintaining other factors close to the current optimum agronomic practice. This is difficult to achieve due to the size and cost of facilities. Also, analyses of crop responses become extremely demanding as the number of factors increases. Thus all analyses are, to some extent, limited. Methods employed (see Rozema et al, 1993; Lawlor, 1996) include a) controlled environments and glasshouse compartments, b) field enclosures and environmental gradient tunnels, c) open-top field chambers, d) open field studies with CO_2 (free air CO_2 enrichment or FACE). Methods in a) and b) generally provide excellent experimental control of atmospheric CO_2 concentrations and temperatures but at the expense of light: spectral quality and total energy profoundly affect plant growth and production. In

a) rooting volume is generally restricted, which is important if plant growth is affected by restricted root growth, also drought effects are difficult to simulate. Methods b), c) and d) avoid limited rooting volume although control of nutrition and water may be difficult. However, b) and, to a smaller extent, c) suffer from reduced and altered light and control of nutrition. Regulation of CO_2 and temperature in b) provides ranges of conditions, which are useful for analysing responses but require careful analysis, whilst control in c) may be limited. FACE methods provide current seasons radiation and temperatures and the nutrition can be regulated but water supply cannot (without automatic rain shelters to ensure deficits). Currently, FACE experiments lack experimental contrast in temperature.

3. Photosynthesis and environment

3.1 Photosynthetic mechanisms Responses to elevated CO_2 and temperature differ between species, but they can be understood by reference to the C3, C4 and Crassulacean acid metabolism (CAM) mechanisms of photosynthesis (Lawlor and Keys, 1993). Many of the photosynthetic responses to climate change are attributable to the enzyme ribulose bisphosphate carboxylase-oxygenase (Rubisco) of the Calvin cycle. This multi sub-unit enzyme (see Lawlor, 1993) has a very slow rate of carboxylation, i.e. CO_2 assimilation, so a large concentration of enzyme is necessary for rapid rates of CO_2 assimilation. The current atmospheric CO_2 concentration is insufficient to saturate Rubisco; indeed as stomatal conductance (gs) decreases inward CO_2 diffusion during photosynthesis (P) is restricted so CO_2 concentration in the leaf (Ci) is only about 0.8 of the ambient concentration. At the enzyme active sites the concentration is even smaller. If gs decreases, due to water stress for example, yet P continues, then Ci and P fall but photorespiration increases. Elevated ambient CO_2 generally decreases gs but despite this Ci rises and P increases. In addition, the oxygenase function of Rubisco, which is greatest at high O_2/CO_2 ratio and small Ci, results in photorespiration which offsets carboxylation and reduces P. The oxygenase is increased, relative to the carboxylase, by warmer temperatures (also the solubility of O_2 increases relative to CO_2). Thus, hot, dry conditions exacerbate the inefficiency of Rubisco, particularly in the current atmosphere with small CO_2 and large O_2 concentrations, and give low net P in C3 plants such as wheat, rice, potato, sugar beet, cassava and pulses.

However, C4 (e.g. maize, sorghum, millet) and CAM plants (e.g. pineapple) have CO_2 concentrating mechanisms and operate with small Ci and gs. C4s have compartmentation of Rubisco in cells which reduce the exposure of the enzyme to O_2 and increase the CO_2 concentration at the active sites many-fold, effectively eliminating photorespiration. They are, therefore, much less sensitive to small gs than C3 plants and have greater rates of P and water use efficiency. CAM plants have CO_2 assimilation in the dark so they can operate with closed stomata during the day, thus avoiding droughts. Rubisco is a large protein, containing much of plant nitrogen. C4 plants have less Rubisco and greater N-use efficiency then C3's. Therefore, increasing atmospheric CO_2 increases rates of P, and substantially increases biomass production and generally yield of C3 plants but has little effect on C4s.

3.2 Photosynthetic acclimation and source-sink relations Increasing ambient CO_2 from ca. 350 to 700 µmol/mol generally increases P at temperatures above 25°C by some 40 to 50% when the exposure is short-term. Plants at 700 µmol/mol CO_2 often show only slightly greater P (and have smaller capacity for P) than plants grown at 350 µmol/mol (Cure and Acock, 1986). This acclimation is ascribed to two types of processes: negative regulation ('down-regulation') in which the photosynthetic system and particularly Rubisco is inhibited by the normal regulatory mechanisms so decreasing the rate of P but without loss of components of the photosynthetic apparatus, and `negative acclimation' in which the composition of the photosynthetic system changes with loss of components, especially Rubisco (Lawlor and Keys, 1993). Both down-regulation and negative acclimation can occur at the same time. These mechanisms for reducing P have been widely observed but are not universal or indeed reproducible. Also positive regulation and acclimation have been demonstrated under some conditions (Delgado et al, 1994). Decreased P will reduce yield potential and also sequestration of carbon: this has implications for the ability of the biosphere to use the rapidly increasing CO_2. Indeed, the current vegetation may become relatively less efficient with time.

Interaction between the source of assimilates and sinks for them is of greatest significance (Lawlor, 1991): it is integral to the production of yield and to the regulation of P via feedback regulation and acclimation discussed above. Source processes produce assimilates while sinks use them for growth and storage (Lawlor, 1995). Probably photosynthesis is regulated to achieve a balance between source and sink. Excessive CO_2 assimilation causes accumulation of starch and sugars and may lead to metabolic imbalances (e.g. in osmoregulation and C versus nitrogen assimilation) which are deleterious to the plant and are responsible for acclimation. As the processes determining sink and source behaviour are very different biochemically and respond to environmental conditions in different ways, it is to be expected that plants and therefore crops will respond to environmental change in rather different and complex ways. Differences between annual and perennial crops in response to environmental change may be important, for annuals have rapid generation time and therefore can be selected more rapidly than the long generation time perennials, such as trees. Perennials also have different source-sink relations but the control mechanisms are not clear, possibly the sink capacity is greater than in annuals so allowing more flexible relationships between photosynthesis and growth. Adaptation of crops to their current environments is the consequence of long term adjustment to many interacting factors. However, it is still not entirely clear how adaptation is achieved and this is a major uncertainty in planning how to adapt crops to environmental change.

4. Effects of environmental conditions on crops

Annual crops provide the major part of human dietary protein and carbohydrate, particularly the gramineae. Wheats of different species are the dominant cereal of world trade and are grown very widely, often in hot, dry environments (wheat belts of north and south America, eastern Europe, Australia) as well as in temperate latitudes. Rice is dominant in tropical regions but also grown widely and to high latitudes, e.g. northern Japan. Maize and sorghum and millet are also of considerable importance. Pulses are of major significance in the supply of protein; many species are grown world wide and are often well adapted to local conditions, thus offering the prospect of flexibility in the face of environmental change. Although in many aspects of biology they differ from the cereals, their responses to environmental change may be rather similar. Root crops such as potato, cassava and sugar beet are important carbohydrate and energy sources (but also protein as well). Flower and fruit crops are less important in terms of tonnage but of considerable importance economically and in providing quality (e.g. vitamins) and dietary variation. These crops are often from woody, perennial woody plants. Cotton is produced by this type of plant and has great economic if not food importance. Such crops, especially long-lived tree species, will experience different conditions over their life and adjustment mechanisms may be very different from annual species. I concentrate on annual crop production. Pests and diseases will be of major significance but are not considered.

4.1 Carbon dioxide. The principal effects of CO_2 on annual crops are now well understood qualitatively but less so quantitatively. The classic literature analysis of Kimball (1983) showed that a range of crops, predominantly those of the southern USA, respond to CO_2 of about 700 μmol/mol compared to 350 μmol/mol by increased biomass production (mean 33%) with considerable range and variability. The effects on yield were smaller and more variable under field conditions (Lawlor and Mitchell, 1991) where environment-crop interactions are complex (Lawlor, 1995). More recent studies have widened the range of crops and increased the number of studies on them and provided greater understanding of the mechanisms of the responses. Effects on weeds will probably be similar to crops with similar biochemistry, growth habit etc. but small changes relative to the crop response may have large impact.

4.1.1 C3 Cereals. Cereals are regarded as determinate crops, with very strictly defined developmental patterns and periods of growth: they do not have large vegetative sinks. Grain size is relatively conservative. Yield variation is mainly in the number of grains produced.

4.1.2 Wheat. Wheat responses to elevated CO_2 generally are somewhat smaller than other crops (Kimball, 1983). Under temperate conditions 700 μmol/mol compared to current ambient CO_2 stimulated biomass production of current bread making winter wheat varieties well supplied with water and nutrients. The increase averaged 22% for *Triticum aestivum* cv. Mercia (Table 1) in studies at IACR-Rothamsted in controlled conditions with ambient temperatures, natural day length and near-natural radiation intensity (Mitchell et al, 1993). The causes of variation in response are possibly differences in radiation and temperature at critical times in development, resulting in imbalance between crop photosynthesis and respiration. Under deficient nitrogen supply the response was negative. The response to elevated CO_2 was similar for another wheat grown in temperature gradient tunnels (Wheeler et al, pers. com.). In the south-western desert region of the USA, growth of wheat in a FACE experiment at 550 μmol/mol CO_2 compared to ambient increased grain yield by a similar proportion (Kimball, pers. com.). Although the percentage stimulation due to elevated CO_2 is variable in different experiments, as expected for the very different conditions, it is nearly always positive when other resources are adequate.

4.1.3 Rice. Experimental studies under near-field conditions (Ziska et al, in press) show that the biomass and grain yield production of rice (*Oryza sativa*) increase by 40% and 27% at 650 compared to 350 μmol/mol CO_2, with differences between growing seasons. Morokuma and. Yajima (1996.) have shown similar effects of CO_2 on production. Earlier studies (e.g. Baker et al, 1992) obtained no effect of CO_2: generally as with other crops the responses have been variable.

Both wheat and rice exhibit similar mechanisms of response to elevated CO_2, the most important being the stimulation of tillering and of flower development or more correctly the greater survival of tillers and flower initials. The additional tillering is the main reason for the increased biomass, and the increased numbers of ears and grains are responsible for the increased grain yields. The mass per grain is generally not increased for either species.

4.1.4 C4 cereals. The C4 cereals do not show very marked increases in production due to elevated CO_2, although the general assumption that C4s do not respond may have prevented proper evaluation.

4.1.5 Pulses and oil crops. Relatively few studies have been made on pulses with the exception of soybean, e.g. Baker et al, (1989) obtained yield increases of 45, 24 and 15% at cool, warm and hot conditions respectively with 660 versus 330 μmol/mol CO_2. General indications are that elevated CO_2 will increase pulse production substantially, probably more than the cereals, possibly because nitrogen fixation in legumes is very energy demanding so the extra availability of assimilates will greatly stimulate productivity. Similar considerations apply to oil crops.

Table 1. Effects of increasing CO_2 and temperature on winter wheat (*Triticum aestivum*) grain yield and on sugar beet (*Beta vulgaris*) dry matter yields of harvested beet. Experiments at IACR-Rothamsted simulating field temperatures and light: water and nitrogen non-limiting.

	Year	Yield for ambient CO_2 + temp (gm^{-2})	Effect of doubling CO_2 (%)	Effect of increasing temp 4°C (%)
Winter wheat	90/91	1173	+16	-19
cv Mercia	91/92	800	+37	-35
	93/94	612	+12	-25
Mean		861	+22	-26
Sugar beet	93	1748	+34	-11
cv Colt	94	1466	+33	-5
	95	1852	+30	-8
Mean		1689	+32	-8

4.1.6 Root crops. Responses for these so-called indeterminate crops with relatively poorly delimited stages or periods of growth and large vegetative sinks should, it is argued, be large compared to the determinate crops. Relatively little attention has been directed to such crops, but they seem to respond as expected of C3 plants, with similar percentage increases in biomass and yield. Recent studies on sugar beet at IACR-Rothamsted have shown (Table 1) that 700 compared to 350 μmol/mol CO_2 increases yield of dry matter by some 25% with similar effects on the sugar production when grown at current ambient temperatures and with optimal nitrogen and water supply (Demmers-Derks et al, 1996). The proportional increase was similar but the absolute increase smaller with deficient N: variation in the response may be caused by different combinations of conditions. The concentration of sucrose in the storage `root' was unaffected by CO_2 but increased with deficient N. Potato has a large response, 38% for tuber yield in dim light and 27% in bright light (Wheeler et al, 1991). Studies of the effects of elevated CO_2 on tropical root crops are few: sweet potato yields increased but were variable (see Lawlor and Mitchell, 1991). Cassava seems not to have been analysed.

4.2 Temperature. Temperature has the most marked effects on plant growth and development, which are generally linear functions of temperature from a base temperature, which is low for temperate species such as winter wheat, somewhat higher, e.g. for sugar beet and much higher for tropical species, e.g. rice. At higher temperatures, the value depending on the species, growth and development may be inhibited. Depending on the species and indeed on the cultivars, cold (freezing) or cool (chilling) and warm to hot temperatures may damage many processes in metabolism, disrupt physiological systems etc. Extreme cold or heat are often responsible for impaired plant development and yield: yields of rice in northern Japan may be decreased by cold, and wheat in the UK and maize in the northern USA may be decreased by high temperatures which damage pollen formation (meiosis), shedding and fertilization. In addition to these perhaps rather direct effects of temperature, warmer temperatures decrease P via the Rubisco mechanism and stimulate dark respiration: both result in decreased production. Fewer studies of the effects of increased temperature on crops have been made than of elevated CO_2.

4.2.1 Wheat. Increasing the temperature throughout growth of winter wheat (cultivar Mercia) crops by 4°C above the current ambient temperatures, increased the rate of early development and tillering and thus straw yield when compared to ambient temperature. However, it decreased total dry matter production and grain yield (Table 1) due mainly to fewer, smaller grains as the rate of grain filling was shortened and ripening accelerated. Interestingly, the decrease due to 4°C warmer temperatures is almost the same as the stimulation due to 700 μmol/mol CO_2 when compared to current conditions (Mitchell et al, 1993; 1995). Wheats differing substantially genetically respond similarly, suggesting that the basic characteristics are very conservative.

4.2.2 Rice. Studies on rice production have shown that increasing the temperatures above current conditions by the order of magnitude expected under climate change, decreases production (Baker et al, 1989; Ziska et al, in press) similarly to wheat. Grain number is most affected whilst grain mass is relatively insensitive.

4.2.3 C4 grains. Although these crops are adapted to warm temperatures it is to be expected that increasing temperatures will adversely affect them, where they are growing close to their optima. Where cool conditions are limiting, production will increase, but where hot conditions limit production yields will decrease.

4.2.4 Pulses and oil crops. As with the other crops it is likely that warmer conditions will be a double edged sword, stimulating production in areas now limited by cold and decreasing it in areas already warmer than the optimum for the crops (Baker et al, 1989).

4.2.5 Root crops. Effects of elevated temperatures on these crops has been little studied. Yields of sugar beet grown at temperatures 4°C above current ambient at Rothamsted were decreased by about 8% compared to the ambient (Table 1), rather less than the decrease for winter wheat, reflecting the known greater sensitivity of beet to cool temperatures. Early growth was stimulated by warmth but maturity was earlier so shortening the growing period and decreasing yield of beet. Also the sugar concentration decreased, possibly as a result of stimulation of respiration (Demmers-Derks et al, 1996). The trend will be the same for other crops: loss of production where a species or variety is optimally suited or are already above the optimum and possibly improvement where current conditions are sub-optimum.

4.3 Effects of UV radiation. Increased UV-B will decrease production of some crops, especially at higher latitudes and elevations. The magnitude of the effects may be similar to those caused by other environmental changes (Krupka and Kickert, 1993).

4.4 Drought. This major limitation to production across the world has been exhaustively studied, but relatively little has been done in relation to environmental change. Crops differ in responses (e.g. potato and sugar beet are very sensitive, wheat less so) and effects of droughts will be very specific, depending on when reductions in water supply occur in relation to developmental stages of crops. Generally drought decreases growth of most crops in their current habitats, even if some fruit trees use relief of stress to signal reproduction. If water deficits increase at particularly sensitive periods, e.g. during rapid growth and development, then the consequences for biomass and harvestable yield will be severe. Increased temperatures, vapour pressure deficits and radiation, which will almost certainly be associated with decreased rainfall, will greatly exacerbate the problems associated with less rain *per se*. The decreased gs in plants as a consequence of elevated CO_2 greatly decreases water loss in experiments but the benefits under field conditions are less sure. The resulting slower transpiration allows the crop to warm by 1 or 2°C and this offsets the saving (Lawlor and Mitchell, 1991; Kimball pers. com.). Where water is currently in excess (e.g. temperate regions in autumn), reduced supply will stimulate production or lead to substitution of existing crops with others more tolerant of dry periods. In currently dry areas, all irrigated crops will be affected by decreasing water availability and those (e.g. irrigated rice) with large water requirements will suffer from increased competition for a scarce and increasingly expensive resource. Of all the consequences of climate the effects of changes in water supply are probably the most difficult to forecast. Tested models of water use under environmental change are an urgent requirement if the consequences are to be assessed properly.

5. Generalizations

Increasing CO_2, changing temperatures and altered rainfall will affect the effective production of all crops and their range particularly where other resources are limiting. Main areas of production will migrate (Rosenzweig and Parry, 1994; FAO, 1994), under economic pressure, to maintain efficiency at rates which have are difficult to assess but probably perceptible on the decadal time scale. Modelling methods have been developed and applied to assess the multi-factorial effects of climate change on crops (Parry et al, 1996). Responses of determinate and indeterminate crops may not differ as greatly as has been suggested but more critical appraisal is needed: rates of production may increase by a few percent per decade with CO_2, decrease with warmer temperatures and thus broadly cancel out. Water is the most important but poorest assessed factor.

6. Plant breeding

As much of human food, fuel and fibre is obtained from a very limited number of species, there is the prospect that limited genetic variability will prevent effective responses to rapidly changing environments. Of major concern is the narrow genetic base of most current crops and the rate and extent to which plants can be altered. Genetic engineering may increase the range and rate of introduction of genes to improve plant responses, but has yet to prove its ability to satisfactorily modify the complex multi-genic traits involved in most plant-environment interactions. Plants have been selected and bred to give the current crops with ability to survive extreme conditions which is crucial. Genetic variation does exist for biochemical and physiological systems conferring a wide spectrum of responses of the major crops to environment. Clearly, traditional plant breeding will play a vital role in adaptation to environmental change. There are grounds for optimism that sufficient genetic variation exists to allow adaptation of crops to novel environments as most have short breeding cycles relative to the likely rate of global environmental change, have already been selected for a wide range of characteristics, quality as well as yield and yield stability in extreme environments, and for resistance to diseases and pests. By identifying and incorporating genetic material from the wide range available it should be possible to introduce favourable characteristics. Adaptation to CO_2 and temperature may involve general, perhaps unconscious, selection. Breeding for large scale commercial production requiring large inputs of water, nutrients and extensive (often expensive and environmentally damaging) pest, disease and weed control, has resulted in genotypes which may be poorly suited to future climates. A substantial part of the world's agriculture is relatively low productivity, simple technology, subsistence farming based on self-saved seed from land races of crops. Such genetic material often has good ability to survive extreme conditions. Future developments must address the need for less resource demanding agriculture. Small scale agriculture in poorer parts of the world may suffer most from lack of access to genetic material for selection: international and national programmes of breeding will be important for improvements but the rate of introduction may be inadequate. Costs of breeding are not trivial although they are if compared to the costs - social as well as directly financial - of not adapting. Testing crop responses to extreme events may provide greater yield stability and avoid catastrophic damage. Commercial plant breeding can only provide the adaptation toglobal environmental change conditions if the needs are clearly defined and it is economical.

7. Conclusions: responses of plants to environmental change

7.1 Elevated CO_2 will generally stimulate C3 plant growth and biomass and yield production provided water, temperature and nutrition are adequate. Differences between `determinate' and `indeterminate' crops may not be large. C4s will be little affected. Protein and oil crops may benefit more from increased CO_2 than other C3s. Responses to elevated CO_2 may be smaller where other factors limit growth. Weeds will respond rather similarly to crops.

7.2 Warmer temperatures will stimulate growth etc if crops are limited by cool temperature in current conditions but decrease productivity if supra-optimal. On balance most crops are likely to suffer loss of production in warmer temperatures: changes in the types of crops grown may be the principal response.

7.3 Water availability will be a crucial aspect of global environmental change. Crop water use may decrease somewhat and water use efficiency will increase for most C3 crops, with smaller benefits for C4s, but decreased rainfall and humidity will drastically reduce production in most areas.

7.4 Increasing UV-B radiation will decrease crop production especially at high latitudes and elevation.

References

Baker, J.T. and Allen, J.R. 1992: Response of rice to carbon dioxide and temperature. *Agricultural and Forest Meteorology*, **60**, 153-166.

Baker, J.T., Allen, L.H. Jr, Boote, K.J., Jones, P. and Jones, J.W. 1989: Response of soybean to air temperature and carbon dioxide concentration. *Crop Science*, **29**, 98-105.

Carter, T.R., Porter, J.H. and Parry, M.L., 1992: Some implications of climatic change for agriculture in Europe. *Journal of Experimental Botany*, **43**, 1159-1167.

Cure, J.D. and Acock, B., 1986 Crop responses to carbon dioxide doubling: a literature survey. *Agricultural and Forest Meteorology*, **38**, 127-145.

Delgado, E., Mitchell, R.A.C., Parry, M.A.J., Driscoll, S.P., Mitchell, V.J. and Lawlor, D.W., 1994: Interacting effects of CO_2 concentration, temperature and nitrogen supply on the photosynthesis and composition of winter wheat leaves. *Plant, Cell and Environment*, **18**, 736-748.

Demmers-Derks, H., Mitchell, R.A.C., Mitchell, V.J., Driscoll, S.P., Gibbard, C., Lawlor, D.W., 1996: Sugar beet under climatic change: photosynthesis and production. In: *Implications of Global Environmental Change for Crops in Europe*. The Association of Applied Biologists, Wellesbourne, Warwick, pp 163-169.

FAO Working Group on Climate Change (1994) *Global climatic change and agricultural production*, Rome: FAO.

Kimball, B.A., 1983: Carbon dioxide and agricultural yield: an assemblage and analysis of 430 prior observations. *Agronomy Journal*, **75**, 779-782.

Krupka, S.V. and Kickert, R.N., 1993: The greenhouse effect: the impacts of carbon dioxide (CO_2), ultraviolet-B (UV-B) radiation and ozone (O_3) on vegetation (crops). *Vegetatio*, **104/105**, 223-38.

Lawlor, D.W., 1991: Responses of plants to elevated carbon dioxide: the role of photosynthesis, sink demand and environmental stresses. In *Impact of climatic changes* *on photosynthesis and plant productivity, Delhi* (ed. by Y.P. Abrol et al). Oxford & IBH Publishing Co. PVY Ltd.

Lawlor, D.W., 1993: *Photosynthesis: molecular, physiological and environmental processes.* 2nd edition, Harlow: Longman Scientific and Technical.

Lawlor, D.W., 1995: Photosynthesis, productivity and environment. *Journal of Experimental Botany*, **46** (Special Issue), 1449-1461.

Lawlor, D.W., 1996: Simulating plant responses to the global greenhouse. *Trends in Plant Science*, **1**, (3), 100-102.

Lawlor, D.W. and Keys, A.J., 1993: Understanding photosynthetic adaptation to changing climate. In *Plant Adaptation to Environmental Stress* (ed. by L. Fowden, J. Stoddart and T.A. Mansfield), pp 85-106.

Lawlor, D.W. and Mitchell, R.A.C., 1991: The effects of increasing CO_2 on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment*, **14**, 807-818.

Mitchell, R.A.C., Lawlor, D.W., Mitchell, V.J., Gibbard, C.L., White, E.M. and Porter, J.R. 1995: Effects of elevated CO_2 concentration and increased temperature on winter wheat: test of ARCWHEAT1 simulation model. *Plant, Cell and Environment*, **18**, 736-748.

Morokuma, M. and Yajima, M., 1996: Effects of ambient CO_2 concentration and air temperature on dry matter production and yield of rice. *Japanese Journal of Crop Science*, **65**, (Extra Issue), 258-259.

Parry, M.L., Hossell, J.E., Jones, P.J., Rehman, T., Tranter, R.B., Marsh, J.S., Rosenzweig, C., Fischer, G., Carson, I.G. and Bunce, R.G.H., 1996: Integrating global and regional analyses of the effects of climate change: a case study of land use in England and Wales. *Climate Change*,**32**, 185-198.

Rosenzweig, C. and Parry, M.L., 1994: Potential impact of climate change on world food supply. *Nature*, **367**, 133-138.

Rozema, J., Lambers, H., van de Geijn, S.C. and Cambridge, M.L., 1993: *CO_2 and Biosphere.* Kluwer Academic Publishers, Dordrecht.

Mitchell, R.A.C., Mitchell, V.J., Driscoll, S.P., Franklin, J. and Lawlor, D.W., 1993: Effects of increased CO_2 concentration and temperature on growth and yield of winter wheat at two levels of nitrogen application. *Plant, Cell and Environment*, **16**, 521-529.

Wheeler, R.M., Tibbitts, T.W. and Fitzpatrick, A.H., 1991: Carbon dioxide effects on potato growth under different photoperiods and irradiance. *Crop Science*, **31**, 1209-1213.

Ziska, L.H., Namuco, O., Moya, T., Quilang, J., (In press): Growth and yield response of field grown tropical rice to increasing CO_2 and temperature. *Agronomy Journal* .