PART III

CONSEQUENCES of CLIMATIC CHANGE for PLANT DEVELOPMENT and GROWTH PROCESSES.

Introduction

In Part I it has been shown that the concentration of CO_2 in the atmosphere has risen and is likely to increase further over the next few decades. Within the expected range of concentrations there will be no direct effects, or only negligible ones, on animals including insects. Only vegetation will be directly affected.

It has also been shown that a likely consequence of that change is an elevation of global temperatures - "global warming". Associated with the raised temperatures there will almost certainly be changes in the hydrological pattern - the levels of precipitation, humidity, and evaporation may change both in absolute level and in seasonal distribution - but the direction of these changes is uncertain. Further, patterns of windspeed and distribution may change. All these changes will affect plant and crop growth. Some of the more problematic consequences for plants are discussed here. The simple direct effects of warming on plant growth are generally well understood and do not require special investigation as the range of temperatures experienced on the globe far exceeds the range of any changes that are currently projected. Where work may be required is in mathematical modelling or simulation of the effects of temperature on temperate crops in parallel with the other changes in the environment. Those problems are considered in Part IV of this document. This Part considers the problems posed by the effects of increased [CO_2] on the development and physiology of plants and the associated problem of water-use-efficiency i.e. water use in relation to carbon gain, in a possibly drier environment.

Above Ground

III.1 The Effects of [CO_2] on Growth.

The enrichment of [CO_2] in the atmosphere as a means to increase plant productivity has been examined in both theoretical (Bravdo, 1986; Black, 1986) and practical studies of glasshouse-grown crops (Cure & Acock, 1986). The applicability of these latter studies to the conditions of globally increased [CO_2] is uncertain, since in these studies [CO_2] has usually been increased only during daylight hours. Indeed, ambient [CO_2] is generally reduced to normal outside levels at intervals throughout the day, during periods of ventilation for temperature control (Willis & Peet, 1989). The frequent cycling between high and ambient [CO_2] almost certainly prevents any possible adaptation by plants to elevated [CO_2]; yet there is evidence that some species of plants adapt to continuously elevated [CO_2] by reducing their stomatal frequency. Such an adaptation could limit any anticipated benefit to photosynthetic rate. Consequently, adaptive changes - morphological and physiological - during leaf development should be examined in some of the major crop species.

The enrichment of [CO_2] in the atmosphere as a means to increase plant productivity has been examined in both theoretical (Bravdo, 1986; Black, 1986) and practical studies of glasshouse-grown crops (Cure & Acock, 1986). The applicability of these latter studies to the conditions of globally increased [CO_2] is uncertain, since in these studies [CO_2] has usually been increased only during daylight hours. Indeed, ambient [CO_2] is generally reduced to normal, outside levels at intervals throughout the day, during periods of ventilation for temperature control (Willis & Peet, 1989). The frequent cycling between high and ambient [CO_2] probably prevents full adaptation by the plants to the elevated [CO_2]. However, plants exposed to elevated levels of CO_2 under special green-house conditions have been shown to develop leaves with reduced stomatal frequencies (number per unit leaf area) (Madsen, 1973; Imai *et al.*, 1984) or increased frequency (O'Leary & Knecht, 1981) and with reduced stomatal conductance (Wong *et al.*, 1985; Delucia *et al.*, 1985: Williams *et al.*, 1986). In a recent growth-chamber study in which [CO_2] was increased only during the light period Apel (1989) found wide inter-specific differences. Growth in an atmosphere of 1500ppmv resulted in stomatal frequencies that were 55% higher than normal in Lycopersicon esculentum (tomato) and in Acer pseudoplatanus (Sycamore, one of the species studied by Woodward, 1987, see below, and the opposite response). In *Vicia faba* (field bean), however, and in *Avena sativa, Secale cereale,* and *Triticum aestivum* (oats, rye, and wheat) the stomatal frequency was within 7% of normal.

Evidence on the effects of continuously different [CO_2] on stomatal attributes of plants growing in the natural environment is both recent and conflicting. Woodward (1987) used herbarium specimens of eight temperate tree species to provide a historical record of changes in stomatal frequency over the last 200 years and found a 29% reduction over the period but Korner (1988), using published records of stomatal frequencies in over 200 herbaceous plant species from as far back as 1864 together with recent data, failed to find statistically significant differences in stomatal frequency. Korner did, however, find large intra-specific variation between sampling sites and suggested that CO_2-effects on natural vegetation are likely to be over-estimated when modelled from monofactorial laboratory responses.

Whatever the morphological response, it is the response of stomatal conductance to changes in ambient conditions that modifies the functioning of the leaf (Wong *et al.* 1979). Adaptive changes in stomatal frequency or aperture leading to changes in stomatal conductance could limit any anticipated benefit to photosynthetic rate from elevated [CO_2]. Consequently, adaptive changes - morphological and physiological - during leaf development should be examined in some of the major crop species.

Given the *caveat* that adaptive changes were not being considered, the practice of atmospheric enrichment with CO_2 has been shown to be beneficial to crop growth when the high concentrations have been maintained for extended periods (Kimball, 1983; Kimball, 1986). Future studies that may be proposed for the study of plant performance and behaviour under long term CO_2 enrichment will need to recognise the possibility of adaptation, and should be conducted using suitably engineered growth environments that allow control of temperature and humidity without recourse to open ventilation.

Studies by Willis & Peet (1989) using the product of [CO_2] and enrichment time to integrate fluctuating [CO_2], suggested that cucumber production is optimised at the equivalent of continuous 600 ppmv. However, no linear relations between [CO_2] and enrichment time could be derived for tomato.

There have been fewer studies on the effects of elevated [CO_2] during conditions of physiological stress of one kind or another. However, Gifford (1979) suggested that, in wheat, water-stress does not eliminate the favourable effect of higher [CO_2] on growth because of improved water relations (in effect a better water use efficiency) leading to greater leaf growth.

Goudriaan & Bijlsma (1987) showed evidence that elevated [CO_2] not only increased total dry matter production in *Vicia faba* but also improved "water use efficiency" (WUE). They also suggested that WUE was independent of water stress but this may reflect on their experimentation, since it is widely recognised that the ratio of dry matter fixed to water transpired is inversely proportional to the saturation deficit of the air (Monteith, 1981).The regulation of water use in relation to carbon gain will be discussed in Section III.4.

Changes in total dry matter fixed do not necessarily lead to proportional changes in the useful harvested product. For example the ratio of root:shoot dry weights has been reported to increase with CO2 enrichment in several crops including sugar beet, barley and kale (Ford & Thorne, 1967) and wheat (Sionit *et al.*, 1981). The effect of nitrogen-stress during growth with elevated [CO_2] was studied by Norby *et al.* (1986) in seedlings of *Quercus alba.* Enrichment of [CO_2] from 362-690 ppmv enhanced growth by 85% with the greatest effect being observed in the root system. They reported no change in absolute water use and hence an apparent improvement in WUE. Concerning nutrient use by the plant, enhanced [CO_2] had no effect on N-uptake (hence at higher [CO_2] the N was used more efficiently) but P and K were absorbed in proportion to growth. From these and similar observations, it follows that the mechanisms that determine partitioning between plant organs and the influence on these of [CO_2] either directly or indirectly through assimilate supply should be an important component of any investigation into the effects of altered [CO_2].

III.2 The Implications of Elevated [CO_2] for Photosynthetic Processes.

There are three principal pathways known for the photosynthetic fixation of carbon from CO_2, known as the C_3, C_4 and CAM mechanisms (Appendix C). There are functional differences in these biochemical processes which give rise to very different physiological responses to light, temperature and water. These physiological responses will be important in determining the whole plant responses to the increasing ambient [CO_2] and the probable higher ambient temperatures.

Since water vapour shares the same stomatal diffusion pathway as CO_2, water is inevitably lost when stomata open and CO_2 is absorbed. Stomatal conductance (gs) appears to adjust in response to the assimilatory capacity of the mesophyll tissue. That is, other things being equal, stomata open to the extent required to provide CO_2 at rates sufficient to meet the CO_2-fixation requirements of the metabolic pathway (Wong *et al.*, 1979).

The association of evaporation (E) and assimilation (A) will be discussed in Section II.4, but the point has been introduced here because the stomata provide the most effective means that plants have to adjust the environment of their photosynthesising organs. The consequences of their action differ in magnitude between C_3 and C_4 plants.

The CO_2 concentrating function of C_4 photosynthesis leads to steady-state [CO_2] of ca. 10 Pa in mesophyll cells and about 200-300 Pa in bundle sheaths (Hatch & Osmond, 1976). Consequently CO_2 fixation in C_4 plants is practically CO_2-saturated in the normal atmosphere. On the other hand C_3 plants in the normal atmosphere function with intercellular [CO_2] of ca. 22 Pa (~ 220 ppmv) (Wong *et al.*, 1979) and under these conditions CO_2 fixation rate is at about 1/2 of the rate when saturated for CO_2, especially in high-N plants (von Caemmerer & Farquhar, 1981; Osmond, Winter & Zeigler, 1982).

The consequence of these differences between the two photosynthetic pathways is that elevated [CO_2] is unlikely materially to modify assimilation or the ratio of the rate of evaporation to assimilation in C_4 plants. Many reports have shown, however, that within C_3 plants elevated [CO_2] results in higher assimilation at given irradiance and higher saturating irradiances. The N-status of plants modifies the differences in performance between C_3 and C_4 plants so that some C_3 plants with increased Rubisco activity as a result of high N nutrition, do not saturate photosynthesis until full sunlight.

Thermal stability of the photosynthetic apparatus, both at high and low temperatures is determined by a variety of properties, none of which is unique to the C_3 , C_4 or CAM pathways of photosynthetic CO_2 fixation (Berry & Bjorkman, 1980). In C_3 plants, oxygenase activity increases relative to carboxylase at higher temperatures, quantum yield is depressed and photorespiration is greater. In cold, low-light environments the lower quantum requirement of C_3 plants may sometimes allow the daily carbon gain to exceed that of C_4 plants. Under such conditions the higher energy cost of C_4 plants can become a liability (Osmond, Winter & Zeigler, 1982). The anticipated changes in temperature within the UK are such that it is unlikely that the balance between C_3 and C_4 species will be altered. Indeed in those areas where C_3 and C_4 species are more equally represented as crop plants the effect of raised ambient $[CO_2]$ may be to shift the balance in favour of C_3 species. In view of the predicted, novel combinations of $[CO_2]$ and temperature, further study should be given to the balance of processes and environmental factors that determine the balance of competitive advantage between C_3 and C_4 species so as to assess the likelihood of a shift in this balance with altered ambient $[CO_2]$.

III.3 Carbon Dioxide and Rate-Limiting Processes in Photosynthesis.

At low levels of intercellular $[CO_2]$, as when stomatal conductance is low, the photosynthetic rate of CO_2 fixation is limited by the RuP_2 saturated rate of Rubisco. At higher intercellular $[CO_2]$ a point is reached where RuP_2 regeneration is limiting and the dependence on $[CO_2]$ changes in nature (Farquhar & von Caemmerer 1982, see Appendix D). The transition from limitations by RuP_2 carboxylation to limitation by RuP_2 regeneration, which is itself dependent on the supply of ATP and NADPH and therefore dependent on the electron transport capacity of the leaf, occurs at a $[CO_2]$ that is dependent on the ratio of the rates of whole chain electron transport (J) and carboxylation of RuP_2 (Vc) in competitive inhibition of O_2 and at saturating RuP_2 (von Caemmerer & Farquhar, 1981) (Appendix D).

The dependence of assimilation on temperature reflects the dependence of its subprocesses. At normal $[CO_2]$ and $[O_2]$ the RuP_2 saturated rate Vc, increases with temperature. This dependence is greater at elevated $[CO_2]$. The temperature dependence of the RuP_2-limited rate is dependent upon the temperature dependence of J_{max}. Farquhar & von Caemmerer (1982) have argued that the long-term effects of environment on leaf photosynthesis are largely mediated through changes in Vc_{max} and J_{max}. For the future, the combination of mathematical modelling with experimental determination of changes to Vc_{max} and J_{max} and studies of the factors determining those parameters offers an approach to predicting some of the consequences of environmental change.

If one wishes to determine stomatal limitation to CO_2 assimilation rate, it is important to know how stomata operate in relation to the region of transition between types of limitation of photosynthetic rate. Cowan and Farquhar (1977) have found that at the region of transition, there is a large change in dA/dC (A = assimilation rate, C = CO_2 concentration). As a consequence, a small change in conductance effects a large change in the marginal water cost of assimilation. If photosynthetic processes are to be modelled at different ambient $[CO_2]$, then experimental studies will be necessary to establish the level of intercellular $[CO_2]$ at which there is transition between types of limitation of photosynthetic rate.

III.4 Water Use Efficiency or the Regulation of Water use in Relation to Carbon Gain.

The apertures of stomata adjust in response to many variables, among the more important of which are the dryness of the air (the saturation deficit) and the intercellular [CO_2]. There is at present uncertainty about the changes in atmospheric humidity and in patterns of precipitation that will accompany the predicted changes in ambient temperature. It is possible that rainfall in the growing season will be increased, unchanged or decreased (see Section I.8). In the case of unchanged precipitation there will probably be a small reduction in atmospheric humidity between rainfall events (increased temperature results in lower RH), increased evaporative demand and generally, more frequent and intense periods of water stress in plants. If precipitation in the growing season is reduced then the problems associated with water-stress will be worsened. Since we do not know what course this important weather element will take, it is important to consider the consequences of each of the possibilities. Clearly however, increased rainfall is not an issue in this Section.

There are plant tactics that may increase the amount of soil water that is available to the plants (changed rooting depth and branching patterns) but irrespective of these however, the problem remains that when plants open their stomata to assimilate CO_2 they lose water.

There tends to be an inverse relation across species, between potential growth rate and capacity for survival (Hall, 1981). Selective adaptation may be thought to have 'optimised' the relation between assimilation (A) and evaporation (E) for particular environments. That is, plants that are successful in a given environment have the characters to grow most quickly without hazarding their survival. Those processes that relate to the temporal regulation of carbon gain and water loss, and so to the water use efficiency have been examined theoretically by Cowan (1977, 1982) and by Farquhar and Sharkey (1982). A brief introduction is given in Appendix E.

Taking optimal variation in assimilation (A) and evaporation (E) to mean that <A> would not be increased without increasing <E>, or that <E> would not be decreased without decreasing <A>, Cowan (1982) has argued that the necessary criteria are that $(\partial E/\partial A)_{s,t}$ is a constant, and that $(\partial^2 E/\partial^2 A)_{s,t} > 0$, where s is a coordinate representing a particular element of leaf surface, and t is time. These conditions are illustrated in Fig. III.1

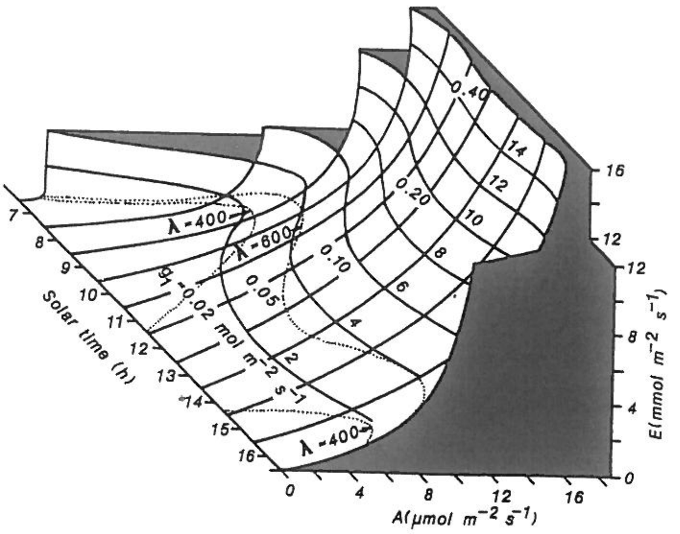

Fig.III.1 Rate of evaporation, E as a function of rate of assimilation, A and time. The dotted lines represent relationships between E and A (Redrawn from Cowan & Farquhar, 1977).

The use of simple expressions for A and E allows an inequality to be stated (Appendix E), defining an upper limit to water use efficiency,

$$A/E < p/\,(\Gamma(T-T_w))$$

where p is the partial pressure of CO_2 in air, Γ is the psychrometric constant, and T and T_w are dry- and wet-bulb temperatures of the air. The maximum value for A/E, the water use efficiency, can vary in direct proportion with p so that if the ambient [CO_2] is doubled, so too is A/E. The question should be posed and work should be undertaken to examine what strategies are available to the plant to approach this limitation. Removal or raising of the other constraints? An operating system for stomata so that leaves assimilate rapidly when evaporative demand is low or when water supply is adequate and assimilate slowly or not at all at other times?

The development of expressions to define E and A (Appendix E) have not as yet defined a unique relation between E and A, because the intercellular partial pressures of CO_2 and H_2O are partly dependent on the fluxes. In practice the relation between E and A must be found numerically or experimentally.

The problem of determining probable water use efficiencies in the predicted atmospheric environment of elevated [CO_2] and reduced humidity is not, as yet, amenable to direct calculation. Experimental studies should be undertaken to assess the relative values of stomatal strategies of operation and transitions between RuP_2 saturated and RuP_2 regeneration limited fixation of CO_2. Advanced modern techniques of isotope discrimination can be used to provide a time averaged determination of water-use efficiency (Farquhar & Richards, 1984; Hubick, Farquhar & Shorter, 1986) which coupled with biochemical and gas exchange measurements of photosynthesis (von Caemmerer & Farquhar, 1981) offers the tools to study the effectiveness of plant strategies to optimise performance in a modified environment.

Inter-species differences occur in experimentally determined water use efficiency, but the most efficient species are not necessarily the most productive (Silcock & Wilson, 1981). These differences have been attributed to a number of characters (Johns & Lazenby, 1973) including differences in stomatal mechanism, but comparative studies fail (Kemp, 1984) to explain why some species are more efficient than others. Integrated studies of the processes determining water use efficiency and the examination of differences between a range of species by incorporation of the appropriate tactical or strategic phenotypic responses through the genotype of these species

III.5 Effects of Climatic Changes on the Growth and Activity of Plant Roots.

(a) Temperature Effects.

Most work on the effects of root temperature on temperate crop species has concentrated on *low* temperatures. Relatively little information is available on the responses to temperatures higher than those which occur at present.

Meristematic activity in root apices can occur over a broad temperature range of *c.* 1°C to 35-40°C. Barlow (1986) presents data showing that the length of the cell cycle in apical meristems of onion roots decreases linearly as the temperature rises from 5 to 25°C, and remains short in duration up to 35°C. Generally, the rate of root extension in many species increases linearly up to 25-30°C (Cooper, 1973), but there is some evidence that different species have different temperature optima for root growth (expressed as rate of root extension or dry weight production): see Table 1. Crops differ more in terms of their *lower* temperature limit for effective root growth than in the upper limit (c. < 33°C: Klepper, 1986).

If future soil temperatures will not fall as low as they do now, it is possible that some species that currently suffer seasonal low-temperature limitations to root growth would be able to sustain growth for longer periods in winter. The possible consequences of this for winter-growing crops could be serious. If root growth of a winter cereal were to continue in winter, the resulting above-ground growth could be more susceptible to damage from strong winds, especially during any periods of low temperature. The effects on perennial vegetation are unpredictable, as these would depend on the precise species composition of the flora. Sustained activity of roots in winter could conceivably shift competitive balances between species whose co-existence depends, in part, on phenological differences (see Rorison *et al.*, 1983). Weed species such as *Elymus repens* (couch-grass) over-winter as young vegetative shoots inter-connected by a system of rhizomes (Grime *et al.*, 1988). These might, as a result of higher soil temperatures, be able to store greater quantities of resources during winter, prior to their mobilisation for early growth in spring, in competition with young cereal crops. In addition, the young, over-wintering shoots of couch-grass are sometimes killed by severe winter temperatures (Grime *et al.*, 1988). Clearly, warmer soil temperatures in winter would mean a greater probability of survival of seedlings into the established phase, with correspondingly greater infestations of arable fields.

Root growth depends also on the partitioning of assimilate from the leaves, a process itself temperature-dependent (Davidson, 1969). Leaf growth can be influenced directly by soil temperature in grasses and cereals in which apical meristems of leaves remain at or below the soil surface. Since air temperature affects photosynthetic activity, the supply of assimilates for root growth depends also on air temperature. Davidson

Table III.1
Optimal temperatures for root growth

Species (°C)	**Optimal temp**	**Reference**
Cassava (*Manihot esculenta*)	35	Marschner (1986)
Cotton (*Gossypium hirsutum*)	30	Pearson *et al.* (1970)
Maize (*Zea mays*)	30	Milthorpe & Moorby (1979)
Rape (*Brassica napus*)	30	Cumbus & Nye (1982)
Potato (*Solanum tuberosum*)	20	Marschner (1986)
Clover (*Trifolium repens*)	20	Davidson (1969)

(1969) and Rorison *et al.* (1983) have shown that the temperature *differential* between air and soil, and the degree and frequency of their diurnal and seasonal fluctuations, can be as important as their absolute temperatures. Experiments on the effects of soil temperature on root growth should, ideally, be conducted in environments that allow both leaf and root temperatures to be controlled in ways that reflect realistic differentials between air and soil.

Nutrient uptake by roots is temperature dependent. For ions absorbed by active transport, Q_{10} values of *c.* 2.0 have been reported over the range 10-30°C (Macduff, 1989). As with photosynthesis, ion uptake is inhibited in temperate crops only above c. 35°C. The optimal root temperature for nutrient uptake varies with genotype (Chapin, 1977). Considerable acclimation of the uptake systems can occur which, eventually, can compensate for the effect of non-optimal temperatures. This process is due to a combination of biochemical changes at the membrane or cell level (White *et al.*, 1988), and to changes in root:shoot ratios (Chapin, 1977).

The growth and development of root systems are notoriously plastic in response to environmental factors, as are ion transport systems. Relatively small changes in soil temperature should, therefore, have little impact on the acquisition of nutrients by existing crops, provided that the availability of nutrients is not itself affected adversely by climatic change (an unlikely event: see Section II.2). It should be noted, however, that the temperature sensitivities of root growth and nutrient uptake in most non-agricultural species are unknown.

(b) CO_2 effects.

An increase, in C_3 plants, of net photosynthetic carbon fixation resulting from elevated atmospheric $[CO_2]$ will lead to increases in the amounts of carbon exported from leaves to roots (Wittwer, 1985). This carbon has several possible fates, all of which are potentially important to the acquisition of nutrients by the plant: synthesis of new root dry matter; respiratory release into the soil; exudation into the rhizosphere; export to mycorrhizal or rhizobial symbionts. Few relevant data are available in the literature.

Moorby *et al.* (1986), O'Neill *et al.* (1987) and Del Castillo *et al.* (1989) showed that in soil-grown white oak (*Quercus alba*), yellow poplar (*Liriodendron tulipifera*) and soybean (*Glycine max*), respectively, root dry weight was increased by elevated $[CO_2]$. In the study by O'Neill *et al.* (the only detailed one to date), a doubling of $[CO_2]$ from 367 (control) to 692 ppmv increased total dry weight by 72% and root dry weight by 100%. This response was associated with increases in the uptake from the soil of all essential nutrients in the CO_2-enriched plants compared with the controls. These increases ranged from 17%, for nitrogen, to 91%, for iron. The most likely explanation for this observation is that the larger root systems of the CO_2-enriched plants had access to greater quantities of nutrients in the soil. The uptake of highly mobile ions like nitrate would be improved to a lesser extent than that of more immobile ions such as iron, by such a modification of the root system geometry in the soil, and this is supported by the data obtained by O'Neill *et al.* However, even if this is the main effect of increased $[CO_2]$ on nutrient uptake, O'Neill *et al.* showed also that CO_2-enrichment increased dry matter production more than the uptake of any nutrient. The result of this difference in response was that the concentrations of nutrients in the dry matter of the CO_2-enriched plants were lower than in the controls: a "dilution" effect. The implication is that serious problems of nutrient deficiency could occur under conditions of increased $[CO_2]$. This could limit the effectiveness with which C_3 species could act as sinks for CO_2.

Nutrient deficiencies are countered by applications of fertilisers, and greater fertiliser usage is predicted if $[CO_2]$ should increase (Wittwer, 1985). An alternative to this environmentally-undesirable proposition would be to select genotypes capable of more effective uptake of nutrients from existing reserves in the soil. This would involve the technically difficult task of selecting genotypes on the basis of root system characters, or plasticity of those characters to give maximum flexibility of response to environmental conditions (O'Toole & Bland, 1987; Robinson, 1988). One requirement would be to select genotypes with root systems capable of exploiting both mobile and immobile ions (Robinson, 1988). No information is available on whether the potential range of root morphologies can be modified by increased [CO_2]. As well as its importance in future breeding programmes, such a response would also be relevant to competitive interactions and vegetation dynamics between plants in natural communities (e.g. uplands, forests), as described by Grime (1979), Strain (1987) and Tilman (1988). Work on screening the growth responses to elevated [CO_2] of a wide range of non-agricultural species is in progress at NERC's Unit of Comparative Plant Ecology at the University of Sheffield. No comparable screening programmes for crop genotypes have been attempted and none, including that at Sheffield, involves the effects of the *interactions* between responses to elevated [CO_2] and temperature, about which little is known (Wittwer, 1985).

Another requirement in any breeding programme would be to examine the potential of roots to modify the chemistry and microbiology of the rhizosphere in ways that enhance the availability of nutrients (Section II.2). The uptake of many micronutrients is possible only by the release of certain root exudates that chelate polyvalent cations, rendering them more available for uptake (Linehan, 1989). Little is known about genotypic variation in such processes, and nothing is known about the scale of root exudation under increased [CO_2]. Similarly, there are no data on the effectiveness of mycorrhizas in nutrient uptake under conditions of increased [CO_2] in the atmosphere. Symbiotic N_2 fixation is responsive to ambient [CO_2], with increases of 570% observed with [CO_2] maintained at up to 1200 ppmv (see Wittwer, 1985).

(c) Moisture Effects.

Soil water content influences the rates at which nutrient ions can be transported through the soil to growing roots by diffusion and mass flow (Nye & Tinker, 1977), and also the rates of mineralisation of those nutrients by soil microbes (see Section II.2). Dry soil inhibits root growth and the physiological activities of many temperate-zone crops (Gregory & Brown, 1989). A decrease in AAP during the growing season will not only make drought a greater threat to the plant, but will also increase the penetration resistance to root growth.

Generally, root growth is limited more by mechanical impedance than by low soil water potential, unless the latter falls below -0.5 MPa (Bengough, 1988). Taylor & Ratcliff (1969) found that matric potentials greater than -1.2 MPa did not limit cotton root growth whereas soil penetration resistance did. Within limits, therefore, plants cope with changes in soil matric potential insofar as they can avoid the effects of drought, but not in terms of mechanical impedance to root growth. Even where irrigation is available, farmers have little knowledge as to whether the crop is mechanically constrained, and irrigation is used only to alleviate or circumvent potential drought.

The relation between the soil's load-bearing capacity (Section II.1) and mechanical constraints to root growth is clear; additional compaction increases mechanical impedance to root growth. An increase in AAP in winter or spring, allied with a decrease in summer, would be the combination most likely to exacerbate problems of mechanical impedance to root growth. Again, soil type is important: certain soils (Mullins *et al.*, 1987) have high resistances to penetration. Such soils are sandy loam in texture and over a very small decrease in moisture content exhibit a correspondingly large increase in penetration resistance (Section III.2).

average
annual
ppt.

These soils have been targetted (Harrod, 1975); Davies, 1975) as having weak structure and high mechanical impedance, and occur as light (80% sand and <20% silt + clay) or silty (low percentage of particles >0.1 mm) soils. The Wash silts of high economic value fall into the latter category. These soils tend to carry high value root crops and are some of the most intensively farmed in the U.K. As they are inherently unstable, they would suffer from further degradation in wet winters due to ill-timed cultivations, as well as developing high strengths in drier summers. Even where AAP increases in the summer, such soils, along with clays, may experience temporal anoxia, further limiting root development.

In general, if rainfall is less as a result of global warming, this will have a greater negative impact on root growth than if rainfall should increase. Many soils in Northern Europe remain at or above field capacity throughout winter, in any case.

An interesting approach was taken by Cowan (1986) who developed a theoretical model of carbon partitioning between leaves and roots based on his work on optimal stomatal conductance (see Section II.4). Cowan derived relations between stomatal conductance, rates of C fixation and water loss, relative growth rate, and, from statistical analyses of rainfall distribution, the probability of desiccation. In principle, it should be possible to predict, from a likely pattern of rainfall events (according to a given change in AAP), how carbon should be apportioned in order to minimise the probability of desiccation whilst maximising, as far as possible, growth rate. This approach could usefully be extended to incorporate the effects of elevated atmospheric [CO_2] and the implications for nutrient uptake.

III.6 Responses of Seed Germination and Tuber Growth to Soil Temperature.

Soil temperature affects not only those processes like root growth important in established plants, but also those involved in regeneration.

Increases in soil temperature caused by global warming would have little effect on the germination response of many pasture species. These tolerate a broad temperature 'window' (Table III.2).

Table III.2

Temperature ranges for at least 50% of the maximum rate of seed germination in common British species (Grime *et al.*, 1988).

Tempera

Species	**Temperature range (°C)**
Pasture:	
Perennial rye-grass (*Lolium perenne*)	<5 - 34
Annual meadow-grass (*Poa annua*)	7 - 31
Clover (*Trifolium repens*)	<5 - 30

Species	**Temperature range (°C)**
Upland:	
Common cotton-grass (*Eriophorum angustifolium*)	16 - 31
Heather (*Calluna vulgaris*)	10 - 28
Purple moor-grass (*Molinia caerulea*)	19 - 39
Mat-grass (*Nardus stricta*)	17 - 36

Warmer soils could, however, have a greater impact in upland habitats where some common species are restricted in the minimum temperatures at which their seeds can germinate effectively.

Tuber growth in potato (*Solanum tuberosum*) is sensitive to high soil temperatures (Reynolds & Ewing, 1989). In the U.K., however, tuber initiation often occurs at temperatures below that (20°C) regarded as optimal. (R.A. Jefferies, private communication). Warmer soils are unlikely to have directly adverse effects on tuber production in the U.K., and may be beneficial.

Some effects of increased temperatures on the regeneration and survival of perennial species over winter were mentioned in III.5(a).

III. 7 Recommendations for Research Priorities.

1. Develop comprehensive theoretical framework to allow physiological and morphological responses of plants to *multiple* environmental factors to be analysed.
2. Determine mechanisms controlling carbon partitioning between roots and shoots and within root systems in response to elevated atmospheric [CO_2] and soil nutrient and water availabilities.
3. Screen genotypes for the extent of adaptive responses to environmental factors.
4. Quantify fate of 'extra' carbon assimilated by C_3 species under elevated atmospheric [CO_2]: determine partitioning between plant structures, respatory losses, root exudates, microbial biomass.
5. Adaptive changes, both morphological and physiological, during leaf development should be examined in some of the major crop species.
6. Studies that may be proposed for the assessment of plant performance and behaviour under long-term CO_2 enrichment will need to be conducted using suitably engineered growth environments that allow control of temperature and humidity without recourse to open ventilation.

Stir into text

7. The mechanisms that determine partitioning between plant organs and the influence on these of [CO_2] either directly or indirectly through assimilate supply should be an important component of any investigation into the effects of altered [CO_2].

8. Attention should be given to the study of CO_2-fixing enzymes and their efficiency under conditions of enhanced [CO_2]. This point is expanded in items 9-11.

9. Further study should be given to the balance of processes and environmental factors that determine the balance of competitive advantage between C_3 and C_4 species so as to assess the likelihood of a shift in this balance with altered ambient [CO_2].

10. The combination of mathematical modelling with experimental determination of changes to Vc_{max} and J_{max} and studies of the factors determining those parameters offers an approach to predicting some of the consequences of environmental change.

11. Experimental studies are necessary to establish the level of intercellular [CO_2] at which the transition between types of limitation of photosynthetic rate occur.

12. Work should be undertaken to examine what strategies are available to the plant to approach this limitation of a conservative relation between assimilation and water use. Removal or raising of the other constraints? An operating system for stomata so that leaves assimilate rapidly when evaporative demand is low or when water supply is adequate and assimilate slowly or not at all at other times?

13. Experimental studies should be undertaken to assess the relative values of stomatal strategies of operation, and transitions between RuP_2 saturated and RuP_2 regeneration limited fixation of CO_2. Advanced modern techniques of isotope discrimination can be used to provide a time averaged determination of water use efficiency (Farquhar & Richards, 1984; Hubick *et al.* 1986) which, coupled with biochemical and gas exchange measurements of photosynthesis (von Caemmerer & Farquhar, 1981) offers the tools to study the effectiveness of plant strategies to optimise performance in a modified environment.

14. Integrated studies of the processes determining water use efficiency and the examination of differences between a range of species could suggest targets that could be attained in other species by incorporation of the appropriate tactical or strategic phenotypic responses through the genotype of these species.

Stir into text