



Review

# Agroecosystem responses to combinations of elevated CO<sub>2</sub>, ozone, and global climate change

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## Abstract

Global climate change, caused by increased emissions of greenhouse gases, is likely to affect agroecosystems in many ways, but the outcome, for instance, as a shift in productivity, depends on the combined effects of climate (temperature, precipitation) and other global change components. The focus of this review is on temperature, soil moisture, atmospheric CO<sub>2</sub> and tropospheric ozone (O<sub>3</sub>). Changes in agricultural productivity can be the result of direct effects of these factors at the plant level, or indirect effects at the system level, for instance, through shifts in nutrient cycling, crop–weed interactions, insect pest occurrence, and plant diseases. Based on results of factorial experiments under a range of experimental conditions, it is difficult to draw generalized conclusions. With respect to C<sub>3</sub> crops, the data suggest that elevated CO<sub>2</sub> may have many positive effects, including yield stimulation, improved resource-use efficiency, more successful competition with C<sub>4</sub> weeds, reduced O<sub>3</sub> toxicity, and in some cases better pest and disease resistance. However, many of these beneficial effects may be lost—at least to some extent—in a warmer climate. Warming accelerates plant development and reduces grain-fill, reduces nutrient-use efficiency, increases crop water consumption, and favors C<sub>4</sub> weeds over C<sub>3</sub> crops. Also, the rate of development of insects may be increased. In grasslands, elevated CO<sub>2</sub> stimulates dry matter production, in particular, in N-fixing legumes, but warming again reduces the positive CO<sub>2</sub> effect. A major effect of climate warming in the temperate zone could be a change in winter survival of insect pests, whereas at more northern latitudes shifts in phenology in terms of growth and reproduction, may be of special importance. However, climate warming disturbs the synchrony between temperature and photoperiod; because insect and host plant species show individualistic responses to temperature, CO<sub>2</sub> and photoperiod, it is expected that climate change will affect the temporal and spatial association between species interacting at different trophic levels. Although predictions are difficult, it seems reasonable to assume that agroecosystem responses will be dominated by those caused directly or indirectly by shifts in climate, associated with altered weather patterns, and not by elevated CO<sub>2</sub> per se. Overall, intensive agriculture may have the potential to adapt to changing conditions, in contrast to extensive agricultural systems or low-input systems which may be affected more seriously.

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## 1. Introduction

Anthropogenic emissions of carbon dioxide (CO<sub>2</sub>), and of other greenhouse gases, have serious implications for the global climate system. In its recent third

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assessment report, the Intergovernmental Panel on Climate Change (IPCC) has concluded that a change in global mean temperature of 1.4–5.8 °C, in combination with changes in precipitation and an increased frequency of extreme weather events, is likely to occur until 2100 (IPCC, 2001). This shift in climate will affect terrestrial ecosystems at different temporal and spatial scales, reaching from effects at the global biosphere level, which may take years to millennia, to localized effects at the level of individual organisms or even organelles, which may take only minutes to a few years. Given the implications for ecosystems with their goods and services, sensitivity analyses are needed to identify areas at risk, and critical conditions and thresholds, and to elaborate mitigation and adaptation options at the scales of interest to decision makers and practitioners. At the smaller spatial scales, effects of climate change may differ from those projected at the larger scales. In fact, high resolution mechanistic ecosystem modeling suggests that the response of a particular system depends on the fine-scale spatial pattern of soil characteristics, and on the nutrient cycling

properties of the soil/vegetation system (Pan et al., 1996; Riedo et al., 1999).

Agricultural ecosystems—or agroecosystems—comprise polycultures, monocultures, and mixed systems, including crop–livestock systems, agroforestry, agro–silvo–pastoral systems, aquaculture, as well as rangelands, pastures and fallow lands. They are found all over the world from wetlands and lowlands to drylands and mountains, and their interactions with human activities are determinant. Today, the agricultural share of the total land area is about 30% in the US, 45% in Europe, and 38% worldwide (FAOSTAT, 1999). Effects of climate change on agroecosystems have received considerable research attention (see Parry, 1990; Rosenzweig and Hillel, 1998), but hitherto the sensitivity of many of the types of ecosystems listed above have not been studied in detail. Most studies focused on cropping systems, and projected effects include changes in yield and spatial shifts of production potentials (Reilly and Schimmelpfennig, 1999), or altered insect pest occurrence (Porter et al., 1991). Changing temperature or rainfall alters the

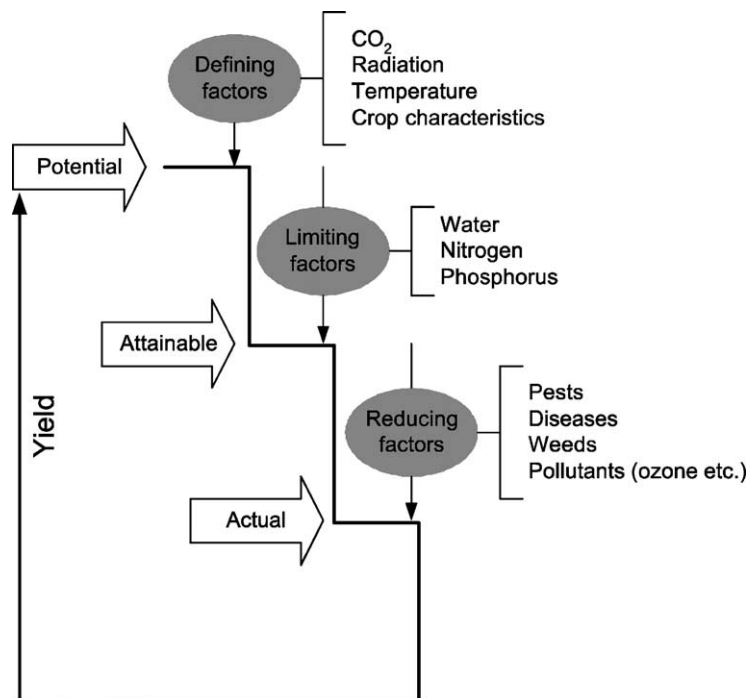


Fig. 1. Crop production levels depending on defining, limiting or reducing factors (see Goudriaan and Zadoks, 1995).

local suitability for specific crops (Rötter and van de Geijn, 1999) and grasslands (Rounsevell et al., 1996), and the need for irrigation and fertilization (Adams et al., 1990). In the case of temperate grasslands, model simulations suggest increased productivity (Riedo et al., 1999; Parton et al., 1995), which may stimulate animal production (Baker et al., 1993). Secondary effects include altered farm profitability and regional costs (Rosenzweig and Parry, 1994).

However, many predictions of climate change effects are confounded by the interactions with direct or indirect effects of elevated atmospheric CO<sub>2</sub>, and with other global change components. An increase in CO<sub>2</sub> adds additional carbon to the ecosystems via photosynthesis, leading to changes in the cycling of water and nutrients, and the energy balance. Moreover, the changing chemistry of the atmosphere affects ecosystem processes. In many industrialized regions, the increase in tropospheric ozone (O<sub>3</sub>) is a key factor of atmospheric change, and the widespread occurrence of visible plant damage across Europe is well documented (Benton et al., 2000). Effects of O<sub>3</sub> pollution on crops received considerable research attention (Heagle, 1989). Direct negative effects of O<sub>3</sub> on photosynthetic C fixation, leading to productivity losses, are well established (e.g. Lehnherr et al., 1997). It is also known that the thinning of the protective stratospheric ozone layer, leading to increased levels of ultraviolet (UV-B) radiation at the earth surface, may have implications for the productivity and quality of sensitive crop species and cultivars (Krupa et al., 1998), but this aspect is not considered in this review.

Following the concept cited in Goudriaan and Zadoks (1995), the *potential yield*, which is determined by climate, CO<sub>2</sub> and crop characteristics, is almost never achieved because of *yield limiting factors* such as low soil moisture and nutrient availability, and *yield reducing factors* such as pests and pathogens, weeds, and air pollutants (Fig. 1). To understand agroecosystem responses, the role these factors may play under altered climatic conditions and elevated CO<sub>2</sub> must be known. The aim of this review is to summarize recent findings with regard to the interactions between various factors, with a focus on agroecosystems productivity. Other relevant aspects such as biodiversity or carbon sequestration are not considered.

## 2. Agricultural yield

### 2.1. Influence of elevated CO<sub>2</sub> and temperature

Atmospheric CO<sub>2</sub> is the sole carbon source for plants. Current levels of CO<sub>2</sub> limit CO<sub>2</sub> assimilation in C<sub>3</sub> crops, and increasing CO<sub>2</sub> concentrations up to about 800–1000 ppm stimulate photosynthesis (Amthor, 2001). However, stimulation of photosynthesis does not directly translate in increased biomass, or yield. In determinate crops such as cereals, grain yield not only depends on photosynthesis but also on the length of the active phase of leaf photosynthesis, and the sink capacity of the grains. Fangmeier et al. (2000) found that in barley (*Hordeum vulgare* L.) elevated CO<sub>2</sub> increased the nitrogen (N) sink capacity of the grains in combination with accelerated flag leaf senescence, which, in turn, reduced the length of the period of photosynthetic carbon acquisition.

Often, the effects of elevated CO<sub>2</sub> have been studied with non-limiting supply of water and nutrients, and temperatures have been kept near the optimum for crop growth. Under these experimental conditions, average yield stimulation for C<sub>3</sub> crops with a doubling of CO<sub>2</sub> has been estimated at 30%, while estimates based on results from field-scale experiments under more realistic conditions were lower. According to the review by Kimball et al. (2002), elevated CO<sub>2</sub> stimulates biomass in C<sub>3</sub> grasses by an average of 12%, grain yield in wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) by 10–15%, and tuber yield in potato (*Solanum tuberosum* L.) by 28%. Yield stimulation in C<sub>4</sub> crops is much lower. Under limiting nutrient supply (mainly N) in free-air CO<sub>2</sub> enrichment (FACE) experiments, a mean stimulation of wheat grain yield by only 7% was observed, in contrast to a higher relative stimulation under water-limited conditions (Kimball et al., 2002). In absolute terms CO<sub>2</sub>-stimulation of wheat grain yield in water-limited plants may nearly compensate for effects of water shortage (Amthor, 2001).

Similar to arable crops, dry matter production in species of temperate grasslands on fertile soils responds positively to an increase in CO<sub>2</sub>. In a FACE experiment, yield of perennial ryegrass (*Lolium perenne* L.) swards with high N-fertilizer input increased from 8% up to almost 30% after 3 years, and in white clover (*Trifolium repens* L.), a legume receiving N via biological N<sub>2</sub>-fixation, yield increased from

11 to 20% (Hebeisen et al., 1997). Yield stimulation of a mixture of both species averaged 18%, regardless of year, fertilization level, or cutting frequency. With a low input of N, N limitation strongly reduced the CO<sub>2</sub>-stimulation of dry matter yield in ryegrass swards to below 10% over a 6-year period, as compared to 25% with high N input (Daepf et al., 2000). Thus, the CO<sub>2</sub> response of grasses, which depends on the carbon sink strength and is highest during reproductive growth, can be overcome by N-fertilizer addition (Daepf et al., 2001). In grass/clover mixtures, biological N fixation contributed significantly to the total system N supply, and in systems with lower N-fertilizer inputs, elevated CO<sub>2</sub> may favor the legumes and restrict the grass component (Zanetti et al., 1997). Biological N fixation by legumes plays a key role in maintaining the C:N balance under elevated CO<sub>2</sub> and accounts for the strong positive response of dry matter yield and N yield of legumes, as evidenced directly by comparing the responses of effectively and ineffectively nodulating lucerne (*Medicago sativa* L.) (Lüscher et al., 2000).

In less productive systems, such as a native tall-grass prairie, elevated CO<sub>2</sub> exposure during several years consistently stimulated biomass production, but the magnitude of the effect differed between individual years mainly because of interactions with variable soil moisture availability (Owensby et al., 1993). In moderately fertile California annual grassland, elevated CO<sub>2</sub> was found to stimulate net primary production (NPP) in the presence of ambient levels of temperature, precipitation, and N input. However, positive effects of increased levels of these factors on NPP were consistently damped by elevated CO<sub>2</sub> (Shaw et al., 2002). The authors suggested that soil nutrient immobilization under elevated CO<sub>2</sub> could be responsible for the suppressive effect. Based on their experience, they stress the importance of multifactor experiments to understanding ecosystem responses to global change.

The effect of elevated CO<sub>2</sub> depends on temperature. Based on the differential temperature sensitivity of the solubility of CO<sub>2</sub> and O<sub>2</sub>, it could be expected that increasing temperature would increase the affinity of ribulose biphosphate carboxylase/oxygenase (rubisco) for CO<sub>2</sub>, leading to an increase in the CO<sub>2</sub>-stimulation of photosynthesis with temperature (Long, 1991). However, this effect may not result

in increased biomass or yield. In individual leaves of soybean (*Glycine max* (L.) Merr.) stimulation of photosynthesis by elevated CO<sub>2</sub> increased as temperature was increased from 25 to 35 °C (i.e. optimal growth rates), whereas both whole plant photosynthesis and total biomass production showed the opposite trend (Ziska and Bunce, 1997). The authors argued that if CO<sub>2</sub> and temperature increase concurrently, self-shading could limit the response of CO<sub>2</sub> assimilation. But the situation is more complex because CO<sub>2</sub> also reduces stomatal conductance and, in turn, transpirational cooling which leads to higher canopy temperatures. In cotton (*Gossypium hirsutum* L.), canopy temperature was increased by an average of 0.8 °C under elevated CO<sub>2</sub>, and in wheat by 0.6 °C, and the increase may even be larger when N is limited (see Kimball et al., 2002). Hence, elevated CO<sub>2</sub> adds further to the increase in leaf temperature caused by higher air temperature.

There is ample evidence that warming generally reduces the yield of grain crops because of accelerated plant development (see Amthor, 2001), and the negative effect tends to be larger for grain yield than for total biomass (e.g. Batts et al., 1997). This may be due to the particular temperature sensitivity of grain-fill. In a recent data analysis for wheat, Amthor (2001) found that warming by only a few degrees may offset the positive effect of elevated CO<sub>2</sub> on yield, and that the combination of doubled CO<sub>2</sub> and a warming of 1.6–4.0 °C has a negative effect on yield (Fig. 2). Similarly, Porter and Perez-Soba (2001) found that sub-optimal temperatures reduced the relative CO<sub>2</sub>-stimulation of growth in herbaceous species. Conversely, elevated CO<sub>2</sub> can counteract the negative effect of higher temperatures, as in the case of cool-temperate grasses. An increase in temperature by 2.5 °C under field conditions strongly reduced (–42%) dry matter yield of a perennial ryegrass sward at ambient, but not at elevated CO<sub>2</sub> (Nijs et al., 1996). Similarly, wheat yield declined with increasing temperature, but less in the presence of elevated CO<sub>2</sub> (Wheeler et al., 1996). However, as studies are often confounded by the different responses of species adapted and acclimated to different temperatures, and the inter-specific differences in growth form and development pattern, evidence for large differences in the response to CO<sub>2</sub> at different temperatures is still limited (Morison and Lawlor, 1999). Polley (2002) suggested that yield

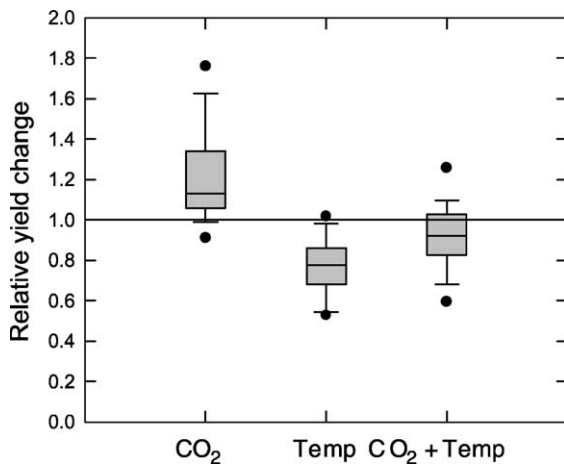


Fig. 2. Effects of elevated CO<sub>2</sub> and increased temperature, singly and in combination, on yield of wheat. The data represent the ratio of yield relative to current ambient CO<sub>2</sub> and temperature (relative yield change). Data are taken from the review by Amthor (2001, Table 7). Plots show median and standard percentiles ( $n = 17$ ).

should be most responsive to CO<sub>2</sub> when temperatures approximate the optimum for crop growth.

The effect of increasing temperature per se on plant growth and development has important consequences for crop production (Porter and Gwaith, 1999), and the implications of warming, for instance, for wheat yields, can be predicted with some confidence. Important aspects include changes in growth rates and phenological development, and effects of shifts in the frequency of occurrence of critical temperature thresholds for specific developmental phases, including germination, vernalization, tillering, spikelet initiation, etc. Given the prediction that climate variability may increase and extremes become more frequent, there is a need to better understand the implications of the combination of increasing mean temperature and more frequent temperature extremes for crop production.

## 2.2. Influence of ozone alone and in combination with elevated CO<sub>2</sub>

It is well known that increasing O<sub>3</sub> levels at ambient CO<sub>2</sub> causes a decline in the yield of many crops species (cf. Fuhrer et al., 1997; Fuhrer and Booker, 2003). This negative effect results from a limitation of photosynthetic C assimilation due to a reduction in the activity and amount of rubisco (Lehnher et al.,

1997; Farage and Long, 1992; Pell et al., 1994), associated with accelerated leaf senescence (Grandjean and Fuhrer, 1989). In addition to detrimental effects of O<sub>3</sub> on rubisco, Grantz and Farrar (1999) and Grantz and Yang (2000) have also shown that impaired translocation of photosynthate from sources to sinks is an early and important effect of O<sub>3</sub> on plant growth. In addition to its effect on yield, O<sub>3</sub> was found to affect the quality of crops; for instance, grain N concentration generally increases with increasing O<sub>3</sub> (Pleijel et al., 1999) leading to a better baking quality of the flower (Fuhrer et al., 1990), whereas in potato, increasing O<sub>3</sub> had a negative impact on tuber quality (Vorne et al., 2002).

The effect of O<sub>3</sub> on photosynthesis interacts with elevated CO<sub>2</sub> (McKee et al., 1995). Therefore, elevated O<sub>3</sub> determines the magnitude of the yield-enhancement by elevated CO<sub>2</sub>. The relative yield stimulation by elevated CO<sub>2</sub> is larger in an atmosphere containing elevated levels of O<sub>3</sub>, or vice versa, in a CO<sub>2</sub>-enriched atmosphere, negative effects of O<sub>3</sub> are less than at ambient CO<sub>2</sub>. This was observed, for instance, in soybean (Heagle et al., 1998), cotton (Heagle et al., 1999), and winter wheat (Heagle et al., 2000), but not in clover (Heagle et al., 1993). The protective effect of elevated CO<sub>2</sub> under O<sub>3</sub> stress could be explained by a reduction in leaf conductance which reduces O<sub>3</sub> uptake, or an increase in the activity of anti-oxidant enzymes (Rao et al., 1995). But most current evidence suggests that the protection from O<sub>3</sub> in a CO<sub>2</sub>-rich atmosphere is primarily due to O<sub>3</sub> exclusion, rather than an increased detoxification capacity (Fiscus et al., 1997; McKee et al., 1997). This is in agreement with the observation that O<sub>3</sub> flux to the plasmalemma in wheat and barley is controlled by stomata rather than by direct reaction of O<sub>3</sub> with detoxifying substances such as cell wall ascorbate (Kollist et al., 2000).

## 3. Resource-use efficiency

### 3.1. Nutrients

The aim of modern agricultural practices is to achieve an optimum efficiency in the use of resources (i.e. minimum amount of a resource used per unit of yield) such as nutrients and water, thereby preserving



resources and minimizing environmental impacts due to resource losses to the environment. Excessive application or low uptake efficiency of nutrients from concentrated inorganic fertilizers or from renewable nutrient sources (e.g. animal manure, cover crops, or green manures) can result in the accumulation of nutrients in the soil. With low nutrient-use efficiency (NUE) nutrients not utilized by the plants may leach to groundwater, be transported in runoff or sediment to surface waters, or be emitted to the atmosphere in the form of nitrous oxide ( $\text{N}_2\text{O}$ ), nitric oxide (NO) or ammonia ( $\text{NH}_3$ ).

Increased NUE was often observed in response to raising  $\text{CO}_2$  (Drake et al., 1997). Nutrient retrieval and nutrient utilization were found to be higher in elevated  $\text{CO}_2$  in field-grown cotton (Prior et al., 1998), and wheat (Fangmeier et al., 1999). However, with increasing NUE under elevated  $\text{CO}_2$ , N yield in cereals does not automatically increase (Kimball et al., 2002) because of the decrease in plant N concentration. This may be caused by the effect of dilution due to the more rapid growth under elevated  $\text{CO}_2$ , or due to changes occurring at the level of the photosynthetic apparatus. Increased plant NUE can lead to lower inorganic N concentrations in the soil, and reduced N loss. Torbert et al. (1996) found that elevated  $\text{CO}_2$  significantly decreased nitrate ( $\text{NO}_3\text{-N}$ ) concentrations below the rooting zone in both soybean and grain sorghum (*Sorghum vulgare* Pers.) crops indicating improvements in N retention in soil organic pools. In ryegrass monocultures, after 4 years elevated  $\text{CO}_2$ , N yield and

NUE were reduced while system N gain decreased at low, and increased at high N-fertilization rate, whereas in clover an increase in N yield and NUE was associated with higher system N gains at both low and high N-input rates (Table 1) (Hartwig et al., 2002). In this case, the higher system N gain was mainly due to higher retention of N in the soil. Assuming that elevated  $\text{CO}_2$  would not increase N availability, the limiting effect of N on the productivity of ryegrass monocultures would become more stringent (Gloser et al., 2000). In an intact  $\text{C}_3/\text{C}_4$  grassland in central Texas (USA), increasing  $\text{CO}_2$  decreased net N mineralization which led to a strong, non-linear decrease in N availability (Gill et al., 2002). In the longer term, this may lead to a decline in plant productivity. These results underline the importance of the influence of elevated  $\text{CO}_2$  on N cycling and N budgets in both annual cropping systems and perennial grassland systems.

There may be important climate feedbacks through effects of elevated  $\text{CO}_2$  on soil nutrient cycling. Higher potential production of the greenhouse gas  $\text{N}_2\text{O}$  could result from direct effects of elevated  $\text{CO}_2$  on soil microbial processes of nitrification and denitrification (Carnol et al., 2002). In ryegrass plots maintained under high N input, elevated  $\text{CO}_2$  increased (+27%), the output of  $\text{N}_2\text{O}$  following the application of ammonium nitrate, thought to be the consequence of enhanced root-derived available soil C, acting as an energy source for denitrification (Ineson et al., 1998). With low N input, Kammann et al. (1999) also observed an increased  $\text{N}_2\text{O}$  output from grassland

Table 1  
Effect of elevated  $\text{CO}_2$  on nitrogen dynamics<sup>a</sup>

Plant species	N fertilization ( $\text{g N m}^{-2}$ per year)	$[\text{CO}_2]$ ( $\mu\text{l l}^{-1}$ )	$\text{N}_{\text{yield}}$ ( $\text{g N m}^{-2}$ per year)	NUE (%)	$\text{N}_{\text{gain}}$ ( $\text{g N m}^{-2}$ )
<i>Lolium perenne</i>	14	350	6.0	21.4	23
		600	5.5	18.2	11
	56	350	22.8	35.5	47
		600	17.4	26.8	86
<i>Trifolium repens</i>	14	350	18.9	11.9	28
		600	28.9	16.7	42
	56	350	17.1	9.9	36
		600	28.9	13.8	45

Nitrogen yield ( $\text{N}_{\text{yield}}$ ), nitrogen use efficiency (NUE) in yield, and system N gain ( $\text{N}_{\text{gain}}$ ) in monocultures of perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) at two levels of N fertilization and exposed to either ambient ( $350 \mu\text{l l}^{-1}$ ) or elevated ( $600 \mu\text{l l}^{-1}$ )  $\text{CO}_2$ . (Plants were grown in the FACE experiment at Zurich-Eschikon, Switzerland.)

<sup>a</sup> Data from Hartwig et al. (2002).

plots, but this was not directly related to fertilizer applications. However, in a study with barley no direct plant-mediated effect of elevated CO<sub>2</sub> on N<sub>2</sub>O fluxes or denitrification activity could be observed, possibly because N uptake by the plants was more efficient under CO<sub>2</sub> enrichment (Martin-Olmedo et al., 2002).

Nutrient cycling may be affected further by elevated CO<sub>2</sub> via changed litter decomposition rates, as suggested by Field et al. (1992). Frederiksen et al. (2001) reported that the decomposition of wheat straw was slower when the plants were grown at elevated CO<sub>2</sub>. Changes in residue quality due to elevated CO<sub>2</sub> may alter soil C and N dynamics, as shown by Torbert et al. (1998) using residues collected from experiments with soybean exposed to either ambient or elevated CO<sub>2</sub>. However, elevated CO<sub>2</sub> has been found to alter the C:N ratio, but not the amount of root litter in the top-soil horizon in grassland after 8 years of exposure, leading to only minor changes in N cycling in the soil (Jastrow et al., 2000). Furthermore, a meta-analysis by Norby et al. (2001) revealed that elevated CO<sub>2</sub> has only a small effect on litter N content, unlike in the case of green leaves, thus indicating that N resorption during leaf senescence is not altered by elevated CO<sub>2</sub> and thus effects on nutrient cycling in the soil may be small. Also, any such effects, if they occur, may be of minor importance in managed agroecosystems because of larger effects from agricultural practice or changing land use and varying crops.

In contrast to elevated CO<sub>2</sub>, warming tends to have a negative effect on plant NUE. This can be due to increased sink limitation with increasing temperature, especially in plants with reproductive sinks (Reddy et al., 1991). At the system level, warmer conditions stimulate soil N availability through higher rates of mineralization which may lead to increased productivity (Parton et al., 1995), but also to higher system N losses if N demand by the plant is not synchronized with N supply. Ozone stress also reduces NUE; in wheat, both the efficiency of N uptake and N assimilation decreased with increasing O<sub>3</sub> (Fuhrer, unpublished data). The combined effect of O<sub>3</sub> stress and elevated CO<sub>2</sub> on NUE remains unknown.

### 3.2. Water

Changes in the water balance and the amount of water available in the soil can be crucial for crop yield.

In grasslands, 90% of the variance in primary production can be accounted for by annual precipitation (see Campbell et al., 1997), and yield of water-limited crops is determined by crop water use and by water-use efficiency (WUE). In a warmer climate and under small interception losses of water, increased evapotranspiration favors soil dryness. Calculations using the Penman–Monteith equation predict that potential evaporation increases by about 2–3% for each 1 °C raise in temperature (see Lockwood, 1999). Thus, sites which are already at the limit with respect to water supply under current conditions are likely to be most sensitive to climate change, leading to an increase in the need for irrigation in dry areas, while more humid areas may be less affected (e.g. Brumbelow and Georgakakos, 2001). This negative effect of climate warming may be counteracted by effects of elevated CO<sub>2</sub> on the crop tolerance to water stress (Woodward et al., 1991), as recently confirmed for sorghum (Wall et al., 2001), wheat, cotton and maize (*Zea mays* L.) (Kang et al., 2002). Among the many effects of increased CO<sub>2</sub> on plants, increased WUE plays a key role (see Kimball et al., 2002).

Improved WUE with elevated CO<sub>2</sub> can be linked to prolonged photosynthetic activity during drought, which, in turn, leads to higher crop yields in rain-fed agricultural systems, for instance, in the semi-arid tropics (Clifford et al., 2000). The increase in WUE tends to be higher under dry as compared to wet soil conditions (Kang et al., 2002), and Ottman et al. (2001) suggested that sorghum yield would increase most with higher CO<sub>2</sub> concentrations in areas where water is limited. However, the nature of the interaction between drought and elevated CO<sub>2</sub> remains unclear. Grant et al. (1995) observed that the decline in stomatal and canopy conductance in wheat as soil dried was greater at the current than at elevated CO<sub>2</sub>. Conversely, Mitchell et al. (2001) provided evidence that the relative response of transpiration and canopy photosynthesis to soil water deficit was unaffected by CO<sub>2</sub> concentration. This is in agreement with the observation that elevated CO<sub>2</sub> may have little or no effect on transpiration or photosynthesis when the response is normalized to soil water content (Serraj et al., 1999). In C<sub>4</sub> plants, however, pronounced drying of soils may cause stomatal closure and thus reduce internal CO<sub>2</sub> concentrations to levels over which photosynthesis is sensitive to CO<sub>2</sub>

(Polley, 2002). This may favor positive CO<sub>2</sub> effects on leaf area development in C<sub>4</sub> species at low soil moisture levels (Samarkoon and Gifford, 1996). The protective effect of elevated CO<sub>2</sub> could also be linked to a greater capacity to extract available soil water and nutrients by roots, thus enabling plants to maintain greater relative water content and less negative total leaf water potentials (Wall, 2001). Wechsung et al. (1999) observed that increased root growth and changes in root morphology caused by elevated CO<sub>2</sub> increased the ability of wheat plants to compensate for effects of water stress. Thus, increased carbon partitioning to roots with elevated CO<sub>2</sub> is an important issue, and was found in field studies with winter wheat (Batts et al., 1998), and in ryegrass (Suter et al., 2002). However, an earlier literature review by Rogers et al. (1996) revealed substantial variation in root:shoot biomass partitioning across crop species, possibly because of differences in crop type, resource supply, or other experimental factors. Effects of elevated CO<sub>2</sub> on root morphology may be equally variable (Pritchard and Rogers, 2000). Because of the lack of a mechanistic understanding of biomass partitioning generalizations about crops responses to elevated CO<sub>2</sub> under limiting soil resources remain difficult.

Improved photosynthetic WUE at the leaf level may not reduce crop water consumption to the same extent because whole canopies may still consume equal amounts or more, instead of less, water due to an increase in total leaf area (Riedo et al., 1999; Hui et al., 2001), particularly in C<sub>3</sub> species such as wheat or cotton (Kang et al., 2002) which are more responsive to increasing CO<sub>2</sub> compared to C<sub>4</sub> plants. The extent of this compensatory effect is influenced by N fertilization because of limitations of the CO<sub>2</sub> enhancement by low nutrient supply (McKee and Woodward, 1994). At a seasonal time scale, elevated CO<sub>2</sub> reduced evapotranspiration of wheat by 9% when fertilized with 35 g N m<sup>-2</sup> or 16% when fertilized with only 7 g N m<sup>-2</sup> (Grant et al., 2001). The increase in crop WUE due to elevated CO<sub>2</sub> typically is less than 75% of that measured at the leaf level (Polley, 2002). In sorghum, crop evapotranspiration was reduced by 10% due to CO<sub>2</sub> enrichment, and WUE based on grain yield increased by 9 and 19% in wet and dry plots, respectively (Conley et al., 2001). This suggests that in the absence of major global warming future water require-

ments for irrigated sorghum will be slightly lower than at present, while dryland productivity may be higher.

An effect of elevated CO<sub>2</sub> on crop water-use affects soil moisture content. Soil moisture tends to be higher under crops exposed to elevated CO<sub>2</sub>, as compared to ambient CO<sub>2</sub>, as observed in tallgrass prairie (Owensby et al., 1999), and in FACE experiments with different crops (Kimball et al., 2002). This increase in soil moisture is important for biological processes in the soil, including litter decomposition (Dukes and Hungate, 2002).

Because of the co-occurrence of high O<sub>3</sub> levels during warm weather, combined with reduced soil moisture, interactions between O<sub>3</sub> stress and WUE are important. Reduced leaf WUE in response to O<sub>3</sub> was found, for instance, in wheat (Saurer et al., 1991; Nussbaum et al., 1995) and soybean (Vozzo et al., 1995). This effect may be linked to direct negative effects of O<sub>3</sub> on stomatal functioning (Leipner et al., 2001; McAinsh et al., 2002), or the stronger sensitivity of photosynthetic CO<sub>2</sub> fixation relative to the stomatal conductance to water vapor (Saurer et al., 1991). But because of a concurrent reduction in crop biomass, O<sub>3</sub> is not likely having an effect on total crop water consumption. Conversely, under dry conditions, stomatal limitation of O<sub>3</sub> uptake is higher and thus the plants are partially protected from short-term O<sub>3</sub> impacts (Tingey and Hogsett, 1985; Bungener et al., 1999).

#### 4. Weeds, insect pests and diseases

The occurrence of plant pests (weeds, insects or microbial pathogens) is an important constraint with global average yield losses estimated at about 40% (Oerke et al., 1994), and production costs significantly dependent on the extent of measures necessary for plant protection. Consequently, changes in the occurrence of pests due to changes in the atmospheric conditions are of both ecological and economic importance.

##### 4.1. Weeds

Weeds cause substantial crop losses particularly in less-developed agricultural production systems (Parker and Fryer, 1975), and most cultivation and tillage practices are for weed control. In general, any direct or indirect consequence of increasing CO<sub>2</sub>



or O<sub>3</sub>, or climate change, which differentially affect the growth or fitness of weeds and crops, will alter crop–weed competitive interactions (Patterson, 1995a). The result may be favoring the weed in one case, or the crop may benefit in another situation. Unfortunately, virtually nothing is known about effects of elevated O<sub>3</sub> on crop–weed interactions (see review by Fuhrer and Booker, 2003), but O<sub>3</sub>, as any environmental factor which affects the growth of agronomically important species, may potentially affect the ability of weeds and crops to compete for common resources.

In the case of aggressive weed species of tropical and subtropical origins, which are currently restricted to Mediterranean environments, future climatic conditions may lead to an expansion of their potential range in to temperate regions. An example would be itchgrass, *Rottboellia cochinchinensis*, which is currently restricted to the sugarcane (*Saccharum* spp.) plantations in the southern US (Patterson, 1995a). But the effect of climate change will likely be different in a high-CO<sub>2</sub> world. Weed and crop species differing in photosynthetic pathway (C<sub>3</sub> versus C<sub>4</sub>) respond differently to elevated CO<sub>2</sub> and other environmental changes (Patterson, 1995b), with C<sub>3</sub> species being favored by increased CO<sub>2</sub> (Patterson et al., 1999). When cultivated together with either of these two weed species, soybean seed yield was reduced at both ambient and elevated CO<sub>2</sub> relative to the weed-free control (Ziska, 2000). The decrease in yield was associated with a 65% increase in dry weight of the C<sub>3</sub> weed at elevated CO<sub>2</sub>, whereas in the combination with the C<sub>4</sub> weed, the yield loss was reduced less at elevated, as compared to ambient CO<sub>2</sub>. The most interesting observation made in this study was that the presence of weeds reduced the ability of soybean to respond positively to elevated CO<sub>2</sub>, particularly in the combination with the C<sub>3</sub> weed (Table 2). A possible explanation would be that weeds compete successfully for resources such as mineral nutrients, water, light, or all three, and thus limit the ability of the crop to assimilate extra carbon. This mechanism may be most important in low-input systems.

From the 18 most problematic weedy species, 14 are C<sub>4</sub> species, whereas the vast majority of important food crops are C<sub>3</sub> species (Holm et al., 1977). As pointed out by Bunce and Ziska (2000), this relationship may differ between regions. For instance, in the US, 9 out of 15 worst weeds in the most important

Table 2  
Effect of elevated CO<sub>2</sub> on crop–weed interactions<sup>a</sup>

Crop–weed interactions	Ambient (CO <sub>2</sub> )	Elevated (CO <sub>2</sub> )	Percentage change
Aboveground biomass			
Soybean (C <sub>3</sub> )	340 ± 13	448 ± 14	+31.8
+C <sub>3</sub> weed	261 ± 18	297 ± 29	+14.0
+C <sub>4</sub> weed	204 ± 17	329 ± 27	+61.3
Seed yield			
Soybean (C <sub>3</sub> )	187 ± 8	228 ± 8	+21.9
+C <sub>3</sub> weed	135 ± 9	141 ± 15	+4.4
+C <sub>4</sub> weed	103 ± 13	158 ± 14	+53.4

Total aboveground biomass and seed yield (±standard error) at maturity for soybean (g m<sup>-1</sup> row) at ambient and elevated CO<sub>2</sub> (ambient + 250 μl l<sup>-1</sup> CO<sub>2</sub>) when grown with or without the presence of a C<sub>3</sub> weed (lambs' quarter, *Chenopodium album* L.) or a C<sub>4</sub> weed (redroot pigweed, *Amaranthus retroflexus* L.).

<sup>a</sup> Data from Ziska (2000).

crops are C<sub>3</sub>, and a substantial fraction of crops are C<sub>4</sub> (maize, sorghum, millet (*Pennisetum* spp.), sugarcane). Thus, the generalized prediction that in a CO<sub>2</sub>-rich atmosphere the world's major crops will compete more successfully with the worst agricultural weeds, which are mostly C<sub>4</sub> species (Dukes and Mooney, 1999), may not be accurate. Furthermore, knowledge of interactive effects of temperature and elevated CO<sub>2</sub> in crop–weed systems is limited. Wild oats (*Avena fatua* L.), a C<sub>3</sub> weed typically competing with wheat, was less responsive to elevated CO<sub>2</sub> at higher compared to lower temperatures. However, the outcome of the crop–weed interaction differed between near-isogenic lines and may thus be determined by the plasticity of the response, which could have adaptive advantages for wild oat at the population level (O'Donnel and Adkins, 2001).

Crop–weed interactions and their management may be influenced by the effect of elevated CO<sub>2</sub> on herbicide tolerance. Ziska et al. (1999) and Ziska and Teasdale (2000) observed that the tolerance to glyphosate, a widely used, phloem mobile, post-emergence herbicide, was higher in the C<sub>3</sub> weed species Lamb's-quarters (*Chenopodium album* L.) when the plants were grown at elevated CO<sub>2</sub>, as compared to the ambient CO<sub>2</sub> treatment. This effect could not be explained by increased plant size alone. Conversely, herbicide tolerance in the C<sub>4</sub> species redroot pigweed (*Amaranthus retroflexus* L.) was unaffected by CO<sub>2</sub>. This observation suggests an increased

presence of certain weeds in herbicide-treated cropping systems with increasing CO<sub>2</sub>.

Establishment of weeds may be favored at elevated CO<sub>2</sub> because of the increase in soil moisture, or slower drying of the soil under non-irrigated crops (see above). Like in any mixed-species competition, the specific CO<sub>2</sub> responses may depend on resource availability. In systems with limiting soil moisture, species that can take advantage of the extra moisture will be favored (Dukes and Mooney, 1999). On grasslands, where effects of stomatal closure may not be negated by an increase in leaf temperature and leaf area, rising CO<sub>2</sub> concentration could slow the depletion of soil water by the grasses and potentially favor shrubs, as discussed by Polley et al. (1997). However, the situation is complicated because of (i) the presence of a large number of interacting species, (ii) the importance of succession, and (iii) the heterogeneity of resource availability. In their review, Dukes and Mooney (1999) pointed out that elevated CO<sub>2</sub> may slow the process of succession in grasslands, which would increase the dominance of non-native species in many ecosystems. Conversely, the results from an experiment in which climate and management were manipulated revealed a hidden potential of native species to establish beyond their current range of distribution and in the absence of eutrophication and disturbance they may achieve dominance over many recognized weeds (Buckland et al., 2001).

The above results stress the complexity of the interactions between weeds and crops or grassland species in relation to global change. Further experiments with different crop–weed systems under a range of atmospheric and edaphic conditions are needed to allow for more accurate predictions. But it seems certain that crop–weed interactions will be affected by global change components, and that weed-induced yield losses may differ from those estimated under current conditions. Thus, estimates of yield stimulation by elevated CO<sub>2</sub> may be too high if effects from competition with weeds are ignored, unless management adapts flexibly. However, problems associated with the spread of weed and alien species under future atmospheric conditions may become even greater with the decline in intensive agriculture and management (Muller, 1996), and a similar trend could occur with the expansion of organic farming practices.

## 4.2. Insect pests

### 4.2.1. Insect life cycles

Effects of climate change, elevated CO<sub>2</sub>, and other global change factors, on insect pests and diseases are rarely taken into account in assessments of possible impacts on agricultural ecosystems. Both pest and beneficial insects can be affected by changing environmental conditions, either directly or indirectly via changes in host physiology and chemical composition, or via effects on predators, competitors, and insect pathogens (Patterson, 1995a). It is generally expected that with climate warming in mid- to high-latitude regions insect pests become more abundant.

Climate warming affects insect life cycles because of the temperature control of the processes involved. Patterson et al. (1999) provided an extensive list of climatic thresholds and responses for the phenological development of pest insects. Exceeding critical thresholds has implications, for instance, for mortality or fecundity, and increased cumulative temperature (in degree-days) potentially increases the number of generations (Porter et al., 1991). The main effect of climate warming in the temperate zone is believed to be a change in winter survival, while at northern latitudes shifts in phenology in terms of growth and reproduction, may be of prime importance (Bale et al., 2002). However, temperature effects may depend on photoperiod, and climate warming disturbs the synchrony between temperature and photoperiod.

In addition to the more local effects on insect populations, shifts in climate are also likely to affect the geographical range. For instance, model simulations predicted that climate change may lead to northwards shift in the potential distribution of the European corn borer (*Ostrinia nubilalis* Hübner) of up to 1200 km, or between 165 and 500 km for each 1 °C raise in temperature, with an additional generation found in all regions where it currently occurs (Porter et al., 1991). Other examples for the expansion of insect ranges were reviewed by Patterson et al. (1999). However, expansions may be limited by the ability of the host plant to move. Each species in a multi-trophic system may respond differently to changing temperature (Fig. 3). Migrant pests may respond more quickly to climate change than plants and could colonize crops already present at distant locations, as suggested by Cannon (1998), who illustrated this possibility by the

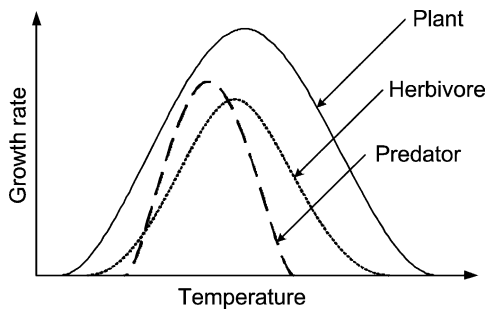


Fig. 3. Hypothetical functions for growth rates of three species in a tritrophic system at constant resource across temperature (after Guitierrez, 2000).

recent changes in the distribution of species from insect orders such as odonata, orthoptera and lepidoptera in NW Europe.

Drought can lead to changes in the host plants, making them more attractive to insect pests, while excessive precipitation associated with water logging may have direct negative effects on soil dwelling insects (Watt and Leather, 1986), or indirect effects through changes in insect pathogens, predators and parasites (Raulston et al., 1992). Higher summer rainfall could result in increased vegetation cover, leading to increased abundance of *Auchenorrhyncha* (homoptera), a major component of the insect fauna of grasslands, while increased summer drought had the opposite effect on vegetation cover with no related effect on the insect (Masters et al., 1998). In some regions such as Australia, the size and quality of insect populations are determined by the high variability in rainfall, which may change over time (Drake, 1994). Extremes like droughts or floods are important triggers for the outbreak of insects within their normal range, and shifts in the probability of such trigger events may be an important aspect of climate change effects on agricultural ecosystems.

Finally, it should be noted that the impact of climate change, involving changes in over-wintering, population growth rates, number of generations, dispersal and migration, host–insect synchronization, etc. may largely depend on insect phenotypic or genotypic flexibility. The direct effects of temperature on insects are likely to differ among species, depending on their current environment and life-histories, and their ability to adapt (Bale et al., 2002), and given the many

interactions between ecosystem processes, human influences, and environmental conditions, long-term predictions remain difficult.

#### 4.2.2. Insect herbivory

Recent research on the effects of elevated CO<sub>2</sub> has revealed some important aspects of insect herbivory associated with changes in plant composition. Relevant changes in the chemical composition of the host include increased C:N ratio, altered concentrations of allelochemicals, non-structural carbohydrates, starch and fiber contents (Lincoln et al., 1993), or increased concentrations of substances involved in disease resistance (Idso and Idso, 2001). In several studies, decreased N and increased carbohydrate concentrations were found to be correlated with increased insect food consumption. Larvae of *Polymmatius icarus* (lepidoptera, lycaenida) feeding on leaves of *Lotus corniculatus* L. (fabaceae) developed faster and were heavier due to more suitable and better digestible leaves containing higher carbohydrate concentrations (Goverde et al., 1999). In contrast, lower protein intake as a result of changed leaf composition under elevated CO<sub>2</sub> decreased the growth rates of Colorado beetle (*Leptinotarsa decemlineata* Say) larvae feeding on potato leaves (see Miglietta et al., 2000). From the analysis of data from 61 plant–herbivore interactions, Bezemer and Jones (1998) concluded that leaf chewers can compensate for decreased N content by strongly increasing their food consumption, in contrast to leaf miners with only a small increase, and seed-eaters showing no effect. The response of leaves-sucking insects such as mites may be affected negatively due to increased epidermis thickness and specific-leaf weight with elevated CO<sub>2</sub>, as suggested by Joutei et al. (2000). However, in white clover elevated CO<sub>2</sub> had not effect on leaf thickness (Fisher et al., 1997). CO<sub>2</sub> enrichment increased the rate of reproduction of twospotted spider mite (*Tetranychus urticae* Koch.) through an increase in the non-structural carbohydrate content (Heagle et al., 2002). Similarly, phloem-feeding aphids often respond positively in terms of population density to elevated CO<sub>2</sub> (Whittaker, 1999). A positive effect of CO<sub>2</sub> was found for the aphid *Myzus persicae* Sulzer on groundsel (*Senecio vulgaris* L.) and annual blue grass (*Poa annua* L.) (Bezemer et al., 1998), and for *Aulacorthum solani* Kalt. on bean (Awmack

et al., 1997) and *Sitobion avenae* F. on winter wheat (Awmack et al., 1996). An increase in aphid performance could lead to larger populations in a high-CO<sub>2</sub> world (Awmack et al., 1997). But, depending on the host plant, the effect on a particular aphid species may also be negative (Bezemer et al., 1999). Abundance of the peach-potato aphid (*M. persicae* Sulzer) was enhanced by elevated CO<sub>2</sub> and increased temperature, whereas one of the aphid's parasitoids, *Aphidius matricariae* Haliday, was stimulated only by warming (Bezemer et al., 1998). The influence of temperature is important because elevated CO<sub>2</sub> causes increased leaf temperatures (see above), and a small increase in temperature can affect fecundity of insects, as suggested by Heagle et al. (2002).

At the whole plant level, the damaging effect of herbivores may be compensated by increased leaf production leading to increased rather than decreased photosynthetic performance in some species, as shown for milkweed by Hughes and Bazzaz (1997). Insect feeding with *Spodoptera exigua* Hübner (beet armyworm) in sugar beet reduced plant growth at ambient but not at elevated CO<sub>2</sub> (Caulfield and Bunce, 1994). At the community level, the situation is even more complex, and preferential herbivore feeding on one species may have an indirect effect on other species less affected by the insects (Diaz et al., 1998). The difference in the re-

sponse to elevated CO<sub>2</sub> between different plant–insect combinations presents a further complication and thus predictions about long-term population responses are not reliable when based on detailed measurements on individual aphids (Bezemer et al., 1999).

Elevated O<sub>3</sub> caused an increase in ovipositioning of eggs on tobacco plants (Jackson et al., 1999), and increased survival and growth response of hornworm moths (*Manduca sexta* L.) larvae (Jackson et al., 2000). Populations of Colorado potato beetle were not affected by elevated O<sub>3</sub> (Costa et al., 2001). While elevated CO<sub>2</sub> tends to reduce the N concentration in leaves, O<sub>3</sub> tends to have the exact opposite effect (Pleijel et al., 1999). Hence, food consumption by herbivores and population development should be lower in O<sub>3</sub>-exposed plants, contrary to the situation with CO<sub>2</sub>, but experimental evidence suggests otherwise. Hummel et al. (1998) found that with increasing O<sub>3</sub> stress, the time required for female mites to develop declined, and increased abundance of twospotted spider mites (*T. urticae* Koch) was observed on O<sub>3</sub>-sensitive clover clones exposed to either increasing O<sub>3</sub> (Heagle et al., 1994) or CO<sub>2</sub> (Heagle et al., 2002) (Fig. 4). The relevant nutritive factor in both cases appears to be the carbohydrate concentration, not nitrogen, because O<sub>3</sub> was found to significantly increase foliar sugars and starch in *T. repens* leaves

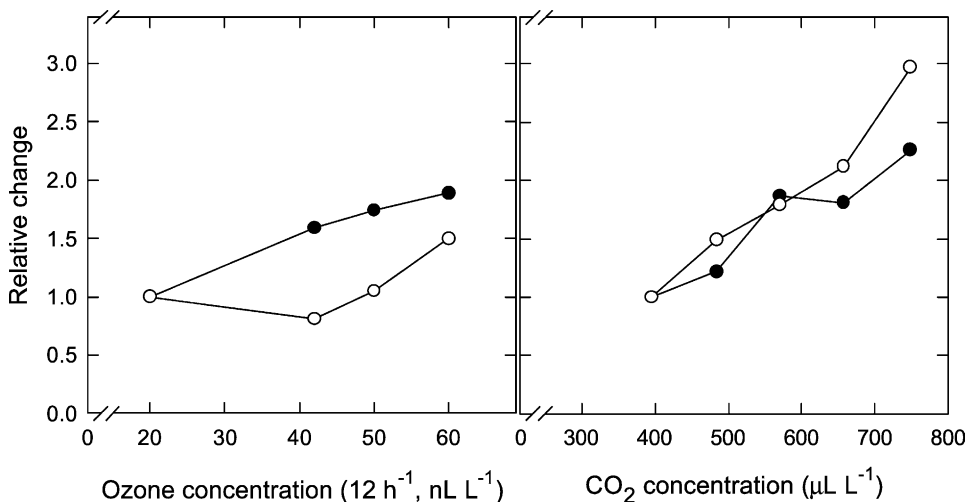


Fig. 4. Effects of increasing O<sub>3</sub> (left) and CO<sub>2</sub> (right) on reproduction of twospotted spider mites (Acari: Tetranychidae) on two white clover clones (●) ozone sensitive clone, NC-S; (○) ozone tolerant clone, NC-R). Data for ozone from Heagle et al. (1994), and for CO<sub>2</sub> from Heagle et al. (2002).

(Burns et al., 1997), and elevated CO<sub>2</sub> did the same (Heagle et al., 2002). Hence, with respect to arthropod herbivores (including *T. urticae*), both O<sub>3</sub> stress and elevated CO<sub>2</sub> may have stimulating effects through similar impacts on foliar chemistry. This suggests that in an atmosphere containing higher levels of CO<sub>2</sub> and O<sub>3</sub>, increased populations of some plant pests seem possible, which would have implications for pest management.

#### 4.3. Plant diseases

The occurrence of plant fungal and bacterial pests depends on climate and weather. Temperature, rainfall, humidity, radiation or dew affect the growth and spread of pathogens, as well as the resistance of the host plant (Patterson et al., 1999). It is likely that climate change will have positive, negative or neutral impacts on specific host–pathogen systems (Coakley et al., 1999). Neglecting the option of using crops with genetic modifications, it could be expected that under climate change conditions milder winters could favor many crop diseases such as powdery mildew, brown leaf rust and strip rust, and warmer summers may provide optimal conditions, for instance, for cercospora leaf spot disease (see Patterson et al., 1999). Alternatively, drier and warmer conditions during the summer would reduce the incidence of several crop diseases, including late potato blight, due to reduced plant susceptibility. But at the same time, the diseases could spread to currently cooler regions.

##### 4.3.1. Influence of elevated CO<sub>2</sub>

Goudriaan and Zadoks (1995) suggested that each (foliar) fungal pathogen has its own N optimum in the leaves, and thus changes in the C:N concentration ratio caused by elevated CO<sub>2</sub> may have differential effects on pathogenic fungi. More recently, Coakley et al. (1999) have provided a detailed review of the interaction between climate change, elevated CO<sub>2</sub> and plant diseases. Their summary presents conflicting results from different studies. Through an increase in canopy density, associated with higher humidity, resulting in more biomass of higher quality, elevated CO<sub>2</sub> could promote foliar diseases such as rust, powdery mildews, leaf spots, and blights. For instance, an enlarged canopy of shrubby stylos (*Stylosanthes scabra*

Schumacher) could trap more conidia of anthracnose (*Colletotrichum gloeosporioides* Penz.) that, together with increased humidity, would lead to more severe anthracnose on plants grown at high CO<sub>2</sub>. However, Coakley et al. (1999) also referred to recent studies of host–pathogen interactions showing that elevated CO<sub>2</sub> can increase host resistance or reduce aggressiveness of the pathogen. This may be due to enhanced production of defense-related substances, or structural changes in the host tissues. In contrast, higher temperature may increase the plant's susceptibility due to inactivation of temperature-sensitive resistance.

##### 4.3.2. Influence of temperature

In forage species, increased lignification under warmer conditions may have a positive effect on plant resistance to fungal attack. However, as in the case of insect pests, impact models predict that higher winter temperatures may favor pathogen survival and, consequently, increase the amount of initial inoculum present, whereas drier conditions during summer time would reduce the risk of infection by pathogens that require leaf wetness or wet soils for infection. However, Coakley et al. (1999) cautioned the value of these predictions because of the many interactions between environment, host, pathogen, and human interference, which are not considered in most models. Based on empirical climate–disease models established with a limited set of observational data, Jahn et al. (1996) predicted that an increase in temperature, combined with less precipitation could (i) increase leaf rust of wheat and barley (*Puccinia triticina*, formerly *recondita* f. sp. *tritici*) and powdery mildew of sugar beet (*Erysiphe betae*), (ii) decrease infestation levels caused by foot rot and leaf blotch diseases, and (iii) cause no change in powdery mildew on small grains. Further analysis of epidemiological data from long-term observations, in combination with climate change scenarios derived for specific sites, may help to improve the reliability of predictions.

##### 4.3.3. Influence of O<sub>3</sub>

Ozone effects on plants lead to altered disease susceptibility, but the effect is variable. As observed by von Tiedemann et al. (1991), powdery mildew (*Erysiphe graminis* DC. f. sp. *tritici* Marchal), leaf spot disease (*Septoria nodorum* Berk.), and spot blotch following inoculation with *Bipolaris sorokiniana*



Sacc. were significantly enhanced by exposure of wheat flag leaves to O<sub>3</sub>. Conversely, Plazek et al. (2001) found a positive effect of O<sub>3</sub> on resistance of barley and fescue to *B sorokiniana*, and in rape to *Phoma lingam*. In a more recent study, leaf rust disease (*Puccinia recondite* f. sp. *tritici*) on wheat leaves was strongly inhibited by O<sub>3</sub>, but was largely unaffected by elevated CO<sub>2</sub> both in the presence and absence of O<sub>3</sub> stress (von Tiedemann and Firsching, 2000). In the field, the incidence of powdery mildew was reduced because of negative effects of O<sub>3</sub> on canopy structure resulting in a drier canopy microclimate, while infections caused by facultative pathogens were generally increased (Fuhrer, unpublished data). This would suggest that under altered climatic conditions favoring infection pressure, plants weakened by O<sub>3</sub> stress may be particularly susceptible. But the interaction between O<sub>3</sub> and pathogens may be determined primarily by the timing of O<sub>3</sub> exposure relative to the presence of the inoculation. Sandermann (2000) suggested that O<sub>3</sub> stress may induce a burst of active oxygen species, which triggers the plant defense system in the leaves (systemic acquired resistance, hypersensitive response). Thus, the outcome of plant–pathogen interactions may strongly vary with timing, stage of plant development, predisposing factors, and environmental conditions.

## 5. Implications for management

Factors which limit productivity today are also subject to future changes, including biotic and abiotic stresses, and the direct effects of increased CO<sub>2</sub>, O<sub>3</sub> or temperature on the plants may be of less importance than effects on the plants' ability to cope with the change in factors limiting or reducing yields. This raises the question of how management may need to adapt in order to mitigate the change in these factors under future atmospheric conditions. Major management adjustments could be necessary in terms of resource management. Irrigation management may need to be adapted to changes in precipitation patterns and amounts. Williams et al. (2001) suggested that in order to preserve soil quality adaptations may include systems that are less prone to erosion and produce higher yielding crops as well as those more adapted to warmer, wetter springs, and hotter summers. Shifts

in the selection of crop cultivars may be necessary to adapt to shorter growing seasons and earlier planting dates (Dale, 1997). Because of the influence of elevated CO<sub>2</sub> and increasing temperatures on nitrogen cycling, adjustments are also necessary in terms of nutrient management. Timing and amount of fertilizer application depend on both crop demand and mineralization–immobilization processes, which are influenced by climate and CO<sub>2</sub>. Furthermore, the use of crops with improved genetics may become increasingly important, and traditional breeding and seed production may produce specific agronomical, morphological and physiological plant traits which could increase or stabilize yields in stressful environments (Kobiljski and Dencic, 2001). However, to define the targets for breeding programs, or genetic improvements, it is important to understand the key plant characteristics. For instance, to cope with increasing risks from O<sub>3</sub> pollution in regions with growing food demands, the use of crops with improved O<sub>3</sub> tolerance would be an option. As discussed by Fuhrer and Booker (2003), this could be achieved by increasing the plant's capacity to detoxify activated oxygen species in the apoplast.

Recent research initiatives have been directed towards increasing the understanding of potential global change impacts on plant pests and developing better predictive capabilities (Scherf et al., 2000). Because insect and plant species show individualistic responses to temperature, CO<sub>2</sub> and other factors, it is expected that climate change will affect the temporal and spatial association between species interacting at different trophic levels (Harrington et al., 1999). While averages of climatic conditions only explain vegetation distribution to a limited extent, it is the frequency, intensity and scale of extreme events that probably most determine ecosystems. Greater fluctuations in the extremes affect the functioning, and phenology and regeneration (Shugart, 1998; Walker et al., 1999), and they can have a marked selection on species or genotypes. This is equally important for plant species and for pests, but the plasticity in the response may be larger in the case of the latter. Extremes can act as important trigger event for pest and disease outbreaks. With the introduction of transgenic crops created for pest and/or disease resistance, the picture drawn here in terms of possible responses of conventional crops may change, but little is known about the sensitivity of

genetically modified plants to increasing CO<sub>2</sub>, O<sub>3</sub> or other factors.

## 6. Conclusions

Global climate change, increasing CO<sub>2</sub>, and regional O<sub>3</sub> pollution are three important aspects of the changing atmosphere with pronounced effects on all agricultural ecosystems, but the exact outcome of the interactive effects cannot be predicted in any generalized way. Information gained from experiments with a single factor have little predictive value because in reality, variable combinations of limiting factors, differing in their temporal and spatial variability, are interacting, and ecosystem responses to interacting global changes may differ greatly from simple combinations of single-factor responses (Shaw et al., 2002). The situation is even more complicated when plant–plant interactions, or feedbacks operating through the soil are considered. The data reviewed here suggest that many of the beneficial effects of elevated CO<sub>2</sub>, including higher yield, improved resource-use efficiency, reduced susceptibility to some fungal pathogens, or increased O<sub>3</sub> tolerance could be reduced or even lost in a warmer world. There is also emerging evidence that in some grassland ecosystems elevated CO<sub>2</sub> may suppress the positive effects of increasing temperature and resource availability on productivity.

Effects of a gradual change in climate may develop slowly and may not be noticeable against the background of impacts of natural multi-decadal climate variability (Hulme et al., 1999). Also, much larger socio-economic effects in the agricultural sector of individual countries (Flückiger and Rieder, 1997) may mask any influence of a slowly developing transient climatic change, and modern societies are able to make technological and economic adjustments (see Rosenzweig and Hillel, 1998). However, as suggested by McMichael (2001), climate change is likely to depress crop yields especially in food-insecure regions, and increased climate variability further increases the risks to future food production. Because the potential for adaptations may be much smaller in less-developed regions, and in regions where agricultural intensity declines due to socio-economic constraints, effects of global climate change and regional air pollution are likely to become more severe.

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