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GLOBAL CLIMATE CHANGE: MODELLING THE POTENTIAL RESPONSES OF AGRO-ECOSYSTEMS WITH SPECIAL REFERENCE TO CROP PROTECTION

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Abstract

Pests and diseases reduce yields to lower levels than those that could have been potentially obtained, given the restrictions of climate, nutrients and crop varieties. Climatic change not only affects the potential yield levels, but it may also modify the effects of pests and diseases. Modelling can serve as a tool to integrate these processes, ranging from simple removal of plant material to subtle toxic and hormonal effects. Modelling can help to quantify different modes of action such as on photosynthesis, root activity, assimilate partitioning, morphology, and their interactions. As to climatic change, little is known about pests, diseases and weeds. If climatic change causes a gradual shift of agricultural regions, crops and their associated pests, diseases and weeds will migrate together, though at different rates maybe. To a limited extent, new outbreaks can be foreseen given the changed environmental conditions. Methodology is available, and some interesting results are on record. Specific changes such as an increase in the CO_2 content in the air and in UV radiation are not likely to have large effects. Increasing atmospheric CO_2 reduces crop nitrogen content, which may retard many pests and diseases, and change the composition of the weed flora which accompanies crops. Some cautionary remarks are made to avoid jumping to conclusions.

Keywords: Carbon dioxide, diseases, greenhouse effect, nitrogen, pests, water, weeds.

INTRODUCTION

A gradual but accelerating increase of CO_2 and of other greenhouse gases in the atmosphere has been well documented to occur since the industrial revolution. The inference is that the natural and life-sustaining greenhouse effect will be enhanced, the earth will warm up, and climates will change (Houghton *et al.*, 1990). For the present discussion we accept this inference as a baseline truth, and therewith the various estimates for rates of change.

This paper considers the effects of climate change on (i) crop production, (ii) yield reduction by pests, diseases and weeds, (iii) distribution of crops, pests and diseases. The use of modelling as a tool will be illustrated throughout.

Present-day knowledge allows for considerable extrapolation regarding weeds, pests and diseases, and certainly permits a warning for some nascent misconceptions. We will first quote some current extrapolations of climatic change, then consider what might happen to agricultural crops, and finally see what such events may mean in terms of weeds, pests and diseases.

CROP PRODUCTION

Physiological effects of rising CO_2

Rising CO_2 in itself has a large effect on plant growth, even if there were no climatic change at all. Atmospheric CO_2 is the sole source of carbon for plant growth. In atmospheric air the concentration of CO_2 is low, only about 0.035% (350 μmol mol^{-1}). Any increase in this low concentration is likely to benefit plant growth, though differences between species exist (Poorter, 1993). However, several other effects of CO_2 exist and interfere with the positive baseline effect. For instance, higher CO_2 levels often lead to a slightly reduced nitrogen content of plant tissue. In its turn, this may affect the impact of sucking insects and pathogenic fungi. We suggest that each (foliar) fungal pathogen has its own nitrogen optimum in the leaves, since, for example, speckled leaf blotch (*Septoria tritici*) of wheat thrives at high nitrogen levels which reduce glume blotch (*Septoria nodorum*) on leaves (Zadoks, unpublished). Sucking insects such as aphids utilize nitrogen and excrete most of the sugars of the phloem sap (Rossing & van de Wiel, 1990; Dik *et al.*, 1991). At lower nitrogen levels

215

J. Goudriaan, J. C. Zadoks

there may be more excretion, more honeydew and more sooty mould, and thus more damage to host plants. Simultaneously the host plants may become less attractive to the insects (Tripp *et al.*, 1992). The net result of these two countervailing effects is unknown. This paper will consider some of these ecophysiological interactions more closely and discuss their potential impacts.

Interaction of rising CO_2 with other limiting factors

There is no doubt about the existence of a positive CO_2 effect on final dry matter formation under favourable conditions for plant growth (Lemon, 1983), as in intensive agriculture. Whether this baseline or CO_2 fertilization effect will remain operative under conditions where plant growth is limited by other factors is questionable. Under most circumstances a part of the growth stimulation by increased CO_2 is maintained, even if growth conditions are not optimal.

In biology and agronomy growth limitation by a single factor is well known and expressed in Liebig's law. This notion is so pervasive that it has supplanted the recognition of the fact that co-limitation by several factors at a time (Mitscherlich's law) exists as well (de Wit, 1992). Figures 1 and 2 show examples of colimitation.
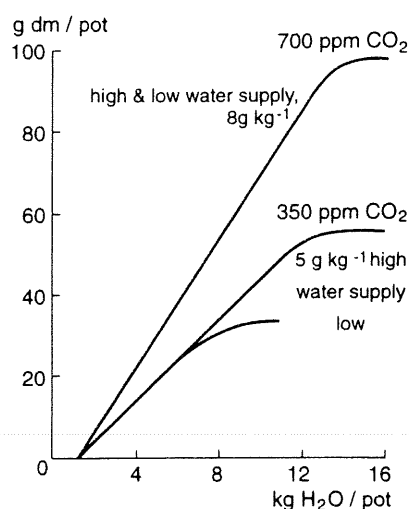
Water

Photosynthesizing plant cells must absorb atmospheric CO_2 by dissolving it in their cell solution for further processing by the photosynthetic machinery. The cell solution is a watery substance, and by exposing the cell surfaces to the air the plant will inevitably lose water by evaporation. The rate of water loss from a wet surface is high indeed. In fact, land plants have protected themselves from drying out by the formation of a dry epidermis on either side of the leaves. This epidermis contains stomatal apertures to permit entrance of CO_2. The surface area occupied by the stomatal apertures

of a leaf is usually less than 1%. Yet the reduction of CO_2 uptake by this impediment is much less than one might think: 10–30% only and definitely not 99%. The reduction of evaporation is much larger, up to 90%, according to circumstances. Clearly, this morphological adaptation of plants to life on land has strongly improved their water use efficiency. A further optimization was achieved by active control of stomatal aperture. During the night, for instance, the stomatal apertures are closed so that almost no water loss occurs during a period when photosynthesis is impossible. A typical secondary effect of raising CO_2 is partial stomatal closure (Raschke, 1975; Morison, 1987). The degree of opening can be considered as a compromise in the balance between limitation of water loss and admission of CO_2 (Wong, 1979).

In spite of these adaptations, the ratio between water loss and carbon gain is still very large, due to the low concentration of atmospheric CO_2. The difference in partial vapour pressure inside and outside the leaves is typically a factor of at least one hundred larger for water than for CO_2 and the gradients run in opposite directions. This simple physical fact explains the very large water requirements of plants, amounting to hundreds of kilograms of water transpired per kilogram of dry matter formed. When the ambient CO_2 concentration rises, this ratio is improved, leading to better plant growth even under conditions of water shortage (Gifford, 1979). This response indicates a Mitscherlich type of interaction between water and CO_2. For water limited conditions, plant biomass increases in proportion to cumulative water consumption, but with a slope that increases for higher atmospheric CO_2 (Fig. 1). Here, the law of the minimum is not valid.

Radiation

Under increased atmospheric CO_2 concentration, the efficiency of other factors is often improved too. Both light and CO_2 are often suboptimal and consequently photosynthesis is stimulated by an increase in ambient

Fig. 1. Schematic representation of dry matter accumulation (subsequent harvests, grams dry matter per pot) of potted *Faba* bean plants in response to water supply (kg water per pot) for two CO_2 levels and two water supply levels. After Goudriaan and Bijlsma, 1987.
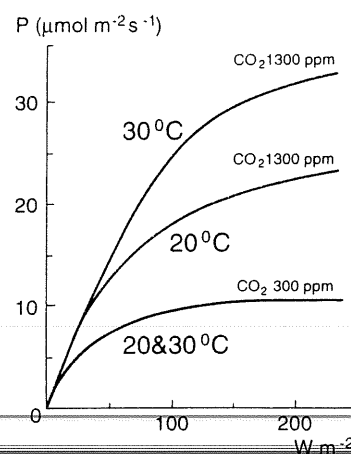
Fig. 2. Schematic representation of photosynthesis in response to incoming radiation at two temperatures and two CO_2 levels. After Goudriaan and Unsworth (1990).
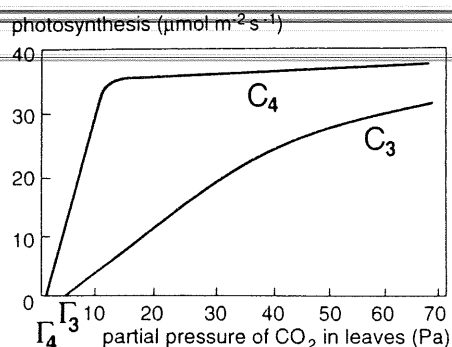
Fig. 3. Schematic representation of responses of CO_2 uptake rate to ambient CO_2 concentration in C_3 and C_4 plants. After Goudriaan and Unsworth (1990). The CO_2 compensation points Γ are indicated for either plant type.

CO_2 (Fig. 3; Farquhar & von Caemmerer, 1981). It appears that this stimulation does not only occur under high but also under low light conditions, at least in C_3 plants. C_3 plants, in contrast to C_4 plants, exhibit photorespiration, leading to a much higher level of the CO_2 compensation point Γ (Fig. 3). In C_3 plants the value of Γ is about 50 μmol mol^{-1} at 25°C in contrast to only 5 μmol mol^{-1} in C_4 plants. The initial light use efficiency increases with CO_2 in proportion with the quotient $([CO_2] - \Gamma)/([CO_2] + 2\Gamma)$ (Goudriaan et al., 1985). This is a major reason why the stimulatory effect of increasing CO_2 on photosynthesis is stronger under high temperatures (Fig. 2). Photorespiration occurs simultaneously with real photosynthesis, and shows up in a reduction in the light use efficiency. This interaction indicates a Mitscherlich type of colimitation by radiation and atmospheric CO_2, rather than the law of the minimum. Saturation of the CO_2 effect does occur, as in C_3-plants the light saturated rate of photosynthesis increases with CO_2, first linearly from Γ up to a CO_2 concentration of about 600–1000 μmol mol^{-1} and then tapers off (Fig. 3).

C_4-plants (Table 1) have a higher affinity to CO_2 (Goudriaan et al., 1985). There is palaeological evidence that the C_4 plants evolved in the late Tertiary (Nambudiri et al., 1978), presumably as an adaptation to CO_2 concentrations as low as 200 μmol mol^{-1}. Although mainly found in tall grasses, the C_4 character independently evolved in other plant genera (Moore, 1982) such as the Chenopodiaceae growing in saline conditions. The C_4 plants mainly grow in hot and dry environments (savanna's), and in physiologically similar habitats such as salt marshes and salt plains (Aber & Melillo, 1991). At a given photosynthetic rate, C_4 plants can close their stomata about twice as much as C_3 plants can, so that their water use efficiency is nearly twice as high (Loomis & Connor, 1992).

Nutrients

When there is a nutrient shortage especially of phosphorus and of potassium, crop growth is severely limited and there is very little stimulation by CO_2. However, nitrogen differs from other nutrients in that a small positive CO_2 effect remains, even under rather severe nitrogen shortage. The background of this observation is that the plants economize on the carboxylation enzyme Rubisco, which normally contains almost half the total leaf nitrogen. In accordance with this photosynthetic role of nitrogen, the nitrogen content in leaf tissue is lower for plants grown under high CO_2 than under low CO_2 (Lemon, 1983; Larigauderie et al., 1988). Also, starch is further accumulated (Ehret & Jolliffe, 1985).

Some 200 years ago the CO_2 concentration was much lower (285 μmol mol^{-1}) than today (350 μmol mol^{-1}). This rise in CO_2 has had an effect on the C:N ratio. Peñuelas and Matamala (1990) found a significantly lower C:N ratio in herbarium material from 200 years ago than in recent plants of the same species growing in similar natural circumstances. Van der Burgh et al. (1993) found evidence of a morphological adaptation of the stomatal index in fossil *Quercus petreae* leaves to atmospheric CO_2 content in material dating back to 10 million years ago. So far, we have no information on the meaning of this morphological adaptation in terms of stomatal functioning, CO_2 uptake and transpiration rate.

Maintenance of the positive CO_2 effect throughout growth

There is evidence of both negative and positive adaptations during prolonged cultivation under increased CO_2. Photosynthesis per unit leaf area was mostly found to be smaller in plants adapted to high CO_2 (Wong, 1979; Mortensen, 1983) than in non-adapted plants (when measured under equal circumstances). Adapted plants seem to be spoiled and lose their high CO_2 response. This loss is attributed to a reduction of the nitrogen containing carboxylation enzymes. However, Valle et al. (1985) and Campbell et al. (1988) found a positive adaptation in soybean, and Arp and Drake (1991) likewise in the salt marsh sedge *Scirpus olneyi*.

In general, leaves grown at a higher CO_2 concentration maintain a higher rate of photosynthesis when that rate is measured at the same higher CO_2 level. In an experimental study during 4 years of continued exposure of a natural salt marsh vegetation to high CO_2, Arp and Drake (1991) found no decline in the CO_2 stimulus of either photosynthesis or water use efficiency (Arp, 1991).

Table 1. Some major C_3 and C_4 plants among crops and weeds (Downton, 1975; Holm et al., 1977)

|	Crops	Weeds
C_3	Rice, wheat Potato, cassava Sugarbeet, soybean	Goosefoot (*Chenopodium album*) Bindweed (*Convulvulus arvensis*) Waterhyacinth (*Eichhornia crassipes*)
C_4	Maize, sugarcane Sorghum, millet	Barnyard grass (*Echinochloa crus-galli*) Nutsedge (*Cyperus rotundus*) Johnson grass (*Sorghum halepense*) Crabgrass (*Digitaria sanguinalis*) Purslane (*Portulaca oleracea*)
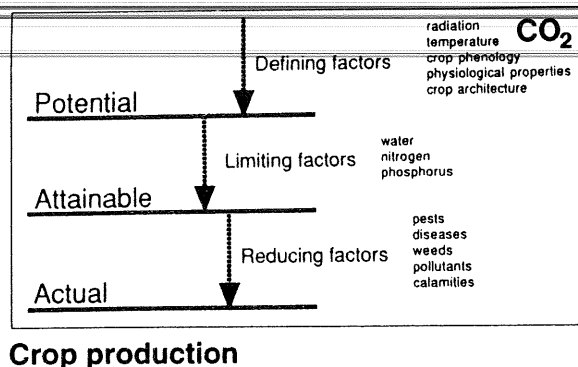
Crop production

Fig. 4. Crop production levels (van der Werf *et al.*, 1990).

Some modelling aspects

Hierarchical modelling

The mechanistic modelling process follows several hierarchies. One hierarchy (Fig. 4) begins with normal, healthy crops not subject to any constraint, and successively introduces yield defining, limiting and reducing factors. Another hierarchy has three steps. The first is the individual leaf, without or with constraint, often measured in a small hand-hold gas exchange chamber. The second is the crop canopy, again without or with constraint, often measured in large, mobile gas exchange chambers placed in the field. The third is the field experiment with continuous crop, pest, disease and environmental monitoring for multilocational and multiseasonal verification. A third hierarchy may be found in the physiological processes affected by the abiotic and biotic constraints (Table 2; Boote *et al.*, 1993).

Carbon assimilation

The process of CO_2-assimilation of a crop canopy is the result of the combined action of all photosynthesizing organs. They respond almost instantaneously to environmental factors, such as radiation, CO_2 and temperature. These external factors can fluctuate rapidly and so can the rate of assimilation. In contrast, plant status variables such as leaf area or nitrogen content are much more stable and vary little within a single day. Accordingly, in a plant growth model, the crop canopy is represented by a set of state variables upon which the environment exerts its influence. Canopy assimilation is modelled by using a subroutine that is called at representative moments during the day. The frequency of such moments will depend on the fluctuation of the environment, especially of radiation (Spitters *et al.*, 1986), and also on the desired precision of the calculations in the time domain.

Light gradients

Within a plant canopy at any one moment an extreme variation in leaf irradiation can occur, especially when the sun shines. Light saturation of leaf photosynthesis must then be taken into account. The effect of scattered light, leading to 'second-hand' irradiance on shaded leaves, is also to be included. The whole range of light intensities that exist at any one moment in a crop

Table 2. Principal processes in plants which can be affected by growth-reducing factors. After Rossing *et al.* (1992) (Table 11.1) which is based on an earlier classification by Boote *et al.* (1983)

Processes	Growth-reducing factors
Carbon economy	
Photosynthesis	
Light interception and distribution	Weeds, foliar fungi, leaf-eating insects
Foliar CO_2 assimilation	Fungal and viral pathogens, phloem-feeding insects, air pollution
Respiration	Fungal and viral pathogens, spidery mites, phloem feeders
Allocation	Biotrophic fungi, viruses, phloem feeders
Transport	Phloem feeders
Water and nutrient economy	
Uptake	Root pathogens, nematodes
Transport	Vascular wilt diseases
Transpiration, stomatal regulation	Leaf diseases
Reallocation	Leaf diseases
Morphogenesis	
Organ initiation	Mycoplasma, galling aphids
Dwarfing	Viruses, fungi, nematodes
Elongation	Fungi

canopy must be included in the model. In fact, radiation is the dominant source of spatial heterogeneity of assimilation rate in a crop canopy, more so than wind, temperature or CO_2.

In addition to variation in irradiance or other external factors, leaf properties themselves may vary. One of the best known examples is that of leaf nitrogen, which affects leaf photosynthetic capacity. It is hypothesized that leaf nitrogen content responds positively to average leaf illumination.

Summarizing the results of detailed models into one equation

As shown in a review by Kimball (1983), responses at the single leaf level to CO_2 are carried over to crop yield, and can be summarized by a mean 40% increase in dry matter for C_3 crops upon doubling of CO_2, and by 15% for C_4-crops. A similar overall response for a C_3 crop was simulated by means of a physiology based model (Goudriaan *et al.*, 1985). This model showed that the resulting overall carbon response could be well described by a logarithmic response to ambient CO_2:

$$Y = Y_o [1 + \beta \ln(C/C_o)]$$

where Y stands for biomass, and C for CO_2 concentration during growth. The subscript o refers to standard conditions at 350 μmol mol^{-1} of CO_2. This equation is only descriptive and has no physiological meaning in itself, but it summarizes many observations and simulation results. The response factor β of modelled crop dry weight was found to be 0·5–0·7 dependent on whether the increased carbon gain was reinvested in productive plant material, or just stored in passive organs such as tubers.

YIELD REDUCTION BY PESTS AND DISEASES

Simple models

Depending on its purpose, modelling can be done at various levels of complexity. In many situations, the approach of describing accumulated dry matter as the integral of intercepted radiation times a radiation conversion coefficient (Russell *et al.*, 1989) is sufficient. Rossing *et al.* (1992) and van Oijen (1991) successfully applied this approach to explain the main route of damage by potato late blight (*Phytophthora infestans*). Such a simplified summarizing approach is equally valid as a detailed reductionist approach in which a complex simulation model is used. It just depends on whether one is interested in the main outline, or in fine (and sometimes decisive) detail. An example of the summarizing approach is the expolinear equation (Goudriaan & Monteith, 1990) which could be successfully applied to describe the effect of SO_2 fumigation on the dry matter accumulation of a *Faba* bean crop (Fig. 5 and Table 3).

Step-wise modelling of a range of impacts

More insight was obtained when the analysis was deepened in the reductionist manner, leading to the conclusion that the reduction in growth rate was largely due to a reduction in light interception (Kropff *et al.*, 1989), mediated by reduced leaf area formation. Leaf photosynthesis itself was not significantly affected by SO_2. Likewise, honeydew had no effect on leaf photosynthesis in sugar beet (Hurej & van der Werf, 1993*a,b*) or in winter wheat (Rossing & van de Wiel, 1990). In such a situation the effect of CO_2 cannot be expected to exhibit any interaction with the growth-reducing factor through photosynthesis, but other interactions remain possible. The growth reducing effects by pests and diseases can be grouped according to their injury mechanism (Table 2).

In crop growth models, daily assimilation tends to exert a feed-back on the formation of new leaf area. This positive feed-back can amplify early effects on leaf

Table 3. Parameter values for *Faba* bean data, fitted to the expolinear equation and plotted in Fig. 5. Only linear growth rate was significantly different. From Kropff *et al.* (1989)

	Control	Fumigated
Maximum relative growth rate (d^{-1})	0·127	0·128
Maximum linear growth rate (g m^{-2} d^{-1})	22·5	18·8
Intercept of linear growth with the time axis (d)	41·3	40·1

photosynthesis by causing a reduction of light interception later on. Separation of immediate effects and accumulated feed-back effects is often difficult, even for the modeller himself, let alone that he could credibly convey his explanation to others. In such a situation modelling is best done in stages, introducing feed-back processes step by step.

First a model run is made for a reference time pattern of leaf area. In a second model run, the pest or disease is introduced, but with an effect on the time course of LAI only. Any modelled reduction in comparison with the reference run that we observe now is entirely due to the modelled reduction of light interception. If a gap remains, this must be due to systemic effects of the disease on plant functioning, such as through reduced leaf photosynthesis (van Roermund & Spitters, 1990; Bastiaans & Kropff, 1991; Bastiaans & Roumen, 1993).

Interaction of CO_2 and a growth reducing agent may not only occur via the direct routes of attack, such as would apply to the group of organisms that affect the carbon economy (Table 2). CO_2 can also help to overcome effects in other groups of processes. For instance, the positive effect of CO_2 on the water economy may help to mitigate the growth reduction due to nematodes (Schans, 1991). Also, the partial stomatal closure induced by CO_2 may render plants less susceptible to access from the ambient air with eventual damaging pollutants, or to entry of pathogens (Royle & Thomas, 1971; Ramos & Volin, 1987). High CO_2 levels stimulate cereal rusts and reduce latency periods up to *c.* 0·3% CO_2 (Gassner & Straib, 1923). Several soil-borne pathogenic fungi can fix CO_2 (e.g. Parkinson *et al.*, 1991). The net effect of an increase in atmospheric CO_2 on fungal pathogens and crop yield cannot yet be predicted.

CLIMATE AND GEOGRAPHICAL DISTRIBUTION OF CROPS, PESTS AND DISEASES

Distribution maps of crops

A warmer climate will obviously have large consequences for the distribution of vegetation and indeed of agriculture (Kenny *et al.*, 1993) on earth. In these agricultural studies the degree-day approach is often used. Crops need a species dependent amount of 'heat' to reach growth stages such as flowering and maturation. Above a minimally required base temperature (T_b) crop development proceeds approximately propor-
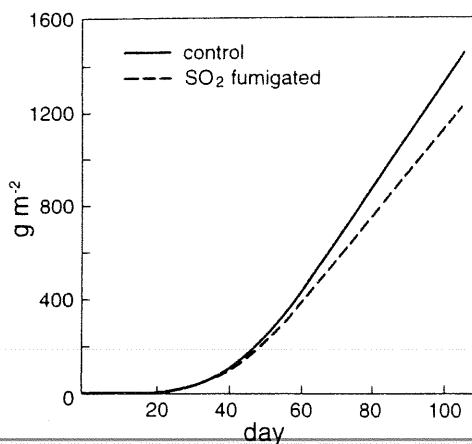

Fig. 5. Schematic representation of expolinear curves for the development of shoot dry matter in two crops of *Faba* bean, with and without SO_2 fumigation. After Goudriaan and Monteith (1990).

Table 4. Required and available temperature sums, expressed in degree-days. Temperature sums are calculated by accumulating the number of degrees Centigrade above a base temperature for each day of the growing season. Base temperature and required temperature sum are crop specific

	Spring wheat	Early potato	Silage maize	Sunflower
Base temperature	0	2	6	7·2
Required temperature sum	1700	1250	1460	1300
Available temperature sum per region				
Iceland	1590	1100	370	215
Netherlands (De Bilt)	3410	2690	1610	1340
France:				
Brest	3930	3200	1750	1390
Strassbourg	3550	2890	1850	1590
Dijon	3830	3120	2010	1730
Lyon	4140	3410	2230	1940

tionally to temperature (at least up to a species dependent optimum level). This means that the accumulated amount of surplus temperature is a good measure for the amount of crop development reached. An example of the result of such a calculation for grain maize, sunflower and potato is given in Table 4 for a few locations in Europe. The potato crop appears to be particularly suitable for a cool climate because it can be harvested even before it has completed its growing cycle. Even on Iceland tuber formation can proceed for a short period before the growing season ends. In The Netherlands, potatoes, *Faba* bean, spring wheat and sugar beet (not shown) can be grown without any difficulty, but sunflower cultivation is barely possible. In practice we will see crop failure in too many summers due to adverse cold weather. Also for silage maize the surplus is very small (not shown), but in view of the destination as fodder grain its maturation does not really matter.

This type of study can be extended to a very detailed geographical map. Kenny and Harrison (1993) found that the northern limit of cultivation of maize will shift to the north by about 300 km for each degree Celsius of temperature increase. In the coastal zone with a maritime climate the effect on the length of the growing season is larger than in the continental centre zone, where the winters are far too cold anyway. It was found that the northern limit of grain maize cultivation would reach the middle of Sweden upon a temperature increase of 3°C.

Shifts in geographical distribution of pests and diseases
Sutherst (1991) used a computerized system, CLIMEX, to produce world-wide maps of an ecoclimatic index EI which integrates growth potential within the limiting effects of extreme climatic conditions. The global distribution of weeds, pests and diseases has been studied thoroughly, be it only for quarantine purposes. Many crops, transferred from one continent to another, left their harmful agents behind, at least temporarily. Later, these agents may overtake their hosts, often with disastrous economic consequences. The sobering conclusion is that most weeds, pathogens, and pests thrive where the host crop thrives. Potato late blight is dangerous in

Mexico, where it came from, in the Netherlands where it came to, but also in the Israelian Negev—a semi-arid area—where potatoes thrive when irrigated.

Nevertheless, the question remains whether we can predict where weeds, pests and diseases may reach the nuisance value. Yes we can (Zadoks, 1991). Weltzien (1972) applied the principles of geophytopathology to sugar-beet mildew, indigenous in Europe, and predicted that California would be a suitable ecotope. A few years later it appeared in California and stayed.

The adaptability of pest and disease organisms and weeds is tremendous, and maybe they exploited as little of their genetic variability as we did of crop plants. Ecotypes do exist but are poorly studied. The Colorado beetle (*Leptinotarsa decemlineata*) seems to have developed into a number of ecotypes in North America according to survival conditions (Hsiao, 1988). Most weeds, pests and diseases of the temperate zone can also be found in the tropics at high altitude, say >3000 m. There they are exposed to high UV radiation, at levels which may kill the same pathogens in the UK (*Puccinia striiformis*; Maddison & Manners, 1972). The lesson is that, if the ozone layer fails, the pathogens may adapt. Similarly, yellow stripe rust (*P. striiformis*), usually extremely sensitive to air pollution, has adapted in Western Europe to air pollution (Stubbs, 1985). Obviously, genetic variation for resistance to adverse conditions is tremendous in weeds, pests and pathogens.

In conclusion, if a crop grows well, the microclimate of the crop favours the standard pests and diseases of that crop. Nitrogen level, stand density and plant ideotype are modifiers with known or supposed effects on the multiplication rate of and thus on the damage done by harmful agents. The mesoclimate determines the rate of oversummering or overwintering of pests and diseases. In this area, the adaptability of pests and diseases seems incredibly large but little studied yet.

Combined effects of climatic change
If climate changes, this means in practice that existing climatic zones shift places. If this change proceeds as slowly as anticipated, the rather mobile pests and diseases will follow without delay (Table 5). For the less mobile soil-borne pests and diseases there may be a

Table 5. Displacement rates in metres or kilometres per growing season

Zero order epidemics (foci)	1–40 m[a]
Forest trees after last glacial period	0·1–2 km[b]
Climate zones (due to greenhouse effect)	7 km[b]
Maize frontier in Europe (due to breeding)	10 km[c]
Second order epidemics—insects	10–50 km[d]
First order epidemics—fungi	100–1000 km[e]
Second order epidemics—fungi	100–1000 km[e]

[a] van den Bosch *et al.* (1988).
[b] Ketner (1990).
[c] Authors' estimate.
[d] Kampmeijer and Zadoks (1977).
[e] Heesterbeek and Zadoks (1987).

welcome delay. Don't be lured into false hope for slow dispersal of pathogens, pests, or weeds, because all are subject to dual or multiple dispersal (Zawolek & Zadoks, 1992). Though the best studied dispersal mechanism may cover short distances only, but at high frequency, most harmful organisms also have at least one long distance-low frequency dispersal mechanism. In these higher order dispersal mechanisms man is often instrumental. Weeds need not but may react differently. Migration rates may be slow because the propagules are heavy, and because weeds face competition where they arrive.

Climatic change implies that at any location the season may become warmer or colder, wetter or dryer, longer or shorter (Ketner, 1990). More important than changes in radiation and precipitation may be changes in the duration of the cropping season, since polycyclic pests and diseases need time to build up their population. Longer vegetation periods will be conducive to more damage by polycyclic agents. The same may be true for some weeds of a polycyclic nature, that is with more generations per year such as common chickweed (*Stellaria media*), annual poa (*Poa annua*) and groundsel (*Senecio vulgaris*) (Ketner, 1990).

Ketner (1990) states that with climatic change present vegetations may dissolve and new associations form. Whatever will happen is largely determined by characteristics of individual weed species. Given the parameters, with due attention for aestivation, hibernation and dispersal, ecosystem changes are amenable to modeling and dynamic simulation. Ecological relationships at the di- and tritrophic level will be changed

Table 6. Responses of brown plant hopper (*Nilaparvata lugens*, macropterous females), a pest of rice and two of its predators, *Cyrtorhinus lividipennis* (females) and the wolf spider (*Pardosa pseudoannulata*). Responses are expressed as mortality versus time at 40°C and subjected to probit analysis. LT_{50} = lethal time in hours. Slope = slope of probit line. n.s. = non significant regression. After Heong and Domingo (1992)

Insect	LT_{50}	Slope
N. lugens	47·3	3·4
C. lividipennis	2·8	11·0
P. pseudoannulata	>280·0	n.s.

(Liljelund, 1990). With climatic change, especially in the tropics, predator-prey may be affected (Table 6; Heong & Domingo, 1992). These effects can be modelled when food webs in tropical agro-ecosystems will be parametrized. Genetic variability is large in weeds (first trophic level) and possibly also in organisms of the second and third trophic level. The effect of selection for adapted ecotypes cannot yet be foreseen.

Some cautionary remarks

Since the 1973 oil crisis, CO_2 fertilization (Enoch & Kimball, 1986) is customary in commercial greenhouses in The Netherlands, especially for growing lettuce. Generally speaking, the CO_2 concentration was increased from 0·03% to 0·08%. No adverse effects are on record with respect to pests and diseases (Glasshouse Crops Research Station, Naaldwijk, personal communication). High CO_2 may reduce the number of greenhouse whiteflies due to a higher C:N ratio (Tripp *et al.*, 1992).

The number of clear-cut examples where climatic change gave a shift in pest and disease patterns is very limited. A well documented case is a series of yellow stripe rust outbreaks in Washington State, associated with a set of cooler and moister years (Coackley *et al.*, 1983).

A false alarm is the rumour that the present expansion of white fly and white fly transmitted gemini viruses from the tropics northward is due to climatic change. A more realistic explanation is the wide-spread use of synthetic pyrethroids, which effectively wiped out the predators and parasitoids of white fly. Similarly, the curious shift from *Septoria* glume blotch to *Septoria* speckled leaf blotch on wheat, observed over a long period in The Netherlands, seems nitrogen-induced and not climate-induced (Zadoks, unpublished).

FINAL REMARKS

Modelling of crop growth and of pests, diseases and weeds is based on understanding formative processes and their causal linkages. Intellectually this approach is more appealing and appears more promising than analysis by statistical methods. However, there is still a long way to go. Not only crop growth must be simulated, but also pests, diseases and weeds, and the interactions between these harmful agents and their host crops. Although individual models for crop growth appear to have been validated at field level, Daamen and Jorritsma (1990) found that the predictive performance of various models at the regional level was still disappointing. It is the explicit objective of the IBPG/GCTE program (Steffen *et al.*, 1992) to improve this rather unsatisfactory situation.

Detailed study of the monocyclic, polycyclic and polyetic adaptability to climatic change of pests, diseases and weeds, and of beneficials to control them, is needed so that we will be better equipped to face the future. The volatility of disease outbreaks necessitates careful, long-
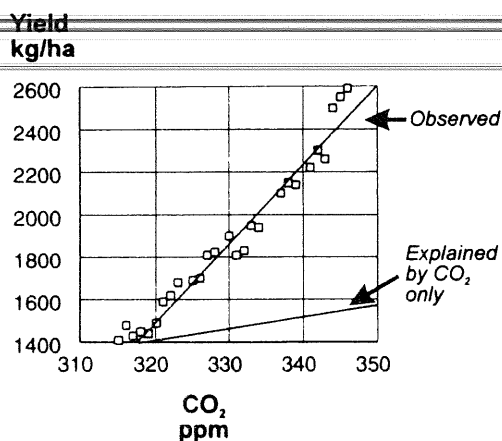
Fig. 6. Average world-wide grain yields (observed) and the yield increase explained by the rise in CO_2 concentration. From Rabbinge *et al.* (1993).

term observations of epidemiological factors. Modeling can contribute, but requires sound knowledge of the causal factors determining spatial distribution, survival, reproduction, dispersal and infliction of damage. Such knowledge is still not sufficiently available.

The dynamics of modern society induce faster changes than the surmized greenhouse effect, as is exemplified by the 'urban heat islands'. Agricultural technology has tremendous possibilities and can yet easily match the ill-effects of global change (Fig. 6). Modelling is one of several ways to guide our judgement.

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