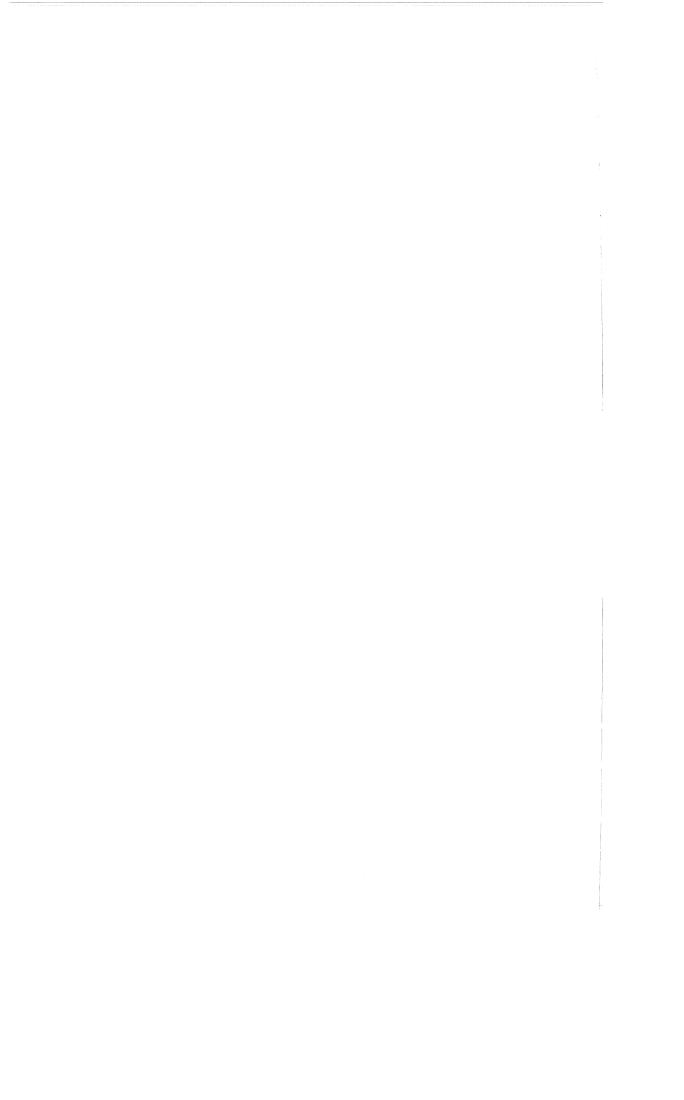The greenhouse effect and primary productivity in
European agro-ecosystems

The greenhouse effect and primary productivity in European agro-ecosystems

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on primary productivity of European
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J. Goudriaan, H. van Keulen and H.H. van Laar (editors)

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Greenhouse effect and society

Preface

Basic conditions of life are normally taken for granted whose preciousness is only appreciated when they are threatened. We live together with the living nature around us in an environment shaped and conditioned by the climate on this planet.

The idle wish is often expressed that the climate should be better, realizing that we cannot do much about it. Now, that mankind finally seems to be able to really induce changes in the climate on this planet, we rightfully fear our inability and our lack of wisdom to exert the right type of control. No wonder that the discovery of the 'greenhouse effect', induced by emissions of CO_2 and other radiatively active gases, has caused a worldwide concern about climatic changes that might turn out to be harmful or even disastrous.

We know that the greenhouse effect is a natural phenomenon that makes this planet habitable. The reason for concern is the fact that the natural greenhouse effect is slightly enhanced. We do not know how such a modification might work out. The term 'greenhouse effect' is a metaphor for a combination of a number of effects. First, there is a climatic effect, due to the absorption of thermal radiation. CO_2 shares this property with many other greenhouse gases (GHGs in general; see Carter et al., this volume), and in fact, at present the contribution of these other gases to the enhancement of the greenhouse effect is almost as large as the effect of the increase in CO_2 itself. The climatic effects of this radiative action are predicted by model studies of different types, with those using General Circulation Models (GCMs) as the most sophisticated ones. Plant growth modellers rely on 'Scenarios' provided by these GCMs, and can give their prognosis on the effects of changes in climatic components such as temperature, precipitation etc. on crop performance. Next, CO_2 itself is an indispensable substrate for plant growth, and usually has a stimulating effect. Plant physiologists and agronomists often call this effect the 'direct' effect of CO_2, in contrast to the 'indirect' climatic effect. The combination of these direct and indirect effects has only been studied to a limited extent, just as the interaction of the direct effect of CO_2 with other stresses such as pollution, shortage of water or of nutrients.

In the Netherlands, a national program on global air pollution and climate change has recently been started. Four years ago a forerunner of this program as a follow-up to the 1985 Villach conference, was organized by the Ministry of Housing, Physical Planning and Environment (VROM), basically as an initiative of Dr G.P. Hekstra. One of the research grants, awarded jointly to the Centre for Agrobiological Research and the Department of Theoretical Production Ecology of the Wageningen Agricultural University, concerned the 'Primary productivity of European agriculture and the greenhouse effect', and it explicitly comprised the organization of a workshop on this same topic. This book presents the results of this workshop, held from 5 to 10 April 1990 in Wageningen. We, the organizers, are grateful to the Ministry of VROM for providing us the financial means, to Dr G.P. Hekstra

for his continuous and personal commitment and enthousiasm, to all participants for their willingness, not only to come and discuss the scientific issues but to also write a manuscript.

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Climatic change and future crop suitability in Europe

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Introduction

We report results from a study to evaluate the broad-scale sensitivity of agriculture to climatic change in Europe. The study involves the use of a simple agroclimatic index, effective temperature sum (ETS), to relate regional temperatures to the temperature requirements of selected field crops. It comprises four main stages of analysis. First, the spatial pattern of crop potential based on ETS is mapped using a geographical information system. Second, a sensitivity analysis is employed to identify the effect of temperature changes on zones of crop suitability. Third, shifts of crop suitability are mapped on the basis of projected temperature changes derived from general circulation models of the atmosphere (GCMs). Finally, estimates are made of the uncertainties surrounding projections of future shifts in crop potential.

Methods

The mapping system employed in this study is based on a 0.5° latitude by 1.0° longitude grid across Europe, an area extending from 35 °N to 72 °N and from 12 °W to 42 °E (Alcamo et al., 1988). The following information, interpolated to the grid, was required for the present study: (a) topographical data on modal and minimum elevation, (b) mean monthly air temperatures for individual years during the period 1951 - 80, (c) standard deviations of daily mean air temperatures around the monthly means and (d) estimates of European climate under present-day and projected atmospheric greenhouse gas (GHG) concentrations derived from three GCMs: the Goddard Institute for Space Studies (GISS - Hansen et al., 1983), Geophysical Fluid Dynamics Laboratory (Manabe & Wetherald, 1987 - two versions) and Oregon State University (Schlesinger & Zhao, 1989) models. For full descriptions of the system, data and interpolation procedures, see Carter et al. (1990).

It is well known that for the successful ripening of crop plants, a critical accumulation of temperatures should be attained during the growing season. The most common measure of this accumulation is the effective temperature sum, defined as the sum of temperatures above a given threshold, commonly the temperature at which significant plant growth begins. We have calculated ETS based on mean monthly temperatures, accounting for within-month temperature variations using information about standard deviations of daily mean temperatures around the monthly mean (Kauppi & Posch, 1988). To illustrate the approach, we consider here the ETS requirements in growing degree-days (GDD) of grain maize: 850 GDD above a 10 °C threshold, cumulated over the whole year (Goudriaan, 1988). Clearly, temperature is only one of a number of constraints on production that are of importance in

considering crop suitability. The use of ETS alone in this study is justified by the large scale of the analysis, and by the dominance of temperature as a limitation for grain maize development in northern Europe. The results are intended to provide a first approximation of the likely shifts in limits of potential cultivation under climatic warming.

Results

Present-day patterns of crop suitability
The pattern of grain maize suitability in Europe under present-day (1951 - 80) mean temperatures is shown in Figure 1. This represents the hypothetical limit based on ETS at the modal elevation in each grid box. It should be noted that warmer conditions would be expected at the lowest grid box altitudes, shifting the suitability limits slightly northwards. The calculated limit appears to lie slightly to the north of the actual limit (the solid line in Figure 1), which has been inferred for western Europe on the basis of national maps of grain maize distribution. The disparity is to be expected, as the commercial limit is determined by a variety of other factors that are not considered in this assessment.

Sensitivity to temperature changes
The shifts of the suitability limits in response to incremental adjustments of the baseline (1951 - 80) temperatures ranging from -1 °C to +4 °C throughout the year have also been mapped. The results imply that a mean annual temperature (MAT) increase of 1 °C, which is within the present-day range of inter-annual variability (approximately ±1.5 °C), would open up large areas of southern England, the Low Countries, northern Germany and northern Poland to potential grain maize cultivation. An increase of 4 °C would move the limit into central Fennoscandia and northern Russia. These represent sensitivities of approximately 200 - 350 km/°C in western Europe and 250 - 400 km/°C in eastern Europe, progress in western Europe impeded by high elevation. Similar sensitivities have also been computed for limits of early-maturing varieties of sunflower, though northward shifts of warmer-loving crops such as soya bean (which are found further south in Europe) are somewhat smaller, due primarily to the steeper north-south temperature gradient in southern than in central and northern Europe.

Shifts under a GCM-derived 2 x CO_2 climate
We have employed four sets of GCM-derived data on the possible equilibrium response of temperatures over Europe to increases in GHG concentrations with a radiative forcing equivalent to a doubling of recent levels of carbon dioxide. Increases in MAT of between about 2 °C and 11 °C (varying by model and by region) are estimated. There can also be large seasonal variations in these changes. The changes over Europe can be compared with a range of global estimates of 1.5 to 5.5 °C (Bolin et al., 1986).

After altering the gridded baseline temperatures according to the GCM estimates of mean monthly temperature changes, ETS was recalculated and the grain maize limit remapped. The range of limits for the four GCM scenarios is shown in Figure 1. Three points can be

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		Limits based on ETS:
	□	Unsuitable under all scenarios
		Baseline suitability (1951-80)
		Min. ext. by 2030s (GISS C)
		Max. ext. by 2030s (GISS A)
		$2 \times CO_2$ climate: min. ext.
		$2 \times CO_2$ climate: max. ext.
		Actual limit of cultivation

Figure 1. Grain maize suitability based on ETS at modal altitude for the baseline (1951 - 80) climate, and minimum and maximum extension under the GISS transient-response scenarios by the 2030s and under four GCM-derived $2 \times CO_2$ scenarios. The actual northern limit of cultivation is denoted by a thick, solid line (AGPM, 1989). For explanation, see text.

noted. First, the minimum shifts implied under these scenarios are comparable with those estimated for a MAT change of between 3 and 4 °C. The maximum extension is considerably in excess of the 4 °C sensitivity limit. Second, at a time considerably before the climate responds fully to an equivalent CO_2-doubling, it is highly probable that there will be potential for widespread cultivation of grain maize in the UK, northern Germany and Denmark. Third, at a time approaching the equivalent doubling response (at the earliest about 2060, and more likely after 2100), there is a strong likelihood that zones of suitability will have extended into southern Sweden, Finland and the Baltic States.

In order to obtain information about temperature changes occurring well before this time, however, it is necessary to make use of information provided by transient-response experiments with climate models.

Rates of shift implied by GCM-derived transient experiments
We have used results from two transient-response experiments with the GISS GCM (Scenarios A and C - Hansen et al., 1988). Scenario A assumes that GHG emissions continue to rise during the period 1958 - 2062 at growth rates typical of the 1970s and 1980s - an exponential increase of 1.5% per annum. This we will take as an 'upper limit'

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scenario. Scenario C (1958 - 2039) imposes drastic reductions in GHG growth between 1990 and 2000, such that radiative forcing is stabilized after 2000 - a 'lower limit' scenario.

Values of ETS have been recalculated for temperatures adjusted according to Scenarios A and C. Figure 1 illustrates the shift in location of grain maize limits between the baseline and the 2030s under the two scenarios. These are considerably less pronounced than for the 2 x CO_2 projections. The map implies a rate of northward shift from the 1960s under Scenario A averaging about 80 - 110 km/decade, and a corresponding rate under Scenario C of 20 - 50 km/decade. Given that we have defined the two scenarios as marking the upper and lower bounds of future projections, while noting that less confidence can be attached to projections of regional than of global temperature changes, it is reasonable to assert that there is a high probability that by the 2030s the limit of grain maize suitability will have shifted to somewhere between the bounds shown in Figure 1.

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Climatic variability and crop development

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The assessment of the impact of climatic change on potential agricultural productivity requires, *inter alia*, models of how the growth and development of crops respond to climatic factors. Broadly, it has been suggested that climatic warming will reduce potential yields of existing varieties of determinate crops because of increased development rate. An additional key question is how the variation of temperatures will change with any increase in means, but little work has been done examining recent inter-seasonal temperature variation and the impact on productivity. Historic climatic records rarely contain enough data to use detailed growth simulation models over periods longer than a few decades, as these models require daily radiation data as well as rainfall, humidity and temperature information. However, models of plant development alone are simpler to use and need only temperature and in some cases daylength information. Further, General Circulation Models (GCMs) at the moment can only give coarse spatial and temporal resolution of temperature, so that the predictions are difficult to relate to crop performance which is determined by the day-to-day time course of conditions.

Recent concern over the impact of mild winters in the UK has stimulated us to look at overwintering crops in particular. As winter temperatures are close to threshold values for development and growth in grass and cereal crops, warmer winters may have profound impacts on the length of the growing season and development rates. In some cases the response of plants to temperature is not solely an increase in development rate caused by increases in temperature above some threshold but interacts also with vernalization requirement and daylength so that the final outcome is not obvious.

We have used long series of daily temperature records to investigate how modelled development of present-day crops would have varied from season to season over past decades. In particular, we used the development submodel of the AFRC-Wheat model of J.R. Porter and colleagues (Weir et al., 1984) to examine how seasonal variability in temperatures is reflected in variability in length of development phases. The model includes a basic degree-day calculation driving development, but degree-days are modified until the vernalization requirement is reached, and by short days.

Figure 1 shows the calculated date of reaching the double-ridge and anthesis stages for winter wheat sown on September 15 in each year at Edinburgh, for 92 years. The dates for double ridges show a maximum spread of 86 days, with the interquartile range of 143 - 171 days after sowing. There is no evidence of a trend, though the last 2 years are certainly exceptionally early. Calculated dates of anthesis are much more compressed owing to the higher mean temperatures and hence daily accumulated temperature values in the spring and summer periods.

The data in Figure 1 for the double-ridge stage can be replotted as a function of mean

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WHEAT DEVELOPMENT AT EDINBURGH

Figure 1. Time series of duration of period to ———— double ridges and ------- anthesis for simulated winter wheat crops at Edinburgh, sown September 15.

WHEAT DEVELOPMENT AT EDINBURGH

$Y = 279.2 - 19.7X$

$Y = 278.2 - 22.5X$

Figure 2. Duration of period to double ridges against mean temperature over the development period (O) and against mean temperature (▲) calculated over fixed October - February period each year.

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temperature over the development period (Figure 2) and show an approximately linear relationship such that for every degree rise in temperature there is a 20 day reduction in duration of the period. The mean temperature over a fixed time period is a variable that comes closer to the scenario information from GCMs, however, though this necessarily introduces more scatter in the relationship (Figure 2), and emphasizes the problems associated with arbitrary summary periods for climatological data. A similar approximately linear relationship between the duration of the period from sowing to anthesis to temperature showed a reduced sensitivity of 13 days per degree.

It should be emphasized that the simulations above include no other aspects of climate change, and imply nothing about the fundamental biology of the processes other than that parameterized in the model. However, it does allow us to ask some pertinent 'what if' questions. Removing the daylength and vernalization influences in the model indicates strongly that the parameterization of vernalization is very important. However, it is an area where we are critically lacking information. We have used two other models: that from SIMTAG (Stapper, 1984) which is similar to CERES-Wheat and the one of Reinink et al. (1986) for comparison, and with this data set they showed substantial differences. SIMTAG gave similar sensitivity to mean temperature over the range of temperatures, with a slight offset in date, whereas Reinink's model gave reduced sensitivity, and substantial scatter. There is, unfortunately no means of true validation of these calculations.

We have also used the AFRC-Wheat model and the Edinburgh daily temperature data to calculate the change in distribution of dates with assumed temperature increases. We arbitrarily chose an increase in daily maximum and minimum temperature of +2.0 and +4.0 °C. No change in the distribution of the temperatures was made. The cumulative probability of dates for the two stages, double ridges and anthesis are shown in Figures 3A and B. While a 2 °C increase reduces the median time period to double ridges by some 40 days, a further 2 °C has little effect because of the daylength and vernalization controls. The distribution

Figure 3. Cumulative probabilities of duration of period from sowing to (A) double ridges and (B) anthesis for current temperatures and with +2 and +4 °C.

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changes as well, with the curves becoming steeper, with a longer tail of 'late' years. The curves of length of time to anthesis show no such upper limit to earlier development caused by an increase in temperature, and no change in the distribution of years.

Such information on the existing and future variability of crop development calendars is important. Primarily it highlights any deficiencies in our understanding of the modelled processes. Secondly, it may be useful in determining risk of crop damage from say pest and disease outbreaks related to weather conditions (Morison & Spence, 1989), or to weather extremes *per se*, such as the early April frosts that caused extensive damage to winter cereals in the UK in 1990 (Morison & Butterfield, 1990). It may also be useful in determining the correct criteria for selection and breeding programs. Perhaps a successful way to 'slow down' cereal crops to optimize solar radiation interception in a warmer climate may be to increase the vernalization requirement, or to increase the degree of photoperiod sensitivity (to strengthen the inhibition caused by short days).

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Effects of climatic changes on growth and development of north European plants

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The predicted global warming suggests an increase in temperature in northern parts of Europe of about 2 °C in summer and 3 - 4 °C in winter by the year 2030. This will lead to a prolonged growing season in Scandinavia of about 60 days (Table 1).

The natural vegetation in the northern temperate and arctic zone is highly adapted to the very specialized local light and temperature conditions, and sensitive to climatic changes.

The great variation in climatic conditions in Norway and the fact that many plant species have their northernmost distribution in this part of the world, create the ideal background for studying the effect of global warming on the natural vegetation in arctic and northern temperate regions. The growing season ranges from less than 2 months in the north with continuous light and an average temperature of 10 - 12 °C, to more than 7 months in the south with daylengths varying from 12 to 18 hours and with an average temperature of 15 - 17 °C. In addition, the maritime climate in the west and the continental climate in the north-eastern mountainous parts exhibit great differences in temperature. In the most continental areas, the maximum difference between the highest summer and lowest winter temperature is nearly 85 °C (+33 to -50 °C) and in the maritime areas in the south-west it is less than 35 °C (+25 to -10 °C).

Table 1. Time of the year and length of the period when average temperature exceeds 6 °C, for different latitudes.

Latitude		Present conditions			Future global warming		
		spring	autumn	length of period	spring	autumn	length of period
58 °N		20/4	23/10	183	25/3	27/11	242
63 °N		10/5	6/10	148	5/4	7/11	212
70 °N		4/6	23/9	110	1/5	18/10	168
61 °N	10 m altitude	25/4	13/10	168	1/4	22/11	232
61 °N	1000 m altitude	25/5	18/9	112	25/4	13/10	168

Adaptation to important climatic and edaphic factors

During the last 15 years experiments have been carried out under controlled climatic conditions in a phytotron (at the Agricultural University of Norway) and in regional field stations at 5 - 8 different locations in Norway to study the responses of maritime, continental, temperate and arctic ecotypes to climatic and edaphic factors. So far, adaptations to the following environmental factors have been found:

1. Climatic factors: light intensity, light quality, photoperiod, temperature, chilling requirement, air pollution.
2. Edaphic factors: soil pollution, nutritional status, heavy metal tolerance.

Photoperiod is obviously the most important factor controlling growth and development of most plant species in the northern temperate and arctic region, and it is especially so for the onset of growth cessation. In an extensive ecotype study on 13 woody ornamentals and two grass species, all indigenous to Scandinavia and collected at three different latitudes, 56, 63 and 70 °N and at different altitudes, it was shown that all species except one responded strongly to photoperiod. The critical photoperiod for shoot elongation varied considerably among ecotypes, from 22 - 24 hours for ecotypes from 70 °N, 16 - 18 hours for types from 63 °N and 14 - 16 hours for ecotypes from 56 °N (Håbjørg, 1972a, b, 1976, 1978). The very strong photoperiodic control of growth makes it difficult to grow northern ecotypes in southern areas. As demonstrated in Figure 1 north Scandinavian ecotypes of *Betula pubescens* completed growth already in July with an annual shoot growth of 10 - 12 cm when grown at 60 °N. Grown at their site of origin 70 °N they had a seasonal shoot elongation of 45 - 50 cm or slightly more than southern ecotypes.

The results also showed that growth cessation of a certain ecotype grown at a defined locality occurred practically at the same time every year. This means that the natural ecotypes

Figure 1. Weekly height growth for three latitudinally distant ecotypes of *Betula pubescens* Ehrh. cultivated at two localities - 60 and 70 °N. (▲ 70 °N; ● 63 °N; ■ 56 °N).

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Table 2. Winter survival (%) of ecotypes of *Betula pubescens* Ehrh. cultivated at latitudes of 60, 64 and 70 °N.

	% Survival Latitude of cultivation		
Latitude of ecotype	60 °N	64 °N	70 °N
56 °N	85	45	0
63 °N	95	100	35
70 °N	55	90	100

of a certain habitat will not be able to utilize a prolonged growing season of one month in autumn. In fact the 'too early' growth cessation causes winter survival problems as demonstrated for *Betula pubescens* in Table 2. In the same experiment arctic ecotypes of *Alnus incana* and *Hippophae rhamnoides* were even more severely affected, they all died within two years of cultivation at 60 °N.

Further experiments have shown that the photoperiodic control of growth and development becomes gradually less important in southern and more maritime ecotypes, and it was also evident that growth cessation in species with an early growth cessation like *Fraxinus*, *Syringa* and *Sorbus* is hardly affected by photoperiod. In fact, field experiments carried out at 59, 63 and 71 °N showed that northern ecotypes of *Sorbus aucuparia* had about the same annual shoot elongation at all localities of 30 - 35 cm.

Light intensity/quality varies seasonally, diurnally and with habitat, latitude, altitude, and aspect. It is evident that great differences exist between ecotypes in photosynthetic light acclimatization. Ecotypes native to open habitat and to densely shaded areas showed that 'shade types' did not acclimate to high light conditions (Bjørkman et al., 1963). Differences in response to light intensity and light quality are also found for photoperiodic reactions. In studies under controlled environmental conditions (Håbjørg, 1972b), north Scandinavian ecotypes had a critical light intensity (PAR) for photoperiodic responses of 1 - 2 W m^{-2} and south Scandinavian ones of 0.06 - 0.4 W m^{-2}. Northern ecotypes also required a greater percentage of red light, thus indicating a difference in 'measuring' daylength. Ecotypes from northern parts of Scandinavia seem to measure daylength from sunrise to sunset while southern ones also include part of the twilight.

Temperature is an important factor for plant growth and since the vegetation in Norway is subject to wide seasonal and diurnal temperature fluctuations, marked differences are found among species and ecotypes in their response in optimum and minimum temperatures for growth and development. Ecotype studies in north European trees have demonstrated adaptation to diurnal temperature fluctuations. Ecotypes from maritime and northern areas, where the diurnal temperature fluctuations are smaller than in southern and continental areas,

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also showed optimum shoot growth when exposed to smaller fluctuations in diurnal temperatures (Håbjørg, 1972a). Ecotype differences in minimum temperature for leaf growth emergence are also demonstrated. As indicated in Figure 1 arctic ecotypes start growth earlier than southern ones. Ongoing experiments in *Ribes rubrum* showed that leaf growth emergence in arctic ecotypes in 1989 and 1990 took place about 20 March, and about 5 weeks later in ecotypes from 56 °N. Also continental ecotypes started growing about 2 weeks earlier than maritime ones. This shows that start of growth is mainly affected by temperature hence the local vegetation can benefit from the one month earlier start of growing season, caused by future global warming. However, a too early start may be hazardous and cause a lot of damage because of late spring frost. Maritime ecotypes might therefore have a greater potential in the future.

Under Scandinavian conditions, differences in response among ecotypes to low temperature stress is crucial. As demonstrated in Figure 1 and Table 2 the response to low temperature stress in autumn is always strongly related to the physiological conditions of the plant at the moment of the first autumn frost. However, early autumn frost damage is not the only crucial moment for winter survival. Stability in winter frost resistance is, as demonstrated in Table 3, extremely important.

Arctic and continental ecotypes, adapted to highly special and stable winter conditions, showed a very strong reduction in winter survival when grown under maritime and southern conditions or at localities with unstable winter conditions. On the other hand, the fjord types exposed to a mixed selection pressure at their place of origin with both maritime and continental climate, also produced very stable ecotypes which could survive and grow fairly well under both maritime and continental conditions. The difference in stability in winter frost resistance seems according to experiments under controlled conditions partly related to differences in chilling requirement (Table 4). The maritime ecotypes of *Picea abies*, from coastal areas needed about 2 weeks longer chilling treatment at 2 °C for breaking bud dormancy than the more continental ecotypes from the same latitude.

The stability in winter frost resistance obviously is of increasing importance in Scandinavia because of the warmer winter climate. The last 2 - 3 years of changing winter climate in southern part of Norway has caused severe damage on typical continental species like *Acer ginnala* and *Berberis thunbergii*. In northern Norway, in the city centre of

Table 3. Differences in adaptability/stability between ecotypes of *Poa pratensis* (%survival).

Ecotype	Place of cultivation			
	Arctic 70 °N	Southern 58 °N	Maritime	Continental
Arctic 70 °N	90	10	0	70
Southern 53 °N	10	90	90	50
Fjord-type 61 °N	70	70	90	80
Continental 61 °N	85	25	40	90

Table 4. Ecotype differences in bud-breaking conditions of *Picea abies* (% bud break).

Ecotype	Weeks at 2 °C					
	0	1	3	5	7	9
Maritime	0	0	2	26	91	99
Continental	0	0	18	98	97	99

Tromsø and Narvik, dramatic tree damage/death of local ecotypes of *Betula pubescens* and *Sorbus aucuparia* has been registered. The damage must partly be due to the unusual warm and unstable winter climate and the lack of stability in winter frost resistance of the local ecotypes. Extensive cambium damage indicated that the ecotypes had broken dormancy, and started growth in late autumn and were subsequently damaged by a frost period. More maritime tree species like *Acer pseudoplatanus*, which ordinarily are not considered so hardy, showed no damage. Heavy air pollution affecting plant growth generally may also account for part of the damage.

Conclusion

This short review shows that the natural vegetation of Scandinavia is well adapted to the local climatic and edaphic conditions. It also shows great differences in adaptability within species. Moreover, arctic and continental ecotypes seem to be poorly adapted to southern and maritime conditions as well as southern ecotypes to arctic and continental conditions. Ecotypes from the fjord areas with a mixed selection pressure showed a wide adaptability. They could grow fairly well both under maritime, arctic and continental conditions.

A possible change in the climate with increasing winter temperatures to above zero, might cause damage on the highly specialized arctic and continental ecotypes. The breeders both of forestry, agricultural and horticultural crops should therefore take that into consideration in future breeding programs.

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Hazards to productivity - the changing risks of crop losses

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The distribution of agricultural activities around Europe is largely determined by climate and soil quality. However, the productivity of crops in any particular season is strongly affected by hazards imposed by the weather, and by the skill with which farmers are able to minimize the impacts of such hazards. Two types of hazards are related to the weather: primary hazards arise from the direct stress of weather elements on crops and soils; in secondary hazards the weather increases the risk of damage to crop production by influencing other stresses that threaten the crops. Examples of primary hazards are frost, drought, flooding and wind damage; secondary hazards include outbreaks of pests and diseases, competition from weeds, and photochemical air pollution. The greenhouse effect is likely to alter the risks of crop losses from both types of hazards.

As a starting point for assessing how climate change will alter the risks of crop losses, it is necessary to estimate how the probabilities of extreme events are related to changes in mean value. The relationship is highly non-linear (Parry & Carter, 1985; Wigley, 1985), so that a small change in the mean may cause large changes in the probability of extremes. For example, the mean summer temperature in central England is about 15.3 °C, and the distribution about the mean is approximately Gaussian. The 1976 summer (T = 17.8 °C) had a probability of about 1 in 1000. Predictions of global warming suggest that the mean central England summer temperature will be about 16.7 °C by 2030. If the variability about the mean was unaltered, the probability of a summer like 1976 would increase to about 1 in 10 (Warrick, unpublished). Using similar assumptions, Wigley (1985) calculated that if the mean rainfall in England and Wales decreased by 100 mm (11%) from its current value (920 mm), a drought that was expected one year in 100 would become roughly 7.5 times more frequently expected.

It is likely to be many years before climate modellers will be able to confirm or falsify the assumption of unchanged variability that underlies these calculations. In the meantime, exploring the sensitivity of extremes to changes in the mean and variability of distributions seems useful, especially since the distributions of some parameters are not Gaussian. Changes in the probabilities of two successive extreme years are even more non-linear, but may be very important as triggers of agricultural change at the margins of current production (e.g. uplands or semi-arid regions). Relationships between the frequency of extreme events where coincidence could be disastrous for agriculture need closer analysis, e.g. high rainfall, snow melt and winds causing tidal surges that could cause flooding around coasts and estuaries.

To make full use of these statistical analyses of the weather it is necessary to establish relationships between crop damage and weather variables. In some cases this may be relatively straightforward, e.g. damage to flowering fruit trees from low temperatures, but in

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other cases the risks of loss depend on combinations of factors, e.g. hazards of drought depend on soil type, timing of water-stress etc. Excessive rainfall may put yields at risk either directly by waterlogging the soil and leaching nutrients, or indirectly by limiting the opportunities for working the land, and so restricting the duration of the season.

Warmer temperatures and more sunshine will favour formation of photochemical pollutants unless emissions are significantly reduced. Although changes in mean temperature (degree-days) might imply opportunities to extend the ranges of crops such as maize and sunflower northward (or to higher land) in Europe, extremes such as frost, or other factors such as sunshine, might be more effective determinants of whether yields are produced. Current winter crops which require low temperatures for vernalization may not get adequate chilling, with consequences for flowering and yield.

It is very likely that the indirect effects of climatic warming on agriculture will be more difficult to manage than direct effects. The ecology of pests, diseases and weeds is likely to alter, and this will require new approaches to their management. Areas where low temperatures currently keep crops disease-free (and consequently suitable for seed production), e.g. Scotland for seed potatoes, are particularly at risk. Similarly, rhizomania on sugar beet in England, currently probably limited by low temperature, may become more widespread.

In the mild winter of 1988 - 89 in the UK (2.5 - 3 °C warmer than average) weeds and 'volunteers' acted as a 'Green Bridge', enabling diseases and pests to overwinter and attack crops early in Spring (Unsworth et al., 1989). The number of aphids trapped at Rothamsted between April and July is a logarithmic function of mean temperature in January and February; numbers in 1989 were nearly three orders of magnitude larger than after a cold winter. Because aphids are vectors of plant virus diseases, the implications of climate warming for crop health are severe.

Diseases such as powdery mildew and yellow rust benefit in warm winters both directly by the influence of temperature on pathogen survival, and indirectly through the more favourable microclimate for growth when the developing crop is more dense than normal. In 1989, substantially larger amounts of fungicides and pesticides were used, with the risk that resistant strains of pathogens might develop. Studies and models of the pest-plant-predator system are needed to develop reliable predictions and improve control in the climates of the 21st century.

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Will there be a weed problem as a result of climate change?

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The increase in atmospheric CO_2 as well as the resulting changes in climate will be of great influence on plant growth and distribution and may prove particularly favourable for weed species. The term weeds is used here to signify species of wild plants able to grow in cultivated soil and by their presence reducing crop yields.

Increased CO_2-levels stimulate photosynthesis, plant growth and water use efficiency. Growth stimulation will be greater under favourable nutrient and light conditions. Eutrophic conditions are generally found in arable fields in countries with a high use of fertilizers.

C_3 species will probably have more advantage than C_4 species. Experimentally it has been shown that increased CO_2 may amongst others, stimulate seed production and seed weight in various weed species, such as *Chenopodium album*, *Abutilon theophrasti*, *Amaranthus retroflexus* and *Setaria* sp. (Bazzaz, 1986; Bazzaz et al., 1985). Increased seed production adds to the seed capital in the soil and may thus contribute to the weed problem.

Warmer conditions and a longer growing season will be of influence on plant performance and will likely stimulate flower and seed production. Two phenomena which are particularly sensitive to a temperature change are seed dormancy breaking and germination (Baskin & Baskin, 1986; 1987a, b; Grime et al., 1981). Earlier emergence and a longer growing season may enhance seed production, such as in *Solanum nigrum*. This species usually emerges late, but can continue seed ripening till the first severe frost in October. In several species higher temperatures will lead to earlier germination and increased germination. C_4 species particularly may benefit from higher temperatures, e.g. *Echinochloa crus-galli*, *Sorghum halepense*, *Digitaria sanguinalis* and *Portulaca oleracea*.

The latter species may be able to produce a second generation, as under warm conditions seeds often germinate immediately after capsule maturation (which takes place soon after first flowering) and thus this species may become troublesome in areas, where at present the species only occurs as adventitious, due to suboptimal temperature conditions.

A longer growing season may be particularly favourable for annual species with a short life cycle, which produce already several life cycles per year (so called therophyta epiteia). The number of life cycles may still increase and thus lead to an increase in seed capital. Several of these species are very troublesome weeds, such as *Stellaria media* and *Capsella bursa-pastoris*.

Temperature change may alter plant distribution patterns. Species with a southern distribution may spread northwards. Many C_4 species, which are predominantly thermophilous species with a more southern distribution, may extend into new areas. Several of these species are classified as the worst weeds of the world, e.g. *Amaranthus* spp., *Portulaca oleracea*, *Cynodon dactylon*, *Cyperus esculentus* and *Sorghum halepensis* (Holm et al., 1977). It should be noted that several of these species are already on the increase within their

present range and are expanding their distribution area, mainly due to human activities. This expansion may be accelerated by climate change.

All these possible effects point to an increase in weed species. This could seriously affect agricultural production, causing crop losses and/or increasing use of herbicides at increasing cost.

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Vernalization and climate change: an application for a simple model of carrot vernalization

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The timing of bolting or flowering of carrots is of interest to commercial root producers who wish to grow early vegetative crops and to breeders and seed producers anxious to secure predictable flowering.

Growth room and glasshouse experiments (Atherton et al., 1990), have shown that in growth room conditions at constant temperatures carrots (cv. Chantenay Red Cored) have a juvenile period of around 760 degree-days above an assumed base temperature of zero. In this period the plants did not show a vernalizing response to cool temperatures. Juvenility is here defined as the period from the date of sowing onwards during which the plants are not yet sensitive to a chilling treatment. In contrast, for non-juvenile carrot plants which had spent a fixed period at cool temperatures after becoming non-juvenile the subsequent rate of progress towards flowering was linearly related to the temperatures experienced earlier. This enabled the critical temperatures for vernalization of base = -1, optimum = 6.1, and maximum = 16.1 °C to be estimated. Thus a thermal time for vernalization could be calculated. The relationship between this thermal time and days to flower appearance provided good predictions of subsequent flowering time for a range of growth room vernalizing temperatures and durations. The flowering times of plants vernalized in the field were also well predicted (Craigon et al., 1990).

Therefore vernalizing thermal time provides an index of the plant's developmental response to its thermal environment and can be used to predict effects of temperature changes. In a simulation of simple climate change 4 °C was added to the mean temperature for each day's data from the original field experiments. In these experiments, run during two successive seasons, plants were transferred to a warm glasshouse (18 °C) on a range of

Figure 1. Influence of climate change on vernalization. Carrots sown 26 Aug. 1981.

Figure 2. Influence of climate change on vernalization. Carrots sown 14 Sept. 1982.

Figure 3. Influence of climate change on vernalization. Variation with time of year 1981/1982.

Figure 4. Influence of climate change on vernalization. Variation with time of year 1982/1983.

dates. The vernalizing thermal times were recalculated for each transfer date and were compared to the original vernalizing thermal times (Figures 1 and 2). The calculations were repeated after shortening the plants' juvenile period in response to warmer temperatures. These comparisons showed that despite vernalization commonly being perceived as a 'chilling' response, increasing the temperature would actually have increased the vernalization stimulus received by many of the plants.

The mean vernalizing degree-days accumulated per day in each of the months from November to March was calculated using the original two years temperature data and then using the modified data (+4 °C) (Figures 3 and 4). This showed that if plants were exposed to the recorded temperatures, the potential for vernalization was greater in March than in the 'cold' months of December to February. Also, in these two years the effect of a 4 °C daily temperature increase on the mean accumulated vernalizing degree-days would not have been the same for all the months. Raising the temperature by 4 °C would have reduced the vernalizing stimulus received by the plants in November, January and March but would have increased it in December and February in both years.

The inconsistency between months of the response to increasing temperature by 4 °C is related to temperatures crossing the thresholds imposed on the model by the critical temperatures for vernalization. This should make us wary of expecting consistent responses to climate change in any other processes in which the ambient temperatures are near to a threshold.

Similarly 'unexpected' results may occur for other crops (e.g. winter wheat, onions) which have similar-shaped vernalization responses to temperature. This preliminary work, therefore, may provide an insight into the complex responses that are observed when crops are moved between temperature zones, either in time or space. If the temperature is raised above the optimum for vernalization then the vernalization responses could result in an increase in the thermal time (°Cd) required to complete subsequent developmental and growth phases. However, if a temperature increase occurs within the suboptimal range of vernalizing temperatures then this will, by increasing the vernalization stimulus, reduce the

thermal time requirement for subsequent development. The work here on carrots for example may cast particular doubt on the wisdom of winter mulching of carrots aimed at increasing temperature in the hope of reducing or delaying subsequent bolting.

The limitations in this model are not in the vernalization response to temperature, which it predicts well, but rather in how the processes it predicts are quantified. The time when juvenility ends is important as it defines when the plants can be vernalized, yet little work has been done to define the duration of juvenility under field conditions. The rate of progress to flowering, in the variable temperature conditions of the field, should be measured with reference to thermal time. Our assumption of a base of zero for both juvenility and thermal time from flower induction to flower appearance needs testing. Photoperiod is also important but was omitted from this part of the work by matching photoperiods in the field and growth room in order to isolate the temperature effect.

However, despite these limitations this simple model and others like it could reveal much about the complex responses of plant development in field conditions to simple temperature changes that may occur as a result of global warming.

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Primary productivity and CO_2

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Introduction

Increased CO_2 (C_a) generally stimulates photosynthesis of leaves and of crop canopies, as well as the subsequent dry matter accumulation in several crop components (Lemon, 1983; Strain & Cure, 1985; Kimball, 1983; Cure & Acock, 1986). Light is indispensable for the process of photosynthetically driven CO_2 uptake by green plants. In the natural environment, light and CO_2 are suboptimally present. Photosynthesis is stimulated by an increase of ambient CO_2, not only under high light, but also under low light conditions.

Leaf responses

There are two major types of plants called C_3 and C_4 plants, which differ in biochemical and anatomical aspects of the way they take up CO_2 from the ambient air. In C_3 plants the enzyme that binds CO_2 with RuBP, can also bind RuBP with O_2, after which RuBP must be recovered (Farquhar & von Caemmerer, 1982). This recovery costs energy and releases CO_2, observable as photorespiration. Since CO_2 and O_2 compete for the same site on the catalysing enzyme, photorespiration is suppressed by higher CO_2. In the other direction, when CO_2 is lowered to the level where CO_2 uptake and CO_2 release just balance each other, this concentration is called the CO_2 compensation point Γ.

The value of Γ is about 50 μmol mol^{-1} at 25 °C and rises with increasing temperature. The level of Γ is proportional with the oxygen concentration. The light saturated rate of photosynthesis is proportional to ($[CO_2]$ - Γ) up to a concentration of about 1000 μmol mol^{-1}, and the initial light use efficiency increases with increasing CO_2 in proportion with ($[CO_2]$ - Γ) / ($[CO_2]$ + 2Γ) (Goudriaan et al., 1985).

In C_4 plants (mostly tall tropical grasses such as millet, maize, sorghum and sugar cane) not RuBP but PEP, which does not bind with O_2, is used as a preliminary binder of CO_2 from the external air. The loosely bound CO_2 is transported from the mesophyll cells to the bundle sheath cells in the form of organic acids and released. The RuBP-CO_2 reaction is concentrated in these bundle sheath cells, where a very high CO_2-concentration is maintained. Oxygen gets practically no chance to bind with RuBP, so that photorespiration is suppressed and Γ stays low (about 5 μmol mol^{-1}). Because of the high affinity of PEP to CO_2, the photosynthetic response to CO_2 is very steep until about 100 μmol mol^{-1}. In the normal natural range of CO_2 of 300 - 500 μmol mol^{-1}, the C_4 leaf assimilation rate rises only little with CO_2, even under high light intensities.

Crop responses

In the course of the growing season several internal mechanisms operate in the plant, modifying the initially observed effects of CO_2. In plants adapted to high CO_2, photosynthesis per unit leaf area is often smaller (Wong, 1979; Mortensen, 1983) than that of non-adapted plants (when measured under equal circumstances), but occasionally stimulation of photosynthetic capacity has been observed (Valle et al., 1985; Campbell et al., 1988). When both grown and measured at a higher CO_2-concentration, leaves have generally a higher rate of photosynthesis than grown and measured at the reference level of CO_2. This is particularly true for nitrogen-fixing plants, that have nodules in their rooting system. The growth response of these plants to CO_2 tends to be particularly strong.

Starch accumulation (Ehret & Jolliffe, 1985) tends to cause some increase of leaf weight per unit leaf area. This rather passive response will not increase light interception, but the more active response of formation of more leaf area by larger leaves or more tillers will further enhance the effect of increased CO_2 when considered at a crop level.

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 of 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 a model (Goudriaan et al., 1985), that considers the physiological mechanisms at the leaf level. More specifically, the model showed that the overall carbon dioxide response could be well described by the following logarithmic equation, at least in the domain of about 200 - 1000 μmol mol^{-1}:

$$W/W_0 = 1 + \beta \ln (C/C_0)$$

In this equation the subscript 0 stands for the reference situation, W for crop dry weight at the end of the season and C for ambient CO_2-concentration. This equation is only indicative and has no physiological meaning, but it serves well to summarize both many observations and simulation results. The response factor β of modelled crop dry weight was found to be 0.7 (see also Allen et al., 1987) when the increased carbon gain was invested again and used for increased tillering, increased leaf number or increased leaf size. When no positive feedback on leaf area growth was assumed, the additional carbon was stored as starch in leaf or tuber, and the value of β was smaller, about 0.5.

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CO_2 effects on fruit crops

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Most fruit species show higher photosynthesis rates with increasing CO_2-concentrations in the atmosphere. CO_2 saturation occurs between 1200 and 1800 μmol mol^{-1} CO_2, depending on development stage, light intensity and temperature. The initial increase in photosynthesis rates may be due to enhanced CO_2-diffusion and reduction of photorespiration.
As a practical application the effect is used to maintain a positive carbon balance of fruit species at extremely high temperatures, in a treatment to eliminate a virus by heat treatment for six weeks.

Prolonged CO_2-treatment for several weeks may result in some decline in photosynthetic rates. An explanation is accumulation of starch in the leaves, which may affect light interception and functioning of grana. But also Rubisco activity could be reduced.

Nonetheless leaf area and total dry matter production of fruit species were higher under increased CO_2-concentrations, but only if the other essential nutrients were sufficiently available for the plant.

The effects of an elevated atmospheric CO_2-concentration on dry matter and nitrogen allocation

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Introduction

Over the last few decades much attention has been paid to the effects of increased atmospheric CO_2-concentrations on plant growth. However, few detailed observations on root growth under these conditions are available. The general assumption is that root/shoot ratios (R/S) increase at higher levels of CO_2 (Enoch, 1990). Wilson (1988) states that responses of R/S to 'carbon dioxide usually conform to Thornley's models'. Thornley (1972) constructed mathematical models of R/S on the basis of the functional equilibrium theory of Brouwer (1962), which predicts a diversion of dry weight to that plant part limiting growth under the prevailing environmental conditions.

This general assumption was tested for *Plantago major* ssp. *pleiosperma* and *Urtica dioica*, two species from natural vegetations, with a different growth form and maximum growth rate (Poorter, personal communication). As nitrogen availability is one of the main factors determining growth rate, the distribution of nitrogen over roots and shoots has been determined as well.

Materials and methods

Seeds of an inbred line (A4) of *Plantago major* ssp. *pleiosperma* and of *Urtica dioica* were germinated on sterilized garden soil in a greenhouse and transferred to a climate chamber immediately after germination. After 3 and 2 weeks respectively seedlings were transferred to a 1/16 Hoagland nutrient solution (Smakman & Hofstra, 1982). One week later this was replaced by a 1/8 Hoagland solution and the plants were randomly distributed over 2 climate chambers at 350 or 700 μmol mol^{-1} CO_2. The nutrient solution was replaced weekly thereafter. Growth conditions were: 20 °C continuously, 12 hours light of 550 μE m^{-2} s^{-1} and 65% relative humidity.

Plants were harvested from the first day of the treatment onwards, with $n = 8$ and double harvests at days 0 and 17 for *P. major* and $n = 16$ for *U. dioica*. At each harvest fresh weight, dry weight after 24 hours at 80 °C and leaf area were determined. Total nitrogen, including NO_3^-, was determined for roots and shoots at each harvest, using a Kjeldahl digestion method followed by an NH_4^+ determination according to Nessler.

Table 1. Total dry weight (± SE) of *Plantago major* ssp. *pleiosperma* and *Urtica dioica* grown at 350 or 700 μmol mol^{-1} CO_2.

	Total dry weight (g)	
Day	350 μmol mol^{-1}	700 μmol mol^{-1}
Plantago major		
0	0.012 (0.0013)	0.012 (0.0020)
3	0.030 (0.0062)	0.035 (0.0056)
7	0.082 (0.0062)	0.125 (0.0160)
10	0.174 (0.0337)	0.306 (0.0328)
14	0.535 (0.0763)	0.742 (0.1103)
17	1.082 (0.1634)	1.639 (0.1633)
Urtica dioica		
0	0.004 (0.0002)	0.005 (0.0002)
7	0.022 (0.0018)	0.035 (0.0025)
14	0.144 (0.0131)	0.326 (0.0340)
22	0.954 (0.0611)	1.808 (0.1335)

Results

Total dry weight of plants at high CO_2 was increased by 39% and 126% (Table 1) after 14 days for *P. major* and *U. dioica*, respectively. This increase was due to a stimulation of the relative growth rate (RGR) from 0.26 to 0.32 g g^{-1} d^{-1} in *P. major* and from 0.25 to 0.30 g g^{-1} d^{-1} in *U. dioica* during the first 10 days of the treatment. The effect on RGR was due to an increase in net assimilation rate (NAR). After 10 days both RGR and NAR at high CO_2 returned to the control levels. The positive effect of NAR on RGR was partly counteracted by a 10% decrease in specific leaf area (SLA). No effect on the distribution of dry matter between plant organs could be detected, as neither leaf weight ratio (LWR) nor R/S were affected by the CO_2 concentration.

Shoot nitrogen-content of *P. major* was reduced soon after the plants were transferred to 700 μmol mol^{-1} CO_2 (Table 2). *U. dioica* shoots showed a decrease in N concentration at the last harvest only. No effect on root N-content was observed in either of the species. The total amount of N taken up was higher at high CO_2 due to the higher growth rates of both species (Table 3).

Discussion

Although both *P. major* and *U. dioica* responded to increased levels of atmospheric CO_2

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Table 2. N concentration (± SE) in shoot and root of *Plantago major* ssp. *pleiosperma* and *Urtica dioica* grown at 350 or 700 μmol mol^{-1} CO_2.

| | N concentration (mg g^{-1} DW) | | | |
| | Shoot | | Root | |
Day	350	700	350	700
Plantago major				
0	51.4 (2.06)		47.1 (0.24)	
3	54.5 (2.03)	46.8 (0.124)	48.5	44.0
7	54.0 (0.45)	47.6 (0.73)	46.0 (0.21)	46.1 (1.11)
10	55.5 (0.40)	45.0 (0.80)	47.5 (0.78)	45.5 (0.13)
14	53.4 (0.80)	41.5 (0.96)	47.6 (0.81)	42.4 (1.58)
17	50.7 (1.01)	39.5 (0.77)	44.7 (0.54)	45.5 (0.89)
Urtica dioica				
0	45.3 (2.59)	43.7 (1.69)	48.8 (0.88)	
7	48.4 (1.91)	46.9 (3.07)	60.0 (1.68)	57.5
14	50.5 (0.60)	50.3 (1.72)	54.2 (2.53)	54.5 (2.23)
22	52.1 (1.68)	47.3 (1.43)	53.6 (2.08)	55.4 (0.25)

with higher rates of dry matter production, as do most other plants (Enoch, 1990), the general assumption that proportionally more dry weight is allocated to the roots did not hold in this case. A comparison of the responses of wheat (*Triticum aestivum*) plants to high CO_2 in different experiments, excluding reproductive parts, can be made. Gifford (1979) found a 27% decrease in R/S, whereas Sionit et al. (1980) found a minimal increase of 6% and Sionit et al. (1981), using the same cultivar, observed a 22% increase. Du Cloux et al. (1987) detected no major shift in R/S within a month after elevation of the CO_2 level, but in the subsequent week a 62% increase was observed. These observations and the data for *P. major* and *U. dioica* point out that R/S values have to be interpreted with care.

Table 3. N content of *Plantago major* ssp. *pleiosperma* and *Urtica dioica* 14 days after the start of the 350 or 700 μmol mol^{-1} CO_2 treatment.

| | N content (mg plant^{-1}) at day 14 | |
	350	700 μmol mol^{-1}
P. major	27.8	31.0
U. dioica	7.4	16.7

R/S estimation is liable to experimental error, because the boundary between shoot and root is not always clear. Small deviations may lead to large shifts in R/S. Also, differences in growth rate may lead to differences in phenological development. Therefore, comparison of morphological variables is only valid between plants in the same growth stage. Probably the most important factor causing the variable response of R/S to higher CO_2-levels is the control of water and nutrient supply in pot experiments. Short periods of drought or water-logging as well as variable nutrient availability may occur. The data on *P. major* and *U. dioica* were collected from water culture experiments during the period of exponential growth of the vegetative plants. Under these conditions, there is a differential effect on weight and area growth leading to a decrease in SLA.

The nitrogen concentration of *P. major* was lower at high CO_2 in the shoots only. A reduction in N concentration was also observed by Cure et al. (1988) in soya bean (*Glycine max*), although no distinction between root and shoot was made. Hocking & Meyer (1985) found a similar effect of CO_2 level on N concentration in the leaves of *Xanthium occidentale*, but not in petiole, stem or root. The small effect of CO_2 concentration on shoot N-concentration in *U. dioica* may be related to its nitrophilic character and the ability to accumulate large quantities of NO_3^- (Rosnitschek-Schimmel, 1982).

Summarizing, it can be concluded that CO_2 level had large effects on growth rate in both species studied. Although roots gained more weight under these conditions, they did so in proportion to other plant organs. Major studies in dry matter distribution and N allocation due to higher CO_2-concentrations only took place in the leaves.

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Effects of elevated CO_2-concentration levels on nutrient contents of herbaceous and woody plants

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Introduction

Although the results of numerous studies on herbaceous, agricultural or horticultural plants as well as some studies on plants grown (cultivated) in silviculture show that more phytomass is accumulated if today's atmospheric CO_2-concentration is doubled (Carter & Peterson, 1983; Overdieck et al., 1984; Overdieck & Reining, 1986; Overdieck & Forstreuter, 1987; Nijs et al., 1988 a, b; Rogers et al., 1983; Dahlmann et al., 1985; Hollinger, 1987; Gaudillère & Mousseau, 1989; Williams et al., 1986), many environmental factors - amongst them nutrient supply - may limit the positive effects of CO_2 on growth and production (Imai & Murata, 1978; Wong, 1979; Goudriaan & de Ruiter, 1983).

Moreover, if for a smooth, undisturbed metabolism in plant tissues approximately constant nutrient concentrations have to be maintained, increasing amounts of nutrient elements should also be incorporated parallel with increasing biomass production. For nitrogen, there are many hints in literature that under elevated CO_2 the mean concentration in dry mass decreases in herbaceous species relative to the concentration of carbon (Sionit, 1983; Overdieck et al., 1988; Larigauderie et al., 1988). Our knowledge about the effects on the concentrations of other, also physiologically important elements, is still incomplete, and so is our information about the composition of woody plants in general. In addition, it is not yet well understood how much nutrients will accumulate per m^2 ground area in a canopy composed of herbaceous species if the phytomass on the same area is evidently increasing under the influence of a higher CO_2-supply. Also some data about the total, absolute content of the most important nutrients in trees growing under CO_2 enrichment would serve as a first step to quantifying the nutrient uptake of entire forests in a CO_2-enriched atmosphere.

Material and methods

In addition to the N concentrations, we therefore determined the P, K, Ca, Mg, and Zn concentrations in *Trifolium pratense* L., var. Lero (red clover) and *Festuca pratensis* HUDS., var. Cosmos 2 (meadow fescue) which were grown at today's CO_2 concentration and at 600 μmol mol^{-1} CO_2. As representatives for deciduous trees from the temperate climate zone we chose *Acer pseudoplatanus* L. (mountain maple) and *Fagus sylvatica* L. (beech) and analysed the N, P, K, Ca, Mg, Mn and Fe concentrations in saplings having grown for about two vegetation periods under about 370, 520, and 670 μmol mol^{-1} CO_2. In all cases the climate inside the CO_2-exposure cabinets was regulated according to the

outside conditions near Osnabrück (52 °N 8 °E) with automatic air conditioning systems. All plants grew up in the same natural sandy garden soil of average fertility. They were not manured and were watered with tap water according to the precipitation rates at the location. The following analytical methods were used for determining the nutrient concentrations: Micro-Kjeldahl, spectrophotometry, atomic emission and atomic absorption spectrophotometry.

The results are based on 10 harvests of red clover and meadow fescue, from the time span 1984 - 1987, and on 21 samples of seedlings and saplings of mountain maple and European beech (partly cloned material) taken from their pots (soil volume: 0.1 - 30 l/young tree) from May until October 1985 - 1988.

For the herbaceous plants the nutrient concentrations were used to calculate the total amount of nutrients in the whole vegetation per m^2 of ground area at the peak of the vegetation period, whereas the values from the analyses of the two tree species were converted to average total amounts in the mean single tree.

Figure 1. Factors for the CO_2 effect upon the concentration of nutrients in the above-ground phytomass of red clover (*Trifolium pratense*) and meadow fescue (*Festuca pratensis*) when elevating the CO_2 concentration level from 353 to 600 μmol mol^{-1} during the entire plant development (mixture of species at germination is 1:1).
Control (353 μmol mol^{-1} CO_2) = 1.0; n = 10 harvests 1984 - 1987.

Figure 2. Amounts of nutrients per m^2 ground area in the vegetation cover (*Trifolium pratense* and *Festuca pratensis*, 1:1) at 353 (open columns) and 600 (hatched columns) μmol mol^{-1} CO_2 at the peak of the vegetation period (1985).

Results

Under elevated CO_2-concentrations the mean concentrations of all nutrients studied tended to be lower in the above-ground parts of red clover and meadow fescue.

Statistically significant were the mean differences in the N and K concentrations for both species (N: -11%, resp. -12%; K: -13%, resp. -8%). The Zn concentration was significantly lower (-13%) only in meadow fescue. In the roots, the mean concentrations of all elements determined showed a slight decreasing tendency with increasing CO_2-concentration but did not differ significantly.

Because of the CO_2-induced increase in the phytomass per m^2 ground area, the mean total amount of all elements was higher in the whole vegetation cover, despite the mostly lower concentrations in the tissues at the peak of the vegetation period (Figure 2).

Compared to the control (370 μmol mol^{-1} CO_2) all nutrient concentrations were lower in *Acer pseudoplatanus* under elevated CO_2-concentrations (520 and 670 μmol mol^{-1}) on the total average of all analysed plants in all their parts (N: -10.2, resp. - 17.3%; P: -6.3, resp. -10.0%; K: -5.4, resp. -9.5%; Ca: -4.2, resp. -12.1%; Mg: -5.3, resp. -10.2%; Mn: -12.0, resp. -20.4%; Fe: -6.0, resp. -5.3%; Figure 3).

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Figure 3. Mean nutrient concentrations in the whole dry phytomass of mountain maple saplings after about two years of CO_2 enrichment under field-like conditions; $n = 21$ harvests, total number of plants: 3000, soil volumina: 0.1 - 30 l/young tree; $* = p \leq 0.05$.

Also in *Fagus sylvatica* saplings the mean concentrations decreased with the exception of P and K (N: -8.7, resp. -10.3%; P: +9.5, resp. +9.7%; K: +3.1, resp. +1.9%; Ca: -6.1, resp. -13.7%; Mg: -6.2, resp. -10.9%; Mn: -10.3, resp. -10.4%; Fe: -19.7, resp. -4.9%; Figure 4).

FAGUS SYLVATICA

Figure 4. Mean nutrient concentrations in the whole dry phytomass of European beech saplings after about two years with CO_2 enrichment under field-like conditions; $n = 12$ harvests, total number of plants: 1000; soil volumina: 0.1 - 30 l/young tree; $* = p < 0.05$.

Table 1. Mean total content of nutrients per sapling of *Acer pseudoplatanus* and *Fagus sylvatica* after about two years with CO_2 enrichment under field-like conditions (mg/tree).

| Species | Element | μmol mol^{-1} CO_2 | | |
		370	520	670
Acer pseudoplatanus	N	86	94	101
	P	10	11	12
	K	73	84	93
	Ca	60	70	75
	Mg	14	16	18
	Mn	1.5	1.5	1.6
	Fe	2.8	4.0	4.3
Fagus sylvatica	N	72	80	87
	P	6	8	9
	K	33	40	44
	Ca	52	59	64
	Mg	9	11	11
	Mn	1.2	1.3	1.5
	Fe	2.4	2.8	3.6

For the trees in our studies the basis for the calculation of the average nutrient uptake was the mean single tree and not the vegetation per m^2 ground area. However, also on this basis both woody species accumulated a larger amount of nutrients in their tissues on the average, in spite of the lower concentrations (Table 1).

Discussion and conclusions

For a number of herbaceous species it is well known that the Kjeldahl-nitrogen as percent of dry weight decreases and the carbon/nitrogen ratio increases if the CO_2 concentration of the ambient air is elevated (Overdieck & Reining, 1986; Overdieck et al., 1988). Most probably this result can be generalized, because also young trees - at least mountain maple and European beech - show the same phenomenon. However, this seems not only to be true for N, but also for a number of other physiologically important nutrients. Certainly this conclusion can be transferred to potassium for the herbaceous species and *A. pseudoplatanus* in our experiments. This element activates numerous enzymes and is osmotically active.

The Ca concentrations in the above-ground phytomass of our herbaceous plants tended to decrease; in the young trees that decline was even statistically significant. Therefore one can conclude that also accumulation of this rather immobile element, which plays a major role in metabolism and building of structures, is affected by CO_2 enrichment, mainly in long-living

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species.

Mn and Fe concentrations, analysed only in the dry mass of the trees, also seemed to decrease.

Up till now trace elements were not sufficiently included in the analyses of plant dry matter after exposure to high CO_2. We could show for Zn that the mean concentrations of this metabolically essential element also was lower at elevated CO_2-concentrations.

Only phosphorus seems to be an exception. In the two herbaceous species and in mountain maple the concentration remained approximately constant and in *Fagus sylvatica* it even was higher under CO_2 enrichment.

However, the general conclusion can be drawn that the stimulating effect of increased atmospheric CO_2-concentration on plant growth and production will not be limited in soils of medium fertility, because the concentration of nutrient elements can decrease at least to a certain degree without obvious negative consequences. Therefore two ecological sequels may be considered:

1. With decreasing nutrient concentrations the nutritive value of the food for herbivores decreases;
2. For the same reason microorganisms in the soil may decompose the litter more slowly and less effectively.

Despite the lower concentrations - up to the time of flowering - the amounts of nutrients in the vegetation per unit ground area are higher, since the total phytomass increased. In the case of the two tree species higher amounts per mean individual were accumulated, at least in the juvenile phase.

Both results lead to the ecological prognosis that in the biogeochemical cycles the flux rates of nutrients are going to increase if the atmospheric CO_2-concentration continues to increase in the coming decades.

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Effect of CO_2 concentration and temperature on photosynthesis and assimilate partitioning of a closed canopy

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Introduction

The beneficial effects of artificially increased atmospheric CO_2-concentrations on plant growth have been exploited at a large scale for the production of greenhouse crops. Extrapolation of these results to a situation of increased atmospheric CO_2-concentration on a global scale, is only partly valid, because there are major uncertainties about the extent of CO_2-induced temperature changes and about changes in the geographical distribution of precipitation. Therefore it is necessary to quantify plant responses in a broad sense, comprising CO_2 concentration, temperature and water status.

In this contribution, environmental variation is restricted to CO_2 concentration and temperature. Experimental results were compared with the output of a simulation model based on CO_2 exchange of individual leaves as a function of photosynthetically active radiation (PAR), temperature and CO_2 concentration.

A photosynthesis model

The model was constructed following the concept of von Caemmerer & Farquhar (1981), but extended for a whole canopy including effects of respiration (Schapendonk & Gaastra, 1984). Two types of experiments were performed to validate the predicted photosynthesis responses and to collect additional information on partitioning of assimilates (Experiment 1) and on senescence (Experiment 2).

EXPERIMENT 1

Assimilate partitioning

Experiment 1 was performed with young tomato plants, growing in artificially lit growth cabinets at high plant density (67 plants m^{-2}) to realize a closed canopy (LAI > 2) at different combinations of photosynthetically active radiation (PAR, 10 - 68 W m^{-2}), temperature (17, 22 and 27 °C) and CO_2 concentration (170 - 1000 μmol mol^{-1}). In each experiment, PAR was kept constant at the top of the canopy by gradually lowering the plants, thus compensating for growth. As such, it was an attempt to simulate a closed canopy under natural daylight conditions. Photosynthesis was measured continuously. After 10 days, the plants were harvested and analysed in terms of dry matter partitioning and specific leaf area (SLA). From the results it was concluded that the effect of elevated CO_2-concentration on SLA was mediated by increased assimilate availability. At a given dry matter production,

SLA (kg/m2)

Figure 1. Specific Leaf Area (SLA), as a function of dry matter production of a tomato 'minicrop' at 17 (●) and 22 °C (▲). The numbers present the CO_2 concentration during crop growth.

SLA was independent of the chosen combination of CO_2 concentration and PAR (Figure 1). In addition, the effect of elevated CO_2-concentration on dry matter partitioning between plant organs was negligible (see also Hertog & Stulen, this volume). However, some caution should join this statement because of the unusual arrangement of young plants in a dense stand and possible interaction between growth rate and developmental stage.

Photosynthesis

The effects of CO_2 concentration and temperature on photosynthesis were adequately simulated by the model. The temperature optimum of crop photosynthesis shifted to higher values at elevated CO_2-concentrations. At a high LAI, the optimum was more smooth due to the lower mean PAR per unit of leaf area, which decreases the beneficial effect of an elevated CO_2-concentration.

EXPERIMENT 2
Extrapolation to greenhouse conditions

Going from the 'minicrop' to a greenhouse crop requires extrapolation both in space and in time. In space, the distribution of young leaves in the canopy changes when side branches develop: older leaves remain in the light at the top of the canopy, but younger leaves appear deeper in the canopy. In time, assimilate distribution and photosynthetic characteristics of leaves change markedly with ontogenetic stage (Ticha et al., 1984). The interaction between ambient CO_2-concentration and these processes was studied in greenhouses. Again special emphasis was given to the photosynthetic side of the topic.

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For the experiment, tomato plants were grown in greenhouses of 600 m^2 in the south of Israel. Planting date was on 2 October. One treatment received supplementary CO_2, the other did not. CO_2 enrichment was achieved by periodical supply from high pressure cylinders. The exchange rate of air with the outside air was determined by releasing tracer gas (N_2O) and measuring its concentration decline between the releases. The data were used for correction of the apparent CO_2-exchange rate of the crop. A detailed description of the measurements and calculations is given elsewhere (Dayan et al., 1985). Until 100 days after planting, when LAI stabilized at a value of about 5, the daily time courses of net CO_2-assimilation for a low and a high CO_2-regime were simulated in accordance with the measurements. The photosynthetic potential of the canopies, expressed here as the gross CO_2-

Figure 2. CO_2 assimilation per unit incoming radiation, plotted against time after planting, pooled for (A) PAR < 40 W m^{-2} and (B) PAR > 160 W m^{-2}. (● low CO_2; ▲ high CO_2).

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assimilation per Joule of incoming PAR on a ground area basis, increased with time at low irradiances (below 40 W m^{-2}) independent of the CO_2 concentration (Figure 2A). At high irradiance, being mainly a direct beam flux (above 160 W m^{-2}) , the photosynthetic potential increased less, due to saturation of the upper leaves and the high extinction value for direct PAR. In that case there was a distinct positive effect of a higher CO_2-concentration (Figure 2B), which can be attributed to higher light-saturation level in the CO_2-enriched atmosphere.

Senescence

From day 100 onwards, the simulated daily photosynthetic rates exceeded the measured values by 50% due to the fact that senescence and the concomitant decrease in the photosynthetic capacity was not accounted for in the model. The actual decrease in photosynthetic potential was more evident at low than at high PAR.

The decay of the photosynthetic potential after day 100 showed that senescence was independent of the CO_2 concentration.

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Effects of CO_2 enrichment on nutrient-deficient plants

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From experiments conducted under optimum supply of water and nutrients, it has been deduced that under elevated CO_2-concentrations, C_3 plants generally show a stimulation of dry matter production and yield while transpiring less water. Extensive literature surveys have demonstrated an average yield stimulation of 33% (Kimball, 1983) and 41% (Cure, 1986). The increased dry matter production and reduced water loss tend to increase the water use efficiency considerably. For C_4 plants, the effects on dry matter production are generally less clear. As in C_3 species, the water loss of C_4 plants is reduced in general.

Only few CO_2-enrichment studies however, have been carried out at suboptimal supply of nutrients. The question is, whether the effects of CO_2 enrichment are absent at low supply of nutrients, as could be expected if low availability of nutrients prevents additional growth, or whether enrichment effects are similar to those under optimal supply of nutrients.

Proportionally similar effects over a range of nitrogen concentrations were found by Wong (1979, Cotton) and Hocking & Meyer (1985, *Xanthium occidentale*). Smaller effects of CO_2 enrichment at nutrient-limited conditions were found by Sionit (1983, Soya bean), Sionit et al. (1981, Wheat) and Patterson & Flint (1982, Soya bean) who supplied different strengths of a nutrient solution containing all the essential elements. In an experiment with NPK fertilizer additions to various annual plant species in soil culture, Zangerl & Bazzaz (1984) also found proportionally smaller effects of CO_2 enrichment at low nutrient supply. Goudriaan & de Ruiter (1983, several crops) and Imai & Murata (1978, Rice) studied the CO_2 effects at different nitrogen supply levels and also found smaller effects of enrichment on dry matter production at lower nitrogen levels. In experiments by Luxmoore et al. (1986, *Pinus virginiana*) and Norby et al. (1986, *Quercus alba*), an effect of CO_2 enrichment on dry matter production at low nutrient levels was found, however, there was no treatment with ample supply of nutrients.

Hence, the information from the literature is conflicting. However, no analysis has been presented of the mechanisms underlying these differences in enrichment effects. At low nutrient supply, plants can still respond with increased growth to CO_2 enrichment either by increased uptake, or by a more efficient use through decreased minimum tissue concentrations. CO_2 enrichment stimulated N-uptake at optimal supply of nutrients in experiments conducted by Masterson & Sherwood (1978) with pea (*Pisum sativum*) and white clover (*Trifolium repens*) at rather unchanged tissue concentrations. In experiments by Lincoln et al. (1986, Soya bean), Overdieck & Reining (1986, Perennial ryegrass and White clover) and Havelka et al. (1984, Wheat) lower tissue concentrations have been found. No information was found of an experiment at suboptimal supply of nutrients that was CO_2 enriched from emergence till maturity and where it was possible to analyse the experiment along the lines of changes in nutrient uptake and efficiency of nutrient use.

To gain more insight in the mechanism of the effect of CO_2 enrichment at suboptimal nutrient supply, several experiments were conducted with various crops of which the results for wheat and barley will be reported here. The results were analysed using a method originally developed by de Wit (1953). (This method relates dry matter production to the uptake of a nutrient, and the uptake to the supply). In this way, much of the variance that normally exists when dry matter production is related to supply can be attributed to specific causes such as differences in fertilizer recovery or differences in potential production.

The experiment comprised spring wheat (*Triticum aestivum* L.) and spring barley (*Hordeum vulgare* L.) plants, grown from seed to maturity at ambient and enriched CO_2 (350 and 700 μmol mol^{-1}), at four different nitrogen levels in two greenhouses under natural light conditions. Five plants were grown in 5.5 liter pots filled with a mixture of sand and the following amounts of basic fertilizers: 2.5 g P_2O_5, 1.5 g K_2O, and 1 g MgO. Nitrogen was mixed with the sand at four different levels: N1: 0.1 g; N2: 0.33 g; N3: 0.8 g; and N4: 1.2 g.

An enrichment effect on total dry matter production was found at all levels of N supply, the enrichment effect, however, correlated to nitrogen supply, low nitrogen supply levels having proportionally less stimulation of dry matter production than higher levels. Analyses of the nitrogen uptake - total dry matter production relations, showed that the enrichment effect was caused by a more efficient use of the nitrogen taken up (a lower nitrogen concentration in the crop) while uptake of N was not affected by CO_2. This could be explained by the fact that the recovery of N was already very high at the ambient CO_2. The total dry matter production per unit N taken up was about 13% higher in the enriched objects. The minimum N-concentrations in the organs, however, did not decrease by enrichment. The more efficient use of N in terms of dry matter production was the result of a change in dry matter partitioning towards organs that are less N-demanding such as stems and roots.

Hence, seed yields of both crops, were not proportional to total dry matter produced when enriched objects are compared to ambient objects: seed yields were lower in the enriched objects in the low N-treatments and higher in the high N-treatments. The relative effect of enrichment at low N-supply on vegetative growth (wheat N1: 17%; barley N1: 33%) was therefore stronger than on total dry matter (wheat N1: 8%; barley N1: 15%).

The lower yield in the low nitrogen, CO_2-enriched objects can be analysed by considering the N concentration and the N uptake of the vegetative parts and the seeds separately. Total nitrogen uptake did not increase after anthesis so that nitrogen in the grain must have been derived from translocation from the vegetative organs during grain filling. This phenomenon has also been observed in the field where on average 65 to 80% of grain N is derived from vegetative parts (Spiertz, 1982). Before anthesis, CO_2 enrichment stimulated growth at all N levels, especially that of stems, roots and to some extent also leaves. That, however, resulted in an increased amount of non-remobilizable N. The fraction of the absorbed N that remained in the vegetative parts is given in Table 1.

The effect on grain yield of a smaller amount of translocatable N in the enriched object was not compensated by lower N-concentrations in the grain (consequently protein contents

Table 1. Percentage of nitrogen in vegetative parts as fraction of total plant uptake at the end of the growing period.

	350 μmol mol^{-1} CO_2				700 μmol mol^{-1} CO_2			
	N1	N2	N3	N4	N1	N2	N3	N4
Wheat	33	33	30	30	42	38	35	34
Barley	39	33	30	34	48	41	33	33

had not decreased). It was therefore concluded that at low N-uptake, the grains have no mechanism to compensate for the reduced N-supply.

A similar response for nutrient solution grown wheat was found in the data supplied by Sionit et al. (1981) although they gave no attention to the observation. In their experiment, wheat plants grown under CO_2-enriched conditions (675 μmol mol^{-1} CO_2) on 1/16, 1/8, 1/2 and 1/1 strength Hoagland solution produced 80%, 106%, 133% and 149%, respectively, of the seed yield of the ambient-CO_2 object (350 μmol mol^{-1}) whereas the enrichment effect on total dry matter was 109%, 109%, 133% and 155%.

Conclusions

In our experiments, total dry matter production was stimulated by CO_2 enrichment at all nitrogen levels but we found no effect on nitrogen uptake. The effect on total dry matter production was caused by a change in dry matter partitioning towards organs with lower minimum N-concentrations (stems and roots). This change in allocation causes the crop to use N more efficiently in terms of amount of nitrogen used per kg crop dry matter (NUE). Due to this mechanism, CO_2-enrichment effects on yield cannot be expected under all circumstances. It is therefore hypothesized that large dry matter effects of CO_2 enrichment at low nitrogen levels are possible only if the extra dry matter has a low nitrogen requirement. In case the economic organ of a crop has a high nitrogen requirement and receives its weight after a period of vegetative growth it can be expected that at low nitrogen supply, enrichment effects on economic yield are absent or can even be negative.

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Influence of climatic change on soil quality; consequences of increased atmospheric CO_2-concentration on carbon input and turnover in agro-ecosystems

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Soil organic matter in arable soils is an important factor for soil structure and fertility of the soil. Continuous turnover of soil organic matter is required to sustain the nutrient cycles and to supply mineral nutrients to plants. The soil microbial biomass is considered to be the driving force for this process. Soil organic carbon is mainly derived from carbon which has been photosynthetically fixed by plants. The plant carbon comes into the soil as litter from above-ground plant material or, after translocation of assimilates from the shoot to the root, as root-derived material (soluble root exudates, mucilage and dead parts of roots). The proportion of carbon released from the roots into the soil varies between 10 and 40% of total net carbon assimilation for arable crops (e.g. Keith et al., 1986). Large variations exist over plant development, plant species and environmental conditions. Estimates of annual input of carbon into the soil range from approximately 900 to 3000 kg ha^{-1} yr^{-1} for both arable crops and forest stands (van Veen et al., 1989; Vogt, 1990)

A doubling of the CO_2 concentration in the atmosphere from 350 to 700 μmol mol^{-1} might result in an average increase in primary production of about 33% for arable crops (Kimball, 1983). The degree of response depends on plant species and several parameters such as nutrient availability, light intensity and soil moisture. The increase in photosynthetic rate is always highest under non-limiting conditions of nutrients and light (Goudriaan & de Ruiter, 1983).

Hardly any research has been done so far on the effects of elevated atmospheric CO_2 on below-ground processes. Due to the high concentrations of CO_2 that are common in soil (several thousands of μmol mol^{-1}) direct effects of a doubling of the CO_2 concentration in the atmosphere are not expected.

However, the indirect effects via the plant are of prime importance for the soil ecosystem, because of the interrelations between primary production, carbon input into the soil, turn-over rate and size of the soil organic matter pool. As a consequence of a higher plant production, the input of organic matter into the soil both as litter and as roots and root-derived material will also increase. Whether this higher input of organic matter will lead to a proportional increase in soil organic matter content largely depends on the activity of microbes.

A large proportion of the root-derived material is easily decomposable for micro-organisms, which utilize the carbon compounds as the main source for biosynthesis and energy. The utilization of this root-derived material by soil microbes is controlled by various soil-related factors like nutrient status, pH and soil texture (e.g. clay content) and also by the

quality of the material. The decomposition processes of soil organic matter are also influenced by climatic factors as temperature and precipitation. Another important factor affecting decomposition processes is cultivation. Campbell et al. (1976) found a decrease by 40 - 60% in organic carbon after 60 - 80 years of cultivation.

The rate and extent of the turnover of organic matter through the microbial biomass will ultimately control the decomposition, and therefore determine the level of retention of soil organic matter. A reduction of the degradability of plant residues, e.g. due to an increased C-N ratio which is expected at elevated CO_2-concentrations, might result in accumulation of soil organic matter. Moreover, both an enhanced competition between plant roots and soil biota and preferential utilization of root-derived organic matter, as compared to more recalcitrant soil organic matter may come into play. The complexity of the organic carbon fluxes between the various pools in soil and biota do not allow a straightforward conclusion. Detailed studies have to be made to decide between two possibilities.

One scenario is that microbial activity will not be affected by the additional carbon input due to other limitations such as poor availability of nutrients and water, induced by increased demand of plants. In this scenario, the plants successfully compete with microbes for limiting nutrients and water by means of extension of the root surface. Consequently, the decomposition of recalcitrant, structural plant debris and native soil organic matter will be reduced, resulting in an increase in the amount of organic material in the soil.

Another scenario states that microbial activity will be stimulated, because more easily decomposable material is available. In this case, the additional carbon input may cause a priming effect, resulting in an enhanced soil organic matter turnover. The amount of organic material in the soil will then increase to a smaller extent than expected according to the extra carbon input. Simultaneously nutrient availability to plants will increase.

First results indicate that indeed the decomposition rate of organic matter in a soil grown to wheat at elevated CO_2-concentration is reduced more than at ambient CO_2-levels (Lekkerkerk et al., 1989). Such short term results should, however, be confirmed by studies over extended periods.

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The impact of changes in weather and CO_2 concentration on spring wheat yields in western Europe

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An increase in atmospheric CO_2-concentration can affect agricultural productivity in two ways. First, a higher CO_2-concentration in itself has a stimulating effect on photosynthesis (Cure & Acock,1986; Strain & Cure,1985) and on water use efficiency of crops (Gifford, 1979; Sionit et al., 1980). Second, being a greenhouse gas increasing CO_2 can induce climatic change. Estimates based on general circulation models predict a rise in global temperature of 2.5 - 5.5 °C, when CO_2 concentration has reached the 700 μmol mol^{-1} level (Wilson & Mitchell, 1987).

A simulation model was constructed to estimate the impact of a rise in temperature and in atmospheric CO_2-concentration on spring wheat yields in The Netherlands and in southern France. The model used is based on SUCROS87 (Spitters et al., 1989). To simulate the impact of higher CO_2-levels on water use efficiency of the crop a soil water balance was included (van Keulen & Seligman, 1987) and transpiration was simulated according to the big-leaf model (Monteith, 1965). The impact of the atmospheric CO_2-concentration on assimilation rate was described in accordance with Goudriaan et al. (1985). The simulation of development rate between crop emergence and heading in the original model was replaced by the Miglietta routine (Miglietta, 1989, 1990a, b), as this routine gave a better description of phenology of wheat cultivars in various climates than the original routine.

yield (10^3 kg/ha)

Figure 1. Spring wheat yield in field experiments (solid line) and simulated yield (broken line) in The Netherlands (see text).

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The model simulates water-limited crop production, and impact of weeds, pests, diseases or nutrient stress on crop production is not taken into account. Daily weather data from Wageningen and Toulouse were used to simulate crop yield in The Netherlands and southern France, respectively.

The present annual variability in weather and crop yields was used to validate the simulation results. Simulation runs were made with weather data from Wageningen from 1954 till 1987 and results were compared with yields in field experiments in those years (Figure 1). Until 1974 the simulated yields were much higher than field production. In 1974, the use of pesticides was introduced in this field experiment and so was an additional nitrogen application. Since then, field production has approached the potential level. Simulation results present a satisfactory picture of the observed inter-annual variability.

The model is very sensitive to the origin of weather data used as input data. It was shown that in The Netherlands weather data of a central weather station could not be used to simulate accurately crop production along the coast.

The impact of temperature rise on crop yield was simulated by increasing the present temperature by 2 °C. Due to the higher temperature, development rate of the crop is accelerated and the growing period shortened. In both regions, in high yielding years the temperature rise resulted in a decline in yield (1000 - 2000 kg ha^{-1}) due to this shorter growing period (Figures 2A and B). A shift in sowing date or the use of other varieties did not eliminate these yield reductions. In low yielding years (water shortage!) yields were not affected, the shorter growing season of the crop reduced the water requirements and counteracted the effects of water shortage.

Figure 2. Impact of changes in climate and CO_2 concentration on water-limited yield in (A) Wageningen and (B) Toulouse. (Temperature + 2 °C (+); 2 x CO_2 (o); 2 x CO_2 and temperature + 2 °C (▲)).

Doubling the atmospheric CO_2-concentration from 350 to 700 μmol mol^{-1} resulted in a simulated yield increase of 3000 kg ha^{-1} (Figures 2A and B). Higher CO_2-concentration resulted in improved growth during the vegetative period which was beneficial to final yield.

Combination of both temperature increase and CO_2 concentration rise, resulted in an increase in yield of about 1000 kg ha^{-1} in high yielding years in The Netherlands (Figure 2A), while in southern France the positive effect of the higher CO_2-levels could not counteract the effect of a temperature rise (Figure 2B). In years with water stress the yield increase was large due to the effect of higher CO_2-concentration on water use efficiency of the crop: in both regions a yield increase of 2000 - 3000 kg ha^{-1} was obtained.

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Uncertainty in prediction of effects of environmental change on wheat yields

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A model of wheat yield, composed of modules of crop development and grain growth taken from the AFRC-Wheat model (Weir et al., 1984), a submodel of canopy photosynthesis developed by Spitters (1986) and a submodel of leaf growth from field observations made at Rothamsted, was used to simulate the effect of environmental change on wheat yield. The model assumed a crop grown under ideal water, nutritional and pest-control conditions. The 30-year average of daily temperature, radiation and sun hours for Rothamsted was used as the starting point for simulations.

The model predicted a 20% increase in yield at a rise in CO_2 of 80 μmol mol^{-1} and a further 15% increase in yield at a temperature increase of +1.5 °C, with greater temperature increases giving smaller benefits. Increasing cloud cover by 10 - 12% was sufficient to negate any positive effects of elevated CO_2 and temperature together.

In an attempt to assess the uncertainty associated with these predictions, the sensitivity of the model output to a number of key parameters was determined for the unperturbed 30-year average conditions. Small errors in measured parameter values probably do not seriously diminish the accuracy of model predictions of relative changes in yield due to an environmental change. However, sensitivity analysis reveals the areas in the model where assumptions are most critical in determining the response of wheat yield to a particular environmental change. For example, the predicted response to CO_2 is largely dependent on the response of leaf photosynthesis to CO_2, which is assumed to remain constant under prolonged exposure to elevated CO_2. However, many of the studies in the literature on wheat grown at elevated CO_2 show a lower level of increase in yield than that predicted by the model. This is presumably due either to an acclimation of leaf photosynthetic activity to high CO_2, or some limitation on growth other than assimilate supply.

The predicted response to temperature is complex because of the multiple sites of action of this factor in the model. However the greatest sensitivity of yield to temperature is due to the effect on the final number of leaves, which is determined by the timing of flag leaf emergence. A data base of growth stages of 70 crops was used to optimize the parameters of a number of alternative routines for predicting flag leaf emergence, and their predictions were tested for 35 further crops grown in 1989. As 1989 was an unusually warm year, these crops represented a good test of predictions for increased temperature conditions.

The predictions of flag leaf emergence from the submodel used in the model of yield were consistently too early for the 1989 crops (left-hand plot in Figure 1). When this submodel was incorporated into the crop model, predicted yield for the 30-year average was increased, but there was little response to temperature increases of up to +2 °C (Figure 2).

Figure 1. Predicted versus observed Julian day of flag leaf emergence (gs37) for two different models. Symbols represent class of crop sowing date: 1 - 28 Sept. (o); 28 Sept - 27 Oct. (□); 28 Oct - 26 Nov. (▲).

Even in a relatively basic model such as that used here, a number of considerable uncertainties remain in the prediction of wheat yield for a given scenario of a future environment. The wide range of responses in yield to elevated CO_2 which has been experimentally observed may indicate that more account has to be taken of varietal differences and acclimation responses. The predicted response to temperature is highly dependent on assumptions about the timing of events. More experimentation is needed in these areas of high sensitivity.

Figure 2. Response of simulated wheat yield to temperature increase for a model incorporating the submodels of flag leaf emergence used in Figure 1.

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Evaluating the effect of climatic change on productivity of agricultural crops in Denmark

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Agricultural production is highly sensitive to weather and consequently to climatic changes. There is not yet evidence that climatic changes induced by the greenhouse effect would seriously restrain global agricultural production (Crossan, 1989). Major regional changes are, however, likely.

The effect of climatic change on crop production is usually evaluated using crop-climate models (Carter et al., 1988). The models differ in complexity and range from purely empirical to completely deterministic. Olesen (1989) used a simple deterministic model for assessing the impact of climate change on productivity of different crop types in Denmark. With the GISS (Goddard Institute for Space Studies) 2 x CO_2 scenario there was generally a small positive effect on productivity of vegetative crops and a small negative effect for grain crops.

The aim of this study was to compare results of two crop-climate models for vegetative growth, and to study the sensitivity of these models to changes in climate likely for Danish conditions in a 2 x CO_2 situation.

Models and meteorological data

The first model used in this study is the WATCROS model (Aslyng & Hansen, 1982). This simple mechanistic model for simulating water use and crop production for different crops was also used in a climatic change study by Olesen (1989). A few changes have been made to the original model, mainly with respect to the calculation of date of growth start.

The second model used here is the HEJMDAL model (Hansen, 1986). This model simulates water use and crop production of vegetative crops using detailed physiological principles, which also include effect of CO_2 concentration. The model has been parameterized and validated for ryegrass under Danish summer conditions. A few changes have been made to the original model to allow simulations during winter and early spring. Vertical root growth is assumed to occur only at soil temperatures higher than 4 °C. In the original model gross photosynthesis was almost constant irrespective of temperature. Several studies, however, suggest this to be strongly temperature-dependent, especially at high solar radiation (Johnson et al., 1983; Woledge & Parsons, 1986). This temperature effect seems, however, in many cases to be masked by a concurrent effect of air humidity (Woledge et al., 1989). In this study gross photosynthesis predicted by HEJMDAL was assumed to hold for leaf temperatures above 6 °C and to decrease linearly to zero at 0 °C.

The WATCROS model requires daily data for temperature, global solar radiation and precipitation. WATCROS uses the Makkink equation for estimating potential evapo-

transpiration. HEJMDAL uses hourly data for temperature, vapour pressure, wind velocity, global radiation, net radiation and precipitation. HEJMDAL also has more detailed requirements for soil parameters than WATCROS.

Data for the relevant weather variables were available from the IHD station at Stevns (55°21' N, 12°11' E) (Aslyng & Hansen, 1982). Daily precipitation was available from the station Endeslev (55°22' N, 12°11' E). The precipitation was corrected to ground level using the method described by Allerup & Madsen (1979). In the hourly data, the precipitation was allocated to midnight and noon.

Results and discussion

The WATCROS model for grass was applied to the daily data set from Stevns, and simulations were carried out for various combinations of changes in temperature, precipitation and global radiation. Temperature was increased 3 °C, precipitation was increased 30% and radiation was decreased 5%. The results are shown in Table 1 for potential and water-limited production on a sandy and a loamy soil. Table 1 shows that the simulated increase in water-limited dry matter yield of grass for a temperature increase of 3 °C varies from -6% to 22% depending on soil type and changes in precipitation and radiation. Similar changes were made to the hourly meteorological data used in the HEJMDAL simulation, cf. Table 2. Relative humidity was kept unchanged from the original. Test runs with HEJMDAL for a doubling of CO_2 concentration from 325 to 650 μmol mol^{-1} were also made.

Table 1. Simulated changes in dry matter yield of grass with the WATCROS model. Temperature changed +3 °C, precipitation changed +30%, global radiation changed -5%. Mean of 8 years.

	Potential production		Water-limited production	
Changed parameter	Sand	Loam	Sand	Loam
	Dry matter yield (kg ha^{-1})			
Original	22100	22500	11100	18200
	Yield change from original (%)			
Temperature rise (3 °C)	9	10	5	2
Precipitation increase (30%)	0	0	20	8
Radiation decrease (5%)	-6	-6	-4	-3
Temp., precipitation	9	10	22	10
Temp., radiation	1	2	1	-6
Temp., precipitation, radiation	1	2	18	3

Table 2. Simulated changes in water-limited dry matter yield of grass with the HEJMDAL model on a loam soil. Temperature changed +3 °C, precipitation changed +30%, global and net radiation changed -5%. Mean of 8 years. Values in brackets are yield change (%) from similar climate at a CO_2 concentration of 325 μmol mol^{-1}.

Changed parameter	325 μmol mol^{-1} CO_2	650 μmol mol^{-1} CO_2
	Dry matter yield (kg ha^{-1})	
Original	14700	22700 (54)
	Yield change from original (%)	
Temperature rise (3 °C)	-27	-13 (85)
Precipitation increase (30%)	32	28 (50)
Radiation decrease (5%)	-1	-2 (53)
Temp., precipitation	7	10 (59)
Temp., radiation	-27	-18 (74)
Temp., precipitation, radiation	6	7 (56)

The dry matter yields of the HEJMDAL runs are shown in Table 2. The yield changes are generally larger with the HEJMDAL model than with the WATCROS model. This seems to be mainly caused by effects of drought, which are stronger in the HEJMDAL model. In HEJMDAL there is a feedback from drought to leaf area development, which is not operative in WATCROS. A part may also be explained by differences in starting date, which turned out to be earlier in the WATCROS simulations compared to HEJMDAL.

The large effect of a doubling of CO_2 concentration of about 50% on dry matter yield in HEJMDAL is larger than the figures of about 30% indicated by Cure & Acock (1986) for wheat and barley biomass, but almost matches the experimental results of Morison & Gifford (1984), who found an increase of 48% in total dry matter for a doubling of CO_2 concentration.

The large differences between the two model's sensitivity to climatic change show that there is large need for further model development and validation.

Acknowledgements

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Modelling the effects of climate change on cereal production

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Introduction

Climate change has important implications for crop production and agriculture (Squire & Unsworth, 1988) of which three facets are discussed in this paper. They are: (i) the importance of growth habit in determining the response of crops to changes in CO_2 concentration and temperature, (ii) the interaction of climate change with other environmental problems and (iii) the systematic comparison of crop growth models.

The influence of growth habit

It is predicted that by the year 2030 there will be an effective doubling of the pre-industrial atmospheric CO_2-level in the atmosphere to about 560 μmol mol^{-1} with an associated increase in mean global temperature of between 1.5 and 4.0 °C. Quantitative changes in other climatic variables, such as precipitation, are predicted with less certainty. Some workers argue that the consensus view of global climate change represents an overestimation of the eventual scale of the effect (e.g. Idso, 1989).

In evaluating the effects such changes may have for the growth, development and distribution of major crops it emerges that an important determinant of a crop's likely response lies with growth habit. Determinate crops, such as cereals and most other arable crops, have a fixed duration for their life cycle. They are predicted to respond differently to changing climate when compared with indeterminate plants, such as perennial grasses, where the seasonal duration of growth is flexible, starting and stopping when environmental thresholds are reached.

With determinate crops higher temperature leads to an increase in the rate of leaf and canopy development and, hence, radiation interception but there is also faster passage towards flowering and final senescence, at least if vernalization is not inhibited by the temperature increase. As a consequence, whereas total dry matter production is predicted to increase in such crops under higher and more optimal CO_2-levels, grain yields may not alter, or may even fall, leading to a rise in the straw/grain ratio. Similarly, indeterminate crops also respond by increasing the rate of formation of their leaf canopy but since their growth duration is limited by low temperatures their growth period would be prolonged in a warmer climate with consequent increase in production. This is assuming that droughts do not become too severe or that temperatures do not increase to the point where respiratory burdens start to sway the carbon balance.

It is likely that other fundamental differences in physiology, such as photosynthetic pathway (i.e. C_3 or C_4), will be instrumental in changing the distribution of plants following

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an anthropogenically altered climate (Goudriaan & Unsworth, 1990). Consequently, we should redirect the emphasis of ecophysiological studies away from the physiological basis of adaptation towards improved definition of the spatial and temporal ranges of species so as to predict their distribution under modified conditions.

The interaction of climate change with other environmental problems

A current matter of concern for many sectors of the arable crop community is the pollution of drinking water with nitrates leached from agricultural land (AFRC Annual Report for 1987/88). In addition to changes to the gaseous and thermal environment of plants it is postulated that the pattern of precipitation will also change in the coming decades. Squire & Unsworth (1988) reported their conclusions on the basis of a maximum 40% increase in rainfall for the UK during the winter months and a +40% to -40% change during the summer. Using these guidelines a version of the AFRC Wheat Model (Weir et al., 1984) incorporating the modifying effects of water and nitrogen on potential productivity was run for three scenarios of climate change:

(i) Baseline: Simulation of a winter wheat crop sown in October 1985 at Rothamsted Experimental Station, Harpenden, UK. The crop was well irrigated and fertilized with nitrogen (ca 150 kg ha^{-1}). The simulation used present-day CO_2 and temperature levels.

(ii) Baseline with doubled CO_2 and a 4 °C increase in mean daily temperature from sowing to maturity but without a change to the pattern or amount of rainfall.

(iii) As (ii) but with a 40% increase (above observed) in rainfall for October 1985 to the end of February 1986 and a 40% decrease (relative to observed) in rainfall for March 1986 until August 1986, thus representing a wet winter and a dry summer.

Where there was a simple increase in temperature and CO_2, prediction was for a slight increase in total crop dry matter but grain yield decreased. In scenario (iii) more than three times as much N ha^{-1} remained as reserves in the soil or was lost from the system compared with the simulation for present-day conditions. From further analysis of the output from the model it is clear that this was because the warmer, wetter winter promoted mineralization from soil organic matter. Also, because of higher temperatures the crop developed faster and was in the field for a shorter period allowing less time for nitrogen uptake.

The implications of such simulations point to problems that stem from the interaction between nitrate leaching and climate change. Further work is needed in this area with particular emphasis on the process of immobilization (also sensitive to temperature and moisture levels) and the role of soil microbes in providing a sink to absorb nitrogenous compounds. Experimental work needs to be congruent with modelling approaches. Such simulations illuminate the importance of synergisms in assessing the overall effect of climatic change on the agricultural and/or natural environment. So far, work has tended to concentrate on first-order effects of either CO_2 levels or temperature on plant performance, often over short time scales. It is likely that our appreciation of the material consequences of climatic change will be fully realized only when also higher-order responses are examined.

The systematic comparison of crop growth models

Comparison of the underlying features and predictions from the five-or-so presently available global circulation models (GCMs) forms an essential part of their development and improvement (Cess & Potter, 1988). In contrast, it is rare for crop simulation models to be run for the same inputs and the results collated and compared (Porter et al., 1987).

There are three principal simulation models available for the wheat crop. They are: (i) V&S, van Keulen & Seligman (1987); (ii) CERES-Wheat, Ritchie & Otter (1985); and (iii) AFRC-Wheat, Weir et al. (1984). Each model describes the growth and development of a wheat crop in a roughly similar degree of detail. In doing so they attempt to mimic the processes of organ formation, the phenological and canopy development of the crop and the production and partitioning of dry matter to roots, stems, ears and grain. However, there are singular differences in approach between them and, thus, alternative and explicitly stated hypotheses about the causal mechanisms underlying the growth and development of wheat crops.

As an example, in AFRC-Wheat the rate of tiller formation is a balance between a potential rate, determined by temperature, and a limiting constraint to production of shoots introduced via the availability of sufficient carbon to allow the next flush of tillering. An age-structured shoot population results in which the life expectancy of a tiller is a function of its age and crop density. Also, in AFRC-Wheat tiller production starts after the third leaf on the main shoot has emerged and ceases following the double ridge stage of the main shoot.

In the V&S model tillering starts at emergence of the crop and continues for longer than in AFRC-Wheat, until the terminal spikelet stage of the main shoot. There is no temperature response and the net number of shoots at any time is a balance between their rates of formation and loss which are, in themselves, a function of carbohydrate availability. For CERES-Wheat a population approach is passed over and the model describes an 'average' plant. As with the V&S model shoot production starts at crop emergence and ends with terminal spikelet.

Space precludes a detailed comparison of the other features of each of the three models. Suffice it to say that the major differences between the models are in leaf, shoot and canopy development, partitioning, CO_2 exchange, respiration and root growth. Similarities are seen in their handling of stage (phenological) development and in the approaches taken to grain growth.

It is clear, in addition to dissection of the ideas behind these crop models that their comparison for the same input conditions would be a valuable but, as yet, unrealized objective.

Conclusions

1. Environmental problems, for example climate change and surplus nitrate in soils, although often separately considered, do not operate in isolation but interact at all levels from that of primary production upwards.
2. The future distribution and performance of a crop is likely to be affected by fundamental

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physiological differences between crop species, and not by minor differences. Factors such as whether a crop is determinate or indeterminate in habit or whether it utilizes a C_3 or a C_4 route for photosynthesis will influence its performance under both transient and equilibrium climatic conditions.

3. In pursuit of their common goals a dialogue between crop modellers and climate modellers needs to be established in order to address the problems resulting from differences in the scale at which each operates.

4. A systematic comparison of different crop models is required and differences in their approach and detail clarified. This is needed to improve our confidence in the predictive ability of such models. The importance of continued model development, in conjunction with experimental studies, should be emphasized.

5. The processes of scientific investigation should be ongoing and proceed in parallel with the establishment of policies designed to deal with global warming. Research into this topic should not cease because it is thought that the 'policy phase' has been entered into. It is certain that there are features and nuances of climate change and its interaction with the biosphere which are unknown at present and for which the best insurance is to be continually reviewing policy in the light of our most recent knowledge.

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The influence of CO_2 and air temperature on agricultural productivity in northern latitudes

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Climatic changes greatly influence crop production in Finnish marginal growing conditions. Increase in air temperature and CO_2 concentration lead to longer growing seasons and higher assimilation rates. Changing growing conditions affect the yielding ability of all crops; both the formation of yield potential and final crop yield.

A simulation model has been developed to predict the effect of CO_2 concentration and air temperature on potential agricultural productivity in northern latitudes. In the first stage, the model computes leaf canopy assimilation. The second step is to calculate the instantaneous canopy assimilation and to integrate this over the whole day. The daily total photosynthesis is converted to dry matter of roots, leaves, stems and storage organs.

Increase in atmospheric CO_2-results in higher photosynthetic rate per unit leaf area. Air temperature has two different effects. Firstly, higher air temperature leads to increased maintenance respiration. Secondly, varieties with longer growing cycles can be cultivated in Finnish conditions which could have greater influence on yield than changes in atmospheric CO_2-concentration.

The University of Helsinki and the Agricultural Research Centre are currently starting a research project aiming at predicting the influence of the greenhouse effect on agricultural productivity in northern latitudes. The development of yield potential of spring barley varieties as influenced by growing time and latitude will be measured in greenhouse experiments. Three different types of cultivars are studied: presently cultivated varieties of Finnish origin, and late cultivars adapted and non-adapted (from middle Europe) to long photoperiod.

The impact of the greenhouse effect on factors limiting primary production

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Primary production and crop yield is the overall result of complex processes, that are influenced by many interactions between the genetic properties of the plant and its environment in the course of the growth cycle. In a schematic way primary production can, however, be described on the basis of a limited number of dominant factors.

Total primary production of a field crop is determined by the length of the growth period, the amount of light intercepted during that period and the efficiency with which light is used to produce plant material. The length of the growth period is determined by the interaction between the genetic properties of the cultivar used and environmental conditions, notably temperature and daylength. Under the expected higher temperatures resulting from global warming, the rate of development, will be higher, leading to shorter growth periods, which would adversely affect the primary production potential. It may, however be possible to breed for cultivars with a lower rate of development at a given temperature, as the genetic variation in this property is rather large.

The amount of light intercepted during the growth period is determined by the prevailing light intensity and the proportion intercepted by the crop, which is a function of the rate of leaf area development. Predicted changes in the level of radiation are uncertain, hence that effect is difficult to quantify. Under higher ambient CO_2 the rate of leaf area development is expected to increase, hence a closed canopy will be reached earlier so that more of the radiation can be utilized.

The efficiency of light utilization for dry matter production is the balance of the processes of assimilation and respiration. Under high ambient CO_2 the rate of assimilation will increase (Goudriaan & van Laar, 1978), but the higher temperatures will also lead to higher rates of respiration. The present insights in the relative effects of these two factors makes it plausible however, that the net balance will be positive, so that the light use efficiency will increase, thus enhancing the production potential.
Under optimum growing conditions primary production is thus expected to increase, provided that adapted cultivars become available.

In many regions of the world, primary production is determined by moisture availability (Le Houérou et al., 1988; van Keulen, 1975). The determinant factors are then the total amount of water available to the crop and the efficiency of water use for dry matter production. The predicted intensification of the hydrological cycle under future weather conditions will lead to shifts in the precipitation pattern. The geographic distribution of the predicted changes is, however, highly uncertain. Under higher ambient CO_2 the water use efficiency will be higher (Goudriaan & Bijlsma, 1987; Gifford, 1979) hence more dry matter will be produced for the same amount of water. In at least part of the present (semi)-

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arid regions, the constraint on moisture availability will be partly released, leading to higher primary production.

In addition to carbon dioxide and water, plants need inorganic nutrients to produce organic material. The major elements in this respect are nitrogen, phosphorus and potassium. Experimental data about the interaction between CO_2 and nutrient supply are relatively scarce, but the available evidence suggests that the improved water use efficiency is retained also under nutrient limitation (Wong, 1979), and that under elevated CO_2 the limiting concentration, of at least nitrogen, in the tissue decreases, hence nitrogen use efficiency improves (Goudriaan & de Ruiter, 1983). It is to be expected therefore that under limited nutrient supply primary production will increase.

Summarizing the effects described here, primary production under elevated atmospheric CO_2 and the associated climatic changes, may be expected to increase, and variability to decrease, while the relative influence of different growth factors may change. There will probably be a possibility to move crop production to presently marginal areas, like droughty or saline soils (Gifford, 1990). However, the modifications in relative importance of the different growth factors will differ, depending on current situation and geographical location (van Diepen et al., 1987)

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The effect of atmospheric CO_2-enrichment and salinity on growth, photosynthesis and water relations of salt marsh species

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The concentration of atmospheric CO_2 is increasing as a result of the combustion of fossil fuels (Strain & Cure, 1985). In the present paper the effect of this increase on a salt marsh vegetation is reported. Growth of halophytes in the salt marsh environment is limited by direct and indirect effects of flooding of the vegetation and soil with sea water. Plant species respond markedly to gradients of salinity and redox status of the soil (van Diggelen, 1988).

Effects of elevated CO_2 on salt marsh species will be modified by environmental factors that limit their growth. For the salt marsh environment the combined effect of CO_2 enrichment and salinity on plants seems to be particularly important. This interaction is also of interest for agriculture where natural or man-induced soil salinity may limit production of crops. Most C_3 plants show increased photosynthesis and growth at elevated CO_2. C_4 species show little or no effect to CO_2 enrichment because their photosynthesis is saturated at the current CO_2-concentration (Strain & Cure, 1985). Salinity generally causes reduction of plant growth. This reduction may result from changed water relations (lowered turgor), ion toxicity or lowered photosynthesis (Bowman & Strain, 1987; van Diggelen, 1988).

Only a few studies report on the combined effect of CO_2 enrichment and salinity on plant growth. Growth increase of the species tested, in response to elevated CO_2, was more pronounced when they were grown in high salt concentrations then in low salt concentrations (Bowman & Strain, 1987; Schwarz & Gale, 1984; Zeroni & Gale, 1984).

Here we present results on the combined effect of CO_2 enrichment and salinity on growth, photosynthesis and water relations of *Aster tripolium*, *Elymus pycnanthus* (both C_3) and *Spartina anglica* (C_4). Plants were grown in the greenhouse at 400 or 750 μmol mol^{-1} CO_2 in soil containing low (0 - 100 mM NaCl) or high (approximately 400 mM NaCl) salt concentration. Growth period was 8 weeks (*S. anglica*), 10 weeks (*E. pycnanthus*) and 14 weeks (*A. tripolium*). At harvest time net photosynthesis, transpiration, water potential and dry weight of shoot, root and total plant were determined. Total plant weight of *A. tripolium* and *E. pycnanthus* increased at elevated CO_2. This increase was expressed as increased shoot weight (*E. pycnanthus*) or also as increased root weight (*A. tripolium*). Total plant weight of *S. anglica* was not affected by CO_2 treatment. Root, shoot and total plant weight of *A. tripolium* and *E. pycnanthus* were reduced at high salinity. Shoot weight of *S. anglica* was lower under saline conditions (Table 1).

Net photosynthesis of *E. pycnanthus* was not affected by CO_2 treatment. In contrast, net photosynthesis of *A. tripolium* increased at elevated CO_2. Salinity did not affect net photosynthesis of either species (Table 2).

Table 1. The effect of increased CO_2 (400 or 750 μmol mol^{-1} CO_2) and salinity (0 - 100 mM (low) or approximately 400 mM (high) NaCl) on shoot weight, root weight and total plant weight of *A. tripolium*, *E. pycnanthus* and *S. anglica*. For every parameter P-values of the CO_2 effect, salinity effect and the interaction CO_2 x salinity from a two way analysis of variance are given.

CO_2 (μmol mol^{-1})	Salinity level	Shoot weight (g)	Root weight (g)	Total plant weight (g)
A. tripolium (C_3 species)				
400	low	1.20	2.22	3.41
750	low	1.28	2.54	3.82
400	high	0.81	1.08	1.90
750	high	0.94	1.44	2.38
P-values				
CO_2		0.163	0.045	0.043
Salinity		0.000	0.000	0.000
CO_2 x salinity		0.773	0.916	0.856
E. pycnanthus (C_3 species)				
400	low	2.47	0.83	3.30
750	low	3.49	0.95	4.44
400	high	1.25	0.33	1.58
750	high	1.73	0.39	2.12
P-values				
CO_2		0.000	0.132	0.000
Salinity		0.000	0.000	0.000
CO_2 x salinity		0.947	0.737	0.922
S. anglica (C_4 species)				
400	low	4.26	2.03	6.29
750	low	3.70	1.95	5.64
400	high	3.10	1.80	4.90
750	high	3.08	2.21	5.29
P-values				
CO_2		0.346	0.499	0.800
Salinity		0.005	0.941	0.095
CO_2 x salinity		0.376	0.301	0.320

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Table 2. The effect of increased CO_2 (400 or 750 μmol mol^{-1} CO_2) and salinity (0 - 100 mM (low) or approximately 400 mM (high) NaCl) on net photosynthesis, transpiration and water potential of *A. tripolium* and *E. pycnanthus*. For every parameter P-values of the CO_2 effect, salinity effect and the interaction CO_2 x salinity from a two way analysis of variance are given.

CO_2 (μmol mol^{-1})	Salinity level	Net photosynthesis (μmol CO_2 m^{-2} s^{-1})	Transpiration (mmol H_2O m^{-2} s^{-1})	Water potential (MPa)
A. tripolium (C_3 species)				
400	low	3.97	2.77	-
750	low	5.68	1.55	-
400	high	4.36	2.21	-
750	high	5.78	1.1	-
P-values				
CO_2		0.000	0.000	-
Salinity		0.511	0.049	-
CO_2 x salinity		0.695	0.701	-
E. pycnanthus (C_3 species)				
400	low	9.55	-	-1.13
750	low	7.49	-	-0.99
400	high	9.61	-	-2.51
750	high	10.90	-	-2.18
P-values				
CO_2		0.793	-	0.057
Salinity		0.244	-	0.000
CO_2 x salinity		0.239	-	0.432

Transpiration of *A. tripolium* was reduced at elevated CO_2 and high salt concentration, leading to increased water use efficiency. Water potential of *E. pycnanthus* became less negative at high CO_2-concentration. At high salinity, water potential was more negative (Table 2). Other experiments show that transpiration of *E. pycnanthus* is reduced at high CO_2 and high salt concentration. There was no significant interaction between CO_2 and salt treatment for any of the parameters measured (Tables 1 and 2).

Results demonstrate a growth increase of the C_3 salt marsh species *A. tripolium* and *E. pycnanthus* of 20 - 30% under CO_2 enrichment while growth of the C_4 species *S. anglica* was not affected. This is in agreement with results reported for other C_3 and C_4 species

(Strain & Cure, 1985). The absence of a CO_2 effect on photosynthesis of *E. pycnanthus* may be the result of acclimation due to long-term elevated CO_2-levels as has been reported by DeLucia et al. (1985) and Bowman & Strain (1987). Photosynthetic rates at elevated CO_2 may have been high immediately after initiation of the experiment. This temporary increase could be responsible for the increased production. Photosynthesis of *A. tripolium* did not appear to show acclimation to CO_2 enrichment.

The improvement of water relations (less negative water potential, reduced transpiration) due to elevated CO_2 may also have affected growth positively. If the improvement of water relations leads to increased turgor, leaf elongation may be stimulated, as has been shown for *A. tripolium* (van Diggelen, 1988).

The extent of growth reduction due to high salinity was not identical for the different species. Growth reduction was more severe for *A. tripolium* and *E. pycnanthus* than for *S. anglica*. *S. anglica* generally shows the highest salt tolerance of these species (van Diggelen, 1988). The growth reduction of *A. tripolium* and *E. pycnanthus* could not be explained by effects on photosynthesis. Negative effects on water relations may have been the main cause of the reduction; more negative water potential leading to lower turgor.

The results presented here did not show a relatively greater growth response to CO_2 enrichment under saline conditions, in contrast with such findings as have been reported for other species (Bowman & Strain, 1987; Schwarz & Gale, 1984; Zeroni & Gale, 1984). Also effects of CO_2 enrichment on photosynthesis and water relations were identical at both salt concentrations. The combined effect of CO_2 and salinity may be species-dependent.

It can be concluded that negative effects of salinity on growth can be partly alleviated by CO_2 enrichment. Therefore, increasing atmospheric CO_2-concentration will probably have positive consequences for agriculture in areas where salinity is limiting production.

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The combined effect of increased atmospheric CO_2 and UV-B radiation on some agricultural and salt marsh species

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Introduction

There is much concern about the possible effects of climatic change on terrestrial and aquatic ecosystems. Numerous studies report the effects of CO_2 and UV-B on plants studied under growth chamber, greenhouse and field conditions. Yield increases are predicted for many C_3 plant species and although wide variability exists, the predicted doubling of the atmospheric CO_2-concentration is expected to increase yields, on the average, by about one third (Strain & Cure, 1985; Morison, 1987). C_4 plants and crops are nearly saturated at ambient CO_2 and do not respond positively to CO_2 enrichment. Increased growth of C_3 plants in a C_3/C_4 mixed salt marsh vegetation in long-term field studies at elevated CO_2 has now been convincingly demonstrated (Curtis et al., 1989). Similarly, the effects of increased UV-B on plants have been studied extensively and in detail. Many plants respond negatively, a few exhibit no effect or a slightly positive effect. Growth stimulation by CO_2 enrichment may be caused by increased photosynthetic rates. Improved water relations as a result of partial stomatal closure also contribute to improved growth under elevated CO_2.

Plant and ecosystem response to climatic change

For terrestrial and aquatic plants, the changing global climate encompasses increase of intensity of UV-B radiation as a result of the depletion of stratospheric ozone, gradual increase in atmospheric CO_2 and other greenhouse gases and global warming. In addition, atmospheric pollution (e.g. SO_2, ozone, nitrous oxide) may locally affect primary production and functioning of natural and agro-ecosystems.

The separate effects of CO_2, UV-B and atmospheric pollution on individual plants have been studied under growth chamber and greenhouse conditions and in a few cases using plant communities under field conditions (Curtis et al., 1989). Models have been developed to predict general trends of changes in primary production (Goudriaan, 1989) and competitive relations between C_3 and C_4 plant groups (Curtis et al., 1989) in response to one of these climatic variables. In these modelling studies it is emphasized that global effects of CO_2 enrichment on plant's primary production may strongly depend on the interaction with other environmental factors such as soil fertility, and water availability.

Therefore, we may conclude that the available knowledge of the impact of the combined climatic variables on plant growth does hardly allow any reliable general conclusions. More importantly we note that not only the interactions of changing climatic factors with nutrient

deficiency and drought are poorly understood, but that hardly any study exists on the combined effect of CO_2 enrichment, UV-B increase, global warming and atmospheric pollution. In a recent excellent review on the greenhouse effect (Krupa & Kickert, 1989) surveying hundreds of recent research papers on the impact of UV-B radiation, CO_2 and O_3 on vegetation it is concluded *'We could find no studies on vegeta.ion response to enhanced UV-B under increased CO_2. This is a surprising and unfortunate gap in the knowledge base considering the importance that society is attaching to the so-called 'Greenhouse Effect', thought to result in part from an increase in ambient CO_2'.*

Here, the combined effects of CO_2 enrichment and UV-B radiation on three plant species under greenhouse conditions is reported and discussed.

Effect of combined CO_2 and UV-B increase in a greenhouse experiment

In a series of greenhouse experiments, 175 μE m^{-2} s^{-1} (PAR), 24 °C day/18 °C night, 70% RH, we examined the combined effect of elevated (760 μmol mol^{-1}) CO_2 and an integrated UV-B radiation of 2.8 W m^{-2} at the pot level on plants. UV-B tubes Philips TL 12/40 were used, which radiate UV-B radiation > 270 nm. Since there is no effective ozone develop-

Table 1. (A) Response of shoot weight (g dry matter) of pea (*Pisum sativum*), tomato (*Lycopersicon esculentum* cv. Moneymaker) and Aster (*Aster trifolium*) to increased concentrations of atmospheric CO_2 (350 and 760 μmol mol^{-1} CO_2) and increased UV-B radiation (0 and 2.8 W m^{-2}). The shoot weight as a percentage of the control is given in parentheses. (B) Statistical analysis of the response of shoot weight of pea, tomato and Aster to increased concentrations of atmospheric CO_2 and increased UV-B radiation. P-values of two way analysis of variance are given.

Treatment		Species		
CO_2 μmol mol^{-1}	UV-B radiation W m^{-2}	Pea	Tomato	Aster
(A)				
350	0	0.82 (100)	1.54 (100)	2.99 (100)
350	2.8	0.11 (13)	1.11 (72)	2.50 (84)
760	0	1.14 (139)	2.19 (142)	2.94 (98)
760	2.8	0.14 (17)	1.39 (90)	2.59 (87)
(B)				
CO_2		0.013	0.001	0.722
UV-B		0.000	0.005	0.026
CO_2 x UV-B		0.465	0.174	0.906

ment at radiation > 242 nm, plant injury due to ozone release by these tubes can be ruled out. On sunny, cloudless days UV-B radiation, measured in Amsterdam may vary from 1.0 $W\ m^{-2}$ in the morning and late afternoon to 3.0 $W\ m^{-2}$ at midday (van de Staaij et al., 1990). UV-B levels vary with latitude and time of year. For the year 2060, when a doubling of atmospheric CO_2 is likely to occur, UV-B radiation at a latitude of $50°$ - $60°$ is expected to show an increase of 8 - 16% (Caldwell et al., 1989), based on the assumption that products, covered by the Montreal Protocol, will be released at a constant flux into the atmosphere after 1985 based on the 1986 production estimates. In fact, in the present greenhouse study no realistic increase of UV-B radiation was applied (0 versus 2.8 $W\ m^{-2}$). In current greenhouse studies the effect of two UV-B radiation levels differing about 15% is assessed. In field studies, the effect of UV-B radiation supplied by UV-tubes, in addition to solar UV-B radiation is studied. Results are summarized in Table 1. Shoot weight of pea and tomato increased significantly with elevated CO_2 ($p < 0.05$) (Figure 1). For the succulent halophyte *Aster tripolium*, no significant effect was found. This is in accordance with
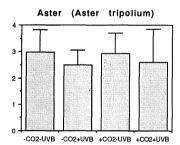

Figure 1. Effect of increased atmospheric CO_2 (350 - 760 μmol mol^{-1} CO_2) and enhanced UV-B (0 and 2.8 $W\ m^{-2}$) on growth (shoot weight, g dry matter) of three plants species.

earlier findings (Rozema et al., 1990). The UV-B radiation reduced shoot weight of all three species significantly. However, there were no significant interactions between the effects of the CO_2 and UV-B treatments ($p < 0.05$). In more detailed studies of the effect of UV-B increase on plants, growth reduction was related to reduced activity of photosystem II (Renger et al., 1986) in isolated chloroplasts and membrane fragments. Transpiration rate is not affected and stomatal effects are not directly involved (Rozema et al., 1990; Strain & Cure, 1985). Increased growth under CO_2 enrichment can be explained by increased rates of photosynthesis and improved water relations due to (partial) stomatal closure. This results in increased water use efficiency and in high turgor values stimulating leaf elongation. The three species differ greatly in sensitivity to increased UV-B-radiation, pea being highly sensitive like other leguminous species (Teramura & Sullivan, 1987). The small growth reduction due to UV-B in the halophyte *Aster tripolium* has been related to the presence of UV-B-absorbing pigments (van de Staaij et al., 1990).

These greenhouse studies indicate that the mode of action of CO_2 enrichment and UV-B increase on the functioning of plants differ, since interactions of the effects were not found.

Although at the moment no generalizations can be made, the findings indicate that the CO_2 and UV-B effect are additive and the possible positive effect of CO_2 enrichment on plant growth can be reduced by negative effects of increased UV-B radiation.

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Climate change and agricultural policy making

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The change in world food production, due to a considerable greenhouse effect, is not a major issue. Water use efficiency in most field crops will increase and the possibilities for crop growth in temperate zones will increase, but these effects will not cause a dramatic change in the world's potential for food production. There may be a change of locations where primary production has most perspectives. This change in perspectives in various areas may cause regional problems, but will hardly affect the world's potential for food production.

Policy makers at various aggregation levels should be familiar with potential changes in regional possibilities and adapt their instruments. On a world scale, food and feed production may not be a problem, but for various continents and political blocks that may be different. For the European Community, for example food self-sufficiency is more than achieved during the last decades and surplus production creates difficulties on the world market. Even without a greenhouse effect, the potentials for agricultural production in the EC exceed the needs for food products and the increase in agricultural productivity per unit area will continue in the next decades. This increase is due to the large gap between potential and actual agricultural production in most agricultural areas of Europe, and to the fact that the efficiency in terms of inputs per unit of output still increases at higher production levels (de Wit et al., 1987). Thus, the increasing over-production in the EC is a major problem for policy makers at the supranational level and as a consequence also for policy makers at the regional level. The increase in agricultural productivity is not the same in various areas of Europe and this may create further divergence of regional economics in Europe. Regional and structural funds are increasingly called upon to mitigate the undesirable socio-economic and environmental effects of the common EC market in agricultural products. However, little or nothing is known about the cost-effectiveness of investments for agricultural development in the various peripherous regions. The need to apply the limited resources from the funds as effectively as possible, requires a more thorough assessment of the different alternatives for the use of resources.

Therefore in 1989 the Netherlands Scientific Council for Government Policy (WRR) started a project on the possible developments of the rural areas in Europe. The general objective of this project is: 'To provide information on the interactions between a number of more or less self-contained technical development processes in agriculture, and objectives from other angles of view such as social economy, environmental protection and nature conservation and the consequences of these interactions for rural areas in Europe'.

This objective is approached in several stages. First a qualitative and quantitative analysis of the long-term agricultural potential of the EC is carried out. Using simulation models, the agricultural production potential of the various European regions is assessed based on soil

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properties and climatological conditions. When the latter change, the results of these simulations may change. Second, these calculated potentials are used to allocate agricultural production considering different policy goals. For this purpose an optimization model (GOAL: General Optimal Allocation of Land use) is developed that incorporates quantified agro-technical, socio-economic and environmental goals (Veeneklaas, 1990). The model is used to calculate the optimum allocation of categories of land use given the technical possibilities within the agricultural sector and the defined preferences for the incorporated goals. Finally, the analysis is completed with the definition a preliminary set of regulatory provisions that are considered necessary to attain the outlined scenarios.

Hence, the study will result in a number of scenarios for a Common Agricultural Policy aiming at solving the problems arising from increasing productivity, market saturation, uneven distribution of production within Europe and increasing concern for the environment and the landscape. At this moment, the land evaluation is completed. The optimization model is defined and the first test runs with the model are completed. An inventory and evaluation of the EC funding and regulations for regional development is also completed. The study can provide information on land use in the EC-12 assuming that the EC aims at food-self-sufficiency. It is also possible to determine expected food production when the EC operates on a liberalized world market. This type of information is needed for a long-term policy choice for the EC.

Climate change as a result of increased greenhouse gases in the atmosphere are not considered yet, but are relatively simple to introduce. The simulation models that generate the potential yield must be run again using modified climate data.

Of course the project does not aim at worldwide scenarios for food supply, but the role of the EC in world food supply can be investigated. The interrelations with other important producing nations (U.S.A., Canada, Australia) and the changes for developing countries can be described within the different scenarios.

The methodology developed and used in this study is not only appropriate for studies where the policy consequences of the greenhouse effect are studied, but has wider applicability. For large scale studies into world food supply this approach may prove to be an important building block.

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Regional analysis of physical potential of crop production in the European Community

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Introduction

The Common Agricultural Policy (CAP) of the European Community (EC) has stimulated agricultural production to a level that surpluses of some major commodities like wheat, sugar, milk and wine have become structural. The agricultural development over the past two decades has led to very intensive land use with associated problems of environmental degradation in some regions and abandonment of land and depopulation in others.

To support EC-policy making the Dutch Scientific Council for Governmental Policy (WRR) is conducting a study on the development possibilities of rural areas within the EC. Different land use scenarios will be evaluated with respect to their impact on rural development, taking into account agricultural, socio-economic, environmental and physical planning aspects. As part of this study, the Winand Staring Centre investigated the physical crop production potential for rural areas in the EC under current climatic conditions. The yield potential of some indicator crops when grown on the major land units suitable for agricultural use, was determined by a combined use of a Geographical Information System (GIS) and models for physical land evaluation. In this paper the procedure for annual crops is outlined and some results for winter wheat are given. The complete study is reported in detail by van Lanen (1990).

Procedures

The starting point was the GIS in which three digitized maps were stored, namely a soil map (CEC, 1985), an agro-climatic map (Thran & Broekhuizen, 1965) and a map of EC-administrative regions at NUTS-1 level (NUTS = Nomenclature des Unites Territoriales Statistiques). The GIS was used to distinguish land units to which the analysis of production potential could be applied. The distribution of such land units was determined by means of a map overlay procedure. This resulted in a new map with some 4200 land evaluation units (LEUs), each a unique combination of soil unit, climatic region and NUTS-1 region. They are distributed over more than 22 000 map polygons (Table 1).

The LEUs are further subdivided on the basis of soil texture, which results in almost 7000 subunits that can be considered homogeneous in their agro-ecological conditions for the purpose of this study at the EC scale. The nature of the LEUs in terms of soil attributes (e.g. soil texture, soil depth) was derived from the EC soil map through an interpretation procedure. Each climatic region was characterized by one weather station for which generally an historical record of 26 years of monthly data was available. The reference to

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Table 1. Number of polygons and mapping units of the three base maps and produced map of land evaluation units covering the EC-12.

Map	Polygons	Map units
Soil map	15 500	544
Agro-climatic map	1 618	109
NUTS-1 map	1 583	61
LEU map	22 208	4 596

administrative regions allows aggregation of basic data and results from LEU level to NUTS-1 level and comparison of results with regional statistics.

A mixed qualitative/quantitative land evaluation procedure was applied to assess the crop production potential of the land evaluation units (van Lanen et al., 1989).

In the qualitative part of this procedure unsuited soils were excluded from further analysis, on the basis of the soil requirements for mechanized cultivation of specific crops. As criteria for this exclusion threshold values were used for soil properties such as slope, stoniness, soil depth, drainage, soil texture, and salinity.

The quantitative part of the procedure consisted of the analysis of the crop production potential of the remaining suitable LEUs with the crop growth simulation model WOFOST (van Keulen & Wolf, 1986; van Diepen et al., 1989). WOFOST simulates the growth and development of a crop from emergence to maturity in daily time steps under prevailing weather and site conditions. For application of the model to the EC, specific data sets were defined with soil and crop parameters. The model was adapted to allow simulation of the dates of sowing and crop emergence. The simulation of the early exponential growth was improved as well. The major simulated processes in the model are phenological development, light interception and resulting assimilation, respiration, partitioning of dry matter increase over plant organs, and transpiration.

Crop yields were calculated for two theoretical production situations: potential and water-limited. The potential crop yield is the integrated expression of the effects of sunlight and temperature on the growth of a defined crop cultivar. The water-limited yield includes the effect of drought stress or waterlogging as well. For this purpose the crop growth model has a soil water balance module quantifying the in- and outflow of water in the rooted soil.

The simulations were carried out as a series for 26 years for each distinct crop/soil weather-station combination. The resulting long-term mean yield was used as indicator for the agricultural potential of each of such land units. The land evaluation procedure described here has been applied to the following crops: winter wheat, sugar beet, potato, maize, oilseed rape, and grass.

The results of the whole procedure were stored in the GIS in the form of yields per land evaluation unit. Within the GIS spatial aggregation can be carried out to calculate weighted mean yields over climatic regions or NUTS-1 regions. The output of the GIS includes tables indicating simulated crop yields for each region and maps showing these yields by yield

class over regions.

Regional production potential of winter wheat

The regional pattern of simulated wheat yields will be used as example to explain regional differences in crop yield potential. The water-limited yields aggregated over NUTS-1 regions will be compared with the actual yield levels.

Potential and water-limited yields

The results of the qualitative selection procedure indicate that less than half of the total EC area is suitable for mechanized cereal cultivation. Large concentrations of suitable land are found in the lowlands of the northern EC-countries on the continent; they are much less widespread in the Mediterranean countries, the UK and Ireland. France has the largest extent of suitable land.

The regional distribution of yields can be related to the major climatic subdivision in temperate and Mediterranean zones, modified by the effects of distance to the sea, altitude and latitude. Mean simulated potential yields are given in Table 2 for some selected climatic regions in the EC. Regional differences in potential yields are caused by differences in solar radiation and temperature regime through their influence on potential growth rate and the length of the grain filling period. The results for wheat indicate that the highest potential yields (more than 10 000 kg ha^{-1} grain dry matter) can be obtained under relatively cool and sunny summers along the Atlantic Coast (e.g. Porto and Plymouth), while lower yields are associated with warmer summers further inland on the continent and in the Mediterranean zone. Above a latitude-specific optimum elevation, potential yields decrease because of suboptimum temperatures for growth.

Simulated yield reductions in the water-limited production situation are related mainly to the occurrence of drought stress during the grain filling period. The severity of the drought stress depends on the earliness of the crop, the rainfall deficit and the moisture supplying capacity of the soil. The latter is related to soil texture, soil depth, groundwater influence and runoff. From the many possible combinations of these factors two are selected to illustrate their influence on wheat yield under various climatic conditions (Table 2): a freely draining coarse-textured shallow soil, and a freely draining medium-textured deep soil. These two soil water conditions mark the range wherein most suited soils of the EC soil map are found.

In the temperate zone the rainfall deficit in summer is rather low and the simulated yield reductions (relative to potential yield) are less than 10% on the widely occurring deep medium-textured soils, but up to 50% on sandy and shallow soils. Aggregation of yields over larger regions results therefore in relatively low yield levels only for regions with a high proportion of shallow, sandy soils such as in Denmark (Copenhagen).

In the Mediterranean zone the summer rainfall deficit is so high that within a climatic region any difference in soil moisture regime leads to differences in yield level. But the overall climate has influence, too. On deep medium-textured soils the reduction in yield due to drought stress varies from 10 to 70%. The strongest yield reductions are calculated for re-

Table 2. Simulated mean harvest dates and yields of wheat on two soils of different water-supplying capacities, and actual yield level on some locations in the EC.

| Climatic region | Harvest date | Yield in kg ha^{-1} (grain dry matter) | | | |
| | | Potential | Water-limited | | Actual[3] |
			Soil I[1]	Soil II[2]	
Athens	6 Jun	6000	600	3600	2000
Rome	20 Jun	8500	1800	7200	2200
Marseille	27 Jun	8600	1100	2200	2600
Madrid	1 Jul	8400	600	2200	1800
Lisbon	6 Jun	9000	1900	7300	1100
Porto	25 Jun	10300	4600	9900	1100
Bordeaux	15 Jul	9200	4000	8800	3700
Paris	1 Aug	8900	2900	7000	5700
Brussels	10 Aug	8200	4600	7900	5200
De Bilt (NL)	20 Aug	8200	4500	8000	6400
Nurnberg	21 Aug	8100	4300	7700	4700
Hamburg	29 Aug	8300	5000	7600	6000
Copenhagen	1 Sep	8000	4000	7800	5500
Plymouth	5 Aug	10400	4300	9900	5200
London	17 Aug	9100	3600	8600	5600
Aberdeen	17 Sep	8600	5500	8500	6000

[1] Soil I = shallow (40 cm), coarse texture, free drainage

[2] Soil II = deep (120 cm), medium texture, free drainage

[3] Actual yield is average over NUTS-1 region (Eurostat, 1987)

gions with a rather cold winter and a hot, dry summer, such as the Spanish high plateau (Madrid). Where the winter is milder, the crop develops earlier, benefits more from the winter and spring rains, and reaches maturity before the severest summer drought. Such a favourable climate is found in some coastal areas (Lisbon, Rome, but much less favourable are Marseille and Athens).

Soil moisture supplying capacity has a strong effect on water-limited yield in the Mediterranean zone. The aggregated regional yield over all soils is relatively low in Portugal due to the presence of a relatively high proportion of shallow or sandy soils among the suitable soils. In Greece there are few suitable soils, but the calculated regional yield is relatively high due to groundwater influence in many of these soils, and the absence of coarse textures.

Water-limited versus actual yields

The calculated aggregated regional water-limited yield levels are all higher than the actual yield level derived from agricultural statistics (Eurostat, 1987). In the northern member states actual yields are of the order of 5000 to 6000 kg ha^{-1} (grain dry matter), and the calculated weighted average water-limited yields are about 40% higher, indicating a large possibility for production increase. Denmark and The Netherlands are closest to the water-limited potential. A larger than average gap between actual and water-limited yields exists for the southern regions of Germany and France, where the difference may reach a factor two.

In southern Europe the actual yields vary from 1200 to 2800 kg ha^{-1} and the water-limited yields are 50 to 500% higher. This indicates that even without additional irrigation development a large increase in wheat production is possible. However, regional differences are large. The smallest yield increases are indicated for regions where the actual yield is already relatively high, such as northern Italy.

Different situations exist in regions with low actual yield levels such as Central Spain and southern Italy. The possibility for production increase is lower in Central Spain because the water-limited yield is more severely affected by drought. But it should also be noted that actual yields in southern Italy refer to durum wheat and simulated yields to common wheat, so that the realization of the regional yield potential would require specific action on crop breeding.

Discussion and conclusion

A constraint for realistic modelling of the soil water balance was the paucity of soil physical data, needed for the estimation of the soil water holding capacity, as no systematic information exists on the soil characteristics of the soil map units, apart from the map code and generalized soil unit definitions. In addition, the map information on soil texture refers only to the dominant soil within each cartographic unit. Most soil data had therefore to be inferred from this generalized soil information, which is at a highly aggregated level compared with the original field observations on which it is based.

In this respect a choice had to be made beforehand between a detailed soil water model representing the current state of process knowledge, but requiring more data than available, or a rather simple model that is designed for use with the available data, but in which process knowledge is incorporated in a rudimentary way only. This boils down to the choice between fitting data to a model, or fitting a model to the data. In the present study a simple soil water model was chosen. But even the application of a simple model could have produced more precise information on water-limited yield levels, if a more detailed soil data base had been available.

The assessment of the possibilities for yield increases based on differences between actual and theoretical production levels could be improved if information on current land use was available. Data on current land use are limited to the NUTS-1 level and at present there is no systematic information available on land use with a geographic resolution comparable to that of the soil map.

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Similarly the lack of a digitized topographic map with altitude data hampers a consistent delineation of climatic regions and hence the identification of more meaningful LEUs.

The procedure developed involving the combined use of GIS and simulation models can also be applied to analyse the effects of climatic change (e.g. change in rainfall or temperature regime, CO_2 concentration) on crop production potential of the EC regions, thus forming a basis for possible future land use scenarios.

A simulation study accounting for current and future climatic conditions has been made earlier for wheat and rice crops for a few locations (van Diepen et al., 1987). The simulation for future conditions requires modification of some crop parameters in the simulation model and the incorporation of the assumed climatic changes in the climate data base. The GIS procedures will remain essentially the same.

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Agriculture, the historian and the future

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When the historian has to answer the question how long-term developments in the future may be illuminated by a comparison with those in the past, he will start to conceptualize the different levels of causation that may possibly influence the object under discussion. To this end, he can dovetail his ideas with those put forward by the French historian, Fernand Braudel (1949), who discerned three clusters of influences on the historical process.

In the first group he put those developments situated outside the scope of human decision-making or that, in any case, only in the long run can be influenced by human action. We may think about developments that take place in the world of natural phenomena such as geological and climatic changes. Mostly the influences of these changes affect social life so slowly that they will pass by unnoticed by the contemporaries. Only the historian will observe them, afterwards, as he will also observe the gradual adaptation of cultures to the new circumstances.

A second group of phenomena comprises developments with a nature of faster change. Nevertheless the word 'fast' has to be understood here in a relative sense. Measured on a human scale, these phenomena seem to move rather slowly. As examples may be considered most of the developments that pertain to the economic, social and cultural life of societies. Mentalities change, but not so quickly. Economic life, too, exhibits developments and has its cycles, but it is only exceptional that it can change overnight. The same is true of demographic and social phenomena. Population growth and population structure are not static phenomena, but it takes decades if not generations for fundamental changes to take place. Occupational structure, incomes, social classes and the relations between them, are all involved in processes of constant but relatively slow and gradual change.

Most volatile prove to be the phenomena of the third group that are the outcome of the struggle for power over people, i.e. the developments caused by political decisions, diplomatic actions and military events. On this level the course of history may be changed suddenly by new treaties, military defeats and victories, and political coalitions. But generally there is also uncertainty as to how long the victor may enjoy the fruits of his victory. Coalitions may break up, parties disrupt, elections be lost, new powerful adversaries unexpectedly arise or agreed measures be revoked. And each of these developments can exert far-reaching influences within a relatively short term.

The course of history may be analysed with the help of this three-level scheme, in which the developments on the first and second level tend to act as limitations for the developments at the next one. This, however, does not exclude the possibility of the existence of influences in the opposite direction. In the long run even climate can be influenced by human action, and political decisions may have a deep impact on social phenomena. But the

historian who wants to look into the future with the help of this analytical tool will be in a stronger position if he first pays attention to developments at the first and second of these levels, rather than to those at the so much more uncertain third one.

This is most probably true for a forecast of agricultural developments in the Common Market. First of all, in this Braudelian scheme of historical forces there is now the often-mentioned change of climate, with its higher mean temperatures, that may deeply influence the long-term developments in agriculture. If it proves to be true that we may expect a rise of 4 - 5 °C, the effects will be so far-reaching that it will be very difficult to assess correctly its impact on agriculture and vegetation in general. But the question is not only whether such a fundamental change will take place, but also, what its rate will be and how far we now want to look ahead in forecasting the future. Climatologists have detected a mean rise of about 0.5 °C during the last 100 years and are inclined to forecast a further rise of 1 - 2 °C up to the middle of the next century. More uncertainty exists about what will happen after that and especially about the expected rate of change. For us, therefore, it seems wise not to extend a forecast of agricultural developments further than the middle of the 21st century.

If the change in climate between let us say 1900 and 2050 is no more than a mean rise in temperature of 1.5 - 2 °C, the consequences for European agriculture will not be disastrous. Although the factor of humidity, which is less easy to evaluate, can spoil our optimistic expectations, on the whole, a limited rise in temperature will probably have more advantageous than disadvantageous effects on agricultural productivity in Europe (this volume). Vegetation with extended leaf growth will especially profit and a double harvest in some crops may well be possible. The zone of possible arable farming will extend further north.

From the viewpoint of the historian of climatic and agricultural change, such a development as predicted to happen up to about 2050 is neither exceptional nor unique. During the last millennia, Europe has undergone climatic changes of a comparable magnitude (Lamb, 1982). During the High Middle Ages cereal crops were harvested on Iceland and vineyards were found in England and Belgium (Slicher van Bath, 1963). The so-called Little Ice Age brought a colder climate after the 15th century, but since the late 17th century, glacier and polar-ice has been retreating. The consequences for agriculture in Europe seem to have been marginal, as far as agricultural historians can observe. We have indeed to take into account the possibility that, in north-western Europe, the consequences of the change of climate between now and the middle of the next century will be felt more in the costs to be spent on defence works against the rising sea-level than in a fundamental change of agriculture.

On the whole, agricultural products are bulky commodities. Consequently, transportation costs are an important factor in consumer prices. The change from the wooden sailing vessel to the iron steamer, with its very much lower transportation costs in ocean shipping, became one of the decisive causes of the agrarian depression in the last quarter of the nineteenth century. But the transportation revolution that began with the railway and steam vessel about 1840 seems to have come to a standstill after the introduction of the mammoth tanker and container traffic. The next century will most probably bring revolutionary developments in electronic communication but not in transportation. It is not even unrealistic to presume that,

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among price components, transportation costs will exhibit an upward tendency. The same is true for the costs associated with the greater care we will be demanding in the near future for the environment. Under these circumstances, with rising price tendencies caused by water management, transport and environmental policy, we cannot expect the share of the producer in the consumer price to show a rising tendency, and certainly not as long as European production prices are above world market prices. On the whole, European farmers would do better not to expect improvements in income. The consequences of long-term changes in the climatic, ecological and geographic factors influencing farmers' incomes tend to be negative.

We have to evaluate the developments at the second level of the Braudelian scheme of influences as being convincingly negative. A central position here is held by the demographic expectations, i.e. the demand for agricultural products. Here we touch on old, long discussed historical questions about the relationship between population and agricultural production. To realize this, it is sufficient to mention the name of Malthus for the 19th century discussion, and that of Ester Boserup for modern development economics (Petersen, 1979; Boserup, 1965).

Friction between the number of mouths to feed and the quantity of food available has been a much-discussed item, too, among economic and demographic historians over the last forty years. They have discovered that, for the last 900 years of Western history, alternate periods with a length of one hundred to three hundred years can be observed in which the friction between population numbers and available quantity of food has undergone a cyclic process. During the periods 1100 - 1350 and 1475 - 1650 population growth was a rather general phenomenon in Europe. Sooner or later this provoked a Malthusian tension with regard to agricultural production. Prices of agricultural products in these periods showed a clear tendency to rise. During the periods 1350 - 1475 and 1650 - 1750 this tension became much less because of a static population or even a decline while, at the same time, agricultural production expanded. During these periods of contraction the prices of the most important agricultural products (cereals, meat and dairy products) showed an unmistakable tendency to fall (Abel, 1935).

Since 1750 until recently population growth was a general Western phenomenon. However, there has also been an unprecedented growth (availability of goods) in production in the Western world thanks to technological innovations and/or expanding import opportunities. This holds for the agricultural market too. Therefore, during that time the standard of living rose formidably, notwithstanding the fast population growth. Hunger has been banished from the Western world and food comprises a much smaller part of the budget than it did 200 years ago. Indeed, even after 200 years of demographic expansion, the surpluses of agricultural products in the Western world never have been so large as at present. But at this same moment of abundance in agricultural home production, Europe seems to be on the brink of a new period of demographic contraction. According to demographers, we have to reckon seriously with a fall of population in Europe of about 10% between now and the middle of the next century (Bourgeois-Pichet, 1989). Consequently, the agricultural home market for food products will decline, and the more so because (hidden) cases of undernourishment no more exist as they did in the past.

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The population decline will express itself in three cumulative ways. It will cause a decline of about 10% in the demand for food, all other things being equal. However, it is well known that, as a consequence of the decline in births, the population structure has been deeply affected, and the European population is ageing. In the beginning of this century about 6% of the population was 65 years and older. This is now about 13%, and it will have increased to about 26% around the year 2040. By then, as much as 15% will be over 75 years of age. But older people eat less than young ones. Although no exact information is available, a guess of a loss in demand for food of 5%, caused by this process of ageing, seems to be on the safe side. A third cause for declining demand can be presumed because better feeding habits will develop over the next generations. If we assume that this means that the general intake of the daily ration of calories will decline from about 2600 to 2500 calories, that seems neglible. But it does mean a further decline of 4%. These three developments taken together suggest a decline in the demand for food in western Europe of about 20% between now and the middle of the next century.

But at this moment, however, our farmers are producing surpluses already! And although it is possible that the further rise in productivity per unit area will slow down, for example, as a result of environmental policy, technology and scientific knowledge certainly will not come to a complete standstill. Therefore, we may expect a further substantial rise in production in the coming decades. If European farmers do not find a solution for this overproduction, by exploiting new export markets or by a change in their crop-mix with a much larger share of industrial products, they will be seriously affected. None of these solutions, however, is likely. A change to more industrial products would imply an expansion of its share in their crop-mix from the present 10% to a future 30 or 40%, before total compensation for losses by the decline in demand for food on the home market would be reached. Such a revolutionary change in the historical trend of a shrinking share of industrial crops in agricultural production is not to be expected. And the exploration of new markets? As long as the price level of European agricultural products does not drop drastically, this too seems highly improbable. On the contrary, the products of European crop farming in many cases need to be protected by customs and export duties.

Here we touch upon the third level of the Braudelian scheme: that of political measures. Can economic policies during the next half century maintain the integrity of the protecting system that has been built around the Common Market? It will immediately be clear that it is unrealistic to expect that public opinion and politicians will be prepared to dump the agricultural surplus production on the world market, at the cost of enormous export duties. As the surplus is likely to exist in the near future without serious adaptation to new circumstances, we even have to go one step further. It also seems highly improbable that, in the long term, the system of protective import levies can be maintained. Such a protection would be contrary to the trend that may be deduced from the international commercial negotiations in the framework of the General Agreement on Tariffs and Trade (GATT). In these negotiations, the political ambition to demolish tariff barriers in the world as strongly as possible dominates. The world community is becoming too small for lasting protective

commercial systems. Here too, European farmers have more to fear than to hope.

Declining demand by smaller populations, in combination with expanding supply by increasing agricultural productivity seems to suggest that we will find ourselves once more in a period of agrarian contraction that strongly resembles the periods 1350 - 1475 and 1650 - 1750. Historians of agriculture have done a lot of research on developments in these periods, characterized by low relative price levels of agricultural products, abandonment of marginal arable lands and depopulation of the countryside, ending in the total disappearance of many agricultural settlements. Twenty-five years ago, Slicher van Bath (1965) summed up much of the phenomena that accompanied the alternating phases of secular agricultural expansion and contraction. A comparison of his findings with on-going developments and existing expectations reveals a number of similarities and, indeed, no contradictions. Most important seems to be the possibility of incongruous developments in agriculture and other sectors of the economy; the gradual, and unequal change from expansion to contraction per country and product; the relatively sharp short-term price fluctuations during the period of contraction; the sharp drop in selling and rent prices of land; the relatively better position of tenant farmers in comparison with farmer owners; the development of the cottar class and the rise in rural and home industries (part-time farmers); the abandonment of marginal lands with its accompanying rise of mean productivity; the decline of the efforts directed against erosion, floods, sand drifts, etc.; the declining interest in agricultural research and instruction; the increase in mean farm size. On each of these points the literature of agricultural history abounds with case studies and examples of past events and developments. They are illuminating for ongoing processes and expected developments.

European agriculture has to prepare for the possibility of a long protracted process of contraction in production (not productivity!) and abandonment of marginal farmlands. This will have to be accompanied by an intensive campaign of reforestation, to avoid massive erosion. This seems to be the only workable alternative solution because, at the moment, timber is the only agricultural bulk product of which Europe still has heavy imports, as well as the possibility of import substitution on a competitive basis, by home production.

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Conclusions and recommendations

The scientific community, especially in its contact with the public and policy makers, should make a clear distinction between the primary physiological effects of increased CO_2-concentrations in the atmosphere, and the secondary climatic effects, that are not only caused by carbon dioxide, but also by other 'greenhouse gases', such as CFKs, nitrous oxides, methane, etc. The primary physiological effects of carbon dioxide are beneficial rather than threatening and hence in itself it is not a polluting gas.

Especially in view of the secondary climatic effects, it is necessary to take measures aiming at reduced emissions of greenhouse gases to the atmosphere. However, such measures will require a basic change in the attitude of policy makers and the general public, aiming at a more efficient use of resources, especially with respect to energy use. At the same time, however, the expected developments in the less developed countries will probably lead to an accelerated rate of increase in the use of energy on a global scale, and because alternative sources (solar energy, etc.) are capital-intensive, it is likely that most of that growth will be covered by the use of fossil energy. Examination of the implications of different scenarios of energy use, i.e. (i) continuation of the present trend, implying a growth rate of about 2% per year, (ii) a mortuarium on growth, or (iii) a decrease in the use of fossil energy by 2% per year, shows that this is of decisive influence on the expected time course of atmospheric CO_2-concentrations. Alternative measures, assuming continuation of the current trend in energy use, such as reforestation or an immediate stop to deforestation, would have a much smaller effect, and could postpone the moment that doubled CO_2-concentrations are reached by ten to twenty years. It is, however, noted that 'buying time' is important for survival and adaptation of society to changing conditions. Hence, any measure that could postpone that moment should be supported.

The present insight in the direct effects of CO_2 concentration on plant performance and the quality of existing quantitative crop growth simulation models enable assessment of the consequences of modified environmental conditions with reasonable confidence for annual agricultural crops. A problem associated with the application of these models is the availability of long-term meteorological records, which are in many instances very difficult to obtain. A strong plea is made therefore for free exchange of meteorological data, at least for research purposes. This is also important for the analysis of trends in meteorological parameters.

An additional problem is associated with the accuracy of prediction of future weather conditions on the basis of results of General Circulation Models (GCMs). Especially with respect to radiation (cloudiness), precipitation and humidity, as well as to extreme events or seasons, great uncertainty exists.

Crop growth simulation models for perennials are far less developed, hence for these

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crops the uncertainty is much greater. The same holds for models that deal with stress conditions, i.e. water shortage, nutrient deficiencies, weeds, pests and diseases. In these models interactions between growth factors are so important that the results of these models should be viewed and used with great caution.

What do we know, what do we need to know (better) and how can that be achieved

Increased CO_2-concentration in itself is beneficial for primary production and the stimulating effect of higher CO_2-concentrations has been demonstrated convincingly both under controlled conditions and in the field.

However, uncertainties exist with respect to long-term effects of high CO_2-concentrations and to the adaptive mechanisms in plants. Experience from horticulture suggests that, at least in some species, the initial stimulation of assimilation fades away after prolonged exposure. Therefore a strong recommendation is made for long-term experimentation, both to study the effects of CO_2 during various phases in the plant's life cycle and to investigate the effects of prolonged exposure. Such experiments should not be restricted to one season, as effects on properties such as seed quality, regrowth potential of perennials, etc., are completely unknown. Experiments should not be restricted to controlled conditions, but should also be executed in the open air, for instance to study the effects on dry matter partitioning to the roots, which can hardly be derived from pot experiments.

A need exists for a more systematic screening of the genetic variability in species with respect to the initial response and the adaptation to increasing CO_2 and temperature.

However, for assessing the overall implications of the greenhouse effect for agricultural production, insight in the interactions between the various factors that influence growth and yield, is of overriding importance. In addition to higher CO_2-concentrations, temperatures will rise, the concentration of polluting gases, such as SO_2 and ozone, in the atmosphere may increase, UV radiation intensity may become higher, etc. The combined effect of these changes is impossible to predict on the basis of current knowledge. Basic experimental research is therefore needed to elucidate the combined influence of these factors on crop performance, complemented by development of simulation models, in which these combined effects can be further investigated. Such activities require research in multi-disciplinary teams, while results should be exchanged and discussed in regular workshops. The changing environmental conditions may affect the relative competitive ability of different species (especially C_3 vs C_4), hence research should be carried out to elucidate the inter-actions between species under different CO_2/temperature combinations. Especially important are germination characteristics and growth in the juvenile phase.

Under the modified environmental conditions new pests and diseases could become a threat to agricultural production, while pests and diseases whose development under the present conditions is checked by low winter temperatures may become more important. There is evidence for modified chemical composition of plant material under future environmental conditions, which may also affect pest and disease development.

An important issue on which uncertainty exists is whether under increased atmospheric CO_2 the C content in soils can be increased. An overall relative increase in soil carbon in arable soils of 1% per year, would result in storage of about 7% of the annual fossil fuel derived CO_2. When also grassland is taken into account, under the same assumption of a relative increase of 1%, as much as 45% could be stored. However, ways and means to increase soil organic carbon contents are scarce, hence there is limited chance for such increases. A major factor in this process will be the relative longevity of the various pools of organic carbon under the modified environmental conditions of temperature, soil moisture and increased carbon dioxide, for which again no solid quantitative information is available.

It is likely that the southern regions in Europe, where at the moment agricultural production is mainly limited by water and nutrient availability, will be more unfavourably affected by the anticipated climatic changes than the northern regions, where temperature and radiation are the major production-determining factors. Estimates with respect to changes in precipitation - quantity, distribution and variability - are uncertain, but they point in the direction of more unfavourable conditions in the south. This may partly be alleviated by the increased water use efficiency, but attention for possible consequences is necessary. Although experimental data on CO_2/nutrient interactions are relatively scarce, existing evidence suggests that under nutrient shortage the beneficial effects of higher CO_2-concentrations on primary production are largely nullified.

The evidence that under elevated CO_2-concentrations the mineral element concentrations in the vegetative material will be lower, has direct consequences for the quality of the material, both for human and for animal consumption. The overall consequences of such different chemical composition are not clear, and need therefore more attention in research. This different chemical composition of the material would entail, among others, a higher C/N ratio. That could have consequences for winter hardening of perennials and winter annuals, and hence for their frost resistance. For the perennials it could also imply relative nutrient shortage during the early period of regrowth, when the substrate mainly consists of components remobilized from the perennial organs.

In the north of Europe, the expected higher temperatures would lead to potentially longer growing seasons - longer frost-free periods-, but phenological development would be accelerated, thus making the actual length of the growing period of the present cultivars of determinate annual crops shorter. However, the genetic variability in this trait seems to be sufficiently high in most agricultural crops, to make breeding of adapted cultivars feasible. The higher temperatures will reduce the permafrost area, which may result in the emission of substantial amounts of methane and CO_2, thus accelerating the greenhouse effect.

'Reciprocal transfer' experiments, both under controlled conditions and under field conditions are strongly recommended. Especially north-south exchange of material would be important. Attention is drawn to the fact that a drawback of such experimentation is, the 'uncoupling' of temperature and daylength. Especially for that aspect, experimentation under controlled conditions is indispensable. It was observed that a gap exists between climate modellers and crop modellers. Climate modellers are not (sufficiently) aware of the requirements of crop growth modellers, who in turn pay insufficient attention to pertinent

data that are available, with a view on development of models that 'fit these data'. Joint meetings, where such problems could be discussed, were therefore strongly recommended. In addition, it is suggested that a European 'clearing house' be established where results of GCMs for European countries and regions are stored and analysed and can be obtained for further application.

It was generally agreed, that insufficient information is available to judge the reliability of predicted and/or anticipated changes in environmental conditions and their possible impact on agricultural production. Long term, uninterrupted monitoring is therefore required to attain long time-series of data.

How to use what we know

There is general consensus that supply of information to the public and to policy makers should be honest, and should include information on the degree of uncertainty attached to the knowledge ('give people the right reason and possibility to worry'). This also means that it should be emphasized that pollution problems are much more acute than the increase in CO_2 concentration.

The changes associated with the greenhouse effect are relatively slow, compared to the changes associated with technological innovation, to which society has in general reasonably well adapted. That may provide some optimism for the flexibility of society to also respond adequately to these changes.

There is consensus that science should not 'follow the fashion of the day', in re-active research, but should emphasize that basic research into causal relationships, proactive anticipation, will provide the best basis to cope with ever-changing problems in a dynamic world.

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