Climate Change Research: Evaluation and Policy Implications
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ASSESSMENT REPORT ON NRP SUBTHEME

"EFFECTS OF CLIMATE CHANGE ON TERRESTRIAL ECOSYSTEMS"

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ABSTRACT

In the projects fostered by the NRP the effects of changed climate (atmospheric CO_2 concentration, temperature) on different terrestrial ecosystems were studied. For forests it was concluded that the initial stimulation of tree growth in general did not persist after two years, and therefore care must be taken not to overestimate the potential contribution of increased carbon sequestration by forests. On the other hand, shifted patterns of carbon distribution in the tree-soil system may lead to a higher soil organic matter content, which will contribute to an improved soil structure and availability of soil moisture. A sensitivity analysis revealed that, for the poor sandy forest soils, improved rooting depth is however more effective for drought prevention than higher soil organic matter.

From the model exercises it was also inferred that with increased precipitation, as predicted under the projected future climate, runoff and recharge of the groundwater will be increased, especially in winter and for deciduous forest stands.

Changed seasonal temperatures will change the timing of phenology but will, in Dutch conditions, not lead to a higher risk for spring frost damage in the period of bud burst. However, competition between tree species may change as the duration of the closed and functional canopy is differentially influenced. For instance for *Larix* and oak the effective growing season is extended, whereas beech and *Tilia cordata* will have a shortened leaf area duration.

Mechanistic forestry production models, adapted to include also the changes in $[CO_2]$, (e.g. in a transient climate scenario), showed that after a transient increase in production, a double-CO_2 climate from GCM calculations caused a subsequent decline in productivity.

A high variability of the growth and production enhancement by rising $[CO_2]$ was also detected in the OTC (Open Top Chambers) and Rhizolab experiments for the crop species studied (potato, wheat, faba bean). The physiological parameters (photosynthesis and respiration) and full season canopy and soil gas exchange measurements showed no growth stage or light and temperature dependent CO_2-enhancement effect. An analysis using crop growth models produced clues as to the origin of the existing confusion about the variability of the CO_2-enhancement factor for biomass production and yield. Using the growth and weather data of different years it could be shown that interactions between growth stage, light and especially temperature in the early growth stages could explain a large part of the variation. Also about half of the differences in growth enhancement between e.g. (winter) wheat (16 - 34%) and faba bean (35 - 56%) could, according to the model outcome, be ascribed to temperature differences in the early (spring) growth stages.

An important and for the carbon cycle very significant finding was that the roots of grass, grown at 700 ppm CO_2 were degraded much slower by the soil organisms

than reference root material. It was shown that this change in properties may fully offset the stimulation of the decomposition of soil organic matter by the projected temperature rise.

In a pilot study the potential distribution within Europe of mosquitoes that can act as a vector for malaria transfer was investigated. The combined effects in the various growth stages of the mosquito, as brought together in a simulation model, indeed point to a highly increased risk for infectious individuals. The probability of an epidemic is considered low, as the European health care system is expected to be sufficiently effective in picking up disease incidence. The concept of "infection potential", developed in this project, offers excellent possibilities to quantify risks also for other, more vulnerable, areas or world wide studies. The methodology developed in this project can be used for other (also agricultural) pests and diseases.

1. INTRODUCTION

1.1 General outline

In the Dutch National Research Programme on Global Air Pollution and Climate Change NRP several aspects of the functioning of widely differing terrestrial ecosystems are considered, varying from physiology, development and productivity of agricultural crops, input and turnover of soil organic matter, characteristics of forest soils and impacts on trees, to the risk of changes in distribution of mosquitoes as vectors for the spreading of malaria. A project aiming at the integration of knowledge at the level of semi-natural ecosystems and thereby to estimate the possible disturbance of the natural succession in such systems was only recently started.

In this assessment a selection of processes, tools and (sub-)systems is considered, and results are discussed that may contribute to a further development of our understanding. Each of the contributions has a merit in its own right, but its added value is realised by linking to the knowledge base of the international scientific community.

After an introduction this report loosely follows the projects within the subtheme "Effects of climate change on terrestrial ecosystems" and discusses the findings in the general context outlined below.

1.2 Ecosystem interactions

Terrestrial managed- or natural ecosystems are by definition functioning and developing in a permanent interaction with external environmental conditions. During their course of development they loose or acquire minerals and organic matter, and thereby modify their internal regulation of the structure and further characteristics. As such they are never in a condition of a stable equilibrium, but essentially in a dynamic and transient state, moving from one stage of development to another. From this general notion it follows that changes in the environment, be it natural or man-made, may perturb or disrupt the development path, destabilize the system or affect the rate of development. Changes may be gradual and difficult to assess, or sudden and substantial when related to instabilities in the system. Transitions to a new quasi-stationary state may be triggered by incidents like storms, droughts, fires or pests. Also socio-economic conditions may be of great influence. Climate change in that respect adds to the environmental factors that determine and change the variability and predictability of ecosystem functioning and stability.

Table 1.1
List of projects in the NRP Subtheme "Effects of climate change on terrestrial ecosystems"

Title	Project leader	Number
The role of organic matter profiles in the effects of climatic changes on the availability of water in forests	W. Bouten	850010
Phenological reactions of the main Dutch tree species to climate change described by a simulation model of the annual cycle	G.M.J. Mohren	850014
Interactions between atmospheric CO_2-concentration, temperature and environmental factors with respect to photosynthesis, assimilate distribution and development rhythm of three agricultural crops	A.H.C.M. Schapendonk	850020
Distribution of carbon over plant and soil compartments during the growth of perennial plants under increased CO_2 concentrations	A. Gorissen	850029
Potential impact of climatic changes on the ecology and distribution of malaria vectors	W. Takken	851057
Integration of effects of climate change on terrestrial ecosystems	F. Berendse	853126
Effect of an increase of greenhouse gases on the water balance of the forested land surface	A.W.L. Veen	850015

Not only the intrinsic value of (natural) ecosystems to mankind (although poorly defined like beauty, ecosystem function) is relevant to the issue of climate change. Changes in ecosystem composition or activity will inevitably have an impact on the pools and fluxes of water and carbon dioxide in the environment. Such changes also may modify greenhouse gas fluxes (N_2O, CH_4, water), production as well as absorption, may be influenced, as the magnitude of the fluxes varies between ecosystem types and with ecosystem functioning. Moreover, characteristics like surface roughness and albedo are of direct relevance to the climatologists. The information on the impact of climate change on terrestrial ecosystems is therefore also of direct relevance for the estimation of feed-backs in the global climate system (see Theme " The climate system").

1.3 Types of ecosystems considered

It may be clear that an assessment of the impacts of climate change on terrestrial ecosystems requires differentiation, depending on the type of system considered. Intensively managed systems like agricultural production systems may require a change in choice of crop type or crop cultivars and a modification of the cropping system, management and market structure. Agricultural systems may also change in productivity and (economic) viability, especially in marginal production areas.

Although impacts of climate change on agriculture in the highly developed technologically advanced Western economies possibly can be absorbed without major risk for food security or shortage, the situation on local and regional markets and with respect to international and intercontinental trade and transportation of food and feed may be affected substantially. A more dramatic situation may arise in regions where local economies do not have access to the economical and technological means to counteract or reduce the threats posed by climate change. Food shortage may lead to starvation or trigger the migration of whole populations. Similarly, measures to protect extensively or unmanaged ecosystems or to counteract unintended developments may also require a substantial economic basis.

However, to judge the risks for the various ecosystems properly, we have to look primarily for the changes in driving forces determining functioning, growth and production potential of e.g. various plant types, crop species, vegetations and forests. Physiological processes, water relations, soil organic matter dynamics and competitive relationships are altered by elevated atmospheric CO_2 concentrations, modified (seasonal) temperatures and precipitation patterns.

1.4 Ecosystem stability

At the next higher integration level from physiological processes in plants and soil, the impact at the level of ecosystem processes should also be taken into account. Forests and semi-natural ecosystems have to be considered as being largely dependent on their internal coherence and consequent resilience to perturbations. As stated, climate change as such is superimposed on top of the existing natural and manmade environmental changes, be it variability or trendwise developments. A proper estimation of the impact therefore requires a complete and coherent picture at a system level and a quantitative description of the selected systems in their present state, their dominant processes and relationships.

The projects on plant- and crop physiology, soil science and soil organic matter dynamics find their application in estimating agricultural and forest productivity, ecosystem functioning and hydrological relationships. Another basis for the estimation of changes in forest ecosystem development is provided by the study of tree phenology in a changed climate.

1.5 Ecosystem evolution and succession

Apart from short term changes and risks, a long term perturbation may happen. Pools and fluxes of carbon and mineral nutrients in nutrient poor systems largely determine the dynamics of vegetation succession. The understanding of the effect of climate change on such ecosystem processes, or ecosystem physiology, is required to estimate the integrated effect on the stability or the rate of development.

A separate study has addressed the potential change in the distribution of the mosquitoes that can act as a vector for malaria. Interpretation of results of the population ecology and other ecological interactions still has to be combined with socio-economic scenarios to estimate the relevance in terms of health risks. As such this type of studies clearly shows the complexity of long-term interactions and the need for caution when interpreting the outcome of sectorial and specialised studies.

2. PLANT GROWTH AND CARBON ALLOCATION IN A SOIL-PLANT SYSTEM

2.1 Introduction

Primary photosynthesis globally takes up as much as 60 - 70 Pg carbon per annum. In addition the oceans have a yearly exchange of the same order of magnitude. Above ground standing biomass is estimated to contain about 500 Pg C, whereas the atmosphere contains about 700 Pg C. These numbers compare with a yearly emission of 6 Pg C from fossil fuel burning. It means that the equivalent of the total carbon content of the standing biomass is turned over by these processes every 8 - 10 years, and of the atmosphere every 6 - 7 years.

The total carbon storage in soil organic matter amounts to approximately 1500 Pg C, of which about half is almost inert. Residence times in various compartments of soil organic matter may range from very short (days to weeks) to extremely long (thousands of years). At the estimated input into the soil the mean turnover time in the active part would be of the order of 30-50 years, but this number has only limited value, given the range of residence times.

Although the dimensions of these numbers give a fair idea about the magnitude of the interactions, the net fluxes are much smaller. Most ecosystems are in a type of steady state, where mean losses of carbon by respiration and decay of organic matter are roughly in equilibrium with C-gains through photosynthesis or other inputs. Even small changes in the balance between C-fixation and release from the storage pools of a system may however have important consequences for the long-year cumulative outcome. Especially the pools in the soil that have long residence times are of interest. Pools and fluxes differ between various ecosystems, and depend on activity and structure of communities. Inputs consist of litter accumulating on the soil surface and in the surface layers and of root material derived from living and dead root systems.

2.2 Primary production

The changed composition of the atmosphere will have a direct effect on plant processes. The most significant impact will be on photosynthesis. As carbon dioxide is the primary substrate for the photosynthetic process a rising concentration in general will enhance the production of assimilates, although not proportional. This is true for plants with the so-called C^3 pathway, where the concentration of carbon dioxide at the site of photosynthesis inside the leaf at present ambient concentrations is limiting. The enhancement is small or absent for C^4 plants. At present most plant species in temperate areas have a C^3 pathway, whereas C^4 plants are predominantly found in warmer climates and tropical areas. For the Dutch and West-European situation the most prominent exception to the general dominance of C^3 plants is maize.

2.3 Effects on transpiration at the level of stomata and canopy

Elevated levels of CO_2 not only enhance the supply of CO_2 as substrate for photosynthesis, but also modify the gas exchange properties of leaves in a canopy in a different way. The opening status of the stomates is a compromise between water loss and uptake of CO_2 from air. The increased levels of carbon dioxide cause a partial closure of stomates, and consequently reduce water loss by transpiration. This is also reflected at a leaf level (30 - 60% lower water loss). However, results at a canopy level are not always clear as many other processes interfere. Because of a reduced transpiration the evaporative cooling is reduced, and canopy temperatures rise. Also, the growth enhancement by elevated CO_2 leads to a larger standing biomass, and an increased evaporating surface. As a result various outcomes are possible, and very much depend on periods of water shortage and the timing thereof.

2.4 Carbon partitioning and soil organic matter dynamics

An increased uptake of CO_2 by the plant biomass may result in a changed supply of root derived products to the soil microbial biomass. The proper quantification of the gradual changes in pools and fluxes of soil organic carbon requires special techniques, as only minor changes may occur, that can accumulate however to significant levels over the years.

Quantitatively, up to 40% of the gross amount of carbon assimilated in the photosynthetic process is allocated directly to the root system and rhizosphere during the season. Root respiration and breakdown of easily decomposable organic compounds in the root rhizosphere return the carbon almost instantly as CO_2. Also part of the biomass built from assimilates produced by photosynthesis is returned in a rather short cycle. In forest systems e.g. the equivalent of the complete fine root system is turned over within one year (Olsthoorn 1991, Olsthoorn & Tiktak 1991). With many annual species of arable crops the full non-harvested biomass is returned as crop residue, and together with the root mass (2 to 4 tons of dry matter per ha), is subject to decay. Up to 60% is easily decomposable, and returns within one year to the atmosphere as CO_2. Part of the remaining material is more resistant to degradation, or is converted into partly humified material by soil organisms, thereby entering the pool with longer residence times in the soil.

It is of great importance to assess the direction and magnitude of changes in the different types of pool sizes and fluxes as a consequence of changed atmospheric CO_2 concentrations and induced by a change in the climate (temperature, moisture). Such changes may be triggered not only through a direct effect on primary productivity, but also through changes in the quality (composition) of the plant material. This quality, reflected e.g. in carbon to nitrogen ratio (C/N) or lignin content of the material, determines the degree of resistance to decomposition by soil fauna and flora (meso-fauna, bacteria, fungi). The quality of the plant material is also of importance for animals (herbivorous macro-fauna) feeding on the plants. The relationship is even more intricate, as the below-ground processes like mineralization re-supply plants with mineral nutrients, thereby closing the nutrient cycle. These pools and fluxes determine to a large extent the productivity and the composition of the vegetation. The complex interactions with moisture, temperature and mineral nutrient availability require a cautious and multi-faceted approach.

3. IMPACTS ON FOREST ECOSYSTEMS

3.1 Introduction

Because of the importance of forest ecosystems a major question in the framework of climate change research within the NRP has been the estimation of the sensitivity of these systems. This applies to growth of individual trees, species composition and stability of the forest ecosystem.

Climate change may affect forests in a complex way (Figure 3.1). Both direct and indirect effects can be envisaged. As stated above, rising CO_2 concentrations will enhance primary production while simultaneously improving water use efficiency. Moreover, rising temperatures may alter phenological development and changing precipitation patterns will also affect growth and hydrological relations. Changes in growth strategy may affect carbon allocation and litter production and distribution as well as litter quality, resulting in modifications of the soil organic matter content, quality and distribution over the soil profile.

It is virtually impossible to create a comprehensive picture of all interactions and processes, and answer in general terms to the questions at hand. Therefore efforts have been concentrated on some major issues.

In the sub-theme "Effects of climate change on terrestrial ecosystems" following aspects of impacts on forests have been specifically studied:

* Douglas fir growth and organic matter dynamics: productivity, quality, conversion rates and pools of organic matter;
* hydrological aspects of changes in organic matter content in forest floors;
* atmospheric exchange and hydrological relations for a forested land surface;
* Phenological development and forest productivity.

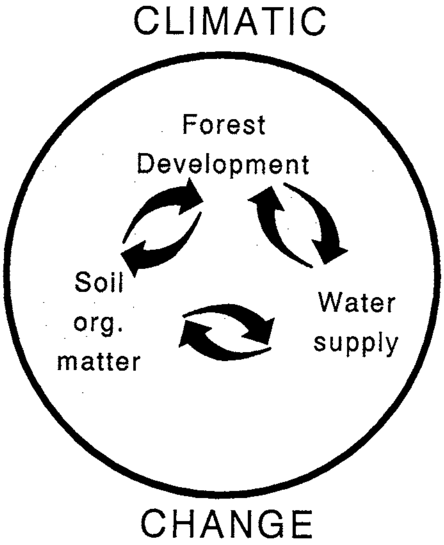

Figure 3.1
Schematic interactions between climate change and forest characteristics

3.2 Growth of Douglas fir trees

Productivity and carbon allocation

To contribute to an improved interpretation of the highly variable results reported in literature concerning persistence of the enhancement of photosynthesis, Douglas fir trees *Pseudotsuga menziesii* were grown at ambient and elevated (double present) CO_2 concentrations. The long term growth enhancement and the partitioning and utilisation of assimilates was followed in time. Using special equipment allowing periodic labelling of the atmosphere with $^{14}CO_2$ at different CO_2 concentrations short term fluxes from the plant to the root and root rhizosphere were studied. The hypothesis was tested that the supply of assimilates to the root and root environment is stimulated at elevated CO_2 concentrations. To ascertain that the effects studied were not (only) transient phenomena, trees and grasses were pre-treated for 14 months at the two experimental CO_2 concentrations. Subsequently, the plants were exposed for a 4-week period to the ^{14}C-CO_2 labelled atmosphere, to trace the fluxes of assimilates. In the experiments with Douglas fir the initial CO_2 uptake, expressed in biomass gain was stimulated by about 25%, but this stimulation fell to lower levels with time.

Exposure to elevated CO_2 for 14 months resulted in 12% more needle biomass and 16% more roots. Root biomass gain is therefore stimulated more than that of branches or needles. Three year old trees appear to have a relatively higher root biomass gain than four year old trees.

However, during the 4 weeks of exposure to a ^{14}C-labelled atmosphere, measurements showed that the total CO_2 uptake of the trees pre-treated and treated at 700 ppm was higher than that at 350 ppm, but that the stimulation of photosynthesis of trees pre-treated at 350 ppm exposed to 700 ppm during the measurement was higher. This was true in both absolute uptake and the more so when expressed per unit needle biomass. When expressed in this way the photosynthesis was reduced by 14% after a pretreatment at 700 ppm CO_2. The reduced photosynthetic activity per unit needle biomass is also found when switching trees from 700 to 350 ppm. Such changes may have important consequences for the potential for carbon storage to be expected in forests. Quantitative conclusions have to wait for the results of additional studies and integration thereof.

Soil and root respiration

In the high-CO_2 treatment at both age classes a higher specific activity was measured in the respiration fluxes from the soil compartment. This may be explained postulating that the soil and rhizosphere organisms in this situation have a preference for the (increased) direct supply of energy rich assimilates from the roots, as compared to the older non-labelled organic material in the soil. It would also mean that the microbial biomass and the organic matter fraction involved in this rapid turnover is not subjected to effects of changes in C/N ratios in the material, or lack of mineral nutrients due to enhanced growth of the trees.

Water use at elevated CO_2

Cumulative water use is changed hardly or not at all, but is lower per unit needle biomass (14-16% lower). Water used for the production of a unit new biomass is also reduced (32% lower). Consequently in unchanged precipitation conditions more biomass can be formed and supported in situations where water poses a serious limitation, or otherwise more water is becoming available to recharge groundwater reserves or contribute to run-off and surface water storage.

Concluding remarks

The general picture can be summarised concluding that initial growth stimulation of Douglas firs does not persist over longer periods. The larger biomass built up initially does not result in a continued higher specific growth rate. It is not realistic to assume that the larger biomass would require proportionally more energy for maintenance, or that tree architecture would lead to a substantial reduction in light interception per unit needle biomass. The latter fact may be at the basis of the high variability of the growth enhancement factor often reported for seedlings in small scale and short duration experiments.

From the detailed results of the present experiments it has been concluded that a limited sink strength of the root system, as proposed in literature, does not play a role. A similar conclusion was also drawn from experiments with crop plants (see Section 5.2).

Physiological and morphological adaptations and effects of changes in the nutrient requirements and nutrient availability have not been considered here, but may have consequences that modify present results, but are difficult to assess systematically.

3.3 Changes in organic matter profiles and availability of water in forest soils

Introduction

Because of the importance of forest ecosystems a major question in the framework of climate change research is the estimation of the sensitivity of these systems. This applies to growth of individual trees, species composition and stability of the forest ecosystem. The question arises also what would be consequences of changes in content and type of soil organic matter due to changed growth characteristics and biomass quality of the trees and of altered organic matter decay rates under climate change (temperature, moisture).

The above discussed potential changes in soil organic matter (Section 2.4) therefore are not only relevant for the global carbon cycle and an improved estimation of the projected changes in carbon storage in terrestrial ecosystems. The organic matter in (forest) soils is also very important for the general soil characteristics, especially for structural properties, fertility and water holding capacity. In other words, changes in the amount and quality of the organic matter deposited on and in the soil have an effect on the quality of the soil for various uses.

Higher organic matter content will lead to better hydrological properties. Depending on the soil type (particle size and size distribution) the effective water storage capacity e.g. is increased. This is especially true for sandy soils with a deep water table, where most of the Dutch forests are located. For most of these forest soils, where the organic matter content is below 2 to 3% the effect of increases in organic matter can be substantial. Organic matter also lowers the bulk density, and enhances possibilities for deep penetration of roots. Again, this helps to supply trees with water in dry periods.

Role of organic matter in sandy forest soils

The organic matter in forest soils is distributed over the profile, and varies in properties from barely decomposed leaf litter and branches, decaying roots and partly decomposed material on and in the forest floor to roots and partly or completely humified organic matter in the mineral soil.

Soil organic matter influences forest hydrology by affecting evaporation from the forest floor, but also by enhancing soil water retention in the root zone. For most conditions on Dutch sandy soils with a deep water table, the amount of required water for evapotranspiration (ca. 400 mm/year) is not available from storage plus summer precipitation, although the year-total of precipitation may be around 800 mm. This water shortage periodically leads to water stress and thus limited growth.

The present project aimed at combining the general understanding of soil physical properties and collecting data in such a way as to allow the evaluation of the sensitivity of the forest hydrological system to climate change. The evaluation itself is not part of this project.

From the soil physical characterisation of a range (8 types) of forest soil profiles quantitative relations have been derived that allow a classification and quantitative description of most Dutch sandy soils. Organic matter lowers the bulk density, and thereby enhances the development of soil structure and its stability. As a consequence the shape of the water retention curve is changed. Dependent on the soil particle characteristics the effective water storage capacity is increased. The effect is stronger for former drift sand soils with uniform particle size distributions than in soils with a non-uniform distribution. This difference is brought about by a better pore size distribution in the latter. For mineral soils with organic matter content below 2 or 3 volume percent the effect is substantial.

An additional effect of soil organic matter is its influence on soil wetting and drying characteristics: the hysteresis gap becomes larger with higher soil organic matter content. The consequences for water availability of this phenomenon still have to be evaluated.

Forest floor evaporation

Direct evaporation from the forest floor can constitute a substantial fraction of the available water. Contrary to expectations, the formation of a dry top layer of the organic forest floor does not limit evaporation losses. Apparently the low-density organic material forming the forest floor acts as a (dense and inverted) canopy, where evaporation takes place at all depths. Moreover water movement from the mineral soil to the organic cover by capillary rise can not be neglected.

The thickness of the forest floor is found to be an important factor for forest floor hydrology. The supply of water down to the mineral soil does not depend on the drainage rate of the forest floor, probably because of the widely diverging time constants.

The estimated evaporation in a dense Douglas fir forest was 85 mm/y, but is expected to be higher in more open forests where both mean radiation level and wind speed at soil level may be higher. Water availability for evapotranspiration depends not only on water storage, rainfall and retention characteristics (3.2), but also on rooting patterns and root growth strategies.

An evaluation of the results in an extended and coupled version of a model for forest hydrology (FORHYD) indicated that the sensitivity of forests for differences in water availability caused by organic matter dynamics is small. Probably trees mostly escape conditions of water shortage by extending roots to greater depths. However, also here organic matter makes a positive contribution, as root growth is enhanced by a lower soil bulk density down the profile.

Ongoing sensitivity analysis, still to be completed, concerning forest floor hydrological dynamics related to future climate scenarios will help to estimate better impacts on forests.

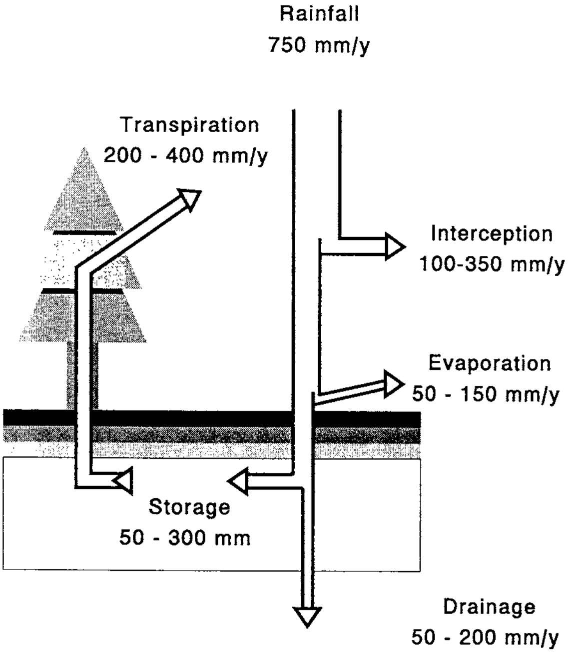

Figure 3.2
Generalised forest hydrological cycle for the Dutch situation

3.4 Water balance of a forested area

The water balance of a forested area very much depends on the structure of a forest, forest canopy and the availability of soil water. A study at a larger spatial scale was also conducted, using a one dimensional computer simulation model. The results are primarily reported in the sub-theme "Regional Hydrology".

For the study at a larger spatial scale a physiologically based model was incorporated to evaluate the direct effect of elevated CO_2 concentrations on photosynthesis, stomatal conductance and water use.

To evaluate the impact of a climate change, a sensitivity analysis and a climate scenario according to the KNMI-2 scenario (with a relatively strong increase in precipitation, especially in winter) were applied. In agreement with the results from other studies in this subtheme, a low increase of productivity was applied by increasing the leaf area index by 5%. The results show a sensitivity to the availability of soil water. Total seasonal water use of forests may change relative to present conditions with between -20% and +10%. Forests suffering water limitation show an increase in water consumption. This may even be stronger when soil water storage is increased as concluded by the study on soil organic matter. Forests with no water limitation consume less water in a changed climate. In general water shortage is reduced, and more of the excess water in the winter period is available to recharge the groundwater.

3.5 Phenological reactions of Dutch tree species in relation to frost sensitivity, growing season and primary productivity

Introduction

Trees are suggested to be in particular vulnerable to climate change because of their long life span and the period of several decades to reach the reproductive stage. Genetic adaptation is therefore too slow and much depends on the plasticity of individual trees and tree species to respond physiologically and/or morphologically to changed local conditions. Important phenomena in the annual life-cycle of deciduous trees are bud burst and leaf area development, and the date of leaf fall or preceding senescence. To study the sensitivity to climate of these events for different species, data were collected and used to develop a phenological model.

A differential response of trees of different species will not only have a direct effect, but may also, or even more importantly, result in changed competitive relations in a mixed stand. This aspect would need further attention as a follow-up of the present study, which has been concentrated on phenology and productivity changes of individual species.

Annual life-cycle of deciduous trees

Important phenomena in the annual life-cycle of deciduous trees are the moment of bud burst and leaf area development, and the date of leaf fall or preceding senescence. These define the physiologically active period, where light intercepted by the foliage is converted into biomass. This period is for deciduous trees also coinciding with a high water demand.

The timing of leaf unfolding is mainly regulated by temperature. For temperate tree species chilling and forcing temperatures are both required to induce leaf unfolding. In other words, a minimum low-temperature exposure and a minimum high-temperature exposure are both required. It is not a priori clear whether warmer winters will advance or delay the date of leaf unfolding: the chilling requirement may be attained later, while the critical temperature sum for leaf unfolding is likely to be reached earlier in spring. Such shifts may have consequences for the occurrence of frost damage. To test the sensitivity of the timing of bud burst to climate several types of models were developed or improved and tested.

Phenology models

The phenology models were calibrated and tested using long-year records of phenological development of beech *Fagus sylvaticus* in the Netherlands and adjacent parts of Germany. Additional data sets of 13 other species but with a shorter record were obtained from phenological gardens in Europe.

The models with the best prediction (modified "sequential" and "alternating" model) were used to test the probability of spring frost damage in the bud burst period under various climate change scenarios. Results were compared with similar studies in the UK and Finland.

Bud burst and frost damage

Based on an analysis of tree clones transferred over Europe, it is argued that the survival of trees is curtailed by spring frosts, and thus that the lowest temperature occurring around leaf unfolding may be a sensitive indication for the geographical distribution of species. Furthermore it is found that trees possess a considerable plasticity, which enables them to accommodate by phenological adaptation a significant change in climate.

With respect to climate warming, in general the probability of frost damage is predicted to be reduced in Dutch, German and UK conditions, for the scenarios and models used (temperature rise uniform throughout the season or temperature rise season dependent).

In Finnish conditions however probability of frost damage is found to be increasing. This disparity is due to local climatic conditions, causing predicted bud burst in Finland to be advanced much more than at the other locations.

The response of bud break of the earlier tree species to temperature is higher than of those which unfold their leaves in the first weeks of May. This enhanced separation in timing may have consequences for the competitive relationships, as competition for light in early spring is changed.

Length of the growing season

As stated, not only bud break but also date of leaf fall is of high significance in tree species performance. Some species (*Larix decidua*, *Quercus robur*) are found to end up with a shortened growing season, while others (*Fagus sylvatica, Tilia cordata*) extend it at higher temperatures as a result of an earlier leaf unfolding without concomitant early leaf fall. Such effects may also have consequences for the competitive relationships.

Primary productivity models

Using a mechanistic model, the combined effect of elevated atmospheric CO_2, temperature and water shortage was explored for Norway spruce. Results showed that the CO_2 response is enhanced in conditions of water shortage. This is due to the fact that water shortage is partly alleviated by the effect of CO_2 on stomatal closure.

Similarly, the larger increase of respiration of the standing biomass with rising temperatures as compared to photosynthesis results in a reduced productivity of cool temperate species when temperatures increase. (6% resp. 2% for potential growth, but 14% resp. 6% in water limited conditions at 350 and 700 ppm CO_2 respectively).

Climate change scenarios were used to evaluate the sensitivity of three tree species (birch, beech and oak) as predicted by process-based tree growth models. Modified current weather data as well as synthetic weather data, modified using GCM output, were used. A transient climate scenario was constructed using a 100 year ramp to the 2 x CO_2 temperature level (mean GCM outcome). Rainfall was modified according to temperature relations, keeping the number of rainy days constant. In these conditions forest productivity was found to increase initially in the transient scenarios, but was reduced at the 2 x CO_2 level, because of an increasing negative effect of temperature on productivity (Figure 3.3).

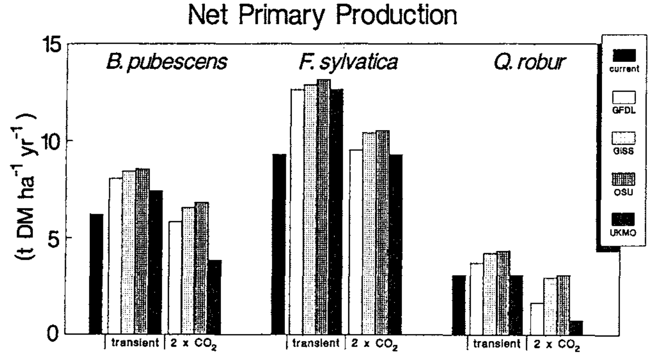

Figure 3. 3
Model prediction of productivity of birch, beech and oak forest under various (GCM-)climate change scenarios

Concluding remarks

Primary productivity models, largely based on correlative relationships, can be used to estimate forest ecosystem productivity in present conditions. More complex mechanistic models of forest growth may also be used to explore the range of effects of climate change on biomass production and carbon storage to be expected. Validation of such models is only partly possible as very few time series of sufficiently detailed forest growth data have been collected. Such more physiological models are however extremely useful tools to explore the possible outcome of the complex reaction of a forest ecosystem to atmospheric [CO_2] and temperature changes. Basic relations derived in this way may subsequently be simplified in summary functions and included in primary production models like the model FORGRO.

Some points should be taken into consideration with respect to these findings. The outcome of these physiological-based models should be interpreted cautiously. A serious drawback is that data to calibrate and validate the forest productivity models are very scarce. Moreover, dry matter partitioning, nutrient relationships and water use are only incorporated in a descriptive way, and the quantitative relationships may itself be modified by climatic conditions.

The impact of temperature on respiration is important when considering long-term effects. Temperatures could deviate considerably from present patterns. It is however still unclear if the short term response of respiration to higher temperature, as used in the model, is also applicable after long-term exposure to higher temperatures. The sensitivity determined in short term experiments amounts to about 7% per °C, and therefore lower values, (e.g. 3% as suggested by Gifford, 1994) might change the picture importantly. Nevertheless the model exercise and literature study has revealed that important changes in forest ecosystem productivity may occur, although the probability of spring frost damage (in Dutch and UK conditions) is decreased.

4. CARBON ECONOMY OF GRASSES

4.1 Introduction

Grasslands dominate an important part of the terrestrial ecosystems, and do play an important role in carbon storage, in some respects with a potential comparable to forests (Goudriaan 1993a, b; Fischer et al, 1994). Especially the below-ground storage of carbon is quantitatively of great importance. Experiments similar in setup to that with Douglas fir (Section 3.2) were also done with different species of grasses (*Lolium perenne* and *Festuca arundinacea*). In these experiments the effect of nitrogen supply was studied using two rates of fertiliser application. Plants were grown in a pretreatment for 14 months at 350 resp. 700 ppm CO_2 in a greenhouse. After acclimation in a special growth cabinet groups of plants were exposed for 24 hours to a ^{14}C-CO_2 labelled atmosphere. During the 24 hour treatment and the succeeding 3 weeks of the experiment the plants were hermetically sealed at the base, to allow the determination of (combined) root and soil respiration separate from CO_2 exchange of the plant tops. Carbon dioxide produced in the soil compartment was trapped in sodium hydroxide, and both absolute amount and specific activity were determined. This allowed the separation of the contribution of different sources of carbon: respiration of labelled recent assimilates from the root and associated soil biomass, and combined non-labelled material from the root and from native soil organic matter.

4.2 Primary production

Elevated CO_2 does stimulate the growth of grasses, but similar to what was found with Douglas fir, the effect is falling over the period of a prolonged exposure. The initial growth enhancement was about 25%, but it dropped to about 16% over a period of 66 weeks. At the final harvest yield differences were almost absent. Both grass species behaved similarly, although the yield response of *F. arundinacea* was somewhat higher. As the effect was similar at both nitrogen levels (135 and 400 kg N/ha) N-limitation as a cause for the falling growth enhancement does not seem likely.

At the highest N-treatment root biomass at final harvest was still strongly stimulated by CO_2, in contrast to the low-N application, where CO_2-enhancement of both root and shoot growth disappeared over time.

The ^{14}C label was used to discriminate between biomass growth during pretreatment, and during and after the labelling period. The results show that most of the larger root systems of the 700 ppm-400 kgN-plants had been formed prior to the labelling. However, as the labelling took place in September an interaction with the season can not be excluded. The analysis of the respiration data showed that the percent distribution of assimilates over the compartments did not change with CO_2 concentration. The higher application of N-fertilisers however reduced root respiration with 29%. Also the percent ^{14}C in the microbial biomass dropped (from 2 to 1% at 350 ppm CO_2). Also at 700 ppm CO_2 the ^{14}C labelled fraction dropped (by 20%). Residual labelled organic material increased by about 100% in the 700 ppm treatment.

4.3 Water use

The pretreatment had an effect on the water use that persisted during the treatment. Grass grown at 700 ppm CO_2 used less water: both total (-16%) and per unit leaf mass (-25%) when exposed to 350 ppm CO_2. At 700 ppm CO_2 the water use was reduced by as much as 35%, independent of pretreatment. *F. arundinacea* was more sensitive, reducing water loss per unit leaf area with 47%, compared to 21% for *L. perenne*. A first extrapolation could be that *F. arundinacea* is capable of taking better advantage of the conditions with higher CO_2 and the more so during periods of water stress.

4.4 Degradation of organic matter grown in elevated CO_2

The above discussed experimental results are obtained with organic matter derived from plants while growing in ambient or double-present CO2 concentrations. The carbon sequestered or released is newly fixed, and only within growing season effects are considered. This might give results that differ in some respects from a normal, more representative growing cycle, where plant residues are left behind at the end of a growth cycle. To test the effects of potential differences in quality of the plant material grown at both CO_2 concentrations, the rate of decay of such material has been analysed. The ^{14}C-labelled plant material therefore has been incorporated into the soil to determine the effect of changes in the composition (quality) of the material caused by growth conditions at elevated CO_2. Two temperatures (14 and 20°C) and soil moisture levels were used. Roots were taken from *Lolium perenne* grown and uniformly labelled with ^{14}C for 4 weeks. The different growing conditions were clearly reflected in the C/N ratio. Roots of *L. perenne* grown at 700 ppm CO_2 had a C/N ratio of 32, whereas for the control plants C/N was 18.

The total production of CO_2 at 2 °C consistently exceeded that at 14 °C, accumulating to 30% difference after 64 days. Root derived respiration increased by 26%. The two levels of soil moisture imposed in the experiments had no significant effect.

The decomposition of roots grown at 700 ppm CO_2 was accelerated during the first two days, but the rate decreased markedly after 8 days. At the end of the incubation high-CO_2 roots had released 24% less ^{14}C-CO_2.

The decomposition of the high CO_2 roots at 20 °C essentially paralleled that of 350ppm root material at 14 °C. The rate of decomposition of the root material had no effect on the decomposition of the native soil-organic matter.

These results show that the change in quality of the plant material as shown here, can hamper decomposition, and possibly partly negate or even annul the accelerating effect of a temperature rise as induced by greenhouse gases.

5. PHYSIOLOGY AND PRODUCTIVITY OF ARABLE CROPS

5.1 General

Introduction

The persistence of the growth enhancement of plants at elevated concentrations of atmospheric CO_2 is still under debate. Although mechanisms have been studied and clarified, the transient nature of the growth enhancement and the variable nature are much less understood. Part of the problems in the experimental studies can be related to experimental conditions, where growth environments have to be created to allow controlled exposure to elevated CO_2 concentrations. In such environments plant characteristics may be modified, leading to changed sensitivity. One aim of the experimental work therefore was to determine the changes in growth characteristics and yield of crop plants in near-field conditions. Therefore three selected arable crops were exposed during the entire growing season to ambient and double-present CO_2 concentrations in OTC's (Open Top Chambers). The research was aimed at answering such questions as the nature of species differences and seasonal variations in plant, crop and vegetation response to climate change conditions ($[CO_2]$, temperature). Detailed studies of source-sink relations, daily and seasonal variations in assimilation, assimilate distribution and total biomass production have been done. The more detailed studies with individual plants and different growth stages and growing conditions were used to support the seasonal studies. The results of the experiments were combined and mechanistic simulation models were used to evaluate the various findings and extrapolations.

Selected crop species and experimental facilities

Rising CO_2 concentrations enhance photosynthesis and thereby the availability of assimilates for various plant processes. Three crop types differing in assimilate utilisation were selected:

* wheat was selected as small grain crop, being a type of "reference crop" used in much of the international climate change research;
* faba beans can develop a symbiosis with nitrogen fixing bacteria which convert atmospheric nitrogen to a plant-available form. To sustain this process the plants have to supply the bacteria in the root nodules with energy in the form of carbohydrates. As such the nitrogen fixation is a drain on the assimilates of the plant;
* potato plants can be characterised as strong starch accumulators during tuber bulking, and were expected to profit specifically from the enhanced assimilate availability.

The effects of elevated $[CO_2]$ were studied experimentally in Open Top Chambers, greenhouses and a Rhizolab facility.

5.2 Basic plant physiological studies

Pot size

To elucidate some aspects of the effect of smaller pot sizes as reported in literature, special tests were set up aiming specifically to avoid shortage of minerals and water. Although for winter wheat a strong reduction in growth was seen for smaller pot sizes (range used: 0.8 to 10L), CO_2-enhancement of growth was not affected. In experiments with faba bean results were more variable, but the general conclusion is that at optimal supply of water and nutrients pot size effects can be avoided.

Interaction with UV-B

Special attention was given to the effect of the presence of UV-B in the solar radiation reaching the plants. To this end OTC's were constructed from special material transmitting UV-B. Results point to an interaction between UV-B and CO_2. Also some effects on plant morphology were detected.

Assimilate distribution and photosynthesis

In the detailed experiments the distribution of sugars over various parts of wheat plants was studied. No differences could be detected in assimilate and nitrogen distribution, apart from an increased carbohydrate content in the wheat leaves in March. Crop architecture was also unchanged. Detailed photosynthesis measurements at the leaf level with wheat and faba beans grown in OTC's and greenhouses as used in Amsterdam (and Wageningen at the canopy level) did not show the occurrence of photosynthetic acclimation.

5.3 Effects of the OTC's

The temperature inside Open Top Chambers is higher than in open field conditions, although this varies over the day. These higher temperatures do have an accelerating effect on plant development, and in general lead to an earlier harvest (about 2 weeks earlier for wheat). The chamber effect on biomass production is however very much influenced by the weather conditions of the specific season. For instance early (or late) high temperatures or drought will affect the crop inside the chamber in a different way, as the development stage or standing biomass is different. For wheat this resulted in 1993 in a clear chamber effect for both winter wheat and faba bean, but in 1994 only for faba bean. A full analysis of the data with crop growth simulation models may reveal whether plants differ in various growth stages regarding their sensitivity to weather conditions.

An unexpected result was the striking effect of the OTC's on the quality (composition) of the plant material. The carbon content was lower (37% as compared to 38.5%), but the effect on nitrogen content was even more prominent. For wheat N-levels at harvest dropped for stems from 8 to 4 mg/g, for leaves from 10 to 6.4 mg/g but for grain it went up from 21 to 23.3 mg/g. Such differences are very important when using plant material for decomposition studies (see above), and may result in misleading outcomes.

In general there was also a slight increase of the harvest index (fraction of the total dry matter in the harvested product). For wheat the effect was stronger than for

faba bean. In 1993 there was no significant effect for faba bean. Differences in harvest index may for faba bean also be influenced by the stage of maturation. It was observed that both with potato and faba bean maturation of the plants tended to be delayed, whereas the faba bean seeds and pods ripened at the same time. Slight differences in moisture content, combined with differences in remaining leaves (including shed leaves) may influence the outcome.
A special aspect of the use of OTC's is the existence of (micro meteorological) gradients within the OTC. In pot experiments, as done in Amsterdam, regular rotation of plants can compensate for non-uniform conditions. However, for field grown plants especially the light gradient causes growth differences that put limits to sampling of plants within the chamber.

As general conclusion it can be stated that although OTC's can be a helpful (and necessary) tool for experimentation in elevated CO_2 conditions, changes in plant growth and development can not be avoided, requiring a cautious interpretation of the magnitude and type of results. In most situations OTC use should be combined with verification experiments at different scales.

5.4 Biomass formation and yield

Growth of winter wheat in winter

The hypothesis was tested that the higher photosynthesis at double-present CO_2 concentrations will result in enhanced growth in autumn, or in higher accumulation of reserve carbohydrates in the plant material. Both from detailed carbohydrate analysis and from biomass determinations it appeared that during the winter period no CO_2-enhancement of growth occurred. Apparently temperatures from late October till early April are prohibitive. This was corroborated by the results with winter rye grown in the Rhizolab. The rye was sown late August, and grown till April. In the winter period no significant differences in growth or rate of photosynthesis could be observed. However, a stepwise increase in temperature in February resulted in a 21% higher biomass in April.

In parallel experiments with grasses it appeared that also there no CO_2-enhancement of growth could be detected, and only in May a clear growth stimulation was found.

From switching experiments (between CO_2-levels) it appeared that the higher accumulation of carbohydrates during winter did not result in a clear advantage.

Differences in response between species

Comparing ambient and double-present CO_2 concentrations with wheat, potato and faba bean (*Vicia faba*) it appeared that the increase in biomass productivity between species and years varied from 16 to 55% (Table 5.1). In general faba bean showed the highest effect, and potato and wheat reacted about equal. Growth enhancements for OTC-grown potato plants were low, and rather variable. In some years no statistically significant differences could be shown.

An analysis of the data using simulation models showed that variations in the weather pattern, but also effects related to light and temperature conditions in the period following emergence could explain a significant part of the year to year variability and also of between-species differences. Model performance for potato crops was rather poor.

Although models could not explain all results, they clearly helped to show the great importance of the timing of local weather (temperature levels, drought) relative to the development stage of the crop.

The generally observed reduction of nitrogen concentrations in the plant biomass was confirmed in our experiments. Therefore the nitrogen harvest (per land area) increased less than the biomass did.

Water use efficiency

In the experimental conditions (optimal water and nutrients) water use efficiency (biomass produced per unit water transpired) was enhanced, but total seasonal water use (per square meter) did not significantly change because of a larger (transpiring) biomass. More detailed analysis showed that nitrogen content in the biomass dropped, but that the harvest index did not change. Full details on the growth of roots and production of CO_2 by respiration of the roots and soil throughout the season can not yet be given.

Table 5.1A
Biomass and yield ($g.m^{-2}$ dry matter) of crops grown in near field conditions in Open Top Chambers, exposed to ambient and double presen [CO_2] in 1994

Crop	ambient [CO_2]	double [CO_2]	statist. signif.	ratio
Winter Wheat				
total biomass	2302	2709	$p<0.001$	1.18
grain yield	1009	1206	$p<0.001$	1.20
Potato				
total biomass	1202	1499	$p<0.001$	1.25
yield (dm)	1036	1284	$p<0.05$	1.24
tuber fresh wht	5011	5725	$p<0.1$	1.14
Faba bean				
total biomass	1116	1641	$p<0.001$	1.47
seed yield	614	733	$p<0.05$	1.20

Table 5.1B
[CO_2] response of biomass production for various years and crops as compared with simulated yield response

	experiental		simulated	
	year	ratio	year	ratio
spring wheat	1991	1.35	1975-1987	1.42
winter wheat	1993	1.19	1993	1.35
faba bean	1992	1.58	1975-1987	1.52

Canopy gas exchange

For the crops grown in the Rhizolab facility gas exchange has been followed throughout the season, allowing the detailed analysis of various interactions with environmental factors. At the canopy level the often reported down-regulation of photosynthesis after prolonged exposure to elevated CO_2 was not detected. The growth enhancement due to CO_2 did not or very little depend on the development stage of the crop. An interaction with light level or temperature during the growing season could not be detected (Figure 5.1). The absence of a growth enhancement at low (winter) temperatures could not be proved, as the photosynthetically active biomass (winter wheat) was too small at that stage. More detailed analysis of data from grass swards and winter rye canopies may shed some light on this point.

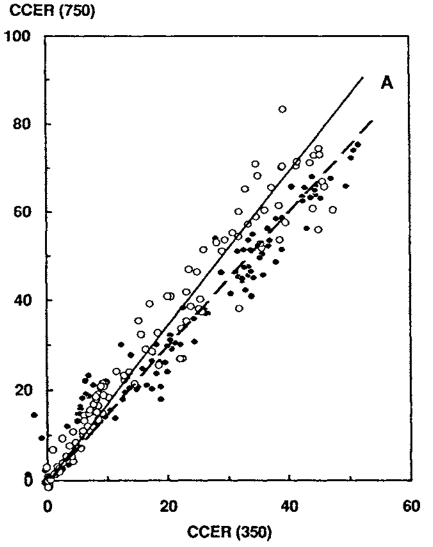

Figure 5.1
Scatter plot of canopy photosynthesis of spring wheat and *faba* bean throughout the season at 350 and 700 ppm CO_2

6. INTEGRATION OF EFFECTS OF CLIMATE CHANGE ON TERRESTRIAL ECOSYSTEMS

6.1 Introduction

Changes in soil acidity and nitrogen supply are held responsible for the strong decline in species diversity in Europe over the past 40 years. Succession of vegetation types is intimately related to changes in nitrogen mineralization, soil acidity and plant biomass production levels, that are a result of soil organic matter accumulation. It is to be expected that changes in CO_2 concentration in the atmosphere will have important effects on the rate of soil organic matter accumulation and nitrogen turn-over. To study the effects on succession in ecosystems, a simulation model is being developed that will help to evaluate effects of changes in $[CO_2]$ and temperature on the succession and biological diversity in nutrient poor ecosystems.

Data for the calibration and validation of the model are collected in an existing chronosequence (0 to 120 years) on a nutrient-poor sandy soil.

6.2 The model

The model simulates carbon and nitrogen flow through plant biomass and soil. It consists of three main modules: a water balance, a soil module, and a plant module. Decomposition and mineralization are calculated in the soil module. In the model species compete for light, water and nitrogen.

The plant model is still under development. Because species will show different responses to climate change because of specific plant traits, competition may change and lead to a modified development course for the ecosystem.

6.3 Progress and plans

The project was started only in late 1993. Although progress is along expected lines, as yet no results are available. Model outcome will be related to biodiversity using the correlation between species diversity and variables like soil moisture content, nitrogen content, pH, vegetation height and vegetation structure. The duration of the development stages of the succession series of the ecosystem will be used as an indication for the potential for maintaining biodiversity during the succession.

Parameter values are obtained from field experiments in five stages in the chronosequence. Among others biomass quantities and decomposition rates are measured for different sources of organic matter.

7. IMPACT ON ECOLOGY AND DISTRIBUTION OF MALARIA VECTORS

7.1 Introduction

This project was started as a pilot study for vector borne diseases. Specifically it aimed at evaluating the effects of climate change on the complex ecology of mosquitoes and, from there, estimate the risk of a future spread of diseases. In itself it is not directly linked to the other terrestrial ecosystem studies.

The main goal of the project was to use detailed information on the habitat and bionics of the relevant *Anopheles* species to develop a simulation model for the population dynamics of malaria vectors in Europe, allowing the estimation of potential changes in location and size of areas with a health risk.

7.2 Simulation models

The model MOSQSIM, describing the population dynamics of vector species, is linked to a model simulating water availability including changed patterns in precipitation. The consequent changes in habitat (moisture, temperature) favouring or hampering the successive stages of mosquito development are calculated. Critical conditions for population development like availability of fresh water pools, and of humans or other blood sources for the blood meal prior to hatching are also quantified in the model.

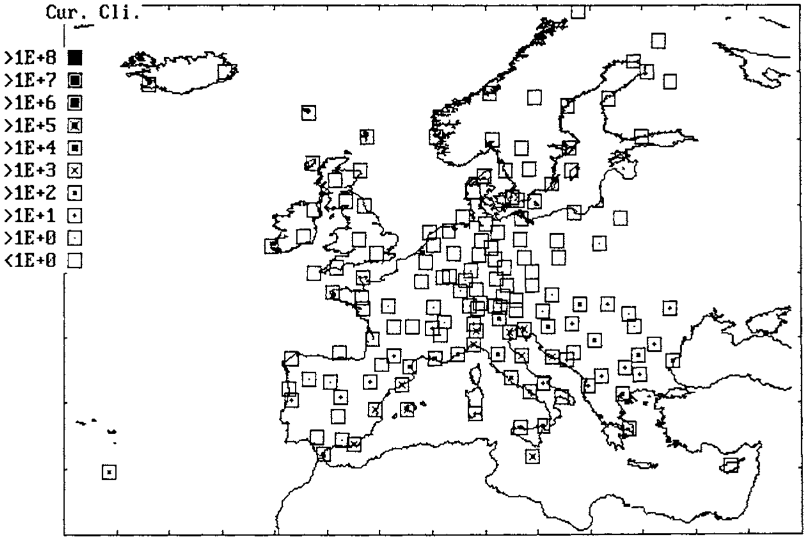

Figure 7.1
Simulated distribution of *Plasmodium vivax* infectious mosquitoes under the current temperature (+ 2 °C) climate scenario

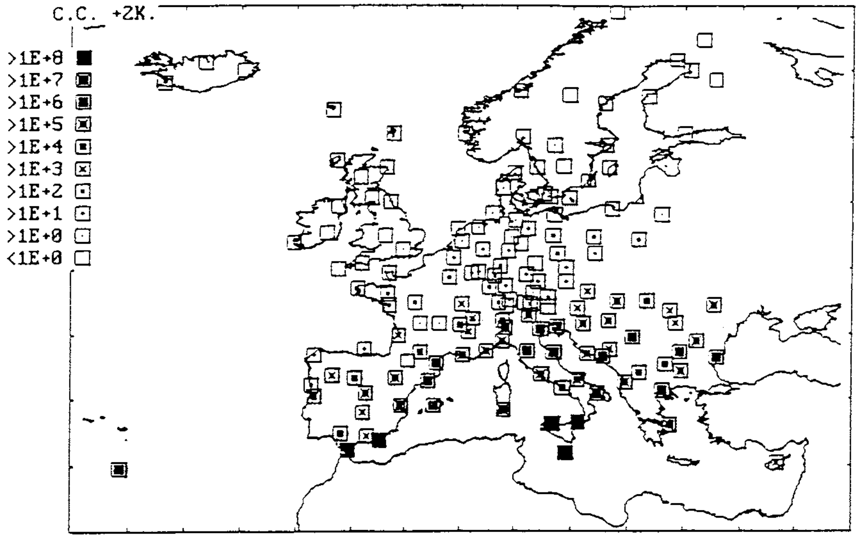

Figure 7.2
Simulated distribution of *Plasmodium vivax* infectious mosquitoes under increased temperature (+ 2 °C) climate scenario

7.3 Distribution of the malaria vector

On basis of a climatological database the model correctly generates the vector distribution and malaria incidence in Europe before World War II. Also, realistic values for the vector distribution were found for the last decade.

When applied to climate change scenarios the validated model predicts a significant change in the vector distribution. Not only present mosquito species will extend in distribution area, but also more dangerous species will move to higher latitudes over Europe. A summer temperature increase of 2 °C may result in a hundred fold or more increase in the number of infected mosquitoes in Southern Europe. The epidemic potential of vectors already present in an area thus may rise drastically.

The techniques developed are suitable for estimating the regionalised malaria risk. As an index the vectorial capacity has been defined, being the number of potentially infective contacts made by a mosquito population per infectious person per day. This index is a powerful tool, as it may also be used to express the regionalised malaria risk at a world-wide scale.

7.4 Concluding remarks

In the project models have been developed for the distribution of mosquitoes as a vector of malaria. The models from this pilot study can be adapted to assess the impact of climate change on other harmful as well as beneficial insects, provided the proper technical coefficients describing critical stages and processes are available. Evaluation of changes in biodiversity as well as questions related to integrated pest management in crop protection could be studied in this way.

8. CLOSING REMARKS

The projects summarised above have not yet been completed at this stage. The project on integration of effects in fact has only started a year ago. As a consequence an assessment can only be preliminary. Further interactions and progress in the analysis and interpretation of the results will help to complete the contribution to the scientific basis for the estimation of the impact of global climate change on terrestrial ecosystems.

Although the subjects and objects under study were different in many respects, the knowledge developed under the programme has made a significant contribution to improve the understanding of the complex terrestrial ecosystems, and has been instrumental for the development of new tools.

It has also helped to establish excellent networks with the international scientific community, and to provide policy makers both nationally and internationally with the latest results. However, the full value of the effort will only be achieved in a follow-up of the programme, where missing information can be added, but certainly a transfer and further integration of knowledge based on the expertise built up in the NRP, and in International Programmes (like IGBP-GCTE, IGBP-BAHC, HDP-LUCC) should take place.

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