

**SIMULATED IMPACT OF GLOBAL CLIMATIC CHANGE  
ON THE GEOGRAPHIC DISTRIBUTION OF PLANT DIVERSITY**

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**ABSTRACT**

Elevated concentrations of atmospheric carbon dioxide ( $p\text{CO}_2$ ) are likely to lead to substantial warming in the coming century with altered hydrological regimes, thereby affecting the distribution of plant species. Here I use an individual-based modeling approach to plant diversity to estimate the impact of global climatic change on the geographic distribution of plant diversity. Differences in temperature, precipitation, and light use efficiency (to represent stimulation of photosynthesis due to higher  $p\text{CO}_2$ ) are used in isolation and in combination in order to investigate the role of these drivers. I find that the general warming associated with elevated  $p\text{CO}_2$  leads to profoundly different responses of simulated diversity in temperature-limited and tropical environments. While the growing season is lengthened in northern latitudes and therefore enables more plant growth strategies to be successful, elevated autotrophic respiration rates lead to higher mortality during plant establishment in the tropics, therefore reducing the range of successful plant growth strategies. The overall impact of elevated  $p\text{CO}_2$  on plant diversity will clearly be a combination of various factors. What these model results nevertheless point out is that global climatic change may alter plant diversity patterns disproportionately by reducing the overall success of plant establishment.

## INTRODUCTION

Elevated atmospheric concentrations of carbon dioxide (pCO<sub>2</sub>) are likely to lead to a global warming of 1.4 to 5.8°C over the period 1990 to 2100, along with an intensification of the water cycle (IPCC 2001a). These environmental changes will inevitably affect plant functioning, resulting in changes in the distribution of plant species and biomes (Pastor and Post, 1988; Still et al. 1999; Cramer et al. 2001; IPCC 2001b). Model simulations suggest a northward shift of vegetation zones in the temperate regions due to a longer growing season (Pastor and Post, 1988; Cramer et al. 2001). So far, only a few studies attempted to estimate the effects of global climatic change on the large-scale patterns of plant diversity (Woodward and Rocheford, 1991; Rocheford and Woodward 1992; Sala et al. 2000). Simulations with a semi-empirical model (Woodward and Rocheford, 1991; Rocheford and Woodward 1992) estimated that the changes associated with elevated pCO<sub>2</sub> would favor higher levels of plant diversity, mainly in semiarid regions due to stimulation of plant productivity with elevated atmospheric pCO<sub>2</sub> leading to a higher water use efficiency. A qualitative analysis on different drivers of biodiversity change (Sala et al. 2000) suggests that the largest impacts of biodiversity change due to climatic change would occur in the arctic, concurring with the suggestion of a poleward shift of vegetation zones.

Here I use a plant diversity modeling approach which focuses on individual plant functioning (Kleidon and Mooney 2000, referred to as the "KM" approach in the following) to investigate how different aspects of global climatic change in isolation, and in combination, affect the simulated geographic distribution of plant diversity. The KM approach is based on an individual-based plant model which simulates plant growth from an initial amount of carbon ("seed") to death using ecophysiological relationships. In the context of a Monte-Carlo simulation, this model is then used to estimate the number of different ways plants can grow and reproduce under a given climate. This number of different ways to grow and reproduce is used as an approximation of plant diversity. Using global climatic forcing, a geographic distribution of plant diversity was obtained which qualitatively reproduces the observed distribution of plant species richness very well (Currie and Paquin 1987, Barthlott et al. 1996), in particular the majority

of hotspot areas as well as a pronounced latitudinal gradient. This simulated pattern is primarily caused by climatic limitations to plant establishment, concurring with the regeneration niche hypothesis of Grubb (1977).

In this paper, a scenario of climatic change for the end of this century is applied to the climatic forcing of the KM approach to simulate the effects of climatic change on plant diversity. Three factors are considered: (i) the general increase of temperature due to the increased concentration of atmospheric pCO<sub>2</sub>; (ii) changes in precipitation associated with the warming; and (iii) changes in photosynthetic pCO<sub>2</sub> uptake ("pCO<sub>2</sub> fertilization", e.g. Koch and Mooney 1986), which is considered here by increasing the model's reference value of light use efficiency. These three factors are used in isolation and in combination in order to investigate the individual and synergistic effects of global climatic change on the geographic distribution of plant diversity.

## METHODS

### *Overview of the plant diversity modeling approach.*

The KM approach is based on an individual based simulation model of a generic plant. A plant is characterized by six carbon compartments representing leaves, fine roots, aboveground- and belowground woody structure (stems, branches, coarse roots), storage and reproduction. These compartments are linked to the physical functioning of the land surface in terms of absorption of solar radiation and soil moisture dynamics which is simulated by a land surface component. For instance, leaf biomass is linked to the amount of absorbed solar radiation, and fine root biomass to the capability of the plant to extract soil moisture from the rooting zone. Both of these examples have functional consequences: more absorbed radiation enhances the supply of energy for photosynthesis and evapotranspiration, and the amount of extracted soil water determines the water status of the plant and the supply of moisture for evapotranspiration. This coupled plant-land surface model is therefore capable of simulating the interaction between plant development, i.e. its strategy to grow, and land surface functioning in a process-based manner. Every new plant starts from an initial amount of carbon (a "seed") and grows once environmental conditions are right. The conditions for germination as well as the way in which the plant grows are defined by a set of



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twelve parameters, forming a plant growth strategy. These parameters determine the particular functioning of the plant such as the amount of carbon from photosynthesis and storage which is allocated to the six plant compartments (allocation) and the response time of the plant to changes in environmental conditions (phenology). All of these parameters are associated with tradeoffs. For instance, a higher allocation to fine roots enhances water availability (if sufficient soil water is available in the rooting zone), but this comes at the expense of lower rates of aboveground allocation. In the model, only limitations through the availability of light, temperature and water are considered.

The plant model was then used in the context of a "Monte Carlo" simulation to test how many plant growth strategies lead to reproductive success. A total of 5000 plant growth strategies assembled from random numbers is tested. The strategies were tested in isolation, that is, the effect of competition in a community setting was not considered. In this respect, the simulated diversity patterns should be seen as a potential diversity that the climate of a particular region permits. The "Monte Carlo" simulation was performed across different geographic regions using daily atmospheric forcing of solar radiation, thermal radiation, temperature and precipitation. The climatological forcing enters this approach directly through its effects on plant physiology and phenology, and indirectly through its effect on land surface functioning. Details of the model and the simulation setup are described in Kleidon and Mooney (2000). The simulation of plant diversity with present-day climatological forcing is referred to as "Control" simulation in the following.

#### *Climate Change Scenario*

The "IS92a" climate change scenario of the coupled ECHAM 4/OPYC3 climate model (Roeckner et al. 1996) was used to represent climatic change for the period of 2070-2099 (available at the IPCC Data Distribution Centre at <http://ipcc-ddc.cru.uea.ac.uk/index.html>). This scenario leads to a global warming of 3°C and an increase in global precipitation by 2% at a mean atmospheric carbon dioxide concentration of 700 ppm. Mean monthly differences to the present-day climate of temperature and precipitation were used to change the climatological forcing of the

control simulation. Temperature differences were directly added to the control forcing while precipitation differences were applied in terms of percentage change. The annual mean differences in precipitation and temperature as simulated by this scenario are shown in Figure 1a and b.

### *Simulation Setup*

Several simulations were performed with the plant diversity model using altered environmental conditions: In the simulations "2085P", "2085T", and "2085L12" the differences in precipitation, temperature, and light use efficiency (of 12.5%) were applied in separation; in the simulations "2085PTL00", "2085PTL12", and "2085PTL25" both, temperature and precipitation differences were applied and light use efficiency was increased by 0%, 12.5% and 25% respectively. For each of these simulations, the Monte-Carlo setup was conducted with the altered climatic forcing as in the "Control" simulation.

## **RESULTS**

The isolated effects of climate change on simulated plant diversity patterns are shown in Fig. 1c and d. In the scenario used, global precipitation increases by 2%. However, this increase takes place in a very heterogeneous fashion, with some regions showing strong increases in precipitation while others experience a decrease. Regions in which precipitation is reduced in the climate change scenario include the western United States, Southeastern Amazonia, South Africa, Western Australia and the mediterranean region of Europe. Taking only these precipitation differences into account, the difference in diversity generally mirrors the difference in precipitation (simulation "2085P" - "Control", Fig. 1c). That is, regions in which a reduction of precipitation is simulated in the climate change scenario can only sustain a reduced level of plant diversity, while regions with increased precipitation show a slight increase in simulated plant diversity. The simulated difference in plant diversity is consistent with the expected shift in vegetation zones associated with the altered hydrologic regimes.

Elevated pCO<sub>2</sub> generally leads to an increased annual mean temperature, with a typical larger increase in the high latitudes while warming is less pronounced in the tropics (Fig. 1b). This

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general warming trend, however, leads to contrasting effects on simulated plant diversity. In cold-limited environments, primarily in the northern latitudes, simulated plant diversity shows a modest increase in simulated diversity due to lengthening of the growing season. This simulated trend is concurrent with previous studies (Woodward and Rocheford, 1991; Rocheford and Woodward 1992; Sala et al. 2000) and the general notion of a northward shift of vegetation zones (Pastor and Post, 1988; Cramer et al. 2001; IPCC 2001b). In contrast, the warming leads to a general reduction in simulated diversity in most tropical regions. This reduction is caused primarily by reduced rates of plant establishment during early plant life (Figure 2) as a result of enhanced rates of autotrophic respiration. Since plants during establishment draw their carbon primarily from the seed, enhanced autotrophic respiration rates associated with warmer temperatures lead to reduced rate of establishment in the model, leading to a lower diversity.

An increase in light use efficiency leads in general to a proportional increase in the simulated capacity of plant diversity (not shown). When forcings were combined, the differences in simulated plant diversity is very similar to the sum of the isolated effects (Fig. 3). This can be understood as a consequence of plant establishment being the primary factor which limits diversity in the model (Kleidon and Mooney 2000). As the isolated forcings lead to differing responses, with precipitation differences leading to both, increases and decreases in simulated diversity, with temperature differences leading to increases in diversity in the extratropics and decreases in the tropics, and with elevated photosynthetic activity leading to generally increased diversity, the overall response depends on the assumed level of increase in light use efficiency. With no increase in light use efficiency, the response to temperature dominates the response, leading to a widespread reduction in simulated plant diversity in the tropics and a modest increase in the extratropics. With increased levels of photosynthetic stimulation, the reducing effects of temperature are offset, so that larger regions in the tropics would be able to sustain higher levels of plant diversity.

Naturally, these simulated results are subject to limitations. For instance, our approach of testing plants in isolation only provides an estimate of potential diversity for a given climate, since competitive effects within plant communities are not considered. Also, other factors such as

historical coincidences are not considered here (e.g. Ricklefs 2004). An increase in simulated diversity merely means that a climatic region would be able to sustain higher levels of plant diversity, that is, more plant growth strategies would be able to establish and reproduce. Whether plant diversity of a region would actually increase depends on factors not considered here, such as dispersal and even the rate of speciation. Large uncertainties are also attached to the climatic forcing, particularly the regional change of precipitation and the response of photosynthesis to elevated pCO<sub>2</sub> (e.g. Koch and Mooney 1996, Mooney et al 1999, Koerner 2000) so that it is not clear to which extent diversity-reducing climatic effects would be offset by the stimulation of photosynthesis and in which regions these would occur. Our model results nevertheless suggest that the global pattern of plant diversity may be considerably altered in the long term by global climatic change through a disproportional effect on the survival during plant establishment, with potential impacts on global ecosystem functioning (Chapin et al. 2000).

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## FIGURE CAPTIONS

**FIGURE 1:** Simulated differences in terrestrial climate with global climatic change for the time period 2070-2099 by the ECHAM4 simulation model (Roeckner et al. 1996) and its impacts on simulated plant diversity. (a) differences in annual mean precipitation; (b) differences in annual mean temperature; (c) differences in simulated plant diversity due to difference in precipitation ("2085P" - "Control"); (d) differences in simulated plant diversity due to difference in temperature ("2085T" - "Control"). Differences in plant diversity are expressed as percentage point differences with 100 being the maximum simulated value of plant diversity for present-day conditions. The climate scenario is available at the IPCC Data Distribution Centre at <http://ipcc-ddc.cru.uea.ac.uk/index.html>.

**FIGURE 2:** Frequency distribution of simulated plant lifetimes for the present-day control simulation (solid line) and for the climate change simulation using temperature differences only (dotted line, simulation "2085T") and the simulation using an increased light use efficiency only (dashed line, simulation "2085L"). The values of approx. 60 million simulated plants were used to derive the distribution for the three simulations.

**FIGURE 3:** Difference in simulated plant diversity using combined forcings. (a) combined effects of differences in precipitation and temperature, using present-day value of light use efficiency (i.e. "2085PTL00" - "CONTROL"); (b) combined effects of differences in precipitation, temperature, and light use efficiency increase of 12.5% (i.e. "2085PTL12" - "CONTROL"); (c) same as (b), but light use efficiency increase of 25% (i.e. "2085PTL25" - "CONTROL").

FIGURE 1:

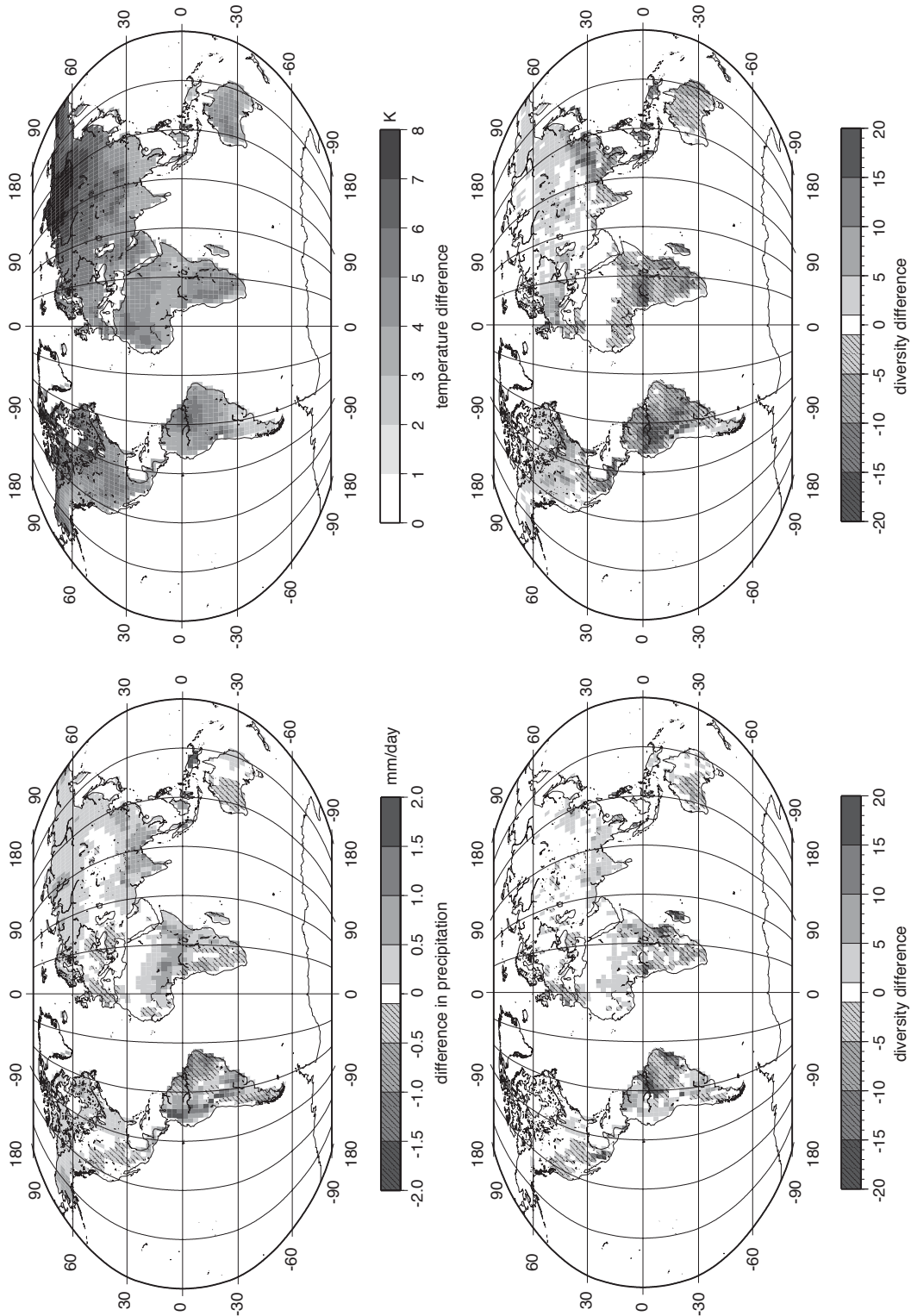
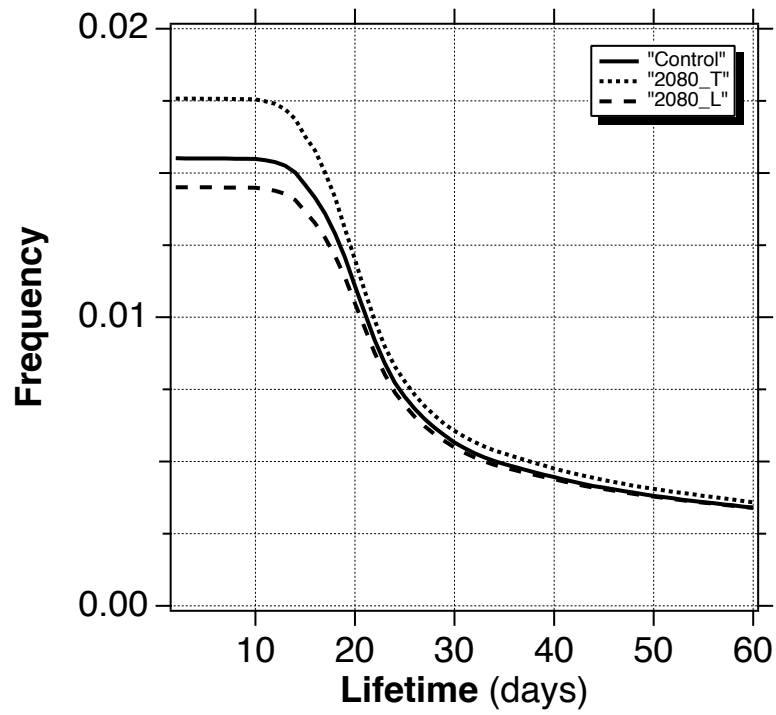


FIGURE 2:





**FIGURE 3:**

