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# Possible impacts of global warming on tundra and boreal forest ecosystems: comparison of some biogeochemical models

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**Abstract.** Global warming affects the magnitude of carbon, water and nitrogen fluxes between biosphere and atmosphere as well as the distribution of vegetation types. Biogeochemical models, global as well as patch models, can be used to estimate the differences between the mean values of annual net primary production (NPP) for present and for future climate scenarios. Both approaches rely on the prescribed pattern of vegetation types. Structural, rule-based models can predict such patterns, provided that vegetation and climate are in equilibrium. The coupling of biogeochemical and structural models gives the opportunity of testing the sensitivity of biogeochemical processes

not only to climatic change but also to biome shifts. Whether the annual mean NPP of a vegetation type increases or decreases depends strongly on the assumptions about a CO<sub>2</sub> fertilization effect and nitrogen cycling. Results from our coupled model show that, given that direct CO<sub>2</sub> effects are uncertain, (i) average NPP of these northern biomes might decrease under global warming, but (ii) total NPP of the region would increase, due to the northward shift of the taiga biome.

**Key words.** Arctic and boreal ecosystems, climate scenarios, global model, NPP, biome distribution.

## INTRODUCTION

Arctic and sub-Arctic regions are expected to undergo severe changes caused by global warming. In Table 1 a number of ecosystem processes are listed along with their expected positive or negative feedbacks on the carbon exchange between atmosphere and biosphere. Most of these effects are linked to changing biogeochemical processes of plant growth and in the soil, but a strong influence is also expected by the change of patterns of the vegetation distribution.

Ecosystem models for the description of these processes may be built around coarse, gridded, spatially comprehensive data bases of the major driving forces (top-down approach) or on detailed descriptions of typical sites in typical biomes (bottom-up approach). Both approaches use widely differing philosophies and have different advantages. Here we compare examples from both approaches. The patch models used by King, O'Neill & DeAngelis, (1989) have a large number of compartments and fluxes. This requires a detailed description of the parameters, which are only available for intensively studied sites, but with the advantage to achieve congruency between simulated and measured values. With global biogeochemical models the behaviour of a small number of compartments

(e.g. carbon and nitrogen in vegetation and soil, and soil water) and the linked fluxes of carbon, water and nitrogen are described. The obtained results represent the average for each grid cell. The two approaches—global and patch models—can be compared with each other by their mean or total values of NPP or other biogeochemical fluxes.

The influence of climate on vegetation is also described by rule-based models that predict the pattern of vegetation types. The advantage of using them instead of prescribed vegetation maps is that they can be used for the present as well as for past and future climate scenarios. Although they can only predict a vegetation that is in equilibrium with climate one can assess the direction of changing patterns. The coupling of rule-based vegetation structure and biogeochemistry models gives, therefore, a first assessment of the magnitude of the influence of shifting vegetation patterns on the carbon cycle and hence its feedback to climate.

## USING PATCH MODELS TO CALCULATE ACTUAL CARBON EXCHANGE RATES

King *et al.* (1989) used two patch models to describe the carbon exchange between the biosphere and the atmosphere: ABISKO II (Bunnell & Scoullar 1975) for tundra

TABLE 1. Possible impacts of a warming at the northern latitudes.

Impact	Consequences on carbon exchange
Deeper thawing of permafrost soils	Release
Prolonged season for decomposition	Release
Prolonged season for vegetation growth	Uptake
Shift of boreal forests to higher latitudes and replacement of tundra plants by trees	Uptake
Temperature dependence of tundra plant net photosynthesis activity	Negligible
Temperature dependence of tundra microorganism activity	Negligible
Temperature dependence of boreal plant net photosynthesis	Uptake
Temperature dependence of boreal microorganism activity	Release
Enhanced nutrient availability (90% of demanded nitrogen and phosphorous derive from decomposition)	Uptake
Enhanced litter production and decomposition due to enhanced plant growth	Release

TABLE 2. King *et al.* (1987) classes of land area between 64°N and 90°N.

Type	Area ( $\cdot 10^6$ km <sup>2</sup> )	Mean NPP (kg C·m <sup>-2</sup> ·a <sup>-1</sup> )
Tundra	6.13	0.053
Boreal forest	3.14	0.169
Ice, polar desert, rock and sand	1.93	
Grassland	0.09	
Cropland	0.02	
Wetland	0.02	
Shore and hinterland	0.01	

and CONIFER (Coniferous Forest Biome Modelling Group, 1977) for boreal forest. ABISKO II and CONIFER calculate photosynthesis and autotrophic respiration as a function of temperature. Photosynthesis is also a function of irradiance. Soil respiration is a function of soil temperature and soil moisture. CONIFER differentiates the vegetation in a large number of compartments, such as new foliage, old foliage, litter from foliage, litter from wood, litter from logs, etc. The photosynthetic and respiratory fluxes are a sum of separately calculated fluxes.

The values of the driving variables as well as their initial values—twenty-eight for the tundra model and ninety-six for the conifer model—are derived from a Monte Carlo simulation with 100 iterations for each model. The authors assume that this is sufficient to describe the heterogeneity of the total region for each of these biomes. In Table 2 the area sizes of all Arctic and sub-Arctic regions as well as the calculated mean annual net primary production of the taiga and tundra are summarized.

#### USING GLOBAL BIOGEOCHEMICAL MODELS TO CALCULATE ACTUAL CARBON EXCHANGE RATES

The Terrestrial Ecosystem Model (TEM; Melillo *et al.* 1993) is used to estimate the spatial and temporal distribution of major carbon and nitrogen fluxes and pool sizes at a global scale. Spatially referenced information in a 0.5° longitude  $\times$  0.5° latitude grid about climate, soils and veg-

etation is used as input. In the TEM each grid cell is differentiated into five compartments (C in vegetation, N in vegetation, C in soil, organic N in soil, inorganic N in soil) and calculates nine fluxes in monthly time steps (gross primary productivity, plant respiration, C in litter production, soil respiration, N input to ecosystem, N uptake by vegetation, N in litter production, net N mineralization, N lost from the ecosystem). The vegetation specific parameters are calibrated at a few intensively studied field sites.

Gross primary production is a function of photosynthetic active radiation (PAR), leaf phenology (actual leaf area relative to maximum leaf area), temperature, nitrogen availability, atmospheric carbon content and water availability. Both autotrophic and heterotrophic respiration are temperature and pool size dependent. In addition the heterotrophic respiration is a function of moisture. For computational reasons, soil moisture is always set to field capacity, and

TABLE 3. In the TEM four vegetation types are distinguished in the Arctic and Sub-Arctic regions.

Type	Area ( $\cdot 10^6$ km <sup>2</sup> )	Mean NPP (kg C·m <sup>-2</sup> ·a <sup>-1</sup> )
Polar desert and alpine tundra	5.0	0.087
Wet/moist tundra	4.7	0.120
Boreal woodland	6.3	0.173
Boreal forest	12.2	0.238

TABLE 4. In the FBM mainly eight vegetation types are distinguished in the Arctic and sub-Arctic regions.

Type	Area ( $\cdot 10^{-6}$ km <sup>2</sup> )	Mean NPP (kg C·m <sup>-2</sup> ·a <sup>-1</sup> )
Tundra	7.6	0.074
Cold deciduous subalpine/subpolar shrubland, dwarf shrubland	0.5	0.226
Evergreen needleleaved/microphyllous shrubland	0.4	0.283
Cold deciduous woodland	2.3	0.253
Evergreen needleleaved woodland	2.3	0.149
Cold deciduous forest without evergreens	5.5	0.501
Cold deciduous forest with evergreens	7.7	0.422
Temperate/subpolar evergreen needleleaved forest	9.5	0.565

actual evapotranspiration equals potential evapotranspiration in Arctic and sub-Arctic regions. Hence the moisture factor remains constant and differs only between soil types. Table 3 shows the areas and mean annual net primary production at normal climate of the Arctic and sub-Arctic vegetation types as used and calculated in TEM.

With the Frankfurt Biosphere Model (FBM; Lüdeke *et al.*, 1994) the spatial and temporal distribution of major carbon and water fluxes and pool sizes are estimated at a global scale. Spatially referenced information in a  $0.5^\circ$  longitude  $\times$   $0.5^\circ$  latitude grid about climate, soils and vegetation is used. In the FBM each grid cell is differentiated into six compartments (C in short living plant parts (leaves, fine roots), C in long living plant parts (wood, coarse roots), C in soil, water in soil) and eleven fluxes are calculated at a daily time step (gross primary productivity, C allocation to short and long living plant parts, autotrophic respiration of both parts, litter fall of both parts, soil respiration, water input to ecosystem, actual evapotranspiration and runoff). The vegetation specific parameters are calibrated using the average of all grid cells of the same vegetation type.

Gross primary production is a function of photosynthetic active radiation (PAR), leaf area index, temperature and water availability. Both autotrophic and heterotrophic respiration are temperature- and pool size-dependent. The heterotrophic respiration uses also soil moisture as a driving force. The temperature dependence of soil respiration is a function of vegetation type, but there is no difference between boreal forests, woodlands and tundra for this

parameter. Areas and mean annual NPP values for normal climate from the FBM are shown in Table 4.

The Potsdam Land Atmosphere Interaction Model (PLAI) is a coupled model of a biogeochemical part derived from FBM and a structural part derived from BIOME 1.1 (Prentice *et al.*, 1992, 1993). The structural part predicts the distribution of vegetation types. At present there is no feedback from biogeochemistry on structure, but this will be built into future versions of the model. The biogeochemical part calculates exchange rates and compartment sizes comparable to the FBM (preliminary description by Plöchl & Cramer, 1995). Differing from the FBM, PLAI uses the soil texture map developed for BIOME and another concept to calculate actual and potential evapotranspiration and hence the soil moisture. In Table 5 the calculated areas and mean annual net primary production for the Arctic and sub-Arctic biome types are listed.

## CHANGING CLIMATIC CONDITIONS

Doubling the atmospheric CO<sub>2</sub> concentration and the concentrations of other greenhouse gases is likely to result in a changed climate. Several groups have estimated the magnitude of this climate change using transient runs of general circulation models with increasing atmospheric CO<sub>2</sub> concentrations (Hansen *et al.*, 1988 (GISS); Manabe & Wetherald, 1987 (GFDL); Mitchell, 1983 (UKMO); Schlesinger & Zhao, 1989 (OSU); Perlwitz, 1992 (MPI)). In these scenarios a doubling of CO<sub>2</sub> concentrations is assumed. Because the MPI model expresses the increase of the concentrations of other greenhouse gases as an equivalent of the actual CO<sub>2</sub> concentration, it is considered a 3\*CO<sub>2</sub> scenario. For simplicity, however, all future climate scenarios are named 2\*CO<sub>2</sub> scenarios. We have interpolated the anomalies (i.e. the differences between control and enhanced CO<sub>2</sub> concentration runs) for temperature and precipitation and combined them with the observed and gridded long-term means. With these five 2\*CO<sub>2</sub> scenarios we have run the PLAI model to obtain new vegetation type patterns and their related NPP distribution. Melillo *et al.* (1993) use the same OSU, GISS and two GFDL scenarios to calculate NPP changes within the arctic biomes. Lüdeke *et al.* (1995) use the same MPI scenario to calculate NPP changes. Both groups do not consider a shift in vegetation

TABLE 5. With the PLAI model areas and NPPs are calculated for the Arctic and sub-Arctic ecosystems.

Type	Area ( $\cdot 10^6$ km <sup>2</sup> )	Mean NPP (kg C·m <sup>-2</sup> ·a <sup>-1</sup> )
Ice/polar desert	1.6	
Semidesert (cold)	1.3	
Tundra	3.7	0.087
Wooded tundra	2.5	0.136
Northern taiga	2.3	0.482
Cold deciduous forest	2.9	0.222
Boreal forest/taiga	10.2	0.546

TABLE 6. With TEM NPP ( $\text{kg C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) for four  $2^*\text{CO}_2$  scenarios without (\*) and with (†)  $\text{CO}_2$  fertilization effect are calculated for the vegetation types in the Arctic and sub-Arctic regions.

Type	Normal	GFDL 1	GFDL Q	GISS	OSU
Polar desert and alpine tundra*	0.080	0.080	0.080	0.080	0.080
Wet/moist tundra*	0.128	0.149	0.149	0.149	0.149
Boreal woodland*	0.175	0.222	0.206	0.206	0.206
Boreal forest*	0.238	0.211	0.295	0.295	0.287
Polar desert and alpine tundra†	0.100	0.100	0.100	0.100	0.100
Wet/moist tundra†	0.128	0.170	0.149	0.149	0.149
Boreal woodland†	0.175	0.254	0.222	0.222	0.222
Boreal forest†	0.238	0.361	0.328	0.303	0.303

TABLE 7. With the FBM NPPs for the MPI  $3^*\text{CO}_2$  scenario without (\*) and with (†)  $\text{CO}_2$  fertilization effect are calculated.

Type	Mean NPP* ( $\text{kg C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ )	Mean NPP† ( $\text{kg C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ )
Tundra	0.077	0.121
Cold deciduous subalpine/subpolar shrubland, dwarf shrubland	0.228	0.352
Evergreen needleleaved/microphyllous shrubland	0.248	0.370
Cold deciduous woodland	0.243	0.355
Evergreen needleleaved woodland	0.139	0.213
Cold deciduous forest without evergreens	0.365	0.534
Cold deciduous forest with evergreens	0.261	0.436
Temperate/subpolar evergreen needleleaved forest	0.474	0.585

type boundaries and they use different observed present-day climatologies.

Comparing the annual courses of temperature and precipitation at a given location or their averaged courses for fixed areas all  $2^*\text{CO}_2$  scenarios show an increase in temperature as well as in precipitation compared to the long-term means. The maxima of temperature tend to occur in July and those of precipitation in August for normal climate and for the  $2^*\text{CO}_2$  scenarios. The increase of temperature in July may lead to an increased dryness for a major part of the vegetational growth period at northern latitudes.

## RESULTS AND CONCLUSIONS

NPP values from the different simulations and models listed in Tables 2–5 are difficult to compare. The considered regions differ strongly from simulation to simulation and the used ecosystem types do not exactly match. King *et al.* (1987) looked only at the areas north of  $64^\circ\text{N}$ , Melillo *et al.* (1993) and Lüdeke *et al.* (1995) took into account the entire area covered by the considered types; in our simulation runs we regarded all areas north of  $50^\circ\text{N}$ . Nevertheless, the obtained average values for comparable tundra areas are similar to  $53\text{--}87 \text{ g C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ . The boreal forest used by King *et al.* (1987) may be more equivalent with the boreal woodlands of the other models; here the values vary between  $169$  and  $253 \text{ g C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ .

Melillo *et al.* (1993) obtained small increases in mean NPP for the northern biomes when they used  $2^*\text{CO}_2$  cli-

mate scenarios and no  $\text{CO}_2$  fertilization effect. When a fertilization effect was considered, these increases were higher, up to 34% for boreal forests (Table 6). In the tundra the NPP increase is only due to the  $\text{CO}_2$  fertilization effect but not driven by temperature increase. In general, Melillo *et al.* assume that the increased nitrogen availability due to increased litter decomposition is the main reason for the increased NPP.

Neither the FBM nor the PLAI model have incorporated nitrogen cycling, therefore other effects are visible. Increased dryness during summer decreases the NPP, and the increase in temperature increases the autotrophic respiration more than the photosynthesis (Lüdeke *et al.* 1995). Hence, the calculations with FBM for the MPI scenario show a decrease in mean NPPs of the northern biomes if no  $\text{CO}_2$  fertilization effect is considered. A  $\text{CO}_2$  fertilization effect could overcompensate the negative effects of dryness and temperature, and mean NPP increases for the MPI scenario compared to normal climate (Table 7).

Fig. 1A–E shows the biome distributions at northern latitudes as they are calculated with the PLAI model at normal climate as well as for the five  $2^*\text{CO}_2$  scenarios. In Fig. 2A–E the NPP distribution at normal climate and the relative changes in NPP for the five scenarios are shown. In all  $2^*\text{CO}_2$  scenarios *tundra* and *wooded tundra* are reduced to very small areas. They are almost completely replaced by *northern taiga* or *southern taiga*, whereas the *southern taiga* is replaced by *cool mixed* and

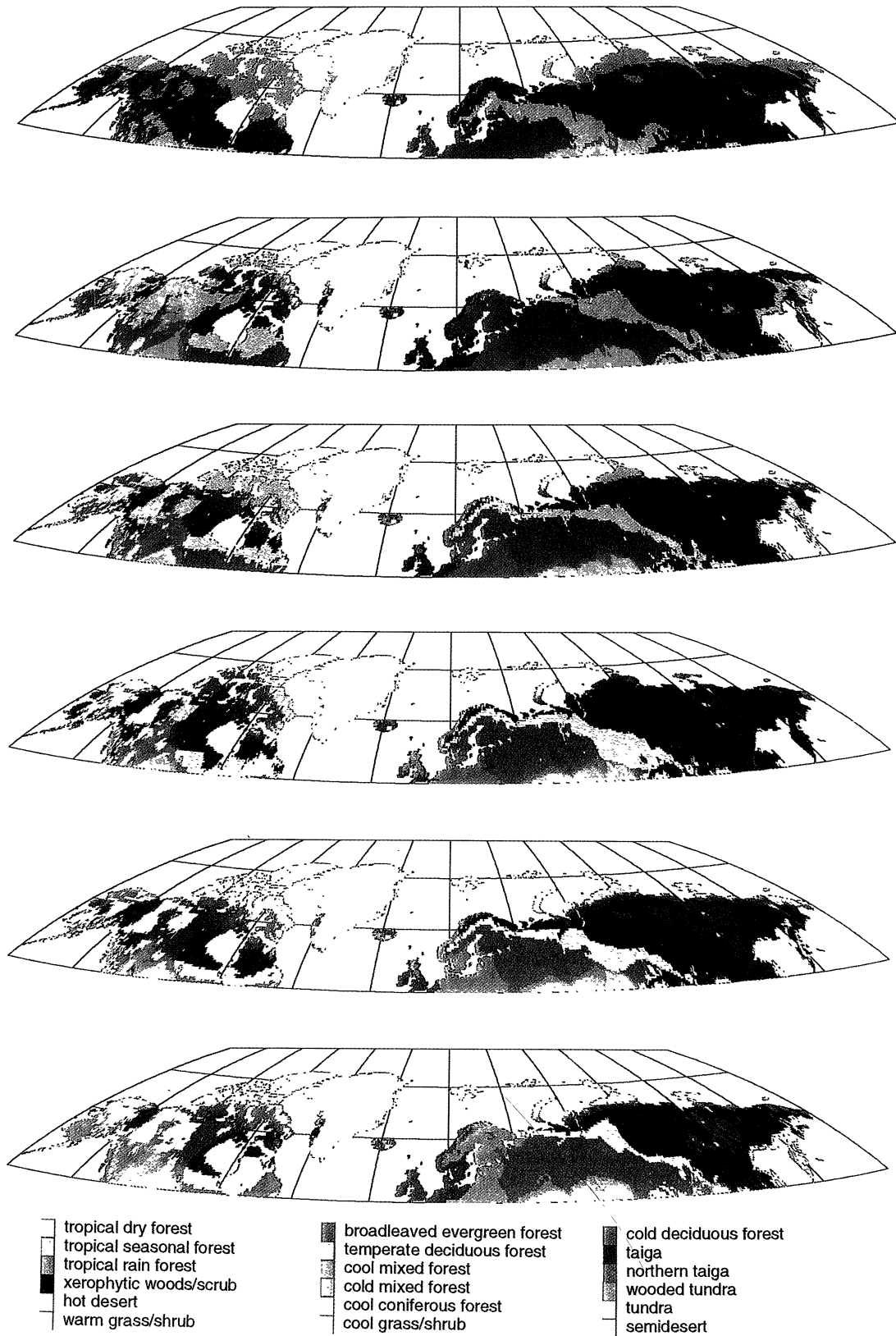


FIG. 1. Geographic pattern of biome types at northern latitudes resulting from calculations with the PLAI model under normal climate (A), GFDL (B), GISS (C), MPI (D), OSU (E) and UKMO (F) climate scenario.

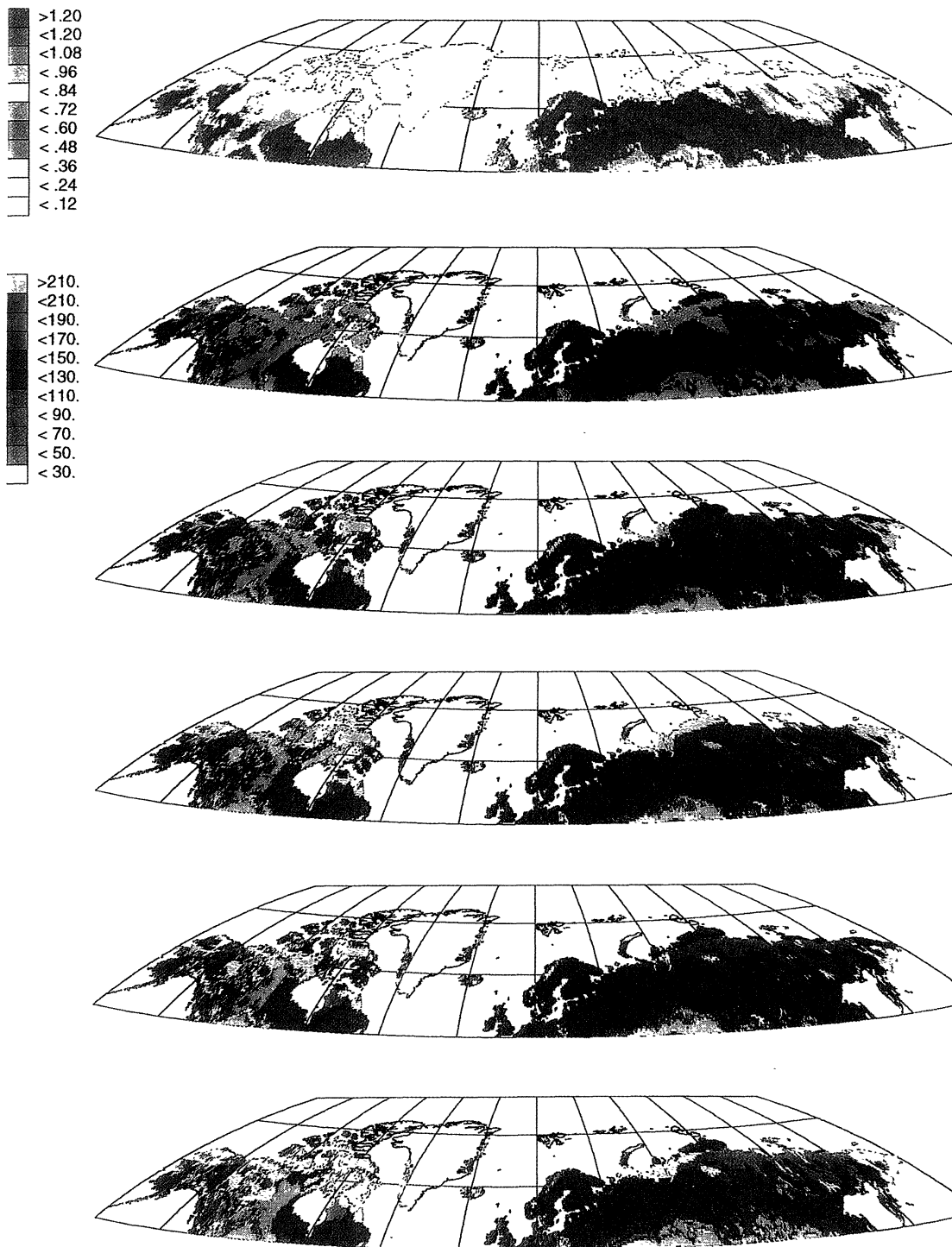


FIG. 2. Geographic pattern of annual NPP (kg C·m<sup>-2</sup>·a<sup>-1</sup>) at northern latitudes resulting from calculations with the PLAI model for normal climate (A), and the geographic pattern of the relative changes in NPP: GFDL (B), GISS (C), MPI (D), OSU (E) and UKMO (F) climate scenario.

*cool coniferous forest*. The area that is covered by *temperate deciduous forest* increases in all 2\*CO<sub>2</sub> scenarios compared to the normal climate (Table 8, Fig. 3). This increase is responsible for the NPP increase for the whole

area of 11.45 Gt C·a<sup>-1</sup> at normal climate to 11.5–12.3 Gt C·a<sup>-1</sup> for the 2\*CO<sub>2</sub> scenarios (Fig. 4). The mean NPP of each biome decreases for the 2\*CO<sub>2</sub> scenarios compared to the normal climate (Table 9). These reductions in mean

TABLE 8. With the PLAI model NPPs ( $\text{kg C}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$ ) are calculated for the five  $2\times\text{CO}_2$  scenarios for the Arctic and sub-Arctic ecosystems north of  $50^\circ$ .

Type	normal	GFDL	GISS	MPI	OSU	UKMO
Ice/polar desert	—	—	—	—	—	—
Semidesert (cold)	—	—	—	—	—	—
Tundra	0.087	0.077	0.068	0.088	0.077	0.068
Wooded tundra	0.136	0.057	0.091	0.061	0.090	0.060
Northern taiga	0.482	0.414	0.404	0.376	0.392	0.373
Boreal forest/taiga	0.546	0.492	0.506	0.481	0.513	0.473
Cold deciduous forest	0.222	0.106	0.148	0.128	0.179	0.122
Cool grass/shrubs	0.292	0.264	0.276	0.200	0.257	0.269
Cool coniferous forest	0.522	0.504	0.521	0.508	0.527	0.485
Cold mixed forest	0.306	0.227	0.276	0.234	0.293	0.247
Cool mixed forest	0.452	0.431	0.458	0.445	0.444	0.416
Temperate deciduous forest	0.625	0.516	0.523	0.485	0.538	0.500
Others	0.092	0.270	0.258	0.131	0.199	0.302

NPP have the same reasons as the decreases of NPP calculated with the FBM. Photosynthesis decreases due to increased dryness, and autotrophic respiration increases due to increased temperature. On the other hand, the shift of vegetation types to more northern latitudes reduces the light availability for each particular biome and, hence, decreases photosynthesis. The decrease in NPP may be compensated if a  $\text{CO}_2$  fertilization effect was considered.

The three approaches using biogeochemical models (global as well as patch) give an impression of the range of carbon (nitrogen and water) fluxes between a large section of the biosphere and the atmosphere. In contrast to the patch model, the global models also provide an image of the geographic pattern. Both model types are based on mechanistic assumptions about the involved biogeochemical processes. The patch models describe them in a more detailed

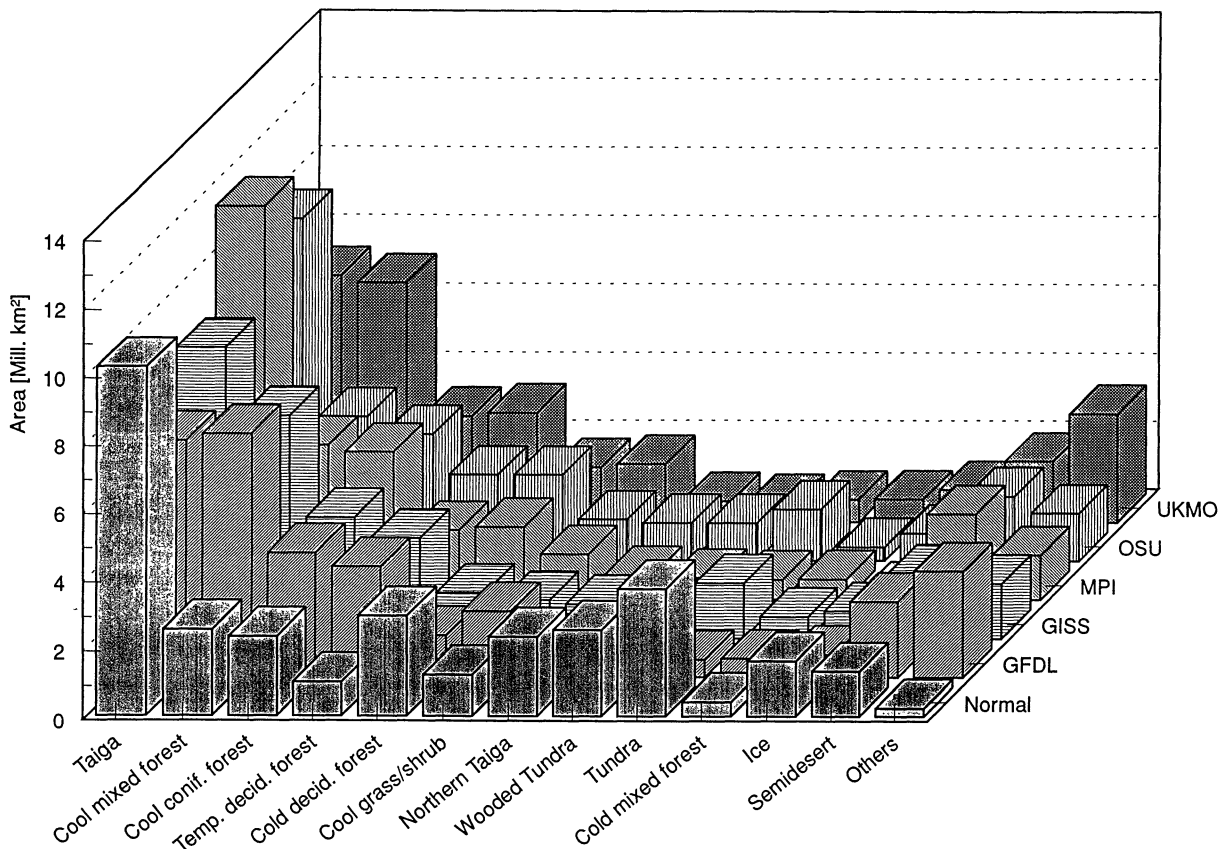


FIG. 3. Areas of biome types at northern latitudes resulting from calculations with the PLAI model for normal climate and five  $2\times\text{CO}_2$  climate scenarios.

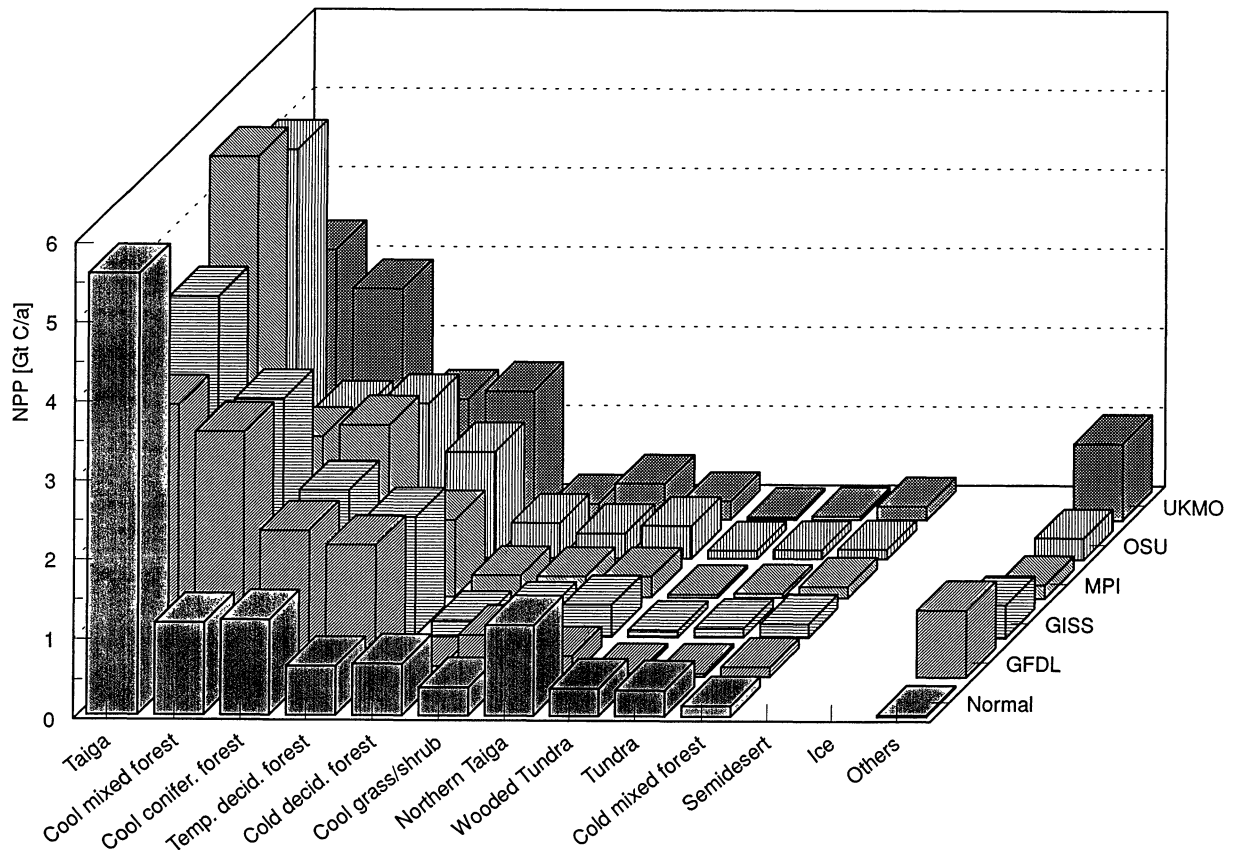


FIG. 4. Annual NPPs of biome types at northern latitudes resulting from calculations with PLAI model for normal climate and for the five  $2^*CO_2$  climate scenarios. The obtained NPP values reflect both the effect of climate and biome redistribution.

way and distinguish between a larger number of compartments than the global models. Therefore the patch models need a large number of driving variables and initial values.

All approaches require prescribed distributions of ecosystem types. Coupling biogeochemical models with rule-based models for ecosystem distribution makes it possible to include effects of climate on ecosystem distribution as well as on NPP directly. The vegetation distribution as well as the carbon flux pattern are, however, only valid if

the vegetation has had the time to reach a new equilibrium with the climate, which is an unrealistic assumption. Using the global models with an age class distribution rather than with climax vegetation, should give a more realistic picture of trace gas fluxes. Developing vegetation, for example, will have a net carbon uptake due to incorporation of carbon in residual tissue. The carbon exchange rate of climax vegetation may or may not be in equilibrium, but the balanced flux between photosynthesis and autotrophic

TABLE 9. With the PLAI model areas ( $\cdot 10^{-6} km^2$ ) are calculated for the five  $2^*CO_2$  scenarios for the Arctic and sub-Arctic ecosystems north of  $50^\circ$ .

Type	Normal	GFDL	GISS	MPI	OSU	UKMO
Ice/polar desert	1.6	0.66	0.79	0.27	0.8	0.95
Semidesert (cold)	1.3	2.2	1.9	2.5	1.9	1.8
Tundra	3.7	0.51	1.6	0.58	1.5	0.66
Wooded tundra	2.5	0.64	0.9	0.59	1.1	0.56
Northern taiga	2.3	0.6	0.99	0.70	1.1	0.61
Boreal forest/taiga	10.2	6.9	8.5	11.5	10.0	7.2
Cold deciduous forest	2.9	1.2	1.3	2.1	2.5	1.6
Cool grass/shrubs	1.2	1.9	1.1	1.3	1.2	1.7
Cool coniferous forest	2.3	3.6	3.5	4.3	3.7	3.1
Cold mixed forest	0.42	0.54	0.63	0.59	0.4	0.67
Cool mixed forest	2.5	7.1	6.5	4.5	4.2	7.0
Temperate deciduous forest	0.98	3.2	2.9	2.0	2.5	3.2
Others	0.24	3.1	1.6	1.3	1.4	3.2

respiration is a basic assumption that only can be made for the equilibrium models.

To cover all the implications listed in Table 1 and to acquire a realistic picture of the consequences of climate change requires a dynamic global vegetation model. Patch models, even if they are dynamic, cannot deliver the global pattern of changes. Present global models, on the other hand, can only describe equilibrium conditions. A dynamic global vegetation model should predict changing biogeochemistry and the change of global vegetation pattern simultaneously. Hence, it has to combine processes with short (plant physiological metabolic processes) and processes with long response times (mortality, migration, etc.).

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## REFERENCES

- Bunyell, F.L. & Scoullar, K.A. (1975) ABISKO II: A computer simulation model of carbon flux in tundra ecosystems. In: Structure and function of tundra ecosystems. *Ecol. Bull.* **20**, 425–448.
- Coniferous Forest Biome Modelling Group (1977) CONIFER: A model of carbon and water flow through a coniferous forest. *Conif. For. Biome Bull.* **8**, 160.
- Hansen, J.E., Fung, I.Y., Lacis, A.A., Rind, D., Lebedeff, S., Ruedy, R., Russell, G. & Stone, P. (1988) Global climate changes as forecast by the Goddard Institute for Space Studies three dimensional model. *J. geophys. Res.* **93**, 9541–9364.
- King, A.W., O'Neill, R.V. & DeAngelis, D.L. (1989) Using ecosystem models to predict regional CO<sub>2</sub> exchange between the atmosphere and the terrestrial biosphere. *Global Biogeochem Cycles* **3**, 337–361.
- Lüdeke, M.K.B., Badeck, F.-W., Otto, R.D., Häger, C., Dönges, S., Kindermann, J., Würth, G., Lang, T., Jäkel, U., Klaudius, A., Ränge, P., Habermehl, S. & Kohlmaier, G.H. (1994) The Frankfurt Biosphere Model (FBM)—a global process oriented model for the seasonal and longterm CO<sub>2</sub> exchange between terrestrial ecosystems and the atmosphere. I. Model description and illustrative results for cold deciduous and boreal forests. *Clim. Res.* **4**, 143–166.
- Lüdeke, M.K.B., Dönges, S., Otto, R.D., Kindermann, J., Badeck, F.-W., Ränge, P., Jäkel, U. & Kohlmaier, G.H. (1995) Responses in NPP and carbon stores of the northern biomes to a CO<sub>2</sub> induced climatic change, as evaluated by the Frankfurt Biosphere Model (FBM). *Tellus*, **47B**, 191–205.
- Manabe, S. & Wetherald, R.T. (1987) Large-scale changes in soil wetness induced by an increase in carbon dioxide. *J. Atmos. Sci.* **44**, 1211–1235.
- Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B. III, Vörösmarty, C.J. & Schloss, A.L. (1993) Global climate change and terrestrial net primary production. *Nature*, **363**, 234–240.
- Mitchell, J.F.B. (1983) The seasonal response of a general circulation model to changes in CO<sub>2</sub> and sea temperatures. *Q.J.R. Meteorol. Soc.* **109**, 113–152.
- Perlwitz, J. (1992) Preliminary results of a global SST anomaly experiment with a T42 GCM. VII General Assembly of the European Geophysical Society Edinburgh, UK, April 6–10, 1992.
- Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.
- Prentice, I.C., Sykes, M.T., Lautenschlager, M., Harrison, S.P., Denissenko, O. & Bartlein, P.J. (1993) Modelling global vegetation patterns and terrestrial carbon storage at the last glacial maximum. *Global Ecol. Biogeogr. Lett.* **3**, 67–76.
- Plöchl, M. & Cramer, W. (1995). Coupling global models of vegetation structure and ecosystem processes—An example from arctic and boreal ecosystems. *Tellus* **47B**, 240–250.
- Schlesinger, M.E. & Zhao, Z.-C. (1989) Seasonal climatic changes induced by doubled CO<sub>2</sub> as simulated by the OSU atmospheric GCM/mixed-layer ocean model. *J. Clim.* **2**, 459–495.