

Coupling global models of vegetation structure and ecosystem processes

An example from Arctic and boreal ecosystems

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ABSTRACT

Many currently available biogeochemical ecosystem process models capture the essential processes of trace gas fluxes between atmosphere and ecosystems, as well as the associated changes in net primary productivity. When used in climate change impact scenarios, one of the most serious limitations of these models is due to the fact that the structure of the ecosystem itself is prescribed from a global data base. Significant shifts of the major biomes of the globe are likely to occur under changed climatic conditions, and, hence, the assumption of stable ecosystem structure could fail. To overcome this problem, we have coupled an ecosystem structure model (BIOME) with a biogeochemical ecosystem process model (the Frankfurt Biosphere Model, FBM). Here we present results for high-latitude ecosystems. The coupled model has an average npp of $343.4 \text{ g C m}^{-2} \text{ a}^{-1}$. The application of the coupled model under a GCM based scenario of changing temperature and precipitation results in major changes of the biome boundaries at these high latitudes. The resulting average npp decreases by 8.8%. If the model is run with changed climate but unchanged biome distribution the average npp decreases by 5.4% only.

1. Introduction

Future trends of a continuing increase in atmospheric CO_2 are likely to cause changes in climate and ecosystem performance. Ecosystems are affected by such changes through changing ambient temperature and moisture availability, and by changes in their ability to use these resources for photosynthesis. There are now numerical simulation models available that describe the major effects of climate on ecosystems. Some models describe the response of major structural characteristics of terrestrial ecosystems to climatic boundary conditions, without reference to the major trace gas fluxes (biome models, e.g., BIOME (Prentice et al., 1992), or its predecessor, developed by E. Box (Box, 1981). Other models

simulate changing uptake and release of carbon and water by ecosystems, and the structure of the ecosystem is a prescribed input variable (biogeochemical ecosystem process models, e.g., the Frankfurt Biosphere Model, FBM (Lüdeke et al., 1994), or the Terrestrial Ecosystem Model, TEM (Melillo et al., 1993). Because much of the current debate about the atmospheric carbon balance is centred around the role of the terrestrial biosphere (Smith et al., 1993), it is desirable to correctly estimate the impact that changing climatic boundary conditions may have on carbon fluxes into and out of the biosphere. This study suggests that an improved performance of biogeochemical process models can be expected, if the initialisation of the ecosystem structural part is improved.

Vegetation maps, either of actual ecosystem complexes (Olson et al., 1983) or potential land cover types (Matthews, 1985) show a more or less

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realistic picture of the structure of the biosphere (Leemans et al., 1995). These maps contain the vegetation and major land use classes of the near past, but they cannot be used to predict the changes in ecosystem structure under changing environmental conditions of the future. Equilibrium models of biosphere structure like the BIOME model (Prentice et al., 1992) predict the potential vegetation of a grid cell based on climatic variables. They reflect no human land use but they can indicate the major directions in potential biome redistribution after climate change. The dynamics of ecosystems under changing boundary conditions are a function of their structure, and this structure may also change due to different biogeochemical processes. Therefore, coupling models of ecosystem structure and of biogeochemical ecosystem processes is a first step of the development towards a dynamic global vegetation model that could describe the transient dynamics of biosphere in a changing world.

The Arctic and boreal regions (especially the border of boreal forest to the Arctic tundra) are likely to be sensitive to climatic change, and they are less influenced by human activities such as cultivation of land or forest management. Therefore, we chose this region as a test case for application of our coupled model. The area of interest for this analysis comprises all areas covered by Arctic or boreal ecosystem types north of 50°N.

2. Model description

The BIOME model (Prentice et al., 1992) is a rule-based model for the fundamental aspects of structure in terrestrial ecosystems. It predicts the global distribution of 14 plant functional types based on a set of climate-derived driving variables, usually with a spatial resolution of 0.5° longitude/latitude. The driving variables act as a filter to predict the plant functional types at the given environmental situation of a grid cell. The plant functional types of the highest, pre-defined dominance value combine with each other to yield the biome type of the grid cell. The model distinguishes 17 biome types. The distribution pattern of the biomes can be predicted for the present time, based on the climate data base of Leemans and Cramer (1991), as well as for future climates basing on GCM scenarios, but always in an equilibrium state.

The Frankfurt Biosphere Model (FBM, (Lüdeke et al., 1994)) is a biogeochemical ecosystem process model. It calculates the exchange fluxes of carbon dioxide and water between atmosphere and biosphere as well as the standing biomasses as a function of climatic input. The gross primary production of vegetation is calculated as a function of temperature, light, soil moisture and atmospheric CO₂, usually with a spatial resolution of 1° longitude/latitude. The C flux from the atmosphere to the biosphere counterbalances the heterotrophic and autotrophic respiration which are also dependent on climatic variables. The fluxes within the vegetation are partitioned to the renewable parts (leaves, fine roots, assimilate storage) and the permanent parts (wood, coarse roots). The litter fall of both vegetation compartments supplies the soil carbon pool. The water fluxes serving as controlling parameters are calculated in parallel. The FBM uses a modified vegetation map of Matthews (1985) for input of ecosystem type and the climate data of Shea (1986).

The validation of global biogeochemical models is extremely difficult, because few data points exist with information about the essential fluxes between the atmosphere and the biosphere. Ecosystem structure models can be compared to existing vegetation maps. The output of the BIOME model fits rather good with the Olson et al. (1983) map of actual vegetation with the major exceptions of agricultural areas (Prentice et al., 1992). The validation of the ecosystem process models can currently not be made by geographical comparison. In the case of FBM several validation possibilities and attempts are discussed by Lüdeke et al. (1994, 1995).

In our coupled model, vegetation zones (biomes) are determined with BIOME. The FBM is then used to calculate the carbon and water fluxes, the standing biomasses and the net primary productivity. It was first necessary to adapt both models to the same data base for long-term mean climate. In this case we used the Cramer et al., climate data* at 0.5° longitude/latitude resolution.

* This database is a greatly modified version of the earlier database by Leemans and Cramer (1991) and will be described in a separate forthcoming publication by Cramer et al.

To analyse how sensitive the combined model reacts on climatic change we use the output of doubled CO₂ transient runs of general circulation models. We present here the results from a test using the data of the GISS runs (Hansen et al., 1988). We use the absolute difference (in the case of temperature) and the ratio (in the case of precipitation), respectively, between the results of the doubled CO₂ scenario and the control run representing the present climate. These anomalies are interpolated to the same grid size and combined with the long-term means of the Cramer et al., data base to obtain scenarios for climate change impact assessments. We compare the results of one scenario with BIOME and FBM driven by the new climate to another scenario where only the biogeochemical part is affected by the doubled CO₂ climate. In the presented calculations we did not consider a CO₂ fertilization effect. The analysis gives us an estimate of the effect of a changed distribution of vegetation types with changed climate although both model parts are still run in an equilibrium mode. Comparing the results of these doubled CO₂ climate scenario calculations may also give some hints about improved parameterization of the component models and the links for feedbacks between the structural and the biogeochemical part.

3. Results

3.1. Comparing the FBM with the coupled model

Using the output of BIOME as input of vegetation structure for FBM requests not only a new

calibration of the free parameters but also a redefinition of the fixed parameters. One possible way is to use the parameters of the most similar Matthews type for its corresponding BIOME type. BIOME and Matthews types as well as the pre-defined and the calibrated parameters are summarized in Tables 1–3. The BIOME types 7 and 8 do not match geographically with particular Matthews types. Therefore, in Table 1, the most similar Matthews types for the predefined parameters are written in brackets.

“Tundra” covers in both vegetation maps nearly the same amount of area but the “tundra” of the BIOME reaches farther north. Consequently, its average npp is 16.2% less than that of the Matthews “tundra” (62 g C m⁻² a⁻¹ versus 74 g C m⁻² a⁻¹). The same is valid for the BIOME type “cold deciduous forest” versus Matthews’ “cold deciduous woodland”. It reaches further north and has a 32% lower average npp, due to the cooler climate. The area of this BIOME type is about 27% larger than that of the Matthews type.

The area of BIOME “taiga” is about 16% larger than the sum of areas covered by the corresponding Matthews types. The average npp is about 1% less than that of the most productive Matthews type 8 and therefore about 15% higher than that of the combined Matthews types. This is due to the fact that the coupled model produces much fewer outliers, i.e., in the Matthews map a large number of grid cells are mapped with a vegetation type that does not fit with the climatic boundary conditions.

The mean npp values of the BIOME types “cool coniferous forest” and “cold mixed forest”

Table 1. Correspondence of BIOME types and Matthews vegetation types

BIOME type	# BT	corresponding Matthews vegetation types	# MVT
Tundra	3	Arctic/alpine tundra, mossy bog	22
Taiga	4	<i>temperate/subpolar evergreen needle-leaved forest</i>	8
		+ evergreen needle-leaved woodland	14
		+ evergreen needle-leaved microphyllous shrubland/thicket	18
		+ cold-deciduous subalpine/subpolar shrubland	20
cold deciduous forest	5	cold-deciduous woodland	16
cool conifer forest	7	(temperate/subpolar evergreen needle-leaved forest)	(8)
cold mixed forest	8	(cold-deciduous forest with evergreen)	(10)
cool mixed forest	9	<i>cold-deciduous forest with evergreen</i>	10
		+ cold-deciduous forest with evergreen	11

Table 2. Prescribed parameter sets for all BIOME types considered in this study

Parameter	BT # 3	BT # 4	BT # 5	BT # 7	BT # 8	BT # 9
GC_{max} [$kg\ m^{-2}$]	0.23	1.62	0.324	1.62	0.252	0.252
RC_{max} [$kg\ m^{-2}$]	0.23	11.88	5.076	11.88	12.348	12.348
SC_{max} [$kg\ m^{-2}$]	19.0	14.0	8.0	14.0	12.0	12.0
NPP [$kg\ m^{-2}\ a^{-1}$]	0.1	0.585	0.36	0.585	0.54	0.54
ResG* [$kg\ m^{-2}\ a^{-1}$]	0.12	0.29	0.18	0.29	0.27	0.27
ResR* [$kg\ m^{-2}\ a^{-1}$]	0.12	0.29	0.18	0.29	0.27	0.27
LpG* [$kg\ m^{-2}\ a^{-1}$]	0.09	0.535	0.259	0.535	0.176	0.176
T_{min} [K]	270.1	270.6	273	270.6	273	273
T_{max} [K]	313.1	311.6	313	311.6	313	313
T_{opt} [K]	288.1	290.6	294	290.6	294	294
k [-]	0.5	0.5	0.5	0.5	0.5	0.5
Φ [$kg\ J^{-1}$]	$2.56 \cdot 10^{-9}$	$2.56 \cdot 10^{-9}$	$2.56 \cdot 10^{-9}$	$2.56 \cdot 10^{-9}$	$2.56 \cdot 10^{-9}$	$2.56 \cdot 10^{-9}$
SLA [$m^2\ kg^{-1}$]	30	12	27	12	40	40
ω [K^{-1}]	0.041	0.0833	0.0833	0.0833	0.0833	0.0833
RG [-]	2	3	3	3	2	2
κ [-]	1.6	1.6	1.6	1.6	1.6	1.6
ξ [$(kg\ m^{-2})^{1/\kappa}$]	2.447	5.49	30.81	5.49	112.04	112.04

GC_{max} RC_{max} SC_{max} Target values for the calibration procedure: maximum short-term and maximum long-term turnover of vegetation carbon, maximum soil carbon, net primary production, mean autotrophic respiration of GC and RC and litter of GC.

T_{min} T_{max} T_{opt} Temperature dependence of net photosynthesis: minimum, maximum and optimum temperature.

k Light absorption coefficient per leaf layer.

Φ Initial quantum yield.

SLA Specific leaf area.

ω Temperature coefficient in the argument of exponential function for autotroph respiration.

RG Soil type with respect to temperature response (after Fung et al. (1987)).

$\kappa\xi$ Parameters determining the allometric relation between GC and RC.

cannot be compared to Matthews types directly. With values of $492.6\ g\ C\ m^{-2}\ a^{-1}$ for BIOME "cool coniferous forest" and $275\ g\ C\ m^{-2}\ a^{-1}$ for BIOME "cold mixed forest" they lie within the range of the expected values. The average npp values and areas of the BIOME type "cool mixed forest" and the Matthews type "cold-deciduous

forest with evergreens" match fairly well (difference of 5%). In Fig. 1 the results of the simulation runs are displayed as area sums of the vegetation types separated in 8 net primary productivity classes. Fig. 2 displays the geographic distribution of the same result.

We conclude that the procedure of using the

Table 3. Parameter sets determined by calibration for all vegetation types considered in this study

	BT # 3	BT # 4	BT # 5	BT # 7	BT # 8	BT # 9
α (C_{AG})	$3.55 \cdot 10^{-8}$	$3.48 \cdot 10^{-8}$	$9.23 \cdot 10^{-8}$	$2.65 \cdot 10^{-8}$	$5.56 \cdot 10^{-8}$	$4.52 \cdot 10^{-8}$
β (C_{GA})	$6.03 \cdot 10^{-13}$	$6.18 \cdot 10^{-19}$	$3.48 \cdot 10^{-18}$	$4.41 \cdot 10^{-19}$	$3.44 \cdot 10^{-18}$	$2.66 \cdot 10^{-18}$
γ (C_{RA})	$3.42 \cdot 10^{-13}$	$8.07 \cdot 10^{-20}$	$1.37 \cdot 10^{-19}$	$5.84 \cdot 10^{-20}$	$4.89 \cdot 10^{-20}$	$3.93 \cdot 10^{-20}$
δ (C_{RS})	$1.01 \cdot 10^{-4}$	$1.16 \cdot 10^{-4}$	$5.46 \cdot 10^{-5}$	$1.16 \cdot 10^{-5}$	$8.13 \cdot 10^{-5}$	$8.12 \cdot 10^{-5}$
ε^* (C_{GS})	—	$9.68 \cdot 10^{-4}$	—	$9.68 \cdot 10^{-4}$	—	—
η (C_{SA})	$3.38 \cdot 10^{-5}$	$1.55 \cdot 10^{-4}$	$2.11 \cdot 10^{-4}$	$1.19 \cdot 10^{-4}$	$8.08 \cdot 10^{-5}$	$6.53 \cdot 10^{-5}$

All fluxes are donor controlled. The greek letters denote the calibrated rate coefficients [s^{-1}]. In brackets are the corresponding fluxes; C_{XY} means flux from compartment X to Y, with A for AC, G for GC and S for SC.

* Continuous litter production rate coefficient, only for evergreen vegetation types.

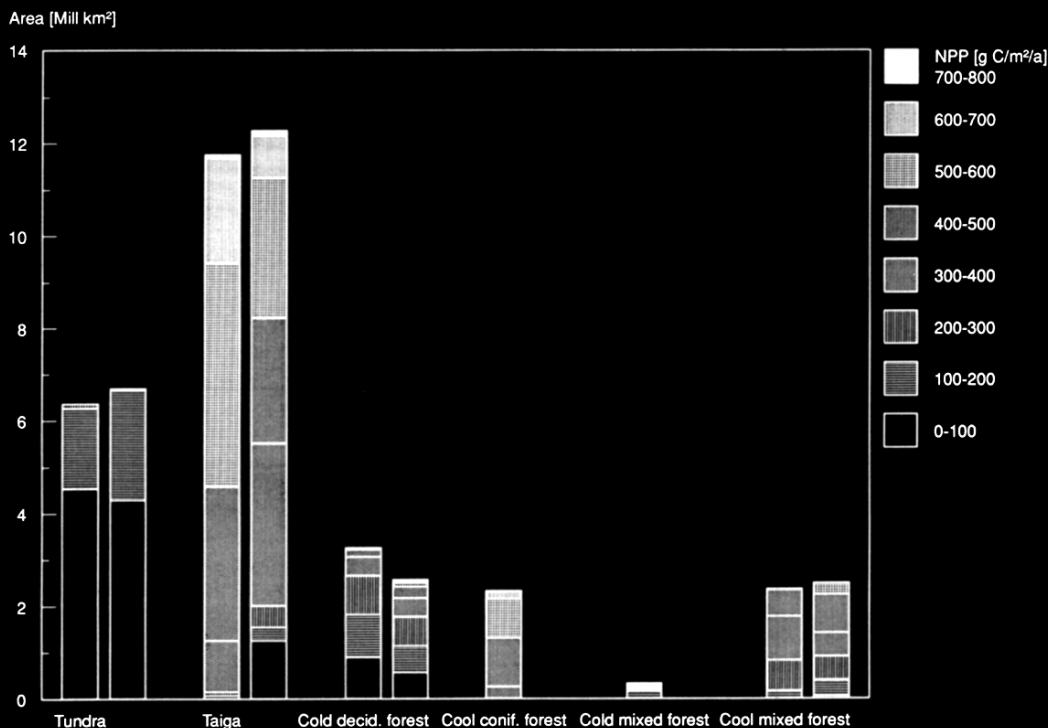


Fig. 1. Comparison of the net primary productivity (npp) areas of northern ecosystem types for the original FBM (right column) and for the coupled model (left column) at current climate, classified into 8 npp classes from 0 to 800 g C m⁻² a⁻¹. Matthews vegetation types are assigned to biome types according to Table 1.

fixed parameters of the nearest corresponding Matthews types leads to acceptable results of the coupled model. The average value of net primary production is with 343.4 g C m⁻² a⁻¹ about 6% higher than that of the original FBM.

3.2. Comparison of coupled model analyses under a warmer climate

The effect of a changed climate is demonstrated by two model runs. Both use climate data that are predicted for doubled CO₂ by GISS (Hansen et al., 1988). The first analysis assumes biome distributions as they are predicted for present climate and productivity simulations for the GISS climate. The second analysis uses also the biome distribution predicted by the GISS climate.

If the biome distribution is not affected by climate change, only the low productive biome types "tundra" and "cold deciduous forest" increase their mean npp, for "tundra" from 62 to 72.6 g C m⁻² a⁻¹ (17%) and for "cold deciduous

forest" from 178.3 to 191 g C m⁻² a⁻¹ (7%). Within all other biomes the npp decreases, strongest with 17% and 24% in "cool conifer" and "cold mixed forest". Total average npp decreases by 5.4% from 343.4 to 324.9 g C m⁻² a⁻¹. Using the biome distribution as it would occur at equilibrium after a climate change, there is an even stronger decrease in npp (to 313.3 g C m⁻² a⁻¹, i.e., 8.8% less).

Although the whole area of the considered biomes north of 50°N decreases only by 4.7%, there are large shifts of the boundaries of the different biomes. "Tundra" is shifted north and its area decreases by 59.9% and is mostly replaced by "taiga". "Taiga" also replaces large parts of "cold deciduous forest", its area decreases by 74.5%. The "taiga" itself is slightly reduced in area (by 12.9%), and is now located far north than at current climate. "Cold mixed forest" occupies under current climate with 0.33 · 10⁶ km² only a small area and is reduced at double CO₂ climate to

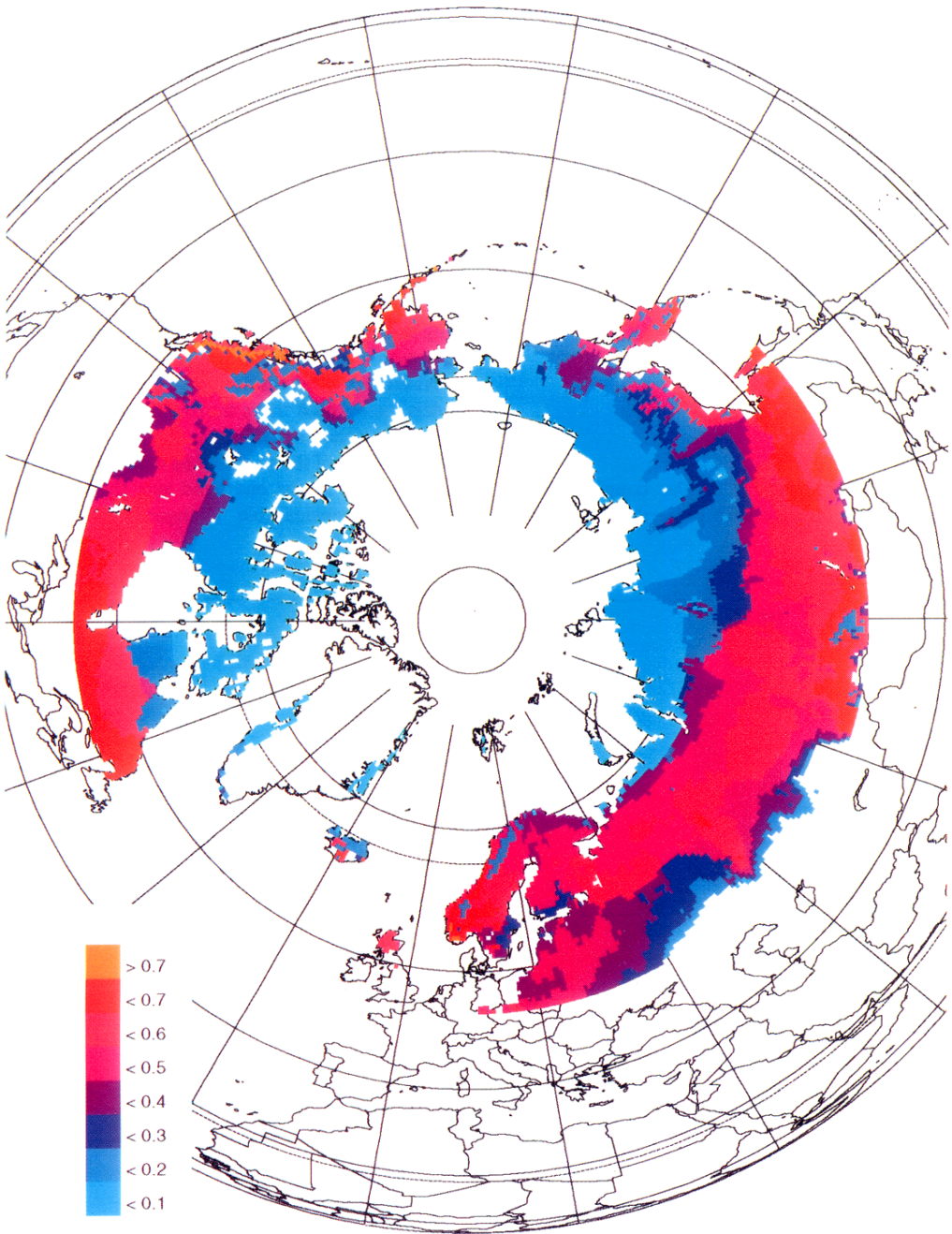


Fig. 2. Geographic pattern of npp in classes from 0 to $0.8 \text{ kg C m}^{-2} \text{a}^{-1}$ of Northern ecosystems (shown only north of 50°N), derived from the coupled model.

Tellus 47B (1995), 1/2

its half. The former "taiga" area is covered by "cool conifer forest" that increases its area by 65% to $3.84 \cdot 10^6 \text{ km}^2$. The largest part of the area (30%) is occupied at double CO_2 climate by "cool mixed forest". It increases its area by 219% to $7.56 \cdot 10^6 \text{ km}^2$.

The mean npp of all biomes except that of the "cold mixed forest" decrease (Fig. 3). The area in the lowest npp class ($0\text{--}100 \text{ g C m}^{-2} \text{ a}^{-1}$) increases for most biomes, i.e., the system does not reach equilibrium in many Northern grid cells, and they have only very small values of both biomass and npp. Fig. 4 shows the geographic pattern of npp change from both simulations compared to current climate.

4. Discussion

The increase in npp of the coupled model, compared to the one with prescribed vegetation,

has two implications. First, there is no longer a discrepancy between the type of ecosystems prescribed by the map and the range of ecosystems that can occur in a given climatic situation. Previously, such discrepancies could occur due to errors in the vegetation map, or due to specific local situations not covered by the climate data base. They could also be due to local disturbances or land use. In the majority of these cases, the coupled model should give more consistent results than the original one because it describes a climate-driven system only. Second, the coupled model generally results in a large fraction of land being assigned higher productivity classes than the vegetation map. This could be a hint to the need of a revised parameterization of either of the two models, based on a more thorough analysis of the ecosystems concerned.

The analysis of the simulations with double CO_2 climate yields on the one hand side the expected result that considerable changes might occur

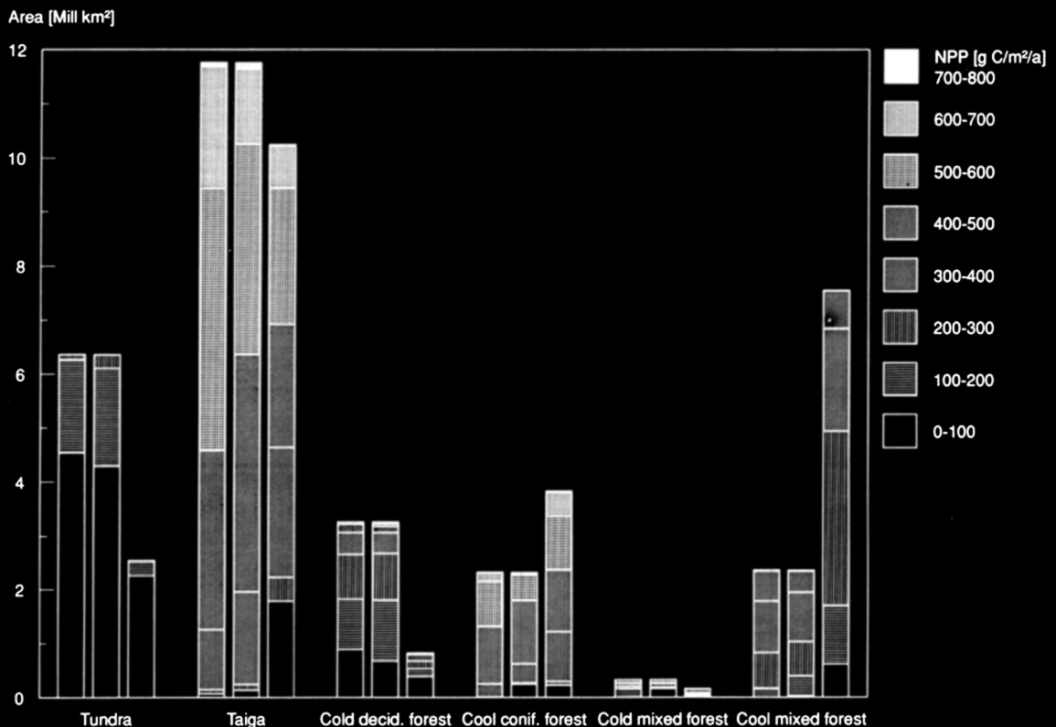


Fig. 3. Comparison of the npp area sums from the coupled model. Left column: current climate, middle column: vegetation structure derived from current climate, C fluxes derived from GISS anomaly climate, right column: both structure and fluxes derived from GISS anomaly climate.

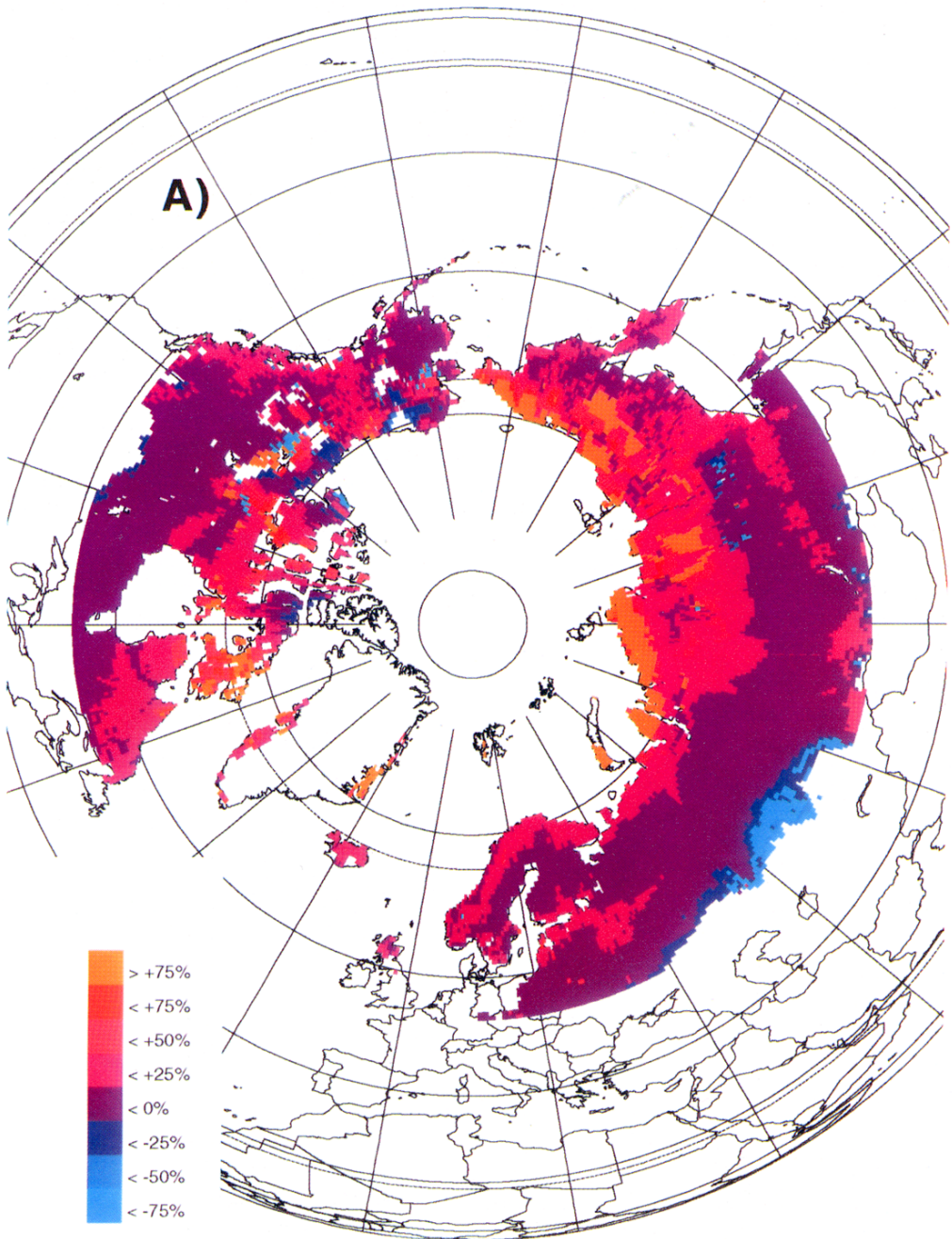


Fig. 4. Difference (percent) in net primary productivity for a double CO_2 scenario, derived from the GISS general circulation model, compared to current climate. (A) Vegetation structure derived from current climate, C fluxes derived from GISS anomaly climate. (B) Both structure and fluxes derived from GISS anomaly climate.

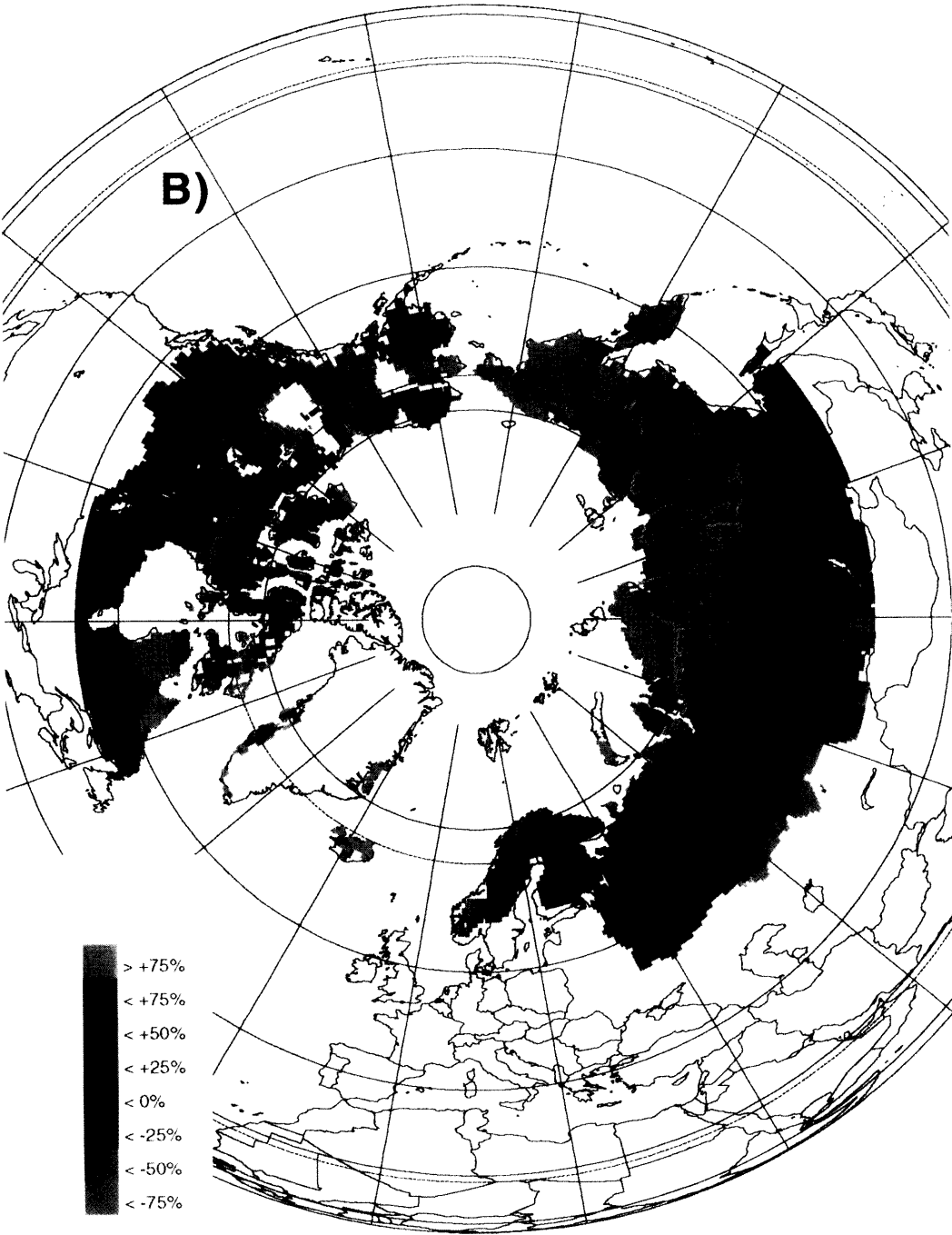


Fig. 4. (cont'd)

within the "tundra" and "taiga" regions. Both biomes are shifted to the north and are reduced to smaller areas.

Both with and without biome boundary shift, the model predicts that npp decreases for the equilibrium situation. The decrease of npp without biome boundary shift corresponds with the results of Lüdeke et al. (1995), who did a similar simulation but using another changed climate scenario. They also obtained small changes for the most Northern biome types, but a large decrease in Matthews types 8, 10 and 11. Melillo et al. (1993) received the opposite results. They used TEM with four different $2 \times \text{CO}_2$ climate scenarios and obtained an increase of npp for the boreal forest of 20 to 31%. In their study, however, the boreal forest is more south than the BIOME "taiga". Melillo et al. (1993) conclude that this increase is due to an increased nitrogen availability as a function of increased temperature. This feature is not built into the current FBM nor into the coupled model.

The decrease in npp of the simulation run without biome boundary shifts has two possible reasons. (i) The FBM reacts very sensitive on water availability and the climate scenario has a warmer and drier summer. (ii) The increased temperatures increase the autotrophic respiration more than the photosynthesis.

The decrease of npp of the scenario affecting both biome boundaries and physiological processes is rather unexpected. One would assume that the biomes in their new climatic equilibrium areas would be as productive as in their previous range. Most biomes, however, were shifted north to more unfavourable light conditions and hence, were less productive in average. Also, the total area of this scenario is smaller than that of the current climate calculations. From the fact that many grid cells of all biome types are in the lowest productivity class two future actions are requested. (i) The parameterization of an improved ecosystem struc-

ture model should be revised or extended to limit the occurrence of biomes at unfavourable light conditions. (ii) The parameterization of the boreal biome types within the biogeochemical part should be reassessed.

For these calculations, we did not consider the possibility of a CO_2 fertilization effect. Melillo et al. (1993) as well as Lüdeke et al. (1995) showed that the increased atmospheric CO_2 content could increase the npp of boreal vegetation types. Lüdeke et al. (1995) also showed that the CO_2 fertilization effect could overcompensate the decrease of npp due to water stress or increased autotrophic respiration.

In contrast to the presented equilibrium calculations, one can expect that during a transient change from current to future vegetation, productivity might increase (temporarily), due to intensive growth in early successional stages. This could contribute to the high latitudes acting as a carbon sink. On the other hand, melting of permafrost might induce mineralization of soil carbon compounds and release of methane or CO_2 . This indicates that a dynamic global vegetation model is required to estimate the medium term carbon balance in a changing global environment.

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REFERENCES

- Box, E. O. 1981. *Macroclimate and plant forms: an introduction to predictive modeling in phytogeography*. The Hague: Dr. W. Junk Publishers, 258 pp.
- Hansen, J. E., Fung, I. Y., Lacis, A. A., Rind, D., Lebedeff, S., Ruedy, R., Russell, G. and Stone, P. 1988. Global climate changes as forecast by the Goddard Institute for Space Studies three dimensional model. *J. Geophys. Res.* **93** (D8), 9541-9364.
- Leemans, R. and Cramer, W. 1991. *The IIASA database for mean monthly values of temperature, precipitation*

- and cloudiness of a global terrestrial grid. International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria. (RR-91-18).
- Leemans, R., Cramer, W. and Van Minnen, J. G. 1995. Prediction of global biome distribution using bioclimatic equilibrium models. In: Melillo, J. M. and Breymeyer, A. (eds.): *C cycling in grassland and forested ecosystems*. New York: SCOPE, John Wiley and Sons.
- Lüdeke, M. K. B., Badeck, F.-W., Otto, R. D., Häger, C., Dönges, S., Kindermann, J., Würth, G., Lang, T., Jäkel, U., Klaudius, A., Ramge, P., Habermehl, S. and Kohlmaier, G. H. 1994. The Frankfurt biosphere model. A global process oriented model for the seasonal and long-term CO₂ 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., Ramge, P., Jäkel, U. and Kohlmaier, G. H. 1995. Responses in npp and carbon stores of the Northern biomes to a CO₂-induced climatic change, as evaluated by the Frankfurt Biosphere Model (FBM). *Tellus* **47B**, 191–205.
- Matthews, E. 1985. *Atlas of archived vegetation, land-use and seasonal albedo data sets*. Goddard Institute for Space Studies. NASA Technical Memorandum.
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore III, B., Vörösmarty, C. J. and Schloss, A. L. 1993. Global climate change and terrestrial net primary production. *Nature* **363**, 234–240.
- Olson, J., Watts, J. A. and Allison, L. J. 1983. Carbon in live vegetation of major world ecosystems. Oak Ridge National Laboratory (ORNL-5862).
- Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A. and Solomon, A. M. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. *J. Biogeogr.* **19**, 117–134.
- Shea, D. J. 1986. Climatological Atlas: 1950–1979. *Surface air temperature, precipitation, sea-level pressure, and sea-surface temperature (45°S–90°N)*. National Center for Atmospheric Research, Boulder, Colorado, USA. NCAR Technical Note.
- Smith, T. M., Cramer, W., Dixon, R. K., Leemans, R., Neilson, R. P. and Solomon, A. M. 1993. The global terrestrial carbon cycle. *Wat. Air and Soil Poll.* **70**, 19–37.