1998

Analyzing climatic and human influences on global terrestrial productivity

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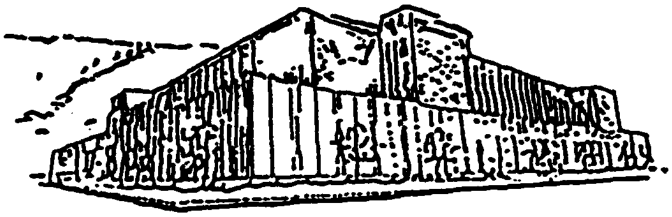

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ANALYZING CLIMATIC AND HUMAN INFLUENCES ON GLOBAL TERRESTRIAL PRODUCTIVITY

by Galina Churkina

M.S., Moscow State University, Moscow, Russia, 1990

presented in partial fulfillment of requirements

for the degree of Doctor of Philosophy

The University of Montana

1998

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10-1-98

Date

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Churkina, Galina, Ph. D., August 1998 Forestry

Analyzing climatic and human influences on global terrestrial productivity

Director: Steven W. Running

The objective of my dissertation is to evaluate climatic and human influences on global NPP. In the first part of my study, I evaluated the different approaches used in global terrestrial biospheric models to introduce water budget limitations on NPP and tested the assumption that moisture availability is a primary driver of the NPP estimated by the current global models. Three methods to restrict NPP by water availability were distinguished; 1) physiological control on evapotranspiration through canopy conductance; 2) supply/demand constraints on ecosystem productivity; 3) water limitation inferred from satellite data. A water balance coefficient, calculated as the difference of mean annual precipitation and potential evapotranspiration, has been compared to NPP for each grid cell in each of fourteen models. While correlation plots revealed similar boundary lines for most global models, there was high variability in these distributions related to other environmental controls on NPP.

In the second part. I assessed relative importance of climatic controls (temperature, water availability, and radiation) in limiting NPP in the array of climatic combinations found globally. The degree of limitation on NPP by climatic controls was defined using an empirical membership function. Results showed that temperature or water availability limited NPP over larger land areas (31% and 52% respectively) than did radiation limitation (5%). Climatic controls appeared to be important in limiting productivity in most vegetation biomes, except for evergreen broadleaf forests. There were areas of the globe (12%) where none of the climatic factors appeared to limit NPP.

In the third part. measurements of extracted timber and modeled forest productivity were used to investigate the relationship between harvested timber and natural forest productivity for current conditions, under doubled CO_2, and climate change scenario. The analysis was confined to coniferous forests and countries that have coniferous forests within their territories. The results of this study suggested that global coniferous forests currently produce more wood than people consume, but this gap would narrow in the future. Wood extraction may reach forest regrowth by the middle of the next century, even though most coniferous forests are located in high latitudes and would have an accelerated stem growth associated with the joint effect of climate change and elevated carbon dioxide concentration in the atmosphere.

Acknowledgements

I would like to thank my major academic advisor, Prof. Steven Running for all the guidance, support, and encouragement he has provided to me over the years since I first came to Montana. I am also very grateful to my committee members, Prof. Paul Alaback, Prof. Carol Brewer, Prof. Rama Nemani, and Prof. Lloyd Quenn for good discussions, helpful advises, and detailed editorial comments on the previous draft of the manuscript. I thank my colleagues and friends, Mike White, Dr. Peter Thornton, Alisa Keyser, Dr. Soizik Laguette, Joe Glassy, Petr Votava, Dr. John Kimball, Pat Andrews, Dr. Kathy Hibbard, Urszula Choromanska, Geoffrey Pool, Renee and Ernst Lundberg, for their useful advises and help. For the technical and administrative support, I thank Saxon Holbrook, Youngee Cho, and Amy Burgess. I have very special thanks to Dr. Detlef Sprinz for encouragements, good advises, and patience in waiting for me to come back to Germany. I am very grateful to my parents Dr. Ludmila Churkina and Dr. Ernst Churkin for setting me out on such a rewarding path. I also thank my parents and my brother Vladimir Churkin for their belief in my success and great moral support from very far away.

The funding for my research was provided from NASA grant.

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Chapter 1

Introduction

Net primary productivity (NPP) represents the greatest annual carbon flux from the atmosphere to the biosphere, and is an important component of seasonal fluctuations in atmospheric CO_2 concentrations, as well as the most critical biotic component of the global carbon cycle. NPP measures products of major economic and social importance such as crop yield and forest production. The mechanisms controlling NPP are complex and not limited to the natural drivers only. Spatial climatic variability dominates large-scale patterns of NPP, which are subsequently modified by soils, plant characteristics, and natural disturbances. People further alter those patterns (use of fertilizers, irrigation, plantations, etc.) while attempting to match the productive capacity of vegetation with their demand for vegetation products.

It is the objective of my dissertation to evaluate climatic and human influences on global NPP. Specifically, I looked at some related questions. Is water availability the primary limiting factor in the recent generation of global terrestrial models? What is the relative importance of climatic controls on global NPP? Can global NPP patterns be explained by climatic influence only? What share of global forest NPP do humans appropriate? Will timber harvest exceed the level available from forest on a sustainable basis?

Review of research problems investigated in Chapter 2

In this chapter, I test the assumption that water availability is the primary limiting factor of NPP in global terrestrial biospheric models. A water balance coefficient (WBC), calculated as the difference between mean annual precipitation and potential evapotranspiration, is compared to NPP for each grid cell (0.5° x 0.5° longitude/latitude) in each of fourteen models. Different approaches to introducing water budget limitations on NPP are evaluated. Three methods to restrict NPP by water availability are distinguished; 1) direct physiological control on evapotranspiration through canopy conductance; 2) climatological computation of supply/demand constraints on ecosystem productivity; and 3) water limitation inferred from satellite data alone.

Review of the research problems investigated in Chapter 3

In this chapter, the biogeochemical model BIOME-BGC is used to simulate global terrestrial NPP and relative importance of climatic controls (temperature, water availability, and radiation) in limiting NPP is assessed in the array of climatic combinations found globally. The degree of limitation on NPP by climatic controls is defined using an empirical membership function. I shall show that, although climate limits NPP over large land areas *none* of the climatic factors appears to limit NPP in some regions of the globe. Other environmental controls such as nutrient availability, disturbance, or biological constraints should then be considered to estimate NPP accurately.

Review of the research problems investigated in Chapter 4

Measurements of extracted timber and modeled forest productivity are used to investigate the relationship between harvested timber and natural forest productivity for current conditions and under a doubled CO_2 and climate change scenario. At this stage, the analysis is confined to coniferous forests and countries that have coniferous forests within their territories. Annual roundwood production from the database of Food and Agriculture Organization (FAO) is used as an approximation of annual timber extraction for each country. Annual stem primary productivity of coniferous forests is estimated using the BIOME-BGC model. Based on the current rates, annual timber extraction is extrapolated for each country for the next 80 years. Then, on a country basis, the timber harvest is related to the modeled forest stem productivity, assuming that the area of coniferous forest would stay unchanged for the next 80 years. Taking into account changing environmental conditions, I shall discuss the natural capacity of coniferous forests to sustain increasing wood extraction by people and attempt to identify countries where wood shortages may occur in the future.

Chapter 2

COMPARING GLOBAL MODELS OF TERRESTRIAL NET PRIMARY PRODUCTIVITY (NPP): THE IMPORTANCE OF WATER AVAILABILITY[1]

Introduction

Net primary production (NPP) is an important quantitative characteristic of the biosphere, since it integrates the greatest annual carbon flux from the atmosphere to the biosphere and is considered to be the main element of seasonal fluctuations in atmospheric CO_2 concentrations (Ciais *et al.* 1995; Keeling *et al.* 1996). The practical importance of NPP estimation is found in its utility to measure crop yield, forest production (Milner *et al.* 1996), and other economically and socially significant products of vegetation growth. Sufficient data have only recently become available, such that NPP can be characterized by something better than an educated guess. At present, NPP receives particular attention in the context of modeling ecosystem parameters at the global scale. Given that neither absolute measures nor direct model validations of global terrestrial NPP are feasible, intercomparison of global NPP models provides an effective tool to check consistency of each model, representations of climatic controls and regional patterns of NPP.

A number of empirical studies suggest that water balance should be a major factor in the NPP pattern for the most of the world's land ecosystems. Rosenzweig (1968)

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[1] Churkina G, Running SW, Schloss A (in press) Comparing global models of terrestrial net primary productivity (NPP): The importance of water availability to primary productivity in global terrestrial models. *Global Change Biology*.

predicted annual aboveground NPP of terrestrial plant communities from actual evapotranspiration (AET) using a single linear equation:

$$log\, NPP = a * log\, AET + b$$

where a and b were constants.

Then, Lieth (1975) determined a curve describing the relationship between mean annual precipitation (P) and NPP of those ecosystems that are not limited by low temperatures:

$$\mathrm{NPP} = a * (1 - \exp(b * P))$$

where a and b were constants.

Later, a water balance formulation, which integrated precipitation input, soil water storage, and atmospheric evaporative demand was found to be the dominant control of leaf area index and NPP in forests of the northwestern United States (Gholz 1982; Grier & Running 1977). Finally, Stephenson (1990) and Neilson *et al.* (1992) illustrated the high correlation between the distribution of North American plant formations and water-balance parameters. Given that these studies, as well as empirical data, strongly suggest that the water balance is the primary driver of variation in NPP, it is interesting to ask if it is also the primary driver in the current generation of global NPP models.

The objectives of this study are to evaluate the different approaches used by modeling groups to introduce water budget limitations on NPP and to test the assumption that moisture availability is a primary driver of the NPP estimated by the current generation of the global models. I first discuss the definitions of actual and potential evapotranspiration and their estimation methods in several global models. This is essential for evaluating approaches introducing water budget limitations on NPP in the next section. Afterwards, I compare the models regarding their time steps and I evaluate the methods for calculating critical water balance parameters such as canopy interception and evaporation, soil moisture, and snowpack. Finally, I analyze the relationship between a water balance coefficient and NPP outputs from the global models.

Materials and methods

Models

Since detailed information about modeling water balance parameters was not available for all models participating in the "Potsdam '95" intercomparison workshop, I confined our study to fourteen models (BIOME-BGC (Hunt *et al.* 1996; Running & Hunt 1993), BIOME-3 (Haxeltine & Prentice 1996), CARAIB (Warnant *et al.* 1994), CASA (Field *et al.* 1995), CENTURY (Parton *et al.* 1993), GLO-PEM (Prince & Goward 1995), (Kohlmaier *et al.* 1997), HRBM (Esser *et al.* 1994), KGBM (Kergoat in press), PLAI (Plöchl & Cramer 1995), SDBM (Knorr & Heimann 1995), SILVAN (Kaduk 1996; Kaduk & Heimann 1996), TEM (Raich *et al.* 1991), and TURC (Ruimy *et al.* 1996)).

Methods for estimating actual and potential evapotranspiration

Potential and actual evapotranspiration (PET, AET) are among the most significant water balance parameters. PET is the amount of evapotranspiration that could occur if the soil of a large area having "vegetation typical of the surroundings" was kept constantly wet (Rosenzweig 1968; Sellers 1965). AET is the amount of water actually entering the atmosphere from soil and vegetation, i.e. evaporation plus transpiration

(Rosenzweig 1968; Sellers 1965). The global NPP models used six methods to calculate PET (Table 1). The Penman-Monteith (Monteith 1973) and Priestley-Taylor (Priestley & Taylor 1972) methods both depend on climatic variables such as temperature and radiation as well as on plant cover type. In contrast, Penman (Penman 1948), Thornthwaite (Thornthwaite 1944; 1948), Jensen-Haise (Jensen & Haise 1963), and Jarvis-McNaughton, which is derived from Penman-Monteith (Jarvis & McNaughton 1986), use climatic parameters only. Calculation of evapotranspiration is based on radiation and temperature in the Jensen-Haise and Jarvis-McNaughton methods, but only on temperature in the Thornthwaite estimation. The Penman and Penman-Monteith approaches also require air humidity data.

Table 1. Methods for estimating potential and actual evapotranspiration (PET and AET) in the fourteen global NPP models[2]

Model	PET	AET
a) canopy conductance control on evapotranspiration		
BIOME-BGC	-	Penman-Monteith (Monteith 1973)
BIOME3	Penman-Monteith (Monteith 1973)	supply/demand (Federer, 1982)
CARAIB	Penman (1948)	f (PET, soil moisture)
KGBM	Penman-Monteith (Monteith 1973)	modified Penman-Monteith (Kergoat, in press)
b) climate supply/demand constraint		
CENTURY	modif. Penman-Monteith (Linacre 1977)	f (PET, live plant biomass, dead plant biomass)
FBM	Thornthwaite (1944, 1948)	f (PET, soil moisture)
PLAI	Priestley-Taylor (1972)	f (PET, soil moisture)
SILVAN	Jarvis-McNaughton (1986)	supply/demand (Federer, 1982)
TEM	Jensen-Haise (1963)	f (PET, soil moisture)
CASA	Thornthwaite (1944, 1948)	f (PET, soil moisture)
SDBM	Jarvis-McNaughton (1986)	supply/demand (Federer, 1982)
HRBM[3]	-	supply/demand (Federer, 1982)
c) moisture limitation inferred from satellite data		
GLO-PEM	-	-
TURC	-	-

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[2] for symbols and abbreviations, cf. Appendix, Table 6.

[3] HRBM calculates monthly AET to redistribute the annual NPP over the 12 months, therefore the estimated AET does not affect annual NPP.

BIOME-BGC and KGBM use the Penman-Monteith method to calculate AET, which allowed the reduction of canopy conductance by plant water stress or soil water limitation. CENTURY calculates AET as a function of PET, live and dead plant biomass. The remainder of the models use either a supply/demand theory by Federer (1982) (BIOME3, HRBM, PLAI, SDBM, SILVAN) or functions of PET reduction through relative soil moisture content (CARAIB, CASA, FBM, TEM) to calculate AET. KGBM and SILVAN distinguish between canopy and soil evaporation, so that estimated AET accounts for the difference in those evaporative processes. Overall, each NPP model's unique method for water budget control on NPP determined the subsequent approach to AET and PET calculation.

Methods for introducing water balance limitation on NPP

The global models introduced water availability restrictions on NPP in one of three ways: 1) direct physiological control on evapotranspiration through canopy conductance; 2) climatological computation of water supply/demand constraints on ecosystem production; 3) water limitation inferred from satellite data alone with no surface climatic data used.

Canopy conductance control on evapotranspiration. The water limitation on NPP through canopy conductance was simulated by BIOME-BGC, BIOME3, CARAIB, and KGBM (Table 2a). Canopy conductance is a complex function of incident radiation, vapor pressure deficit, air temperature, leaf water potential, and leaf area index and, therefore, exerts a significant physiological control over plant productivity. Wellhydrated leaves allow stomata to remain open, facilitating CO_2 uptake and nutrient transport. Decreasing water content in leaf tissue forces stomata to begin closure and the leaf photosynthesis rate to decline. When leaf water potential reaches a threshold value, the stomata close completely and the carbon uptake is halted. With all other factors held constant, an increase in leaf area results in increased canopy conductance, because canopy conductance is the sum of those conductances in different canopy layers working in parallel (Nemani & Running 1989b).

Climatological supply/demand control on ecosystem productivity. CENTURY, FBM, PLAI, SILVAN, TEM, CASA, SDBM, HRBM used a more direct approach to infer moisture restriction on NPP and used scalars describing climatic supply/demand control on ecosystem productivity (Table 2b). The ratio of actual to potential evapotranspiration (AET/PET) was a scalar widely used by the modeling groups. This ratio provides a measure of how much water is evaporated or transpired from a site relative to the evapotranspiration that would occur with an unlimited water supply. In hot and dry environments this ratio may be close to zero, while in cool and rainy climates this ratio can reach one (Aber & Melillo 1991). CASA and SDBM, both satellite-driven models, accounted for water restriction on NPP incorporating both an explicit scalar dependent on AET/PET and an implicit water limitation through a light interception efficiency coefficient. HRBM used the simplest version of climatic supply/demand controls on ecosystem productivity, a factor dependent on soil type which modified NPP obtained from an empirical relationship between annual NPP and mean annual precipitation.

Water limitation inferred from satellite data. TURC and GLO-PEM inferred water availability limitation on NPP entirely from satellite data (Table 2c). Although Garcia (1988) showed that water stress limits the Normalized Difference Vegetation Index (NDVI) using a hand-held radiometer, subsequent research by Nemani and Running (1989a) and Nemani *et al.* (1993) demonstrated a method to estimate surface moisture status at satellite resolutions more accurately using the relationship between NDVI and surface temperature (T_{surf}). For moist environments, T_{surf} provided no distinction between soils and leaves. In dry conditions, green foliage increased NDVI, but decreased T_{surf} because of the increasing amount of evaporated water. TURC incorporated water limitation on NPP solely through a light interception efficiency coefficient derived from NDVI data. GLO-PEM included water restrictions on NPP through a moisture index dependent on NDVI/T_{surf}. In contrast to the other models, GLO-PEM simulations were based on time-specific observations rather than biome means or climatologies.

Table 2. Methods for introducing water limitation (WL) on NPP in fourteen global NPP models[4]

Model	Effect of WL on NPP	WL calculation	Input data
a) canopy conductance control on evapotranspiration			
BIOME-BGC	canopy conductance (soil moisture, VPD)	online	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler 1986) wind speed (constant) air humidity (Friend in press)
BIOME3	canopy conductance (soil moisture, AET)	online	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler 1986)
CARAIB	canopy conductance (soil moisture or relative humidity)	offline	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler 1986) wind speed (ECMWF[5]) air humidity (ECMWF)
KGBM	canopy conductance (soil moisture, VPD)	online	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler 1986) wind speed (constant) humidity (interpolated from NCDC[6])
b) climate supply/demand constraint			
CENTURY	scalar dependent on AET/PET (soil moisture)	online	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler 1986]
FBM	scalar dependent on AET/PET (soil moisture)	offline	T, P (Leemans & Cramer 1991) soil texture (FAO/UNESCO 1977; Zobler 1986)
PLAI	scalar dependent on AET/PET (soil moisture)	offline	T, P, R_s (Leemans & Cramer 1991) soil texture (FAO/UNESCO 1977; Zobler, 1986)
SILVAN	scalar dependent on AET/PET (soil moisture)	online	T, P, R_s (Leemans & Cramer 1991) soil texture (Webb et al. 1992]
TEM	scalar dependent on AET/PET (soil moisture) AET/PET	online offline	T, P, R_s (Leemans & Cramer 1991) soil texture (Zobler, 1986) vegetation, elevation
CASA	scalar dependent on AET/PET (soil moisture) light interception efficiency	offline	T, P (Leemans & Cramer 1991) soil texture (Zobler, 1986) NDVI (AVHRR)
SDBM	scalar dependent on AET/PET (soil moisture) light interception efficiency	offline	T, P, R_s (Leemans & Cramer 1991) soil texture (Webb et al. 1992) NDVI (AVHRR)
HRBM	directly through precipitation, soil factor	online	P (Leemans & Cramer 1991) soil type (FAO/UNESCO 1977)
c) moisture limitation inferred from satellite data			
GLO-PEM	scalar dependent on NDVI/T_{surf}	online	T_{surf} (AVHRR) NDVI (AVHRR)
TURC	light interception efficiency	online	NDVI (AVHRR)

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[4] for symbols and abbreviations, cf. Appendix, Table 6.

[5] data supplied by the European Center for Medium Range Weather Forecast, Reading, UK

[6] data supplied by the National Climatic Data Center

Other hydrologic variables

Time step. Time step length plays a significant role in calculating the water balance and therefore NPP. Although monthly precipitation data provide the average amount of water entering the system, there is no information regarding rain frequency, which varies dramatically between different regions of the globe. Rainwater partitioning includes canopy interception, snowmelt, evaporation, and subsequent throughfall processes represented within a daily time step model. Plants may experience water stress and rehydration all in one month, but these dynamics cannot be shown using monthly time steps. Therefore, using daily time step improves calculation of water related variables.

As summarized in Table 3, the process-based NPP models are capable of determining hydrologic processes such as potential and actual evapotranspiration, interception, runoff, and soil water availability on a daily or even an hourly basis. In this comparison, models required daily climate data inputs either generated weather data stochastically (Friend in press), or interpolated monthly data, or distributed monthly precipitation into "events" using a statistical method (Rastetter *et al.* 1992). As a result, input climate data adjustments influenced models' performances.

Table 3. Time steps for calculating water balance variables by the fourteen global NPP models[7]

	NPP	PET	AET	Int	runoff	SW
a) canopy conductance control on evapotranspiration						
BIOME-BGC	d	-	d	d	d	d
BIOME3	m	d	d	d	d	d
CARAIB	2h	d	d	d	d	d
KGBM	d	d	d	d	d	d
b) climate supply/demand constraint						
CENTURY	m	m	m	m	m	m
FBM	d	d	d	d	d	d
PLAI	d	d	d	d	d	d
SILVAN	6d	d	d	d	d	d
TEM	m	m	m	m	m	d
CASA	m	m	m	m	m	m
SDBM	m	d	d	d	d	d
HRBM	m	-	-	-	-	-
c) moisture limitation inferred from satellite data						
GLO-PEM[8]	m	-	-	-	-	m
TURC	m	-	-	-	-	-

Canopy interception and evaporation. Only seven models treated vegetation canopy interception or evaporation (Table 4). Precipitation, leaf area index (LAI) and vegetation type can be used to estimate canopy interception. To calculate canopy interception, KGBM included all three parameters, whereas BIOME-BGC and CENTURY used precipitation and LAI. CARAIB treated canopy interception as a function of precipitation. Calculation of canopy interception in PLAI was dependent entirely on vegetation type.

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[7] for symbols and abbreviations, cf. Appendix, Table 6.

[8] The temporal resolution of GLO-PEM is dependent upon the temporal resolution of the satellite data used. Monthly satellite data were used for the intercomparison.

Table 4. Methods for canopy interception, evaporation and snow pack treatment in the fourteen global NPP models[9]

Model	Canopy interception	Evaporation of intercepted rain	Snow pack model	Snow transformation to water
a) canopy conductance control on evapotranspiration				
BIOME-BGC	f (P, LAI)	transpiration with zero stomatal conductance	included	f (T, R_s)
BIOME3	-	-	included	f ($T>-2$ °C)
CARAIB	f (P)	interception	included	f (T)
KGBM	f (P, LAI, veg)	transpiration with zero stomatal conductance	-	-
b) climate supply/demand constraint				
CENTURY	f (P, LAI)	interception	included	f ($T>-9$ °C)
FBM	f (P, veg)	-	-	-
PLAI	f (veg)	-	-	-
SILVAN	-	-	-	-
TEM	-	-	included	f ($T>-1$ °C, *elevation 500 m*)
CASA	-	-	included	f ($T>0$ °C)
SDBM	-	-	-	-
HRBM	-	-	-	-
c) moisture limitation inferred from satellite data				
GLO-PEM	included in canopy temperature	-	-	-
TURC	-	-	-	-

Snowpack dynamics. Only liquid water reaching the soil is potentially usable by plants. While snow is precipitation at the time it falls, it is not accessible to plants until it melts. During the winter season, water is not used by plant to grow, despite the considerable amount of precipitation fallen as snow. Snowpack accumulated during the winter presents a potential water storage that will be available to the plant as meltwater in spring and may supply the plant with water even during the summer depending on the original snowpack size and water-holding capacity of the soil. Incorporating snowpack treatment allows NPP models to capture this feature. As summarized in Table 4, the transformation of snow to water was treated differently by the global models. It was

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[9] for symbols and abbreviations, cf. Appendix, Table 6.

dependent upon threshold temperatures (BIOME3, CARAIB, CASA, and CENTURY), or temperature and radiation (BIOME-BGC), or threshold temperatures and site elevation (TEM).

Soil moisture and soil textural controls on vegetation growth. Soils are primary stores for water usable by plants. By definition, the water available to a plant is the total amount of liquid water reaching the soil minus the net change in water stored in the soil. Thus, the water balance cannot be calculated accurately unless the water holding capacity of the soil is considered (Stephenson 1990). All models except TURC accounted for soil moisture in some way (Table 5). Although most of them employed one layer bucket models, BIOME3 defined two and CENTURY simulated six soil layers. Most models with water limitation through canopy conductance included soil textural controls on vegetation growth excluding CARAIB. The models with a supply/demand water limitation included soil moisture in AET calculations, but used simpler soil moisture constraints on vegetation (e.g., available water capacity or field capacity and wilting point were constants). GLO-PEM, a model with moisture limitations from satellite-derived data, used a simple one-layer bucket model in combination with the slope of NDVI/T_{surf} ratio.

Table 5. Methods for soil moisture treatment and soil textural controls on vegetation growth in the fourteen global NPP models[10]

Model	Soil layers	Bucket depth	Rooting depth	Soil texture control on vegetation	FC, WP, AWC
a) canopy conductance control on evapotranspiration					
BIOME-BGC	1	1 m	1 m	SW	FC= f(text, RD) WP= f(veg)
BIOME3	2	0 - 0.5 m 0.5- 1.5 m	f (grass, woody plants)	SW, water percolation rate	AWC= f(text)
CARAIB	1	RD	f (veg, text) 1 - 2 m	-	FC= -33 kPa WP= -1500 kPa
KGBM	1	RD	0.6 m grass 1.2 m (temp.for.) 1.5 m (trop.for.)	SW	AWC= f(text)
b) climate supply/demand constraint					
CENTURY	6	0 - 0.15 m 0.15- 0.3 m 0.3 - 0.45 m 0.45- 0.6 m 0.6 - 0.9 m 0.9 m <	-	SW	FC= -33 kPa WP= -1500 kPa
FBM	1	RD	f (veg, text) <2 m	SW	FC= f(text, RD) WP= f(veg, text, RD)
PLAI	1	1 m	1 m	implicit	FC= f(text, RD) WP= f(veg, text, RD)
SILVAN	1	1 m	≤ 1 m	-	FC= -10 kPa WP= -1500 kPa AWC= f(text)
TEM	1	RD	f (veg, text) 0.5 - 2.5 m	SW, C_{max}, N_{max}	FC= f(text, RD) WP= f(text, RD)
CASA	1	RD	0.5 m (grass, crops, tundra) 1 m (forest)	SW	FC= f(text) WP= f(text)
SDBM	1	RD	≤ 1 m	-	FC= -10 kPa WP= -1500 kPa
HRBM	1	1 m	-	-	AWC= 150 mm
c) moisture limitation inferred from satellite data					
GLO-PEM	1		f (aboveground biomass)	-	-
TURC	-	-	-	-	-

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[10] for symbols and abbreviations, cf. Appendix, Table 6.

Comparison of estimated annual NPP in relation to water availability

Since empirical data suggest that water balance is the primary driver of variation in NPP (Neilson & Marks 1994; Stephenson 1990; Woodward 1987), I test if it is also the primary driver in the current generation of global NPP models and if the models show large differences in the dependence of NPP on water balance. As demonstrated above, there were vast differences in the logic employed by the models to account for water limitation on NPP. A direct comparison of simulated water balances was, therefore, not possible and I had to compare general characteristics of the models.

Methods for the comparison

To compare estimated annual NPP in relation to water availability among global models, I introduced a simple scalar or water balance coefficient (WBC), which differentiated sites with surplus from sites with deficiency of available water. This scalar could be used with all models, regardless of their individual hydrologic computations with the advantage of being independent of any models and reliant on input climate data only. Calculation of a water balance index including AET and runoff was not appropriate in this case, because it required land cover classification and soil texture data to be involved in the calculation and could lead to certain biases in the results associated with different land cover maps used by global models.

The WBC reflecting water availability was defined as the difference between precipitation (P) and potential evapotranspiration (PET):

$$\mathrm{WBC} = P - \mathrm{PET} \qquad (1)$$

Potential evapotranspiration was computed as a function of temperature and radiation from the method by Priestley & Taylor (1972):

$$\lambda\ \mathrm{PET} = \alpha\ [s/(s+\gamma)]\ (\boldsymbol{R}_s + \boldsymbol{G}) \qquad (2)$$

where λ PET is the latent heat flux density, α is the Priestley-Taylor parameter, R_s is the net radiation above the surface, G is the soil heat flux, s is the slope of the saturation vapor pressure-temperature curve at the dry bulb temperature, and γ is the psychrometer constant. I used the Priestley-Taylor method without land cover dependency (with α=1.26 for all vegetation types). R_s was calculated as a proportion of solar radiation and G was a function of temperature.

The global annual water balance coefficient was calculated at each grid cell of 0.5° x 0.5° longitude/latitude (Fig. 1). Global data for mean annual precipitation, temperature, and solar radiation were obtained from the common input data set (Cramer *et al.* submitted).

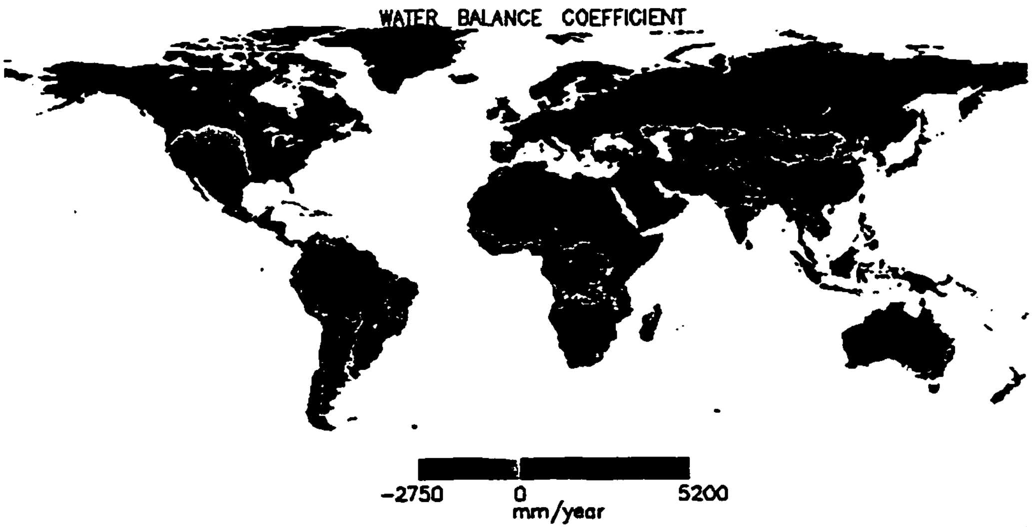

Figure 1. Water balance coefficient (WBC) computed as the difference between annual precipitation and potential evapotranspiration (eq.1). WBC was calculated at each 0.5° x 0.5° longitude/latitude

grid cell. Potential evapotranspiration was computed by Priestley-Taylor method (eq. 2) using the global data set (Cramer *et al.*, in press).

Assuming that water availability was the primary controlling factor of global NPP patterns, I examined if models showed large differences in the dependence of NPP on WBC. In dry regions, gradually increasing water availability facilitates the regular increment of maximum potential vegetation productivity. If an ecosystem receives sufficient water available for plant growth, then moisture does not limit plant productivity and the maximum NPP saturates. When WBC is high, then NPP below maximum reflects control by other climatic variables. For example, although there is plenty of available water in the high latitude ecosystems, low radiation and low temperatures restrict photosynthesis and NPP. In addition, low nutrient content may limit optimum NPP in some areas.

Results and discussion

A comparison of modeled NPP to WBC for all grid cells of the globe (Figs. 2, 3a, 3b, 4) indicates low correlation ($r^2 = 0.05\text{-}0.3$) between these two variables in all models. Nevertheless, a closer examination of these correlation plots reveals some general characteristics of the dependence of WBC on NPP for the models. As WBC becomes more negative, the upper boundary of NPP estimates decreases in all models. It indicates that water is the ultimate limiting factor of NPP in these grid cells. The wide distribution of NPP estimates between zero and the upper boundary implies that secondary factors (temperature, solar radiation, nutrient constraints, etc.) simultaneously limit NPP at these grid cells. Spatial variations in the density of NPP estimates reflect different methods to simulate interaction among environmental controls on NPP used by the global models.

As WBC becomes more positive, NPP estimates of most models reach a maximum of 1500 - 3000 g C m^{-2} yr^{-1} (Figs. 2, 3a, 3b, 4). The high density of NPP estimates at this maximum indicates that the models assume optimal environmental conditions for NPP in some regions (e.g., the wet tropics). Several models have much higher variability in NPP estimates in those regions indicating the importance of secondary factors such as nutrient constraints or land use. Interestingly, half of the models (BIOME3, CARAIB, CASA, FBM, GLO-PEM, SILVAN, and TURC) estimated the maximum NPP in regions with a negative water balance. The other half of the models (BIOME-BGC, CENTURY, HRBM, KGBM, SDBM, TEM, and PLAI) predicted the maximum NPP to occur where the water balance was positive.

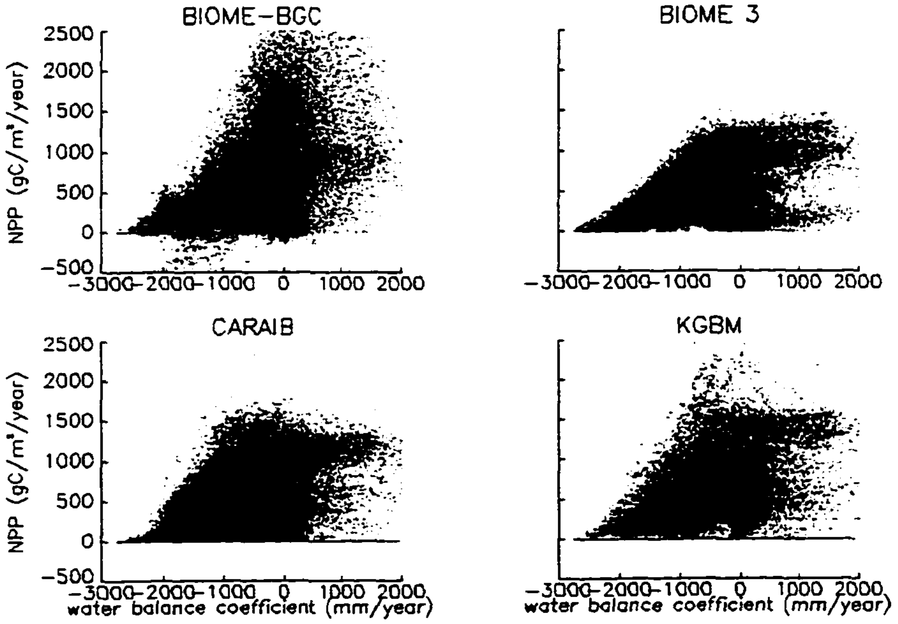

Figure 2. Relationship between estimated NPP and WBC for models with physiological control on evapotranspiration through stomatal control.

A number of reasons can account for the differences in the comparison results discussed above. First, the WBC used for this comparison provided only a general scale of potential water available in an ecosystem. It did not give an absolute measure for water balance, because it was calculated on an annual basis and did not account for precipitation seasonality or the interaction between precipitation seasonality and PET. The model sensitivities to climatic factors, however, can change depending on the temporal scale at which the comparisons are made (Schloss *et al.* in press). Second, to estimate PET, models used methods which differed from the approach in the WBC computation, thus the variations in the relationship of maximum NPP to the WBC may be a result of these differences. Different PET methods may give substantially different PET estimates for the same climate and land cover type, and influence AET and NPP computations. Federer *et al.* (1996) showed that although nine different PET methods agreed in the general magnitude of PET over a range of climates and cover types, differences among methods were hundreds of millimeters per year. Between methods, annual PET varied from about 400 mm at Fairbanks, Alaska to about 1500 mm at Phoenix, Arizona and San Juan, Puerto Rico. Methods dependent on land cover type (e.g. Penman-Monteith and Priestley-Taylor) were suggested as more appropriate for regional or global modeling, because they gave the highest values of transpiration and soil evaporation for wet soils.

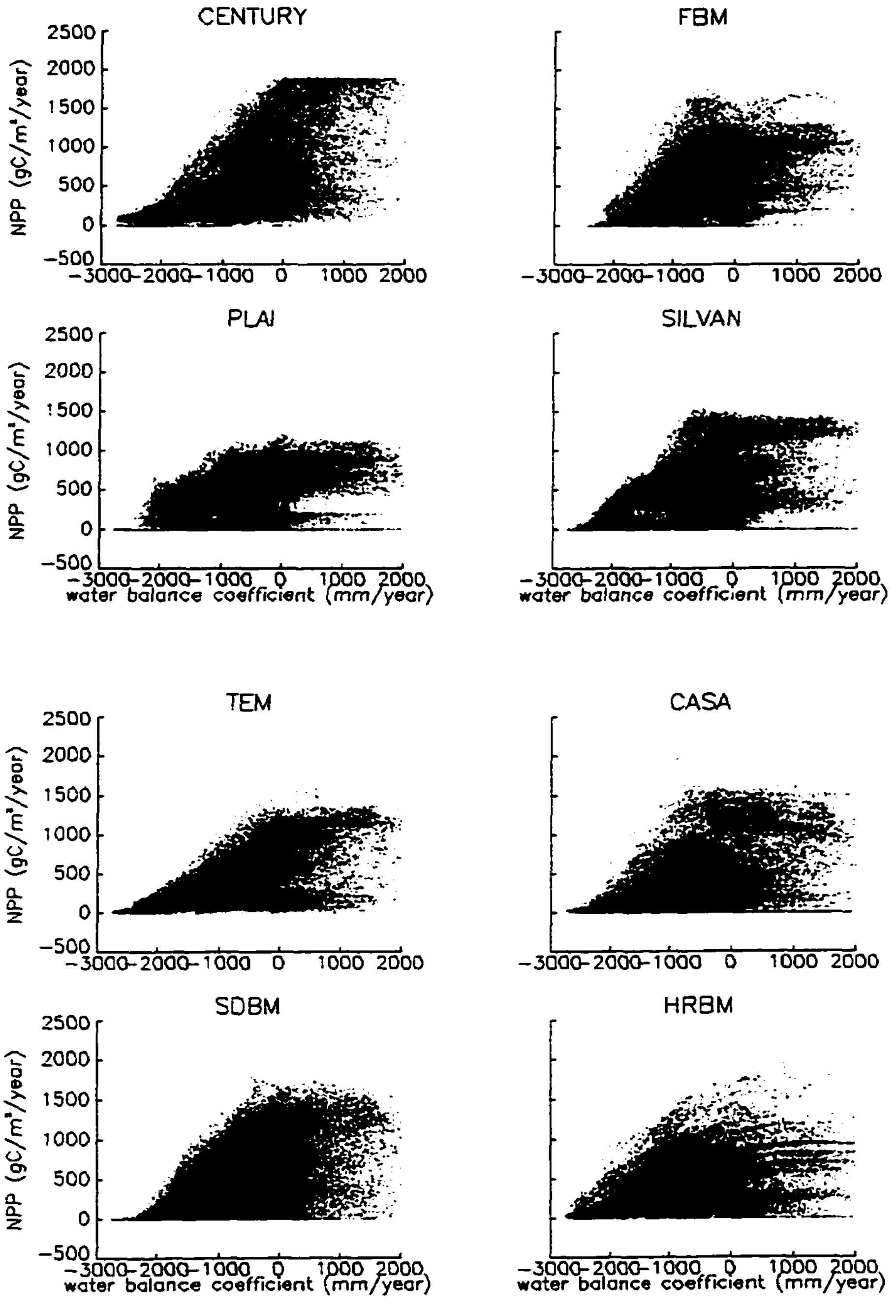

Figure 3 a, b. Relationship between estimated NPP and WBC for models with climatic supply/demand control on ecosystem productivity.

In addition, the methods used to estimate water budget limitation on ecosystem productivity also had a significant effect on the model outputs. Models with physiological controls over evapotranspiration and NPP (Fig. 2) predicted a smooth increase in the range of NPP with the increasing WBC and the slope of the edge of NPP versus WBC was steeper (except BIOME3). It suggests that the deficit of water available to plants set the upper limit on ecosystem productivity. Correlation plots for a few models with the climatic supply/demand control on NPP featured the appearance of concentric lines (Figs. 3a and 3b), which biome or soil types with set productivity limitations could explain. Plots of the relationship between NPP and WBC from the models based on satellite data revealed distinct differences between the two models (Fig. 4). In contrast to TURC, GLO-PEM showed an even distribution of NPP versus water balance coefficient with the monotonic growth of vegetation productivity following the increase in ecosystem water supply. These results suggest that soil moisture status can be more accurately represented by the relationship between NDVI and T_{surf} versus NDVI alone.

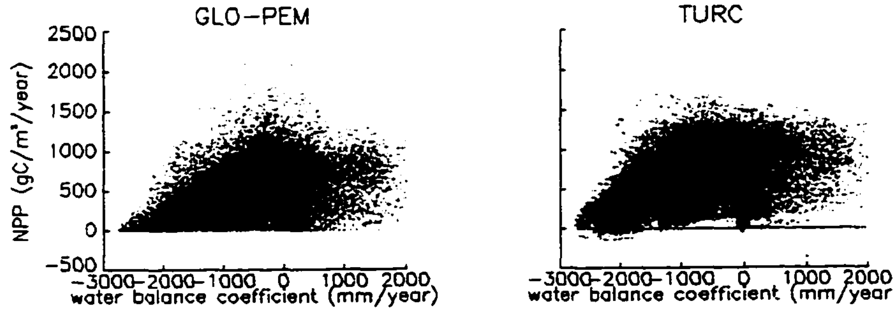

Figure 4. Relationship between estimated NPP and WBC for models with water availability limitation inferred through satellite data.

While water availability may be the most influential variable for NPP, multivariate environmental factors interact and restrain NPP in non-linear and discontinuous ways. Analysis of measured atmospheric carbon dioxide and satellite-derived measurements of temperature and the vegetation index suggested that nutrient effects on the carbon cycle could delay ecosystem response to changing climate by as much as two years (Braswell *et al.* 1997). Vogt *et al.* (1996) attempted to determine what climatic and nutrient variables drove fine root productivity using measured NPP data. They found no significant or consistent patterns for above- and belowground NPP change across the different climatic forest types and by soil order, even though they suggested that nutrient concentration in the forest floor controlled belowground NPP. These studies imply that vegetation productivity is a result of the interaction of several environmental factors and I should *not* expect a generic dependence between a single environmental control and NPP. The strong correlation between NPP and water balance found from empirical data in the earlier studies (Lieth 1975; Rosenzweig 1968) can be attributed to the location of the sampling sites in the water limited parts of the globe. After all, water availability is the dominant constraint on NPP over a larger part of the globe (52%) than any other environmental factor (Churkina & Running 1998).

Conclusions

Reflecting our improved understanding of terrestrial ecosystems, global NPP modeling has evolved from a simple linear regression between NPP and a climate variable to sophisticated simulation of NPP as a result of multiple environmental factor interaction. Consequently, in future model comparison, I should focus more on the methods to simulate these interactions rather than on the influence of a single environmental control on NPP.

To understand better the differences between approaches to account for water limitation on NPP in global models I suggest that the outputs with hydrological parameters (which were not available for this intercomparison) should be developed concurrently with NPP in the future model comparisons. These additional outputs would help to quantify the relationships between NPP and water balance variables as well as to investigate the differences between daily and monthly models (e.g., Schimel *et al.* 1997).

Another important issue is the accurate determination of maximal annual NPP. The simulated maximal NPP values (1500-3000 g C m^{-2} yr^{-1}) do not agree well with the highest measured values (1680-2300 g C m^{-2} yr^{-1}, cf. Ajtay *et al.* 1979; Olson *et al.* 1983). Large discrepancies can arise from the computational method of the areally averaged NPP over 1000-3000 km^2 grid cells, which often represent a mixture of mature and/or disturbed vegetation. Although the delineation of the globe into 0.5° x 0.5° grid cells helps to capture some of the heterogeneity of terrestrial ecosystems, a model which assumes that each grid cell is occupied by a single vegetation type and has a mean climate may subsequently overestimate or underestimate NPP. Models using satellite data may provide more accurate NPP estimates for each grid cell, since they average actual vegetation cover present in the grid cell.

Although roots are primary pathways for water and nutrients uptake by plants, root treatment was greatly simplified in the global models (Table 5) because of the lack of relevant information. A database containing global root biomass and distribution has recently become available (Jackson *et al.* 1996; 1997) and can now be included in the standard input package for the global models. Use of this database could refine NPP estimates (e.g., improve maximal NPP estimates) as well as standardize rooting depth data used by the models, which would simplify future model comparisons.

Appendix

Table 6. Common abbreviations, symbols, and acronyms.

AET	actual evapotranspiration
APAR	absorbed photosynthetically active radiation
AVHRR	Advanced Very High Resolution Radiometer
AWC	available water capacity
C_{max}	Maximum carbon assimilation rate
d (6d)	daily (every six days)
ET	evapotranspiration
FC	field capacity
FPAR	fraction of photosynthetically active radiation absorbed by the canopy
G	soil sensible heat flux
GAIM	Global Analysis, Interpretation and Modeling (IGBP Task Force)
GCM	General Circulation Model
GCTE	Global Change and Terrestrial Ecosystems (IGBP Core Project)
GPP	gross primary productivity (flux)
GVI	Global Vegetation Index
h (2h)	hourly (every two hours)
IGBP	International Geosphere-Biosphere Programme
Int	interception
Nmax	Maximum nitrogen uptake rate
LAI	leaf area index
Leaf-N	nitrogen content of leaves
LUE	light use efficiency
m	monthly
NDVI	Normalised Difference Vegetation Index
NEP	net ecosystem production (annual integral)
NPP	net primary productivity (flux - net primary production refers to the annual integral)
PAR	photosynthetically active radiation at the top of the canopy
PET	potential evapotranspiration
P	precipitation
R_A	autotrophic respiration
RD	rooting depth
R_H	heterotrophic respiration
R_s	solar radiation
Soil C&N	both carbon and nitrogen in soil organic matter
SW	soil water
T	(air) temperature

T_{surf}	surface temperature
text	Soil texture
veg	Vegetation type
Veg C	vegetation carbon (i.e. carbon in leaves, sapwood, heartwood, roots etc.)
Veg N	nitrogen content in leaves and roots
VPD	vapour pressure deficit
WBC	water balance coefficient
WP	wilting point

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Chapter 3

CONTRASTING CLIMATIC CONTROLS ON THE ESTIMATED PRODUCTIVITY OF GLOBAL TERRESTRIAL BIOMES[11]

Introduction

Terrestrial net primary productivity (NPP) represents the greatest annual carbon flux from the atmosphere to the biosphere and is considered to be the main cause of seasonal fluctuations in atmospheric CO_2 concentrations (Ciais *et al.* 1995; Keeling *et al.* 1996). In addition, terrestrial biospheric productivity is critical for the life of humankind and all heterotrophic organisms on Earth because it provides potential food resources and a source of wood for construction, fabrication, and fuel. Population growth and industry, however, have potentially negative effects on biospheric productivity and may reduce it dramatically. Between one-third and one half of the land surface has already been transformed by human action (Vitousek *et al.* 1997). Consequently, estimating global primary productivity and monitoring changes will play an important role in detecting the state of biospheric health.

There are two common experimental ways to estimate NPP: (1) as biomass produced during the growing season (Landsberg & Gower 1997) or (2) as net gas exchange of plants, namely the difference between gross primary production and autotrophic respiration (Baldocchi *et al.* 1996) [gross primary production (net photosynthesis) is the rate of atmospheric carbon fixation by vegetation; autotrophic

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[11] Churkina G, Running SW (1998) Contrasting climatic controls on the estimated productivity of different biomes. *ECOSYSTEMS*, 1, 206-215.

respiration is the rate of carbon return from live vegetation to the atmosphere]. Importantly, NPP should not be confused with net ecosystem production (NEP), which is the difference between net atmospheric carbon fixation by plants (NPP) and heterotrophic respiration. A number of difficulties prohibit precise NPP measurements. Direct measurements of biomass involve the challenge of quantifying belowground processes and measuring large units of biomass in forests. Given that gross primary production and both autotrophic and heterotrophic respiration are occurring simultaneously, it is very difficult to isolate NPP from total gas exchange. In either case, the scale of experimental methods is usually limited to single plants or small plots. Thus, direct measures of NPP at large scales remain problematic, and model-based estimates are essential at global scales.

Many modeling attempts have been made to predict global terrestrial NPP from environmental parameters. First, NPP was estimated empirically from climatic data (Lieth 1975; Rosenzweig 1968). Subsequently, a number of ecosystem process models were developed from theory linking climate, soil properties, and biome specific characteristics to responses in biogeochemical processes of vegetation (Haxeltine & Prentice 1996; Kaduk & Heimann 1996; Knorr & Heimann 1995; Kohlmaier *et al.* 1997; Melillo *et al.* 1993; Parton *et al.* 1993; Running & Hunt 1993; Warnant *et al.* 1994; Woodward *et al.* 1995). A few models have been recently designed to compute global NPP directly from remotely sensed data (Field *et al.* 1995; Prince & Goward 1995; Ruimy *et al.* 1996). Overall, NPP models range in complexity from fairly simple regressions between key climatic variables and one or several biospheric gas fluxes to quasi-mechanistic models which attempt to simulate the biophysical and ecophysiological processes occurring at the plant level. Each approach is based on simplifying assumptions about how ecosystems are structured and how vegetation may respond to changes in various environmental parameters. Consequently, the differences in model performance stem from these various simplifying assumptions.

A comparison of NPP estimated by 17 global biospheric models was conducted at two workshops of the Global Analysis, Interpretation and Modeling (GAIM) activity of the International Geosphere-Biosphere Program (IGBP) (W. Cramer, *submitted*). The comparison used standardized input variables wherever possible. Large differences in sensitivity to precipitation, temperature, and solar radiation were identified among the models, even among those that estimated similar global values of NPP (A.L. Schloss, *submitted*). Systematic biases associated with the fundamental modeling strategy, however, were not found, although the inclusion of nutrient constraints reduced NPP in some regions (D.W. Kicklighter, *in press*). Participants of the Vegetation/Ecosystem Modeling and Analysis Project (VEMAP) compared changes in annual NPP of the continental USA with climate change scenarios and current and altered atmospheric CO_2 concentrations (VEMAP 1995). For the altered CO_2 and climate scenarios, large variability in carbon cycle responses was observed among the biogeochemistry models (e.g. NPP ranged from no response to increase of 40%), despite a common input database (soils, vegetation classification, and climate). This variability was attributed to the different model formulations of the hydrologic and nitrogen cycles. These studies imply that environmental factors controlling NPP influence one another, resulting in broad correlations among those factors. NPP models, including richer suites of controlling parameters, should therefore be more sensitive to conditions that disrupt the broad correlation.

Several studies have analyzed the relative strengths of biotic and abiotic factors in limiting vegetation productivity from very different perspectives. Schimel et al. (1996) demonstrated an "equilibration" of water with nutrient limitation on NPP based on the Century model run under quasi-steady state conditions. Analysis of measured atmospheric carbon dioxide and satellite-derived measurements of temperature and the vegetation index suggested that nutrient effects on the carbon cycle could delay ecosystem response to changing climate by as much as 2 years (Braswell *et al.* 1997). Interestingly, there was also an attempt to determine what climatic and nutrient variables drove fine root productivity using measured NPP data (Vogt *et al.* 1996). The authors of the latter study found no significant or consistent patterns for above- and belowground NPP change across the different climatic forest types and by soil order, even though they suggested that nutrient concentration in the forest floor controlled belowground NPP. The results of all these studies strongly suggest that vegetation productivity is a result of the interaction of several environmental factors, so that I should *not* expect a generic dependence between a single environmental control and NPP from field data.

In this paper, I attempted to quantify the relative fractions of environmental controls exerted on productivity in various biomes. I set the stage by spatially representing climatic controls (temperature, water availability, and radiation) on net primary productivity. Afterwards, I determined areas of the globe where climatic controls on NPP were important and areas where other factors like nutrient availability or biological constraints limited NPP more than climate. Finally, I analyzed relative contributions of temperature and water availability to potential vegetation productivity patterns around the globe and to the productivity of different biomes.

Methods

Modeling NPP

In this study, the ecosystem process model BIOME-BGC (Hunt *et al.* 1996; Running & Hunt 1993) was used to estimate vegetation productivity around the globe. The BIOME-BGC model simulates three vital biogeochemical cycles: carbon, nitrogen, and water within an ecosystem. NPP was calculated in terms of gas exchange, as a difference between gross primary production (GPP) and autotrophic respiration (R_a). GPP and R_a were computed for each grid cell at 0.5°x0.5° spatial resolution. NPP of each grid cell was determined by the difference between these two values. All computations were based on the results of a one-year model run for the whole globe with daily climate; daily climate was stochastically generated from monthly mean climate data obtained from the CLIMATE database (*unpublished manuscript* by Cramer, W.P., M.F. Hutchinson, R. Leemans, and B. Huntley, an improved version of IIASA climate database; (Leemans & Cramer 1991).

The BIOME-BGC model was parameterized for seven structural vegetation biomes (Running *et al.* 1995). The potential vegetation classification used for the model run included deciduous needle leaf and broad leaf forests, evergreen needle leaf and broad leaf forests, shrubs or deserts, and C_3 and C_4 grasslands. This structural vegetation classification was based on a combination of three primary attributes of plant canopy structure: permanence of above-ground biomass (forests versus grasses), leaf longevity (evergreen versus deciduous), and leaf type or shape (broadleaf versus needleleaf).

The BIOME-BGC method for NPP estimation is key to understanding the results of this study. This estimation results from the interactions of numerous environmental controls simulated by the model [as it was mentioned further above, BIOME-BGC computed NPP as the difference between gross primary productivity and autotrophic respiration]. Consequently, climate, nutrient availability, and vegetation type influence NPP through controls on *both* photosynthesis and respiration processes. In BIOME-BGC, the gross photosynthesis limited by climate and nutrients was calculated as:

$$GPP = f(T, VPD, SW, SRAD, CO_2, LAI, LEAFN),$$

where T was the air temperature, VPD was the vapor pressure deficit, SW was the soil water content, $SRAD$ was the solar radiation at the top of canopy, CO_2 was the carbon dioxide concentration in the atmosphere, LAI was the leaf area index, and $LEAFN$ was the nitrogen concentration of leaves. Air temperature, leaf, and root nitrogen contents controlled autotrophic respiration:

$$R_a = f(T, LEAFN, ROOTN),$$

where $ROOTN$ was the nitrogen concentration of roots. Thus, BIOME-BGC was able to capture effects of a number of abiotic (temperature, vapor pressure deficit, soil water, solar radiation, and CO_2 concentration) and biotic (leaf area index, leaf, and root nitrogen contents) controls on NPP.

Dominant environmental controls on NPP

Terrestrial primary productivity is sensitive to a number of environmental controls such as climate, soils, plant characteristics, natural and human disturbances, as well as many other factors. Nevertheless, spatial climatic variability dominates patterns of NPP. Given the focus of this study on estimating NPP of potential vegetation, I tested the relationship between climatic variables and NPP, but did *not* account for NPP variability associated with the other environmental factors. Nitrogen limitation on NPP was inferred by eliminating other causal factors because a comprehensive spatially distributed global database of any nitrogen cycle variable is not available. Consequently, I contrasted only temperature, water, and radiation controls on NPP in this article.

Because measured vegetation productivity is a result of the interaction of several environmental factors, I did not expect a generic dependence between a single environmental control and NPP from field data. Thus, I quantified the degree of environmental factor limitation on NPP using the functions shown in Figure 1. To determine these functions, I defined measures of climatic factor limitations on NPP analogues to membership functions in fuzzy set theory (Terano *et al.* 1991). The membership function quantifies the degree of an element inclusion in the fuzzy subset for each element of a given set. The values of the membership function range between 0 and 1. In this study, I considered a set of all possible values of a climatic parameter (e.g. entire range of mean annual temperatures) and its fuzzy subset containing climatic parameter values limiting vegetation productivity (e.g. low or very high mean annual temperatures). Then, I defined a membership function on the set of all possible climatic parameter values. The closer the function value was to 1 (Figure 1), the greater the likelihood that the value of the climatic parameter belonged to the fuzzy subset and was more limiting to vegetation productivity.

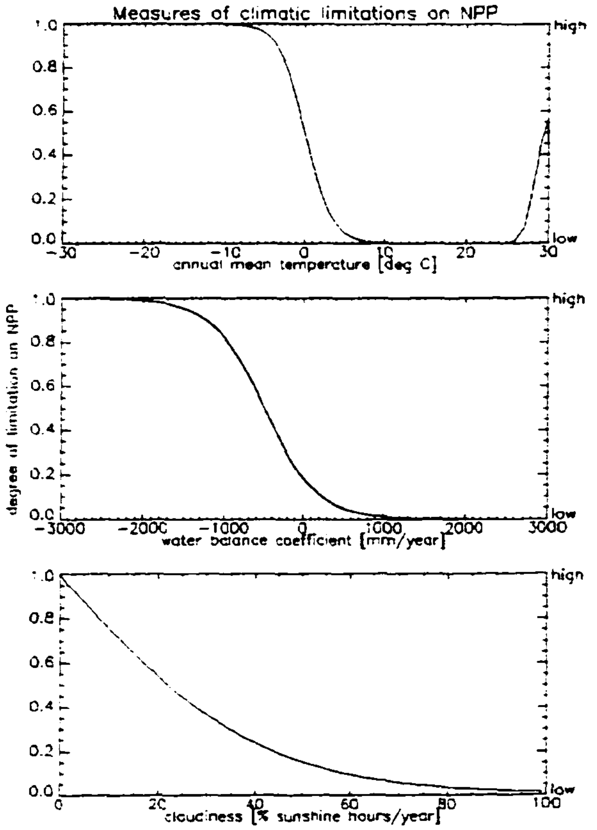

Figure 1. Measures of climatic limitations on net primary production defined by membership functions. The membership function gives the degree of element inclusion, a value from 0 to 1 of each element of the set X, where 0 is the lowest degree of inclusion and 1 is the highest degree of inclusion.

Many studies of vegetation physiognomy, productivity, and climate have described climate in terms of measures related to annual energy supply (such as temperature, potential evapotranspiration, radiation) or annual water supply (precipitation) (Lieth 1975; Stephenson 1990). These studies showed strong relationships between either annual climate means and vegetation distribution or annual climate and productivity patterns. Although these annual measures do not provide information about seasonal variability and extreme events, they show the central tendency of climate events during a year and average climate conditions suitable for the existence of a biome. Any change in these annual means can have significant implications for plant growth and biome stability. Thus, it seemed reasonable to use annual climatic means as indicators of NPP limitation.

Temperature partially determines photosynthetic and respiration rates of vegetation as well as the amount of nutrients available for plant uptake through the influence on litter decomposition rate. Consequently, plants growing in environments with low daily temperatures are usually less productive then plants growing in warmer climates. Thus, one can suggest that the NPP of plants from cold regions is primarily limited by temperature. In plant biogeography, the commonly used northernmost thermal limit was defined by mean monthly temperature and separated boreal forest from treeless tundra (no month has a mean monthly temperature higher than 10° C) (Bailey 1996). This limit was not quite appropriate for this study, because biogeographical thermal zones delineated areas with similar vegetation types, not with similar limitations on vegetation productivity. Indeed, low temperatures limit productivity of tundra as well as boreal forest. Though extreme low mean annual temperatures obviously restrict vegetation productivity, less extreme low temperatures may also limit plant productivity during the period of maximum growth. The degree of thermal limitation on NPP gradually declines as the annual temperatures rise; the limitation increases again when the annual temperatures get too high. Vegetation productivity can be limited by temperature in very hot environments as a result of an abrupt decrease in gross photosynthesis (specific changes in chloroplast and enzyme activity) and a continuous increase in respiration (Waring & Schlesinger 1985). These considerations are represented in the function defining temperature limitation on NPP (Figure 1). Global mean annual temperatures were obtained from the CLIMATE database.

Although precipitation is traditionally considered to be another important climatic driver of vegetation productivity, evapotranspiration primarily determines plant growth. Water from precipitation is never completely available to vegetation, but represents the maximum possible amount of accessible water. In contrast, available water for plant growth depends on the amount and seasonality of precipitation, soil type, vegetation type, and atmospheric evaporative demand. Not all rainfall reaches the soil, but this water is partitioned into canopy interception, evaporation, and subsequent throughfall processes. Plants may experience water stress at a site with sufficient precipitation because a high fraction of incoming water has been intercepted and then evaporated by canopies. Consequently, NPP is controlled not by the amount of precipitation, but by the *water available* to plants.

To estimate the amount of available water, I computed a water balance coefficient (WBC) as a difference between mean annual precipitation and potential evapotranspiration (Churkina G., S.W. Running, and A. Schloss, *in press*), where potential evapotranspiration was a function of mean temperature and net solar radiation (Priestley & Taylor 1972). WBC computation was based on global means of annual precipitation, solar radiation, and temperature from the CLIMATE database. This water balance computation has the advantage of being independent of any models and can be derived purely from climate data. To develop the relationship between NPP limitation and water balance coefficients I followed a logic similar to the one suggested by

Stephenson (1990). Stephenson showed the importance of the annual deficit limit (the evaporative demand that is not met by the available water supply) in North American plant distribution and discussed its role in primary productivity of different plant formations. In this study, I suggested that vegetation productivity of areas with extreme negative water balance coefficients was limited by moisture availability and this limitation declined as water balance coefficients approached zero. Sites with positive water balance coefficients were not moisture limited or were limited very slightly. The function describing the dependence of the degree of the water limitation on NPP (Figure 1) clearly delineated sites with available water deficiencies versus excesses.

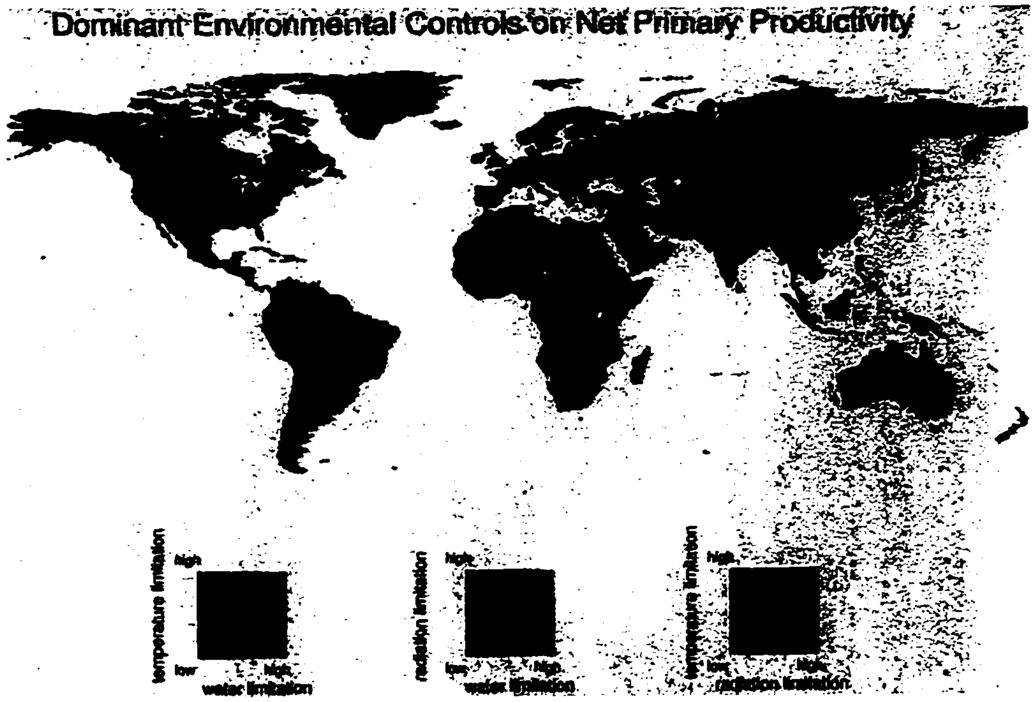

Figure 2. Map of weighed climatic controls on net primary productivity determined from water availability, average temperature and cloudiness. Each data point represents three values of the membership functions based on annual mean temperature, water balance coefficient, and percentage of sunshine hours per year one 0.5°x0.5° grid cell.

Radiation is another important environmental control on NPP because photosynthesis occurs only in environments with a sufficient amount of light. Although clouds can dramatically reduce the amount of incoming photosynthetically active radiation, plants still assumed that cloudiness considerably reduced incoming solar radiation and NPP in areas with low percentages of sunshine hours per year. Vegetation productivity was not limited by radiation in areas without clouds or with negligible cloud cover. Cloudiness data, expressed in sunshine hours per year, were derived from the CLIMATE database.

According to the aforementioned assumptions made, I mapped weighted climatic controls (temperature, water availability, and radiation) on NPP over the land surfaces of the globe (Figure 2). The value of each 0.5° x 0.5° grid cell on this map is a result of an integration of three variables that were calculated from the three membership functions of temperature, water availability, and radiation limitation. Temperature limitation on NPP was coded in blue, water availability limitation in red, and radiation in green. To investigate the relationship between climatic controls and the productivity estimated by the BIOME-BGC model, I plotted estimated NPP in the climate space of temperature and water availability (Figure 3).

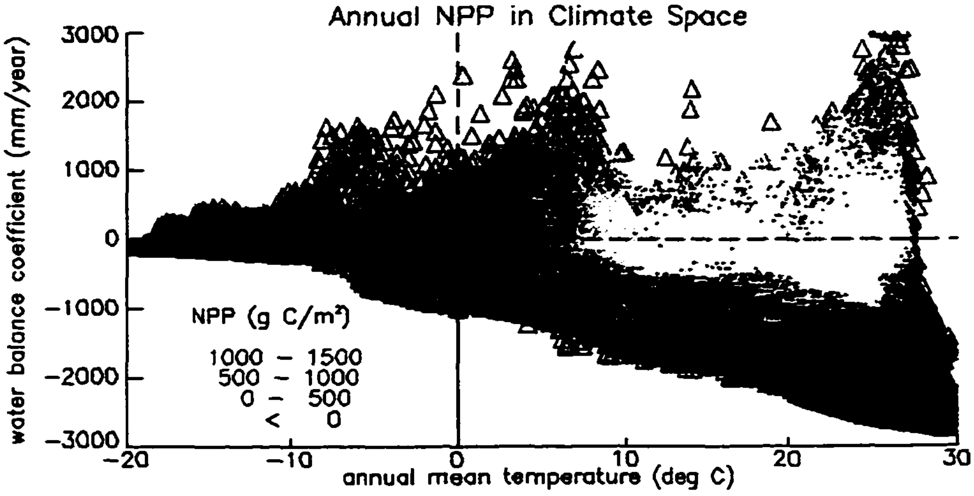

Figure 3. Annual global NPP simulated by BIOME-BGC in climate space represented by mean annual temperature and water balance coefficient.

To analyze the relationships between environmental controls and productivity of different vegetation biomes, I determined the relative importance of each climatic factor to biome productivity. First, I determined which of the three membership functions had the largest value for each 0.5° x 0.5° grid cell. The climatic factor for which the membership function had the largest value for a grid cell was defined as the dominant control for this grid cell. For example, if the value of the temperature limitation function was 0.8 and the values of radiation and water limitation functions were 0.6 and 0.3, respectively, for a grid cell, temperature limited NPP of this grid cell. Second, I overlaid the biome classification map with the map of environmental controls on NPP and determined how many grid cells of each biome were limited by temperature, water availability, or radiation. Finally, the environmental factor limiting productivity of the majority of biome grid cells was defined as a dominant environmental control on biome productivity (Table 1). The grid cells where the values of all three membership functions were below 0.3 were identified as cells with no climatic limitations on productivity.

Nutrient availability, or biological constraints, or limited absorption of photosynthetically active radiation by multi-layer canopies (shaded lower canopy layers) might limit vegetation productivity in those areas.

Table 1. Biome types and environmental controls on their productivity.

Biome type	Temperature	Water availability	Radiation reduction	No climate limitation	Environmental controls
C3 grassland	**76%**	21.5%	1.5%	1%	**temperature**, water
C4 grassland	<1%	**99%**	0%	<1%	**water**
Deciduous broadleaf forest	11%	**64%**	8%	17%	**water**, other controls than climate
Deciduous needle leaf forest	**80%**	8.5%	4.5%	7%	**temperature**, water
Evergreen broadleaf forest	4%	31%	12%	**53%**	**other controls than climate**, water
Evergreen needle leaf forest	**74%**	4%	16%	6%	**temperature**, radiation limitation
Shrubland / Desert	4.5%	**95%**	<1%	<1%	**water**

Results and discussion

The map of weighted climatic controls (Figure 2) showed that the productivity of most terrestrial ecosystems was controlled by more than one climatic factor, while the NPP of some ecosystems was not controlled by climate at all. In the high latitudes, temperature (indicated by dark blue on the map) appeared to be the primary control on NPP. However, a combination of either temperature and radiation (shades of cyan) or temperature and water availability (shades of magenta) limited NPP in the middle latitudes. In the low latitudes, water availability (bright red) became more dominant than either of the other environmental factors. Interestingly, none of the climatic factors were limiting in the tropical regions of South America, Africa and South-East Asia (dark gray to black on the map). Among the climatic controls considered, temperature and water availability controlled the vegetation productivity over more land area (31% and 52% respectively) than did radiation (5%). This conclusion can be easily visualized using the map of climatic controls on NPP (Figure 2) where large areas are bright red and blue, but none of the areas are bright green.

Given that temperature and water availability controlled larger areas of the globe than radiation reduction, I focused on contrasting temperature and water availability limitations on modeled global NPP. NPP estimates obtained from BIOME-BGC simulations were plotted for each grid cell in the climate space represented by mean annual temperature and water balance coefficient (Figure 3). The overall picture of NPP distribution in climate space was quite satisfactory, even though a few outlier values were detected. The lowest NPP values were typical for environments limited by moisture availability, or low temperatures, or a combination of both factors. These low productivity ecosystems might correspond to high latitude biomes such as tundra with negative mean annual temperatures or desert areas, where evaporative demand greatly exceeded the amount of precipitation entering the ecosystem during a year. The highest productivity occurred in areas with excess available water (positive WBC) and moderate temperatures (mean annual temperatures from 10° to 25° C). A few NPP estimate outliers could be attributed to possible errors in data layers used for simulations, or a prolonged growing season (Hunt *et al.* 1996).

Forest biomes with different leaf types and C_3 versus C_4 grasslands were clearly distinguished in the climate space composed of mean annual temperature and water balance coefficient (Figure 4). Shrub/desert vegetation was the only biome that stretched through the whole temperature interval from -20°C up to 27°C, but featured negative water classification scheme, which combined cold and hot deserts into one class, could possibly explain the long temperature stretch of the shrub/desert biome. Both temperature and water availability clearly discriminated C_3 from C_4 grassland. Low mean annual temperatures (below 10°C) and moderate water availability (WBC between -1000 and 1000 mm/year) characterized climates suitable for C_3 grasslands, while C_4 grasslands were located in warmer (temperature above 5°C) and dryer (negative WBC) areas. Mean annual temperature was the best

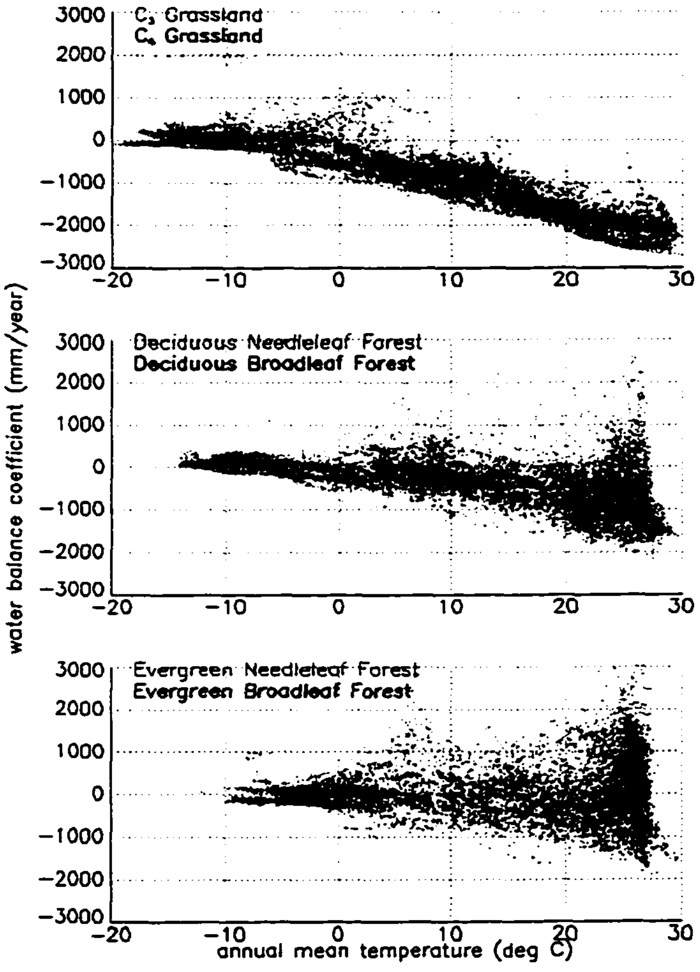

Figure 4. Biomes in climate space represented by mean annual temperature and water balance coefficient. Each data point represents one 0.5°x0.5° grid cell.

discriminator for needleleaf versus broadleaf forests. Deciduous and evergreen needleleaf forests occupied regions with annual mean temperatures below or close to the freezing point and with evaporative demand close to precipitation. In contrast, broadleaf evergreen and deciduous forests occurred mostly in the environments with positive mean temperatures and WBC scattered in a wide range of values ranging from negative to positive.

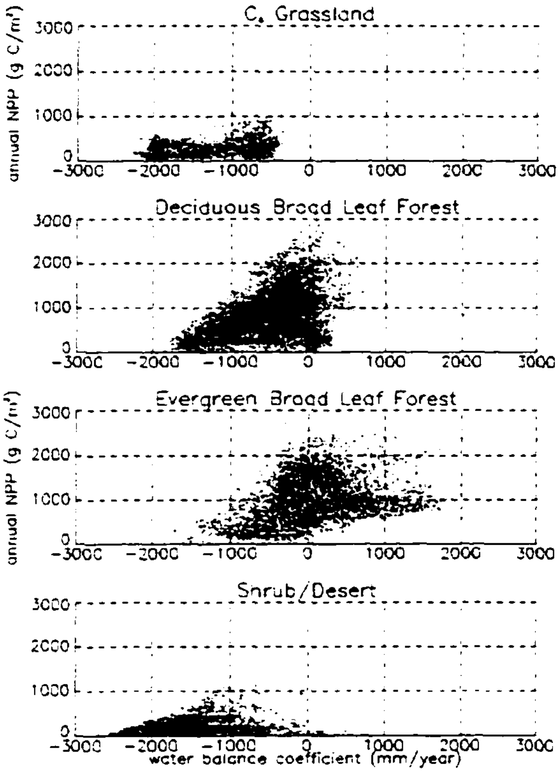

Figure 5. Relationship between estimated annual NPP and water balance coefficient for the water limited biomes such as C4 grassland, deciduous broadleaf forest, schrubland/desert, and evergreen broadleaf forest. Each data point represents one 0.5° x0.5° grid cell.

Water availability largely controlled productivity of the vegetation biomes such as C_4 grassland (99% of the biome area), deciduous broadleaf forest (64%), and shrub/desert (95%) (Table 1). Environmental controls other than climate were of secondary importance (17%) for deciduous broadleaf forest. Evergreen broadleaf forest productivity was mostly limited by environmental factors other than climate (53%); water availability held the secondary priority for this biome (31%). An important feature of the correlation between the productivity of the water limited biomes and WBC (Figure 5) was a restriction on the maximum NPP estimates set by the WBC values. The upper boundary of NPP estimates increased following increases in WBC up to zero value. The situation when NPP did not reach the maximum for a given water balance value indicated that the biome productivity in this cell was limited by some other factors as well.

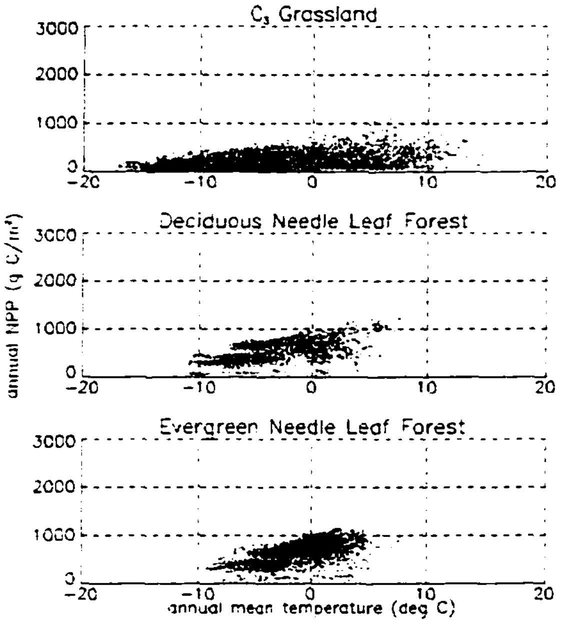

Figure 6. Relationship between estimated annual NPP and annual mean temperature for the temperature limited biomes such as C3 grassland, deciduous and evergreen needleleaf forests. Each data point represents one 0.5°x0.5° grid cell.

This study showed that temperature was the major limiting factor for the productivity of C_3 grassland (76% of the biome area), deciduous (80%), and evergreen needleleaf forests (74%) (see Table 1). Water availability holds the secondary priority for C3 grasslands (21.5%) and deciduous needle leaf forest (8.5%). Radiation limitation was of secondary importance to the productivity of the evergreen needle leaf forest (16%). Although the correlation between productivity and mean annual temperature of these biomes was weak (Figure 6), the tendency of a linear increase in maximum NPP values with an increase in mean annual temperatures was evident. The distribution of productivity values between zero and its potential maximum for a given temperature suggested that other environmental controls reduced NPP below its potential maximum.

Conclusions

The results of this study illustrate the complexity of the interactions between different environmental factors influencing ecosystem productivity. The map of environmental controls has shown that the productivity of most terrestrial ecosystems is controlled by more than one environmental factor. Temperature and water availability represented primary environmental controls on NPP for larger areas of the than radiation. None climatic parameter appeared to limit vegetation productivity in some areas on the globe. Other environmental controls (e.g. nutrient availability, biological constraints, or limitation on PAR by multi-layer canopies) should be considered for accurate NPP modeling in those areas. The map of environmental controls on NPP resulting from this study can also be helpful in determining where environmental factors other than climate would be especially important for accurate NPP modeling and to locate more precisely sites for future field studies. Moreover, the logic I developed for the BIOME-BGC model analysis can be useful for intercomparison or analysis of complex terrestrial biospheric models.

The map of environmental controls proposed in this paper reveals their relative importance to global NPP for mean climate, however changing climate conditions may alter these environmental controls over NPP. For instance, a warmer climate can result in increased evaporative demand and decreased water availability. As a result, water limitation may become a dominant limiting factor in the regions where it was not limiting before. Furthermore, elevated nitrogen deposition can also change the hierarchy of environmental controls over NPP. Nitrogen deposition has the potential to alleviate nitrogen limitation of productivity in terrestrial ecosystems and stimulate plant production (Townsend *et al.* 1996). Faster growing plants will require more water and, eventually, may become water limited.

With respect to the BIOME-BGC analysis, I conclude that temperature and water availability represent the ultimate limiting factors of NPP for certain biomes, since the upper boundary of NPP estimates decreases as the water availability or temperature becomes lower. The wide distribution of NPP estimates between zero and the upper boundary values in the correlation plots indicate that the BIOME-BGC model captures the influence of secondary multivariate environmental factors relevant to biosphere productivity.

Given the natural intricacy of an ecosystem, a mechanistic modeling approach might be considered most appropriate to capture these numerous interactions, since it involves a very detailed description of most physiological ecosystem processes. Interestingly, a new generation of much simplified NPP models, primarily driven by remote sensing (Field *et al.* 1995; Prince & Goward 1995; Ruimy *et al.* 1996), are able to provide large-scale actual vegetation productivity estimates and can also account for certain environmental controls on NPP. Importantly, models of this type embody the effects of climatic drivers implicitly through light use efficiency and remotely sensed Normalized Difference Vegetation Index (NDVI) data. Such simplified, remote sensing driven NPP modeling will be used to produce a standard, weekly NPP map of the world from the Earth Observing System beginning late in 1998 (Running *et al.* 1994).

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Chapter 4

INVESTIGATING THE BALANCE BETWEEN TIMBER EXTRACTION AND PRODUCTIVITY OF GLOBAL CONIFEROUS FORESTS

Introduction

A widely held assumption in forest economics is that the demand for timber will exceed the maximum level available from forests on a sustainable basis (Williams 1994). Sharma (1992) estimated that demand for wood products would increase by 50% with an increase of the world's population by about 70% during 1987 - 2025. Demand for fuelwood and building poles will increase most in absolute terms, while demand for industrial wood products will increase most in percentage terms (Sharma *et al.* 1992). The global trend since 1950 has been continued forest cover loss associated with rapid clearance in the developing countries, and stability or increase in forest area in most of the developed countries (Riebsame *et al.* 1994). An increase in forest area, however, may not necessarily lead to an increase in net forest productivity because the forests might suffer from air pollution or adverse effects of changing climate. About six million hectares of European forests have been destroyed or severely damaged because of air pollution originating from poorly equipped, old, or inefficient factories (Mackenzie & Mackenzie 1995).

One can argue, however, that human beings will solve the environmental crisis they created through scientific and technological innovations, and probably through some implicit influence on the environment. "Science and technology have liberated humans from the harshness of the environment. They will now liberate the environment from humans" (Ausubel 1998). Wernick et al. (1998) suggest that foresters have leverage to grow trees faster and thus use less forest land to grow and harvest timber. Moreover, a number of recent studies suggest an increase in the vegetation productivity in the Northern Hemisphere, which may not be unrelated to human activities. Based on long-term field measurements, forest growth increase at specific sites was noticed by several European scientists (Elfving *et al.* 1996; Mielikäinen & Sennov 1996; Skovsgaard & Henriksen 1996). An unprecedented increase in growing stock of European forests was reported as well (Kauppi *et al.* 1992). Increased vegetation growth in the high latitudes of the Northern Hemisphere from 1981 to 1991 was suggested from analysis of remotely sensed data (Myneni *et al.* 1997).

To see which prediction might be closer to the truth, both the current balance between timber extraction and forest natural productivity of global coniferous forests, and the balance between extrapolated timber demand and forest productivity under doubled CO_2 and climate change scenario, are investigated in this study. First, annual stem productivity of coniferous forests is estimated using the BIOME-BGC model (Running & Hunt 1993; Hunt *et al.* 1996; Thornton 1998). Second, on a country basis, the amount of harvested softwood is related to modeled forest productivity. Then, the natural capacity of coniferous forests to sustain increasing wood extraction by people is discussed, taking into account changing environmental conditions. Finally, the countries are identified where wood shortages may occur in the future if the timber products continue to be consumed at the current rates.

Methods

The analyses of this chapter were confined to the global coniferous forest and to countries that have coniferous forests within their territories. In particular, I have focused my analysis on seven countries with the largest coniferous forest productivity (former USSR, Canada, USA, China, Sweden, Finland, and Norway). Countries with smaller coniferous forest productivity[12] will be referenced as "other countries".

Estimation of forest productivity from biophysical data

First, forest productivity was estimated using the biogeochemistry model BIOME-BGC for current environmental conditions. Subsequently, the results obtained were compared to published data. Finally, projections of forest productivity were made using global change scenarios.

Modeling forest productivity

Model

Various environmental factors including climate, soil composition, fire, as well as anthropogenic factors such as air pollution, acid deposition, fertilization, and management practices influence forest growth. Different methods exist to estimate forest productivity from environmental conditions. A traditional method is to estimate forest growth and yield from stand age, density and site index. This method works well for natural stands and individual trees where data on past growth can be used to predict future growth. Under changing environmental conditions this method is not very useful. Gap forest modeling is based on the dynamics of individual trees: disturbance, recruitment, and mortality processes, which are determined by site variables including climate (Bugmann *et al.* 1996). These models, however, are of limited use at a large spatial scale because of the increasing complexity of simulations.

Biogeochemical models estimate forest growth using seasonal dynamics of canopy carbon and nitrogen balances. An advantage of the biogeochemical modeling approach is that it not only allows estimates of forest productivity over large areas, but it also quantifies causes of possible decline or increase in forest growth. In this study the biogeochemical model BIOME-BGC (Running & Hunt 1993; Thornton 1998) was used to estimate stem primary productivity *(SPP)* of global coniferous forests, which is driven by the following factors:

$$SPP = f(T, VPD, SW, SRAD, CO_2, NDEP, LAI, SOILC, SOILN),$$

where T is the air temperature, VPD is the vapor pressure deficit, SW is the soil water content, $SRAD$ is the solar radiation at the top of canopy, CO_2 is the atmospheric carbon dioxide concentration, $NDEP$ is the atmospheric nitrogen deposition, LAI is the leaf area index, $SOILC$ is the carbon concentration of soil, and $SOILN$ is the nitrogen concentration of soil. Thus, BIOME-BGC is able to capture effects of a number of abiotic (temperature, vapor pressure deficit, soil water, solar radiation, atmospheric CO_2 concentration, and atmospheric nitrogen deposition) and biotic (leaf area index, soil carbon and nitrogen contents) controls on stem productivity.

Input data and model parameterization

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[12] Chile, Japan, Mongolia, New Zealand, Argentina, Australia, Austria, Turkey, UK, Poland, North and South Koreas, Italy, former Yugoslavia, France, Germany, former Czechoslovakia.

The model was parameterized for a coniferous forest with a maximum projected leaf area index below 0.6. For each grid cell, the leaf carbon pool was initialized from the maximum leaf area index. Fine root carbon was assumed to be equal to the leaf carbon. Coarse root and stem carbon pools were initialized at 0.

The distribution of coniferous forest at 1.0° x 1.0° spatial resolution was derived from a map at 8 km resolution for 1987 (DeFries *et al.*, *in press*) using a cubic convolution resampling method. Nitrogen deposition distribution used in this study included wet and dry nitrogen deposition (NO_y, and NH_x) simulated by the three-dimensional chemical transport model MOGUNTIA (Dentener & Crutzen 1993; Dentener & Crutzen 1994; Holland *et al.* 1997; Lelieveld *et al.* 1998) for both 1985 and the pre-industrial times. Daily climate data (precipitation, maximum and minimum temperatures) used for BIOME-BGC simulations were for 1985-1987 (Piper & Stewart 1996). "Global Distribution of Country Codes at 1°×1° Resolution" (Matthews E, *unpublished manuscript*) was used to estimate stem primary productivity of different countries. This data reflect the political boundaries of the world in 1993.

Stem increment calculation

To convert predicted annual stem primary production (*SPP*) to equivalent increment of wood volume (*IWV*) the following equation was used:

$$IWV\,[m^3] = SPP\,[kgC] * BtoC\,[kg/kgC]\ /\ WD\,[kg/m^3],$$

where *BtoC* is biomass to carbon ratio, and *WD* is wood density.

The BIOME-BGC model estimated *net stem primary productivity*. *Biomass to carbon ratio* was set to ***2 kg/kg C***. *Wood density* varies among tree species, within one tree family (Yanchuk & Kiss 1993; Khasa *et al.* 1995; Dean & Baldwin 1996), and even within one tree stem (Rueda 1992; Castro *et al.* 1993; McDonald *et al.* 1995). Most coniferous trees or softwoods have lower wood density (360-660 kg/m^3) than broad-leaved trees or hardwoods (410-990 kg/m^3) (Young & Giese 1990). It was also shown that tree age can have a considerable effect on wood density (Castro *et al.* 1993). Given that it was problematic to distinguish between different conifer species or ages of the trees at the global scale, a wood density of a mature conifer tree of ***434 kg/m^3*** was used in this study. This wood density was calculated as an average of the wood densities of the most common in the United States' coniferous species (Turner *et al.* 1995).

Corrections to modeled stem primary productivity

The current version of the BIOME-BGC model simulated stem productivity taking into account natural forest mortality associated with pest and disease outbreaks and but not other natural and anthropogenic factors affecting forest growth. The *natural factors* omitted from model simulations were tree competition with other tree species, wood increment changes with tree age and stand structure, and forest fire losses. The excluded *anthropogenic factors* encompassed degradation of forests associated with pollution from industrial and transportation sources. In addition, I had to correct stem productivity for harvest efficiency (subtract wood residues left behind after a harvest from modeled stem growth). The latter correction was necessary for making the estimated stem growth comparable to roundwood production from economic data, because wood residues comprise a considerable part of a typical harvest and ignoring this variable could lead to the overestimation of wood available for consumption.

Forest Growth. Although it is difficult to say if inclusion of tree age, stand structure, or species competition would increase or decrease estimated annual stem increment, forest fire losses certainly decrease the amount of wood available for harvest. Fire is the major disturbance regime in boreal forests, with a natural fire cycle of 50-200 years in the North American boreal forests. An average of 5-6 million hectares of North American and Eurasian boreal forests was burned annually in the 1980's (Stocks 1991). One to two million hectares of forest were burned annually in the USA (Powell *et al.* 1994). The coniferous forest area burned by fire in Canada was 2.4 million hectares on average in the 1980's (FAO/ECE, 1988). In Russia, fire annually burned from up to 2.7 million hectares of forest (Korovin 1996). Enormous forest fire losses in Siberia were documented in the 1900's; the largest fire occurred in 1915 with 12 million hectares burned (Valendik 1996). The forest area burned annually in China averaged at about 0.9 million hectares and could reach up to 2.8 million hectares in a dry year (1994). Sweden reported that between 400 to 6887 hectares of forest were burned from 1975 to 1980 (the collection of forest fire statistics was discontinued in 1980) (FAO/ECE, 1988). In Finland, fire losses of coniferous forest were between 100 and 300 hectares in the 1980's. Coniferous forest area burned was much lower in Norway (31-126 hectares). For countries where published forest fire losses did not distinguish between different forest types, I assumed that all forest burned were coniferous. Then, based an average stem productivity, the forest productivity losses associated with fire may reach 3-10 million m^3 in Canada, 2-3.5 million m^3 in the USA, 2-6 million m^3 in China, 0.5-3 million m^3 in the former USSR, 520-8953 m^3 in Sweden, 150-450 m^3 in Finland, and 43-176 m^3 in Norway. Consequently, only 0.5-2 % of annual stem productivity, on average, may be lost after a fire in Canada, the USA, China, and the former USSR. Fire losses are much lower (0.01-0.3% of annual stem productivity) in Scandinavian countries. To account for fire losses in this study, annual stem productivity was reduced by 1% in Canada, the USA, China, and the former USSR; it was decreased by 0.1% in Sweden, Finland, and Norway.

The *anthropogenic factors* not included in the forest growth estimates in this analysis encompassed degradation of forests associated with pollution from industrial and transportation sources. Although pollution effects can be really damaging to a forest (17% stem growth decline in one year as a result of acidic precipitation; Smith 1990), distribution of these areas is unknown at the global scale. Moreover, some studies suggest that these areas are not significant at a continental scale (Kauppi *et al.* 1992) with, for instance, only 0.5% severely damaged forest of the total forest area in Europe.

Harvest Efficiency. Although timber-harvesting practices have improved dramatically in the recent years, large volumes of wood residues and salvable material remain unused in the logged areas. Forest residues remaining on logged sites include small trees, cull and broken logs, tops, and dead timber. A primary barrier to more efficient utilization is the added cost of recovering residue material. Typically, the value of residues will not cover the costs of harvesting them, unless the volume of recoverable material is extremely high. The amount of residues left after logging depends on the type of logging operation, topography, forest type, logging crew skills, and some other factors (Barger & Benson 1979). In the US, at least 15% of the wood fiber in a typical timber harvest is left behind as broken or defective (Harmon 1990). In the former Soviet Union, the efficiency of logging operations is much lower; 30-50% of all cut logs are left on the ground and lost during transportation (Isaev *et al* 1996, WRI 1996). In this study, I assumed that countries with more advanced harvest technologies had 15% residues and the countries with low timber harvest efficiency lost 40% of harvest. To obtain the wood volume that will be actually available for consumption, net forest productivity (after fire losses) was reduced by 15% in Canada, the USA, Sweden, Finland, and Norway; it was decreased by 40% in the former USSR and China.

Corroboration of modeled forest productivity

The reliability of the BIOME-BGC model has been tested in a number of studies where FOREST-BGC, a stand-level version of BIOME–BGC, was used to estimate forest growth. Korol et al. (1991) simulated the 5-year growth increments of 176 Douglas-fir trees in British Columbia, Canada, using the FOREST-BGC model. They found that individual tree stem growth increments from field measurements were in close agreement with those from the model simulations (r^2=0.95). Running (1994) used FOREST-BGC to simulate the accumulation of stem biomass over a century for mature forests on seven sites across the Oregon transect in the United States. A range of stem biomass (10-700 t/ha) measured along this climatic gradient was replicated well by the model (r^2=0.79). Milner et al. (1996) correlated the modeled stem productivity to the site index for two climatic regions in Montana, USA, and found a relatively good correspondence (r^2= 0.67).

Two comparisons were made to corroborate the results of the BIOME-BGC simulations. First, I compared the areas of coniferous forest distribution used for the model simulation to statistics available on a country basis; second, I compared modeled forest annual growth to data from the national forest inventory. Both comparisons were done at a country level because of data availability.

Forest area

The coniferous forest distribution data used for the model simulation were from a land cover classification derived from the NASA/NOAA Pathfinder Land data set with a spatial resolution of 8 km. This data set has a length of record of 14 years (1981-1994), providing the ability to test the stability of classification algorithms (DeFries *et al. in press*). Furthermore, this data set includes red, infrared, and thermal bands, in addition to Normalized Difference Vegetation Index (NDVI). In addition, 156 high resolution scenes from Landsat Multispectral Scanner System, and a few from Landsat Thematic Mapper and Linear Imaging Self-Scanning Sensor (LISS), were used to identify the pixels to be used for training of Pathfinder data. In this classification, a pixel was defined as evergreen or deciduous needleleaf forest if 60% was covered by one of these vegetation types.

Both coniferous forest definitions, and mapping techniques from ground measurements, vary by country and sometimes even within the same country. For example, in the former USSR, a land with 50-80% of forest cover is classified as forest (Kolchugina & Vinson 1993). For China and Finland, the data on coniferous forest area were available only for closed forests. The term "forest", however, does not necessarily mean the same term for these two countries, because it includes all lands with minimum tree crown cover of 10% in developing regions and 20% in developed regions (WRI 1996). Different definitions of "forest" are possible even within the same country, especially in vegetation transition zones (e.g., tree line). For instance, in Canada, various limits of tree size and density were used to estimate the forest area in different provinces (Lowe *et al.* 1994).

Stem primary productivity

All possible adjustments to the modeled forest growth and to the estimated forest growth were undertaken to make modeled and estimated forest growth comparable. Nevertheless, a strict comparison of modeled and reported coniferous forest growth remained problematic, because different countries provided different statistics of coniferous forest growth. Estimation of the average annual growth of coniferous forests in the former Soviet Union (619 million m^3) was based on forest statistical data, which did not include coniferous forests in the Southern regions (Kolchugina & Vinson 1993). It was unknown, however, if these estimates were for timber productive timber land only or for the entire forest. Net annual growth of coniferous forest of growing stock on timberlands in 1991 (340 million m^3) was known for the United States (Powell *et al.* 1994). For Canada, annual average growth of coniferous forests was estimated from reported average annual forest growth of timber productive forests (364 million m^3) assuming that coniferous species contribute 78% of this growth and timber productive land was 60% of Canada's total forest area (Lowe *et al.* 1994). Various statistics are cited for gross annual growth in China's forests; they differ between 150 and 300 million cubic meters per year (Richardson 1990). Therefore, gross coniferous forest growth in China was estimated as between 105 and 210 million cubic meters per year (assuming 70% of the total growing stock was coniferous forest). Gross average increment of growing stock of coniferous forests in Finland for 1921-1994 (46 million m^3) was obtained from the National Forest Inventories (Tomppo 1997). For Sweden, gross annual growth of coniferous forests (59 million m^3) was averaged over 1923-1982 (Bengtsson *et al.* 1989). Coniferous forest mortality data were unavailable for China, Finland, and Sweden. To obtain net forest growth in these countries, I reduced their gross forest growth by fire losses (1% in China, 0.1% in Finland and Sweden). Only estimations of the average annual growth were available for Russia and Canada. Forest growth statistics were inaccessible for Norway.

Forest productivity under global change

Global change scenarios

The climate change scenario used in the simulations was based on an atmospheric general circulation model (GCM) experiment for doubled CO_2 in the atmosphere and an equilibrium climate. The scenario was taken from the Canadian Center for Climate Modeling and Analysis (CCCMA) at 3.7° x 3.7° lat/long spatial resolution (Boer *et al.* in press). In this simulation experiment, the GCM was implemented with an ocean representation at 1.8°x1.8° spatial resolution and 29 vertical levels. In addition, the direct forcing effect of sulfate aerosols was included by increasing the surface albedo. Changes in monthly mean temperature were represented as first differences (Figure 1) and those in precipitation as change ratios (Figure 2). The GCM grid point values were derived from the archives of the CCCMA and interpolated to a 1.0° grid representation. This provided smoothed monthly change fields that were applied to the base climate (1985-1987 climate data) to generate altered-climate inputs (three years of altered monthly maximum and minimum temperatures and precipitation). Then, daily climate values were generated from monthly means using MTCLIM (Running *et al.* 1987; Kimball *et al.* 1997; Thornton & Running 1998).

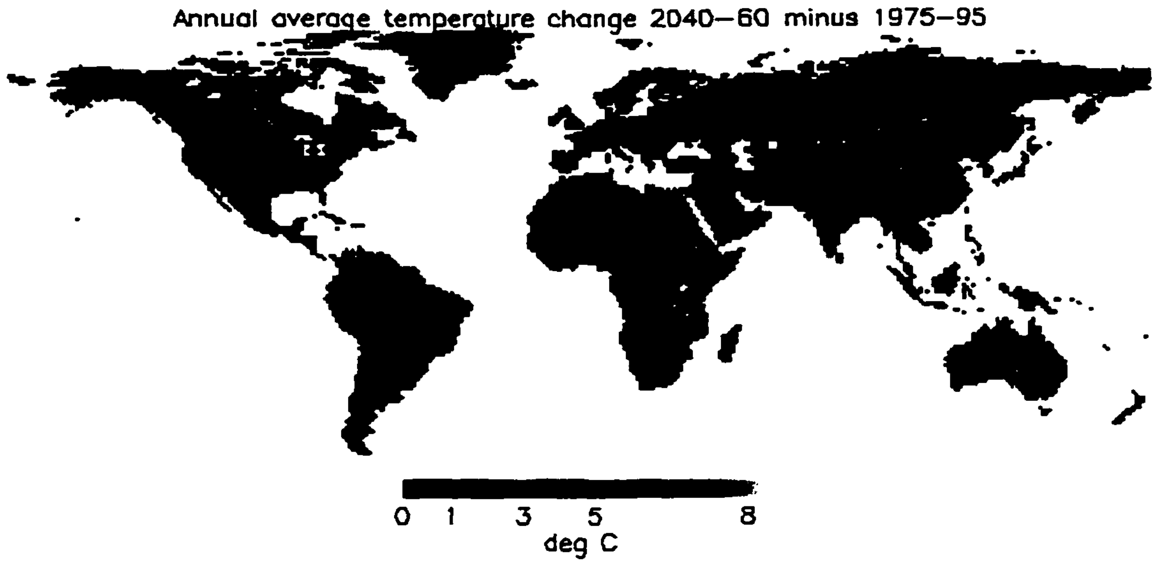

Figure 1. Annual average temperature change 2040-60 minus 1975-95 at 3.7°x3.7° lat/long grid for CCCMA climate change scenario.

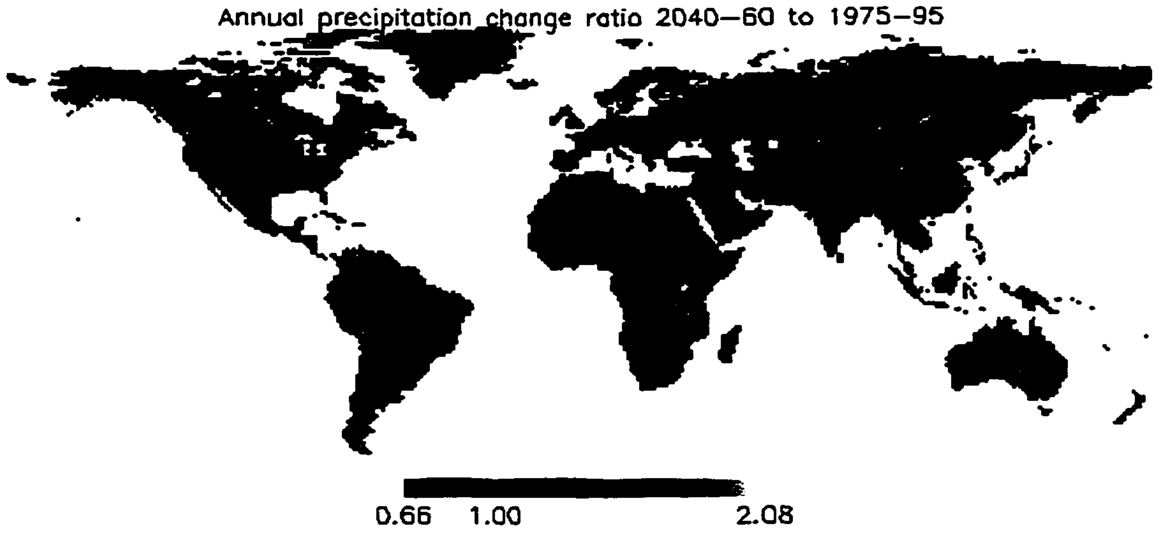

Figure 2. Annual average precipitation change ratio of precipitation for 2040-60 and for 1975-95 at 3.7°x3.7° lat/long grid for CCCMA climate change scenario.

To evaluate the single and joint effects of doubled atmospheric CO_2, altered climate, and enhanced nitrogen deposition on forest growth, the model was run with the following scenarios:

1) ***Reference***: industrial nitrogen deposition, current atmospheric CO_2 concentration (350 ppm), contemporary climate (1985-1987);
2) ***Pre-industrial N***: pre-industrial nitrogen deposition, current atmospheric CO_2 concentration, contemporary climate;
3) ***Climate Change***: industrial nitrogen deposition, current atmospheric CO_2 concentration, altered climate;
4) ***2xCO₂***: industrial nitrogen deposition, doubled atmospheric CO_2 concentration (700 ppm), contemporary climate;
5) ***2xCO₂ and Climate Change***: industrial nitrogen deposition, doubled atmospheric CO_2 concentration, altered climate.

For each scenario the BIOME-BGC model was run for 100 years with 3-year climate input repetitively. Then, stem productivity of each grid cell was averaged over the 100-year period (Figure3).

An important component of global change, the change in coniferous forest cover was assumed to be negligible in this study. This assumption was based on the evidence for stabilization or even slight increase of temperate forest cover within developed regions from 1980 to 1990 (WRI 1996). This internal conservation was possibly achieved not only because of improved harvest and wood processing technologies, but also at the expense of the producers in the tropical world, who are ready to supply hardwood for hard currency (Williams 1994). Of the countries considered in this study only China lost under four percent of its natural forest cover between 1980 and 1990 (WRI 1996).

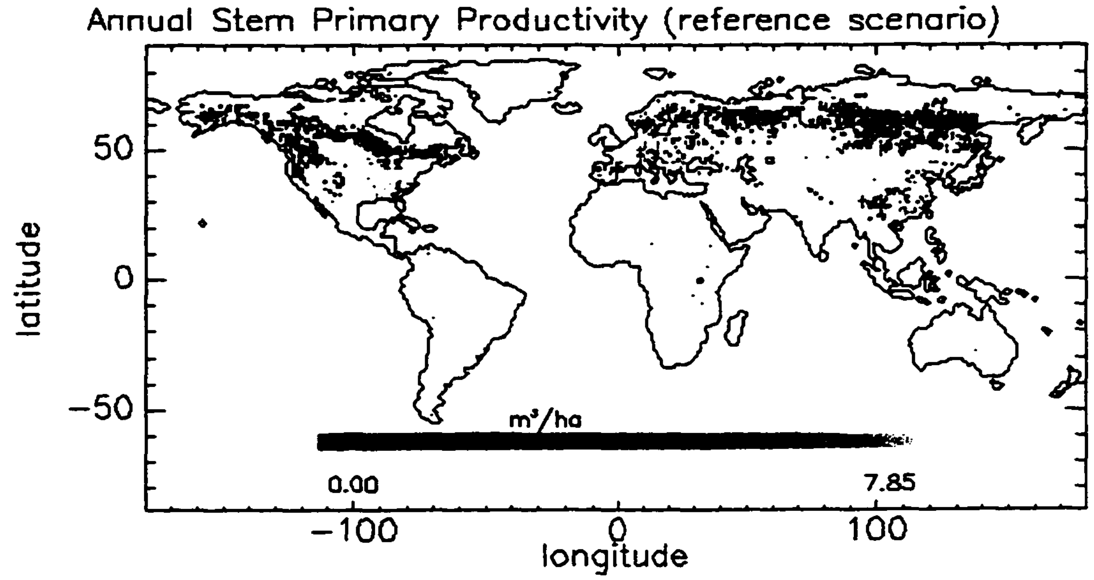

Figure 3. Annual stem primary productivity of coniferous forest simulated by the BIOME-BGC model for the *reference* scenario at 1.0°x1.0° lat/long resolution.

Analysis of forest productivity responses to global change

To analyze the response of forest productivity to changing environmental conditions, the stem ratio was related to environmental controls (annual average temperature and water balance coefficient; Churkina & Running 1998), to changes in annual temperature (difference between annual average temperatures for 2040-60 and for 1975-95), and precipitation ratio (ratio between annual average precipitation for 2040-60 and for 1975-95). The stem growth ratio (*SGR*) was calculated for each grid cell (1°x1° lat/long) and for each global change scenario as:

where *CSP* was stem productivity for this scenario, *RSP* was stem productivity for reference scenario.

Estimation of timber extraction from economic data

Data

Wood production in any country is driven by the demand for wood products and is limited by forest resources availability. Wood demand is defined by factors such as country population, its affluence, and market prices (Laarman & Sedjo 1992). To account for all social and political factors influencing wood production, a country-based socio-political model would be a desirable tool. Regretably, an appropriate model to predict wood production in each country producing softwood was not available for this study, and a simpler method was used to project wood production of different countries. *Roundwood* (unprocessed primary wood) production was chosen to be an indicator of wood demanded in the countries. Roundwood is wood at an intermediate stage between tree harvest and wood products. It can become lumber, composites, pulp, fuel, plywood, or veneer for furniture and construction.

Extrapolation of wood extraction

To extrapolate into the future and to estimate current roundwood production, a time series analysis of roundwood production by countries was used (FAO quarterly bulletin of statistics, 1980-1996). For extrapolation of roundwood production, **an assumption** was made that the social factors (e.g., politics, population, income) of the current year have more influence on roundwood production then ones of the previous year, that the economic situation in a country in the previous year has more influence than the year before, and so on. Weights from 0.0 to 1.0 were assigned to roundwood production for each year and each country[*] following this assumption. Roundwood production in 1985 had the smallest weight (0.06), and roundwood production in 1996 had the largest weight (1.0). Weighted linear regressions of roundwood production were performed for each country and country roundwood productions were extrapolated from obtained linear equations for the next 100 years (Figure 4). Two distinct regression lines were plotted for the former USSR. The first regression line represented wood production rate, if it were to stay at the level it was before the collapse of the USSR and its economy (1989). The second regression line depicted the recent trend in wood production in the former USSR based on the data for the last years (1994-1996).

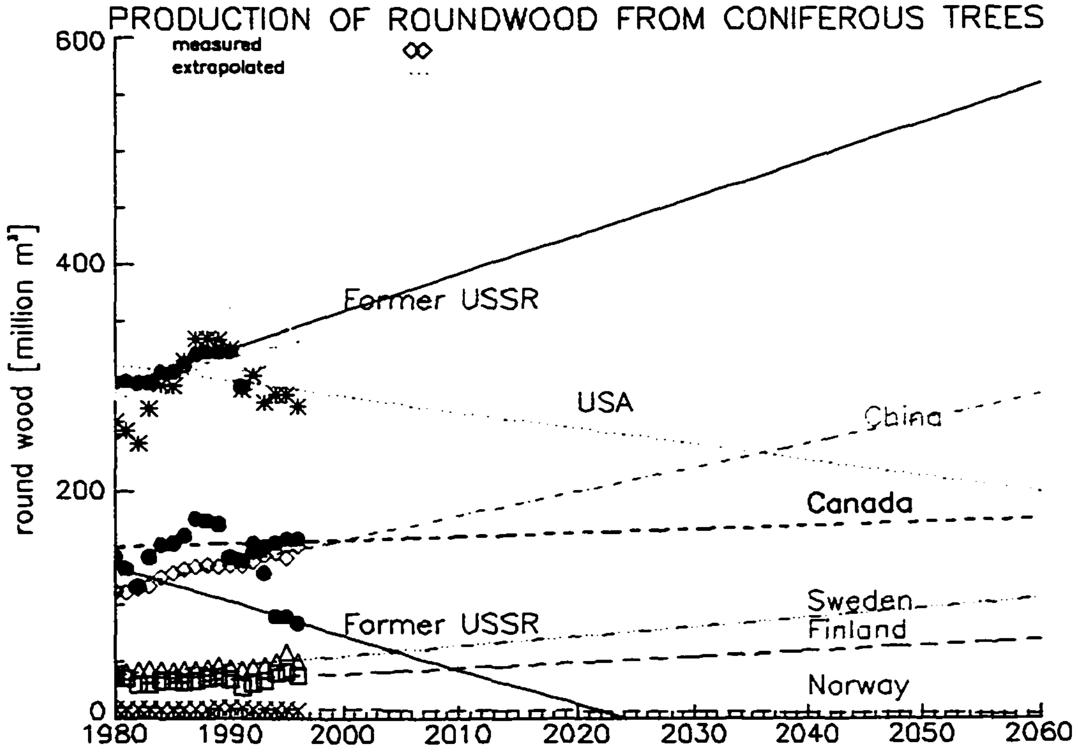

Figure 4. Extrapolated and measured production of roundwood from coniferous trees for different countries.

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[*] Wood productivity data for the last three years (1994-1996) were used in the case of the former USSR.

Results and Discussion

Corroboration of the modeled forest productivity

The two comparisons, area of coniferous forest distribution used for model simulations to the country statistics, and modeled forest annual growth to the data from national forest inventory data yielded satisfactory results.

Forest area

The areas of coniferous forest estimated from satellite observation data were similar to the published data (Table 1). For most countries, forested areas were slightly higher based on the satellite-derived map as compared to those from ground measurements, except for the former USSR and the USA. Given that various literature sources offered different estimates of the forested area in the former USSR, it was unclear if the area used for model simulations was over- or underestimated. For the USA, the coniferous forest area from remotely sensed data was consistently lower than the area reported by the US Forest Service. Various definitions of coniferous forest used in the satellite-derived classification and in the ground measurement (see Methods section) can partially explain existing discrepancies. In addition, the vegetation classification algorithm, conversion between different map projections, and an aggregation from a finer (grid cell area = 64 km^2) to a coarser (grid cell area = 100-8000 km^2) spatial resolution could potentially contribute to the error in the final estimation of coniferous forest area. Errors of the *vegetation classification algorithm* arise from a definition of conifer forest (i.e., what proportion of pixel should be covered by conifer forest to define it as a conifer forest). Errors associated with *map projection conversion* occur from stretching or compressing of some pixels. Errors of *resampling* the vegetation classification to the coarser spatial resolution originate from an aggregation of several pixels into one. Forest area, therefore, may be underestimated in the countries with sparse forest cover and overestimated for countries with contiguous forests. Edge effect and country size can also contribute to the error value. The larger the country area, the smaller the error of over- or underestimation (Table 1).

Table 1. Comparison between coniferous forest areas derived from countries' statistics and calculated from a satellite derived map. Forest areas from remotely sensed data and those from ground measurements are not strictly comparable because of differences in classifications (see Methods section). The percentage difference between area from remotely sensed data and from ground measurement data is calculated based on ground measurements as 100%.

Country	Area from remotely sensed data [10^6 ha]	Area from ground measurements [10^6 ha]	% difference
Former USSR	553	516-593[13]	± 7
Canada	272	262[14]	+ 4
USA	168	170-190[15]	- 0.7-(-13)
China	120	110[16]	+ 8
Sweden	26.5	23[17]	+ 13
Finland	22	18[18]	+ 18
Norway	10	8.5[19]	+ 15

Stem productivity

For most countries, the magnitude of the modeled annual growth increment was comparable to the values published (Table 2). The annual growth increment simulated by the BIOME-BGC model was lower then the one obtained from forest inventory in the United States, Sweden, and Finland; it was higher in the former Soviet Union, Canada,

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[13] Kolchugina, 1993, Richardson, 1990.
[14] Estimated from Lowe (1994)
[15] Estimated from Powell (1994)
[16] Richardson, 1990
[17] Estimated from UN/ECE timber database.
[18] Richardson, 1990
[19] Estimated from UN/ECE timber database.

and China. Several causes may underlay the results from the comparison. First, the model simulations were performed on a relatively coarse grid (spatial resolution of 1° x 1° lat./long) and each input data layer could add aggregation errors. Second, modeled stem productivity was averaged over 100 years; the stem annual growth from country statistics was not necessarily a long term average. Third, the only controls simulated by BIOME-BGC for stem primary productivity were the direct effects of climate and soil type. It did not account for a number of anthropogenic factors, such as forest fertilization and various management practices that enhance forest growth. The forest cover definition can significantly contribute to the final estimates of stem growth (Table 2). For instance, although the discrepancy in forest area estimates of the former Soviet Union did not seem significant relative this country area (7%), the forest productivity of this "discrepancy" area (47 million m^3 assuming this forest has average productivity) could be comparable to the productivity of the entire Sweden.

Table 2. Modelled annual growth compared to the annual growth of coniferous forests estimated for countries with the largest coniferous forest productivity. Differences between modelled and reported by country *stem growth may originate from different definitions of stem growth and forest cover.*

Country	Modeled stem annual growth [$*10^6$ m^3]	Stem annual growth from countries' statistics [$*10^6$ m^3]	Possible discrepancies from forest cover definition [$*10^6$ m^3]
Former USSR	658	619[20]	± 47
Canada	412	350[21]	- 18
USA	283	340[22]	+3.5-(+38)
China	262	105-210[23]	- 18
Sweden	42	58[24]	- 5
Finland	26	45[25]	- 6

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[20] Average annual growth of coniferous forest (Kolchugina, 1993)

[21] Average annual growth of coniferous forest (Lowe, 1994)

[22] Net annual growth of the coniferous forest (Powell, 1994).

[23] Net annual growth of coniferous forest estimated from Richardson (1990), incl. fire losses.

[24] Net annual growth of coniferous forest estimated from Bengtsson (1989), incl. fire losses.

[25] Net annual growth of coniferous forest estimated from Tomppo (1997), incl. fire losses.

Forest productivity response to global change

The model simulation results suggested that individual and joint changes of environmental conditions considered in this study (enhanced nitrogen deposition, doubled CO_2, and climate change) would favor stem growth in most cases (Table 3).

Table 3. Responses of stem productivity to pre-industrial nitrogen deposition, doubled CO_2, climate change, and both doubled CO_2 and climate change as estimated by the BIOME-BGC model.

	Estimated stem annual growth [$*10^6$ m^3]								
	Global coniferous forests	**Former USSR**	**Canada**	**USA**	**China**	**Sweden**	**Finland**	**Norway**	**Other countries**
Reference scenario	2039	657	413	283	262	42	26	14	341
Response to pre-industrial nitrogen	-17.9	-13.4	-15.3	-19.9	-17.7	-31.2	-15.3	-27.6	-26.2
Response to climate change	+10.5	+30.4	+16.5	-22.4	-6.0	+20.5	+25.3	+25.5	+1.7
Response to $2xCO_2$	+10.2	+8.9	+7.2	+18.5	+12.8	+5.2	+4.6	+5.5	+ 8.3
Response to climate change & $2x\ CO_2$	+25.4	+44.3	+27.1	+3.8	+12.5	+26.2	+30.7	+31.0	+13.8

Industrial nitrogen deposition increased forest growth especially in Sweden (31%), in Norway (27%), and in the USA (20%). This result was not surprising given that the largest increase in nitrogen deposition from pre-industrial times was documented in Europe and the South-Eastern United States (Figure 5).

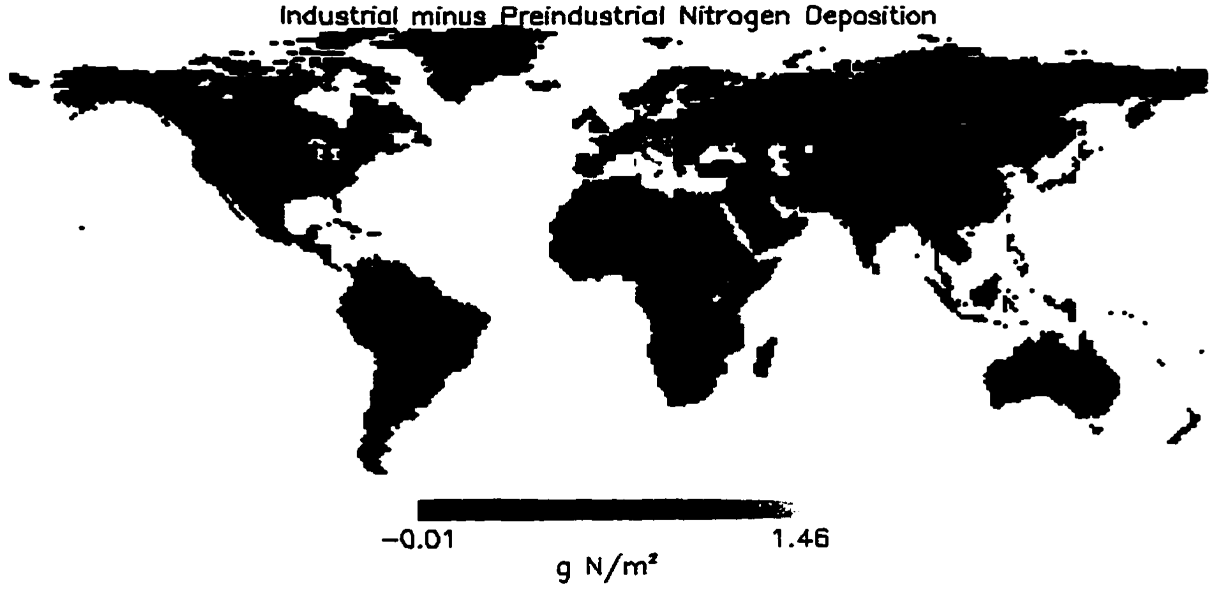

Figure 5. Industrial minus pre-industrial wet and dry nitrogen depositions at 10°x 10° lat/long grid from the MOGUNTIA model.

Changes in climate decreased forest growth in the USA (-22%) and China (-6%), but increased stem productivity in all other countries, with the largest increase in the former USSR (30%). Forest growth decreased in the USA and China because vegetation productivity in a large part of these countries was not temperature limited, but was instead water limited (Churkina & Running 1998). Temperature increases, therefore, lead to enhanced water limitations and, consequently, to decreased stem production (stem growth ratio <1; Figure 7a). The largest increase in stem productivity (stem growth ratio > 2) under changing environmental conditions occurred in the areas with annual average temperatures below zero (Figure 6a) and temperature increase of 3-4° C (Figure 6b). Thus, countries with temperature limited territories (the former USSR, Norway, and Finland) benefited from the climate change the most.

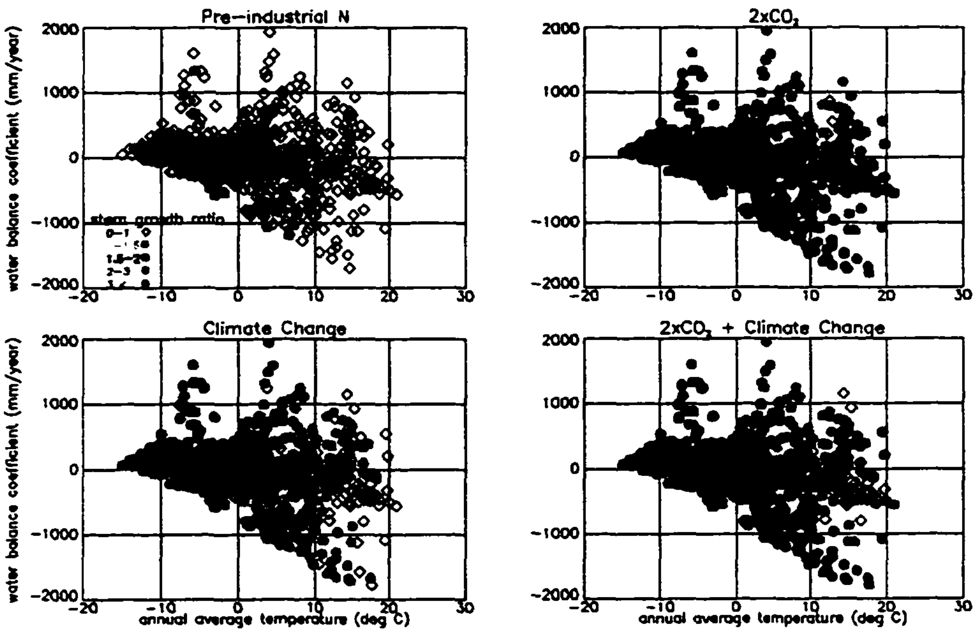

Figure 6 a. Relation of stem growth ratio to climatic controls on vegetation productivity for *pre-industrial nitrogen*, *climate change*, *2xCO$_2$*, and *2xCO$_2$ + climate change* scenarios. Each data point represents one 1.0° x 1.0° longitude/latitude grid cell.

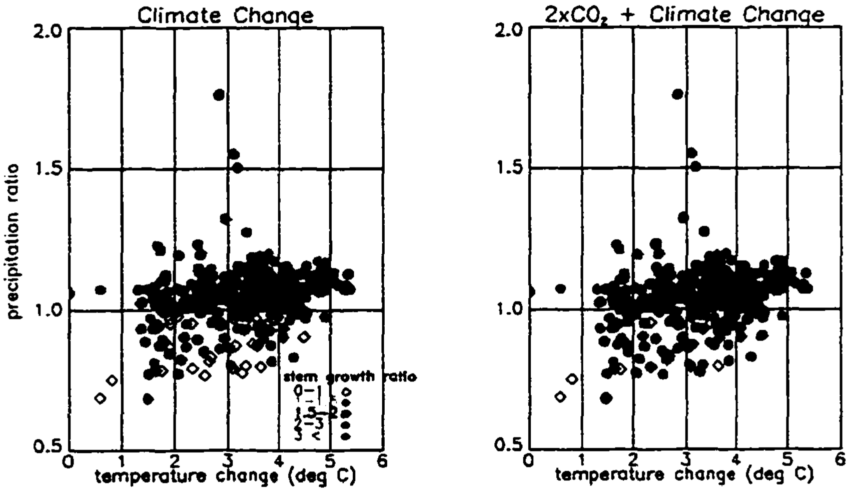

Figure 6 b. Relation of stem growth ratio to precipitation ratio (ratio of precipitation for 2040-60 to 1975-95) and temperature change (temperature difference between 2040-60 and 1975-95) for both *climate change* and *2xCO$_2$ + climate change* scenarios. Each data point represents one 1.0° x 1.0° longitude/latitude grid cell.

The *doubled CO$_2$* concentration in the atmosphere elevated forest growth in all countries. The greatest increases in stem productivity were in the USA (18%) and China (13%) (Figure 7), because of a stronger CO$_2$ fertilization effect in dry and warm areas (Figure

6a). The *joint effect of climate change and doubled CO_2* enhanced stem productivity in all countries. The former USSR, Norway, Finland, Canada, and Sweden benefited from this combination of global changes the most, with increases in forest productivity of 44%, 31%, 31%, 27%, and 26%, respectively. The effect of climate change on stem productivity was enhanced by the CO_2 fertilization effect in countries located in high latitudes (former USSR, Canada, Norway, Finland, and Sweden). Countries located in mid-latitudes (the USA and China) had a smaller increase in stem productivity because the negative influence of increased temperatures offset the CO_2 fertilization effect. The former USSR benefited from these changes the most, because 65 percent of the Siberian forests are located in the permafrost zone.

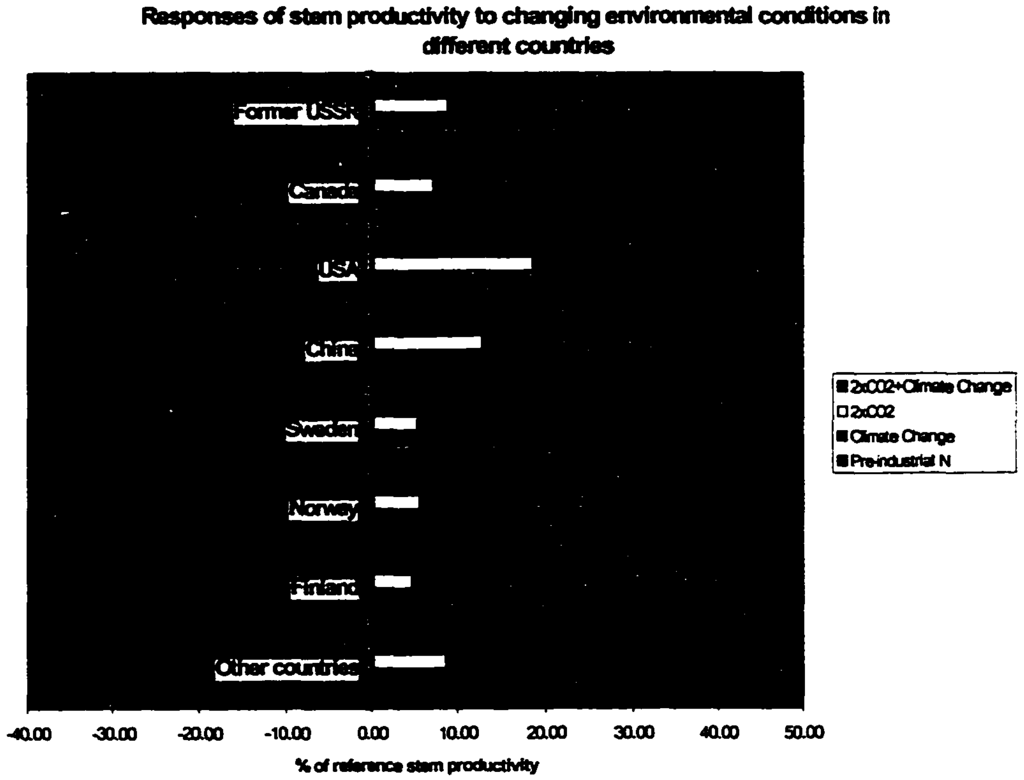

Figure 7. Responses of stem productivity to *pre-industrial nitrogen*, *climate change*, *2xCO*$_2$, and *2xCO*$_2$ + *climate change* scenarios in different countries.

Projections of timber harvest

Results of the extrapolation of roundwood production indicated that by the year 2060, softwood extraction *slightly increased* in Canada and Finland, and *dramatically increased* in Sweden and China, assuming constant rates of timber harvest (Figure 4). A decline in timber harvest was predicted in the USA and Norway. Harvest of coniferous trees would increase in the former USSR and be doubled by 2060 if the softwood extraction rate returned to its 1980's level (upper red line on Figure 4). As a result of the USSR's collapse in the late 1980's, by 1996, roundwood production plunged to 30% of the 1989 level. A negative trend in roundwood production in the early 1990's would lead to zero forest production by 2025 (lower red line on Figure 4). This situation, however, is not realistic given that forest industry has always been an important part of the Russian economy and accounted for about 5 percent of total industrial output (World Bank, 1997). There also is a chance that a good part of harvested timber was not reported to and documented by Russian authorities, so that numbers published by FAO are severely underestimating the amount of harvested timber.

Comparison between modeled forest productivity and timber extraction

The model results suggested that at an aggregated level, the amount of extracted softwood remains and will remain well below the estimated productive capacity of the global coniferous forests (Figure 8). About 75% of the total modeled forest growth (corrected for harvest efficiency) was harvested in 1995; this share is significantly higher than was suggested earlier (Waring & Running 1998) for global forests (15%). This proportion, however, reached 100% of the total coniferous forest growth by 2060 in modeled projection if timber continued to be consumed at the constant rates, the climate changed, and atmospheric carbon dioxide concentration increased according to the scenario used in this study.

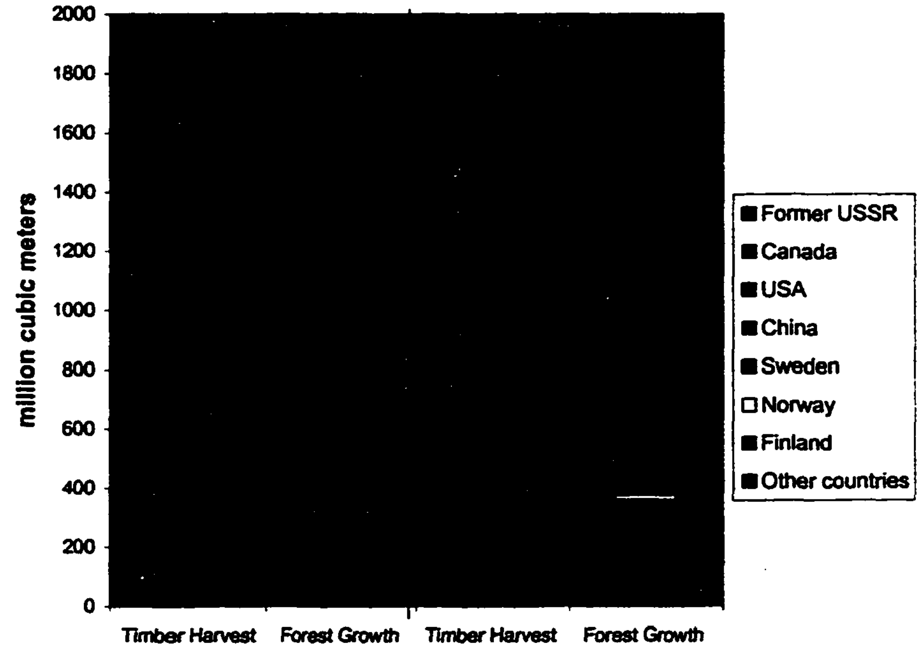

Figure 8. Comparison of timber harvest in 1995 and 2060 to stem productivity for *reference* and *$2xCO_2$ + climate change* scenarios for different countries.

The difference between timber harvest and modeled forest productivity changed from country to country (Figure 9, Table 4). Under the *$2xCO_2$ and Climate Change scenario*, the modeled productivity of coniferous forests exceeded the value extrapolated for extraction of softwood in the former USSR, Canada, and Norway. In the USA and the USSR, the difference between extrapolated timber harvest and forest growth under global change, however, was not as prominent. In the future, these countries may achieve a negative balance between forest growth and timber harvest if climate change has stronger adverse effects on forest productivity, mortality or both than suggested by the scenario used in this study, or if the rates of roundwood extraction increase. The modeled productivity of coniferous forests was lower than the timber extraction in Finland and Sweden, because neither the use of fertilizer nor management practices were considered in this analysis (Kauppi *et al* 1992; Mielikäinen & Sennov 1996).

Sweden, because neither the use of fertilizer nor management practices were considered in this analysis (Kauppi *et al* 1992; Mielikäinen & Sennov 1996).

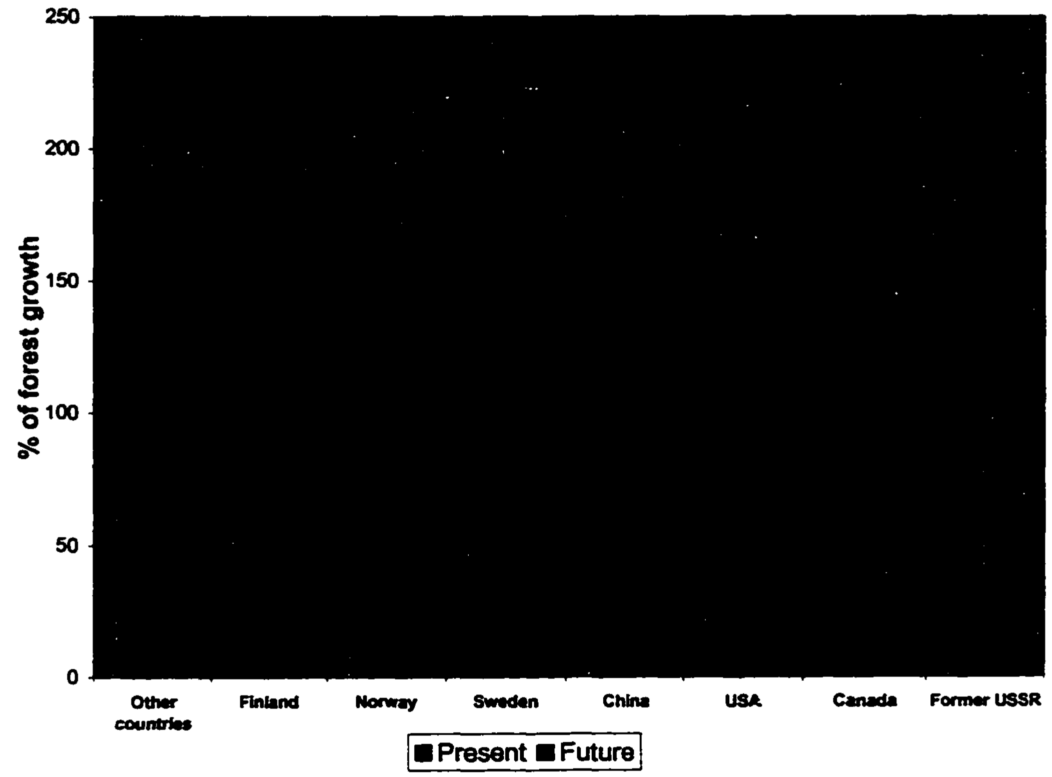

Figure 9. Timber extraction as a percentage of forest growth (corrected for harvest efficiency) for different countries

The literature, however, provided evidence that these factors might be additional important drivers of elevated forest productivity in these countries. The forest growth analysis conducted in Finland showed an increase of more than 40% in annual forest volume growth from 1950 to 1990 (Mielikäinen & Sennov 1996). Moreover, a steady increase in the estimated productivity of forested lands was documented by the Swedish National Forest Inventory since the inventory began in 1923 (Elfving *et al.* 1996). A relative increase of about 60% was observed in this country between 1920 and 1990. Although in both cases changes in silvicultural practices and stand structure were suggested as the main reasons for this increase, global change was on the list of possible causes as well.

Table 4. Modelled stem primary productivity of coniferous forest (incl. harvest efficiency) for global change scenario compared to measured timber harvest in 1995 and projected timber harvest in 2060.

	Timber Harvest [$*10^6$ m^3]		*Forest Productivity*	*[$*10^6$ m^3]*
Country	In 1995	In 2060	Reference Scenario	$2xCO_2$ and Climate Change Scenario
Former USSR	91	550	394	569
Canada	158	170	351	446
USA	287	200	241	250
China	143	270	157	177
Sweden	54	100	36	45
Finland	42	60	22	29
Norway	8.5	8	12	16
Other countries	344	500	344	290
Total	**1127**	**1858**	**1503**	**1862**

Conclusions

According to model estimates, global conifer forests have currently the capacity to satisfy people's demand for softwood. At the same time, this study suggests that the gap between timber harvest and forest growth will be getting smaller and smaller in the future. The accelerated stem growth under the joint effect of climate change and elevated carbon dioxide concentration in the atmosphere will not be able to compensate for the increasing timber extraction. Unless people improve harvest efficiency and decrease timber harvest rates, we may reach the dangerous margin, when forest extraction equals growth, by the middle of the next century. Importantly, global change would have differential effects on forest productivity in different countries. The USA may reach a negative balance between forest growth and harvested softwood if the current rates of roundwood consumption increase and climate change has more adverse effects on coniferous forest productivity and mortality that this study suggested. Timber extraction may exceed forest regrowth even faster than predicted in this study if the forest cover declines. The projections for China's wood production look the most discouraging, because of deforestation (of all the countries considered here, there is an evidence for forest cover decline in China only, WRI 1996) accompanied by adverse climate change effects on forest growth. In contrast, the coniferous forests of the former USSR, the major beneficiary from predicted global change, may be producing one third of the wood to be consumed in 2060. On the other hand, given extrapolated high wood extraction rates and inefficient wood harvest techniques, the wood production in the former Soviet Union may become dangerously close to forest regrowth.

Clearly, there will be winners and losers from the ongoing global change. If Russia, the major winner, is to take the full advantage of the effects of global change on forest production, it may become the single leading producer of roundwood from coniferous trees in the next century. China and the USA, losers from global change, may become more dependent on imported wood and become the largest consumers of wood from Russian forests. The following trends corroborate these model predictions. For example, there is evidence that the total amount of roundwood imported into China from Russia increased by almost 40 percent from 1973 to 1993 (WRI 1996). In 1995, US markets were finally opened to Russian roundwood imports after the US Department of Agriculture enacted new rules lifting the ban on the import of raw logs (WRI 1996). According to these rules, Russian raw logs must be sterilized to kill pests prior to reaching US shores.

An increase in stem productivity associated with climate change and CO_2 fertilization, however, can be offset by contamination from industrial plants and uncontrolled logging of areas that can not be reforested, especially in countries with ineffective management policies and uncertain property rights. The 1986 Chernobyl nuclear power plant accident contaminated 4 million hectares of forest located within Russia, Belarus, and Ukraine. The process of logging itself is another significant source of degradation; for example, approximately 65% of Siberian forests are in the permafrost zones and are particularly sensitive to disturbances. Logging exposes frozen soils to sunlight, and once the top layer of permafrost melts, these areas often convert to swamp, making reforestation impossible. Mountain areas are also prone to soil erosion when tree cover is removed.

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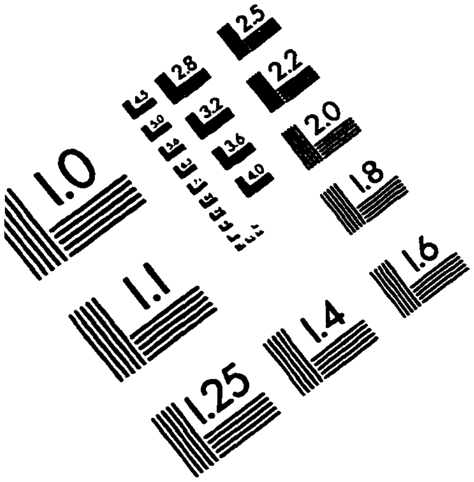
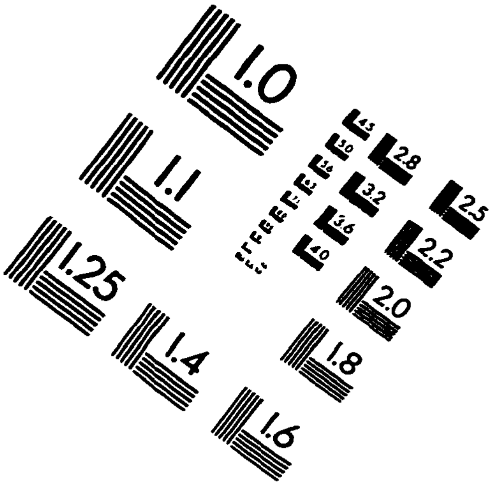
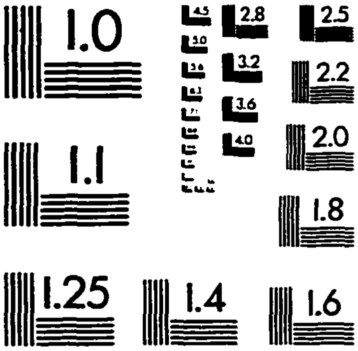
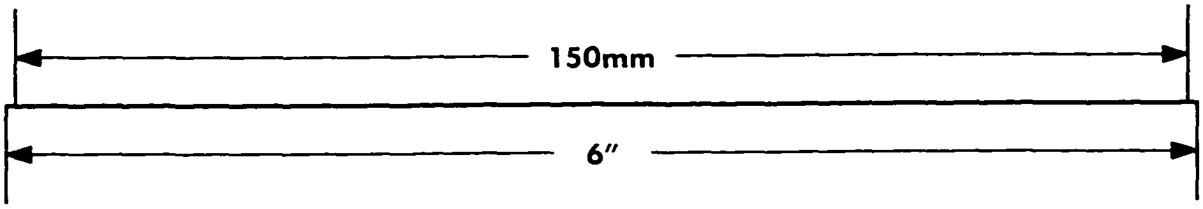
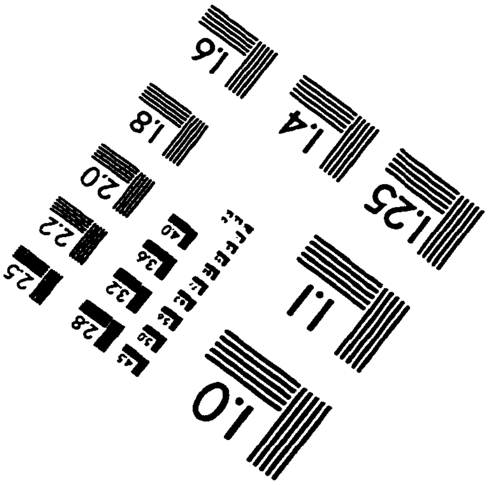
IMAGE EVALUATION TEST TARGET (QA-3)











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