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Physiological derivation of the observed relationship between net primary production and mean annual air temperature

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ABSTRACT

Empirical observations show that when examined along a climatic gradient, the annual net primary production (NPP) of terrestrial ecosystems increases with warmer mean annual air temperature (MAAT). This relationship has been used in models to calculate annual NPP and also its seasonal cycle by assuming some prescribed seasonality. However, the physiological processes causing the relationship and its applicability to climate change studies have not been examined. A mechanistic model of daily carbon exchange in forest ecosystems was used to derive the relationship between NPP and MAAT and to identify the physiological processes represented in this relationship. The model reproduced the observed empirical relationship and showed that it reflected, at least for boreal and temperate coniferous forests growing on moist soils, the length of the growing season, nitrogen limitation for NPP, and lower maintenance respiration rates in warm climates than in cold climates. NPP and the seasonal cycle of CO_2 uptake and release were relatively insensitive to the temperature dependencies of photosynthesis except at the beginning and end of the growing season. These analyses demonstrate that simple physiological assumptions can result in reasonable predictions of NPP over a wide range of climates. The seasonal cycle of CO_2 uptake and release and the empirical relationship between NPP and MAAT are consequences of the physiological assumptions and hence are validations of the NPP calculations rather than direct parameterizations of NPP. The NPP component of this model may provide the framework to integrate terrestrial carbon fluxes with the land surface schemes used in global climate models.

1. Introduction

Annual net primary production (NPP) is an important component of the carbon exchange between the atmosphere and the terrestrial biosphere, and accurately predicting the effects of air temperature and precipitation on NPP is crucial to understanding the sensitivity of terrestrial carbon storage to climatic change. Empirical relationships between annual climatic factors and annual carbon exchange may, in part, provide a simple means to parameterize terrestrial carbon exchange for global models. In particular, when gathered from a variety of climatic regions empirical observations show NPP increases with warmer mean annual air temperature (MAAT) and higher annual precipitation (Fig. 1). These empirical relationships form part of the annual NPP calculations for two global carbon cycle models (Esser, 1987; Friedlingstein et al., 1992) and can be used for seasonal calculations by assuming some seasonality to NPP (Esser, 1987). However, the physiological processes subsumed by these simple empirical relationships and their usefulness for climate change studies have not been explored.

The physiological relationships between CO_2 assimilation and environmental factors such as air temperature, photosynthetic photon flux, foliage water potential, and nitrogen concentration are well understood (Larcher, 1980; Landsberg, 1986). These principles can be incorporated into ecosystem process models and integrated from

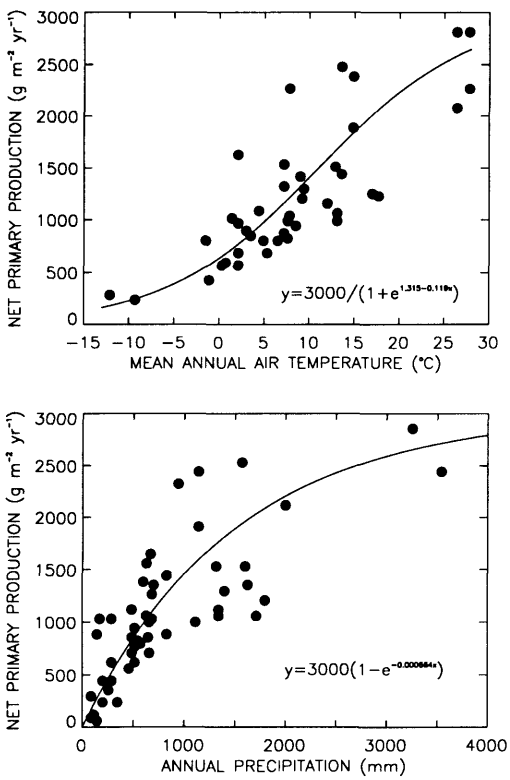

Fig. 1. Net primary production (above- and below-ground) in relationship to mean annual air temperature and annual precipitation. Data are fom Lieth (1975). Independent data for 57 sites show similar relationships (O'Neill and DeAngelis, 1981).

daily, or sub-daily, photosynthesis and respiration to annual NPP (e.g., Running and Coughlan, 1988; Running and Gower, 1991; Bonan, 1991b, 1993). Physiologically-based ecosystem process models can be criticized for their complexity (e.g., Box, 1988), but these models demonstrate that simple physiological principles can accurately simulate NPP over a wide range of climatic conditions (Running and Coughlan, 1988; Running and Nemani, 1988).

In this paper, I use the TCX (Terrestrial Carbon Exchange) forest ecosystem process model to examine the physiological controls of NPP along a climatic gradient in North America east of the Mississippi river, from subarctic Quebec to Florida. For coniferous forests growing on moist soils, I use the model to derive Lieth's empirical relationship between NPP and MAAT (Fig. 1), to identify the important physiological processes represented in this relationship, and to determine the usefulness of this relationship for climate change studies.

2. Methods

2.1. The model

The model is conceptually similar to the FOREST-BGC model (Running and Coughlan, 1988; Running and Gower, 1991). It combines the exchange of energy, heat, moisture, and momentum between forests and the atmosphere, moisture and heat flow in the soil, decomposition and nitrogen mineralization, CO_2 assimilation and respiration, and whole-tree carbon allocation to calculate the daily CO_2 balance of forest ecosystems. The simulation of surface energy exchange, soil temperature, and soil moisture has been described in Bonan (1991a). Early versions of tree and microbial CO_2 fluxes have been described in Bonan (1991b, 1992). These have been recently modified by Bonan (1993) to include a more mechanistic representation of assimilation, decomposition, and nitrogen mineralization. The model is briefly summarized below.

The exchange of energy, heat, moisture, and momentum between a forest and the atmosphere provides the overriding framework with which to study biosphere-atmosphere exchange of CO_2. The forest canopy is divided into 3 layers: an upper canopy (height h_1), a lower canopy (height h_2), and the ground surface (height $h_3 = 0$). The energy, heat, and moisture fluxes at each height are each a function of three unknown temperatures (T_1, T_2, T_3) at heights h_1, h_2, and h_3, respectively. At each height, these fluxes sum to zero, and the three equations are solved simultaneously for the unknown temperatures.

Long-wave radiation is absorbed and emitted by foliage and the ground surface in proportion to temperature raised to the fourth power. Solar radiation is divided into visible and near-infrared wavelengths and direct beam and diffuse components. Solar radiation is absorbed, transmitted, and reflected by foliage. The wind profile above and within the canopy is calculated from simple mixing theory. Sensible heat fluxes are proportional to the temperature gradient and boundary

layer and aerodynamic resistances. The boundary layer resistance controls heat flux from foliage to canopy air; the aerodynamic resistance controls heat flux between canopy heights. The boundary layer resistance increases with larger leaf size and smaller wind speeds. The aerodynamic resistance decreases as canopy height and wind speed increase. Evaporation of intercepted water is proportional to the vapor pressure gradient and the boundary layer resistance. Water loss during transpiration is proportional to the vapor pressure deficit and stomatal resistance. Stomata close when the soil is frozen or air temperature is less than -5°C and otherwise open as a continuous function of irradiance, vapor pressure deficit, and foliage water potential. As with sensible heat, an aerodynamic resistance regulates water fluxes between canopy heights.

Soil temperature and moisture are calculated for a multi-layer profile consisting of snow (if present), humus, and mineral soil. Soil temperature is calculated using an implicit finite difference solution to the heat conduction equation. Phase change (i.e., the freezing and thawing of soil) is included through an apparent heat capacity term. The water content of each soil layer is based on the difference between water input as snowmelt and throughfall and water loss through evaporation, transpiration, and drainage. Water accumulates as snow if air temperature is below a critical value. Snow melts based on available energy.

NPP is directly proportional to CO_2 uptake during foliage assimilation, integrated over the forest canopy, and CO_2 loss during foliage, stem, and root respiration. Bonan (1993) modified foliage assimilation to use the theory of Farquhar et al. (1980) and Farquhar and Von Caemmerer (1982) (see Appendix for details). Photosynthesis is integrated over the two canopy layers and multiplied by daylength to get the daily total. CO_2 is lost during maintenance and growth respiration. These fluxes are calculated separately for foliage, stem, and root biomass. Daily maintenance respiration is proportional to biomass and increases exponentially with canopy temperature for foliage and stem respiration and soil temperature for root respiration. Growth respiration is proportional to dry matter increment. Growth is adjusted so that a critical carbon-to-nitrogen (C:N) ratio is maintained for foliage, stem, and root biomass.

The nitrogen available to support growth is the sum of nitrogen fixation, nitrogen contained in precipitation, retranslocated nitrogen stored in plant tissue, and mineralized nitrogen. Bonan (1993) changed the calculation of decomposition and nitrogen mineralization to include the concepts of Bosatta and Ågren (1985) and Ågren and Bosatta (1987). Their work describes decomposition and nitrogen mineralization in terms of the relative quality of soil carbon, which decreases over time. The rate of decrease, and hence the rate of decomposition and nitrogen mineralization, depends on initial litter quality, soil temperature, and soil moisture.

The model has been validated using data from boreal forests near Fairbanks, Alaska. These forests consist of a variety of coniferous and deciduous stands growing on cold, wet, nutrient-poor soils underlain with permafrost and warm, mesic, nutrient rich, permafrost-free soils. Simulated soil temperatures, annual soil respiration, annual forest floor decomposition and

Table 1. *Comparison between observed and simulated aboveground tree production ($g^{-2}\ yr^{-1}$) in boreal forests near Fairbanks, Alaska*

	Observed			Simulated		
	n	range	mean ± SE	*n*	range	mean ± SE
black spruce	4	72–148	113 ± 17	9	86–234	154 ± 20
white spruce	4	238–540	366 ± 63	5	263–436	347 ± 28
quaking aspen	2	363–760	565 ± 199	2	366–756	561 ± 195
paper birch	3	343–572	470 ± 61	2	438–641	539 ± 102
balsam poplar	3	264–952	552 ± 206	3	512–649	599 ± 44

Simulated and observed data are not significantly different at $p = 0.05$.
See Bonan (1993) for more details.

nitrogen mineralization, annual above-ground tree production, and annual moss production were not significantly different from observed data (Bonan, 1993). The fraction of soil respiration that was due to roots was also consistent with observed data. The model also successfully reproduced features of observed fertilization, soil warming, and litter transplant experiments in these forests. An example model validation is shown in Table 1.

2.2. *Climate data*

The model requires daily averaged air temperature, precipitation, vapor pressure, cloudiness, wind speed, and air pressure. These data were estimated from long-term climatological monthly means for 35 sites located from subarctic Quebec to Florida in North America east of the Mississippi river (Court, 1974; Hare and Hay, 1974). MAAT ranged from -3°C to 21°C.

Daily rainfall was estimated from a combination Markov chain-probability distribution model (e.g., Richardson, 1981). A given day was wet or dry based on the conditional probabilities of a wet day given the previous day was wet or dry. These conditional probabilities were estimated from the number of wet days in a month (Geng et al., 1986). Precipitation for a wet day was estimated from a two-parameter gamma distribution based on the mean precipitation for that month and assuming the variance equals the mean. For each site, daily precipitation was generated for 100 years, and the average daily precipitation was used to approximate the climatological mean daily precipitation.

Daily air temperature and vapor pressure were estimated from monthly means through linear interpolation, assuming the midday of each month had a value equal to the monthly mean. For lack of better data, daily cloudiness for a particular month was set equal to the monthly mean. No attempt was made to account for correlations among precipitation, temperature, vapor pressure, and cloudiness. That is, I assumed NPP was more related to seasonal changes in temperature, vapor pressure, and cloudiness that to day-to-day variation caused by the occurrence of rain.

Simulated NPP is insensitive to small changes in air pressure and wind speed (Bonan, 1992). Neither of these varied greatly seasonally or among climate stations. Both were held constant with an air pressure of 101,300 Pa and a wind speed of 4 m s^{-1}. Ambient CO_2 concentration was 340 μmol mol^{-1}. Intercellular O_2 concentration was 0.209 mol mol^{-1}.

2.3. *Vegetation and soil parameters*

Following the approach of Running and Coughlan (1988) and Running and Nemani (1988), required vegetation and soil parameters were constant for all 35 sites; only climate varied from site-to-site. Stand parameters were set to a leaf area index (projected area) of 3 m^2 m^{-2}, a stem biomass of 11,111 g m^{-2}, and a root biomass of 1667 g m^{-2}. Each stand was located on a horizontal surface with a 25-m canopy height and a 5-cm humus layer. Soils were fine-grained, with

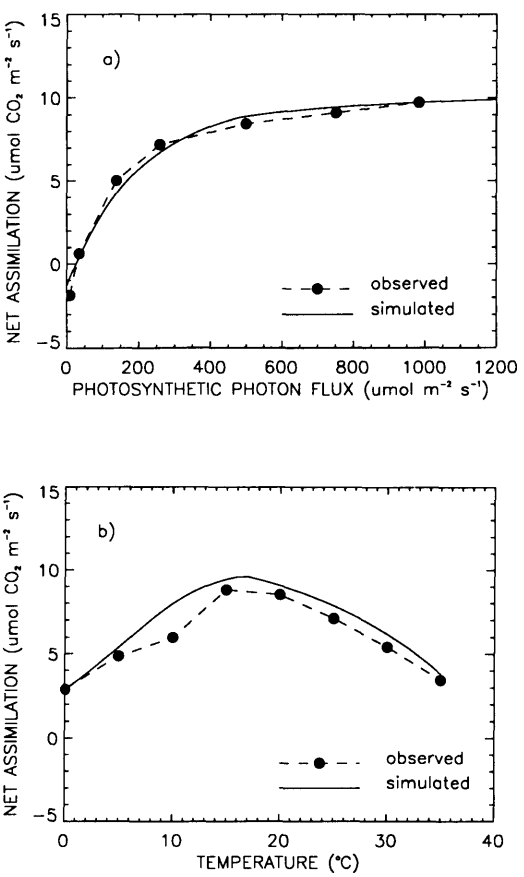

Fig. 2. Observed and simulated net foliage CO_2 assimilation per unit leaf area. (a) photosynthetic photon flux response at 15°C. (b) temperature response at a photon flux density 740 μmol m^{-2} s^{-1}. See Bonan (1993) for more details.

volumetric moisture contents of 50.2%, 19.1%, and 7.1% at saturation, field capacity, and wilting point, respectively. Moisture contents were initialized at field capacity. Each stand had approximately 40 g N m^{-2} in the forest floor. There was no mineral soil nitrogen. Nitrogen input from precipitation was 0.35 g N m^{-2} yr^{-1}. Nitrogen fixation was set to zero.

Physiological parameters for white spruce (*Picea glauca* (Moench.) Voss), as estimated by Bonan (1993), were used for the simulations. Appropriate values for photosynthesis are $V_{cmax,25} = 412\ \mu$mol CO_2 m^{-2} s^{-1}, $J_{max,25} = 210\ \mu$mol photons m^{-2} s^{-1}, $K_{o,25} = 15500$ Pa, $K_{c,25} = 31$ Pa, $a_{vcmax} = 5.6$, $a_{jmax} = 1.7$, $a_{ko} = 1.2$, and $a_{kc} = 2.1$. These parameters provide a reasonable fit between observed and simulated foliage assimilation (Fig. 2). Relative allocation of carbon to foliage, stem, and root growth are 0.18, 0.32, and 0.50, respectively. Carbon-to-nitrogen (C:N) ratios for foliage, stem, and root biomass are 66:1, 370:1, and 325:1, respectively. As in Running and Coughlan (1988) and Running and Nemani (1988), respiration rates were adjusted so that annual maintenance respiration at the warmest site was 30% of annual canopy assimilation. For a given temperature, this resulted in maintenance respiration rates that were 82.5% lower than the parameters given in Bonan (1993) (Fig. 3).

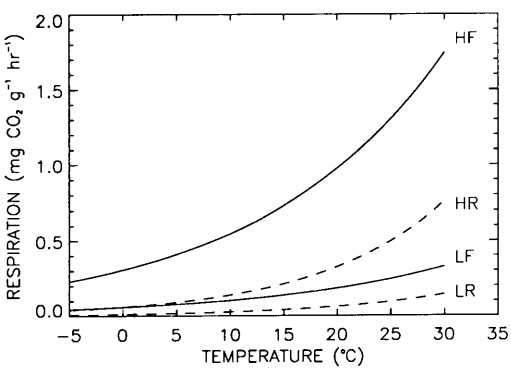

Fig. 3. Foliage and root maintenance respiration rates per unit gram biomass as a function of temperature. High foliage (HF) and high root (HR) rates were used in Bonan (1993). The current analyses used low foliage (LF) and low root (LR) rates. Stem maintenance respiration is 100 times less than foliage and root respiration and for convenience is not shown.

3. Results and discussion

3.1. Net primary production

With the low respiration rates and with approximately 40 g N m^{-2} in the forest floor, simulated NPP as a function of MAAT was similar to the Lieth relationship (Fig. 4). The most striking difference was that Lieth's data showed much more scatter about his empirical relationship than did the simulated data. For Lieth's observed data, the average squared deviation from his empirical relationship was 160,609. The average squared deviation of simulated NPP from the Lieth relationship was only 20,729. This reflects the fact that Lieth's data came from a variety of sites. In some of these sites, soil moisture may have limited growth. However, soil moisture did not limit NPP for the simulated sites. Moreover, Lieth's data may have come from forests in different stages of development whereas forest structure was constant for all the simulated sites. So presumably the simulated sites did not reflect the same range of conditions as Lieth's sites.

The correspondence of simulated NPP with Lieth's empirical relationship reflected two features. First, maintenance respiration rates (per unit biomass and for a given temperature) were adjusted so that annual maintenance respiration was equal to 30% of annual gross canopy assimilation at the warmest site. For a given temperature, this resulted in maintenance respiration rates (per unit biomass) that were 82.5% lower

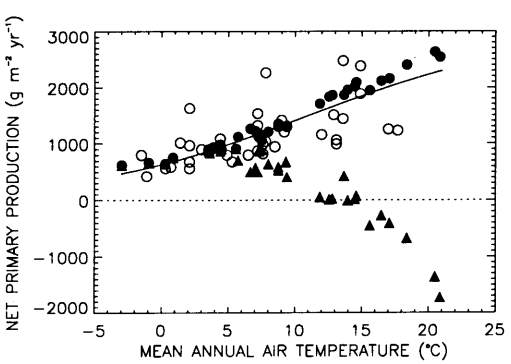

Fig. 4. Observed and simulated NPP in relationship to MAAT. ○: observed data (Lieth, 1975). ●: simulated NPP for low respiration rates. ▲: simulated NPP for high respiration rates. The solid line is Lieth's (1975) empirical relationship.

than the rates used in Bonan (1993) for white spruce growing near Fairbanks, Alaska (Fig. 3). When maintenance respiration was increased to the higher values, there was no difference in NPP for sites with MAAT < 5°C (Fig. 4). However, the increased respiration loss caused a lower NPP for sites with MAAT > 5°C, and for sites with MAAT greater than approximately 12°C respiration exceed CO_2 uptake during photosynthesis (i.e, there was a negative NPP).

For sites with MAAT < 5°C, simulated NPP was insensitive to the prescribed high or low rates of maintenance respiration. However, for sites with MAAT > 5°C, correspondence with Lieth's relationship required a low rate of maintenance respiration. Thus, to match Lieth's observed relationship the trees growing in a cold climate had to have a rate of maintenance respiration (per unit biomass and for a given temperature) that was greater than or equal to that of trees growing in a warm climate. An important component of Lieth's relationship, therefore, is the physiological distinction between cold- and warm-adapted plants in their respiration rates. Experimental studies suggest that this distinction is real. Empirical data for *Pinus radiata* and Arctic and mountain ecotypes of *Oxyria digyna* show a similar temperature dependency of respiration (Larcher, 1980; Figs. 3.41 and 3.43) in which respiration rates per unit mass and at a given temperature were lower for warm-adapted plants than for cold-adapted plants.

Available nitrogen was another factor affecting agreement with Lieth's relationship. At each site, 40 g N m^{-2} was available to be mineralized. The actual amount mineralized depended on soil moisture and soil temperature. When the nitrogen pool was increased so that nitrogen did not limit growth, simulated NPP was overestimated compared to Lieth's relationship (Fig. 5a). This suggests that available nitrogen sets the limit to growth at these sites. Other studies also show that nitrogen limitation to NPP is common in forest

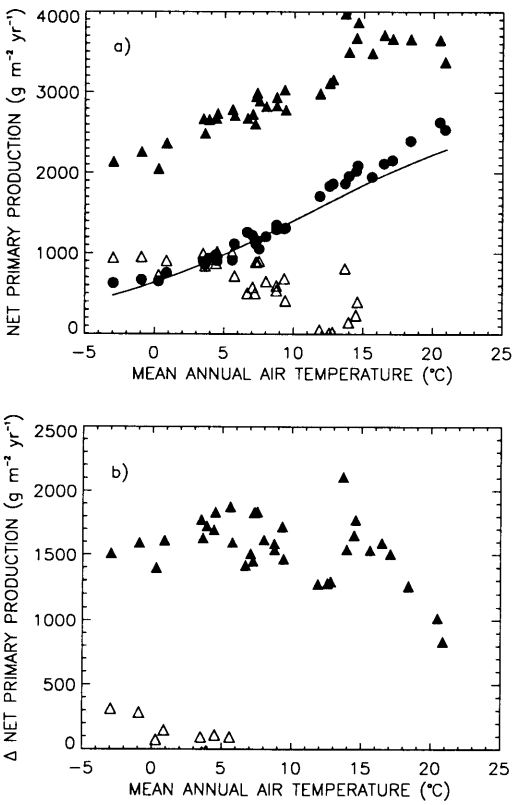

Fig. 5. (a) Simulated NPP in relationship to MAAT. ● : low respiration NPP when nitrogen limited tree growth. ▲ : low respiration NPP when tree growth was not limited by nitrogen. △ : high respiration NPP when tree growth was not limited by nitrogen (only for sites with NPP > 0). The solid line is Lieth's (1975) empirical relationship. (b) Increase in NPP, relative to simulation "●" in Fig. 5a, caused by removing nitrogen limitation to tree growth.

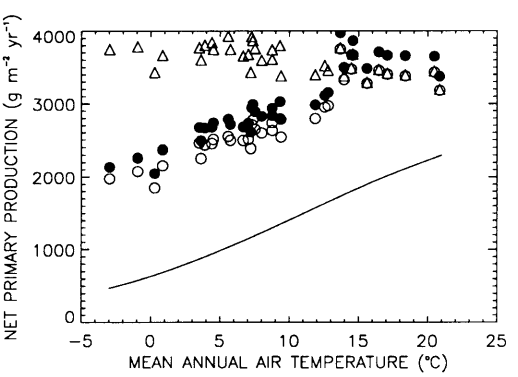

Fig. 6. Simulated NPP in relationship to MAAT when nitrogen did not limit tree growth and with low respiration rates. ● : NPP with the temperature of dependencies of assimilation and stomatal resistance. ○ : NPP when K_o, K_c, V_{cmax}, and J_{max} were independent of temperature and set to values for 25°C. △ : NPP when K_o, K_c, V_{cmax}, J_{max}, and r_s were independent of temperature. The solid line is Lieth's (1975) empirical relationship.

ecosystems (Pastor and Post, 1986; Bonan, 1990; Vitousek and Howarth, 1991; McGuire et al., 1992).

In addition, there was a significant interaction between NPP, nitrogen availability, and MAAT. With low respiration rates and for MAAT < 13°C, the increase in NPP when nitrogen did not limit tree growth was independent of temperature (Fig. 5b). However, for MAAT > 13°C the increase in NPP caused by removing the nitrogen limitation decreased with warmer temperatures. This suggests that higher rates of nitrogen mineralization in the warm climates cause NPP to be less limited by available nitrogen than in the cold climates.

There was also a significant interaction between NPP, nitrogen availability, and respiration rates in which the increase in NPP caused by unlimited nitrogen was greater for low respiration rates than for high respiration rates (Fig. 5b). In particular, for the 4 sites with MAAT < 1°C, NPP increased by 226% when nitrogen did not limit NPP and when low respiration rates were used. However, for these cold sites high respiration rates are appropriate (Bonan, 1993), and with high respiration rates NPP increased by only 30%. This is consistent with empirical fertilization studies that show aboveground production for white spruce forests near Fairbanks, Alaska, increases by approximately 50% in response to high levels of nitrogen fertilization (Van Cleve and Zasada, 1976) and modeling studies that show mean increases in NPP in response to no nitrogen limitation of approximately 50% and 25% in boreal and temperate forests, respectively (McGuire et al., 1992). Thus, it appears that cold-adapted trees, with their higher respiration rates, can respond less to nitrogen addition than warm-adapted species with the lower respiration rates.

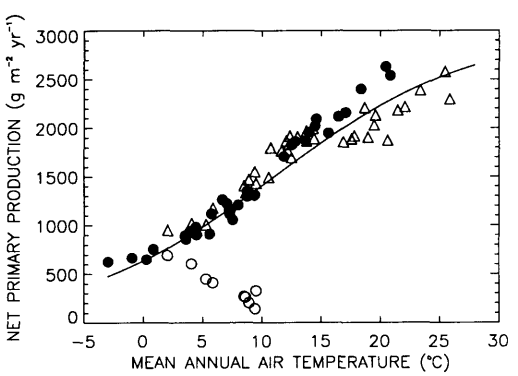

Fig. 7. Simulated NPP in relationship to MAAT when nitrogen limited tree growth. ●: NPP for long-term climatological data and with low respiration rates. △: NPP when daily air temperatures were increased by 5°C and with low respiration rates. ○: NPP when daily air temperatures were increased by 5°C and with high respiration rates. The solid line is Lieth's (1975) empirical relationship.

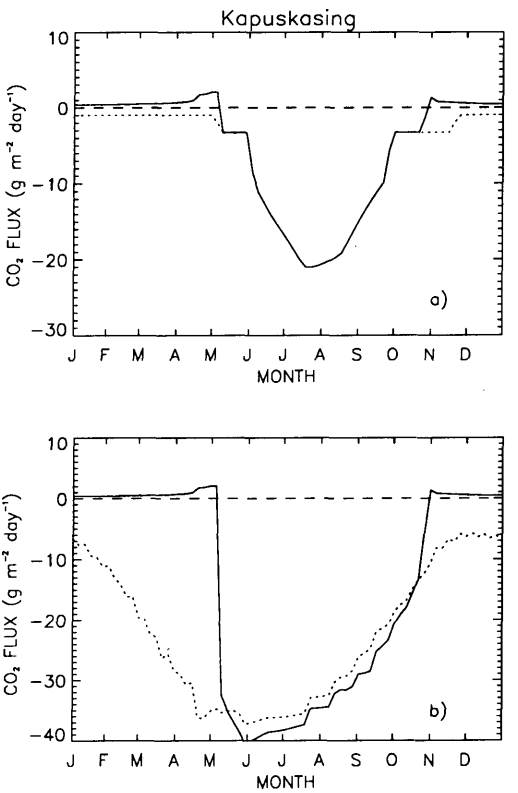

Fig. 8. Daily net tree CO_2 flux from 1 January to 31 December simulated at Kapuskasing, Ontario. Fluxes are smoothed to a 5-day average. Tick marks indicate the first day of each month. Net tree CO_2 flux is the difference between CO_2 uptake during assimilation and CO_2 loss during maintenance and growth respiration. A negative flux indicates CO_2 uptake. (a) Simulations when NPP was limited by available nitrogen. (b) Simulations when NPP was not limited by available nitrogen. —: seasonal cycle when either (1) assimilation and stomatal resistance were temperature dependent or (2) K_o, K_c, V_{cmax}, and J_{max} were independent of temperature (i.e., set to values for 25°C). ···: seasonal cycle when K_o, K_c, V_{cmax}, J_{max}, and r_s were independent of temperature.

Simulated NPP was insensitive to the temperature dependencies of photosynthesis and stomatal resistance when NPP was limited by available nitrogen. This was because annual nitrogen mineralization, not CO_2 assimilation, set the bounds on simulated NPP. When NPP was not limited by available nitrogen, NPP was sensitive to the temperature dependencies of photosynthesis and stomatal resistance, primarily to the stomatal response to temperature (Fig. 6). When K_c, K_o, J_{max},and V_{cmax} were held constant to values at 25°C, simulated NPP decreased by 183 g m^{-2} yr^{-1} at each site. When stomata were open regardless of temperature, NPP increased by as much as 1610 g m^{-2} yr^{-1}. The greatest increase was in cold regions.

To explore the relationship between MAAT and NPP, daily air temperatures were increased by 5°C for each site. With low respiration rates, the simulated NPP tended to fall along the Lieth relationship (Fig. 7). However, the deviation of the simulated data from the Lieth relationship increased. For the control simulations with the long-term climatological data, the average squared deviation of simulated NPP from Lieth's relationship was 20,729; for the +5°C simulations, the average squared deviation was 33,574. The greatest differences occurred for MAAT > 15°C, where simulated NPP was underestimated compared to Lieth's relationship. This reflected the decrease in assimilation with warmer temperatures (Fig. 2) and the exponentially increasing loss of CO_2 during respiration with warmer temperatures (Fig. 3).

For the 9 sites with MAAT < 5°C, where simulated NPP was consistent with Lieth's data regardless of whether high or low respiration rates were used (Fig. 4), the climate warming caused NPP to increase when low respiration rates were used but decrease when high respiration rates were used (Fig. 7). Low respiration rates are inconsistent with the observed physiology of cold-adapted tree species (Bonan, 1993), suggesting that at these sites climate warming will cause a decrease in NPP until the trees adjust their maintenance respiration rates to the warmer climate.

3.2. *Seasonal CO_2 fluxes*

The seasonal cycle of tree CO_2 uptake and release is illustrated for a cold and warm site. At the cold site (0.9°C MAAT), the simulations with the temperature dependencies of assimilation and stomatal resistance showed a standard seasonal cycle in which trees lost small amounts of CO_2 during the winter and took up large amounts of CO_2 during the growing season (Fig. 8a). This seasonal cycle was not sensitive to the temperature dependencies of assimilation, but was sensitive to the beginning and end of the growing season as defined by when the stomata opened or closed (Fig. 8a). The convergence of seasonal cycles during the growing season reflected the fact that nitrogen mineralization, not air temperature or irradiance, limited assimilation.

Without nitrogen limitation to plant growth, the seasonal cycle was also sensitive to changes in

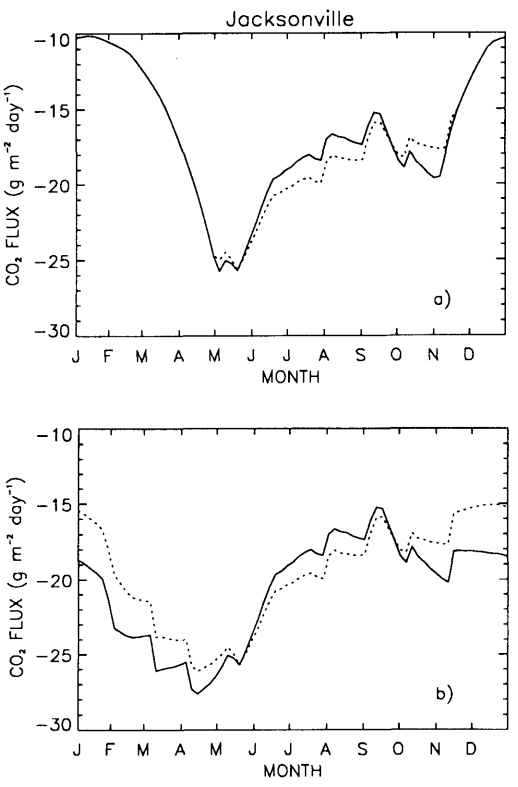

Fig. 9. Daily net tree CO_2 flux from 1 January to 31 December simulated at Jacksonville, Florida. As in Fig. 8 except —: seasonal cycle with the temperature dependencies of assimilation and stomatal resistance. ···: seasonal cycle when either (1) K_o, K_c, V_{cmax}, and J_{max} were independent of temperature (i.e., set to values for 25°C) or (2) K_o, K_c, V_{cmax}, J_{max}, and r_s were independent of temperature.

stomatal resistance (Fig. 8b). Moreover, maximum CO_2 uptake occurred in early-June and declined during the remainder of the growing season. This was in contrast to the simulations with nitrogen limiting NPP, where CO_2 uptake increased during the growing season, reaching maximum uptake in late-July and early-August (Fig. 8a).

At the warm site (20.9°C MAAT), the seasonal cycle was independent of the beginning and end of the growing season as defined by stomatal resistance because the soil was never frozen and air temperature was never below −5°C (Fig. 9). The seasonal cycle was not very sensitive to the temperature dependencies of assimilation. In both the nitrogen limited and nitrogen unlimited simulations, maximum CO_2 uptake occurred in May and declined for the remainder of the year. The most striking difference was that there was a larger decrease in CO_2 uptake during the winter months, relative to the summer months, for the nitrogen limited simulation than for when nitrogen did not limit tree growth. This reflected decreased nitrogen mineralization during the colder months.

4. Conclusion

The current analyses show that physiological models of ecosystem processes can provide meaningful insight into the factors controlling NPP. In particular, these analyses show that Lieth's empirical relationship between NPP and MAAT reflects, at least for boreal and temperate coniferous forests growing on moist soils, the length of the growing season as defined by the period in which stomata are open, nitrogen limitation for NPP, and lower respiration rates in warm climates than in cold climates. The seasonal cycle of CO_2 uptake and release is also sensitive to the beginning and end of the growing season and nitrogen limitation to tree growth. NPP and the seasonal cycle of CO_2 uptake and release are relatively insensitive to the temperature dependencies of assimilation.

Vegetation varies greatly in important physiological characteristics, both spatially over large climatic gradients and temporally with seasonal climatic changes. One of the concerns in applying detailed physiological models over large climate regions is how to account for these spatial and temporal changes in physiology. The current analyses suggest that for boreal and temperate conifer forests growing on moist soils geographic and seasonal changes in physiology are not important when calculating NPP and its seasonal cycle, except as geography affects respiration rates. That is, simple physiological assumptions can result in reasonable estimates of annual and seasonal NPP over wide climatic gradients. Independent work with the FOREST-BGC physiological ecosystem model points to a similar conclusion (Running and Coughlan, 1988; Running and Nemani, 1988).

Although the model reproduced Lieth's relationship between NPP and MAAT, these analyses show that process-based models are more general than this simple empirical relationship. In particular, the current analyses show the different sensitivity of NPP to climatic warming depending on whether maintenance respiration rates decrease with warmer climates and the different effects of nitrogen limitation on NPP for low and high maintenance respiration rates. In addition, empirical relationships can only be applied to the conditions for which they were derived. Process models allow simulation of changes in several climatic variables (e.g., temperature, precipitation, CO_2 concentration, relative humidity) and changes in physiological behavior (e.g., water use efficiency, nutrient use efficiency, carbon allocation) using known physiological principles rather than ad hoc constraints.

The empirical relationship between NPP and MAAT and an assumed seasonal cycle has been used as a parameterization of NPP for global models (Esser, 1987). In contrast, the current analyses have derived this relationship from simple physiological principles. Thus, the observed relationship between NPP and MAAT and the seasonal cycle of NPP have become tests of the model not a means to parameterize NPP. If the physiological approach can be extended to other vegetation types (e.g., savanna, tropical evergreen, tropical deciduous, grassland, tundra), it will provide a powerful research tool with which to study biosphere-atmosphere CO_2 exchange.

Although the links between canopy physiology, surface energy exchange, and gas exchange have long been recognized (e.g., Campbell 1977; Gates, 1980; Landsberg, 1986), global biosphere NPP models lack detailed surface energy exchange processes and canopy physiology (e.g., Esser,

1987; Fung et al., 1987; Box, 1988). Likewise, the initial development of land surface parameterizations for atmospheric general circulation models focused on the exchanges of energy, moisture, and momentum (Dickinson et al., 1986; Sellers et al., 1986). Carbon fluxes are only now being incorporated into these models (Dickinson, pers. comm.; Sellers, pers. comm.). This study suggests that this will be a fruitful approach.

5. Appendix

The temperature dependencies of several physiological parameters that define the rates of photosynthesis and respiration were removed to examine their importance when calculating NPP. For clarity, these parameters are defined below. The reader is referred to Bonan (1993) for a complete description of the model.

The rate of gross CO_2 assimilation per unit foliage area, A (μmol CO_2 m^{-2} s^{-1}), is

$$A = (1 - \Gamma_*/C_i) \min\{W_c, W_j\} \quad (1)$$

where W_c and W_j are the Rubisco-limited and RuBP regeneration-limited rates of carboxylation, respectively (μmol CO_2 m^{-2} s^{-1}), Γ_* is the CO_2 compensation point (Pa), and C_i is the partial pressure of CO_2 in the chloroplast (Pa). The Rubisco-limited rate of carboxylation is

$$W_c = \frac{V_{cmax} C_i}{C_i + K_c(1 + O_i/K_o)}, \quad (2)$$

where V_{cmax} is the maximum rate of carboxylation (μmol CO_2 m^{-2} s^{-1}), O_i is the partial pressure of oxygen in the chloroplast (Pa), and K_c and K_o are the Michaelis-Menten constants for CO_2 and O_2, respectively (Pa). The maximum rate of carboxylation allowed by the capacity to regenerate RuBP is:

$$W_j = \frac{JC_i}{4C_i + 8\Gamma_*}, \quad (3)$$

where J is a potential rate of electron transport (μmol electrons m^{-2} s^{-1}). J varies with absorbed photosynthetic photon flux I_a (μmol photons m^{-2} s^{-1}) as

$$0.7J^2 - [J_{max} + 0.38I_a]\, J + J_{max}\, 0.38I_a = 0, \quad (4)$$

where J is the smaller of the 2 roots and J_{max} is the maximum potential rate of electron transport (μmol electrons m^{-2} s^{-1}). Intercellular CO_2 is eliminated from eq. (1) by

$$A = \frac{C_a - C_i}{1.37r_b + 1.65r_s} \frac{1}{P}, \quad (5)$$

where P is the ambient air pressure (Pa) and r_b and r_s are the boundary layer and stomatal resistances to water vapor diffusion, respectively (s m^2 μmol^{-1} H_2O).

The parameters K_c, K_o, Γ_*, V_{cmax}, and J_{max} vary with temperature. A general temperature response is

$$p = p_{25} a_p^{(T-25)/10} \quad (6)$$

where p_{25} is the value of a given parameter at 25°C and T is temperature (°C). Carboxylation is inhibited at high temperatures, and V_{cmax} and J_{max} from eq. (6) are multiplied by the function $f(T)$, which mimics thermal breakdown of metabolic processes

$$f(T) = \left\{1 + \exp\left[\frac{-220000 + 710(T+273)}{8.314(T+273)}\right]\right\}^{-1}. \quad (7)$$

The CO_2 compensation point is:

$$\Gamma_* = \frac{1}{2} 0.21 O_i \frac{K_c}{K_o}. \quad (8)$$

Stomata are fully open for $T \geq -5$°C, and fully closed for T < -5°C. Maintenance respiration rates (μmol CO_2 g^{-1} s^{-1}) increase with higher temperatures according to eq. (6), although respiration rates at 25°C vary for foliage, stem, and root biomass.

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REFERENCES

Ågren, G. I. and Bosatta, E. 1987. Theoretical analysis of the long-term dynamics of carbon and nitrogen in soils. *Ecology* **68**, 1181–1189.

Bonan, G. B. 1990. Carbon and nitrogen cycling in North American boreal forests. II. Biogeographic patterns. *Can. J. For. Res.* **20**, 1077–1088.

Bonan, G. B. 1991a. A biophysical surface energy budget analysis of soil temperature in the boreal forests of interior Alaska. *Water Resour. Res.* **27**, 767–781.

Bonan, G. B. 1991b. Atmosphere-biosphere exchange of carbon dioxide in boreal forests. *J. Geophys. Res.* **96D**, 7301–7312.

Bonan, G. B. 1992. Comparison of atmospheric carbon dioxide concentration and metabolic activity in boreal forest ecosystems. *Tellus* **44B**, 173–185.

Bonan, G. B. 1993. Physiological controls of the carbon balance of boreal forest ecosystems. *Can. J. For. Res.*, in press.

Bosatta, E. and Ågren, G. I. 1985. Theoretical analysis of decomposition of heterogeneous substrates. *Soil Biol. Biochem.* **17**, 601–610.

Box, E. O. 1988. Estimating the seasonal carbon source-sink geography of a natural, steady-state terrestrial biosphere. *J. Appl. Meteorol.* **27**, 1109–1124.

Campbell, G. S. 1977. *An introduction to environmental biophysics.* New York: Springer-Verlag.

Court, A. 1974. The climate of the conterminous United States. In: *Climates of North America. World survey of climatology vol. 11* (eds. R. A. Bryson and F. K. Hare). Amsterdam: Elsevier, 193–343.

Dickinson, R. E., Henderson-Sellers, A., Kennedy, P. J. and Wilson, M. F. 1986. *Biosphere-atmosphere transfer scheme (BATS) for the NCAR Community Climate Model.* Tech. Note NCAR/TN-275 + STR. Boulder, Colorado: Nat. Center for Atmos. Res.

Esser, G. 1987. Sensitivity of global carbon pools and fluxes to human and potential climatic impacts. *Tellus* **39B**, 245–260.

Farquhar, G. D. and von Caemmerer, S. 1982. Modelling of photosynthetic response to environmental conditions. In: *Physiological plant ecology (II). Water relations and carbon assimilation. Encyclopedia of plant physiology vol. 12B* (eds. O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler). Berlin: Springer-Verlag, 549–587.

Farquhar, G. D., von Caemmerer, S. and Berry, J. A. 1980. A biochemical model of photosynthetic CO_2 assimilation in leaves of C_3 species. *Planta* **149**, 78–90.

Friedlingstein, P., Delire, C., Müller, J. F. and Gérad, J. C. 1992. The climate induced variation of the continental biosphere: a model simulation of the last glacial maximum. *Geophys. Res. Let.* **19**, 897–900.

Fung, I. Y., Tucker, C. J. and Prentice, K. C. 1987. Application of advanced very high resolution radiometer vegetation index to study atmosphere-biosphere exchange of CO_2. *J. Geophys. Res.* **92**, 2999–3015.

Gates, D. M. 1980. *Biophysical ecology.* New York: Springer-Verlag.

Geng, S., Penning de Vries, F. W. T. and Supit, I. 1986. A simple method for generating daily rainfall data. *Agric. For. Meteorol.* **36**, 363–376.

Hare, F. K. and Hay, J. E. 1974. The climate of Canada and Alaska. In: *Climates of North America. World survey of climatology vol. 11* (eds. R. A. Bryson and F. K. Hare). Amsterdam: Elsevier, 49–192.

Landsberg, J. J. 1986. *Physiological ecology of forest production.* New York: Academic Press.

Larcher, W. 1980. *Physiological plant ecology*, 2nd Edition. Berlin: Springer-Verlag.

Lieth, H. 1975. Modeling the primary productivity of the world. In: *Primary productivity of the biosphere* (eds. H. Lieth and R. H. Whittaker). New York: Springer-Verlag, 237–263.

McGuire, A. D., Melillo, J. M., Joyce, L. A., Kicklighter, D. W., Grace, A. L., Moore, B. III and Vorosmarty, C. J. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles* **6**, 101–124.

O'Neill, R. V. and DeAngelis, D. L. 1981. Comparative productivity and biomass relations of forest ecosystems. In: *Dynamic properties of forest ecosystems* (ed. D. E. Reichle). Cambridge: Cambridge Univ. Press, 411–449.

Pastor, J. and Post, W. M. 1986. Influence of climate, soil moisture, and succession on forest carbon and nitrogen cycles. *Biogeochemistry* **2**, 3–27.

Richardson, C. W. 1981. Stochastic simulation of daily precipitation, temperature, and solar radiation. *Water Resour. Res.* **17**, 182–190.

Running, S. W. and Coughlan, J. C. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange and primary production processes. *Ecol. Modelling* **42**, 125–154.

Running, S. W. and Gower, S. T. 1991. FOREST-BGC, a general model of forest ecosystem processes for

regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* **9**, 147–160.

Running, S. W. and Nemani, R. R. 1988. Relating seasonal patterns of the AVHRR vegetation index to simulated photosynthesis and transpiration of forests in different climates. *Remote Sens. Environ.* **24**, 347–367.

Sellers, P. J., Mintz, Y., Sud, Y. C. and Dalcher, A. 1986. A simple biosphere model (SiB) for use within general circulation models. *J. Atmos. Sci.* **43**, 505–531.

Van Cleve, K. and Zasada, J. 1976. Response of 70-year-old white spruce to thinning and fertilization in interior Alaska. *Can. J. For. Res.* **6**, 145–152.

Vitousek, P. M. and Howarth, R. W. 1991. Nitrogen limitation on land and in the sea: How can it occur? *Biogeochemistry* **13**, 87–115.