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A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems

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Summary. PnET is a simple, lumped-parameter, monthly-time-step model of carbon and water balances of forests built on two principal relationships: 1) maximum photosynthetic rate is a function of foliar nitrogen concentration, and 2) stomatal conductance is a function of realized photosynthetic rate. Monthly leaf area display and carbon and water balances are predicted by combining these with standard equations describing light attenuation in canopies and photosynthetic response to diminishing radiation intensity, along with effects of soil water stress and vapor pressure deficit (VPD). PnET has been validated against field data from 10 well-studied temperate and boreal forest ecosystems, supporting our central hypothesis that aggregation of climatic data to the monthly scale and biological data such as foliar characteristics to the ecosystem level does not cause a significant loss of information relative to long-term, mean ecosystem responses. Sensitivity analyses reveal a diversity of responses among systems to identical alterations in climatic drivers. This suggests that great care should be used in developing generalizations as to how forests will respond to a changing climate. Also critical is the degree to which the temperature responses of photosynthesis and respiration might acclimate to changes in mean temperatures at decadal time scales. An extreme climate change simulation (+3°C maximum temperature, –25% precipitation with no change in minimum temperature or radiation, direct effects of increased atmospheric CO₂ ignored) suggests that major increases in water stress, and reductions in biomass production (net carbon gain) and water yield would follow such a change.

Key words: Conductance – Foliar nitrogen – Water balance – LAI

One goal of global change research is the development of models that can predict the effects of simultaneous changes in several environmental variables on the inter-

actions among several critical ecosystem processes. Reaching this goal will require that models of individual processes or sets of processes be as simple as possible while still capturing the essential dynamics of those processes. To be applied extensively, these models must also require only a few widely available parameters as input.

One critical set of interactions in terrestrial ecosystems is that between the development of leaf area within the canopy and the exchanges of carbon and water between that canopy and the atmosphere. Relatively few models provide estimates of both water and carbon balances for forest ecosystems for annual or longer periods (e.g. Running and Coughlan 1988; McMurtrie et al. 1990; Pastor and Post 1986). These models generally drive water balances with equations from soil and atmospheric physics (e.g. the Penman-Montieth equation) or large-scale hydrology (e.g. the Thornthwaite-Mather equation), and drive carbon gain separately with physiological data on photosynthesis or tree growth. The two processes are incompletely coupled in such models (cf. physiological model of Tenhunen et al. 1990).

Ecophysiological research over the last decade has provided a new synthesis of the interactions among foliar nitrogen content, photosynthetic rate, leaf longevity and stomatal conductance (e.g. Mooney and Gulmon 1982; Field and Mooney 1986; Evans 1989). These relationships offer a useful approach to the development of relatively simple models that explicitly link carbon gain, transpiration and the development of canopy leaf area, and that emphasize the nature and degree of biological control over transpiration.

In this paper, a simple, monthly-time-step model of water and carbon fluxes which makes use of these relationships (PnET) is presented and applied to 10 temperate and boreal forest ecosystems. The model minimizes the number of input parameters required, but captures important interactions between nitrogen availability (as represented by foliar N concentrations) and leaf physiology, as they affect photosynthesis and transpiration.

PnET is similar to the CENTURY model (Parton et al. 1988) in that it operates at a monthly time-step, uses a single set of parameters to define the physiology of the

plant community, produces biomass only by tissue type (e.g. foliage, wood and fine roots), and predicts seasonal changes in leaf area display in response to climatic drivers. It is also similar in structure to the carbon and water portion of the FOREST-BGC and BIOMASS models (Running and Coughlan 1988; McMurtrie et al. 1990), but differs from these in the methods used to link the photosynthetic and transpiration processes, and in that a monthly, rather than a daily, time step is used.

PnET borrows conceptually from the MAGIC model of Cosby et al. (1985) and the nutrient flux density models of Agren and Bosatta (1988), in that an effort has been made to retain only as much structural complexity as is required to capture the major dynamics in the ecosystems. In a sense, this model is a test of the hypothesis that a monthly-time-step, lumped-parameter (Federer and Lash 1978a; Cosby et al. 1986) model can capture the essential variation among ecosystems and across seasons that are relevant to the monthly water and carbon balances of forest ecosystems (see discussions on the relevance of lumped-parameter models for large-scale models by Hunt et al. 1991, McNaughton and Jarvis 1991 and Dickinson et al. 1991).

The leaf nitrogen-photosynthesis-transpiration relationship

Several papers by Mooney and coworkers (summarized in Field and Mooney 1986) have identified a generalized relationship between foliar nitrogen content and rates of maximum net photosynthesis. We examined the literature for similar data from major broad-leaved species of eastern North American forests. While studies reporting both photosynthetic rates and foliar nitrogen content are relatively rare, data from Reich et al. 1990; Hinkley et al. 1978; Amthor et al. 1990; Bahari et al. 1985; Abrams et al. 1990; and Aubuchon et al. 1978 yield the equation:

$$\text{NetPsn}_{\text{Max}} = -5.98 + 4.86 * \text{N}\% \quad (1)$$

$(n = 20, R^2 = .44, p = .0002)$

where $\text{NetPsn}_{\text{Max}}$ is maximum net photosynthesis in $\mu\text{mole CO}_2 \cdot \text{m}^{-2} \text{ leaf area} \cdot \text{sec}^{-1}$ and $\text{N}\%$ is percent nitrogen in foliage (dry weight).

Data in the literature demonstrate an even stronger relationship between the absolute rate of net photosynthesis and measured leaf conductance in C_3 plants (Amthor et al. 1990; Bahari et al. 1985; Abrams et al. 1990; Aubuchon et al. 1978; Hinkley et al. 1978; Reich et al. 1990; Schulze and Hall 1982). Based on this concept, Sinclair et al. (1984, see also Tanner and Sinclair 1983 and Bierhuizen and Slatyer 1965), conclude that water use efficiency (WUE) should vary only with atmospheric water vapor and CO_2 concentrations. If atmospheric CO_2 is considered a constant, then WUE becomes a function only of vapor pressure deficit (VPD) and has the form:

$$\text{WUE} = \text{WUEConst}/\text{VPD} \quad (2)$$

where WUEConst is a constant, WUE is water use efficiency in $\text{mg C fixed per g H}_2\text{O transpired}$ and VPD is vapor pressure deficit in kPa . Baldocchi et al. (1987) applied this theory to eddy-correlation data from a decid-

uous forest and determined that a calculated value of 10.9 for WUEConst was not inconsistent with measured values. A similar value (10.4) has been reported for soybeans (Zur and Jones 1984).

Using these two relationships (photosynthesis as a function of foliar N and WUE as a function of VPD) greatly simplifies the calculation of transpiration in the PnET model, and provides a direct link between carbon gain and transpiration (see also discussion by Monteith 1988).

Structure of the model

General

PnET operates at a monthly time step, and has no specified spatial dimension. It is applied here at the stand-to-small watershed scale.

There are 5 compartments in the model, and 11 fluxes, 3 for carbon and 8 for water (Fig. 1, net photosynthesis includes separation of daytime and nighttime carbon fluxes). All fluxes are calculated monthly except carbon allocation to wood and fine roots, to which excess carbon accumulated by net photosynthesis is allocated at the end of the year.

There are four major computational components to PnET. Climate calculations are performed first in each month. This routine uses latitude, month, average maximum and minimum temperature and measured insolation to compute vapor pressure deficit, day-length, mean daytime and nighttime temperatures, and radiation per second of daylight period.

The foliage production routine uses radiation, temperature, water stress during the previous month and nitrogen content of foliage to derive a potential gross photosynthesis rate and day and night respiration rates for leaves at the top of the canopy. These are combined with a light attenuation coefficient, a photosynthetic light response curve, and foliar longevity to determine the production and shedding of foliar mass, and a potential gross photosynthesis (in the absence of water stress) for the whole canopy.

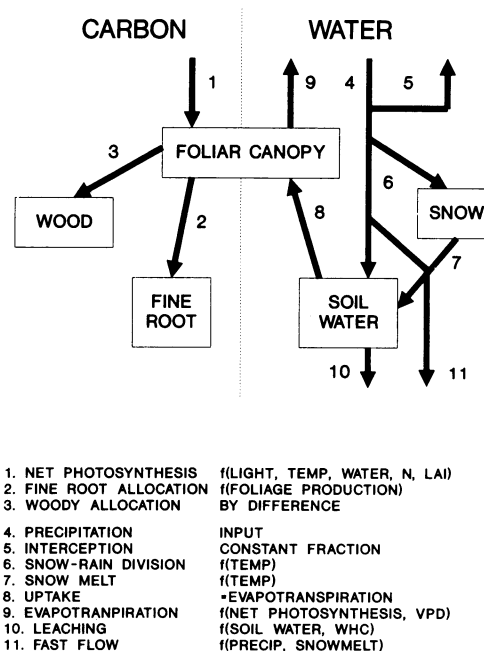


Fig. 1. Compartments, flow paths, and controlling variables within the PnET model

The carbon and water balance routine partitions precipitation between rain and snow, calculates snowmelt, total water input to the soil, and a fast, non-Darcian, drainage volume to determine water availability over the month. It then performs a numerical integration (daily time step) of water inputs to soil and transpirational demand (a function of gross photosynthesis and WUE from Eq. 2) over the month to produce changes in water storage, the degree of actual water stress on vegetation, and realized transpiration and net photosynthesis. Water remaining beyond water holding capacity at the end of this integration is drained away.

Finally, the carbon allocation routine accumulates carbon canopy gain over a year and allocates this to wood and root tissues. Net primary production of these tissues is calculated, but not accumulated year-to-year. PnET does not at this time produce successional patterns of biomass accumulation.

Environmental calculations

All calculations for a month time period are made on the basis of an average day represented by mean climatic conditions for that month. DayLength (seconds) is calculated from latitude and day-of-year (midpoint of each month) using equations from Swift (1976) and Sellers (1965). Maximum and minimum temperatures are used to calculate a mean daily temperature (T_{mean}), and mean daytime and nighttime temperatures:

$$T_{\text{day}} = (T_{\text{mean}} + T_{\text{max}})/2 \quad (3)$$

$$T_{\text{night}} = (T_{\text{mean}} + T_{\text{min}})/2 \quad (4)$$

Daytime and nighttime temperatures are used in calculations of leaf respiration and photosynthesis. Vapor pressure deficit (VPD) is the difference between the saturated vapor pressures at T_{day} and T_{min} using the equation of Murray (1967). Daily solar radiation (I_0) is converted to a per second value by dividing by DayLength.

Foliage production and estimated gross photosynthesis and day and night foliar respiration

Maximum photosynthesis and respiration per unit leaf area. Maximum net photosynthesis for broad-leaved, deciduous forests is calculated as in Eq. 1. Insufficient data were found to derive a similar relationship for needle-leaved evergreen species. For these, a maximum rate for net photosynthesis of field grown trees from the literature was used for the dominant species in each forest types.

Basal respiration of foliage is assumed to be 10% of the maximum net photosynthesis rate, so

$$\text{GrossPsn}_{\text{max}} = 1.1 * \text{NetPsn}_{\text{max}} \quad (5)$$

Resp_{day} and $\text{Resp}_{\text{night}}$ are calculated as 0.1 times $\text{NetPsn}_{\text{max}}$ modified by a Q_{10} factor of 2 using 20°C as the reference temperature and T_{day} and T_{night} respectively as actual temperatures. $\text{GrossPsn}_{\text{max}}$ and Resp_{day} are multiplied by DayLength (in seconds) and $\text{Resp}_{\text{night}}$ by $(86400 - \text{DayLength})$ to obtain values in $\mu\text{moles CO}_2 \cdot \text{m}^{-2} \cdot \text{leaf} \cdot \text{day}^{-1}$.

Maximum gross photosynthesis per unit leaf area is modified for suboptimal environmental conditions as:

$$\text{GrossPsn} = \text{GrossPsn}_{\text{max}} * \text{DTemp} * \text{DWater} * \text{DVPD} \quad (6)$$

where DTemp, DWater and DVPD vary between 0 and 1 and express the effects of temperature, water availability and vapor pressure deficit.

Temperature effects on gross photosynthesis (DTemp) are described by the parabolic equation:

$$\text{DTemp} = \frac{(\text{PsnT}_{\text{Max}} - T_{\text{day}})(T_{\text{day}} - \text{PsnT}_{\text{Min}})}{(\text{PsnT}_{\text{Max}} - \text{PsnT}_{\text{Min}})^2} \quad (6)$$

where DTemp is a factor between 0 and 1, PsnT_{Max} and PsnT_{Min} are

the maximum and minimum temperatures at which net photosynthesis occurs and T_{day} is the mean daytime temperature. In addition, DTemp is set to 0 for any month in which T_{min} is below 0. DWater expresses the effect of soil water stress on stomatal closure. For the calculation of leaf area display in this month, DWater is set to the mean level of water stress experienced in the previous month (see carbon and water balance section for determination of water stress).

DVPD expresses the direct effect of vapor pressure deficit on stomatal conductance, and hence on both photosynthesis and transpiration. The effect is generally linear, and is incorporated in PnET as a system-specific constant (VPDEffK) which reduces both net photosynthesis and transpiration as a function of VPD (Baldocchi et al. 1991):

$$\text{DVPD} = \text{VPDEffK} * \text{VPD} \quad (7)$$

where VPD is in kPa.

Light attenuation and total potential photosynthesis

GrossPsn represents a light-saturated rate of carbon fixation per day per unit leaf area under given conditions of temperature, mean water stress and VPD. This rate is converted to a whole canopy (or per unit ground area) value by defining the amount of leaf area in the stand, light attenuation and its interaction with a defined photosynthetic light response curve.

Light attenuation is calculated using the equation:

$$I_i = I_0 \cdot e^{-k(\text{LAI}_i)} \quad (8)$$

where I_i is radiation in $\text{J} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ at level i , I_0 is radiation at the top of the canopy (a monthly input parameter), k is the attenuation coefficient and LAI_i is total LAI above layer i . The effect of light on gross photosynthesis is described by the exponential function:

$$\text{LightEff} = 1.0 - e^{-(I_i \ln(2)) / \text{HalfSat}} \quad (9)$$

where LightEff is a value between 0 and 1, I_i is the radiation intensity at this level and HalfSat is the specified half saturation light level.

These equations are used in two ways. The first is to determine the amount of leaf area to be displayed, which is the value at which the bottom-most layer will have a zero net carbon balance. Computationally, this is where LightEff is low enough to reduce GrossPsn to the sum of the two respiration terms, or where:

$$\text{LightEff}_{\text{ZBal}} * \text{GrossPsn} = \text{Resp}_{\text{day}} + \text{Resp}_{\text{night}} \quad (10)$$

Then:

$$\text{LightEff}_{\text{ZBal}} = (\text{Resp}_{\text{day}} + \text{Resp}_{\text{night}}) / \text{GrossPsn} \quad (11)$$

and, from Eq. 9:

$$I_{\text{ZBal}} = -(\ln(1 - \text{LightEff}_{\text{ZBal}})) / (\ln(2) / \text{HalfSat}) \quad (12)$$

where I_{ZBal} is the light level at which gross photosynthesis equals respiration. Finally (from Eq. 8):

$$\text{LAI}_{\text{ZBal}} = \ln(I_{\text{ZBal}} / I_0) / (-k) \quad (13)$$

where LAI_{ZBal} is the LAI at which the carbon balance at the bottom of the canopy is zero for the month.

The second use of Eqs. 8 and 9 is to calculate the potential rate of carbon fixation, in the absence of water stress, for this month. For this, GrossPsn is divided by DWater (from the end of the previous month) to produce a non-water-stressed rate. This is then used in a numerical integration (100 layers) over the canopy to calculate the effect of light attenuation (Eq. 8) and photosynthetic response (Eq. 9) on total gross photosynthesis over the entire canopy. This value (PotGrossPsn in $\mu\text{moles CO}_2 \cdot \text{m}^{-2} \cdot \text{ground} \cdot \text{day}^{-1}$) is converted to $\text{g CO}_2 \cdot \text{m}^{-2} \cdot \text{ground} \cdot \text{day}^{-1}$ and is passed to the carbon and water balance routine.

To summarize, these algorithms accomplish two things. The first uses this month's temperature, radiation and VPD, and last month's soil water stress to calculate this month's leaf area display and the

production or shedding of leaf area. The second then removes the effects of water stress to calculate a non-water-stressed (or potential) rate of total gross photosynthesis for the constructed canopy.

Phenological and developmental limitations to total LAI

The above routine uses only the current month's carbon balance to determine how much leaf area is to be displayed. The assumption is that foliage will be produced whenever its carbon balance in the first month will be positive. This does not allow for the development of phenological and carbon allocation controls that might assure that a produced leaf acquired enough carbon in excess of respiration over its lifetime to "repay" the cost of producing that leaf.

Several complex carbon optimization schemes were attempted. However, two rather simple concepts are actually employed in PnET to constrain intra-annual variation in leaf area display, and to assure positive carbon balances of produced leaves.

The first is that the shedding of foliage at the end of the growing season or due to stress during the growing season, is limited to the maximum amount of foliage displayed divided by FolReten, where FolReten is the foliage retention time in years. This limits the intra-annual variation in leaf area display and reduces total carbon demand for foliage production in evergreen species. Respiration continues outside of the growing season for retained foliage.

The second concept is that it is non-adaptive to produce foliage which is not retained for the majority of the growing season (as determined by $DTemp > 0$). This is accomplished by an iterative algorithm involving two years in which a maximum LAI (LAI_{max}) for each system is calculated. In the first year of a simulation, LAI in each month is allowed to be equal to the value determined by this month's carbon balance alone (LAI_{ZBa1}). In systems with significant mid-summer soil water stress or large VPD, this means that LAI fluctuates widely over the course of the growing season. At the end of the year, LAI_{max} is calculated as the mean LAI during the growing season.

In the second year, LAI in any month is equal to the lesser of LAI_{ZBa1} and LAI_{max} . Again an average of LAI values for months with $DTemp > 0$ is calculated and this becomes the new LAI_{max} , which is used in all subsequent years, in conjunction with the limitations due to foliage retention times discussed above.

This algorithm has the effect of decreasing photosynthesis and transpiration early in the season and decreasing water stress and increasing photosynthesis late in the season (a "feed-forward" control system not unlike the direct effect of VPD on stomatal conductance), while minimizing the total carbon cost of producing foliage.

Carbon and water balances, and water availability

A simple monthly water balance is used in PnET. A constant fraction of precipitation (PrecIntFrac) is intercepted and evaporated. This includes both rain interception and evaporation (sublimation) from canopy and ground level snow. The remaining precipitation is divided between snow and rain as follows (all values are in cm). If the mean temperature for a month (t_{mean}) is above 2°C , then all precipitation is as rain. If t_{mean} is below -5°C , then all precipitation is as snow. When t_{mean} is between these two values, then:

$$\text{SnowFrac} = (T_{mean} - 2) / -7 \quad (14)$$

where SnowFrac is the fraction of precipitation falling as snow. If $T_{mean} > 1^\circ\text{C}$, then snow melt is calculated as:

$$\text{SnowMelt} = 4.5 * (T_{mean}) \quad (15)$$

which is equivalent to 0.15 cm snow melted per degree per day, a value equivalent to that produced for late winter/early spring under evergreen forests by the more detailed snowmelt routine in BROOK (Federer and Lash 1978a). When a snow pack is present and T_{mean} is less than 1°C , the value of 1°C is used in place of the actual T_{mean} to

represent the lack of soil frost due to the insulating effect of snow. The timing and quantity of snowfall and snowmelt are among the most difficult to predict from standard weather data, but also are not critical to the predictions of photosynthesis and transpiration by this model.

Inputs to the available soil water pool in a month are equal to snowmelt plus non-intercepted rainfall. However, as non-Darcian or macro-pore flow through forest soils is increasingly recognized as an important component of forest water balances, PnET contains a parameter (FastFlowFrac) which directs a constant fraction of WaterIn to drainage, by-passing the plant available soil water pool. FastFlowFrac is set to 0.1 for all simulations reported here. Thus the input of water to the plant available pool is:

$$\text{WaterIn} = ((\text{Rain} * (1 - \text{PrecIntFrac})) + \text{Snowmelt}) * (1 - \text{FastFlowFrac}) \quad (16)$$

This is converted to a daily rate (WaterIn_d) by division by number of days per month. Daily potential transpiration in the absence of plant water stress is calculated as:

$$\text{PotTrans}_d = \text{PotGrossPsn} / \text{WUE} \quad (17)$$

Where WUE is as calculated in Eq. 2.

To calculate the combined effects of water inputs and transpirational demand on soil water storage and water stress, a simulated daily water balance is performed. The degree of water stress is calculated based on this balance. Water availability on a simulated day is:

$$\text{Water}_i = \text{Water}_{i-1} + \text{WaterIn}_d \quad (18)$$

where Water is plant available water (cm) and i is the simulated day of the month.

There is no standard way to calculate and apply water stress in ecosystem models. Existing models use the Palmer Drought Index at a monthly time-step (e.g. LINKAGES; Pastor and Post 1984), ratios of precipitation to predicted ET at a monthly time-step (e.g. Century, Parton et al. 1988) combinations of pre-dawn water potential and daytime VPD at a daily time-step (e.g. FOREST-BGC, Running and Coughlan 1988), or ratios of transpirational demand to total available water at a daily time step (e.g. BROOK, Federer and Lash 1978a).

Building on the experience with BROOK, we define a soil water release parameter f which has units of day^{-1} and expresses the fraction of plant available soil water which can be removed in one day without water stress occurring ($D\text{Water} = 1$). The value of .04, derived for watersheds at Coweeta, is used for all sites in this model. A similar number (.036) was derived for the Hubbard Brook watersheds.

Using this approach:

$$\text{Trans}_i = \text{PotTrans}_d \quad \text{when } \text{Water}_i \geq (\text{PotTrans}_d / f) \quad (19)$$

$$\text{and:} \quad \text{Trans}_i = (\text{Water}_i * f) \quad \text{when } \text{Water}_i < (\text{PotTrans}_d / f) \quad (20)$$

Then:

$$D\text{Water}_i = \text{Trans}_i / \text{PotTrans}_d \quad (21)$$

where Trans_i is actual transpiration (cm/day), PotTrans_d is the prorated, unstressed transpirational demand (cm/day), and Water_i is the total plant available soil water storage (cm) on day i . This algorithm has the advantages of reproducing a soil water draw-down curve, given a constant PotTrans_d , with both a linear or unstressed phase (Eq. 19) followed by a logarithmic (increasing water stress) phase (Eq. 20), and has been validated for two of the systems simulated here (Coweeta and Hubbard Brook). $D\text{Water}$ for the month is the mean of all $D\text{Water}_i$.

At the end of the hydrological balance routine, both potential gross photosynthesis (PotGrossPsn) and potential transpiration (PotTrans_d) are converted to realized values by multiplication by $D\text{Water}$. Transpiration for the month is the sum of Trans_i . If Water_i

at the end of the month is greater than the soil water holding capacity (WHC), the difference is removed by drainage.

Finally, monthly totals for Resp_{day} and $\text{Resp}_{\text{night}}$, which are not affected by water stress, are subtracted from realized gross photosynthesis to yield a monthly carbon balance over the entire canopy.

Carbon allocation

Monthly carbon gain by the canopy is accumulated over the year. At the end of the year, accumulated carbon is allocated in the following way:

$$\text{Leaf Carbon} = \text{LAI produced} \cdot \text{Specific leaf weight} \\ \cdot \text{Carbon concentration in foliage} \quad (22)$$

$$\text{Fine Root Carbon} = 130 + 1.92 \cdot \text{Leaf Carbon} \quad (23)$$

$$\text{Wood Carbon} = \text{Total Accumulated Carbon} - \text{Leaf Carbon} \\ - \text{Fine Root Carbon} \quad (24)$$

Eq. 23 is based on the relationship between above ground litter production and carbon allocation to roots from Raich and Nadelhoffer (1989). Both Fine Root and Wood Carbon are converted to biomass production by removing growth and maintenance respiration and dividing by the carbon fraction content of biomass. Wood Carbon allocation has lowest priority and should accumulate any differences between predicted and observed rates of photosynthesis,

respiration and carbon allocation. Thus it is the least constrained variable and should provide the most stringent test for validation of the model.

Parameterization

PnET has been parameterized and validated for 10 well-studied forest ecosystems (Table 1) which cover a wide range of vegetation types, geographic locations and climatic conditions. Climatic data were obtained from site publications for Hubbard Brook (Federer et al. 1990), Coweeta (Swift et al. 1988), and the taiga sites (Slaughter and Viereck 1986), and from site records for the Harvard Forest (E. Boose, pers. comm.). Precipitation data for H.J. Andrews are from Sollins et al. (1980). For the lodgepole pine system total precipitation data are from Fahey and Knight (1986), while the seasonal distribution is from climatic data for Missoula, MT. Similarly, Temperature data for H.J. Andrews, and the lodgepole pine system, and all data for other sites, were taken from the nearest U.S. Weather Service Station.

Beyond climatic data, PnET requires 28 input variables (Table 2a). Of these, 17 are held constant for all runs presented here, and may be thought to represent generalized relationships for forest ecosystems. Of those var-

Table 1. Ecosystem types and sources of data for 8 forest ecosystems simulated

1.	The Coweeta Hydrologic Laboratory, Otto, NC Watershed # 18 Vegetation: Oak-hickory (<i>Quercus</i> , <i>Carya</i> , <i>Acer</i>), admixture of evergreen trees and shrubs (<i>Tsuga</i> , <i>Rhododendron</i> , <i>Laurel</i>) Sources of Data: Monk and Day 1988, Swift et al. 1988
2.	The Hubbard Brook Ecosystem Study, West Thornton, NH Watershed # 6 Vegetation: Northern hardwoods (<i>Acer</i> , <i>Fagus</i> , <i>Betula</i>) Sources of Data: Whittaker et al. 1974, Likens and Bormann 1970, Federer and Lash 1978a, Federer et al. 1990
3 and 4.	The Harvard Forest, Petersham, MA Prospect Hill Tract Vegetation: Transition hardwoods (<i>Quercus</i> , <i>Acer</i> , <i>Betula</i> , <i>Castanea</i>) and red pine plantation (<i>Pinus resinosa</i>) Sources of Data: Aber et al. 1992
5.	University of Wisconsin Arboretum, Madison, WI Stand: Wingra Woods Vegetation: Mesic oak-maple (<i>Quercus</i> , <i>Acer</i>) Sources of Data: Nadelhoffer et al. 1983, 1985, Aber et al. 1991, Fownes 1986
6.	Slash pine plantations, near Gainseville, FL Vegetation: slash pine plantation (<i>Pinus elliottii</i>) Sources of Data: Gholz and Fisher 1982, Gholz et al. 1991
7.	Lodgepole pine stands, southeastern WY Stand: Nash Park Vegetation: Natural stands of lodgepole pine (<i>Pinus contorta</i>) Sources of Data: Fahey et al. 1985, Pearson et al. 1984, Fahey and Young 1984, Running 1980
8.	H.J. Andrews Experimental Forest, near Blue River, OR Watershed 10 Vegetation: Douglas-fir (<i>Pseudotsuga menziesii</i>) dominant Sources of Data: Sollins et al. 1980, Marshall and Waring 1986, Gholz 1982, Brix 1972, Leverenz 1981
9 and 10.	Taiga aspen and white spruce stands near Fairbanks, AK Stands: Mean values for each forest type Vegetation: Aspen (<i>Populus Tremuloides</i>) and white spruce (<i>Picea glauca</i>) Sources of Data: Viereck et al. 1983, Van cleve et al. 1983, Hom and Oechel 1983, Lawrence and Oechel 1983, Slaughter and Viereck 1986

Table 2a. List of parameters required to run the PnET model. A numerical value for the parameter indicates that variable is the same for all runs reported here. An asterisk indicates a variable that differs between runs. See Tables 2b and c for a list of values for these parameters for each system

Name	Definition (units)	Value
<i>Site and soil variables</i>		
Lat	Latitude (degrees)	*
WHC	Water holding capacity, plant available water (cm)	*
<i>Canopy variables</i>		
k	Canopy light attenuation constant (no units)	*
LeafNCon	Foliar nitrogen (percent)	*
FolReten	Foliage retention time (years)	*
LeafSpecWt	Leaf specific weight (mg · cm ⁻²)	*
<i>Photosynthesis variables</i>		
NetPsnMaxA	Intercept / relationship-foliar N-max photosyn. rate	*
NetPsnMaxB	Slope \ (μmoles CO ₂ · m ⁻² leaf · sec ⁻¹)	*
BaseLeafRespFrac	respiration as a fraction of maximum photosynthesis	0.1
HalfSat	Half saturation light level (J · m ⁻² · sec)	*
PsnTMax	Maximum temp. for photosynthesis (°C)	40
PsnTOpt	Optimum temp. for photosynthesis (°C)	20
PsnTMin	Minimum temp. for photosynthesis (°C)	0
<i>Water balance variables</i>		
VPDeffk	Constant for effect of VPD on photosyn. and transpiration	*
PrecIntFrac	Fraction of precipitation intercepted	*
WUEConst	Constant in equation for WUE as a function of VPD	10.9
FastFlowFrac	Fraction of water inputs lost directly to drainage	0.1
f	Soil water release parameter	0.04
<i>Carbon allocation variables</i>		
CFracLeaf	Carbon as fraction of foliage mass	0.45
CFracWood	Carbon as fraction of wood mass	0.5
CFracRoot	Carbon as fraction of fine root mass	0.45
RootAllocA	Intercept / of relationship between	130
RootAllocB	Slope \ foliar and root allocation	1.92
LeafGRespFrac	Foliar growth respiration, fraction of allocation	0.25
WoodGRespFrac	Wood growth respiration, fraction of allocation	0.25
RootGRespFrac	Fine root growth respiration, fraction of allocation	0.25
RootMRespFrac	Fine root maintenance resp., fraction of allocation	0.5
WoodMRespFrac	Wood maintenance resp., fraction of allocation	0.35

Table 2b. Parameter values for broad-leaved deciduous forest ecosystems

Forest Type	Nothern Hardwood	Oak-Maple Hardwood	Pine, Mixed Hardwood	Oak-Maple Hardwood	Aspen
Location	Hubbard Brook, NH	Harvard Forest, MA	Coweeta, NC	Blackhawk Island, WI	Central AK
<i>Parameter</i>					
lat	44	42	35	44	65
WHC	12	12	65	24	10
k	.5	.5	.5	.5	.5
LeafNCon	2.40	1.8	1.8	2.4	2.1
FolReten	1.0	1.0	1.34	1.0	1.0
LeafSpecWt	5.8	5.8	9.1	7.7	5.5
NetPsnMaxA	-5.96	-5.96	-5.96	-5.96	-5.96
NetPsnMaxB	4.86	4.86	4.86	4.86	4.86
HalfSat	60	60	60	60	60
VPDeffK	0	0	0	0	0
PrecIntFrac	.11	.11	.12	.11	.11

Table 2c. Parameter values for needle-leaved evergreen forest ecosystems

Forest Type	Slash Pine	Red Pine	Lodgepole Pine	Douglas-fir	White Spruce
Location	Central Florida	Harvard Forest, MA	Wyoming	H.J. Andrews Forest, OR	Central AK
Parameter					
lat	30	42	43	44	65
WHC	15	12	9	8	10
k	.4	.4	.4	.4	.4
LeafNCon	—	—	—	—	—
FolReten	2.0	2.5	5.0	4.5	7.0
LeafSpecWt	8.5	9.0	14.3	13.5	15.0
NetPsnMaxA	2.4	2.2	2.2	2.0	2.25
NetPsnMaxB	0.0	0.0	0.0	0.0	0.0
HalfSat	70	70	40	40	70
VPDefK	0	0	0.21	0.21	0
PrecIntFrac	0.15	0.15	0.15	0.15	0.15

ables which do change between systems (Tables 2b–c), many are constant among either broad-leaved deciduous or needle-leaved evergreen species. Thus the actual number of parameters which vary between sites, and which determine the differences discussed below, is very small.

For the evergreen stands, NetPsnMaxB is 0, and NetPsnMaxA represents a measured maximum rate of net photosynthesis for the dominant species (field grown) in the system. Because of this, the foliar N concentration has no real effect in the model for the conifer systems.

An effect of VPD on stomatal conductance (VPDefK) is included for the two western conifer species modeled (Douglas-fir and lodgepole pine). For these two, and for several other western U.S. coniferous evergreens (e.g. sitka spruce, western hemlock, englemann spruce and ponderosa pine), it has been shown that partial stomatal closure occurs in the field as a direct response to increased VPD, even in the absence of soil water stress (Running 1980). For these same species, conductance does vary linearly with photosynthetic rate at a given VPD (Monson and Grant 1989), so that the calculation of water use efficiency below is still valid, once the additional effect of VPD is included in the calculation of gross photosynthesis.

DVPD is set to zero for broad-leaved species and for eastern pines. While it is thought that nearly all species reduce stomatal conductance in response to VPD (Tenhunen et al. 1987; Schulze and Hall 1982), this response is less pronounced in plants of humid environments (Schulze and Koppers 1979; Schulze and Hall 1982). In Combination with reduced VPDs in humid environments, this causes VPD to have relatively little effect on total photosynthesis or transpiration (e.g. less than 1% reduction from optimal for a *Fagus sylvatica* stand in Germany, Schulze and Hall 1982).

Validation

PnET predicts LAI, foliage production, transpiration and water yield (drainage), total net photosynthesis and net

primary production of foliage, wood and fine roots. Not all of these data are available for all sites.

Foliar and woody net primary production

Both total foliar and foliar-plus-wood production are predicted very well by PnET (Figs. 2 and 3). With foliar retention times and leaf specific weights derived from field data, estimates of LAI should also be predicted with equal accuracy. As mentioned above, wood production is not constrained in any way, and represents the difference between net photosynthesis and all other carbon sinks. This agreement is remarkable considering the crude nature of the distribution between growth and respiration of carbon allocated to wood (c.f. Ryan 1991).

The validation for taiga spruce is against data for the white spruce type which dominates on well-drained sites,

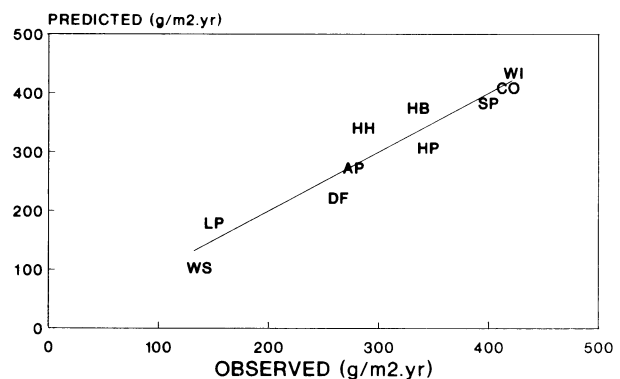


Fig. 2. Predicted versus observed foliar production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) for 10 temperate and boreal forest ecosystems (solid diagonal is the 1:1 line, site initials are CO-Coweeta, HB-Hubbard Brook, WI-Wisconsin, HH-Harvard Forest Hardwood, AP-Alaska Aspen, DF-H.J. Andrews Douglas-fir, SP-Slash Pine, LP-Lodgepole Pine, HP-Harvard Forest Red Pine, WS-Alaska White Spruce)

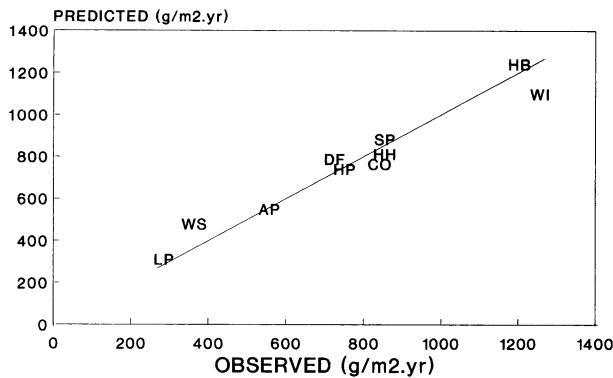


Fig. 3. Predicted versus observed total net primary productivity above ground for the 10 forest ecosystems used in this study (solid diagonal is the 1:1 line, site initials are CO-Coweeta, HB-Hubbard Brook, WI-Wisconsin, HH-Harvard Forest Hardwood, AP-Alaska Aspen, DF-H. J. Andrews Douglas-fir, SP-Slash Pine, LP-Lodgepole Pine, HP-Harvard Forest Red Pine, WS-Alaska White Spruce)

not against data for black spruce. NPP values for black spruce are much lower under identical climatic conditions due to the saturated and cold soil conditions under which this species comes to dominate (Van Cleve et al. 1983). This suggests that PnET does not currently apply to systems where soil processes, other than those summarized by foliar N concentration, control NPP.

Water yield

Complete water budgets were only available for the three watershed sites (Hubbard Brook, Coweeta and H.J. Andrews). In these sites, ET is calculated as precipitation minus streamflow, such that if streamflow or drainage is predicted accurately, then the calculated ET would be the same for both model and data. Predicted and observed drainage ($\text{cm} \cdot \text{yr}^{-1}$) were 76 and 87 at Hubbard Brook (watershed 6), 159 and 155 at H.J. Andrews (watershed 10), and 108 and 103 at Coweeta (watershed 18).

PnET also mimicked seasonal patterns of drainage at Hubbard Brook quite well (Fig. 4a). For Coweeta (Fig. 4b) predicted drainage both declined and recovered about a month before measured. The early decline may be due mainly to the occurrence of leaf out in March in the model, compared with April in the field. However, the lag in increasing drainage in the fall would have to result from a hydrological lag time within the watershed, which then also would affect the spring differences. This type of time lag was incorporated into the simulations of the Coweeta watersheds by Federer and Lash (1978b). In both cases, hydrology is predicted well during the growing season, which is the part of the year which affects photosynthesis.

These validations suggest that a simple model such as PnET can accurately capture the effect of monthly mean climatic variation on canopy development, mean ecosystem water balance and net primary production over a wide range of forest ecosystem types. The model may then be useful in predicting mean ecosystem responses to changes in mean climatic conditions such as those generated by general circulation models (GCMs).

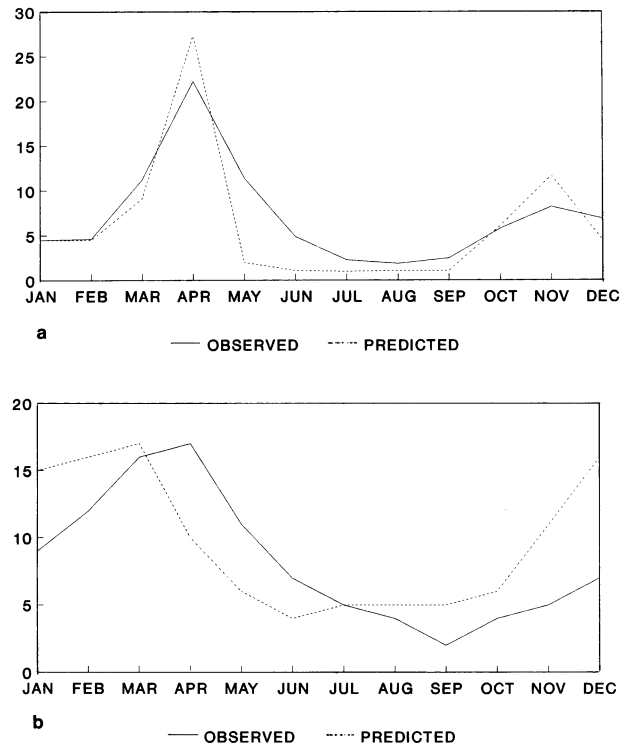


Fig. 4a, b. Predicted versus observed seasonal discharge for 2 ecosystems used in this study: **a** Hubbard Brook, and **b** Coweeta

Sensitivity analysis and response to climate change

Water stress under ambient climate

Both climate and maximum potential photosynthesis determine the degree of water stress occurring under ambient conditions. For example, the Harvard Forest hardwood simulation did not produce water stress because of the low foliar N concentration and thus low maximum net photosynthesis. In contrast, the Hubbard Brook simulation, although run under slightly more humid climatic conditions, does develop water stress because of the higher foliar N value. Both the Harvard Forest pine system and the slash pine system do not develop water stress because of low maximum rates of net photosynthesis. The Coweeta system also does not develop water stress, partly because of a low foliar N concentration, and partly because of the large soil water holding capacity used (65 cm, c.f. Federer and Lash 1978b). Significant water stress (reductions in photosynthesis of up to 60% in June and July), occur in the taiga aspen stand, but not in the spruce stand, with an equivalent leaf area but a much lower maximum photosynthetic rate.

In the two most severely water stressed systems, H.J. Andrews, and lodgepole pine, the degree of reduction in photosynthesis and transpiration due to the VPD effect was greater than for soil water stress, demonstrating the value of this adaptation in limiting transpiration in the early part of the growing season so as to minimize soil water stress late in the season.

Sensitivity of primary production to individual parameters

PnET can be used to determine the sensitivity of net primary production in each of these ecosystems to four important components of climate which are predicted to change due to human modification of the Earth's atmosphere (Mitchell et al. 1990).

Maximum and minimum temperatures were changed both separately and together in this sensitivity analysis (Table 3). Minimum temperature determines the length of the growing season for systems in which this variable drops below 0 in winter. Maximum temperature affects the balance between gross photosynthesis and leaf respiration. The *difference* between maximum and minimum temperatures determines vapor pressure deficit, which affects water use efficiency in all sites and stomatal conductance in the western conifer sites.

Simulated responses at Hubbard Brook show that this system is currently poised at the edge of significant water stress. Increasing maximum temperature or decreasing precipitation caused large declines in NPP, while the opposite changes produced relatively small increases in NPP. Similarly, the beneficial effects of increases in both maximum and minimum temperatures (extending the length of the growing season) or increasing radiation were partially offset by increased water stress, and yielded relatively small increases in NPP.

Responses of the two Harvard Forest systems were similar to each other. Increasing maximum temperature induced mild water stress, while reducing both maximum and minimum temperature reduced NPP through a shortened growing season. Decreased precipitation resulted in slight water stress in the hardwood stand, but not in the pine stand because of lower NPP in the pine stand under current climate.

As with all systems without water stress in the ambient climate runs, increasing precipitation at Coweeta had no effect. A 25% decrease in precipitation also did not induce water stress, this time due in part of low foliar N and low rates of photosynthesis. Increasing both maximum and minimum temperatures converted this system to a 12 month growing season, and increased NPP. Reducing both temperatures shortened the season and reduced NPP. The decrease in NPP with increasing maximum temperature alone is not a water stress effect, but results from higher respiration rates in mid-summer.

The Wisconsin system shows extreme responses to changes in either amount of precipitation or VPD. Increasing both maximum and minimum temperatures decreases growth because of higher respiration and the water stress limitation on gross photosynthesis. Because of the extreme water stress effects, radiation effects are minimal.

Although the slash pine system did not exhibit water stress in the control condition, it did with decreasing precipitation or increasing VPD. Again, increasing both maximum and minimum temperatures increased respiration and reduced NPP.

The lodgepole pine system showed both a strong negative response to increasing water stress and a positive response to a lengthening of the growing season caused by increasing maximum and minimum temperatures. Response to changes in precipitation were less than might be

expected because ambient precipitation amounts are very low during the growing season. Increasing or decreasing these amounts by 25% does not cause a large change in total precipitation.

The H.J. Andrews system responded positively to increased precipitation and reduced VPD, while both increases and decreases in maximum and minimum temperatures caused reduced NPP. Again, the response to altered precipitation was small because of low ambient values during the growing season.

Both taiga systems responded strongly to reductions in precipitation, which induced water stress in the spruce stand, and increased stress in the aspen. The effect was even greater with increased maximum temperature which increased both VPD and respiration. Reducing temperatures caused reductions in the length of the growing season and reduced NPP. Decreasing maximum temperature increased growth in aspen but had no effect in spruce, in which water stress was not present in the ambient climate run.

That these systems show a diversity of responses to identical climatic changes suggests that great care should be used in developing generalizations as to how forests will respond to a changing climate. In addition, it is clear that the temperature effects on both photosynthesis and respiration are important in the responses described. This suggests that the degree to which temperature responses of these processes will acclimate within mature trees to altered temperatures over decadal time scales is an important research topic.

Combined effects – an extreme treatment

Climate change involves the simultaneous alteration of each of the four parameters which were changed individually in the sensitivity analysis. The direction and degree of change in these four for any one location cannot yet be accurately predicted (Mitchell et al. 1990). To examine the effects of combined changes in climate drivers, we have devised something approaching a worst-possible combination for temperate and boreal forest ecosystems, and tested the effects of this combination on our set of 10 systems.

The scenario used includes a 3 degree increase in maximum temperature and a 25% decrease in precipitation, applied evenly throughout the year, with no change in minimum temperature or radiation. This combination produces the negative effects of increased VPD and mid-season respiration resulting from higher maximum temperatures, without an offsetting increase in length of growing season (controlled by minimum temperature). It also increases the potential for water stress through decreased precipitation without an offsetting increase in radiation which might be expected to occur in the real climate system.

Only the Coweeta site did not develop water stress under this climate change scenario. Water stress contributed to reduced NPP in all other systems (Fig. 5a). For 7 of the 10 systems, the effect of the combined treatment was nearly equal to the sum of the individual effects (Table 3). For both Harvard Forest sites, and for the slash pine

Table 3. Predicted sensitivity of net primary production above ground to different changes in climatic variables for the eight forest ecosystems used in this study (values are percent change in NPP)

Ecosystem	Climate variable change							
	Temperature				Precipitation		Radiation	
	Max T	Max T	Max T	Max T	+25%	-25%	+10%	-10%
	Min T	+30	-30	-30				
Hubbard brook	+4	-29	-5	+2	+5	-18	+2	-6
Harvard forest (Hardwood)	-2	-10	-15	-3	0	-3	+7	-8
Coweeta	+12	-8	-18	+2	0	0	+7	-8
Wisconsin	-18	-33	+5	+45	+19	-31	+1	-1
Taiga aspen	-23	-33	-24	+37	+17	-21	+2	-2
Slash Pine	-21	-21	+7	+2	0	-6	+9	-10
Harvard forest (red pine)	0	-6	-20	-3	0	0	+8	-10
Lodgepole pine	+14	-45	-19	+35	+4	-15	+4	-8
Douglas-fir	-9	-16	-11	+15	+5	-5	+5	-5
Taiga spruce	-18	-26	-67	0	+5	-13	+3	-8

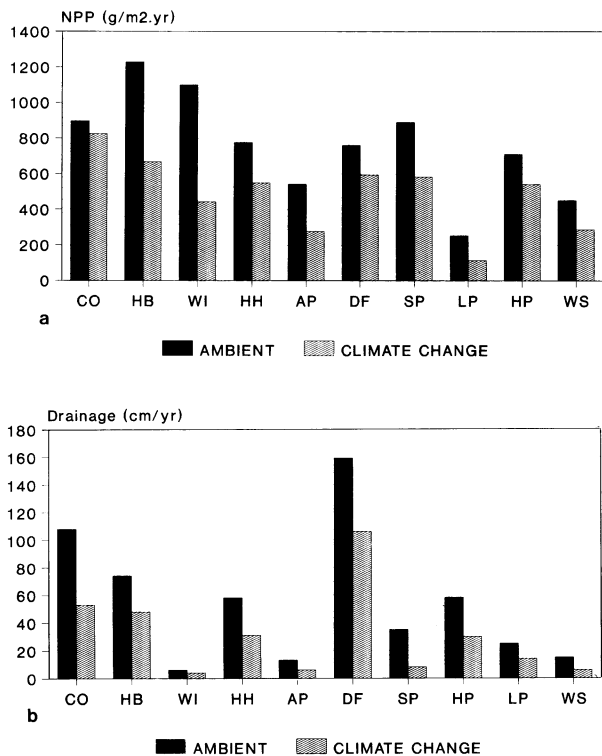


Fig. 5a, b. Predicted change in ecosystem function for 10 forests in response to an extreme climate change scenario (+3°C maximum temperature, -25% precipitation, minimum temperature and radiation unchanged): **a** change in net primary production above ground, and **b** change in annual water yield (site initials are CO-Coweeta, HB-Hubbard Brook, WI-Wisconsin, HH-Harvard Forest Hardwood, AP-Alaska Aspen, DF-H.J. Andrews Douglas-fir, SP-Slash Pine, LP-Lodgepole Pine, HP-Harvard Forest Red Pine, WS-Alaska White Spruce)

system, the combined effects were greater than the sum of the individual effects. Decreases in NPP ranged from 8% at Coweeta (due solely to increased respiration) to 60% in Wisconsin. For the lodgepole pine systems, predicted

wood production went to zero, suggesting that systems at the forest biome boundary might give way to non-forested systems such as grasslands or shrublands.

Predicted drainage also decreased significantly in all systems (range=33–77%, Fig. 5b). Those systems experiencing the most water stress (Wisconsin and Lodgepole pine) showed the smallest decrease in drainage. Most of what little drainage that does occur in these systems is due to fast flow, which is independent of transpiration. The largest decreases in drainage occurred in systems with long growing seasons and no water stress under ambient conditions (Coweeta and slash pine).

Conclusions

PnET has been validated against field data for foliar and wood production and for drainage from a number of forest ecosystems. This suggests that a simple model with a coarse temporal resolution can capture and describe the range of variation in these ecosystem-level processes as they exist in the field. Stated differently, aggregation of climatic data to the monthly scale and biological data such as foliar characteristics to the ecosystem level apparently does not cause a significant loss of information relative to long-term, mean ecosystem responses.

Sensitivity analyses suggest that a wide range of responses to identical changes in climatic drivers can be expected from different temperate and boreal forest ecosystems. Such responses will depend on the degree to which the different climatic variables (temperature, precipitation, radiation) control NPP and water balance on a given site. Simple generalizations regarding the response of temperate and boreal forests to climate change should be avoided. However, the success of the validations presented here shows that this variability can be represented in a relatively simple model. Dealing with other limiting factors ignored by this analysis, such as nutrient limitations, will require additional complexity.

Those forests which occur near boundaries with drier biomes (e.g. the lodgepole pine system), are predicted to

realize large reductions in NPP, and may no longer support the tree growth form. Results suggest that sizable areas of dry conifer forest ecosystems in the intermountain west might become unsuitable for forest growth under the rather extreme climatic change simulated here.

The fact that predicted declines in water yield are greater than predicted declines in NPP for many systems in humid areas may be of special concern. In the more densely populated, and generally more humid, areas of the eastern U.S., the production of potable water by forested ecosystems is often more important than wood production. From a policy perspective, reductions in water yield may be the first critical effect of climate change on these systems.

These predictions apply only to mean climatic conditions. As forests approach climatic limitations on function, the importance of extreme years, or a series of extreme years may increase. PnET is currently being applied to a long-term timeseries of actual climatic data for the Hubbard Brook ecosystem, to see if inter-annual variability in water balance (from drainage data) and NPP (from tree ring growth data) can be accurately predicted. If so, the model may also be useful for prediction of the effects of extreme events and short-term climatic fluctuations.

Finally, this analysis has ignored perhaps the most significant and best documented global change likely to affect ecosystems function, that of increasing atmospheric CO₂ (Bazzaz 1990; Mooney et al. 1991; Bazzaz and Fajer 1992). Increasing CO₂ concentration will affect both the maximum rate of net photosynthesis and the instantaneous water use efficiency. The direct link between photosynthesis and transpiration employed here and the underlying theory based on gradients in CO₂ concentration between foliage and the atmosphere (Sinclair et al. 1984) make the inclusion of direct CO₂ effects on WUE relatively straightforward. An analysis of the direct effects of CO₂ and other gases (e.g. ozone) on net photosynthesis and NPP is currently under way.

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