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Loblolly pine hydrology and productivity across the southern United States

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Abstract

Concern over future changes in water yield and timber production in southern pine forests has increased the need for a well tested and validated forest ecosystem model which can be used to predict potential climate change effects on forest processes. However, before a model is used to project potential climate change impacts on forests, it should first be validated across a wide range of climates and site conditions. We used PnET-IIS, a physiologically-based, monthly time-step model that uses soil, vegetation, and climate parameter inputs to predict evapotranspiration, drainage, soil water stress and net primary productivity for loblolly pine (*Pinus taeda)* stands across the southern United States. Sensitivity analyses and model validation of predicted net primary productivity (NPP) were conducted. Predicted hydrology and productivity were most sensitive to temperature driven parameters (e.g. optimal temperature for photosynthesis, and changes in air temperature). Values of PnET-IIS predicted NPP were compared with measured annual site basal area growth from 12 stands located from eastern Texas to eastern Virginia, from the year of site canopy closure to 1990. Annual basal area growth ranged from 4.2 to 26.8 cm^2 per tree $year^{-1}$. Annual basal area growth was significantly correlated with predicted NPP (r^2 = 0.30, $P < 0.005$, n = 164), and the correlation improved when annual basal area growth was averaged by site (r^2 = 0.66, $P < 0.005$, n = 12). Total annual precipitation was the single climate variable which best correlated with annual basal area growth (r^2 = 0.14, $P < 0.005$, n = 164). These result indicate that PnET-IIS could be useful in predicting the effect of changing patterns of precipitation and air temperature on southern pine hydrology and productivity.

Keywords: PnET-IIS; *Pinus taeda;* Model; Hydrology; Net primary productivity; NPP

1. Introduction

The southeastern United States is one of the most rapidly growing regions in US, and as the population increases, the demand for commercial, industrial and residential water will also increase (United States Water Resources Council, 1978). Forest species type, stand age, and climate all influence the amount of water use and yield (Swank et al., 1988). Because forests comprise approximately 55% of the southern US (USDA Forest Service, 1988), changes in forest water use could significantly alter water yield and potentially lead to water shortages within the region.

In addition to water, timber is an important forest resource. Accurate estimates of future southern pine forest productivity are essential for the development plans that provide enough timber to meet consumer demands. Southern forests may not be able to main-

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tain (or increase) current levels of productivity. Radial growth of loblolly pine (*Pinus taeda)* decreased during the years from 1949 to 1984 in Piedmont stands (Zahner et al., 1988). If pine productivity decreases by 10%, annual timber production would be reduced by 2.9 million m^3, across the southern US (USDA Forest Service, 1988).

A physiologically based forest hydrology and productivity model that is sensitive to climate change is needed to project how forests may respond to potential changes in precipitation and air temperature. However, before a forest process model is used for projecting potential climate change impacts on forests, the model should first be well validated across a wide range of climates and site conditions. We used PnET-IIS, a physiologically-based, monthly time-step model that uses soils, vegetation and climate parameter inputs to predict evapotranspiration, drainage, soil water stress and net primary productivity (NPP) for loblolly pine (*Pinus taeda)* stands across the southern United States.

This paper describes, and tests PnET-IIS annual predictions of NPP and hydrology, and validates model predictions of NPP across the southern US. PnET-IIS is a derivation of the PnET-II model (Aber et al., 1996) which was originally developed and validated in the northeastern United States. Discussion of the original model (PnET-II) structure and algorithms have been published, so we will limit our discussion to the changes made in the original model which were necessary for the development of PnET-IIS for predicting hydrology and productivity in southern United States loblolly pine stands.

Sensitivity analysis and a validation of predicted NPP across a wide geographic, inter-annual air temperature and precipitation range were conducted with PnET-IIS. The range in inter-annual climate data used to parameterize the model is greater than the predicted average annual variation in air temperature and precipitation from most general circulation models (GCMs). The use of many sites with diverse inter-annual and inter-site climates for validation of model predicted NPP, in necessary if future uses of the model include predicting the potential affects of climate change on forest NPP.

Therefore, the objectives of this paper are to discuss how: (1) PnET-IIS was modified from PnET-II (Aber et al., 1996) to predict hydrology and productivity in southern pine forests; (2) test model sensitivity to changes in model parameterization and climate; (3) predict annual changes in forest growth and water use for 12 loblolly pine sites located across the southern US; (4) validate model prediction of NPP using measured basal area growth data from the 12 sites.

2. Methods

2.1. Model description

Given the importance of timber and water supply in the southern US we wanted to predict the potential that inter-annual changes in air temperature and precipitation could have on forest productivity. However, within the southern region, no physiologically based model existed which could be easily parameterized, so we looked outside of the region for a model to use in predicting southern US hydrology and productivity.

Aber and Federer developed PnET (Aber and Federer, 1992) and its successor PnET-II (Aber et al., 1996), which are process-based hydrology and productivity models, which predict evapotranspiration, drainage, NPP, and leaf area index (LAI), at monthly intervals, for northeastern US forests. PnET-II uses four site specific climate parameters, one soil parameter, and generalized vegetation parameters for calculating ecosystem processes for a variety of forest types. When PnET (Aber and Federer, 1992) or PnET-II (Aber et al., 1996) were applied across a range of environmental conditions and species types (excluding loblolly pine), the results of their simulations indicated good agreement between predicted and measured hydrology and productivity. However, PnET-II performed poorly when we attempted to predict hydrology and productivity in loblolly pine forests cross a range of southern US sites.

Compared with the northeastern US, southeastern forests have developed under very different climatological conditions, so we developed PnET-IIS (i.e. PnET-II south) from PnET-II, to better predict ecosystem processes in southern US pine forests. The model structure and all of the algorithms of PnET-II are incorporated in PnET-IIS, except where noted. PnET-IIS uses modified controls of gross photosynthesis, respiration, and litter fall which better reflect physiological characteristics for loblolly pine. With the exception of the changes noted below, the complete PnET-II model has been fully described previously (Aber et al., 1996).

2.2. *PnET-IIS: general structure and variations from PnET-II*

PnET-IIS calculates the maximum amount of leaf area which can be supported on a site based on the soil, climate and parameters specified for the vegetative type. Leaf area is a major component in calculating NPP and water use. PnET-IIS assumes all stands are fully stocked and that leaf area is equal to the maximum amount of foliage that can be supported due to soil and climate limitations. Predicted NPP is defined as total gross photosynthesis minus growth and maintenance respiration for leaf, wood and root compartments. PnET-IIS calculates respiration as a function of the current and previous months minimum and maximum air temperature. Given the difference in species composition and climate, we replaced the day and night time respiration rates in PnET-II with respiration rates derived specifically for loblolly pine by Kinerson (1975) (Eqs. (1) and (2))

$$\mathrm{DayResp} = e^{(3.2 + 0.072 \times \mathrm{Tday})} \tag{1}$$

$$\mathrm{NightResp} = e^{(3.2 + 0.072 \times \mathrm{Tnight})} \tag{2}$$

DayResp and NightResp are leaf respiration (mg CO_2 m^{-2} foliage h^{-1}), Tday is average daily air temperature, Tnight is average nightly air temperature (Aber et al., 1996).

Across the southern US, loblolly pine have the ability to acclimate to seasonal variations in air temperature. PnET-IIS uses a curvilinear function to simulate the relationship between increasing air temperature, optimal temperature for gross photosynthesis, and maximum air temperature for gross photosynthesis (Fig. 1) (Strain et al., 1976). As temperature increases beyond the optimal photosynthetic temperature, the respiration rate increases while gross photosynthesis increases slightly or decreases, so proportionally less net carbon per unit leaf area is fixed (Kramer, 1980). Total gross photosynthesis is a function of gross photosynthesis per unit leaf area, and total leaf area. Changes in water availability and plant water demand place limitations on the amount of leaf area produced, so as vapor pressure deficit and air temperature increase above optimal levels, leaf area and total gross photosynthesis decrease. Predicted NPP, expressed as t biomass ha^{-1} $year^{-1}$, was compared with site measured annual basal area growth in cm^2 $year^{-1}$.

PnET-IIS also incorporates a forced timing of autumn/winter needle fall. Because loblolly pine grows across a wide geographic range (Fig. 2), leaves fall after a wide range of growing degree days, with peak litterfall in November. PnET-IIS uses average monthly minimum temperature of less than 5°C as a stimulus for leaf senescence. Leaf senescence is forced if the temperature conditions for leaf fall are not met by November of each year.

The same model structure and algorithms used in PnET-II were also used in PnET-IIS for predicting forest hydrology. Annual transpiration was calculated from a maximum potential transpiration which was modified by plant water demand (a function of gross photosynthesis and water use efficiency). Interception loss was a function of leaf area and total precipitation. *ET* was equal to transpiration and interception loss. Drainage was calculated as water in excess of *ET* and soil water holding capacity

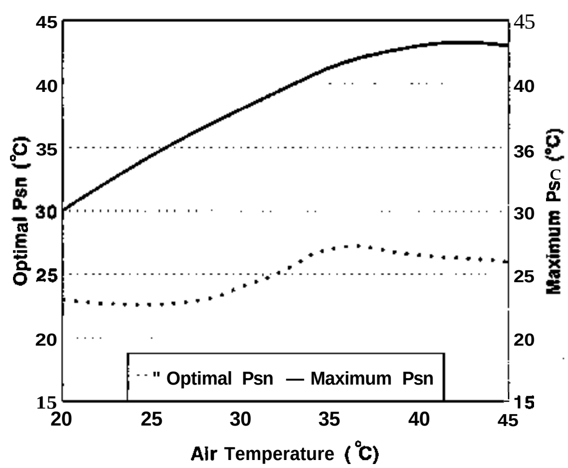

Fig. 1. Relationship between changing air temperature (°C) and changing maximum and optimal gross photosynthetic leaf temperature (°C), from Strain et al. (1976).

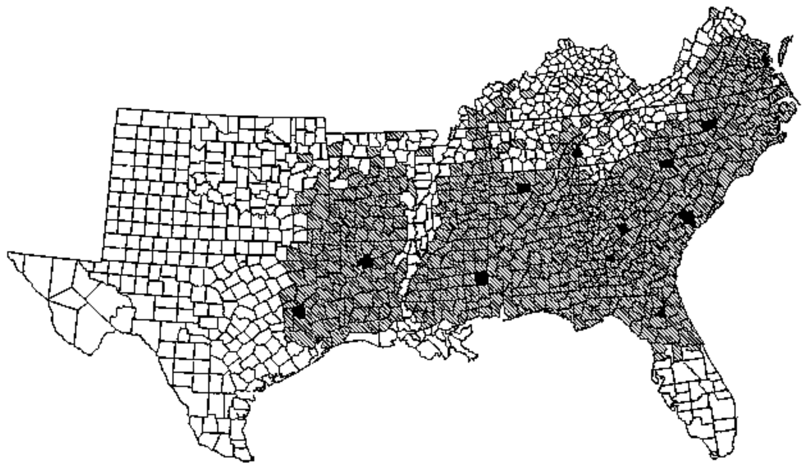

Fig. 2. Site locations of the 12 pine sites sampled in study, overlaid on range map of loblolly pine (gray shaded zone).

(SWHC). Plant water demand was dependent on monthly precipitation and water stored in the soil profile. If precipitation inputs exceed plant water demand, the soil was first recharged to the SWHC and if water was still available, water was output as drainage. Monthly drainage values are summed to provide an estimation of annual water outflow. Growing season soil water stress (GSSWS) was defined as 1 - (average growing season soil water/SWHC). Average growing season soil water equals the sum of monthly calculated soil water, which was less than or equal to SWHC, divided by the number of months in the growing season. Growing season and annual soil water deficit ranged from 0.00 (no water stress) to 1.00 (maximum water stress).

2.3. Input data

PnET-IIS uses constant generalized species-dependent process parameters (e.g. light extinction coefficient, and optimal temperature for gross photosynthesis) and site specific soil and climate data. Table 1 summarizes the constant parameters used in model predictions of loblolly pine hydrology and productivity at 12 sampled sites in the southern US (Fig. 2).

Soil series data were derived from a GIS-based Soils Atlas compiled by the Soil Conservation Service (Marx, 1988). The soil series were hand digitized from a paper source at a scale between 1:500000 and 1:1 500 000, depending on the state. Soil information associated with each series includes SWHC to a depth of 102 cm (Table 2), the only site-specific soils data used in our simulations. All other soil parameter values were held constant across all sites and years (Table 1).

PnET-IIS also requires four monthly climatic drivers; minimum and maximum air temperature, precipitation and solar radiation. The Forest Health Atlas provided cooperator and first-order station data from 1951–1984, which was originally acquired from the National Climatic Data Center (NCDC) (Marx, 1988). Cooperator station data include average minimum and maximum monthly air temperature and total monthly precipitation, while first-order station records include relative humidity. Because these data had error rates between 5 and 40% (Marx, 1988), a large proportion of the data was removed prior to usage. After checking for accuracy, the database was interpolated on a 0.5° X 0.5° grid across the southern US (Marx, 1988). The gridded databases of minimum and maximum air temperature, relative humidity and precipitation were compiled into a single database and run through a program to calculate monthly solar radiation (Nikolov and Zeller, 1992) on a 0.5° X 0.5° grid. Solar radiation values were then combined with average monthly maximum and minimum air temperature and total monthly precipitation and input into PnET-IIS.

Table 1
PnET-IIS model parameters used to predict productivity and hydrology for loblolly pine stands

Parameter name	Parameter abbreviation	Model default value	Sensitivity analysis values
Light extinction coefficient	*k*	0.5	0.4, 0.5, 0.6
Foliar retention time (years)		2.0	
Leaf specific weight (g)		9.0	
NetPsnMaxA (slope)		2.4	
NetPsnMaxB (intercept)		0	
Light half saturation (J m^{-2} s^{-1})	*HS*	70	60, 70, 80
Vapor deficit efficiency constant	VPDK	0.03	0, 0.03, 0.05
Water use efficiency constant	WUE C	10.9	10, 10.9, 12.0
Canopy evaporation fraction		0.15	
Soil water release constant	*F*	0.04	0.03, 0.04, 0.05
Maximum air temperature for photosynthesis (°C)	TMAX	Variable	35, 45
Optimal air temperature for photosynthesis (°C)	TOPT	Variable	17, 23
Change in historic air temperature (°C)	DTEMP	0	+2, -2
Change in historic precipitation (% difference)	DPPT	0	+10, −10

Climate data (i.e. air temperature, precipitation and relative humidity) from 1985 to 1990 for the three first-order or cooperator stations located closest to each of 12 sampled loblolly pine sites were extracted from the NCDC microfiche. These data were averaged to estimate climate for each site, and solar radiation from 1985 to 1990 was calculated. The 1951-1984 and 1985-1990 climate databases were combined to produce a continuous monthly climate database from 1951 to 1990.

2.4. Sensitivity analysis

PnET-IIS runs using numerous user defined parameters, and varying degrees of certainty are associated with these parameter estimates. These parame-

Table 2
Climatic data for 12 measured loblolly pine sites. Standard errors are included in parentheses

Site	YOR	Lat. (deg.)	Grow. seas. avg. solar radiation (J m^{-2} s^{-1})	Grow. seas. avg. temp. (°C)	Annual avg. temp. (°C)	Grow. seas. avg. PPT (cm H_2O)	Annual avg. PPT (cm H_2O)	GS SWHC (cm H_2O per 102 cm soil)	Avg. basal area growth (cm^2 $year^{-1}$)
Bradford, FL	21	30.0	465 (10)	25.3 (0.2)	20.2 (0.2)	80 (2)	130 (3)	6	11.4 (0.5)
Bienville, LA	15	32.3	446 (5)	24.3 (0.2)	18.0 (0.2)	67 (7)	149 (9)	14	11.3 (0.9)
Chatham, NC	14	35.6	414 (6)	21.8 (0.1)	15.0 (0.2)	61 (4)	117 (6)	14	11.8 (0.5)
Chester, SC	8	34.8	432 (10)	22.6 (0.2)	16.2 (0.3)	66 (5)	120 (6)	13	13.1 (0.4)
Colleton, SC	11	32.9	436 (6)	24.5 (0.2)	18.7 (0.2)	68 (3)	121 (4)	13	21.1 (1.3)
Glouchester, VA	13	37.5	400 (7)	22.0 (0.2)	15.0 (0.3)	62 (4)	117 (7)	12	11.7 (0.7)
Dooly, GA	11	32.1	466 (8)	26.6 (0.2)	20.2 (0.3)	50 (2)	108 (4)	14	8.7 (0.8)
McMinn, TN	14	35.5	417 (9)	21.7 (0.2)	14.8 (0.2)	63 (6)	134 (9)	9	11.3 (0.7)
Morgan, AL	10	34.5	424 (9)	21.8 (0.2)	15.0 (0.2)	63 (4)	136 (5)	14	13.6 (0.4)
Walker, TX	12	31.0	477 (8)	25.3 (0.3)	19.5 (0.2)	55 (2)	114 (7)	11	14.2 (1.6)
Wayne, MS	28	31.6	432 (4)	24.1 (0.2)	18.2 (0.2)	72 (3)	149 (6)	16	17.4 (0.7)
Wilkinson, GA	14	32.8	449 (6)	24.0 (0.6)	17.9 (0.2)	50 (3)	111 (4)	13	11.4 (0.6)

YOR, years of record since canopy closure; Lat., latitude; Grow. seas. avg. solar radiation, growing season solar radiation; GS SWHC, site soil water holding capacity derived from a Soil Conservation Service map of the soils on each site; Avg. basal area growth, average annual basal area growth for the measured trees on each site.

ters may have varying impact on model predictions of hydrology and productivity. To determine model sensitivity to changes in input parameter values, the light extinction coefficient, light half saturation, vapor pressure efficiency constant, water-use-efficiency constant, soil water release constant, and temperatures of maximum and optimal gross photosynthesis, were individually set at different values while all other variables remained static (Table 1). Additionally, historic air temperature and precipitation were changed to observe changes in predicted annual transpiration, evapotranspiration, soil water drainage, soil water stress, maximum LAI, and NPP.

2.5. Validation of predicted NPP

We sampled 12 loblolly pine stands in 1991 and 1992 to validate PnET-IIS NPP predictions (Table 2). These sites represented a wide range of climate and soil conditions. Sites met the following selection criteria: (1) stands were fully stocked at the time of sampling; (2) over 95% of the stand basal area was comprised of loblolly pine; (3) the site had not been thinned, burned, fertilized, or damaged by insect or disease; (4) all sites were on relatively level terrain (less than 10% slope).

Two tree core samples were collected 1.4 m above the forest floor (DBH) from each of 20 trees per site. The trees selected were located randomly within the plot, but represented the dominant or co-dominant size class. The first core was selected at a random azimuth, and the second core was extracted at 90° to the first core. Cores were returned to the laboratory, mounted and sanded prior to ring width measurements. The cores were cross dated, and ring width was measured using a Model 3 increment measurer (Fred C. Henson Co., Mission Viejo, CA) [1], which has an accuracy of 0.01 mm. All cores were measured twice and if the difference in measured annual ring width was over 10% between the two readings, the core was measured a third time. Annual basal growth (cm^2) was calculated as π X (tree radius)^2 of the current year ring area - π X (tree radius)^2 of the previous year ring area.

[1] The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Department of Agriculture of any product or service.

PnET-IIS was run on each of the 12 sites using climate data from 1951 to 1990. Predictions of annual NPP were compared with annual basal area growth (n = 165), and average annual basal area growth (n = 12), from each site. Although annual basal area growth varied between sites, all sites exhibited a pattern of rapidly increasing basal area growth during the early years of stand development, followed by a decline in growth, and then a fluctuation in growth about a longer term average rate. Once the period of rapid basal area growth had subsided, it was assumed that inter-tree competition for water, nutrient and light had the greatest influence on tree growth rates and that the stand had reached canopy closure. PnET-IIS assumed closed canopy conditions for model predictions of productivity and hydrology.

3. Results and discussion

3.1. Sensitivity analysis

Changing the values of input parameters had both direct and indirect effects on PnET-IIS output values. Of the six observed PnET-IIS outputs, GSSWS was the most sensitive to changes in model input parameter values (Table 3). Compared with ambient GSSWS, the change in GSSWS ranged from -28% when optimal air temperature for photosynthesis was reduced to 17°C, to a + 12% increase in GSSWS when the light extinction coefficient (k) was reduced to 0.4. Reducing the optimal temperature for gross photosynthesis (TOPT) reduced NPP and maximum LAI (MXLAI). As LAI was reduced, total evapotranspiration and GSSWS were also reduced. Reducing the light extinction coefficient (k) increased maximum LAI and evapotranspiration, and as this water demand increased, GSSWS increased. In addition to k and TOPT, the vapor pressure deficit constant (VPDK), soil water release parameter (F), and air temperature of maximum photosynthesis (TMAX) also affected GSSWS.

The other hydrology output values (i.e. transpiration, evapotranspiration and soil water drainage) were most strongly influenced by k and TOPT. Both of these parameters directly influence LAI, transpiration and, therefore, water use. Predicted NPP and MXLAI

Table 3
Changes in PnET-IIS predicted hydrology and productivity corresponding to changes in input parameter values. Numbers in parentheses are the percent deviation from ambient values. Abbreviations for input parameters are the same as Table 1

Variable	Annual					Growing season
	Transpiration (cm)	Evapotranspiration (cm)	Drainage (cm)	NPP (t biomass)	Max.LAI ($m^2 m^{-2}$)	GSSWS
Ambient	61.2	80.3	47.2	11.0	5.7	0.32
k = 0.4	65.5 (+7)	83.3 (+4)	44.2 (-6)	11.7 (+6)	6.5 (+14)	0.36 (+12)
k = 0.6	59.0 (-4)	76.7 (-5)	50.8 (+8)	10.2 (-7)	5.0 (-12)	0.34 (-16)
HS = 60	64.0 (+4)	81.7 (+1)	45.8 (-3)	11.5 (+5)	5.9 (+4)	0.34 (+6)
HS = 80	60.6 (-1)	78.5 (-1)	49.0 (+4)	10.4 (-5)	5.5 (-4)	0.30 (-6)
VPDK = 0	63.0 (+2)	80.7 (0)	46.8 (-1)	11.3 (+3)	5.7 (0)	0.33 (+3)
VPDK = 0.05	60.5 (-1)	78.3 (-2)	49.2 (+4)	10.5 (-5)	5.5 (-4)	0.29 (-10)
F = 0.05	64.2 (+5)	80.9 (0)	46.6 (-1)	11.2 (+2)	5.7 (0)	0.36 (+12)
F = 0.03	60.5 (-1)	78.3 (-2)	49.2 (+4)	10.6 (-4)	5.6 (-2)	0.26 (-19)
WUE C = 12	60.4 (-1)	78.6 (-2)	48.9 (+4)	11.8 (+8)	5.8 (+2)	0.30 (-6)
WUE C = 10	63.8 (+4)	81.8 (+2)	45.6 (-3)	10.1 (-9)	5.5 (-4)	0.34 (+6)
TMAX = 45	62.1 (+1)	81.2 (+1)	46.3 (-2)	11.2 (+2)	5.7 (0)	0.34 (+6)
TMAX = 35	58.7 (-4)	77.9 (-3)	49.6 (+5)	10.4 (-6)	5.6 (-2)	0.27 (-16)
TOPT = 17	54.3 (-11)	73.6 (-9)	53.9 (+14)	9.4 (-15)	5.4 (-5)	0.23 (-28)
TOPT = 23	59.9 (-2)	79.0 (-2)	48.3 (+2)	10.6 (-4)	5.8 (+2)	0.31 (-3)
DTEMP = +2	63.0 (+3)	81.9 (+2)	46.5 (-1)	9.5 (-14)	5.2 (-9)	0.31 (-3)
DTEMP = -2	59.1 (-3)	77.3 (-4)	50.2 (+6)	11.7 (+6)	6.0 (+5)	0.31 (-3)
DPPT = +10%	64.5 (+5)	101.1 (+8)	54.0 (+14)	11.6 (+5)	5.8 (+2)	0.28 (-12)
DPPT = −10%	59.6 (-3)	88.6 (−10)	41.0 (−13)	10.3 (-6)	5.6 (-2)	0.36 (+12)

were most strongly influenced by *k*, water use efficiency constant (WUE C) and TOPT. Changes in the light half saturation point *(HS)* had the least influence on predicted hydrology and productivity. A 16% change in HS produced a 1-6% change in model outputs.

Generally, changes in air temperature had a greater impact on productivity outputs while changes in precipitation had a greater influence on predicted hydrology (Table 3). Increasing average annual air temperature by 2°C decreased LAI, transpiration, GSSWS and NPP, while increasing average annual drainage (Table 3). Increasing average annual precipitation by 10% increased LAI, transpiration, average annual drainage, and NPP. When precipitation was increased by 10%, PnET-IIS predicted only a 8% increase in evapotranspiration, so predicted GSSWS decreased.

3.2. NPP validation sites

Across the 12 sites, canopy closure occurred between 1963 (Wayne County, MS site) and 1983 (Chester County, SC site). The climate from 1963 to 1990 was very dynamic, including some of the hottest, driest and wettest years on record (Marx, 1988). In addition to inter-site climate variability, climate also varied along longitudinal and latitudinal gradients. Generally, the lower latitude sites were warmer, but during the years of measurement, no clear regional trend in precipitation was observed (Table 2).

The greatest average annual air temperatures were recorded at the Bradford County, FL site, and the Dooly County, GA site. The lowest average annual air temperature occurred on the McMinn County, TN site. The Bradford County, FL site received the highest average annual precipitation while the Wilkinson County, GA site received the lowest. Across the 12 sites, average SWHC was 12.4 cm, but ranged from 6.0 cm at the Bradford County, FL site, to 16.0 cm at the Wayne County, MS site.

3.3. Predicted hydrology

Predicted annual evapotranspiration (*ET*) ranged from 55.3 cm during 1988, at the Walker County, TX site, to 104.0 cm during 1979, at the Wayne

Table 4
Predictions of growing season evapotranspiration (*ET*), drainage and soil water stress (GSSWS) and annual evapotranspiration, drainage and net primary productivity (NPP) for the 12 measured loblolly pine sites. Standard errors are included in parentheses

Site (state, county)	Average growing season			Average annual		
	ET (cm)	Drainage (cm)	GSSWS (%)	*ET* (cm)	Drainage (cm)	NPP (t biomass ha^{-1})
Bradford, FL	51.8 (1.5)	28.0 (1.9)	0.17 (0.02)	83.0(1.7)	47.6 (2.6)	11.4 (0.9)
Bienville, LA	55.4(1.1)	12.7 (2.7)	0.37 (0.03)	83.0 (1.4)	53.6 (4.6)	10.2 (0.7)
Chatham, NC	54.1 (1.1)	11.2 (1.4)	0.35 (0.05)	73.6(1.4)	43.2 (3.2)	10.8 (0.9)
Chester, SC	51.7 (2.0)	12.1 (1.8)	0.37 (0.08)	73.8 (2.1)	46.0 (4.2)	10.3 (1.3)
Colleton, SC	56.4 (1.6)	14.5(1.3)	0.31 (0.05)	83.1 (1.3)	38.5 (2.6)	12.8 (1.2)
Gloucester, VA	51.7(1.3)	15.6(1.8)	0.30 (0.05)	69.1 (1.4)	48.2 (3.9)	10.8 (0.9)
Dooly, GA	50.8 (1.9)	6.7 (0.5)	0.44 (0.03)	79.1 (1.4)	29.5 (2.6)	9.4 (0.8)
McMinn, TN	50.3 (1.5)	15.1 (3.2)	0.26 (0.04)	70.3 (1.3)	60.8 (5.6)	9.3 (0.8)
Morgan, AL	56.7 (1.4)	14.3 (2.0)	0.33 (0.05)	79.8 (1.5)	59.0 (4.4)	11.9 (0.9)
Walker, TX	48.1 (1.7)	11.3(1.8)	0.38 (0.05)	76.0 (2.1)	39.8 (3.7)	9.9 (0.8)
Wayne, MS	62.6 (0.7)	15.2 (1.6)	0.28 (0.03)	94.1 (0.8)	55.2 (2.9)	13.1 (0.5)
Wilkinson, GA	51.9 (1.6)	6.2 (0.5)	0.44 (0.05)	76.9 (1.6)	34.3 (2.2)	9.1 (0.8)
Average	54.2 (0.5)	14.5 (0.6)	0.32 (0.01)	80.3 (0.7)	47.2 (1.2)	11.0 (0.3)

County, MS site. The lowest average annual predicted evapotranspiration occurred at the Glouchester County, VA site (mean + SE 69.1 + 2.1 cm H_2O, n = 14), and the highest average annual evapotranspiration rate occurred at the Wayne County, MS site (94.1 + 1.0 cm H_2O, n = 28), (Table 4). Total annual drainage was a function of precipitation, SWHC and plant water demand. Annual drainage ranged from 5.2 cm in 1988 for the Walker County, TX site, to 86.0 cm in 1989 for the McMinn County, TN site. Average annual drainage was least in the Dooly County, GA site (29.5 + 2.6 cm, n = 11) and greatest in the McMinn County, TN site (60.8 + 5.6 cm, n = 14), (Table 4).

Predictions of GSSWS ranged from 0.15 (little water stress) for various years on the Bradford County FL, Glouchester County VA and Wayne County MS sites, to 0.63 in 1986 on the Dooly County, GA site and 0.68 in 1988 on the Walker County, TX site. The lowest predicted average annual GSSWS occurred on the Bradford County, FL site (0.17 + 0.02, n = 21), and the greatest predicted average annual GSSWS occurred on the Dooly County (0.44 + 0.04, n = 11) and Wilkinson County, GA sites (0.44 + 0.03, n = 13), (Table 4).

Soil water stress may be a useful indicator of plant stress and susceptibility to insects, pollutants or disease. For example, Lorio and Sommers (1986) found that soil water stress was related to oleoresin production in loblolly pine. Moderate water stress increases oleoresin production and decreases tree susceptibility to southern pine beetle (*Dendroctonus frontalis*, Zimm.) attack. Areas of predicted high GSSWS correlate with sections of the southern US which historically have high rates of southern pine beetle infestation (Price et al., 1991). These results suggest that given potential climate change scenarios, the model could predict future areas of southern pine beetle outbreak, based on GSSWS (McNulty et al., 1997a).

3.4. Predicted NPP

Predicted NPP ranged from 2.4 t ha^{-1} $year^{-1}$ for 1978 at the Walker County, TX site to 18.6 t ha^{-1} $year^{-1}$ in 1975 at the Wayne County, MS site, with the average NPP across all sites equal to 11.3 t ha^{-1} $year^{-1}$. Predicted average annual NPP was greatest on the Colleton County, SC and Wayne County, MS sites, and least in the Dooly County GA, McMinn County TN, and Wilkinson County GA sites (Table 4).

Predicted NPP in this study agrees closely with measurements of NPP. Teskey et al. (1987) measured a range of above ground NPP between 2 and 10 t dry matter ha^{-1} $year^{-1}$ on loblolly pine sites.

Other studies have estimated that below ground production equals approximately 40% of above ground NPP (Whittaker and Marks, 1975; Nadelhoffer et al., 1985). Multiplying Teskey et al. (1987) measurements of above ground NPP by 1.5 (60% above ground NPP/40% below ground NPP) yields a measured range of total (above and below ground) NPP between 3.0 and 15.0 t biomass ha^{-1} $year^{-1}$, with most site NPP (above ground only) over 8.5 t biomass ha^{-1} $year^{-1}$ (Teskey et al., 1987). PnET-IIS predicted NPP ranged from 2 to 18 t biomass ha^{-1} $year^{-1}$, with an average annual NPP value of over 9 t biomass ha^{-1} $year^{-1}$. Although NPP was always positive on an annual basis, the model predicted that NPP would be negative on some sites during the hottest months (average monthly maximum air temperature over 30°C).

In PnET-IIS, predicted gross photosynthesis is a function of photosynthesis per unit leaf area, and total leaf area. Optimal air temperature for loblolly pine photosynthesis is 17°C and 23°C, beyond which point, gross photosynthesis begins to decline (Strain et al., 1976). As temperature increases beyond the optimal level for gross photosynthesis, the rate of respiration continues to increase, therefore, proportionally less photosynthate per unit leaf area will be gained (Kramer, 1980). Within the model, changes in water availability and plant water demand place limitations on the amount of leaf area produced (Aber and Federer, 1992). Therefore, as air temperature increases above an optimal level, both photosynthesis per unit leaf area and total leaf area decline, while respiration continues to increase, which causes a reduction in NPP.

3.5. *Measured basal area growth*

The years of record (YOR) that basal area growth could be compared with predicted NPP varied between sites, due to differences in plantation establishment time and rate of canopy closure. The shortest record of basal area growth was from the Chester County, SC site and the longest was from the Wayne County, MS site (Table 2). Basal area growth ranged from 4.5 cm^2 per tree for 1980 at the Bienville Parish, LA site, to 26.4 cm^2 per tree in 1982 at the Colleton County, SC site. The Colleton County, SC site also had the largest average annual basal area growth, while the Dooly County, GA site had the smallest average annual basal area growth (Table 2).

3.6. *Basal area growth vs. predicted NPP*

Across all sites and years, predicted NPP was significantly (r^2 = 0.30, P < 0.005, n = 165) correlated with annual basal area growth (Fig. 3). Average annual basal area growth was highly correlated (r^2 = 0.66, P < 0.005, n = 12) with average annual predicted NPP (Fig. 4). Predictions of NPP may be more closely related to average annual basal area across all sites when compared with inter-annual basal area growth, because factors influencing growth not accounted for in PnET-IIS average out over long time periods. For example episodic O_3 events are known to influence growth of loblolly pines (Faulkner et al., 1990; Kress et al., 1992), but are not accounted for by PnET-IIS. Additionally, changes in C portioning are not accounted for by measuring basal area alone. During drought years, a greater percentage of the NPP may be placed into root production, compared with years with average or above average precipitation when proportionally more NPP could be allocated into basal area growth (Boyer, 1970). Over time, variation in C portioning is averaged into the basal area growth.

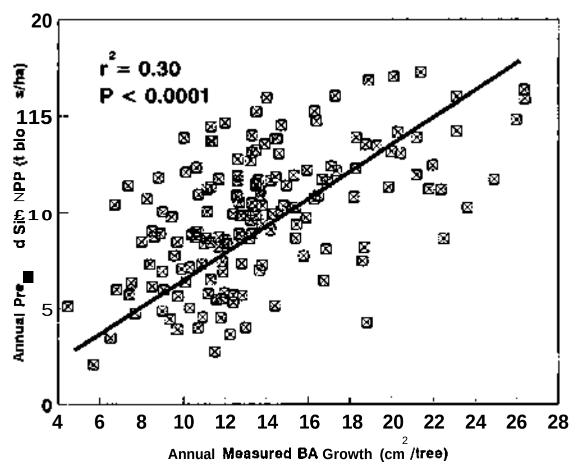

Fig. 3. Annual predicted NPP (t biomass ha^{-1} $year^{-1}$) vs. annual measured basal area growth (cm^2 per tree $year^{-1}$) for all 12 measured loblolly pine sites and years.

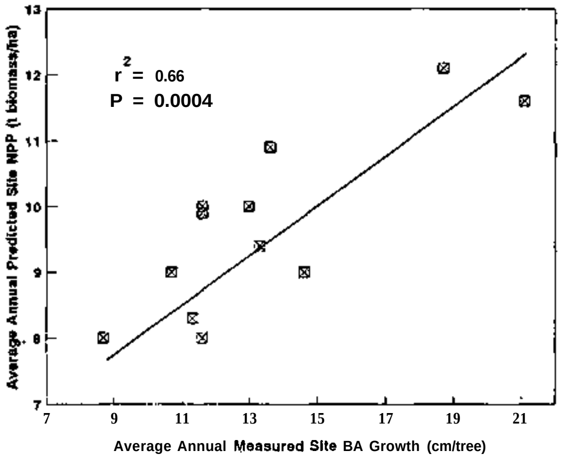

Fig. 4. Average annual predicted NPP (t biomass ha^{-1} $year^{-1}$) vs. average annual measured basal area growth (cm^2 per tree $year^{-1}$) for all 12 loblolly pine sites.

3.7. Basal area growth vs. other ecosystem parameters

In comparison with predicted NPP, other predicted and measured factors were less well correlated with measured annual basal area growth. Total growing season precipitation was the climate variable most strongly correlated with measured annual basal area growth ($r^2 = 0.14$, $P < 0.005$, $n = 165$), but no relationship ($P > 0.05$) between average growing season precipitation and average annual basal area growth was shown. The poor correlation with any single climate variable and basal area growth demonstrates the advantage of using plant water demand and soil water holding capacity for modeling forest growth.

Annual evapotranspiration was the hydrologic output that had the highest correlation with measured annual basal area growth ($r^2 = 0.34$, $P < 0.005$, $n = 164$). Total annual evapotranspiration was also the only hydrologic or climate variable which correlated with average annual basal area growth for the 12 sampled sites ($r^2 = 0.32$, $P < 0.05$, $n = 12$). Many of the same soil, climate and vegetation factors needed to predict NPP are also used to predict evapotranspiration. Thus, a good correlation between predicted NPP and predicted annual evapotranspiration exists ($r^2 = 0.55$, $P < 0.0001$, $n = 165$).

3.8. Hydrology validation

Precipitation was the only hydrologic variable measured on or near each of the 12 sampled sites, so validation of PnET-IIS predicted hydrology was not possible with these sites. However, predictions of site hydrology have been validated at the stand level with PnET (Aber and Federer, 1992) and PnET-II (Aber et al., 1996), and at the landscape scale with PnET-IIS (McNulty et al., 1994, 1996, 1997b).

4. Conclusions

PnET-IIS predictions of hydrology and productivity were most sensitive to changes in temperature-related model parameters. Sampling 12 loblolly pine sites across the southern US yielded a wide range of annual basal area growth rate. PnET-IIS was significantly correlated with measured annual and average annual basal area growth across the region. These results, along with previous research, indicate that PnET-IIS prediction of ecosystem hydrology are well correlated with measured ecosystem function. Future uses of this model could include prediction of climate change affects loblolly pine productivity and hydrology.

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References

Aber, J.D. and Federer, C.A., 1992. A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. Oecologia, 92: 463-474.

Aber, J.D., Ollinger, S.V., Federer, C.A., Reich, P.B., Goulden, M.L., Kicklighter, D.W., Melillo, J.M. and Lathrop, R.G., Jr., 1996. Predicting the effects of climate change on water yield and forest production in the northeastern U.S. Climate Res., 5: 207-222.

Boyer, W.D., 1970. Shoot growth patterns of young loblolly pine. For. Sci., 16 (4): 472-482.

Faulkner, P., Schoeneberger, M.M. and Kress, L.W., 1990. Belowground changes in loblolly pine as indicators of ozone stress. Sixth Biennial Southern Silvicultural Research Conference, Memphis, TN.

Kinerson, R.S., 1975. Relationships between plant surface area and respiration in loblolly pine. J. Appl. Ecol., 12: 965-971.

Kramer, P.J., 1980. Drought, Stress and the Origin of Adaptations. Adaptation of Plants to Water and High Temperature Stress. John Wiley, New York, pp. 7-20.

Kress, L.W., Allen, H.L., Mudano, J.E. and Stow, T.K., 1992. Impact of ozone on loblolly pine seedling foliage production and retention. Environ. Toxicol. Chem., 11: 1115-1128.

Lorio, P.L. and Sommers, R.A., 1986. Evidence of competition for photosynthates between growth processes and oleoresin synthesis in *Pinus taeda* L. Tree Physiol., 2: 301-306.

Marx, D.H., 1988. Southern forest atlas project. In: The 81st Annual Meeting of the Association dedicated to Air Pollution Control and Hazardous Waste Management (APCA), Dallas, TX, 1988, pp. 1–24.

McNulty, S.G., Vose, J.M., Swank, W.T., Aber, J.D. and Federer, C.A., 1994. Landscape scale forest modeling: Data base development, model predictions and validation using a geographic information system. Climate Res., 4: 223-231.

McNulty, S.G., Vose, J.M. and Swank, W.T., 1996. Prediction and Validation of Forest Ecosystem Processes at Multi-Spatial Scales Using a GIS. In: D.A. Quattrochi (Editor), Scaling of Remote Sensing Data for GIS. CRC Press, Boca Raton, FL, in press.

McNulty, S.G., Lorio Jr., P.L., Ayres, M.P., Reeve, J.D., 1997a. Predictions of Southern Pine Beetle Populations Under Historic and Projected Climate Using a Forest Ecosystem Model. In: S. Fox and R.A. Mickler (Editors), Global Change and the Forests of the Southeastern United States. Springer-Verlag, New York, NY, in press.

McNulty, S.G., Vose, J.M. and Swank, W.T., 1997b. Predictions and Projections of Pine Productivity and Hydrology in Response to Climate Change Across the Southern United States. In: S. Fox and R.A. Mickler (Editors). Global Change and the Forests of the Southeastern United States. Springer-Verlag, New York, NY, in press.

Nadelhoffer, K., Aber, J.D. and Melillo, J.M., 1985. Fine roots, net primary production, and soil nitrogen availability: a new hypothesis. Ecology, 66: 1377-1390.

Nikolov, N.T. and Zeller, K.F., 1992. A solar radiation algorithm for ecosystem dynamic models. Ecol. Modelling, 61: 149-168.

Price, T.S., Doggett, C., Pye, J.M. and Holmes, T.P., 1991. A history of southern pine beetle outbreaks in the southeastern United States. Georgia Forestry Commission, 67 pp.

Strain, B.R., Higginbotham, K.O. and Mulroy, J.C., 1976. Temperature preconditioning and photosynthetic capacity of *Pinus taeda* L. Photosynthesis, 10: 47-53.

Swank, W.T., Swift, L.W., Jr., Douglas, J.E., 1988. Streamflow changes associated with forest cutting species conversions and natural disturbances. In: W.T. Swank and D.A. Crossley, Jr. (Editors), Forest Hydrology and Ecology at Coweeta. Springer, New York, pp. 297-312.

Teskey, R.O., Bongarten, B.C., Cregg, B.M., Dougherty, P.M. and Hennessey, T.C., 1987. Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine *(Pinus taeda* L.). Tree Physiol., 3: 41-61.

USDA Forest Service, 1988. The South's Fourth Forest: Alternatives for the future. Rep. 24, US Government Printing Offfice, Washington, DC, 512 pp.

United States Water Resources Council, 1978. The nation's water resources, 1975-2000. Vol. 1: Summary. US Government Printing Office, Washington, DC, 86 pp.

Whittaker, R.H. and Marks, P.L., 1975. Methods of assessing terrestrial productivity. In: H. Lieth and R.H. Whittaker (Editors), Primary Production of the Biosphere. Springer, New York, pp. 55–118.

Zahner, R., Saucier, J.R. and Myers, R.K., 1988. Tree-ring model interprets growth decline in natural stands of loblolly pine in the southeastern United States. Can. J. For. Res., 19: 612-621.