Fertilization effects on forest carbon storage and exchange, and net primary production: A new hybrid process model for stand management

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Abstract

A critical ecological question in plantation management is whether fertilization, which generally increases yield, results in enhanced C sequestration over short rotations. We present a rotation-length hybrid process model (SECRETS-3PG) that was calibrated (using control treatments; CW) and verified (using fertilized treatments; FW) using daily estimates of H_2O and CO_2 fluxes, canopy leaf area index (L), and annual estimates of tree growth and dimension. Herein, we focus on two decades of loblolly pine (*Pinus taeda* L.) growth and establishment for stands growing on a nutrient poor, droughty soil (SETRES; Southeast Tree Research and Education Site) in North Carolina, USA, on a site previously occupied by a ∼30-year-old natural long-leaf pine (*P. palustris* Mill.) stand. The SECRETS-3PG model combines: (1) a detailed canopy process model with hourly and daily resolution, (2) a biometrically accurate tree and stand growth module for monthly allocation, 3-PG, and (3) empirical models of soil CO_2 efflux (R_S). Simulated L, quadratic mean tree diameter, and total standing biomass all tracked field measurements over a 10-year period. Simulated maintenance respiration, canopy transpiration, and R_S mirrored, with minor exceptions, short-term independently acquired data. Model correspondence with the independent measurements provided a basis for making short-term estimates of net ecosystem productivity (NEP) and longer-term estimates of net primary production (NPP) over the 20-year period from planting. Simulations suggest that optimum fertilization amendments; (1) increased NEP by more than 10-fold over control – FW (952 g C m^{-2} a^{-1}) and CW (71 g C m^{-2} a^{-1}) – at maximum NPP and (2) increased NPP two-fold (1334 and 669 g C m^{-2} a^{-1} for FW and CW, respectively) at maximum L. Seasonal patterns in NEP suggest that autumn and winter may be critical periods for C uptake in nutrient-limited loblolly pine stands. We conclude that increased L in response to improved nutrition may enable loblolly pine to achieve positive annual NEP earlier in rotation.

1. Introduction

Sustainable forest practices assume, among other prerequisites, that the net carbon (C) balance over a rotation will be positive or at least neutral. This applies not only to intensively managed forests but also to forests that could be managed to sequester C on lands unsuitable for agriculture or intensive cultivation (cf. Huston and Marland, 2003). Intensive forest management has thoroughly demonstrated that dramatic increases in short- and long-term yield can be achieved by improving soil site nutrition (Albaugh et al., 1998, 2004; Jokela

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and Martin, 2000; Boarders et al., 2004). Improved soil nutrient availability increases leaf area index (L) and, therefore, yield. On nutrient poor sites optimum fertilization treatments can increase annual stem volume increment by 10 m^3 ha^{-1} L^{-1} (Albaugh et al., 1998). When nutrition is less limiting, others have found even greater responses to fertilization (Jokela and Martin, 2000; Boarders et al., 2004). Improved soil nutrient availability also increases below ground coarse root biomass (Johnsen et al., 2001a). The relationships among soil nutrient availability, canopy leaf area, and the fluxes and long-term storage of C in mineral soil, however, remain largely unknown. High rates of soil CO_2 evolution associated with frequent disturbance on sites with low soil nutrient availability will likely limit significant accumulation of mineral soil C in intensively managed plantations. Thus, whether intensively managed forests are net sources or sinks for atmospheric C remains an unresolved question that can be addressed using an integrated, process based, modeling approach that accounts for novel environmental conditions and changing forest management (Johnsen et al., 2001b).

A suite of process models is available to predict short- and longer-term C fluxes in forest trees, stands, and ecosystems. Most of these models were originally developed as research tools. Accordingly, they address specific, and often rather narrow, questions of interest defined by the study objectives and the experimental design of field research sites. For instance, short-term gas exchange may best be studied using detailed canopy models such as MAESTRO (Wang and Jarvis, 1990) or MAESTRA (Luo et al., 2001). Longer-term (days to years) simulations are more suited to stand- or ecosystem-scale models such as SECRETS (Sampson et al., 2001), BIOMASS (McMurtrie and Landsberg, 1992), BIOME-BGC (Running and Hunt, 1993) or PnET (Aber and Federer, 1992), to name a few. The effects of soil C and nutrient cycling on long-term ecosystem C storage are best studied in decadal simulations (e.g. CENTURY: Parton et al., 1988 and G'DAY: Comins and McMurtrie, 1993). It is not surprising, then, that these models vary in their outputs, time-step, and process resolution. Canopy models accurately predict instantaneous radiation at the leaf surface (and thus CO_2 exchange) (i.e. Wang and Jarvis, 1990), however they, naturally, lack a unified approach for long-term C allocation. Conversely, ecosystem models such as BIOME-BGC (Running and Hunt, 1993) – a 'big leaf' model – allocate C and they estimate daily fluxes but finer resolution underpinnings are, by design, ignored, and thus cannot be validated.

We use ecosystem models to synthesize and integrate knowledge gained from intensive, short-term monitoring and experimentation – such as eddy-covariance measurements – to extrapolate to broader landscapes for long-term projections. Developing these models in concert with direct measures of gas exchange (e.g. Lai et al., 2002) has provided a means to validate short-term (days to years) model outputs (e.g. Wang et al., 2004). However, upscaling processes that occur at small-scales (leaves) to large spatial and temporal-scales (ecosystems) is subject to large errors due to functional non-linearity and heterogeneity in the distribution of processes (Jarvis, 1995). Accordingly, long-term validation of ecosystem models is

warranted. Moreover, models written as research tools are not oriented to address management related questions; they neither provide outputs that are useful to foresters (e.g. annual changes in stem volume, tree diameters, and stand density) nor do they enable silvicultural prescriptions. Research questions aimed at C sequestration and long-term sustainability may require new approaches in ecosystem modeling.

A model that is structured to enable validation of processes such as photosynthesis and respiration and stand attributes such as diameter, height, and volume growth – to name a few – using field measurements over years to decades would increase confidence in longer-term predictions. Simultaneously estimating daily (or hourly) canopy gas exchange, monthly growth and turnover, and annual conventional biometric attributes of stand properties throughout a rotation is suited to a hybrid modeling approach (Mäkelä et al., 2000). Linking standardized processes of gas exchange (e.g. SECRETS, Sampson et al., 2001) with a robust, and biometrically accurate C allocation schema (e.g. 3-PG—physiological principles predicting growth; Landsberg and Waring, 1997) (Landsberg et al., 2001, 2003; Law et al., 2001) in a management-oriented hybrid model would permit silvicultural decisions for management related questions while maintaining the components of ecosystem structure and function for short- and long-term validation.

In this study, we document the formulation of the SECRETS-3PG model and demonstrate its accuracy in predicting short- and long-term responses (daily gas exchange and annual and decadal growth) for loblolly pine plantations in North Carolina growing on an infertile site at Southeast Tree Research and Education Site (SETRES). We use the model to evaluate annual net primary production (NPP) over a short rotation for control (CW) and fertilized (FW) treatment plots at SETRES and a hypothetical fertilization-at-planting (FWP) scenario. We also examine the role of nutrition and stand development on net ecosystem productivity (NEP) during a 4-year period. Symbols referenced more than once in this study are listed in Table 1.

2. Materials and methods

2.1. Site description

All field data were acquired on loblolly pine stands established in 1985 on the sand hills of Scotland County, North Carolina (34°54′N, 79°29′W). In 1992, a factorial (SETRES) experiment (four replicated blocks) with combinations of fertilization and irrigation treatments, along with controls, was installed. Fertilizer was applied as needed to maintain optimum nutrition, defined by a foliar N concentration of 1.3% with other macro- and micro-nutrients in balance (e.g. Ingestad, 1987). Details on the study design, site, and treatments are provided by Albaugh et al. (1998, 2004).

Annual precipitation averages 1210 mm and is generally evenly distributed throughout the year, although occasional droughts do occur. Average annual temperature (T, °C) is 17 °C, June–August is 26 °C, and December–February is 7 °C. Each year an average of 62 days have a minimum T below freezing.

Table 1
A list of symbols referenced more than once in this study

Symbol	Description	Units
A_N	Net canopy assimilation	g C m^{-2} d^{-1}
CUE	Carbon use efficiency (NPP GPP^{-1})	Unitless
CW	Control plots	N.A.
delWR	Dry mass production of fine and coarse roots	g ha^{-1} month^{-1}
delWCR	Dry mass production of coarse roots	g ha^{-1} month^{-1}
delWFR	Dry mass production of fine roots	g ha^{-1} month^{-1}
DBH	Diameter at breast height	cm
Dq	Quadratic mean diameter	cm
Dq$_{AREA}$	Basal area of the tree of mean Dq	m^2 tree
E_C	Canopy transpiration	mm d^{-1}
$E_{C,N}$	Canopy transpiration, normalized leaf area basis	mm d^{-1}
fCR	Soil texture modifier on pCR	Unitless
F_R	Fertility ratio found in 3-PG	Unitless
FR_pCR	Fertility influence on pCR	Unitless
fracBB	3-PG fraction of branch and bark biomass	Proportion
fracBB$_{MOD}$	Fertility modified fracBB	Proportion
FW	Fertilized plots	N.A.
FWP	Fertilized at planting scenario	N.A.
GPP	Gross primary production	g C m^{-2} a^{-1}
H	Tree height	m
H_{BLC}	Height to the base of the live crown	m
$\bar{H}$	Mean tree height	m
HD	Dominant tree height	m
L	Leaf area index	m^2 m^{-2}; projected
L_E	Water balance	mm d^{-1}
LCE	Light capture efficiency (faPAR L^{-1})	Unitless
m	A soil fertility variable found in 3-PG	Unitless
m0	The value of m when SFRi is equal to zero	Unitless
N	Stand density	Stems ha^{-1}
NCE	Net canopy exchange (GPP minus Rd)	µmol CO$_2$ m^{-2} s^{-1}
NEP	Net ecosystem productivity	g C m^{-2} d^{-1}
NET$_{BIO}$	Biomass partitioned into tissue structures	g biomass m^{-2} d^{-1}
NPP	Net primary production	g C m^{-2} a^{-1}
pBark	The relative fraction of biomass allocated to bark	Unitless
pCR	Coarse root allocation coefficient	Unitless
pCR$_{MAX}$	Maximum coarse root allocation fraction	Proportion
pCR$_{MIN}$	Minimum coarse root allocation fraction	Proportion
P_N	Net photosynthesis	µmol CO$_2$ m^{-2} s^{-1}
pR	Root allocation coefficient	unitless
Rd	Foliage respiration	µmol CO$_2$ m^{-2} s^{-1}
R_{C_AG}	Above-ground construction respiration	g C m^{-2} d^{-1}
R_H	Heterotrophic respiration	g C m^{-2} d^{-1}
R_M	Maintenance respiration	g C m^{-2} d^{-1}
R_{M_AG}	Above-ground maintenance respiration	g C m^{-2} d^{-1}
R_S	Soil respiration	µmol CO$_2$ m^{-2} s^{-1}
SC	Soil class variable of 3-PG	Unitless
SFRi	Soil fertility index	Unitless
SI$_{25}$	Site index, base age 25	m
T	Temperature	Celsius
TDR	Time domain reflectometry	Hertz
θ_D	Volumetric soil water content	m^3 m^{-3}

2.2. Environmental measurements

A 10 m meteorological tower located at the site provides half-hourly measurements of photosynthetically active radiation (PAR) (LI-COR LI-190SA Quantum Sensor), shortwave radiation (LI-COR LI-200SB pyranometer), *T*, and relative humidity (Campbell Scientific HMP45C *T* and relative humidity probe). Soil temperatures at a 5 cm depth (mineral soil) are measured with a copper-constantan thermocouple and recorded on a CR21x Campbell data logger at half-hourly intervals.

Meteorological data collected at SETRES were available for the period from 1993 through 2001. To conduct a 20 year analyses – a short rotation – it was necessary to obtain meteorological data for the period from planting (1985) through 1992, and 2002 through 2004. Meteorological data from a continental-scale modeling program were available from an on-line source (Schimel et al., 2000; www.daymet.com) for the period prior to study installation. These data included daily shortwave radiation (W m^{-2}), average daily minimum and maximum ambient air *T*, daily precipitation (cm), daylight average saturated vapor pressure (Pa), and day length (s). Daily estimates of shortwave radiation were converted to standard units (MJ m^{-2} d^{-1}) (Anon., 1992). We calculated daily average saturated vapor pressure from average *T*. We then used daily maximum and minimum *T* to estimate daily minimum and maximum relative humidity following Murray (1967). We used an average year (a year whose monthly average fell within the 40th and 60th percentiles of the 10 year average) for *T* (1984) and a 'typical' year for precipitation (a year with average total rainfall and monthly sums similar to the 10 year record) (1996) for the 2002–2004 calendar years.

3. Model–data comparisons: empirical measurements

Independently acquired estimates of projected leaf area index (*L*), stand dimensional and biomass measurements, tissue maintenance respiration (*R*$_M$), soil respiration (*R*$_S$), and canopy transpiration (*E*$_C$) were available for model–data comparisons. Acquisition and use of these data are briefly discussed below.

3.1. Structural measurements of stand properties

Monthly estimates of *L* were attained for 1993–2000 using a statistical model formulated from empirical estimates of foliage biomass, LI-COR LAI 2000 plant canopy analyzer (PCA) measurements, and measurements of needle phenology (Sampson et al., 2003). Uncertainty in the *L* estimates was evaluated as discussed in Sampson et al. (2003).

Stand inventory data are collected at SETRES in December of each year. These include: (1) tree height (*H*; m), (2) diameter at breast height (DBH; cm), and (3) height to the base of the live crown (*H*$_{BLC}$; m). For each inventory year we calculated quadratic mean diameter (diameter of the tree of mean basal area) (Dq; cm), average tree height (*H̄*), and stand density (*N*; stems ha^{-1}) and we estimated dominant height (HD) (cf. Radtke and Burkhart, 1999) using Proc Univariate in SAS

(SAS, SAS Institute Inc., 1999). Inventory data for this paper were available for the period 1991 through 2001. Estimates of stand biomass used in the model–data comparisons were obtained from Albaugh et al. (2004).

3.2. Physiological measurements

Estimates of stem, foliage, and fine root R_M for 1996 from Maier et al. (2004), Maier (2001), and Maier (2000), respectively, were derived from tissue specific equations developed from trees sampled at the SETRES site. Stem R_M was based on stem T, and biomass and nitrogen content (Maier, 2001) while foliage and fine root R_M were based on tissue T and biomass (Maier, 2000). The seasonal patterns in tissue component respiration were developed for 1996 using site T data and estimates of component biomass (Maier et al., 2004).

Independent estimates of R_S for 1995 and 1996 and estimates of E_C for a 48-day period during 1996 were available for model–data comparisons. The R_S simulations and measurements are more fully discussed below. The E_C estimates, normalized on a unit leaf area basis ($E_{C,N}$), were obtained from the author (Ewers et al., 1999).

4. The SECRETS-3PG hybrid biogeochemical model

The SECRETS-3PG hybrid model represents an adaptation of the process model SECRETS (Sampson and Ceulemans, 1999; Sampson et al., 2001) and the process-based model physiological principles predicting growth (3-PG) (Landsberg and Waring, 1997). The SECRETS model is a multi-species, multiple-structure process model that simulates stand-scale C and water fluxes using process algorithms adapted from several sources. Namely: (1) Farquhar photosynthesis (P_N) (sun/shade model; de Pury and Farquhar, 1997), (2) R_M, and water balance (L_E) formulations (BIOMASS; McMurtrie and Landsberg, 1992) with L_E described fully in Meiresonne et al. (2003), and (3) empirical or mechanistic (GRASSLANDS DYNAMICS; Thornley, 1998) R_S. Empirical models of R_S are often site-sensitive. We incorporated another empirical model of R_S into SECRETS for use herein (Maier and Kress, 2000). The SECRETS model simulates P_N hourly, and R_M, L_E, and R_S daily. The 3-PG model is a simplified forest growth model developed with the specific objectives to obtain detailed stand-level properties useful to foresters (e.g. annual changes in stem volume, tree diameters, etc.). Strong yearly correspondence between 3-PG model outputs and empirical measurements are typically found (Landsberg et al., 2001, 2003; Law et al., 2001), consistent with forest inventory data acquired periodically throughout a full rotation (Landsberg et al., 2003; Waring and McDowell, 2002). Moreover, the 3-PG model has been well received and is widely used; there are currently over 20 peer-reviewed publications on 3-PG.

The SECRETS-3PG hybrid was designed to be useful as a forest management tool while, at the same time, maintaining the physiological mechanisms and outputs of interest to researchers. Thus, SECRETS-3PG links the process-level functions from SECRETS and the C allocation algorithms
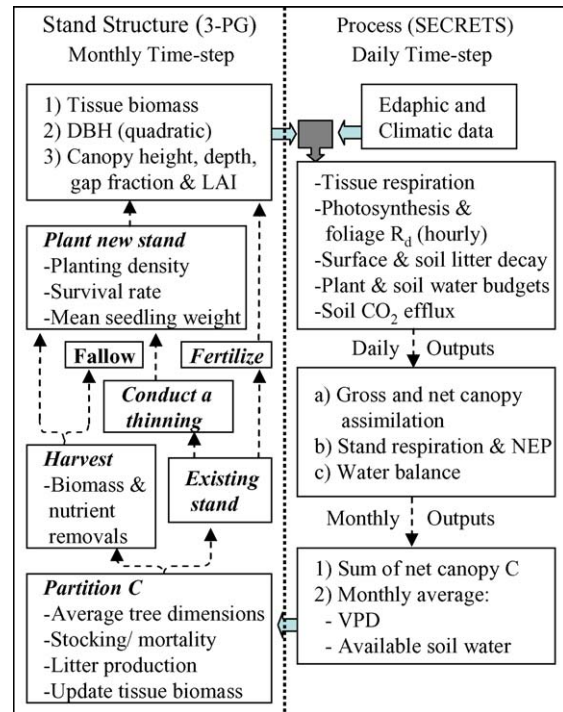

Fig. 1. A generalized flow diagram of SECRETS-3PG depicting the model structure and linkages between the process variables (SECRETS) simulated daily and the components of stand structure (3-PG C allocation schema).

(and associated functions) from 3-PG (Fig. 1). This model structure: (1) enables silvicultural prescriptions (i.e. planting, harvesting, fertilization amendments), (2) permits stand growth and dimensional estimates useful to managers (i.e. volume growth, DBH, HD, etc.), (3) provides estimates of pertinent ecosystem fluxes (C and H_2O) of interest to researchers, and (4) makes possible model–data comparisons of stand structure attributes and process-level mechanisms using field measurements at scales appropriate to both. The SECRETS-3PG model also incorporates a dynamic needle litter-fall representative of a three foliage cohort pine that can also be verified using needle litter-fall collections. These adaptations are described below.

4.1. Three-cohort needle phenology

The SECRETS-3PG model can either input L from a computer hard disk, when daily estimates of L are available, or simulate L based on the 3-PG algorithms adapted for use here. When L is simulated, standard 3-PG needle litter-fall or a cohort specific needle litter-fall approach following Sampson et al. (2003) may be used.

4.2. Carbon allocation

To link the two models, it was necessary to develop new equations and to derive the parameter estimates central to the C allocation and stand structure schema. These equations and parameters are associated with: (1) biomass partitioning, (2) root turnover, (3) stem mortality, (4) fertility effects on C

allocation, and (5) canopy structure (Sands, 2002). These are discussed in order, as follows.

4.2.1. Biomass partitioning

The 3-PG model allocates biomass into roots, stems, and foliage. However, SECRETS differentiates standing biomass into fine (<2 mm) roots, coarse, and tap roots combined (>2 mm) (hereafter referred to as 'coarse root'), stem, branch, and foliage tissues. It was thus necessary to add allocation coefficients for coarse roots, branches, and bark to the SECRETS-3PG hybrid model.

The net rate of dry mass production for fine and coarse roots combined (delWR; g ha^{-1} month^{-1}) is expressed as:

$$\text{delWR} = \text{NET}_{\text{BIO}} \cdot \text{pR}$$

where NET_{BIO} is net biomass available to distribute each month (g ha^{-1} month^{-1}) and pR is the root allocation coefficient that is scaled from zero to one (Landsberg and Waring, 1997). The process side of SECRETS-3PG (Fig. 1) passes the monthly sum of net canopy assimilation (A_N) to the structure (allocation) side of the model with biomass (NET_{BIO}) assumed to be 47% C.

The original Landsberg and Waring (1997) equation to estimate pR was modified for use in SECRETS-3PG; simulated root production was consistently greater than the empirical estimates at SETRES (see Albaugh et al., 2004; Maier and Kress, 2000). We added an exponent (η) to the original formulation to increase sensitivity of the algorithm to m and the physiological modifier (PhysMod) as:

$$\text{pRz} = \left[\frac{(\text{pRx})^{\eta^{-1}}}{1 + \left(\left(\frac{\text{pRx}}{\text{pRn}} \right)^{\eta^{-1}} - 1 \right) \cdot m \cdot \text{PhysMod}} \right]^{\eta}$$

where pRz is the adjusted root allocation coefficient, m is the fertility variable (discussed below), and PhysMod is a physiological modifier that considers soil water content and vapor pressure deficit (Landsberg and Waring, 1997).

The model adaptation required differentiation of delWR into fine (delWFR) and coarse (delWCR) root production. First, m (see Eq. (15); Landsberg and Waring, 1997) is calculated as:

$$m = m0 + (1 - m0) \cdot \text{SFRi} \tag{1}$$

where $m0$ is the value of m when the soil fertility index (SFRi) is equal to zero, and SFRi (FR as used in 3PG) is a measure of the soil nutritional status effecting root production (Landsberg and Waring, 1997).

We estimate a coarse root allocation coefficient using two equations, one of which accounts for the effect of soil nutrition (as reflected by SFRi) on the coarse root fraction of total root production. They are:

$$\text{pCR} = \frac{\text{CR}_{\text{MAX}}}{1 + \left(\frac{\text{CR}_{\text{MAX}}}{\text{CR}_{\text{MIN}}} - 1 \right) \cdot \text{FR\_pCR}}$$

where the proportional maximum (CR_{MAX}) and minimum (CR_{MIN}) allocation to coarse roots are user-defined while

FR_pCR is the soil nutrition scalar variable that is expressed as:

$$\text{FR\_pCR} = \frac{1}{(1+m)^{\varepsilon}} \tag{2}$$

where ε is a parameter to be estimated and m is discussed above. Finally, coarse root production, then, is estimated as:

$$\text{delWCR} = \text{delWR} \cdot \text{pCR}$$

The other variables are as before. The model then estimates delWFR as the difference between delWR and delWCR.

Because SECRETS-3PG differentiates stem, branch, and bark production explicitly we retained, but modified, the original formulation that estimates the fraction of above-ground woody biomass allocated to stems as one minus the proportion allocated to branch and bark production (fracBB), with fracBB influenced by stand age (Landsberg and Waring, 1997). We added a fertility modifier to fracBB (fracBB$_{\text{MOD}}$), or:

$$\text{fracBB}_{\text{MOD}} = \text{fracBB} \cdot \left(\frac{1}{1+m} \right) \tag{3}$$

The variable m was previously defined. Bark production (pBark) is estimated as a constant fraction of fracBB ($\sim$8%; Albaugh et al., 2004). The approach to estimate stem production was unchanged.

4.2.2. Root turnover

Because we differentiate between fine and coarse roots, it was necessary to estimate fine and coarse root litter; both are estimated as constant fractions of standing biomass (Table A.4).

4.2.3. Stem mortality

Random mortality has been occurring at SETRES while density-induced thinning has not (Albaugh et al., 2004). The 3-PG model incorporates density dependant mortality. To maintain accuracy but retain simplicity we added a term to reflect random tree mortality. Because SECRETS and 3-PG are both stand-level models – they simulate conditions for an 'average' tree – we can mimic random mortality by removing a constant number of trees each month. Our stand inventory data indicated that, on average, 6 trees ha^{-1} a^{-1} were lost between 1991 and 2001. Thus, 6 trees year^{-1}, or 0.5 trees month^{-1}, are removed starting when stand basal area reaches 5 m^2 ha^{-1} (cf. Albaugh et al., 2004).

4.2.4. Stand intervention and site fertility

The SECRETS-3PG hybrid model structure enables management intervention. Specifically, simulations may be interrupted to conduct a thinning, to harvest and then plant, or to change parameters of biomass allocation such as the soil fertility index (Fig. 1). The soil fertility parameter is an important allocation parameter in the 3PG approach (e.g. Landsberg and Waring, 1997). Landsberg and Waring (1997) note that although there is evidence to suggest that nutrition affects the amount of C allocated to roots, quantifying the relationship is difficult. They created a tractable solution to

modify C allocation to roots as influenced by site growing conditions (Eq. (15); Landsberg and Waring, 1997). In SECRETS-3PG, the soil fertility parameter, SFRi, may be altered to mimic changes in site fertility.

4.2.5. Stand structure and canopy height

Landsberg and Waring (1997) estimated Dq from average stem mass for a stand of 1000 trees ha^{-1} as:

$$Dq_{3-PG} = \left(\frac{AvgStemMass}{StemConst} \right)^{1/StemPower}$$

where StemConst and StemPower are allometric constants. We found this equation to be insensitive to changes in SFRi as used in this model (fertilization events in SECRETS-3PG). We thus added a variable to describe an apparent change in the relationship between AvgStemMass and Dq when SFRi is altered. The modified equation is:

$$Dq = \left(\frac{AvgStemMass \cdot Dq_M}{StemConst} \right)^{1/StemPower}$$

with Dq_M estimated as:

$$Dq_M = \sqrt{\frac{1}{(1-m) + m0}}$$

where m and $m0$ were discussed above. This equation was generated using the FW test data set.

The SECRETS-3PG hybrid estimates $\bar{H}$, HD, and live crown length from stand dimensional measures. We used non-linear regression procedures in SAS and the SETRES stand inventory to derive the parameter estimates for an equation to estimate $\bar{H}$ and HD as:

$$\bar{H} \text{ or } HD = \frac{Volume}{Dq_{AREA}^{\gamma_1 \cdot Dq^{\gamma}}} \cdot N^{-\gamma_3}$$

where γ_1, γ_2, and γ_3 are parameters to be estimated, Volume (v) is total stand volume (m^3 ha^{-1}; inside bark), Dq_{AREA} is basal area (BA) of the tree with mean BA (m^2), and the other variables are as before. We estimated v for each plot and year at SETRES using the standard equations found in the allocation schema of 3-PG. The tree height equation had an approximate r^2 of 0.99. To enable predictions of live crown length we used a modified Chapman–Richard's equation in SAS, and the stand inventory data, to predict mean height to the base of the live crown ($\overline{H_{BLC}}$) as:

$$\overline{H_{BLC}} = \kappa_1 \cdot (1 - e^{-\kappa_2 \cdot Volume})^{\kappa_3} \cdot \kappa_4^N \cdot Dq^{\kappa_5}$$

where $\kappa_1 - \kappa_5$ are parameters to be estimated. This regression equation had an approximate r^2 of 0.98. Live crown length, then, is estimated in the model as the difference between $\bar{H}$ and $\overline{H_{BLC}}$.

4.3. Soil respiration

Our daily estimates of soil respiration for CW and FW plots for these analyses used the equation developed by Maier and Kress (2000). At the time of measurement (1995–1996), rates of R_S were significantly greater in the CW than in FW plots; higher rates in CW plots were attributed to differences in soil temperature rather than from a direct effect of fertilization on root or soil metabolism (Maier and Kress, 2000). The response of soil CO_2 efflux to fertilization is mixed ranging from a reduction (Mattson, 1995; Haynes and Gower, 1995; Lu et al., 1998; Butnor et al., 2003), no effect (Vose et al., 1997; Pangle and Seiler, 2002) to increases (Griffin et al., 1997; Mikan et al., 2000) in R_S. Fertilization of a mid-rotation loblolly pine plantation in the North Carolina Piedmont resulted in a brief stimulation (several weeks) followed by a long-term suppression of R_S (Butnor et al., 2003). These mixed results are likely due to the complex and differential effects of fertilization (type and amount) on root growth, root specific respiration rates, microbe population, and metabolism. Some of these component responses may offset one another resulting in no net change in R_S (Maier and Kress, 2000; Gough et al., 2005), thus R_S may be remarkably stable over a rotation (Gough et al., 2005). Because we cannot verify or validate R_S for the FWP scenario no estimates of R_S for FWP simulations were possible.

4.4. Model parameterization, fitting, and validation procedures

The SECRETS-3PG parameters may be found in Tables A.1–A.6. We used control plots (CW) at SETRES to calibrate the model. For biomass allocation we used starting values similar to those used by others for loblolly pine (e.g. Landsberg et al., 2001) and incrementally adjusted them until we achieved agreement ($\pm 5\%$) between the model outputs; and (1) L, (2) Dq, and (3) fine and coarse root standing biomass (cf. Albaugh et al., 1998, 2004). A SFRi value of 0.01 was used to fit the model for the CW treatments.

We separated the data from the FW plots to create a ''test'' data set for use in model fitting and data used for the model–data comparisons (to evaluate model performance). At present (and similar to the difficulties in obtaining an estimate of the fertility index of 3-PG) we have no a priori estimate of the SFRi fertility parameter for the fertilized treatments. Thus, to estimate SFRi for the FW plots we conducted a simulation using the test data set, interrupting the run in March of 1992 to set the SFRi value to 0.1 and then let the model run through 2004. We then examined the peak simulated L achieved for 1997. We then iteratively changed the SFRi value in subsequent simulations until we were within $\pm 5\%$ of our empirical estimate of peak L. This current ''Achilles' heel'' of the model and its implications are briefly discussed below.

Because fertility influences the delineation between fine and coarse root allocation in SECRETS-3PG, it was necessary to estimate the ε parameter of Eq. (2). This parameter was altered until simulation outputs for coarse root standing biomass was within $\pm 5\%$ of the measured estimates at the end of 1992 and 2000 for the CW and the FW plot test data set (Albaugh et al.,

2004). The FWP simulations used the FW SFRi value at planting. This approach to model fitting was, at present, necessary in order to provide the best estimates of NEP possible during our 4-year scrutiny of C balance. It does not suggest that we have current capabilities of accurately simulating an extant fertilized stand without parameter iteration. At present, we have an approach to estimate SFRi for unfertilized stands (unpublished data). Current model development is incorporating an approach to estimate SFRi for fertilized stands and a Bayesian approach to model-parameter uncertainty.

We conducted a sensitivity analyses to examine the effect of changes in SFRi on model outputs. We increased and decreased the SFRi value for FW plots (at the time of model intervention) by 5, 10, and 20% to examine the effect on L, NPP, and NEP.

5. Simulations

5.1. Approach

Initial stand characteristics are provided in Table A.1. Simulations for these analyses used hourly PAR estimated from daily shortwave radiation. Meteorological data included daily estimates of shortwave radiation, minimum and maximum ambient air T, minimum and maximum soil T, precipitation, and minimum and maximum relative humidity.

5.2. Simulations conducted

Simulations included model–data comparisons, estimates of NPP and of heterotrophic respiration (R_H), and short-term projections of net ecosystem productivity (NEP). We calculated R_H as the difference between total soil CO_2 efflux estimated with the empirical equation and root autotrophic (maintenance and construction) respiration. For these analyses we calculated NEP as:

$$NEP = GPP - (R_{M\_AG} + R_{C\_AG} + R_S)$$

where GPP is gross primary production, and R_{M_AG} and R_{C_AG} are above-ground maintenance and construction respiration, respectively. The other variable is as before.

Model performance was evaluated using the empirical measurements as discussed above. First, we compare model outputs with empirical estimates of L (Sampson et al., 2003), total standing biomass, and estimates of Dq (Albaugh et al., 1998, 2004) for FW plots. We also compared simulated HD for CW and FW treatments using inventory estimates. We included simulated HD for FWP plots for treatment comparisons and we estimated site index (SI_{25}) (Amateis et al., 2001). Second, model–data comparisons for the physiological processes included: (1) tissue R_M for 1996 (Maier and Kress, 2000; Maier, 2001), (2) normalized transpiration ($E_{C,N}$) for multiple days during 1996 (Ewers et al., 1999), and (3) R_S measurements as discussed above for a 12 month period during 1995 and 1996 (Maier and Kress, 2000). Third, we present 20 years of NPP and model estimates of carbon use efficiency (CUE; the ratio of NPP to GPP) and we projected 4 years of NPP and NEP for CW

and FW plots at SETRES (1994–1997; inclusive) and R_H for the FW treatment. For this we assume that 1-year prior to, and following, the empirical measures of soil respiration are accurately represented using the regression. Lastly, results from the sensitivity analyses of SFRi on L, NPP, and NEP are presented.

6. Results

6.1. Model performance

6.1.1. Carbon partitioning

Simulated stand development closely mimicked observed C partitioning and biomass accumulation in the FW plots. Synchrony in annual foliage production and a three-cohort needle litter-fall phenology yielded temporal patterns in simulated L that were within the confidence intervals of the empirical analyses (Fig. 2A). Our approach, however, cannot adequately capture short-term changes in L as a result of severe drought or hurricane disturbance. Simulated standing biomass was closely aligned with our available estimates from empirical measurements (Fig. 2B). Finally, the stand inventory estimates of Dq and those simulated also compared well with the empirical measures (Fig. 2C).

We found good correspondence between the model estimates of HD and the empirical measurements for FW
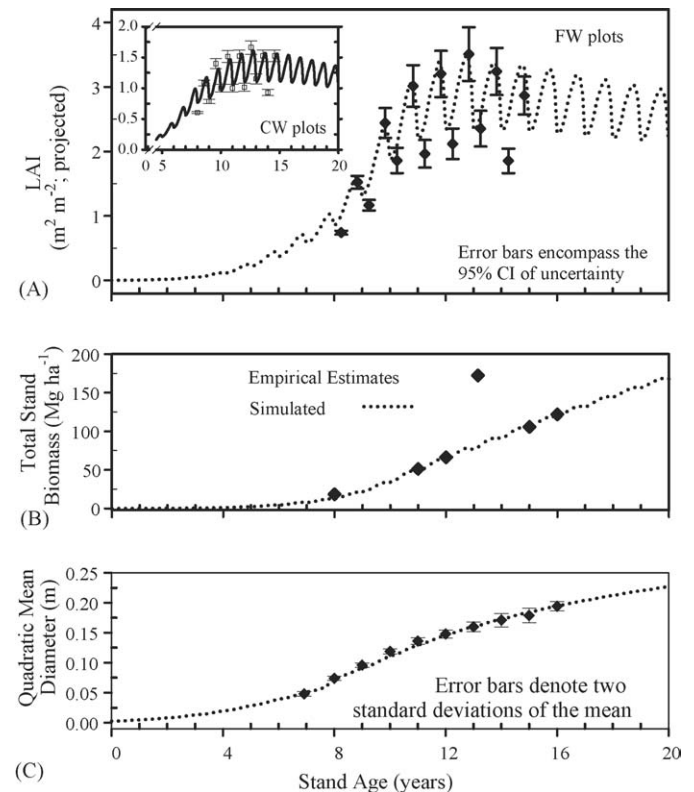
Fig. 2. Simulated leaf area index (L) (A), quadratic mean diameter at breast height (Dq) (B), and standing biomass (C) from the hybrid process model SECRETS-3PG for fertilized plots (FW) from planting in 1985 through 2004 vs. stand inventory data at SETRES, a loblolly pine research site located in Scotland County, North Carolina.
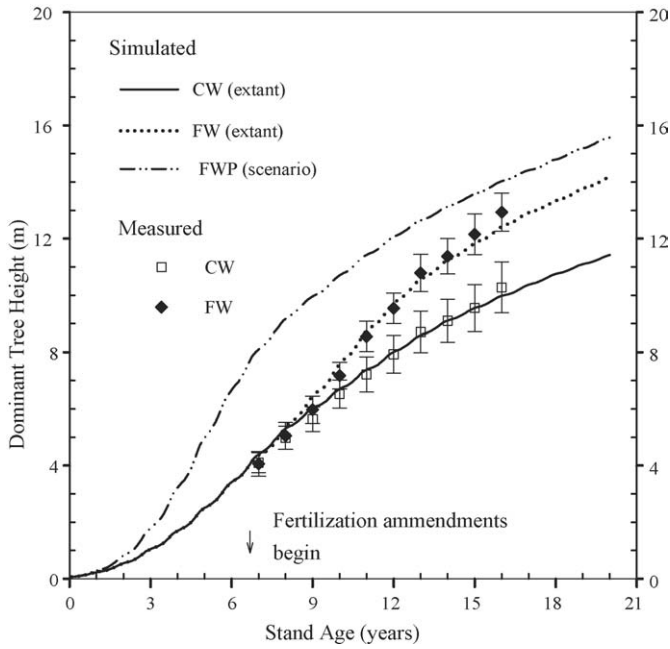
Fig. 3. Simulated dominant tree height (HD) for control (solid line), fertilized (dashed line), and a hypothetical fertilized-at-planting scenario (dotted line) at SETRES using the hybrid process model SECRETS-3PG from planting in 1985 through 2004. Empirical measurements were obtained from stand inventory data.

plots (Fig. 3) (the model was fit using CW estimates of HD). Simulated HD for the control plots suggest that the base site index (SI$_{25}$) for SETRES is about 14 m. Fertilization 8 years post planting increased SI$_{25}$ by 3 m. However, the fertilizing at planting scenario suggests that SI$_{25}$ could be increased by almost 5 m at SETRES through optimum nutrition amendments.

6.1.2. Physiological and tissue biomass comparisons

Model validation of the base physiological processes had variable, but favorable results. In general, simulated R_M corresponded well with the empirical estimates. From mid-May to October, however, simulated foliage respiration (Rd) was higher than the empirical estimates; empirical estimates of Rd approached 4 μmol CO_2 m^{-2} s^{-1} while simulated Rd approached 5 μmol CO_2 m^{-2} s^{-1} during 1996 (Fig. 4A). Absolute differences in L (between that used in the empirical analyses and that simulated here) may explain much of this variation. Stem (Fig. 4B) and fine root R_M (Fig. 4C) comparisons were more closely aligned with minor exceptions. The empirical estimates of stem R_M were moderately higher that that simulated during the spring and early summer for 1996 (Fig. 4B). Minor departures between simulated outputs and the independently acquired measurements could be explained by abiotic factors (e.g. T) but they may also be attributed to differences in the way that tissue R_M was calculated. For instance, the empirical estimates of stem R_M were based not only on T, but also on nitrogen concentration.

Discrepancies between empirical and simulated Rd led us to examine the T response functions for dark respiration of foliage. Empirical estimates of Rd used three separate equations,
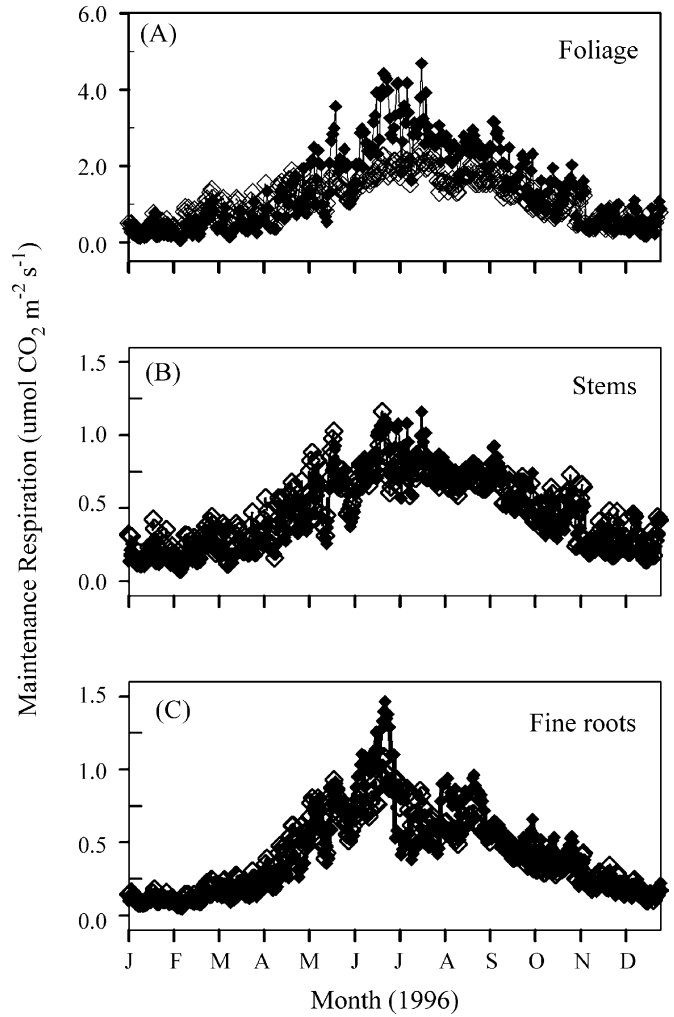

Fig. 4. Comparisons of simulated tissue maintenance respiration for foliage (A), stems (B), and fine roots (C) for fertilized plots vs. those estimated by Maier et al. (2004) for 1996 at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from the SECRETS-3PG hybrid process model.

depending on the season. For instance, the slope for the January equation was greater than that for August (Fig. 5). The SECRETS-3PG model uses one Arrhenius function, with a stronger T response for summer than that used in the empirical analyses (Fig. 5). Thus, differential responses in Rd to leaf T
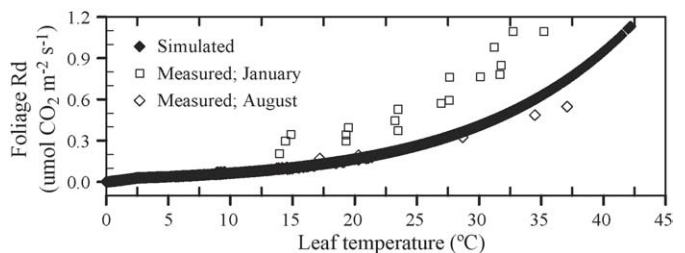

Fig. 5. The relationship between foliage respiration estimates (Rd) and leaf temperature for simulated (filled triangles), and measured (empty triangles and squares) for fertilized plots (Maier, 2000) at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from the SECRETS-3PG hybrid process model.

would be expected. Slope differences from the empirical analyses, however, suggest that empirical estimates for winter should be higher than those simulated. This discrepancy, and the others mentioned above, may be also explained by differences in leaf T. Simulated leaf temperatures were estimated from daily minimum and maximum data while the empirical analyses used measured leaf temperatures at the time the study was conducted.

We observed a strong correspondence between the simulated and empirical estimates of normalized transpiration ($E_{C,N}$) for FW plots (Fig. 6). During the 49 day comparison period in 1996 simulated $E_{C,N}$ was often similar to that up-scaled from sapwood area and xylem water flux measurements. On several days, however, the model underestimated the empirical estimates. Proportional departures in $E_{C,N}$ between the simulated and empirically estimated values were examined, in detail, for 15 days during the comparison period (Fig. 6B). Reduced $E_{C,N}$ as simulated by SECRETS-3PG corresponded with days exhibiting lower incident PAR (IPAR) (Fig. 6C) and thus reduced P_N (Fig. 6D) and, in particular, those days of proportionally greater canopy photosynthesis by shaded leaves

(Fig. 6B–D). For instance, decreased IPAR on day of year (doy) 273 through 275 (29 September–1 October) resulted in decreased P_N on those days with an accompanying increased proportion of total canopy P_N from shaded versus sun lit leaves (Fig. 6C and D).

We found favorable comparisons between measured and simulated estimates of θ_D, T, and R_S. Simulated θ_D was generally similar to the TDR measurements (Fig. 7A). It is worth noting that the soil site water balance comparison for the 1995–1996 comparison represents a cumulative accounting of soil available water and the various fluxes from the start of the simulation cycle in 1985. Model estimates of soil T at 5 cm were also comparable with those used in the empirical analyses (Fig. 7B). Despite minor differences in predicted θ_D and soil T (compared to the measurements), the model estimates of R_S were consistent with the point estimates from the infrared gas analyzer measurements (Fig. 7C).

Our model–data comparisons for stem, branch, and coarse root standing biomass serve to illustrate model performance in allocating daily C on a monthly basis (Table 2).

6.2. Simulated NPP and net ecosystem productivity

Optimum nutrition increased annual NPP two-fold in the fertilized plots by peak production. Annual NPP for CW plots
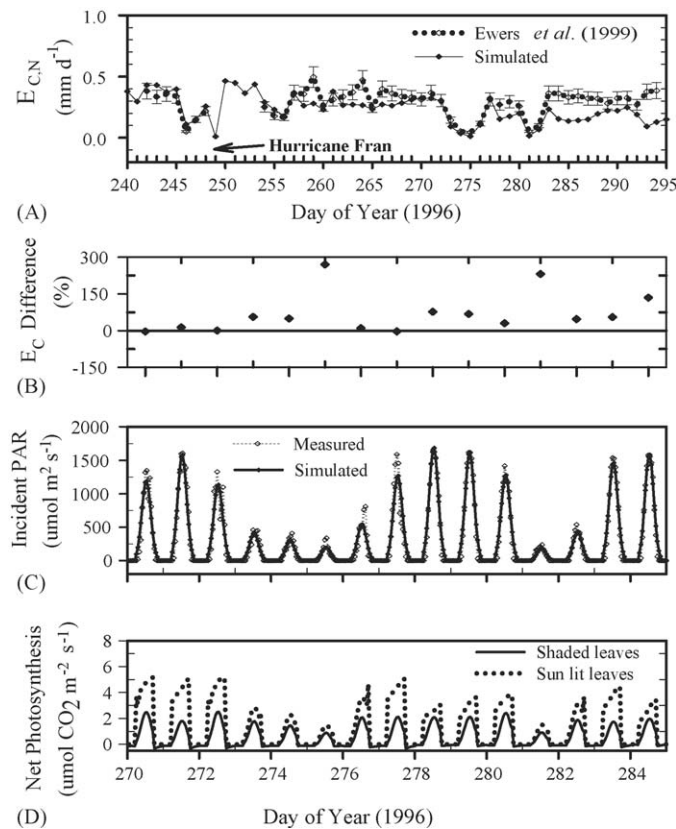

Fig. 6. A comparison of simulated canopy transpiration ($E_{C,N}$) vs. those estimated by Ewers et al. (1999) for fertilized plots for 47 days during 1996 (A), the percent difference between simulated and estimated $E_{C,N}$ for 15 days during the 1996 comparison (B), estimated hourly incident PAR vs. measured (C), and simulated net photosynthesis for sun and shade leaves over the same period (D) at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from the SECRETS-3PG hybrid process model. Transpiration was expressed on a unit leaf area basis. Error bars denote one standard error of the mean.

Fig. 7. Simulated vs. measured volumetric soil water content (θ) to a depth of 15 cm (A), soil temperature at 5 cm (B), and daily (dashed line) and mean monthly (open squares) soil CO_2 efflux (R_S) (C) for fertilized plots (FW) for 1996 at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from SECRETS-3PG, a hybrid forest process model. Empirical measurements are from Maier and Kress (2000).

Table 2
An end-of-year comparison of standing biomass for stems, branches, and coarse roots (includes tap roots) between empirical measures from destructive harvests at the Southeast Tree Research and Education Site (SETRES) and that simulated by the hybrid process model SECRETS-3PG

Plot	Tissue	Mg biomass ha^{-1}	
		Empirical[a]	Simulated
End of 1996			
CW	Stems	14.85	13.73
	Branches	6.91	6.73
	Coarse roots	5.76	5.40
FW	Stems	30.96	28.68
	Branches	10.38	12.13
	Coarse roots	13.87	12.12
End of 2000			
CW	Stems	25.93	26.28
	Branches	12.07	12.02
	Coarse roots	10.00	9.91
FW	Stems	58.78	60.44
	Branches	22.40	24.12
	Coarse roots	24.93	24.76

[a] Albaugh et al. (2004).

peaked 12 years following planting (Fig. 8, panel A). Optimum nutritional amendments that began in 1992 enabled FW plots to achieve maximum NPP 5 years later (Fig. 8, panel A). Annual NPP for the FWP scenario peaked 7 years following planting with declines following 4 years later (Fig. 8, panel A). The ratio of simulated NPP to GPP (carbon use efficiency—CUE) for the 20-year period decreased with stand age (Fig. 8B). Slight divergence among the treatments began 6–7 years after planting, with FWP treatment exhibiting the lowest CUE while CW and FW plots were nearly identical, but higher. A value of 0.47 – used in the 3-PG
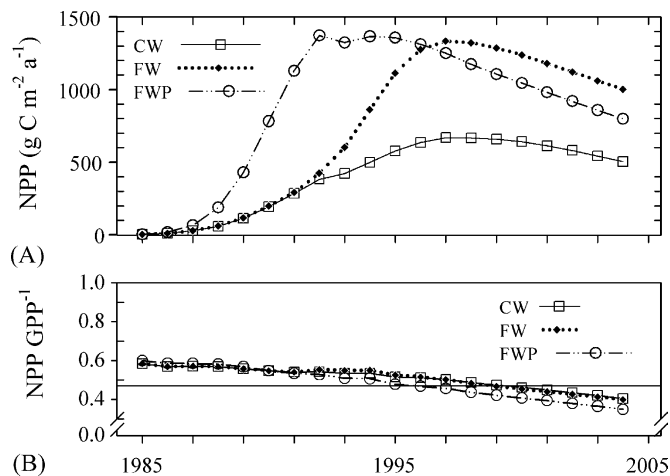
process-based model – was reached 11–14 years post planting (Fig. 8B).

Simulated bi-monthly estimates of NPP demonstrate the seasonal variability in net C gain and the influence of biotic controls over productivity in these intensively managed loblolly pine stands (Fig. 9, panel A). Simulated NPP in FW plots was roughly twice that of CW plots (Fig. 2A). High plasticity in foliage production and indeterminate growth for this three-cohort pine permit fairly rapid adjustments in L in response to improved soil nutrition and climate.

A 4-year "window" into net C balance depicts the seasonal dynamics and the effect of optimum nutrition on net ecosystem productivity (NEP) for loblolly pine growing on a droughty, nutrient poor site. The CW plots exhibited typical seasonal responses for a coniferous species with, in general, net C loss not only during the summer of each year but also on occasion

Fig. 8. Annual net primary production (NPP) (A) and the ratio of NPP to gross primary production (B) for control (CW—soil line, open squares) (A and B) and fertilized (FW—dotted line, filled diamonds) treatments (A–C), and a hypothetical fertilized-at-planting scenario (open circles) (A only) at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from the SECRETS-3PG hybrid process model.

Fig. 9. Mean daily NPP (A), net ecosystem productivity (NEP) (B), heterotrophic respiration (R_H)(C), and the ratio of R_H to total soil respiration (D) averaged bi-monthly over a 4 year period for control (CW—soil line, open squares) (A–C) and fertilized (FW—dotted line, filled diamonds) treatments (A–D), at SETRES, a loblolly pine research site located in Scotland County, North Carolina. Simulations were from the SECRETS-3PG hybrid process model. The FWP plots were omitted because no empirical model of soil respiration was available for this scenario. The CW plots were omitted from panels C and D to increase clarity by reducing redundant overlap in the estimates.

loss during winter 'dormancy', especially during 1994 and into 1995 (Fig. 9, panel B). At near peak and peak L for the stand and, thus, maximum NPP (1996 and 1997) net positive NEP during autumn and winter for CW plots suggest that autumn and winter C uptake may be critical periods for nutrient-limited stands. The FW plots, of course, having greater L had greater NEP; FW plots during this period only exhibited net C (averaged bi-monthly) losses during 1994. The FWP plots were excluded from these analyses for reasons mentioned above.

The increased trend in NEP with time for both treatments is, of course, attributed to increased L (Fig. 2) and, thus, increased NPP (Fig. 8A) over this period. The seasonal patterns are due to the strong temperature (and incident shortwave) signal; less obvious are soil moisture effects on soil CO_2 efflux. Increased NEP in 1997 (when compared to the previous years) for both plots can also be attributed to reduced soil C losses during 1997 (Fig. 9, panel C); precipitation was 17% lower in 1997 (1159 mm a^{-1}) as compared to 1995 (1395 mm a^{-1}). Estimates of R_H for FW plots suggest a decrease over time as root growth – coarse roots increased by ∼280% over this period – accelerates. The ratio of R_H to R_S approached 40% 12 years after planting (Fig. 9D). Seasonal variation suggests a reduced contribution of R_H during April and October of each year.

Annual simulated GPP, NPP, and NEP increased from 1994 through 1997 (Table 3). CW plots exhibited a few negative NEP years but were in near short-term equilibrium while NEP for FW plots nearly tripled over this period (Table 3). Of course, because NEP represents the difference between two large but apposing fluxes, dramatic changes in NEP can occur from minor changes in either gross C uptake (GPP) or total ecosystem respiration (TER). Between 1994 and 1997 NPP was increasing more rapidly than TER (data not shown).
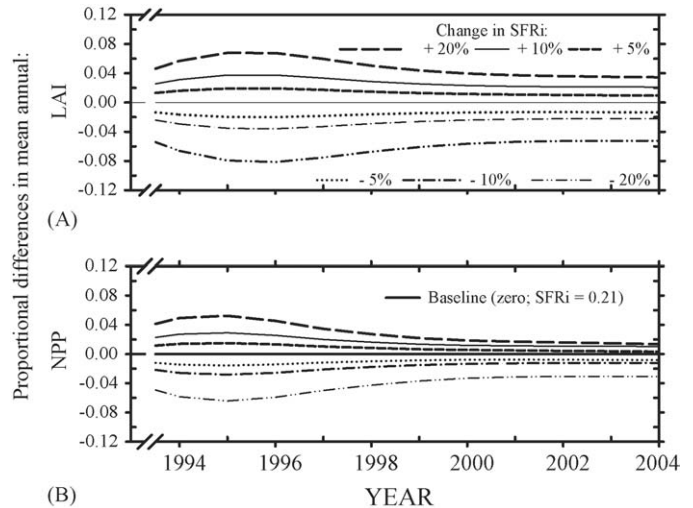

Fig. 10. A sensitivity analysis of the effect of the soil fertility variable (SFRi) found in SECRETS-3PG on leaf area index (LAI) and net primary production (NPP). The results portray the proportional differences (ΔSFRi-baseline/baseline) in mean annual LAI and NPP as influenced by increasing and decreasing SFRi by 5, 10, and 20% of the baseline used in the FW simulations (0.075).

We examined proportional differences in L, NPP, and NEP in our sensitivity analysis of the soil fertility variable (SFRi) in SECRETS-3PG. A 5 or 10% change in SFRi increased or decreased L by 2–4% at peak L for these stands (Fig. 10A). In contrast, a 20% increase in SFRi increased L by ∼7% while a 20% decrease in SFRi decreased L by 8%. These differences were all reduced by the end of the rotation (Fig. 10A). We found a similar pattern in the NPP response to changes in SFRi although the magnitude of the response was diminished (Fig. 10B).

The effect of changing SFRi on NEP, then, would be expected to follow the patterns observed with changes in L and NPP. Reducing SFRi by 20% resulted in a maximum reduction in NEP of about 19% in 1994 (Table 4). The minimum response observed was a 2% increase in NEP for a

Table 3

Gross and net primary production (GPP, and NPP, respectively) for control (CW) and fertilized (FW) plots, and one scenario (fertilized at planting; FWP), and net ecosystem productivity (NEP) at the Southeast Tree Research and Education Site (SETRES) for 1994 through 1997 using the hybrid process model SECRETS-3PG

Treatment	Year	GPP	NPP	NEP
CW	1994	933	499	−131
	1995	1119	577	−100
	1996	1243	637	−26
	1997	1331	669	71
FW	1994	1568	862	323
	1995	2120	1115	592
	1996	2475	1276	803
	1997	2659	1334	952
FWP	1994	2696	1366	N.A.
	1995	2844	1357	N.A.
	1996	2806	1312	N.A.
	1997	2741	1250	N.A.

Units are g C m^{-2} a^{-1}. N.A., no analysis of NEP for FWP plots were considered; we had no means to model soil respiration for this scenario.

Table 4

A sensitivity analyses of the soil fertility variable (SFRi) in SECRETS-3PG and its effect on simulated net ecosystem productivity (NEP) (g C m^{-2} a^{-1}) (and the percent change in NEP) for fertilized (FW) plots at the Southeast Tree Research and Education Site (SETRES) located in Scotland County, North Carolina

FW plots	Year			
	1994	1995	1996	1997
NEP	323	592	803	952
SFRi = 0.075[a]				
Δ				
SFRi − 20%	262 (−19.1)	501 (−15.4)	705 (−12.2)	863 (−9.3)
SFRi − 10%	296 (−8.4)	552 (−6.8)	761 (−5.3)	914 (−3.9)
SFRi − 5%	308 (−4.7)	570 (−3.8)	780 (−2.9)	931 (−2.2)
SFRi + 5%	338 (+4.5)	613 (+3.6)	825 (+2.7)	970 (+1.9)
SFRi + 10%	352 (+8.8)	634 (+7.0)	846 (+5.3)	987 (+3.7)
SFRi + 20%	375 (+16.0)	666 (+12.5)	878 (+9.3)	1013 (+6.4)

[a] The fertility was increased to 0.075 from the control value (0.01) starting in March of 1992.

5% increase in SFRi. As observed in the other comparisons, decreasing SFRi resulted in greater negative impacts on NEP (overall lower NEP) than increasing SFRi had on increasing NEP (Table 4). Moreover, these analyses underscore the importance of soil respiration on NEP estimates. A 20% reduction in SFRi reduced L and NPP by 7–8% but the concomitant decrease in NEP was roughly 19%.

7. Discussion

Fast growing, intensively managed pine plantations offer promise for sequestering carbon (Johnsen et al., 2001a). Intensive site management (i.e. fertilization, vegetation control, bedding, and improved genetics) has increased the production potential of southern pine plantations by three-fold (Boarders and Bailey, 2001) or more (Jokela and Martin, 2000). Increased productivity has largely been achieved through increased foliage production from improved soil site nutrition (Xiao et al., 2003; Albaugh et al., 2004). Cannell (2003) suggests that considerable sink capacity could be created through afforestation. This may be particularly true for marginal or degraded land (Huston and Marland, 2003; Grace, 2005). Results presented here suggests that nutrient poor soils may offer the potential to sequester large amounts of C when provided adequate nutrition, however Grace (2005) recommends caution because too little is know on the net impact of positive and negative feedbacks on terrestrial C cycling. Of course, we have focused on short-term responses in an intensively managed system; we have not addressed the long-term fate of soil C nor do we discuss forest products removed from a site.

Model ''validation'' serves to increase confidence in short- and long-term simulation projections. The SECRETS-3PG hybrid model enables validation of basic physiological processes at field measurement scales (i.e. hourly photosynthesis) in conjunction with many of the typical silvicultural metrics of interest to forest managers (i.e. annual DBH, volume, etc.). SECRETS-3PG partitions photosynthesis between sun and shade leaves as developed by de Pury and Farquhar (1997). Our findings suggest that the model may underestimate transpiration on those days where shaded leaves account for the greatest proportion of net canopy C gain. This finding suggests that separate leaf conductance models – perhaps apart from the Ball–Berry–Leuning approach – may be needed for shade leaves when using the ''sun/shade'' approach.

Observed seasonal differences in simulated versus the empirical estimates of foliage Rd may, in part, be explained by model-measurement differences in T, and the T response functions used; our findings are consistent with others who suggest that a seasonal-invariant T response function for Rd may be inappropriate (Radoglou and Teskey, 1997; Teskey and Will, 1999). The thermal environment experienced by a plant during tissue development appears to control the maximal thermal acclimation of respiration (Atkin and Tjoelker, 2003). Medlyn et al. (2002) suggested that T response functions for photosynthesis may need to vary by season, depending on the

species and plant type. However, they found no significant differences in their loblolly pine parameter estimates. Greater simulated Rd when compared to the empirical analysis is likely also due to differences in L. Of course, greater foliage Rd results in less C available for partitioning.

There is evidence to suggest a downward trend in the carbon use efficiency (CUE) (NPP GPP^{-1}) after crown closure (Mäkelä and Valentine, 2001). Our estimates were somewhat stable prior to 1988, 4 years after planting, although FW stands did not reach crown closure until ~10 years following planting; CW plots have not achieved true crown closure. Our CUE estimates are within the range reported by Curtis et al. (2005) for a mixed deciduous forest, but slightly higher than that estimated by Maier et al. (2004). Further analyses indicated reduced light capture efficiency (LCE) (faPAR L^{-1}) over time and, thus, a reduction in the ratio of net canopy exchange (NCE) per unit L^{-1} (data not shown). Sampson and Allen (1998) and Sampson and Smith (1993) demonstrated lower LCE with increasing L. Treatment separation in CUE can be attributed to treatment differences in LCE, especially at greater L (Sampson and Allen, 1998).

Empirical models of total soil CO_2 efflux do not partition the mechanisms of soil C and mineral transformation, however both their utility and their limitations are readily apparent. Empirical equations are useful because they enable temporal projections of R_S when climate data are limited to soil T and, if available, soil water information. They often explain one-half to two-thirds of the variation in R_S (Lloyd and Taylor, 1994; Maier and Kress, 2000; Butnor et al., 2003). However, because of the importance of the soil CO_2 signal on NEP projections – perhaps especially in these systems where net soil C losses can exceed 15,000 g C m^{-2} a^{-1} (Gough et al., 2005) – extrapolation of an empirical model for those years where direct measurements were not made is unadvisable. Nonetheless, we are confident in our short-term projections. Our simulated estimates of R_S were well correlated with the empirical measurements; we would expect similar results because in these analyses we used the equation and parameter estimates reported by Maier and Kress (2000). SERETS-3PG over-estimates R_S on those days when actual θ_D is lower than that simulated, however our analyses for 1995–1996 suggests that this may be infrequent. Not shown in Fig. 7B, Maier and Kress (2000) reported soil CO_2 effluxes exceeding 8 μmol CO_2 m^{-2} s^{-1}.

Newly established stands may initially be C sources (Harmon, 2001; Kolari et al., 2004) followed by a sink that declines with age (Janisch and Harmon, 2002; Law et al., 2003; Kolari et al., 2004). We were unable to examine NEP during the first 9 years of growth. Soil respiration has been demonstrated to be significantly greater than NPP in loblolly pine after planting and early in rotation (Gough et al., 2005). Our NEP analyses, coincidentally, focused on the 1994 through 1997 years when CW and FW plots both reached maximum NPP (Fig. 8, panel A; Table 3). This, of course, corresponds to when Maier and Kress (2000) measured soil CO_2 efflux at SETRES. Although we found minor increases in NEP for CW plots over the 1994–1997 period, NEP was

close to zero. However, if annual soil C losses do not decline with time (as observed by Gough et al., 2005) from the 1995 to 1996 flux estimates, while annual NPP declines from peak production (Fig. 8A), CW plots will likely again become net C emitters by the end of the rotation although we cannot yet confirm this. A rotation-complete analysis of NEP would require accurate estimates of soil CO_2 efflux that our empirical model cannot, at the moment, provide outside our focus period.

Gough et al. (2005) examined R_S in a chronosequence of loblolly pine stands growing on the Virginia Piedmont and on the South Carolina Coastal Plain (Gough and Seiler, 2004). They concluded that the degree of soil disturbance during site preparation largely determined their observed changes in R_S associated with stand age. On sites where the residual slash material was retained, R_S decreased slightly with stand age, but was remarkably stable from age 10 through the end of rotation ($\sim$25 years). They suggested that the relative contributions of microbial respiration likely decreased as residual labile slash material was consumed, and root respiration increased with increased root biomass associated with stand development. Our analyses support this hypothesis (Fig. 9D and Table 2). Our estimates of R_H were within those commonly observed (Hanson et al., 2000). Thus, it is reasonable to assume that soil respiration remained relatively stable at SETRES following peak NPP. However, this needs to be examined with an easily parameterized mechanistic formulation to be incorporated into this model.

Few meaningful, direct comparisons of NEP for these loblolly pine plantations could be made. Maier et al. (2004) developed component carbon budgets to estimate NEP for CW and FW plots during 1996 at SETRES using empirical measures of tissue respiration, standing biomass, and soil CO_2 efflux measurements. They estimated 28 and 634 g C m^{-2} a^{-1} for CW and FW plots, respectively. We simulated -26 g C m^{-2} a^{-1} for CW plots and 803 g C m^{-2} a^{-1} for FW plots. Although these estimates are fairly similar there are at least two reasons why our results here do not directly match with Maier et al. (2004). First, they estimated GPP as the sum of NPP and total autotrophic respiration (R_A), however in this case NPP was 27% less than R_A which resulted in a CUE of 0.42. Our simulations found CUE to be ca. 0.51 in 1996 (Fig. 8B). This discrepancy helps to explain differences in the FW estimates but not the CW results. Second, Maier and Kress (2000) estimated daily θ_D by linear interpolation of periodic point data. In contrast, we have demonstrated that our simulations provide accurate daily estimates of θ_D (Fig. 7A). A component analysis for a mid-rotation piedmont loblolly pine plantation estimated NEP to be 430, 580 and 650 g C m^{-2} a^{-1} at ages 15 (Hamilton et al., 2002), 16, and 17 (Schafer et al., 2003), respectively. These estimates include contribution of a well-established hardwood under-story. In our analyses, NPP would have decreased ca. 15% for FW plots and ca. 17% for CW plots for a similar age comparison. Finally, Lai et al. (2002) used a combination of empirical (eddy flux, soil CO_2 efflux, stem respiration, and net photosynthesis) and modeling approaches to examine net ecosystem exchange (F_C) in

adjacent 8-year-old loblolly pine stands at SETRES. They report that CW plots ($L = 1.65$) were a source of C of about -170 g C m^{-2} a^{-1} while FW plots ($L = 3.5$) were weak C sinks (92 g C m^{-2} a^{-1}). Finally, Lai et al. (2002) reported an NEP of 605 g C m^{-2} a^{-1} for a 17-year-old loblolly pine stand at Duke Forest.

Gathering evidence suggests that a time trajectory in NEP is associated with stand development following disturbance and stand replacement. As mentioned above, following disturbance developing stands are initially C sources followed by a strong sink that declines with age (Janisch and Harmon, 2002; Law et al., 2003; Kolari et al., 2004). If disturbance consists of a harvest followed by planting, then initially high rates of C loss attributed to R_H would decline with stand age as C, either left on the site as slash residues or from legacy root biomass, decays. High soil temperatures and favorable soil moisture early in stand development and prior to canopy closure facilitate microbial decomposition (Lloyd and Taylor, 1994; Hanson et al., 2000; Gough et al., 2005). Roughly 80% of the total root biomass decomposition can occur within the first 20–30 years following harvest in loblolly pine (Ludovici et al., 2002). After disturbance, and in our case harvest and then planting, developing stands must reoccupy the site. It follows, then, that if R_S remains relatively constant over a rotation (Gough et al., 2005) then carbon release will exceed C uptake until an equilibrium leaf area – gross C uptake equals gross C loss – is achieved. With stand development NEP will continue to increase until maximum L is achieved at canopy closure (e.g. Gower et al., 1994; Law et al., 2003). A subsequent decline in NEP would coincide with a reduction in the canopy-integrated gross C uptake as stands mature (Mäkelä and Valentine, 2001; Binkley et al., 2002) associated with decreasing L or decreased photosynthetic efficiency due to various processes associated with aging (Bond and Franklin, 2002). The L signal is apparently stronger than compensatory signals of reduced R_H but increased R_C and R_M from coarse and fine root biomass as stands age (cf. Hanson et al., 2000).

Climate exerts a strong influence on the seasonal patterns in NEP (Wang et al., 2004). Simulated NEP for CW plots for 1996 and 1997 suggest that autumn and winter, with low temperatures but favorable incident shortwave radiation, may be important periods for C uptake as they influence the annual C budget (Fig. 9B), however because these stands have not achieved site equilibrium (as measured by inter-annual L) this speculation needs conformation. Gough et al. (2004) suggest that 20% of annual C fixation for loblolly pine at SETRES may come from the 'non-growing season'.

Complete vegetation control for all treatments at SETRES removes understory influences on NEP. In the absence of mechanical or herbicidal control of competing vegetation can represent a significant portion of early stand biomass (Quicke et al., 1999; Lauer and Glover, 1999). When present, competing vegetation must contribute substantially to NEP however their impact on net C balance remains largely ignored. The process model SECRETS (Sampson et al., 2001), and now SECRETS-3PG, can simulate sub-canopy and under-story

contributions to total stand C and water fluxes. On-going research is focused on the impact of sub-canopy species on total stand C exchange.

One apparent limitation in this modeling approach is a priori estimates of the soil fertility index (SFRi). Ongoing analyses using 45 loblolly pine stands from across the Southeast (Amateis et al., 2001) indicates that we can now explain almost 80% of the variation in SFRi for unfertilized plots using estimates of soil physical properties (unpublished data). These results also suggest that independently acquired estimates of the SFRi parameter for a limited range of specific fertilization treatments will be possible (e.g. NCSFNC, 1993).

We must stress that our analyses utilized several simplifying assumptions. Specifically, (1) although we demonstrate strong correspondence between measured and empirically derived estimates of stand structure and physiological processes with that simulated, it is difficult to confirm our results beyond our comparison periods, (2) developmental differences that may exist in photosynthetic rates and tissue respiration were not used in these analyses, and (3) problematic issues that pertain to fine root dynamics (production and mortality) reduce our certainty in model outputs. Although we have point-in-time fine root standing biomass from soil sampling using the sequential coring technique (data not shown), inherent variation in soils and much uncertainty in both standing fine root biomass and fine root turnover does reduce the strength of our NEP arguments (e.g. Gill and Jackson, 2000).

8. Implications for management

The magnitude and temporal variation in our simulations of NPP for CW and FW plots are supported by destructive harvest sampling at SETRES (Albaugh et al., 1998, 2004). The NPP response at SETRES demonstrates the strong, dynamic plasticity in foliage production and C allocation, for intensively managed loblolly pine. These simulations augment the empirical measurements by demonstrating the potential long-term impacts of management on net biomass accumulation, C storage, and thus undoubtedly net ecosystem productivity (NEP) over short rotations. At SETRES, optimum nutrition amendments increased NEP by two-fold at peak stand leaf area index, emphasizing the plasticity of short-term C sequestration potential in this system.

Thus, plantation management may be a viable option to increase short-term C sequestration (Johnsen et al., 2001a). However, whether or not intensively managed plantations function as C sinks will depend on management activities (e.g. site preparation, vegetation control, fertilization) and their effect on long-term soil C and the type and fate of harvested products. From an ecological perspective, increased site productivity from fertilization will increase short-term C sequestration by increasing NPP as well as storage in the residual coarse root pools (Albaugh et al., 1998; Johnsen et al., 2001a). Additionally, increased productivity will increase soil organic matter inputs (foliage and roots) enhancing the labile and

recalcitrant soil C pools potentially leading to increased long-term retention of mineral soil C, especially on nutrient poor soils (Carlyle, 1993; Sanchez et al., 2003). Including C sequestration as a management objective may modify land management, by changing management intensity, rotation-length, and/or product objectives.

Our simulations suggest that fertilizing loblolly pine growing on a droughty, nutrient poor site may enable them to become net annual carbon sinks (positive NEP) earlier in the rotation (Table 2 and Fig. 8). However, it is also important to emphasize that SETRES should be considered "off-site" for growing commercial loblolly pine. Even with optimum fertilization treatments above-ground biomass accumulation after 16 years for both the CW and the FWP scenario was 27% less than that observed by Jokela and Martin (2000) for loblolly pine of similar management history in Florida. The fertilized at planting scenario (FWP) – although unsubstantiated – would have increased the SI_{25} to $\sim$19 m, corresponding to an average site for loblolly pine in the Southern United States (Schultz, 1997). Of course, growth responses to fertilization on better sites would likely shorten the time interval required to achieve net annual C balance. This needs considerably more work. In addition, optimum fertilization is not operational management for loblolly pine. Thus, simulations using a matrix of soil types across the loblolly pine cover-type, supported by empirical measurements, are needed to clarify the fertilization–L–soil nutrition interactions on net annual and cumulative C balance.

9. Conclusions

The SECRETS-3PG hybrid process model offers a new approach in stand-level carbon and water flux modeling and forest growth projections. The model structure provides outputs of basic physiological processes and stand growth projections at appropriate temporal-scales suitable for validation with empirical measurements. Correspondence of simulated estimates of daily C and water flux estimates with independently acquired data, and yearly estimates with stand inventory data suggests that the model performs fairly well for this site. Confirmation of model performance for other soil and site conditions is needed.

Our results suggest that plantation management may be a viable option to increase short-term C sequestration. Optimum nutrition amendments doubled net primary production (NPP) at maximum stand leaf area index (L). Increased productivity resulted from increased L with improved soil nutrition. However, because net ecosystem productivity (NEP) is the difference between two large, but opposing fluxes, dramatic, short-term changes in NEP can result from minor changes in either gross C uptake or net C release. We found a 10-fold increase in NEP for fertilized stands. Increased NPP, inter-annual variation in climate, and changes in soil heterotrophic respiration (R_H) can explain our NEP response observed. Increased L (and thus increased NPP) and decreased R_H over a 4-year period increased annual NEP.

A sensitivity analysis examined the influence of the soil fertility variable (SFRi) in SECRETS-3PG on model outputs. Results demonstrated the importance of soil respiration on these NEP estimates; a 20% decrease in SFRi and, subsequently, a 6% reduction in NPP resulted in a 19% reduction in NEP.

We hypothesize that slow growing loblolly pine on nutrient poor sites may be net C sources over a rotation. Although our 4-year analysis of NEP for CW plots provides some evidence to support this hypothesis a rotation-length analysis of NEP (unavailable at this time) is required for true evidence. Because the CW plots were in an approximate (short-term) equilibrium during the 4-year period and because the NEP response is not proportional to NPP, minor errors in our production estimates or our estimates of ecosystem respiration would dramatically alter the NEP estimates.

Our inability to estimate NEP for the entire rotation may be overcome by including a semi-mechanistic approach to soil C modeling such as that used by the CENTURY or the BGC models. Although SECRETS-3PG currently includes the Thornley (1998) surface and soil C and N model, the heavy dependence on parameters precludes its use for all but the most intensive, short-term research sites.

Acknowledgements

Appendix A

Tables A.1–A.6.

Table A.1
Estimated initial stand characteristics at planting (1985) for control (CW) and fertilized (FW) plots at SETRES, a loblolly pine research site located in Scotland County, North Carolina

Parameter description	Abbreviation	Method of calculation	Value and units	Source
Mean seedling weight	W_{SEED}	Input	10.0 g	1
Initial stocking	Stock	Input	CW = 1170, FW = 1200 stems ha^{-1}	2
Total biomass	TOT_{BIO}	W_{SEED}·stock	g ha^{-1}	
Standing biomass			g ha^{-1}	
Foliage	WFi	0.39 TOT_{BIO}		3
Stems/branches	WSBi	0.23 TOT_{BIO}		3
Stems	WSi	WSBi-WBi		
Branches	WBi	0.5 WSBi		3
Fine roots (⩽2 mm)	WFRi	0.28 TOT_{BIO}		3
Coarse and tap roots (>2 mm)	WCRi	Subtraction		
Mean tree height	avgHT		0.1 m	4
Live crown length	Live_Crown		0.1 m	4
Canopy gap fraction	GapFrac		99%	4

They were used as starting values for input into the hybrid process model SECRETS-3PG. 1, personal communication (Dr. Philip Dougherty); 2, Albaugh et al. (1998); 3, Samuelson (2000); 4, assumed.

Table A.2
Physiological parameters associated with photosynthesis and stomatal conductance used in the hybrid process model SECRETS-3PG

Parameter description	Abbreviation	Value and unit	Source
Cosine-corrected light extinction coefficient	G	0.5 L^{-1}	1
Canopy foliage dispersion coefficient	Ω[a]	0.65 dimensionless	2
Albedo	ALBEDO	0.15 dimensionless	2
Sigma	σ	0.17 dimensionless	3
Maximum RuBP carboxylase activity	V_{CMAX_25}	20.0 μmol m^{-2} s^{-1}	4
Maximum electron transport at 25 °C	J_{MAX_25}	47.4 μmol m^{-2} s^{-1}	4
Projected to total leaf area	v	2.45	5
Empirical coefficient	g_1	4.84 dimensionless	6
Empirical coefficient	g_0	0.005 mol m^{-2} s^{-1}	6

1, Sampson and Allen (1998); 2, Sinclair and Knoerr (1982); 3, assumed; 4, Palmroth and Maier (unpublished data); 5, Ellsworth, personal communication, 6, Katul et al. (2000).

[a] The dispersion coefficient is estimated as a function of *L*.

Table A.3

Parameters associated with biomass allocation within the hybrid process model SECRETS-3PG

Parameter definitions	Parameter and parameter description	Value and units	Source
Allometric and partitioning coefficients			
Foliage:stem partitioning ratio @ $D = 2$ cm	pFS2	0.75[a]	1
Foliage:stem partitioning ratio @ $D = 20$ cm	pFS20	0.56	1
Constant in the stem mass vs. diameter relationship	StemConst	0.039	2
Power in the stem mass vs. diameter relationship	StemPower	2.60	2
Maximum fraction of NPP to roots	pRx	0.80	1
Minimum fraction of NPP to roots	pRn	0.36	1
Soil water modifier (fSW)			
Moisture ratio deficit for $f_\theta = 0.5$	SWconst	0.7	3
Power of moisture ratio deficit	SWpower	9	3
Fertility effects			
Value of 'm' when SFRi = 0.0	$m0$	0.01	4
Fertility rating	SFRi		
Control plots		0.01	4
Fertilized plots		0.075	4
Age modifier (fAge)			
Maximum stand age used in age modifier	MaxAge	200 years	5
Power of relative age in function for fAge	nAge	1.5	5
Relative age to give fAge = 0.5	rAge	0.5	5
Mortality			
Max. stem mass per tree @ 1000 trees ha^{-1}	Wsx1000	254 kg tree^{-1}	4
Power in self-thinning rule	ThinPower	1.78	3
Fraction mean singe-tree foliage biomass lost per dead tree	mF	1.0	5
Fraction mean singe-tree root biomass lost per dead tree	mR	1.0	5
Fraction mean singe-tree stem biomass lost per dead tree	mS	1.0	5
Canopy structure			
Specific leaf area at age 0.0	SLA0	4.80 m^2 kg^{-1}	6
Specific leaf area for mature trees	SLA1	3.32 m^2 kg^{-1}	7
Age at which specific leaf area = (SLA0 + SLA1)/2.	tSLA	3.5 years	1
Branch and bark fraction (fracBB)			
Branch and Bark fraction at age = 0.9	fracBB0	0.69	2
Branch and bark fraction for mature stands	fracBB1	0.35	2
Age at which fracBB = (fracBB0 + fracBB1)/2	tBB	3.0 years	2
Basic density	Density	0.42 t m^{-3}	8

1, model fit; 2, model fitting using data from the Virginia Tech loblolly pine growth and yield research cooperative; 3, Landsberg and Waring (1997); 4, assumed; 5, personal communication (Dr. Richard Waring); 6, personal communication (Dr. Rod Will); 7, Sampson et al. (2003); 8, McKeand et al. (1997).

[a] When no units are provided, the value is dimensionless.

Table A.4

Parameters associated with biomass allocation for the hybrid process model SECRETS-3PG

Parameter and parameter description	Value and units	Source
Root production and turnover		
Maximum coarse and tap root production	0.97 dimensionless	1
Minimum coarse and tap root production	0.09 dimensionless	1
Coarse and tap root turnover	1e−09 month^{-1}	1
Fine root turnover	0.29 month^{-1}	1
Reference month for needle litter-fall	3 month	2

1, model fit; 2, Sampson et al. (2003).

Table A.5
Physiological parameters associated with respiration in the hybrid process model SECRETS-3PG

Parameter and parameter description	Value and units	Source
Ratio of leaf respiration to photosynthetic capacity $(R_l/V_l)^1$	0.012 dimensionless	1
Tissue maintenance respiration (R_M) rates at 25°C		2
Stems	0.026 mg CO_2 g dwt h^{-1}	2
Branches	0.026 mg CO_2 g dwt h^{-1}	2
Coarse and tap roots	0.025 mg CO_2 g dwt h^{-1}	3
Fine roots (<2 mm)	0.224 mg CO_2 g dwt h^{-1}	4
Tissue construction respiration	0.25 dimensionless	5
Tissue Q_{10} values for R_M		
Stems	1.67	6
Branches	1.67	6
Coarse and tap roots	2.0	6
Fine roots	2.0	6
Empirical soil respiration parameters		
CW plots		
Q	2.37	6
R_{MAX}	1.289 μmol CO^2 m^{-2} s^{-1}	6
K	0.187 dimensionless	6
FW plots		
Q	2.395	6
R_{MAX}	1.088 μmol CO^2 m^{-2} s^{-1}	6
K	0.278 dimensionless	6

1, Lai et al. (2002); 2, Maier (2001); 3, assumed; 4, Maier (2000); 5, Ryan (1991); 6, Maier and Kress (2000).

Table A.6
Initial soil water and soil water parameters for seedling to maturity simulations using the hybrid process model SECRETS-3PG at SETRES, a loblolly pine research site located in Scotland County, North Carolina

Parameter and parameter description	Value and unit	Source
Total profile depth	2.5 m	1
Depth of the top profile	0.15 m	1
Maximum H_2O storage at field capacity		
Total profile	302 mm	2
Top layer of the profile	17.3 mm	2
Minimum H_2O storage of rooting zone		
Total profile	70 mm	2
Top layer of the profile	4.27 mm	2
Maximum available water		
Total profile	232 mm	2
Top layer of the profile	14.03 mm	2

1, assumed; 2, Abrahamson et al. (1998).

References

Aber, J.D., 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.

Abrahamson, D.A., Dougherty, P.M., Zarnoch, S.J., 1998. Hydrological components of a young loblolly pine plantation on a sandy soil with estimates of water use and loss. Water Resour. Res. 34, 3503–3513.

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., King, J.S., 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. 44, 317–328.

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Johnsen, K.H., 2004. Long-term growth responses of loblolly pine to optimal nutrient and water resource availability. For. Ecol. Manage. 192, 3–19.

Amateis, R.L., Burkhart, H.E., Allen, H.L., Montes, C., 2001. FASTLOB: a stand-level growth and yield model for fertilized and thinned loblolly pine plantations. Loblolly Pine Growth and Yield Research Cooperative Report No. 115, 26 pp.

Anon., 1992. Standard Practice for Use of the International System of Units (SI) (the modernized metric system). American Society for Testing and Materials, Publication E 380-92. Philadelphia, PA.

Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351.

Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R., Fownes, J., 2002. Age-related decline in forest ecosystem growth: an individual-tree, stand-structure hypothesis. Ecosystems 5, 58–67.

Boarders, B.E., Bailey, R.L., 2001. Loblolly pine—pushing the limits of growth. S. J. Appl. For. 25, 69–74.

Boarders, B.E., Will, R.E., Markewitz, D., Clark, A., Hendrick, R., Teskey, R.O., Zhang, Y., 2004. Effect of complete competition control and annual fertilization on stem growth and canopy relations for a chronosequence of loblolly pine plantations in the lower coastal plain of Georgia. For. Ecol. Manage. 192, 21–37.

Bond, B.J., Franklin, J.F., 2002. Aging in pacific Northwest forests: a selection of recent research. Tree Physiol. 22, 73–76.

Butnor, J.R., Johnsen, K.H., Oren, R., Katul, G.G., 2003. Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. Global Change Biol. 9, 849–861.

Cannell, M.G.R., 2003. Carbon sequestration and biomass energy offset: theoretical, potential, and achievable capacities globally, in Europe and the UK. Biomass Bioenergy 24, 97–116.

Carlyle, J.C., 1993. Organic carbon in forested sandy soils: properties, processes, and the impact of forest management. New Zealand J. For. Sci. 23, 390–402.

Comins, H.N., McMurtrie, R.E., 1993. Long-term response of nutrient-limited forests to CO_2 enrichment. Equilibrium behavior of plant–soil models. Ecol. Appl. 3, 661–681.

Curtis, P.S., Vogel, C.S., Gough, C.M., Schmid, H.P., Su, H.B., Bovard, B.D., 2005. Respiratory carbon losses and the carbon-use efficiency of a northern hardwood forest, 1999–2003. New Phytologist 167, 437–456.

de Pury, D.G.G., Farquhar, G.D., 1997. Simple scaling of photosynthesis from leaves to canopies without the errors of big-leaf models. Plant Cell Environ. 20, 537–557.

Ewers, B.E., Oren, R., Albaugh, T.J., Dougherty, P.M., 1999. Carry-over effects of water and nutrient supply on water use of *Pinus taeda*. Ecol. Appl. 9, 513–525.

Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems. New Phytol. 147, 13–31.

Gough, C.H., Seiler, J.R., Johnsen, K.H., Sampson, D.A., 2004. Seasonal photosynthesis in fertilized and non-fertilized loblolly pine. For. Sci. 50, 1–9.

Gough, C.M., Seiler, J.R., 2004. The influence of environmental, soil carbon, roots, and stand characteristics on soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations located on the South Carolina Coastal Plain. For. Ecol. Manage. 191, 353–363.

Gough, C.M., Seiler, J.R., Wiseman, E.P., Maier, C.A., 2005. Soil CO_2 efflux in loblolly pine (*Pinus taeda* L.) plantations on the Virginia Piedmont and South Carolina Coastal Plain over a rotation-length chronosequence. Bio-geochemistry 73, 127–147.

Gower, S.T., Gholz, H.L., Nakane, K., Baldwin, V.C., 1994. Production and allocation patterns of pine forests. Ecol. Bull. 43, 115–135.

Grace, J., Taylor and Francis Group, 2005. Role of forest biomes in the global carbon balance. In: Griffiths, H., Jarvis, P. (Eds.), The Carbon Balance of Forest Biomes. Taylor and Francis (Cromwell Press), Trowbridge, UK, pp. 19–45.

Griffin, K.L., Bashkin, M.A., Thomas, R.B., Strain, B.R., 1997. Interactive effects of soil nitrogen and atmospheric carbon dioxide on root/rhizosphere carbon dioxide efflux from loblolly pine and ponderosa pine seedlings. Plant Soil 190, 11–18.

Hamilton, J.G., Delucia, E.H., George, K., Naidu, S.L., Finzi, A.C., Schlesinger, W.H., 2002. Forest carbon balance under elevated CO_2. Oecologia 131, 250–260.

Hanson, P.J., Edwards, N.T., Garten, C.T., Andrews, J.A., 2000. Separating root and soil microbial contributions to soil respiration: a review of methods and observations. Biogeochemistry 48, 115–146.

Harmon, M.E., 2001. Carbon sequestration in forests: addressing the scale question. J. For. 99, 24–29.

Haynes, B.E., Gower, S.T., 1995. Below ground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. 15, 317–325.

Huston, M.A., Marland, G., 2003. Carbon management and diversity. J. Environ. Manage. 67, 77–86.

Ingestad, T., 1987. New concepts on soil fertility and plant nutrition as illustrated by research on forest trees and stands. Geoderma 40, 237–252.

Janisch, J.E., Harmon, M.E., 2002. Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. Tree Physiol. 22, 77–89.

Jarvis, P.G., 1995. Scaling processes and problems. Plant Cell Environ. 18, 1079–1089.

Johnsen, K.H., Weir, D., Oren, R., Teskey, R.O., Sanchez, F., Will, R., Butnor, J., Markewitz, D., Richter, D., Rials, T., Allen, H.L., Seiler, J., Ellsworth, D., Maier, C., Katul, G., Dougherty, P.M., 2001a. Carbon sequestration and southern pine forests. J. For. 99, 14–21.

Johnsen, K.H., Samuelson, L., Teskey, R.O., McNulty, S., Fox, T., 2001b. Process models as tools in forestry research and management. For. Sci. 47, 2–8.

Jokela, E., Martin, T., 2000. Effects of ontogeny and soil nutrient supply on production, allocation, and leaf area efficiency in loblolly and slash pine stands. Can. J. For. Res. 30, 1511–1524.

Katul, G.G., Ellsworth, D.S., Lai, C.-T., 2000. Modelling assimilation and intercellular CO_2 from measured conductance: a synthesis of approaches. Plant Cell Environ. 23, 1313–1328.

Kolari, P., Pumpanen, J., Rannik, U., Ilvesniemi, H., Hari, P., Berninger, F., 2004. Carbon balance of different aged Scots pine forests in Southern Finland. Global Change Biol. 10, 1106–1119.

Lai, C.-T., Katul, G., Butnor, J., Ellsworth, D., Oren, R., 2002. Modelling night-time ecosystem respiration by a constrained source optimization method. Global Change Biol. 8, 124–141.

Lauer, D.K., Glover, G.R., 1999. Stand level pine response to occupancy of woody shrub and herbaceous vegetation. Can. J. For. Res. 29, 979–984.

Landsberg, J.J., Waring, R.H., Coops, N.C., 2003. Performance of the forest productivity model 3-PG applied to a wide range of forest types. For. Ecol. Manage. 172, 119–214.

Landsberg, J.J., Johnson, K.H., Albaugh, T.J., Allen, H.L., McKeand, S.E., 2001. Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. For. Sci. 47, 43–51.

Landsberg, J.J., Waring, R.H., 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance, and partitioning. For. Ecol. Manage. 95, 209–228.

Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M., Hultman, N., 2001. CO_2 and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. Tree Physiol. 2, 299–308.

Law, B.B., Sun, O.J., Campbell, J., Van Tuyl, S., Thornton, P.E., 2003. Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. Global Change Biol. 9, 510–524.

Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Funct. Ecol. 8, 315–323.

Lu, S., Mattson, K.G., Zaerr, J.B., Marshall, J.D., 1998. Root respiration of Douglas-fir seedlings: effects of N concentration. Soil Biol. Biochem. 30, 331–336.

Luo, Y., Medlyn, B., Hui, D., Ellsworth, D., Reynolds, J., Katul, G., 2001. Gross primary productivity in Duke Forest: modeling synthesis of CO_2 experiment and eddy-flux data. Ecol. Appl. 11, 239–252.

Ludovici, K.H., Zarnoch, S.J., Richter, D.D., 2002. Modeling in-situ pine root decomposition using data from a 60-year chronosequence. Can. J. For. Res. 32, 1675–1684.

Maier, C.A., 2000. Respiratory carbon use in loblolly pine plantations. DS Thesis. North Carolina State University, Raleigh, North Carolina, 107 pp.

Maier, C.A., 2001. Stem growth and respiration in loblolly pine plantations differing in soil resource availability. Tree Physiol. 21, 1183–1193.

Maier, C.A., Albaugh, T.J., Allen, H.L., Dougherty, P.M., 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Global Change Biol. 10, 1335–1350.

Maier, C.A., Kress, L.W., 2000. Soil CO_2 evolution and root respiration in 11-year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Can. J. For. Res. 30, 347–359.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D., Puttonen, P., 2000. Process-based models for forest ecosystem management: current state of the art and challenges for practical imple-mentation. Tree Physiol. 20, 289–298.

Mäkelä, A., Valentine, H.T., 2001. The ratio of NPP to GPP: evidence of change over the course of stand development. Tree Physiol. 21, 1015–1030.

Mattson, K.G., 1995. CO_2 efflux from coniferous forest soils: comparison of measurement methods and effects of added nitrogen. In: Lai, R., Kimble, J., Lavine, E., Stewart, B.A. (Eds.), Advances in Soil Science: Soils and Global Change. CRC Press, Inc., Boca Raton, FL, pp. 329–342.

McKeand, S.E., Eriksson, G., Roberds, J.H., 1997. Genotype by environment interaction for index traits that combine growth and wood density in loblolly pine. Theor. Appl. Genet. 94, 1015–1022.

McMurtrie, R.E., Landsberg, J.J., 1992. Using a simulation model to evaluate the effects of water and nutrients on the growth and carbon partitioning of *Pinus radiata*. For. Ecol. Manage. 52, 243–260.

Medlyn, B.E., Loustau, D., Delzon, S., 2002. Temperature response of parameters of a biochemically based model of photosynthesis. I. Seasonal changes in mature maritime pine (*Pinus pinaster* Ait) Plant Cell Environ. 25, 1155–1165.

Meiresonne, L., Sampson, D.A., Kowalski, A.S., Janssens, I.A., Nadezhdina, N., Cermak, J., Van Slycken, J., Ceulemans, R., 2003. Water flux estimates from a Belgian Scots pine stand: a comparison of different approaches. J. Hydrol. 270, 230–252.

Mikan, C.J., Zak, D.R., Kubiske, M.E., Pregitzer, K.S., 2000. Combined effects of atmospheric CO_2 and N availability on the below-ground carbon and nitrogen dynamics of aspen mesocosms. Oecologia 124, 432–445.

Murray, F.W., 1967. On the computation of saturation vapour pressure. J. Appl. Meteorol. 6, 203–204.

NCSFNC, 1993. Six-year growth and foliar nutrient responses of midrotation loblolly pine plantations to N and P fertilization. NCSFNC Report No. 29. College of Forest Resources, North Carolina State University, Raleigh.

Parton, W.J., Stewart, J.W.B., Cole, C.V., 1988. Dynamics of C, N, P and S in grassland soils: a model. Biogeochemistry 5, 109–131.

Quicke, H., Glover, G., Meldahl, R., 1999. Loblolly pine growth response to herbaceous vegetation control at different planting densities. Can. J. For. Res. 29, 960–967.

Radoglou, K., Teskey, R.O., 1997. Changes in rates of photosynthesis and respiration during needle development of loblolly pine. Tree Physiol. 17, 485–488.

Radtke, P.J., Burkhart, H.E., 1999. Basal area growth and crown closure in a loblolly pine spacing trial. For. Sci. 45, 35–44.

Ryan, M.G., 1991. A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. Tree Physiol. 9, 255–266.

Running, S.W., Hunt Jr., E.R., 1993. Generalization of a forest ecosystem model for other biomes, BIOME-BGC, and an application for global-scale models. In: Ehleringer, J.R., Fields, C. (Eds.), Scaling Physiological Processes: Leaf to Globe. Academic Press, San Diego, CA, pp. 141–158.

Sampson, D.A., Albaugh, T.J., Johnsen, K.H., Allen, H.L., Zarnoch, S.J., 2003. Monthly leaf area index from point-in-time measurements and needle phenology for *Pinus taeda*. Can. J. For. Res. 33, 2477–2490.

Sampson, D.A., Janssens, I.E., Ceulemans, R., 2001. Simulated soil CO_2 efflux and net ecosystem exchange in a 70-year-old Belgian Scots pine stand using the process model SECRETS. Ann. For. Sci. 58, 31–46.

Sampson, D.A., Ceulemans, R., 1999. SECRETS: simulated carbon fluxes from a mixed coniferous/deciduous Belgian forest. In: Ceulemans, R., Veroustraete, F., Gond, V. (Eds.), Forest Ecosystem Modelling. Upscaling and Remote Sensing. SPB Academic Publishing, The Hague, the Netherlands, pp. 95–108.

Sampson, D.A., Allen, H.L., 1998. Light attenuation in a 14-yr-old loblolly pine stand as influenced by fertilization and irrigation. Trees 13, 80–87.

Sampson, D.A., Smith, F.W., 1993. The influence of canopy architecture on light penetration in lodgepole pine (*Pinus contorta* spp. *latifolia*) Forests. Agric. For. Met. 64, 63–79.

Samuelson, L.J., 2000. Effects of nitrogen on leaf physiology and growth of different families of loblolly and slash pine. New For. 19, 95–107.

Sanchez, F.G., Carter, E., Klepac, J.F., 2003. Enhancing the soil organic matter pool through biomass incorporation. Bio. Bioenergy 24, 337–349.

Sands, P., 2002. 3PGPJS—a user-friendly interface to 3-PG, the Landsberg and Waring model of forest productivity. Technical Report No. 29. CSIRO, Hobart, Tasmania, Australia.

SAS Institute Inc., 1999. SAS/STAT® User's Guide Version 8. No. 3884. SAS Institute Inc., Cary, North Carolina.

Schafer, K.V.R., Oren, R., Ellsworth, D.S., Lai, C., Herrick, J.D., Finzi, A.C., Richter, D.D., Katul, G.G., 2003. Exposure to an enriched CO_2 atmosphere alters carbon assimilation and allocation in a pine forest ecosystem. Global Change Biol. 9, 1378–1400.

Schimel, D.S., Melillo, J., Tian, H., McGuire, D.A., Kicklighter, D., Kittel, T., Rosenbloom, N., Running, S., Thorton, P., Ojima, D., Parton, W., Kelly, R., Sykes, M., Neilson, R., Rizzo, B., 2000. Contribution of increasing CO_2 and climate to carbon storage by ecosystems in the United States. Science 287, 2004–2006.

Schultz, R.P., 1997. The ecology and culture of loblolly pine (*Pinus taeda* L.) USDA Agriculture Handbook, vol. 713. US Government Printing Office, Washington, DC.

Sinclair, T.R., Knoerr, K.R., 1982. Distribution of photosynthetically active radiation in the canopy of a loblolly pine plantation. J. Appl. Ecol. 19, 183–191.

Teskey, R.O., Will, R.E., 1999. Acclimation of loblolly pine (*Pinus taeda*) seedlings to high temperatures. Tree Physiol. 19, 519–525.

Thornley, J.M., 1998. Grasslands Dynamics: an Ecosystem Simulation Model. CAB International, Wallingford, UK.

Xiao, Y., Jokela, E.J., White, T.L., 2003. Growth and leaf nutrient responses of loblolly and slash pine families to intensive silvicultural management. For. Ecol. Manage. 183, 281–295.

Vose, J.M., Elliot, K.J., Johnson, D.W., 1997. Soil respiration response to three years of elevated CO_2 and N fertilization in Ponderosa pine (*Pinus ponderosa* Doug. ex Laws) Plant Soil 190, 19–28.

Wang, Y.P., Jarvis, P.G., 1990. Influence of crown structural properties on PAR absorption, photosynthesis, and transpiration in Sitka spruce: application of a model (MAESTRO, radiation and PSYN model). Tree Physiol. 7, 297–316.

Wang, K.-Y., Kellomaki, S., Zha, T.S., Peltola, H., 2004. Component carbon fluxes and their contribution to ecosystem carbon exchange in a pine forest: an assessment based on eddy covariance measurements and an integrated model. Tree Physiol. 24, 19–34.

Waring, R.H., McDowell, N., 2002. Use of a physiological process model with forestry yield tables to set limits on annual carbon balances. Tree Physiol. 22, 179–188.