

Edaphic and climatic effects on forest stand development, net primary production, and net ecosystem productivity simulated for Coastal Plain loblolly pine in Virginia

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[1] We used SECRETS-3PG to simulate net primary production (NPP) and net ecosystem productivity (NEP) of loblolly pine (*Pinus taeda* L.) growing on the Virginia Coastal Plain, focusing on the effects of soils and climate, and stand age over a 30-year rotation. Soil type was influential, with heavier soils having greater NEP earlier in the rotation than lighter, sandier soils, although these differences disappeared by the rotation end. Climate had only a small effect. Stand age had the largest effect, with simulated annual NEP strongly negative during the first 5 to 8 years of development but peaking at +600 g C m⁻² a⁻¹ by age 13. Modest declines in NEP after 13 years were associated with declines in LAI as stands aged. The 30-year mean annual NEP was positive over most of the study area but in a few cases was indistinguishable from zero for northwestern portions of the study. Simulated annual NPP rose from zero to over 2300 g biomass m⁻² a⁻¹ by age 12, after which it declined to ~1700 g biomass m⁻² a⁻¹ by rotation end. These results suggest that loblolly pine plantations on the Coastal Plain of Virginia may become net annual C sinks 5 to 9 years after planting but that when averaged over a whole rotation the net carbon accumulation during the baseline rotation simulated here is indistinguishable from zero. Our results also suggest, however, that this finding is sensitive to the length of the rotation, soil type (and thus fertility), and climate, implying that changes in management practices could significantly influence the carbon balance in managed loblolly pine plantations.

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1. Introduction

[2] Empirical and process modeling and eddy covariance (EC) measurements suggest that site disturbance (and soil site characteristics) and stand development influence the attainment of positive, annual net carbon (C) balance in forest ecosystems [Harmon, 2001; Law et al., 2001; Kolari et al., 2004; Sampson et al., 2006]. Young and disturbed mature stands are typically C sources while mature, undisturbed stands are thought to be C sinks that decline in strength with age [Janisch and Harmon, 2002; Law et al., 2003; Kolari et al., 2004]. For plantation loblolly pine (*Pinus taeda* L.) the dominant mechanisms that influence this proposed time trajectory in net C balance are fairly well understood, but they are temporally limited in scope; the current knowledge base has been derived from 1- to 3-year (a) snapshots of net ecosystem productivity (NEP) from short-term field studies [Hamilton et al., 2001, 2002; Lai et al., 2002; Schafer et al., 2003; Maier et al., 2004; Siqueira et al., 2006].

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[3] Developmental patterns in NEP for loblolly pine can largely be explained by temporal changes in gross canopy assimilation associated with phenological changes in stand leaf area index (LAI) and total soil CO₂ efflux. Young (seedlings and small saplings) loblolly pine stands growing on infertile soils may be C sources [Lai et al., 2002; Maier et al., 2004; Sampson et al., 2006] due to high soil CO₂ efflux rates [Maier et al., 2004; Gough et al., 2005] relative to gross canopy assimilation [Sampson et al., 2006]. Improved site fertility, however, can increase their sink capacity [Lai et al., 2002; Maier et al., 2004; Sampson et al., 2006]. Older “midrotation” (ages 15 to 17) loblolly pine stands are typically C sinks [Hamilton et al., 2002; Lai et al., 2002; Schafer et al., 2003; Siqueira et al., 2006]. Suspected declines in sink strength with age can be attributed to declines in maximum stand LAI following canopy closure [Vose and Allen, 1988; Albaugh et al., 2004] and the attainment of maximum annual net primary production (NPP) [Sampson et al., 2006]. Punctuated estimates of NEP are available for mature stands, seedlings, and saplings. Missing, however, are rotation length estimates of NEP, especially as influenced by soils and climate.

[4] Our objective was to examine the influence of soils, climate, and stand age on C sequestration for loblolly pine

stands growing on the Virginia Coastal Plain. We used the hybrid forest process model SECRETS-3PG [Sampson *et al.*, 2006], combined with empirical estimates of soil respiration, to simulate NPP and NEP for a 30-year period for stands that were assumed to be uniformly planted across the study area in 1969. This approach enabled direct comparisons of the temporal effects of stand development on NPP and NEP as influenced by the spatial variability in soils and the spatial and temporal variability in climate across the study area; we focused on an area that encompasses the Chesapeake Rivers Conservation Area of eastern Virginia. These analyses included an assessment of uncertainty in the model outputs as determined by uncertainty in the baseline soils information and thus uncertainty in our estimates of inherent soil fertility across this study.

2. Methods and Materials

[5] Our simulations described herein required soils information and daily climate data for a 30-year simulation period for the study area, and changes to the hybrid forest process model SECRETS-3PG. We used the U.S. Department of Agriculture (USDA) Forest Service Forest Health Monitoring (FHM) hexagonal sampling grid (each plot grid represented 642 km²) [White *et al.*, 1992] to define the spatial grain of the simulations. Within the study area 39 hexagonal polygons were identified. Each hexagon, then, determined the boundaries for the soil classification data and the minimum spatial resolution of the climate data. Model changes and soil and climate data acquisition are discussed in detail below.

2.1. Study Area

[6] The study area roughly corresponds to the Chesapeake Rivers Conservation Area, a region of broad interest for forest research by a consortium of agencies under the aegis of the Virginia Department of Forestry. Our focus area extends beyond the conservation area, extending from the North Carolina border to the south, and bounded by the Chesapeake Bay on east, the Potomac River on the north, and the Piedmont–Coastal Plain boundary (roughly the 78th meridian) to the west (Figure 1).

2.2. Soil Classification and Climate Data

[7] We intersected the FHM grid with the USDA Natural Resource Conservation Service (NRCS) soils data map (STATSGO) to extract the individual soil series within each hex. Using the online USDA-NRCS Soil Survey Division, Soil Series Name Search (<http://ortho.ftw.nrcs.usda.gov/cgi-bin/osd/osdnamequery.cgi>), individual soil series were evaluated to obtain soil texture and depth information for two soil profiles that were differentiated as the Ae horizon and then everything else to bedrock (or 2 m, whichever applied). We used the soil texture triangle of Brady [1990] and the soil texture classification to obtain the “average” (polygon-centered) estimate of percent clay and the percent sand for each profile. The forested portion within each hex (J. Scrivani, Virginia Department of Forestry, personal communication, 2006) was intersected with the soils layer to define applicable “cells” for the model outputs.

[8] Meteorological data from a continental-scale modeling program were available from an online source [Schimel *et al.*, 2000; <http://www.daymet.com>] for 1980 through 1997. These data included daily shortwave radiation ($W m^{-2}$), average daily minimum (T_{MIN}) and maximum (T_{MAX}) ambient air temperature (T), daily precipitation (cm), daylight average saturated vapor pressure (Pa) and day length (s). Daily estimates of shortwave radiation were converted to standard units ($MJ m^{-2} d^{-1}$) [American Society for Testing and Materials, 1992]. We calculated daily average saturated vapor pressure from average T [e.g., Murray, 1967]. We then used daily T_{MAX} and T_{MIN} to estimate daily minimum and maximum relative humidity following Murray [1967].

[9] Climate data were downloaded for each hex using the latitude and longitude coordinates for hex center. We used 1969 as the start year for our 30-year simulations to maximize use of the historical climate data. We estimated the monthly average of mean daily temperature (average of T_{MIN} and T_{MAX}) and the average monthly precipitation over the 18-year record for each hexagonal climate cell as follows: (1) The temperature averages and precipitation totals for each month for each of the 18 years were iteratively compared to select the years in which mean monthly temperatures and precipitation totals were closest to the long-term averages, and (2) These selected years were then duplicated to fill in the period between 1969 and 1980 and 1998 and 1999.

2.3. Forest Process Model SECRETS-3PG

[10] The SECRETS-3PG hybrid model [Sampson *et al.*, 2006] 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 model simultaneously estimates hourly canopy gas exchange, daily C budgets, and monthly growth and turnover; the 3-PG module provides monthly estimates of conventional stand properties throughout a rotation (Figure 2).

[11] This hybrid structure provides a management-oriented model that enables silvicultural decisions for management related questions. Stand structure and soil site information, and daily meteorological data are required to simulate a stand from seedling to maturity. Mean seedling weight, height, and planting density are used to establish the initial stand conditions. Soils information is limited to the texture and depth for two soil profiles. The daily meteorological data includes (1) shortwave radiation, (2) minimum and maximum ambient air temperature, (3) minimum and maximum relative humidity, and (4) precipitation. Soil temperature is estimated from air temperature and day of year. Hourly photosynthetically active radiation (PAR), in the absence of measured PAR, is calculated from daily shortwave radiation assuming that hourly PAR is normally distributed over the daylight period.

[12] The SECRETS model uses the Farquhar *et al.* [1980] approach to simulate hourly net photosynthesis and dark respiration of foliage as found in the sunshade model [de Pury and Farquhar, 1997]. Daily gross primary production (GPP; $\mu mol CO_2 m^{-2} s^{-1}$ and/or $kg C ha^{-1} d^{-1}$) is

Map of the study area

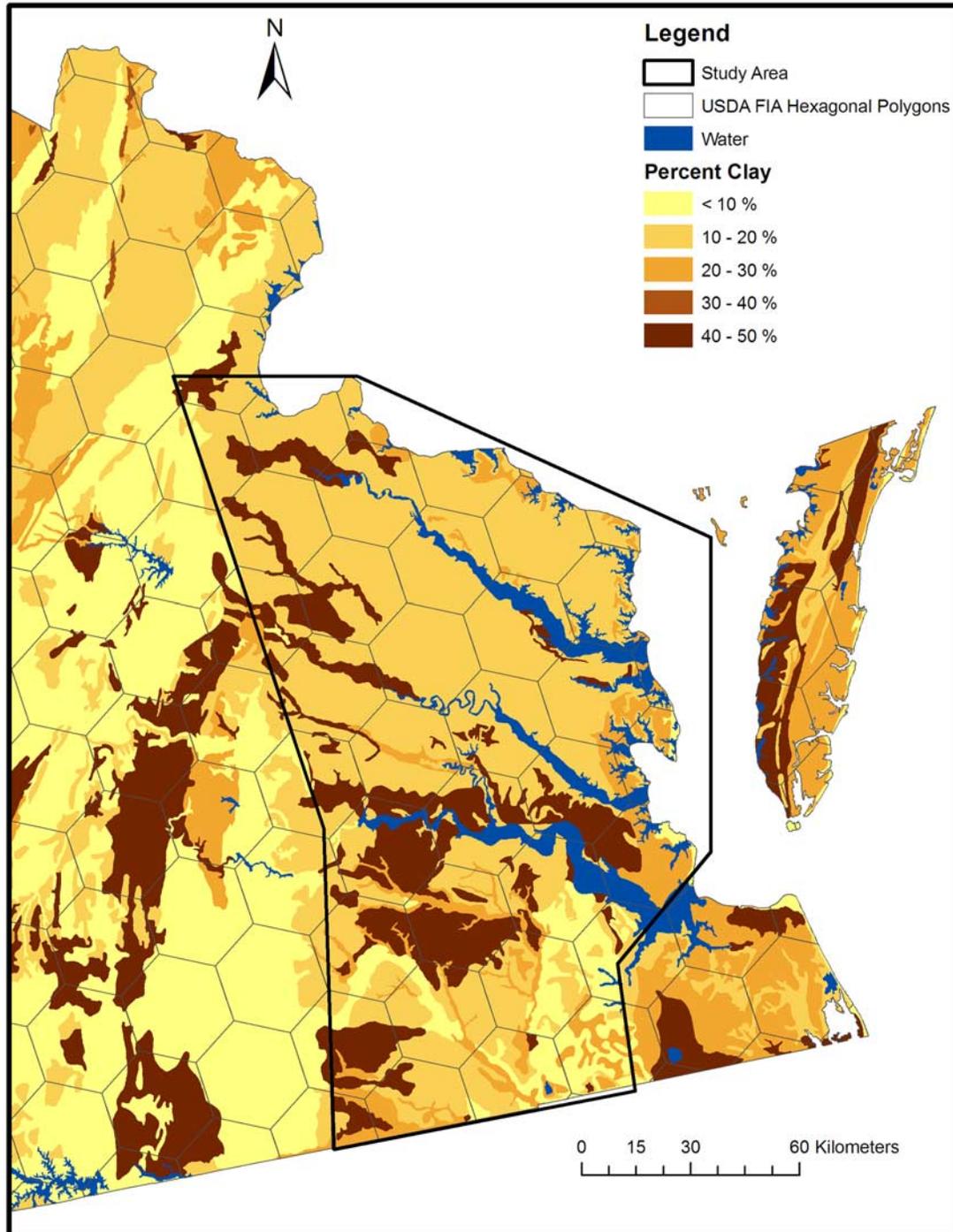


Figure 1. Map of the study area that encompasses most of the Coastal Plain of Virginia. The percent clay for each of the soil series present in the study area is depicted as irregular polygons. Hexagonal polygons based on the USDA Forest Inventory and Analysis program were used to define the spatial grain for the simulations. Thus separate climate data for each hexagon were used in these analyses. Image boundaries (box) are as follows: top left, $77^{\circ}54'45.91''\text{W}$ longitude and $39^{\circ}15'39.37''\text{N}$ latitude and bottom right, $75^{\circ}34'14.82''\text{W}$ longitude and $36^{\circ}13'18.84''\text{N}$ latitude.

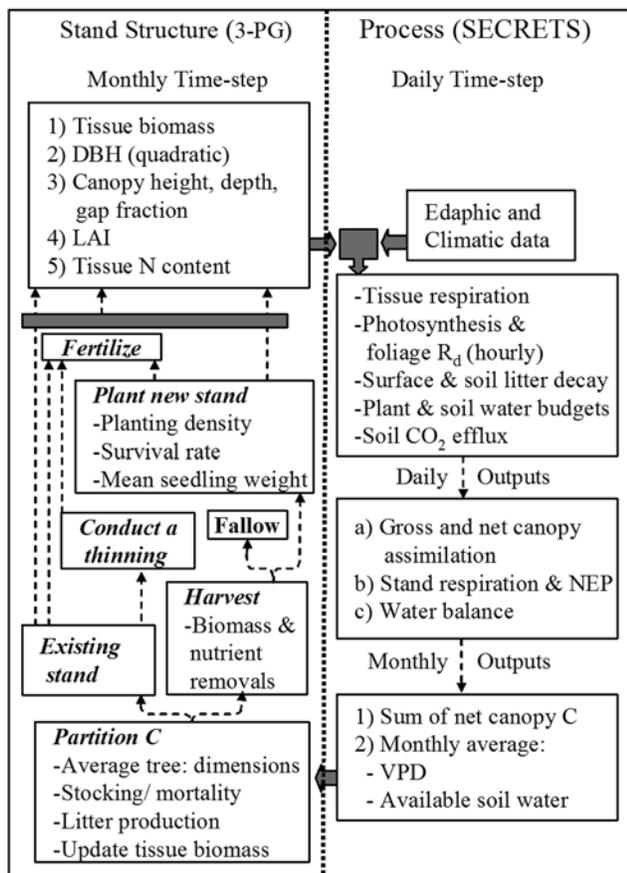


Figure 2. Diagram of the SECRETS-3PG hybrid forest process model (adapted from *Sampson et al.* [2006]).

estimated as the sum of net photosynthesis plus dark respiration of foliage scaled to the daily time step. Maintenance respiration (R_M) of stem, branch, coarse (and tap) root, and fine root biomass follows the formulations found in the BIOMASS process model [*McMurtrie and Landsberg*, 1992]. Construction respiration is estimated as a constant fraction of tissue production following *Ryan* [1991]. Net primary production (NPP; $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ and/or $\text{kg C ha}^{-1} \text{ d}^{-1}$) then, is estimated as GPP minus R_M , R_C , and an estimate of root exudates following *Thornley* [1998]. The 3-PG module of SECRETS-3PG estimates monthly C allocation to stems, branches, fine and coarse roots (including tap roots), bark, and foliage using allometric and resource-limiting relationships described by *Landsberg and Waring* [1997] and *Sampson et al.* [2006].

[13] In the model we calculate carbon use efficiency (CUE) as NPP GPP^{-1} averaged on an annual basis. The model estimates heterotrophic respiration (R_H) as

$$R_H = S_R - (R_M + R_C) \quad (1)$$

where S_R is total soil CO_2 efflux. Of course, in this case we assume that the soil respiration can reliably be extrapolated from another Coastal Plain site managed similarly. Both R_C and R_M were discussed above. For these analyses we

estimate NEP as the difference between NPP and heterotrophic (R_H) respiration, or

$$\text{NEP} = \text{NPP} - R_H \quad (2)$$

The model maintains the components of ecosystem structure and function for short- and long-term validation of fluxes and attributes of stand structure at scales appropriate to both. We have previously demonstrated favorable correspondence between simulated and measured estimates of C [*Sampson et al.*, 2006; *Siqueira et al.*, 2006] and water [*Meiresonne et al.*, 2003] fluxes, the canopy light environment [*Sampson et al.*, 2007], and various components of stand structure (i.e., standing biomass, quadratic mean diameter, leaf area index) [*Sampson et al.*, 2006].

[14] These simulations required special attention to the model estimates of S_R , and an approach to estimate baseline soil fertility. Below we describe (1) our approach to estimate S_R and (2) additions to the model that were necessary to derive a soil fertility index, a surrogate for soil fertility, as required for the 3-PG biomass allocation module.

2.3.1. Soil Respiration

[15] At present SECRETS-3PG has no mechanistic soils module for regional simulations. Thus no soil C pools (e.g., soil organic matter (SOM), surface and soil detritus, etc.) are used in the estimates of S_R . As such, SECRETS-3PG requires an empirical estimate of S_R in order to estimate NEP (i.e., equation (2)). Repeated measurements of S_R for the Virginia Coastal Plain were not available for these analyses. However, S_R estimates for a loblolly pine age chronosequence from the South Carolina Coastal Plain [*Gough et al.*, 2005] were available. *Gough et al.* [2005] describe their estimates of root volume density and coarse woody debris (CWD) content from soil samples taken with each measurement. Because site preparation and stand management are similar for Coastal Plain soils and because soil type is generally similar along the Coastal Plain of the eastern seaboard we used the South Carolina data to develop an equation to estimate S_R for the Coastal Plain of Virginia. Site preparation can and does incorporate a substantial amount of fine and coarse woody debris [*Gough et al.*, 2005]. We used a modification of the *Lloyd and Taylor* [1994] approach by adding a scalar variable to the equation using nonlinear procedures in SAS© [*SAS Institute Inc.*, 1999], or

$$S_R = \eta_1 \exp \left[308.56 \left(\frac{1}{56.02} \right) - \left(\frac{1}{K - 227.13} \right) \right] \quad (3)$$

where η_1 is the scalar parameter to be estimated and K is soil temperature (kelvin). The exponents in equation (3) are from *Lloyd and Taylor* [1994]. Residuals from equation (3) were plotted against other variables in the data set such as volumetric soil water content and stand age.

[16] We used estimates of S_R from a 1-d field campaign for a range in stand ages for loblolly pine growing on the Virginia Coastal Plain [*Tyree et al.*, 2006] to examine if the temperature response in soil respiration from South Carolina was similar to that observed for Virginia.

2.3.2. Soil Fertility Index

[17] Because SECRETS-3PG incorporates the C allocation algorithms (and associated functions) as found in 3-PG,

it was necessary to derive an approach to estimate the 3-PG fertility index (FR). This index, scaled from zero (poor fertility) to one (maximum fertility), represents a simplified approach to model the complex functional relationship between root production and soil fertility [Landsberg and Waring, 1997]. The FR variable is typically estimated for a site by iteratively fitting test data sets until good agreement is reached between modeled and measured data (i.e., stem volume, leaf area index, etc.). However, for SECRETS-3PG our goal was to estimate the soil fertility index (SFRi) from readily available baseline soils information.

[18] We used growth, yield, and edaphic data for 53 field studies from the Loblolly Pine Growth and Yield Cooperative at Virginia Tech (http://www.cnr.vt.edu/g&y_coop/), to develop an empirical model to estimate SFRi from standard soils information. These data included: 1) soil texture and profile depth, 2) stem diameter at breast height (m), 3) standing volume ($\text{m}^3 \text{ha}^{-1}$), and 4) stand density (stems ha^{-1}) information. Accordingly, the stand level biometrics from 53 loblolly pine plantations for control treatments (no management interventions) were used to heuristically derive individual stand estimates of SFRi for these 53 stands for the development of a generalized algorithm.

[19] Specifically, to estimate the SFRi for each of the 53 stands, we used visual optimization procedures that compared model outputs with measured stand attributes. This technique required stand-specific estimates of (1) initial LAI, (2) the average stem mass at which density-dependent mortality commences, and (3) the rate of random mortality. Stand-specific estimates of SFRi were derived by changing the model input for SFRi while iteratively manipulating each of these parameters, one at a time, and then visually comparing model outputs with measured estimates of standing volume, quadratic mean diameter (Dq) (m), and stem density. An SFRi value was considered acceptable when each of the output response variables were within $\sim 5\%$ of the measured values over the time trajectory available for each stand. On the basis of these criteria, we were able to utilize 36 of the 53 stands examined. The 17 stands that we were not able to fit represented either stands with too few data points or stands that, for one reason or another, did not conform to the restrictions imposed by our model fitting approach. While this task could have been automated, any errors associated with our visual optimization approach were minor in comparison to the variability (error) associated with the soils information needed to conduct regional simulations.

[20] We used nonlinear procedures in SAS[®] [SAS Institute Inc., 1999] to develop a generalized equation to estimate SFRi from basic soils information. After multiple regression analyses using all available soils information we converged on a final model that used the percent clay and the percent sand of the Ae horizon normalized for profile depth (i.e., divided by the Ae profile depth). The relationship between clay and SFRi was described as

$$f_{\text{clay}} = \left[a \left(\frac{e^{(-b \text{clay})} - e^{(-a \text{clay})}}{a - b} \right) \right] \quad (4)$$

where a and b were parameters to be estimated. The effect of sand on SFRi was modeled simultaneously as

$$f_{\text{Sand}} = c \frac{\text{sand}}{d} \quad (5)$$

where c and d were parameters to be estimated. The combined model was

$$\text{SFRi} = f_{\text{Clay}} f_{\text{Sand}} \quad (6)$$

where SFRi is the SECRETS-3PG soil fertility index, scaled from zero to one where zero is extremely unfertile and one is maximum fertility for the species.

[21] We also used the USDA STATSGO soils database to extract specific biological variables for each study that could correlate with site productivity. These included soil C, bulk density, pH, and water holding capacity. However, none of these variables were useful in predicting SFRi in these analyses.

2.3.3. Soil Class

[22] The SECRETS-3PG model requires an estimate of soil class (SC) for the 3-PG portion of the C allocation module. Soil class as used in 3-PG is differentiated into four discrete classes: (1) sand, (2) sandy loam, (3) clay loam, and (4) clay. Our adaptation of the 3-PG approach to allocate biomass uses SC as a continuous variable; a continuous response in SC enables greater sensitivity of the model to variation in soil texture. Soil texture is a model input that establishes minimum and maximum soil water availability. We therefore developed an equation to estimate SC from soil texture. We assigned a SC value of 1 to 4.5 for various combinations of the percent clay and the percent sand from the soil texture triangle to create a response surface. We then used nonlinear procedures in SAS[®] (PROC NLIN) and the data assignments for 87 texture combinations to fit

$$\text{SC} = K_0 \text{clay}^{K_1} \text{sand}^{K_2} \quad (7)$$

where SC is the soil class (1–4.5), clay and sand are the percent clay and the percent sand of a soil profile, respectively, and K_0 , K_1 , and K_2 were parameters to be estimated.

2.4. Uncertainties in the Model Estimates

[23] For these analyses we focus on two ways to examine uncertainty in our SFRi estimates as they influence our model outputs. First, the SFRi model regression has sample variance in the regression parameter estimates a , b , c , and d (equation (6)). Second, soil texture classification based on soil series resulted in broad uncertainty in what would be the actual site estimate of the percent clay and the percent sand needed for the SFRi regression. To accommodate these two sources of uncertainty, we conducted nine separate simulations for each climate-soil combination. This 3×3 matrix, three for each source of uncertainty, was represented as (1) the mean of the regression model parameter estimates of equation (6), (2) \pm two standard errors of the mean for the regression model parameter estimates of equation (6), (3) the “average” percent clay and percent sand for each soil series, and (4) $\pm 5\%$ for the percent clay and $\pm 7\%$ for the percent sand of the average texture

Table 1. Percent Change in the Soil Fertility Index (SFRi) From the Baseline Estimate as Influenced by Uncertainties in Soil Texture and in the SFRi Model Parameter Estimates

Uncertainty in the Parameter Estimates of Equation (4)	Uncertainty in Soil Texture, %		
	Minus ^a	Mean	Plus ^b
Lower ^c	-93	-91	-91
Mean	-37	-	-19
Upper ^d	119	165	184

^aSoil texture estimate minus 4% sand and 3% clay.

^bSoil texture estimate plus 4% sand and 3% clay.

^cMean minus two standard errors of the mean for each parameter statistic.

^dMean plus two standard errors of the mean for each parameter statistic.

classification for each soil series (Table 1). The influence of profile depth as used in equation (6) was ignored in these analyses.

2.5. Simulations Conducted

[24] Simulations and model comparisons included (1) a comparison of the temperature response in S_R for the *Gough*

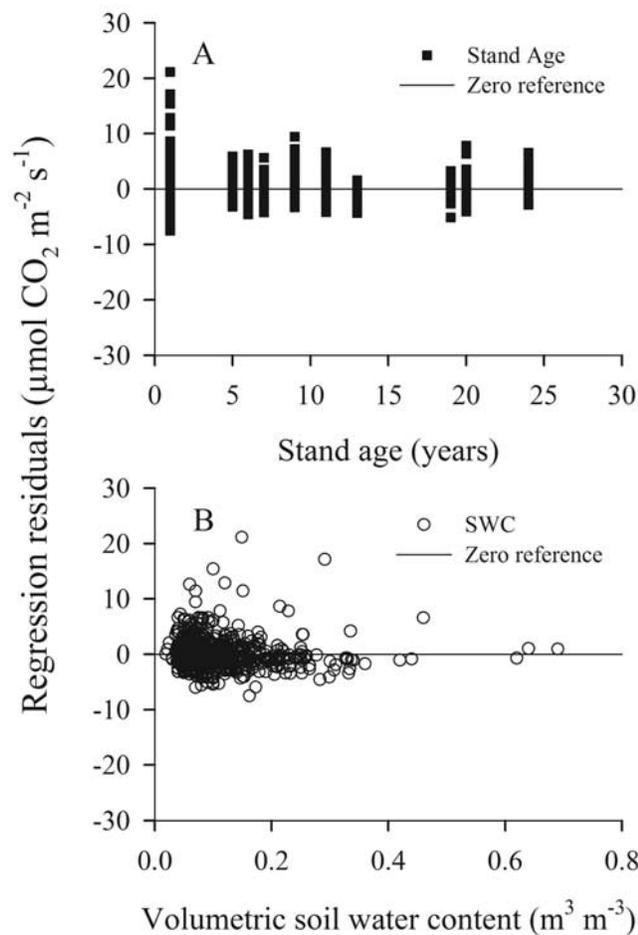


Figure 3. Comparison of the regression residuals from equation (3) using the *Gough et al.* [2005] soil respiration measurements from South Carolina with estimates of (a) stand age (solid squares) and (b) volumetric soil water content (open circles). No bias in the independent measures was observed.

et al. [2005] data and a 1-d field campaign for the Virginia Coastal Plain, (2) verification of the soil fertility index (SFRi) estimates, (3) model verification of simulated stem volume ($\text{m}^{-3} \text{ ha}^{-1}$) with measured estimates, and (4) the influence of stand development, soils, and climate on simulated NPP, CUE, and NEP over a 30-year rotation.

[25] The nine simulations for each soil series-hex combination described above enabled us to generate measures of central tendency and dispersion; we used the univariate procedures in SAS[®] to derive these estimates. Soil effects on mean annual NEP, and \pm one standard error of the mean are presented for three soils of varying texture for one climate cell (latitude $36^\circ 34' \text{N}$, longitude $77^\circ 35' \text{W}$) for the 30-year rotation. The 30-year trends in mean annual NPP for the entire study area and \pm one standard error of the mean for a silt loam soil are presented for the 5th to 95th percentiles, inclusive, of NPP for each hexagonal climate polygon averaged over the study area. The modest restriction in the data analyzed removed outliers and extreme, potentially biologically infeasible outcomes. Simulated LAI for the three soils, over the short rotation, for the one climate cell studied in detail is also presented. Finally, we present the 30-year mean annual NEP for the forested portion of the Virginia Coastal Plain.

3. Results

3.1. Soil Respiration

[26] We found no bias in the regression residuals with respect to either volumetric soil water content or stand age for the *Gough et al.* [2005] soil respiration data from the South Carolina loblolly pine age chronosequence (equation (3)) (Figure 3). The scalar parameter estimate (i.e., lower 95% confidence limits, estimate, upper 95% confidence limit) was significant; $n1 = 1.863$ ($1.782 < n1 < 1.944$) (equation (4)). The regression explained about 52% of the variation in total soil CO_2 efflux (S_R) (Figure 4). A comparison of regression

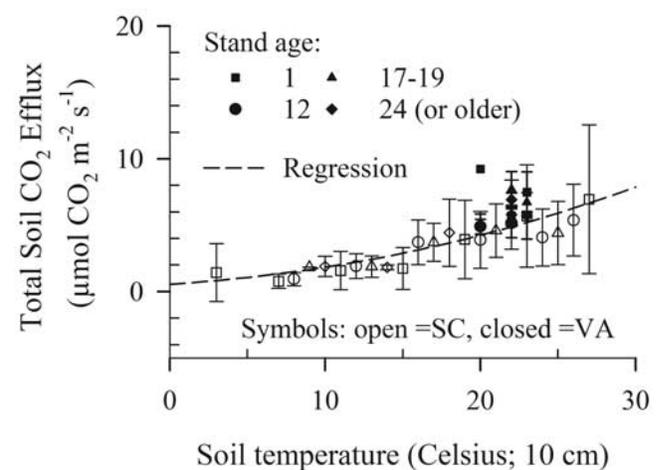


Figure 4. Comparison of measured CO_2 fluxes for the South Carolina Coastal Plain (open symbols) across four age groups with those obtained from a 1-d field campaign for the Virginia Coastal Plain (solid symbols). Total soil CO_2 efflux was modeled using the *Lloyd and Taylor* [1994] equation (dashed line) that was fit using the South Carolina data.

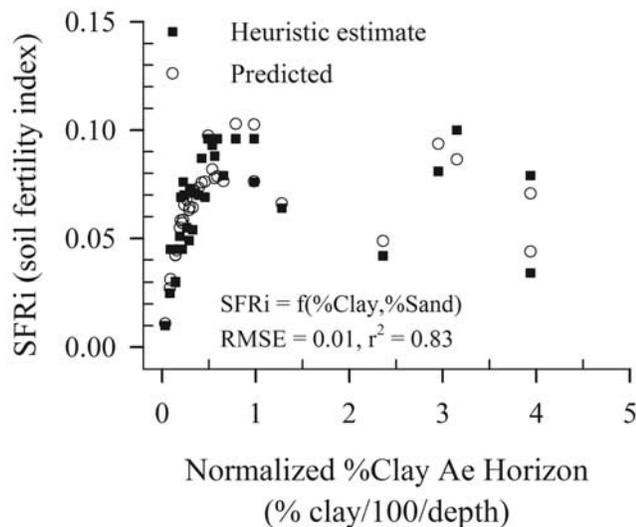


Figure 5. Relationship between heuristic (solid squares) and predicted (open circles) estimates of the soil fertility index (SFRi) (for unmanaged stands) used in the SECRETS-3PG hybrid process model and the percent clay of the Ae horizon. We used visual optimization procedures to derive the heuristic estimates by comparing destructively sampled measurements of stem volume, quadratic mean diameter, and stem density with those simulated from the SECRETS-3PG model until minimum departures among all three were obtained. Thirty-six loblolly pine stands of varying age and productivity from the Virginia Tech Loblolly Pine Research Cooperative were used for these analyses.

model estimates with measurements from South Carolina and from a 1-d field campaign for the Coastal Plain of Virginia suggests that the regression underestimates S_R for these Virginia sites. However, the small sample size of the Virginia Coastal Plain measurements restricts the interpretation of these comparisons. On the basis of these limited data we would conclude that our estimates of S_R were conservative and that stand age did not influence the respiration measurements (Figure 4).

3.2. Soil Fertility, LAI, and Model Verification

[27] Regression estimates of the soil fertility index (SFRi) predicted by equation (6) were strongly correlated and unbiased with those derived from the manual optimization procedures. The regression parameter estimates, estimate and (lower 95% confidence limits, estimate, upper 95% confidence limit), were $a = 0.1844$ ($0.0700 < a < 0.2890$); $b = 2.8604$ ($1.8251 < b < 3.8958$); $c = 2.1140$ ($0.6939 < c < 3.5340$); $d = 0.2452$ ($0.1551 < d < 0.3354$). The regression explained 83% of the variation in SFRi. We found a unimodal response in SFRi to the percent clay of the Ae horizon, normalized for depth of the Ae profile (Figure 5) with decreased productivity observed with increased percent sand of the Ae soil horizon. These paired comparisons in SFRi demonstrated our ability to replicate our soil-site fertility index for a wide range of soils using baseline soils information.

[28] The 30-year mean, maximum annual LAI increased with SFRi, with an asymptotic response in simulated LAI

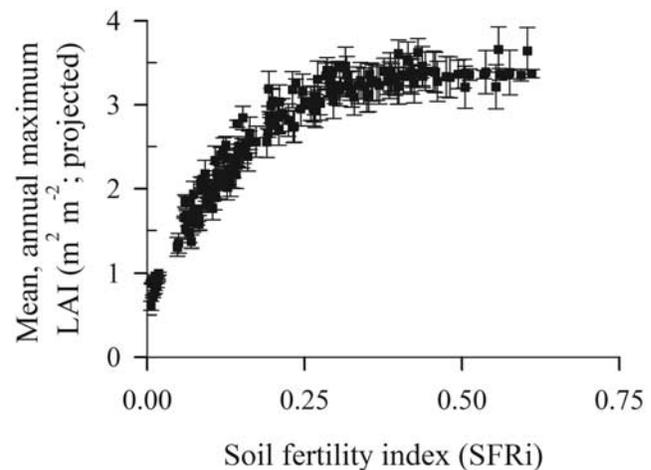


Figure 6. Effect of the soil fertility index (SFRi) on mean, maximum annual leaf area index (LAI) simulated by the SECRETS-3PG hybrid process model over the 30-year rotation.

observed (Figure 6). The hyperbolic relationship demonstrated a linear increase in annual maximum LAI for low SFRi associated with low clay content soils.

[29] We observed close correspondence between measured and simulated standing volume for three stands of varying productivity that were used for the development of the generalized equation to estimate SFRi (Figure 7). Of course, high agreement between the two estimates would be expected because standing volume was used as an optimization metric in the visual optimization procedure.

3.3. Stand Development and Soils on the Temporal Estimates

[30] Net ecosystem productivity was more sensitive to stand development than to soil type (texture and depth)

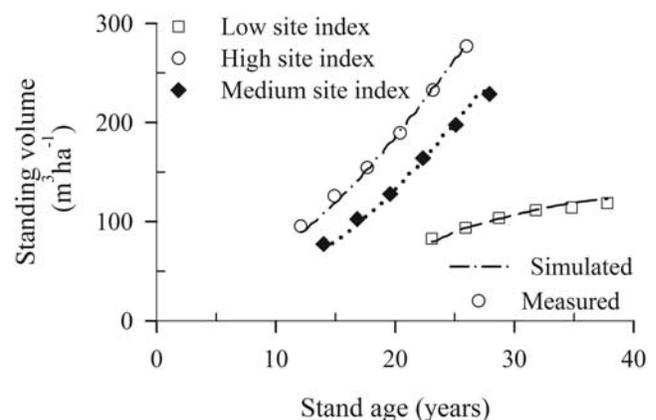


Figure 7. Comparison between measured (symbols) and simulated (lines) estimates of standing stem volume for three loblolly pine stands of varying age and productivity used in the derivation of the heuristic estimates of the soil fertility index (SFRi). This correspondence (among others) was obtained from optimization procedures and enabled the development of the regression equation to predict SFRi from soils information as used in the hybrid process model SECRETS-3PG.

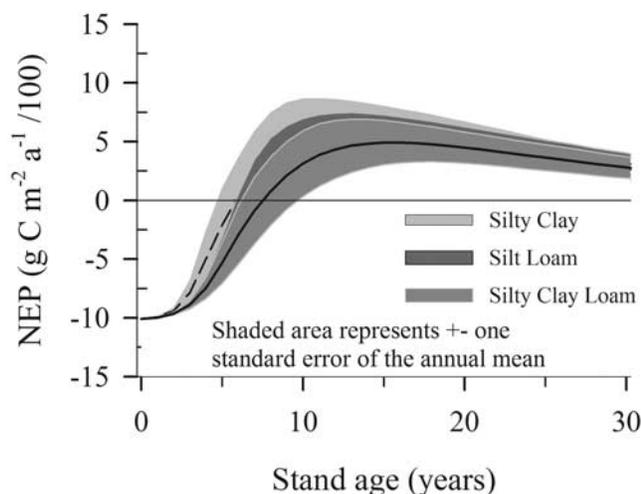


Figure 8. Effect of soil type and stand development on mean simulated net ecosystem productivity (NEP) \pm one standard error of the annual mean for $36^{\circ}39'N$ latitude and $76^{\circ}40'W$ longitude.

when evaluated over the entire rotation. However, there were minor differences in NEP as influenced by soil texture after 2 years but prior to about age 10 (Figure 8). Heavier, shallower soils had somewhat greater NEP than deeper,

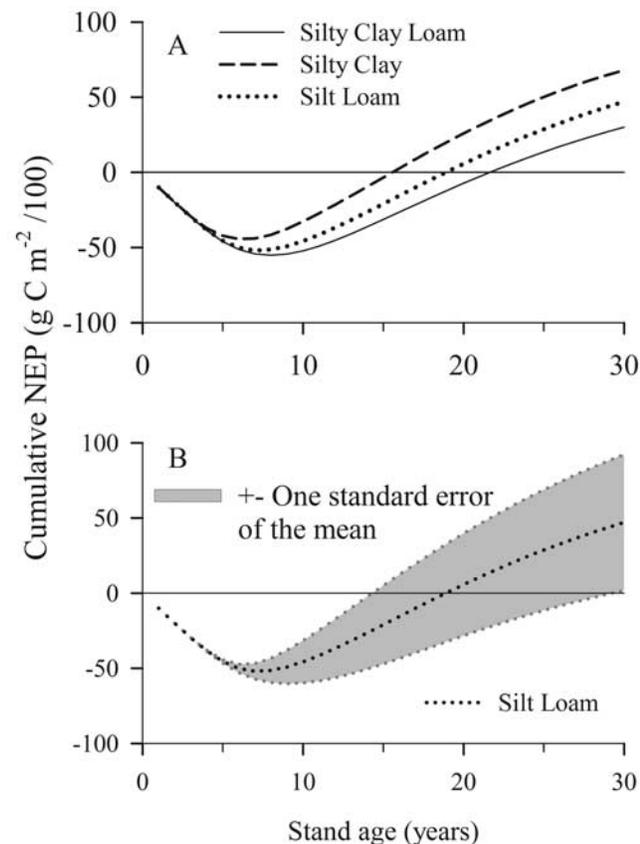


Figure 9. Cumulative net ecosystem productivity (NEP) simulated for $36^{\circ}39'N$ latitude and $76^{\circ}40'W$ longitude for (a) three soils and (b) the mean plus and minus one standard error of the mean for a silt loam soil.

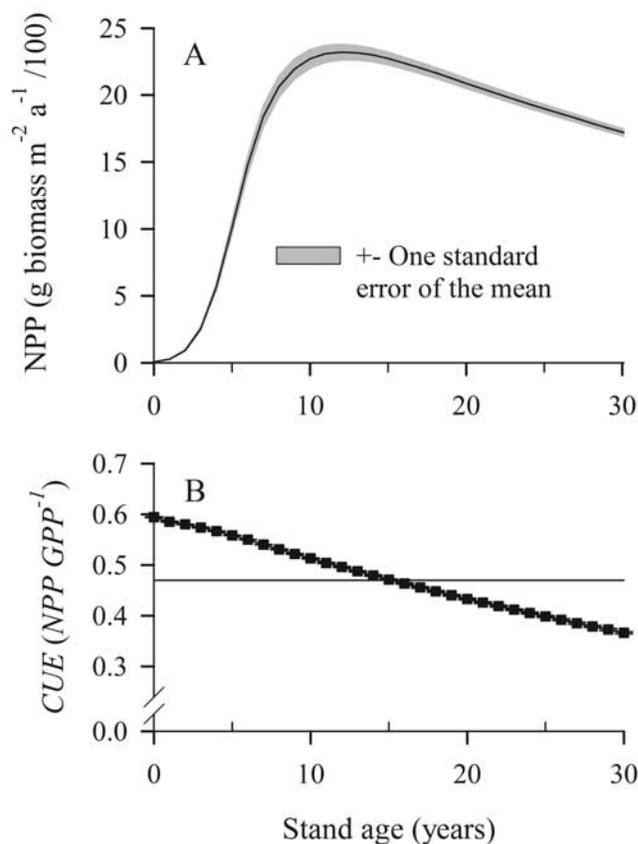


Figure 10. (a) Net primary production (NPP) and (b) carbon use efficiency (CUE) over a 30-year rotation for a silt loam soil for loblolly pine stands in the Coastal Plain of Virginia.

sandier soils. However, uncertainties in the fertility index as a result of sample variance in the model parameter estimates from equation (6) and in soil texture, because of the coarse resolution in the basic soils information, yielded broad variation in the NEP estimates. These simulations suggested annual net C release for these stands prior to about 9 years of age, depending on the soil texture class (Figure 8). Annual variation in NEP was dramatically reduced by the end of the rotation (Figure 8).

[31] Only minor differences were observed in mean cumulative NEP for the three soils examined (Figure 9a). Lighter, sandier soils did achieve positive C balance earlier than heavier clay soils, but these outputs suggested that loblolly pine growing at this latitude and longitude were net sources of C for 16 to 22 years following planting, depending on the soil texture class. However, our uncertainty assessments demonstrated broad variability in cumulative NEP (summation of the annual net ecosystem C fluxes over the 30-year period) for a silt loam soil. Namely, for portions of the southeastern Coastal Plain of Virginia, loblolly pine stands growing on a silt loam or silty clay loam could be net C sources when evaluated over a short rotation (Figure 9b).

[32] Stand development exhibited a strong influence on the study average net primary production (NPP) for a silt loam soil (Figure 10a). Mean NPP approached $2400 \text{ g biomass m}^{-2} \text{ a}^{-1}$ with a moderate decline observed following peak production after 13 years of growth. Climatic effects on NPP for the study area are reflected in the

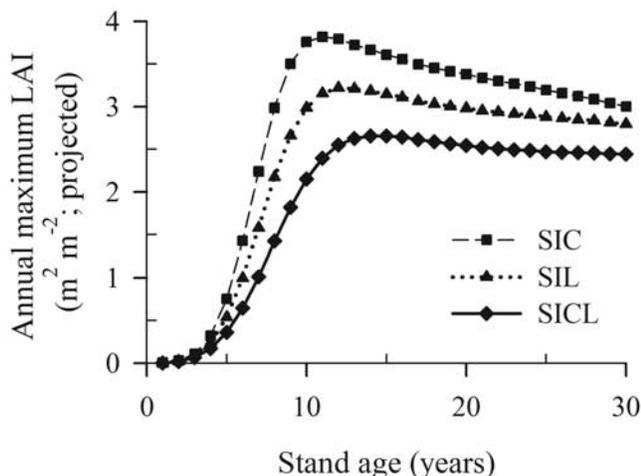


Figure 11. Annual, maximum leaf area index (LAI) over a 30-year rotation simulated with the process model SECRETS-3PG using the baseline soil fertility index (SFRi) from the uncertainty assessment for silty clay (SIC; solid square, Ae horizon 0.66 m deep), silt loam (SIL; solid triangle, Ae horizon 0.19 m deep), and silty clay loam (SICL; solid diamond, Ae horizon 1.75 m deep) soils used in our model output comparisons.

variance about the mean, 30-year projection (Figure 10a). Thus simulated NPP was less sensitive to climate when compared to developmental changes in stand structure over time (based on the width of the confidence interval). Carbon use efficiency (CUE) declined from about 0.6 to about 0.35 as these stands grew from seedlings until age 30 (Figure 10b). Increased C costs of maintaining an ever increasing biomass resulted in decreased CUE as stands aged (data not shown).

[33] Developmental differences in simulated LAI determined the magnitude and temporal responses in NEP and NPP observed for the three soils examined in detail (Figure 11). Peak annual LAI was greatest for the SIC soils, with maximum LAI achieved earlier in stand development (Figure 11) using the baseline estimate of SFRi. Conversely, peak LAI for the SICL soil occurred nearly 5 years later with maximum LAI about 32% lower than that estimated for the SIC soils present in our study. Simulated LAI for the SIL soil fell in between that observed for the SIC and SICL soils (Figure 11).

3.4. Regional Estimates

[34] Mean annual NEP averaged across the study was highly sensitive to stand development, similar to the trajectories as found in Figure 8. The study average NEP decreased from a maximum of about $600 \text{ g C m}^{-2} \text{ a}^{-1}$ at age 12 to about $300 \text{ g C m}^{-2} \text{ a}^{-1}$ by the end of the rotation. Annual variation in NEP for the study was, however, quite small.

[35] The study average ratio of simulated mean annual R_H to S_R was tightly coupled to stand development, decreasing from almost 100% of the total soil CO_2 efflux immediately following planting to about 46% by age 16 (Figure 12). The study average annual R_H (displayed as a negative flux) varied from $-270 \text{ g C m}^{-2} \text{ a}^{-1}$ to $-170 \text{ g C m}^{-2} \text{ a}^{-1}$ over

this period. Simulated R_H increased slightly following a minimum at age 16, associated with a decrease in LAI for maturing stands; root production increased at a decreasing rate following peak annual LAI (data not shown).

[36] The 30-year mean annual NEP for the study area varied from zero to almost $4500 \text{ g C m}^{-2} \text{ a}^{-1}$. Carbon sequestration increased with increased latitude and decreased longitude (Figure 13). Decreased C sequestration patterns over the 30-year averaging period were associated with decreased mean annual temperature and reduced incident shortwave radiation (data not shown). On an annual basis, these simulations suggest that loblolly pine stands on the Virginia Coastal Plain that receive no management intervention were, in general, net C sinks over a 30-year rotation, although northwestern portions of the study area departed from this finding. Specifically, our simulations demonstrate that short rotation loblolly pine stands in this region of the Coastal Plain may be C neutral (Figure 13).

4. Discussion

[37] Simulations from the hybrid forest process model SECRETS-3PG for Coastal Plain loblolly pine stands of Virginia support the generally suspected time trajectory in net C balance. Namely, it is thought that newly established stands may initially be annual 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]. In these analyses the stage in stand development exerted a strong influence on the annual estimates of loblolly pine NPP and NEP for the Virginia Coastal Plain. Soil type was influential, but to a lesser extent (although uncertainty in the soils information masked any potential differences). Our estimates of NPP and NEP were least sensitive to climate (although gap filling of the climate data, due to a restricted climate data record, may have diminished the overall climate effect), but climate was still important. This 30-year simulation analysis provides evidence to suggest that Coastal Plain loblolly pine of Virginia may, on an annual basis, become C sinks 5 to 9 years after planting. However, our 30-year mean annual estimates of NEP for northwestern portions of the study area, and

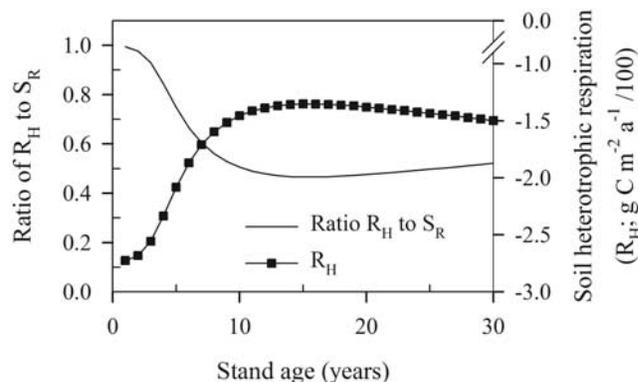


Figure 12. Ratio of mean annual soil heterotrophic respiration (R_H) to total soil CO_2 efflux (S_R) for the study area over the 30-year simulation (left axis), and mean annual R_H for the same data and period (right axis).

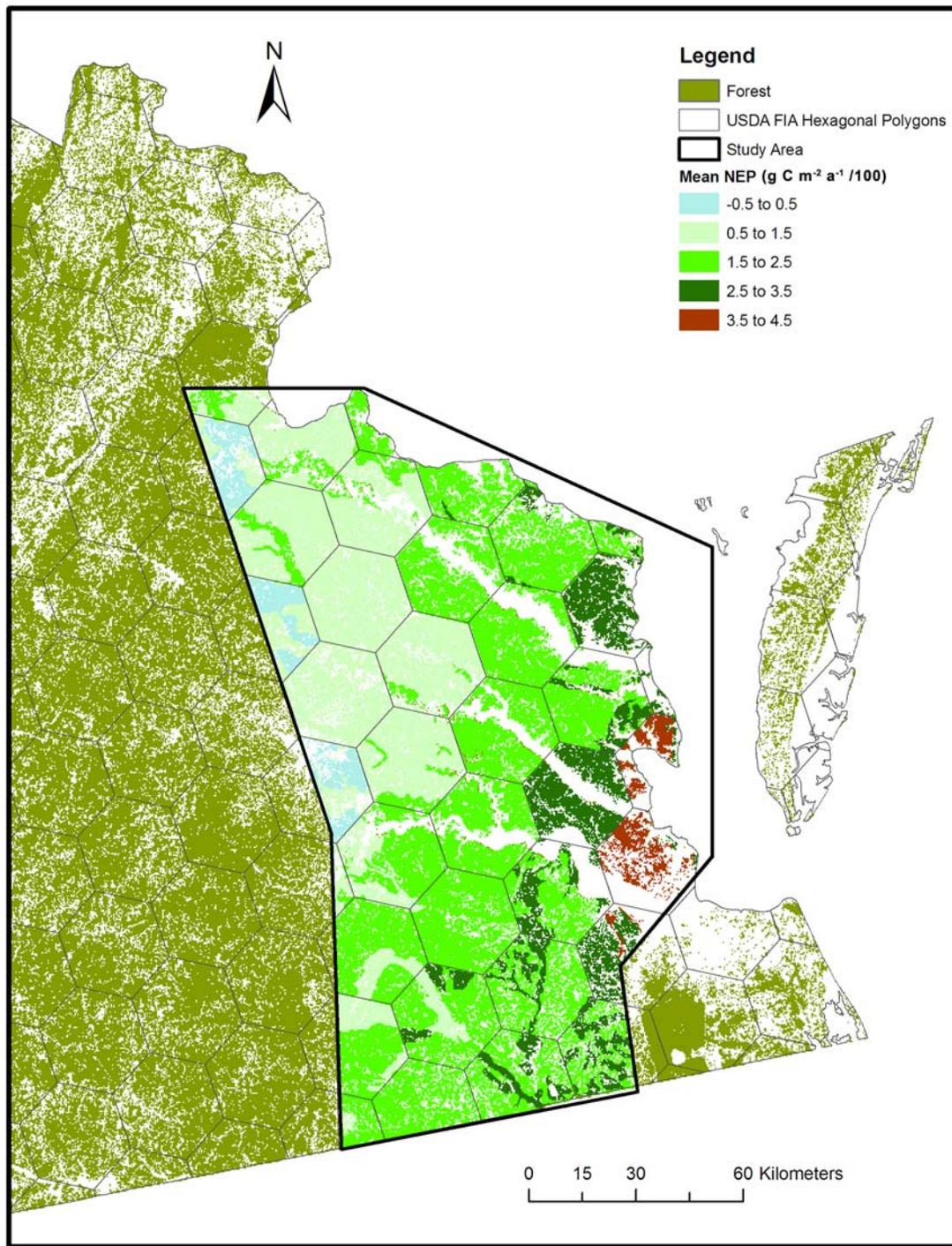


Figure 13. The 30-year mean net ecosystem productivity (NEP) simulated for the forested portions of the Virginia Coastal Plain for loblolly pine. Simulations assumed that all stands were planted in 1969 using similar initial starting conditions. Image boundaries (box) are as follows: top left, 77°54'45.91"W longitude and 39°15'39.37"N latitude and bottom right, 75°34'14.82"W longitude and 36°13'18.84"N latitude.

cumulative NEP (annual summation of net C flux) simulated over a short rotation suggest that untreated loblolly pine stands growing on the Virginia Coastal Plain may be net C sources, depending on soil type (and thus fertility) and climate.

[38] In these analyses NEP is calculated as the difference between NPP and heterotrophic respiration (R_H). For this exercise the model estimates R_H as the difference between total soil respiration (S_R) and root maintenance (R_M) and construction (R_C) respiration. Thus the implications and

meaningful interpretation of our NEP findings relies on our confidence in our estimates of NPP, S_R , root R_M , root R_C , and on the assumption that soil respiration can reliably be extrapolated from another Coastal Plain site managed similarly (South Carolina Coastal Plain measurements of Gough *et al.* [2005]). It is important to note that in this study our S_R estimates assume similar site preparation for our Virginia soils and that these soils would have a similar temporal response in heterotrophic respiration rates from sources other than soil (e.g., dead trees and woody detritus), especially early on in stand development, as observed in the Gough *et al.* [2005] study. Specifically, the fact that we observed no age effect in the empirical regression to estimate S_R can be explained by offsetting effects between soil heterotrophic respiration and root respiration as stands age as suggested by Gough *et al.* [2005] for the bedded South Carolina Coastal Plain soils. The S_R data used in these analyses were from bedded Coastal Plain sites that had a large amount of coarse woody debris incorporated into the beds; soil CO_2 efflux attributed to heterotrophic respiration was initially very high. As stand development proceeds, however, respiration attributed to oxidation of legacy C diminishes as root autotrophic respiration increases (as simulated in Figure 12). The net result is that total S_R has little to no correlation with stand age for bedded Coastal Plain sites where harvested debris has been incorporated into the soil during site preparation.

[39] Previous work has demonstrated that SECRETS-3PG can accurately estimate photosynthesis, biomass allocation and tissue respiration, and thus NPP [Sampson *et al.*, 2006]. Also, a model-data comparison found good correspondence between simulated and measured S_R from an empirical soil respiration model [Maier and Kress, 2000] used in SECRETS-3PG [Sampson *et al.*, 2006]. The degree of soil disturbance following site preparation influences S_R , especially early in rotation [Gough *et al.*, 2005]. Gough *et al.* [2005] studied soil respiration on the Piedmont and Coastal Plain of Virginia and South Carolina for a loblolly pine age chronosequence. They found that on sites where the residual slash material was retained, S_R decreased slightly with stand age but was remarkably stable from age 10 through the end of rotation (~ 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 and thus were offsetting. The regression residuals from equation (3) were unbiased with respect to stand age and volumetric soil water content in this analysis. Also, while measurements from our 1-d field campaign support this finding, we acknowledge that these short-term, spatially limited results may not be indicative of the potential response that could be observed across the Virginia Coastal Plain. Nonetheless, the higher temperature response found for the Virginia Coastal Plain study suggests that our S_R estimates may be conservative.

[40] Empirical models of S_R rely on the correlation between S_R and temperature as observed in field measurements and, in many cases, also on correlations with soil water content (SWC) [cf. Fang and Moncrieff, 2001; Janssens *et al.*, 2003]. As an empirical estimate, these measurements do not directly record the process level

mechanisms of total soil CO_2 efflux associated with autotrophic and heterotrophic respiration. Rather, they represent a reliable time-averaged estimate of S_R when substrate supply and soil moisture are nonlimiting and when temperatures are below a critical threshold. Davidson and Janssens [2006] and Davidson *et al.* [2006b] discuss, in detail, the processes and conditions that influence instantaneous rates of soil CO_2 efflux. Many suspect that current or recent photosynthate influences soil CO_2 release [Ekblad and Högberg, 2001; Bowling *et al.*, 2002; Bhupinderpal-Singh *et al.*, 2003; Ekblad *et al.*, 2005]. An empirical analysis that focused on longer timescales and broader spatial scales found within-year variability in the basal rate of soil respiration (R_B) [Curiel Yuste *et al.*, 2004]. Curiel Yuste *et al.* [2004] demonstrate that seasonal changes in the Q_{10} of soil respiration and in R_B were coupled to variation in LAI. Sampson *et al.* [2007] advanced this work in an empirical and modeling analysis. They found strong correlations between Q_{10} and GPP and R_B and GPP; R_B was more closely associated with GPP than to soil temperature, especially for deciduous oaks. Thus, although the existence of these processes and their influence on S_R are known, their ecological importance remains to be tested [Davidson *et al.*, 2006a].

[41] The empirical measurements used in these analyses represent hundreds of measurements taken in an age chronosequence over many seasons. Accordingly, these measurements capture the average inherent responses of soil respiration for a range of stand age and site conditions; these measurements represent the average, integrated response of the soil site conditions overtime. Thus, although we have not directly modeled the instantaneous influence of “actual” buried and partially buried woody biomass, live roots, dead roots, SWC, and any inherent S_R process, such as photosynthate activation of microbial biomass or substrate limitations to S_R , over longer spatial and temporal scales these processes are indeed reflected in the empirical measurements taken [e.g., Maier and Kress, 2000; Butnor *et al.*, 2003; Davidson *et al.*, 2006a]. Also, although the Lloyd and Taylor [1994] formulation provides unbiased estimates of S_R that are theoretically sound and empirically robust [Fang and Moncrieff, 2001], many more field measurements of S_R for the Virginia Coastal Plain are needed to confirm our S_R estimates.

[42] Model outputs of NEP from these analyses relied on a heuristic algorithm to estimate the soil fertility index (SFRi), a measure of site fertility and thus C allocation and stand growth in SECRETS-3PG. Our results suggest that we may be able to accurately estimate the SFRi variable for control stands that receive no management interventions. The regression model predicts decreased estimates of the SFRi variable as the percent sand of the Ae horizon, normalized for profile depth, increased (data not shown). The empirical form of the functional relationship between SFRi and the percent clay of the Ae horizon is conceptually consistent with structural and functional relationships among soil texture and depth, soil organic matter content, and soil nutrition. Soil organic matter and soil clay content have been shown to be inversely correlated, while soil N content and clay content are directly correlated [e.g., Vejre *et al.*, 2003]. Moreover, soil organic matter has been demonstrated to decrease with increased profile depth.

Inherent sampling error in the regression parameter estimates of the SFRi algorithm, and uncertainty in the actual soils information provided a means to evaluate uncertainty in our model outputs. Our analyses suggested greater variability in NEP due to this uncertainty than to the regional influences of climate, for a given soil type, on NEP (and on NPP). Further validation of this empirical approach is warranted. Because the empirical soil respiration model used only temperature in the regression (equation (3)), soil type had no influence on the S_R rates. Thus soil influences on NPP and NEP reflected soil differences in site fertility as estimated using the SFRi variable. Use of a simple temperature function for rotation length simulations may have overly simplified these analyses, although age was not significant in the regression analyses [also see Gough *et al.*, 2005] and did not appear to be biased in the available S_R data for the Virginia Coastal Plain comparison.

[43] Increased soil site fertility results in increased LAI and thus increased productivity of loblolly pine [Vose and Allen, 1988; Albaugh *et al.*, 2004; Jokela *et al.*, 2004]. The SFRi in these analyses represents a first approximation to estimate inherent site fertility for regional modeling exercises. Mean annual maximum LAI (Figure 6) in these analyses was comparable to the maximum values observed by Jokela *et al.* [2004] for control stands based on empirical studies for various southern pine species. Modeling intensively managed stands will require an approach to estimate soil nutrient availability as influenced by silvicultural treatments such as control of competing vegetation and fertilizer amendments.

[44] Light use efficiency model estimates of NEP for Virginia are comparable to our simulation findings. Masek and Collatz [2006] used Landsat data and the CASA (Carnegie-Stanford-Ames) model to estimate NEP for central and eastern portions of Virginia. Their simulations predict ~ 80 to ~ 130 $\text{g C m}^{-2} \text{a}^{-1}$ NEP for “peak-to-peak” variability due to climate and fPAR (fraction of absorbed photosynthetically active radiation) drivers for pine. However, they go on to suggest that the annual “biologic carbon sink” in this region of ~ 80 $\text{g C m}^{-2} \text{a}^{-1}$ could be nearly neutralized due to cold weather or low PAR conditions. Our 30-year mean estimates of NEP over the study area ranged from neutral (or slightly negative) C in the northwestern portions of the study area (extreme northern extent for the cover type) to a C sink approaching ~ 400 $\text{g C m}^{-2} \text{a}^{-1}$ for a limited portion of southern and eastern regions (Figure 13). Masek and Collatz [2006] suggest that climate variability accounted for 75% of NEP variability. Their simulations, however, were assessed using static stand conditions. In our simulations stand development exerted a strong influence on NEP, but climate was important in determining the mean response when evaluated over a short rotation (Figure 13).

[45] Point-in-time estimates of NEP from Piedmont loblolly pine stands of North and South Carolina and Virginia are available for comparison. Newly planted stands (seedlings) are thought to be C sources on the order of 800 to 1200 $\text{g C m}^{-2} \text{a}^{-1}$ [Gough *et al.*, 2005] based on soil CO_2 efflux measurements and destructive harvesting. Unfertilized 6-year-old loblolly pine stands on infertile sandy soils in North Carolina were a C source, but became minor sinks when receiving optimum fertilization [Lai *et al.*, 2002]. Annual NEP for an adjacent 12-year-old unfertilized

loblolly pine stand was a minor sink of about 28 $\text{g C m}^{-2} \text{a}^{-1}$ while fertilized stands for the same soils were a strong sink of 634 $\text{g C m}^{-2} \text{a}^{-1}$ based on component analyses [Maier *et al.*, 2004]. A modeling study found somewhat similar results [Sampson *et al.*, 2006]. Component analyses for a midrotation piedmont loblolly pine plantation estimated NEP to be 430, 580, and 650 $\text{g C m}^{-2} \text{a}^{-1}$ at ages 15 [Hamilton *et al.*, 2002], 16 and 17 [Schafer *et al.*, 2003], respectively. Finally, Lai *et al.* [2002] reported an NEP of 605 $\text{g C m}^{-2} \text{a}^{-1}$ for a 17-year-old loblolly pine stand at Duke Forest.

5. Conclusions

[46] In our simulations the stage in stand development had a strong influence on annual net primary productivity (NPP) and net ecosystem productivity (NEP) for these Coastal Plain soils. Soil type was also influential. Lighter soils had, in general, lower NPP and NEP than soils with greater silt and clay content. This finding was due to differences in the model estimates of soil fertility (i.e., lighter soils had lower intrinsic fertility as estimated by equation (6)). Climate, although of lesser importance, determined the influence of soil texture (and depth) on the regional estimates of simulated NEP. Reduced C sequestered was associated with decreased mean annual temperature and decreased incident shortwave radiation. Of course, our NEP estimates depended on our empirical estimates of total soil CO_2 efflux (and in our estimates of root NPP and root autotrophic respiration). Also, although we demonstrated reasonable correspondence between our modeled estimates of soil respiration and measurements for the Virginia Coastal Plain collected during a 1-d field campaign, more measurements are required to bolster these findings.

[47] Our simulations suggest that following planting, young loblolly pine stands may be net annual C sources of about 1000 $\text{g C m}^{-2} \text{a}^{-1}$ but after 5 to 8 years (on average) they may become net annual C sinks on the order of 500 to 800 $\text{g C m}^{-2} \text{a}^{-1}$ at maximum stand LAI depending on soil type. Stands became a C sink following achievement of a leaf area index (LAI) threshold (data not shown) that corresponded to a mean annual NPP of 1600 to 1700 $\text{g C m}^{-2} \text{a}^{-1}$. These findings were for stands that receive no management intervention (i.e., fertilization or thinning). Declines in NEP after about nine to 13 years were associated with declines in stand leaf area index (LAI) with age. Fertilization would likely increase the sink strength of these stands, both earlier in rotation and total stand C sequestration throughout the rotation [Sampson *et al.*, 2006]. However, cumulative estimates of NEP (the net cumulative effect at the end of the 30-year rotation) suggest that unmanaged loblolly pine stands may be a net sink in some cases, a net source in others, and is on average indistinguishable from zero (based on our uncertainty assessments) depending on soil type and thus soil fertility and climate. This finding needs collaboration with more intensive measurements.

[48] Our findings suggest that forest management (e.g., bedding) and/or inherent site characteristics exert a considerable and lasting influence on the rate of C efflux from the soil and directly impact the relationship between soil C efflux and stand age. We acknowledge, however, that our

NEP estimates assume that we have adequately characterized the temporal trajectory in soil C efflux dynamics for the Virginia Coastal Plain soils. Namely, these analyses assume that soil respiration can reliably be extrapolated from another site where species, age and structure, soils, and site harvest and preparation would be similar. However, it is very unlikely that these assumptions could be met for other forested landscapes that exhibit dissimilar species or structure, soils, and site harvesting and preparation techniques.

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