Linking Growth and Yield and Process Models to Estimate Impact of Environmental Changes on Growth of Loblolly Pine

V. Clark Baldwin, Jr., Harold E. Burkhart, James A. Westfall, and Kelly D. Peterson

ABSTRACT. PTAEDA2 is a distance-dependent, individual tree model that simulates the growth and yield of a plantation of loblolly pine (*Pinus taeda* L.) on an annual basis. The MAESTRO model utilizes an array of trees in a stand to calculate and integrate the effects of biological and physical variables on the photosynthesis and respiration processes of a target tree on an hourly basis. PTAEDA2 sums the quantities for individual trees to obtain stand results; MAESTRO computes values for one tree at a time. These models were linked to provide a tool for further understanding stand, climatic, and edaphic effects on tree and forest productivity. PTAEDA2 predicts the characteristics of trees grown at a given stand density, on a given site, for a given length of time. These characteristics (outputs) are then used as direct inputs into MAESTRO which assesses the expected impact of environmental changes on tree function. The results from MAESTRO are fed back into PTAEDA2 to update future predictions by modifying the site index driver variable of the growth and yield model. An equation that predicts changes in site index as a function of net photosynthesis, age, and trees per unit area is the backbone of the dynamic linkage. The model changes required to link PTAEDA2 to MAESTRO were developed and reported earlier. This article reviews the earlier work and reports research results quantifying the relationships between net photosynthesis and the PTAEDA2 growth predictors, thus providing the basis for the MAESTRO to PTAEDA2 feedback process and integration of these two models. FOR. SCI. 47(1)77–82.

Key Words: *Pinus taeda*, climate change, forests.

MODELS ARE NEEDED TO PREDICT growth and yield of trees and stands that are, or have recently been, influenced by environmental changes. Of course, the environment changes constantly and the resulting growth response can be measured. But methods to unlock the cause-effect relationships because of historical changes, other than dendrochronology, are lacking. Consequently, researchers are looking more toward understanding and modeling the growth processes of tree and stand components as they are influenced by environmental factors, and then assembling and summarizing this information to predict how future growth would change due to changes in the environment (Blake et al. 1990). This modeling procedure is referred to as a "bottom-up" approach (Jarvis 1993). Jarvis also noted the

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advantages of a different approach to the problem, called "top-down." Here one starts with base information and works back to piece together the components and relationships that created the result. Jarvis concluded that ideally one would combine the bottom-up and top-down approaches to achieve the best of both worlds. Zeide (1999) presented a strong case for the top-down approach and the need to "start with the given outcome-tree size or number-and infer the processes that produce this result." In this study, we assume that a classical growth and yield model is a practical model to begin with in a top-down approach at the stand level. It fits the definition described by Zeide, it quite accurately predicts tree or stand growth based on measured data, and at a minimum it should be usable as a growth constraining function for a purely bottom-up approach.

In this article, we describe a model system that dynamically links a canopy process model (MAESTRO) with a growth and yield model (PTAEDA2). The objectives were to develop a model system based on existing models that would (1) further our understanding of stand, climatic, and edaphic effects on tree growth and forest productivity, (2) identify knowledge gaps in information required to scale from one measurement and time scale to another and determine future research needs to fill these information gaps, and (3) provide a test of the present state of modeling sciences for creating model systems to predict responses to natural and human-based disturbances.

Starting with these general objectives, a linked model system was developed. The prediction process is as follows: PTAEDA2 generates a planted loblolly pine stand for a given age, site index, and planting density. The resulting stand and tree information are then input into MAESTRO, along with environmental data for the location and period, and net photosynthesis is determined for that period. Net photosynthesis and other variables are used to estimate change in site index, which is then fed back to PTAEDA2 to update that model's predictions, which were initially based only on historical data that reflected average growth resulting from ambient environmental influences. Growth and yield are then recalculated using the new information, and the updated predictions are output and/or the process is repeated for further projections.

This article summarizes the earlier work, and then reports research results quantifying the relationships between net photosynthesis and the PTAEDA2 growth predictors, thus providing the basis for the MAESTRO to PTAEDA2 feedback process and integration of these two models. Comparisons of model predictions with measured loblolly pine growth results were made to illustrate the utility of modifying the driver variables in a growth and yield model to account for changing environmental conditions.

The Models

PTAEDA2 is an individual tree distance-dependent model that simulates the growth and yield of planted loblolly pine (Burkhart et al. 1987). It can be used to either simulate a plantation from the time of planting through a desired rotation, or to accept data from an existing stand and project that stand through desired time periods. When simulating a plantation from the time of planting, the model employs two main subsystems. The first subsystem generates an initial precompetitive stand at age 8 yr modeled by a diameter distribution technique. The second subsystem develops the growth and dynamics of that stand by evaluating individual tree competition and simulating the growth of individual trees on an annual basis. In general, growth in height and diameter is assumed to follow some theoretical growth potential. An adjustment or reduction factor is applied to this potential increment based on a tree's competitive status (as measured by the competition index) and photosynthetic potential (as expressed by the crown ratio). A random component, representing microsite and genetic variability, is then added. The probability that a tree remains alive in a given year is assumed to be a function of its competition index value and crown ratio. Survival probability is calculated for each live tree every year and is used to determine annual mortality.

MAESTRO (Wang and Jarvis 1990) utilizes an array of trees in a stand to estimate the net carbon gain of a target tree. The model requires the positions of all individual trees in the stand as specified by their x and y coordinates, and individual descriptions of each tree by the crown radii in the x and y directions, crown length, height to the crown base, and the total area of leaves within the tree crown. The positions of the leaves in both the vertical and radial directions are defined by functions describing the leaf area density distribution. The slope of the ground in the x and y directions and the orientation of the x axis are also specified. The time scale for MAESTRO is in hours, and the spatial scale involves up to 120 subvolume grid points within each tree crown. For every tree, radiation is estimated at the selected number of grid points within the crown, which takes into account both within-tree and between-tree light penetration. Foliage density in each of the selected crown grids within the tree crown is estimated, and foliage is classified with respect to age, position, and attendant physical and physiological properties. First, MAESTRO calculates the radiation absorbed by the leaves and the CO, and water vapor exchanges between the leaves and the ambient air for each of the selected grids. After integrating these factors to the crown level, MAESTRO then outputs daily amounts of (1) radiation absorbed, (2) photosynthesis minus leafrespiration, (3) respiration amounts for leaves, branches, the bole, and course and fine roots, and (4) transpiration of the defined target tree. Multiple runs of MAESTRO that designate different target trees can then be performed, and the output values calculated to acquire stand-level predictions.

Initial Linkage

The initial linkage from PTAEDA2 to the loblolly pine version of MAESTRO (Jarvis et al. 1991) was described in Baldwin et al. (1993). New relationships were fitted to facilitate the linkage and improve the linked-model system. Changes to the MAESTRO model were made in an effort to improve the description of canopy structure. A crown radius model was developed, and a new crown shape model was investigated. At the time, an effective crown shape model was not found, and the standard half-ellipsoid model, already incorporated into MAESTRO, was used based on observations from the Piedmont and Coastal Plain regions. MAESTRO originally used the beta function fitted to leaf area pooled from all sample trees to independently describe the vertical and horizontal distributions of leaf area (Wang and Jarvis 1990). A tree dependent Weibull function was used to replace the vertical beta distribution, while a discrete distribution based on branch horizontal one-thirds was used to replace the horizontal beta distribution.

An effective crown shape model for MAESTRO was developed and reported in Baldwin and Peterson (1997). This polynomial model provides the maximum crown radius, height at which this crown radius occurs, and the average symmetrical vertical cross-sectional profile for each tree. A comparison of the model to the original MAESTRO crown shape alternatives was made in the article. To adequately describe the location of the crown base, an equation predicting the height to live foliage (based primarily on the standard height to live crown measure) was also developed.

MAESTRO uses a phenology routine to describe the quantity of foliage on a tree at any given time of the year. This requires an estimate of each tree's leaf area at the time of full flush for each foliage age class. Prediction equations providing these values and other crown component information appeared in Baldwin et al. (1997). New methods to describe the horizontal and vertical distributions of foliage were incorporated into the MAESTRO model. The vertical distribution was changed to a truncated Weibull function to ensure that all foliage was contained between the crown base and the tree tip. Vertical placement of foliage within the crown was based on actual location, not where the branch was attached to the bole, which is valid only if the branches extend out horizontally. The discrete horizontal distribution was altered to model the crown horizontal one-thirds rather than branch horizontal one-thirds.

Code changes incorporating the new prediction equations were made to both PTAEDA2 and MAESTRO. A routine was added to PTAEDA2 that created a stand output file describing each tree in detail. This file was then used as a direct input file to MAESTRO. The resulting linked model allows microeffects on stand structure and function to be considered that would have been impossible to predict using stand-process models. This linkage was used to illustrate the predicted response of loblolly pine to elevated temperatures and carbon dioxide concentration (Cropper et al. 1998) and to investigate the effects of site index and thinning on the trends in tree-structure components and their effects on carbon gain and carbon loss (Baldwin et al. 1998).

Dynamic Linkage

To complete the linkage process, it is necessary to determine a relationship between one or more of the MAESTRO output variables to one or more key driver variables in PTAEDA2. We surmised there should be a relationship between net photosynthesis gain (NPS) and site index (SI). If true, then changes in NPS predicted by MAESTRO could be used to update SI in PTAEDA2 on a regular basis, and a dynamic system would result. Such a relationship could be found and modeled through simulations of the existing systems.

Initially, 10 MAESTRO simulations (10 different stands randomly generated from PTAEDA2) were completed at a planting density of 500 trees/ac (1,235 trees/ha) for each SI-Age combination in the target stand on yearly and monthly (May l-May 30) bases. The site index values used were 40, 60, and 80 ft. (12, 18, 24 m) and NPS amounts were output at ages of 10, 15, 20, 25, and 30 yr. Variation among the SI-Age-Time runs resulted from the stochastic mechanism of generating stands built into PTAEDA2. Plots of mean NPS over Age for yearly and monthly time periods were consistent—NPS increased gradually through age 20 and then appeared to begin leveling off at the later ages. Furthermore, NPS trends over time were distinctly separate for each SI class, with little crossover, i.e., trend lines were higher in the higher SI classes (Figure 1). We surmised increasing the number of simulations for each SI-Age combination would further decrease variation between the slopes of each SI class.

An investigation was also conducted to determine the best "average" tree to use. Simulations indicated the tree of average NPS was one within the 56th percentile of the dbh distribution; however, differences between the 56th percentile tree and the tree of quadratic mean diameter (QMD) were considered negligible so we elected to use the QMD tree as the target tree in all cases. Figure 2 shows the relationship between NPS and a target tree from various percentile classes from the 10th through the 90th percentile.

The next step was to determine a sufficient, but manageable, number of runs to be made for any SI-Age-Time combination. Trials led to the selection of 30 runs to reduce variability to an acceptable level (Figure 3). We then considered the advantage or necessity of using a certain time length run to establish the final relationship to be parameterized. Because the MAESTRO yearly runs are very time-consum-

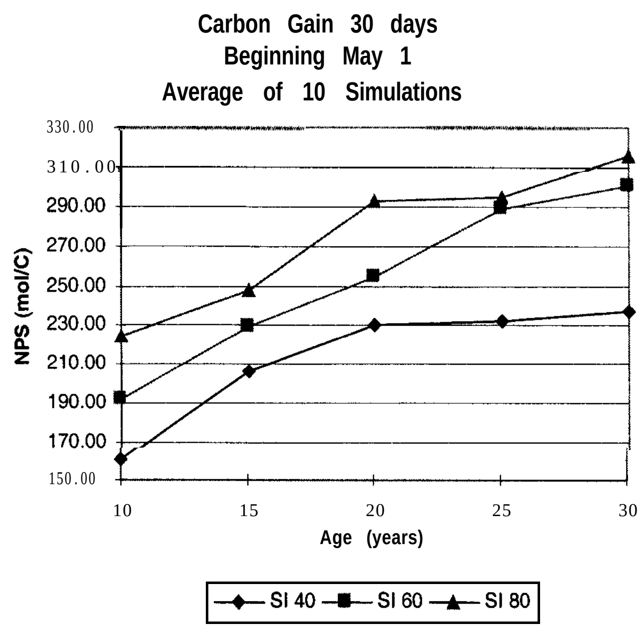

Figure 1. Relationships of site index (40, 60, 80 ft or 12, 18, 24 m), net photosynthesis, and stand age based on mean values of ten simulations for the month of May.

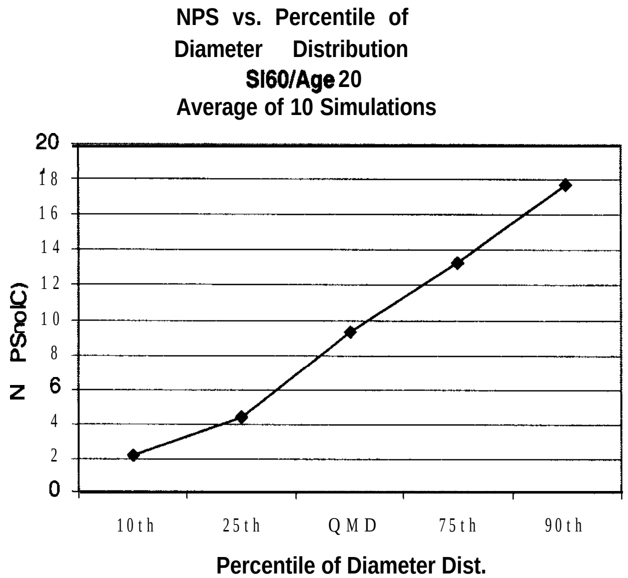

Figure 2. Net photosynthesis for trees of different positions in diameter distribution based on mean values of ten simulations.

ing, and the general relationships did not change from yearly to monthly runs, that option was discarded, and monthly values were used for further simulations.

We used six available 1 yr weather datasets to determine the time of year and time period to simulate when developing the experimental dataset. Four of the weather datasets were collected in Louisiana, one in South Carolina, and one in Georgia. The SI and Age values specified previously were used for a total of 90 repetitions where the tree nearest the QMD tree dimensions was selected as the subject tree. From the data generated by these simulations, a stepwise regression predicting yearly NPS from monthly NPS values, correlations of all NPS values, a principal components analysis of monthly NPS values, and a stepwise regression predicting SI from monthly NPS values and age were performed. For predicting yearly NPS, May, August, and October was the best three-parameter model. May NPS was the best single predictor of yearly NPS, with April a close second. May was the month with the highest correlation to yearly NPS, followed again by April. May was clearly the month with the highest NPS. The principal components analysis provided similar results: May and April had the two highest eigenvectors, respectively. The first five variables to enter the stepwise regression to predict SI from all of the variables considered were February NPS, Age, November, April, and May NPS. This ancillary information provided justification for the use of May as a representative month to make the runs to generate the modeling dataset.

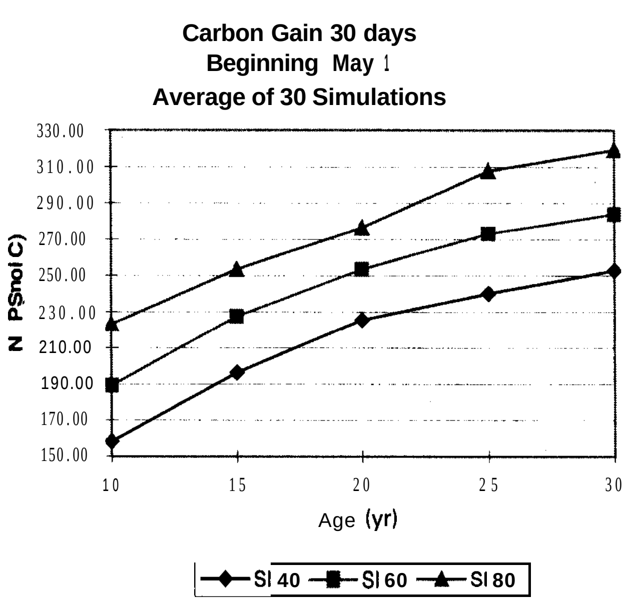

Figure 3. Relationships of site index (40, 60, 80 ft or 12, 18, 24 m), net photosynthesis, and stand age based on mean values of 30 simulations for the month of May.

Initially, number of trees planted was held constant at 500/ac (1,235/ha) and the relationship between NPS, SI, and age was explored. Figure 1 shows the initial relationships between NPS and SI. What is needed is the reverse relationship—SI needs to be expressed as a function of NPS. An equation to predict SI from A and NPS was fitted:

$$SI = b_0 + b_1 \log(A) + b_2 NPS \qquad (1)$$

where SI = site index of the stand at base age 25; log is natural logarithm function; A is the age of the tree in years; NPS is the net photosynthesis of the tree in mols; and b_0–b_2 are parameters estimated from the data

Equation (1) was fitted to data generated for the tree of quadratic mean diameter. It is possible, however, that trees of different relative sizes in the stand might respond quite differently. Thus, Equation (1) was also fitted to data for the tree representing the 10th percentile of the dbh distribution and for the tree at the 90th percentile. These percentiles should represent the range of response that might be expected from the smallest to the largest tree. If the response is similar, then a single site index adjustment can be made for all trees on the PTAEDA2 simulation plot; otherwise, the adjustment in site index will need to account for relative tree size.

For a common site index adjustment across all tree sizes, the product of mean NPS times the fitted slope coefficient b_2 in Equation (1) should be approximately the same, while lacking a systematic trend across the tree sizes. Repeating the same procedures as followed for fitting model (1) to the data for the tree of quadratic mean diameter, and computing the appropriate mean NPS values for trees of each size class, gave the results in Table 1.

Although the value for the tree of QMD is somewhat higher than the comparable figure for the small tree and the large tree, the values at the extremes are the same, and there is no compelling evidence for a differential response across the diameter distribution. Hence, we concluded that a single, plot-level adjustment in site index for all trees in a PTAEDA2 simulation plot should be sufficient.

Table 1. Response across the diameter distribution.

Tree of	b_2 Equation (1)	Mean NPS	Product ($b_2 \times NPS$)
QMD	17.412	8.844	154
10th percentile	57.241	2.296	131
90th percentile	7.817	16.788	131

Exploration indicated that not only is SI an important determinant of NPS, but age and numbers of trees per unit area are also critical. Thus, any equation relating SI and NPS must also take into account the stand age and density.

We simulated growth using PTAEDA2 for all combinations of SI values 40, 60, and 80 ft (12, 18, and 24 m), ages 10, 15, 20, 25, and 30 yr, and initial planting densities of 250,500, 750, 1000, and 1250 stems/ac (618, 1235, 1853, 2470, and 3088 stems/ha) . The simulated area was 20 rows x 20 rows. The subject tree for MAESTRO was selected as the tree having dbh closest to the quadratic mean dbh of the simulated plot, and not located in the outside 2 rows to eliminate edge effect problems.

Based on means of 30 repetitions for the month of May for the 75 SI-Age-N combinations already considered, the following model was fitted:

$$SZ = b_0 + b_1 \log(A) + b_2\,NPS + b_3\,(1000/N),$$

$$R^2 = 0.39,\ \text{Root MSE} = 13.06,\ n = 75, \qquad (2)$$

where SZ= site index of the stand (ft) at base age 25 yr; log is natural logarithm function; A is the age of the tree in years; NPS is the net photosynthesis of the tree in mols; $1000/N$ is 1000 divided by number of trees per acre (scaled); b_0–b_3 *are* parameters estimated from the dataset.

By expressing model (2) in mean difference form for the equation fitted using the QMD tree as the subject tree one obtains:

$$\Delta SZ = -12.771742(\log(A_2) - \log(A_1))$$
$$+ 0.309065(NPS_2 - NPS_1)$$
$$- 22.747977(1000/N_2 - 1000/N_1) \qquad (3)$$

Equation (3) can be used to express change in site index for specified changes in NPS and stand density over a time period represented by ages A_1 and A_2.

Application

As a demonstration of how this model can be utilized, simulations based on observed existing stand conditions were performed. One hundred unthinned control plots from a regionwide thinning study (Burkhart et al. 1985) that have 15 yr of observed growth data were analyzed. Each plot was used as an existing stand at plot establishment and 15 yr later for input into MAESTRO. The resulting NPS values, along with differences in density and age, were input into Equation (3) to obtain a ΔSZ value for each plot. Plantation ages at time 1 and 2 (A_1 and A_2) as well as numbers of trees at ages 1 and 2 (N_1 and N_2) were known. In this demonstration, the number of trees at the beginning of the simulation (N_1) was used, and N_2, the number of trees at the end of the growth period, was predicted from the PTAEDA2 model. Weather conditions were assumed to remain constant over the time period, but an average rate of CO_2 increase of 1.6 ppm/yr was assumed to have occurred (Conway et al. 1991), thus affecting the NPS values over time and, consequently, the site index over time. While changing CO_2 values may be confounded with changes in climate, plots of CO_2 concentration, mean temperature, and mean rainfall over the region for the time period covered by the growth observations showed no systematic trend except for the approximately linear increase in CO_2 concentration. The average estimated ΔSZ over the 100 plots was 0.278 ft/yr (0.0847 m/yr). This estimated increase in site index due to increasing CO_2 concentration is very similar to that obtained by Valentine et al. (1999) using the carbon-balance model Pipestem.

Simulations based on these existing stands were done using PTAEDA2 in order to compare predicted volume estimates with observed values. The initial set of simulations utilized PTAEDA2 with no yearly increase in site index. A second set of simulations was performed where site index was increased by 0.278 ft/yr (0.0847 m/yr). A summary of observed and simulated total volume per unit area is shown in Table 2.

These statistics show that holding site index constant over the 15 yr growth period resulted in an underprediction of total volume. The implementation of an annual increase in site index results in a mean predicted volume that is not significantly different than the observed volume at the 95% confidence level. In this example, utilization of the ΔSI Equation (3) clearly leads to improvements in simulated stand volume estimates. While the underprediction could be a result of inadequacies in the PTAEDA2 model itself, it seems plausible that the increase in CO_2 over the projection period has resulted in accelerated growth which must be accounted for in order to achieve unbiased projections.

Summary and Conclusion

The utility of using a growth and yield model to provide tree detail and stand structure information for process-level modeling was demonstrated previously (Baldwinet al. 1993). However, to be fully useful, a two-way linkage is needed whereby changes in processes can be used to modify predictions from the growth and yield model. The objective of this study was to develop methods for using estimates of net photosynthesis from a process model (MAESTRO) to modify growth and yield predictions from PTAEDA2.

Table 2. Observed and predicted values.

	Observed (plot data)		PTAEDA2 (constant SI)		PTAEDA2 (SI increase 0.278 ft/yr or 0.0847 m/yr)	
	ft^3/ac	m^3/ha	ft^3/ac	m^3/ha	ft^3/ac	m^3/ha
Mean	4,891.3	342.2	4,284.1	299.8	4,875.2	341.1
SE	130.6	9.1	81.3	5.7	90.3	6.3

From this exercise we conclude that site index, a commonly used driver variable in growth and yield models, can be related to net photosynthesis as predicted by the process model MAESTRO. The impact of changing environmental conditions on net photosynthesis can then be used to modify predictions in a growth and yield model by changing site index values. Integration of existing growth and yield and process models provides a relatively quick and efficient means of estimating the impact of changing environmental conditions on stand productivity.

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