
Applying 3-PG, a Simple Process-Based Model Designed to Produce Practical Results, to Data from Loblolly Pine Experiments

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ABSTRACT. 3-PG is a simple process-based model that requires few parameter values and only readily available input data. We tested the structure of the model by calibrating it against loblolly pine data from the Control treatment of the SETRES experiment in Scotland County, NC, then altered the Fertility Rating to simulate the effects of fertilization. There was excellent correspondence between simulated values of stem mass and the values obtained from field measurements, and good correspondence between simulated and measured stem diameters and Leaf Area Index values. Growth efficiency values derived from the model were similar to those obtained from field data. We used the model, without further calibration, to predict tree growth in terms of stem diameter at SETRES 2, a genotype x environment interaction trial in the same locality. Simulated mean stem diameters of two provenances did not differ significantly, over 3 yr, from those observed in the Control (unfertilized) treatments, but rates of change were lower than those of fertilized provenances. We then used 3-PG to simulate fertilized stand growth for an entire rotation length, and these results corresponded to those obtained with a traditional growth and yield model. This study showed that the model can simulate accurately the behavior and responses to environmental factors of loblolly pine and that it has considerable potential value as a management tool, for scenario analysis and as a research tool. *FOR. SCI.* 47(1):43–51.

Key Words: *Pinus taeda*, fertilization, process modeling, growth simulation.

L OBLLOLY PINE (*PINUS TAEDA* L.) IS THE leading timber species in the United States and is both extensively and intensively managed for wood production in the Southeast (Schultz 1997). Stand management of loblolly pine has been based on standard growth and yield prediction models derived from empirical measurements and relation-

ships among stand density, dominant tree height, and some measure of site quality. Site quality is usually estimated using site index, typically based on age 50 for natural stands and age 25 for plantations.

These growth and yield models have been developed for naturally regenerated stands, old field plantations and cutover

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plantations (see Schultz 1997), but loblolly pine management is evolving rapidly and it is unlikely that modern stands will grow at the same rates, and with similar levels of mortality, as those the models were derived from. It has been estimated that, relative to natural stands harvested in the 1950s, the productivity of cutover stands harvested in the 1970s had increased, on average, by 100%. In plantations established in the 1970s that are currently being harvested, growth rates have again approximately doubled. Even in natural stands with no intensive management, environmental conditions may be changing and affecting stand growth. For instance, atmospheric CO₂ is increasing steadily and is likely to influence forest management in future rotations (Groninger et al. 1999) and atmospheric inputs of N are altering stand nutrient budgets (Richter and Markewitz 1996). Considerable increases in management intensity are also having dramatic impacts on loblolly pine plantation productivity. These include fertilization (NCSFNC 1999), site preparation (Schultz 1997), competition control (Zutter et al. 1999), and genetic improvement (Li et al. 1999). Some companies are talking of aiming at another doubling of productivity in the next 20 yr (Anonymous 1999). As a result of these changes and developments, conventional, empirically based growth and yield models are becoming less and less useful for scenario analysis and forward projection of probable forest growth.

Over the last two decades, there has been considerable progress in developing process-based models to predict forest productivity. Process-based models aim to simulate the growth of stands in terms of the underlying physiological processes that determine growth, and the way stands are affected by the physical conditions to which trees are subject and with which they interact. Process-based models have the potential to be far more flexible than empirical relationships and can be used in a heuristic sense to evaluate the consequences of change and the likely effects of stimuli (Landsberg and Gower 1997, p. 247). These models fit into several different major categories; individual tree models such as TREGRO (Weinstein and Yanai 1994), canopy models such as MAESTRO (Wang and Jarvis 1990a,b, Cropper et al. 1998), stand-level models such as BIOMASS (McMurtrie and Landsberg 1992, Sampson and Allen 1999), G'Day (Comins and McMurtrie 1993) and Pipestem (Valentine et al. 1997), "hybrid" models (Baldwin et al. 1998) and regional "stand-alone" models such as PnET (Aber and Federer 1992), and FOREST-BGC (Running and Gower 1991). In general, these models have proved useful for integrating different processes and scales of knowledge, for honing research hypotheses, and even for making broad predictions of relative productivity regionally or under different environmental change scenarios. However, they are of limited utility for practical forest management because they usually require large amounts of input data and parameter values that are not readily available or economically obtainable. They also do not produce results in terms useful to forest managers.

The model called 3-PG (Physiological Principles Predicting Growth), developed by Landsberg and Waring (1997), is a simple process-based model requiring few parameter values and only readily available data as inputs. The output

variables it produces are those of interest to forest managers. Since the model embodies a number of hypotheses about the processes governing tree growth, and the way they respond to environmental factors, any calibration against observed data provides a test of the structure of the model and the operation of those processes, while comparison of the results obtained from the model, compared to data not used in calibration, provides a test of the model as a whole. We calibrated the model against data from unfertilized *Pinus taeda* (loblolly pine) trees at the Southeast Tree Research and Education Site (SETRES), located in Scotland County, North Carolina and adjusted the Fertility Rating (but no other parameters) to account for fertilizer applied at age 8. We then used the model to predict tree growth at SETRES 2 (McKeand et al. 1999), a genotype \times environment interaction trial in the same locality, where fertilization was initiated at planting. 3-PG was also run for the period of a complete rotation and the results compared to those obtained using a traditional growth and yield model. We discuss the potential value of this model as a management tool for loblolly pine.

Model Outline and Study Sites

Model Outline

3-PG requires, as inputs, monthly average values of solar radiation, atmospheric vapor pressure deficit, rainfall, frost days per month, and average temperature. All these are routinely available, except, in some cases, solar radiation, which can be calculated from temperature data (Bristow and Campbell 1984, Coops et al. 1998a). Calculation time step is a month and output is monthly or annual values of Leaf Area Index (L*), stem mass and volume, stem growth rate, mean annual (volume) increment (MAI), and stem number. Given the appropriate geometrical relationships 3-PG can also provide estimates of stand height. The model can be run for any number of years, using monthly weather data for each year or monthly averages for the year. Using long-term averages is far faster and is the normal procedure unless there is particular interest in specific events, such as droughts. All the analyses presented in this article used average monthly weather data for the SETRES site, which were representative of the southeastern part of North Carolina.

The model calculates gross primary production (GPP) from a simple (linear) relationship between absorbed photosynthetically active radiation (PAR) and carbon fixed by the canopy. The conversion factor (canopy quantum efficiency) is constrained by atmospheric humidity, through its effects on stomatal (and hence canopy) conductance, as well as by air temperature, water balance, and nutrition. The effects of soil water balance and atmospheric vapor pressure deficit (VPD) are not additive or multiplicative—the most limiting factor in any interval is the one that applies: i.e., if soil water is more limiting than VPD, growth is assumed to be constrained by soil water during that period. Nutrition is described in 3-PG by a rating (FR), based on assessment of site fertility. Nutrition affects canopy quantum efficiency as well as carbohydrate allocation and is therefore a potentially important variable

but unfortunately, despite many years of research effort all over the world, our ability to describe soil nutrient status in terms usable in quantitative models of plant growth is extremely limited. The FR, while based on the best information available, including expert opinion, therefore remains a somewhat problematical and **unsatisfactory**—albeit pragmatic—approach. It can also be used as a **tuneable** parameter in the model, and in this mode holds out some prospect of providing information about effective site fertility.

Net primary production (NPP) is calculated from a simple ratio of NPP to GPP (see Waring et al. 1998) and then allocated to roots, stems, and foliage. The carbon partitioning procedure is central to 3-PG. Allocation to roots is on the basis of the now well-established influence of growing conditions [see, for example, Beets and Whitehead 1996; for a review, Landsberg and Gower (1997, p. 150)]; the proportion of NPP allocated to roots increases if nutritional status and/or water relations are poor. Allocation to stems and foliage in 3-PG is self-regulating; it relies on the ratio of the derivatives of the allometric equations describing leaf (W_f) and stem (W_s) mass in terms of stem diameter at breast height (dbh, denoted B when used as a mathematical symbol by Landsberg and Waring, 1997; see their equation 14 *et seq.*, p. 219). The parameters of the equation describing W_f in terms of dbh are among those used to tune the model; their values may vary from those established by analysis of sample data. Carbon allocation to foliage varies according to stand age (tree size) and growing conditions (soil moisture, VPD, soil fertility).

The model calculates monthly changes in stem mass; the allometric equation is then inverted (solved for average dbh), so the relationship between dbh and W_s determines stand basal area and volume at any time, depending on the geometric or empirical relationships being used. The parameter values for this equation are therefore important to the practical user.

Initial stand density is specified and changes in stem populations calculated using the well-established $-3/2$ power law. The position of the line is estimated from information about the largest tree size (greatest individual stem mass) likely to be attained in the area of interest, at low stem populations.

The allometric parameters—particularly those for the foliage/dbh equation—may vary with species, although extensive investigations indicate that the range is surprisingly small (see also Ter-Mikalian and Korzukhin 1997). They are the most important of the “tuneable” parameters in the model. Because of the nonlinearity of the equations, small variations in the coefficients of the equation describing stem mass in terms of diameter can cause significant differences in the values of parameters such as basal area and stand volume, particularly if—as is usually the case—stem sizes are not normally distributed.

3-PG is calibrated by fitting to individual sets of observational data, using an iterative procedure to optimize parameter values—mainly the foliage allometric values—with weather data relevant to the site and best available estimates of soil water holding capacity and fertility. The values for the

constant and power of the stem allometric equation should, if possible, be based on experimental data to give the best estimates of stem diameter when the equation is solved for dbh from mean stem mass. Time series of observations are preferable for calibration, but the model can be calibrated to reproduce a single set of measurements made at some specified age.

Study Sites

The Southeast Tree Research and Education Site (SETRES) is located in the Sandhills of Scotland County, North Carolina (35°N lat., 79°W long.). SETRES is located on an infertile, excessively drained site and was hand planted on a 2 x 3 m spacing in 1985 using a mix of ten open-pollinated families originating from the North Carolina Piedmont. More details on the site and stand can be found in Albaugh et al. (1998).

In 1992, sixteen 50 x 50 m (0.25 ha) treatment plots containing 30 x 30 m measurement plots were established. The 16 plots were evenly spaced as 4 blocks, each with 4 plots. A 2 x 2 factorial, randomized complete block experiment was established across the 4 blocks. Treatments, applied from 1992, were: fertilized vs. unfertilized and irrigated vs. nonirrigated. Fertilization was applied to achieve a foliar N concentration of 1.3% (with other nutrients in balance) and unfertilized trees had foliar N concentrations of approximately 0.95%. Irrigation was applied to achieve a target value of 40% of available water content in the upper 50 cm of the soil profile. More details on initial plot tree occupancy, weed control, fertilization, and irrigation prescriptions, and treatment efficacy can also be found in Albaugh et al. (1998). Observations included yearly measurements of tree height, diameter, stem populations, root, stem and foliar biomass, and leaf area index (L^*). Biomass estimates were derived from allometric relationships established from a subset of trees destructively sampled in 1992, 1994, and 1996. These relationships were applied to yearly individual tree height and diameter measurements as in Albaugh et al. (1998).

SETRES 2 is a larger scale **genotype** x environment experiment with ten blocks, located adjacent to SETRES. A split-split plot design was used with fertilization treatments, applied at planting, as main plots, provenances as subplots and families within provenances as sub-subplots. Nutrition treatments were again fertilized vs. unfertilized, with fertilization applied to achieve the same target foliar values as SETRES. Unlike SETRES, where fertilizer was applied in growing year 8, it was applied at establishment in SETRES 2. The provenances in the trial were Atlantic Coastal Plain and Texas Lost Pines; there were five families per provenance. More details on SETRES 2 can be found in **McKeand** et al. (1999).

Data

3-PG was fitted to data from the Control (unfertilized, unirrigated) treatment of SETRES. We assumed that the stands did not reach effective canopy closure until year 7; Beers Law (used in the model to calculate the radiation absorbed by the canopy) assumes horizontal homogeneity, i.e., it assumes that L^* is spread evenly over the land surface.

This is clearly not the case in the early stages of loblolly pine growth on this poor soil, so it was assumed that canopy cover increased from a low value (small trees at establishment) to unity over a 6 yr period, and this was used to correct radiation absorption. When canopy cover is complete (in these terms) Beers Law applies without correction. (Note that, because the model uses a monthly time step, radiation absorption is integrated over that period, which greatly reduces the effects of nonuniform canopy cover.)

Data from SETRES 2 (McKeand et al. 1999) were used to test the model; i.e., growth was simulated without further calibration of the model and the results compared to observations. Environmental data were obtained from the SETRES site.

Results

Model Performance on SETRES Data

Figure 1a is a plot of observed against simulated stem mass, for Control and Fertilized treatments in the SETRES experiment, at the end of years 7-12 (1991-1996 inclusive) after calibration of 3-PG using data from the control treatment of that experiment. This established the values of the parameters that determine carbon allocation, and hence growth patterns. The value of FR used for the Control was near zero.* To calculate growth in the Fertilized and Fertilized + Irrigation treatments, the value of FR was increased, from the beginning of growth year 8, in successive runs until rates of biomass production matched those observed. This occurred when FR = 0.4. No other parameter values were altered. The line on Figure 1 a goes through zero. The relationship between observed and simulated stem mass values is excellent—essentially a 1: 1 relationship with $r^2 = 0.99$.

The leaf area index is an important variable determining radiation interception, and hence carbon assimilation and stand growth rate, as well as transpiration rates. It is essential, during calibration procedures, to try to ensure that the maximum L^* produced by a stand, and the time course of L^* , are consistent with observations (or knowledge about the species where direct observations are not available). Figure 1b shows that simulated values of L^* were slightly lower than observed values in the middle of the range of observed L^* in the fertilized plots, where the difference is about half a unit. Otherwise the relationship is good. Regression analysis indicated no significant difference between the slopes of lines fitted to the data for Control and Fertilized treatments separately; they can be described by a single line (slope = 0.95—not significantly different from unity— $r^2 = 0.90$) with a slight positive bias—the intercept is 0.42 ± 0.41 .

Accepting the calibration results, the time course of stem mass and L^* , as calculated by 3-PG, is shown in Figure 2a and 2b, which illustrate the growth response produced by the

¹ The use of a zero value for the fertility rating (FR) does not imply no nutrients in the soil. It is the baseline condition, with the lowest value of canopy quantum efficiency used by 3-PG, and a relatively high proportion of carbohydrate allocated to roots rather than aboveground growth (see Landsberg and Waring 1997). Increasing FR increases canopy quantum efficiency and alters the pattern of carbohydrate allocation.

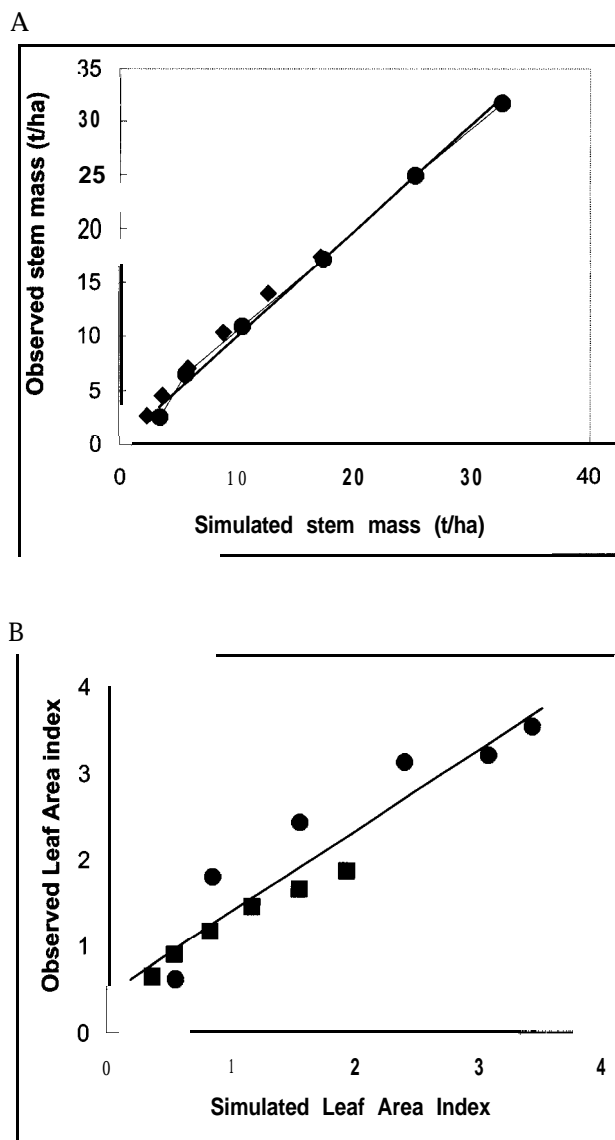


Figure 1. Simulated stem mass (A) and Leaf Area Index (B) at the end of years 1991 to 1996, inclusive for control and fertilized treatments in the SETRES experiment. Simulated values were calculated using 3-PG after calibration against the control treatment. The values for the fertilized treatment were calculated with FR = 0.4 Other parameter values were those established for the control. Correlation statistics are given in the text.

alteration of the fertility rating (FR) after fertilizer was applied.

There were large responses to fertilization, in terms of wood production, in this experiment (see Albaugh et al. 1998), with smaller additional responses to irrigation, reflected in Figure 2. Increases in L^* were smaller, but the higher values in 1995 and 1996, and the increase in available water in the root zone that resulted from irrigation, caused significantly increased water use. This was documented by Ewers et al. (1999), who noted that “mean daily E_c (transpiration) . . . was the same for C (Control) and I (Irrigated), higher for F (Fertilized), and highest for IF (Irrigated + Fertilized). Thus the effect of nutrient addition was to increase L^* sufficiently to nearly double the latent heat flux from the stand (comparing F to I and C); while the effect of providing water during dry periods, in

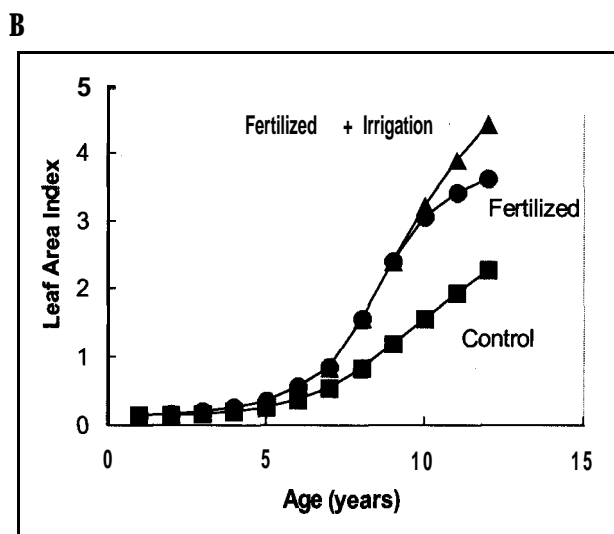
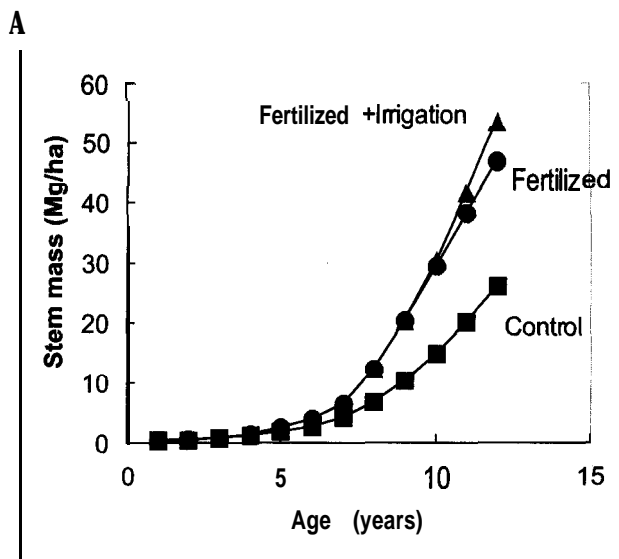


Figure 2. Simulated time course of stem mass (A) and leaf area index (B) for control, fertilized and irrigated + fertilized treatments. The fertility rating (FR) in the model was changed at the beginning of 1992 (growth year 8).

addition to nutrient, was to increase water use by 50%, when soil moisture was sufficiently high (comparing IF to F). Providing water without nutrients did not affect L^* or E_c , only changing the diurnal pattern of canopy transpiration."

We noted earlier that "because of the nonlinearity of the (allometric) equations, small variations in the coefficients of the equation describing stem mass in terms of diameter can cause significant differences in the values of parameters such as basal area and stand volume." In this study, simulated and observed values of dbh are very similar (Figure 3; $r^2 = 0.9$; the relationship is essentially 1:1), as we would expect from the fact that the parameter values for the allometric equations were derived from trees harvested in the SETRES experiment.

One of the stand growth characteristics investigated by Albaugh et al. (1998) was the growth efficiency of the various SETRES treatments (their Figures 1 and 2). They plotted

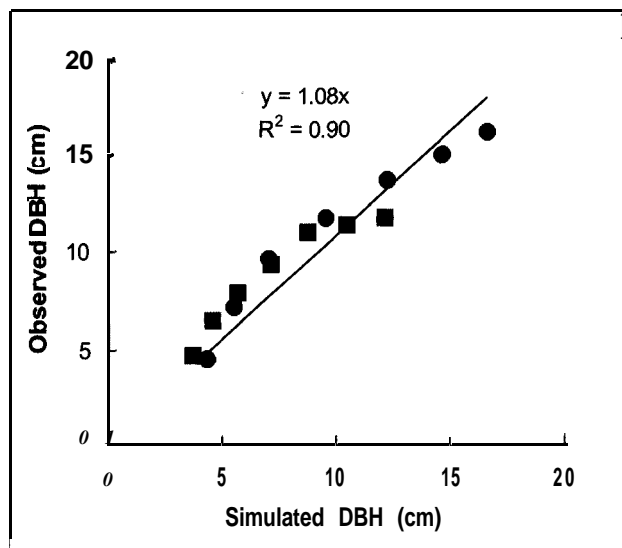


Figure 3. Simulated vs. observed stem diameters in the SETRES experiment. The line projects through the zero point on the axes.

annual stem volume increments against peak annual L^* , fitted linear regressions to their data, and found that stem volume growth efficiency increased from $7.1 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ per unit L^* in control plots to $9.2 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ in fertilized and irrigated plots. We produced a similar graph, plotting simulated annual aboveground stem volume increments (current annual increments, CAI) against average L^* , for each of the years in this study (Figure 4). (We used wood density values determined during the SETRES study to convert stem biomass to stem volume.) Since the relationships were clearly nonlinear, we fitted curves of the form $\text{CAI} = c_1 L^{*2} + c_2 L^* \pm a$ (where c_1 and c_2 are constants) to the three sets of data in Figure 4. To estimate growth efficiency from the modeled curves, we took derivatives of these equations and calculated the values of $d(\text{CAI})/dL^*$ for values of L^* spanning the range covered [i.e., $d(\text{CAI})/dL^*(i)$]. These results are shown in Table 1. The growth efficiency values are very similar to

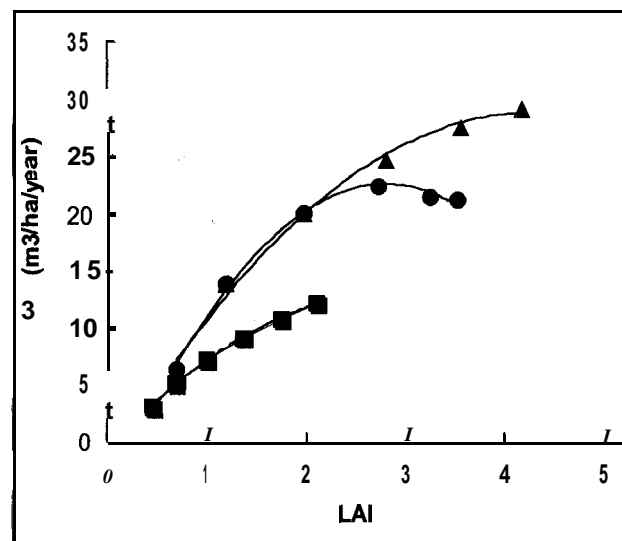


Figure 4. Simulated annual aboveground biomass production plotted against average Leaf Area Index for each of the treatments in SETRES, for the growing years 7 (1992) to 12 (1996), inclusive. The lines are fitted polynomials (see text).

Table 1. Growth efficiency as estimated as slopes ($\text{m}^3 \text{ha}^{-1} \text{year}^{-1}/\text{unit LAI}$) at three points in the quadratic curves shown in Figure 4. Numbers in parentheses indicate the exact LAI that the slope was derived.

Treatment	Point 1	Point 2	Point 3
Control	9.1 (0.5)	5.6 (1.5)	3.8 (2.0)
Fertilized	15.2 (1.0)	6.8 (2.0)	-1.6 (3.0)
Fertilized+irrigated	9.9 (1.0)	5.8 (2.0)	1.8 (3.0)

those obtained by Albaugh et al.; if we take the average of the first two values in each case (i.e., in the L^* range 0.5–2.0), we get 7.3, 11, and $7.8 \text{ m}^3 \text{ha}^{-1} \text{yr}^{-1}/\text{unit LAI}$, although the change in efficiency with treatment is not consistent. It seems unlikely that the negative value, at $L^* = 3$ in the Fertilized treatment reflects reality, but overall the reduction in growth efficiency at the higher values of L^* is to be expected, since as leaf mass increases, the fraction of foliage in the canopy subjected to shading increases. The results are presented to illustrate the potential of this approach, and that of the model as an analytical tool. One of the applications of this approach may be in analyzing the performance of different tree families and/or provenances.

Tests Against SETRES2 Data

There were two differences between SETRES and SETRES2, besides the fact that SETRES2 was designed to evaluate the performance of families and provenances. Firstly, tree densities were double those used in SETRES, and second, fertilizer was applied beginning at stand establishment.

To simulate SETRES2 results, 3-PG was run with the appropriate stem population (about double that used in SETRES), and the assumption that the canopies could be considered sufficiently homogeneous for the application of Beers Law after 36 months. FR was set to zero for the unfertilized stands, and 0.4 for the fertilized stands—the values used to analyze SETRES—from the beginning of the simulations. Allometric parameters were unchanged from those derived from SETRES, and we used the same (average) weather conditions. Comparisons between 3-PG output and experimental data are shown in Figure 5, which compares simulated and measured stem diameter,² the most direct and reliable measurement available from SETRES2. (The usual range of 3-PG outputs, such as L^* , stem mass, and hence, assuming wood density is known, volume was calculated, but these data are not presented here.) No attempt was made to allow for possible differences between the *P. taeda* provenances. The experimental data were averaged to produce mean values for provenance stem diameter; these values do not show significant differences between provenances, although when subjected to detailed analyses by year, dbh varies significantly between provenances.

The lines on Figure 5a show that 3-PG simulated accurately ($r^2 = 0.97$) the growth patterns of unfertilized trees, although the rate of increase in measured stem diameters

² These values are not strictly dbh; the trees were too small to measure stem diameter at (about) 1.4 m; the data relate to measurements made at about 30 cm height.

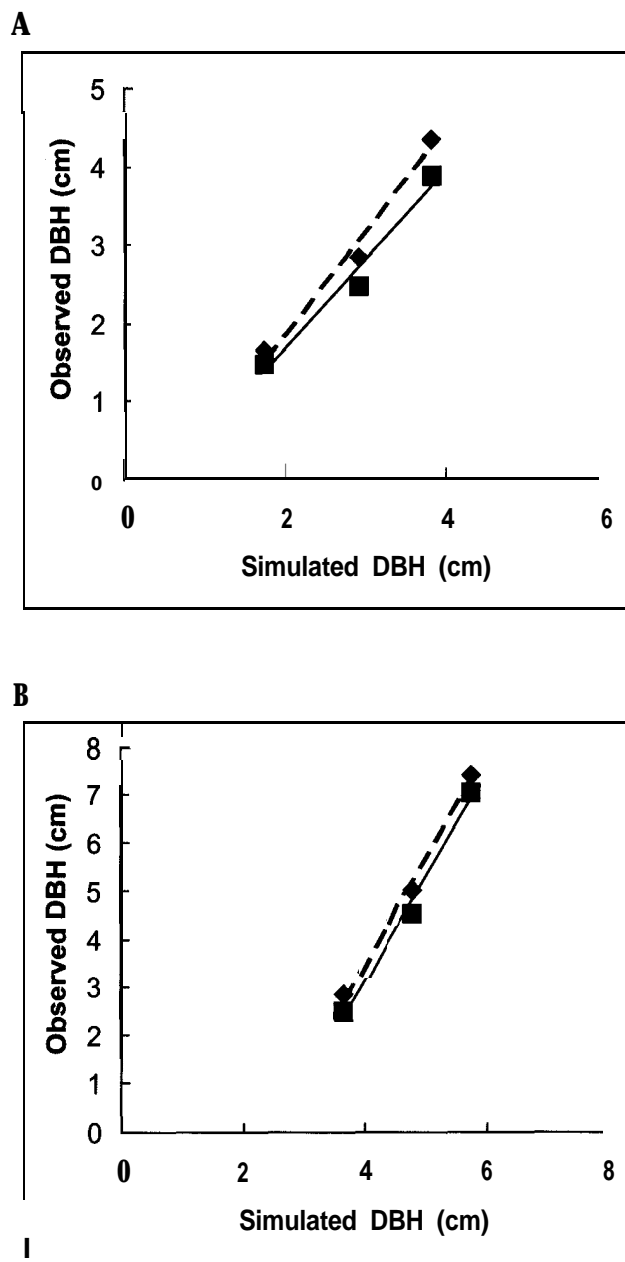


Figure 5. Simulated and observed time course of stem diameters in SETRES2, for both the genetic families (Atalantic Coast Provenance \blacklozenge ; Texas, \blacksquare) in the unfertilized Control (A) and fertilized (B) treatments.

was faster, in year 3, than simulated rates. Regression analysis showed no significant differences between provenances. In the fertilized treatments the correlation between simulated and observed values was very strong ($r^2 = 0.99$), but in this case the rate of change in stem diameter was considerably greater in the measured than in the simulated values. The test, therefore, indicated that the model could simulate the growth patterns of unfertilized young trees accurately, but questions remain in relation to the fertilized trees. There may be a number of possible reasons for the differences: fertilizer was applied at planting in this experiment, unlike SETRES, where it was applied in year 8, and stem populations were double those used in SETRES. Further investigation is warranted.

Discussion

As with any model, some of the assumptions made in 3-PG are debatable. The model embodies simplifications that cause concern to some scientists, prominent among which is the assumption that the NPP:GPP ratio is a constant, taken as 0.47 (say 0.5). Clearly this is not true for short periods, and there are likely to be significant deviations from this value in particular instances. Nevertheless, the data collated by Waring et al. (1998), for a number of species, strongly support a constant value (however, also see Medlyn and Dewar 1999). It is also supported by detailed studies on *P. radiata* (Arneth et al. 1998) and *P. ponderosa* (Law et al. 1999a, b) and by data reviewed by Malhi et al. (1999). Therefore we accept the constant NPP:GPP ratio as a pragmatic, robust and useful assumption. There are, currently, no compelling reasons to abandon or change it.

The physiological mechanisms underlying carbon allocation are not yet well understood, but because 3-PG uses a procedure based on the observed allometric relationships between different part of trees, carbon allocation is constrained within "reasonable" limits. The procedure is not entirely fixed. The allocation of carbohydrate to roots depends on growing conditions, and allocation to foliage and stems is a dynamic procedure and also responds to growing conditions. The patterns of L^* shown in Figure 2b were generated by the model as a consequence of the increased availability of carbohydrate and changes in its allocation. The fact that the model produced good estimates of L^* for fertilized plots (Figure 1b) without alteration of the allometric (C-allocation) parameters obtained by calibration against data from unfertilized plots, indicates that the allocation mechanism is robust and sound. Results such as these, and others obtained from analyses using 3-PG, have brought into sharp focus the importance of carbon allocation in trees; it is possible to get significantly different growth rates and patterns by varying carbohydrate allocation. Tree breeders have known for a long time that genetic variation and genotype \times environment interactions can be attributed to differences in carbohydrate allocation (Bongarten and Teskey 1987, Li et al. 1991). Differences in the growth of genotypes have less often been attributed to photosynthetic variation (Johnsen et al. 1999) and hence growth efficiency. It may be possible to use 3-PG to evaluate the relative contributions of these factors causing genetic variation in productivity.

The fact that the fertility rating (FR) in the model is relatively crude was noted earlier. Loblolly pine responds strongly to differences in site fertility, primarily by generating large amounts of foliage on fertile sites (see Figure 2b); foliar N concentrations tend to remain within a relatively narrow range (about 1.1 to 1.2 %). This is in contrast to *P. radiata*, which can maintain large differences in foliar N concentrations (see Crane and Banks 1992), as well as developing greater foliage mass (and hence L^*) in well-fertilized stands (Raison et al. 1992). The value of FR = 0.4, used to simulate responses on the fertilized site, was established empirically, as described in the Results section. It cannot be taken to represent all fertile sites, nor is it necessar-

ily associated with a particular value of foliage nitrogen concentration. The development of satisfactory and dependable relationships between FR ratings and conventional measures of soil fertility for loblolly pine, as well as other species, will probably come from understanding and quantifying the responses of foliage, both in terms of mass dynamics and nutrient concentrations, to site fertility and nutrient availability. The use of dynamic soil organic matter models may also contribute to solving the problem of modeling soil nutrition and tree nutrient uptake.

3-PG has another application in relation to nutrition: given, as shown here, that the model can be calibrated to simulate tree growth patterns accurately, it provides the biomass information needed for use in the NUTREM model (Ducey and Allen, this volume). This allows calculation of the nutrient content of various components of *P. taeda*, and hence of nutrient use efficiency and the nutrients likely to be removed from a site when trees are harvested.

If 3-PG is to be adopted and used as a tool for the study of loblolly pine, and prediction of its performance at various sites and under different conditions, it will be necessary to improve the description of litterfall used in the model for this species. The default setting has litterfall evenly distributed through the year, and this was the situation in the simulations that form the basis of this article. However, this is incorrect for *P. taeda* in the southeastern United States. New foliage grows during the spring/early summer period (March-June), and the foliage of the previous season starts to fall towards the end of the summer; i.e., the average life of a foliage cohort is about 15 months (Vose and Allen 1991, Hennessey et al. 1992). This pattern of foliage growth and litterfall results in the age distribution of the foliage on the trees changing markedly through the growing season, accompanied by dynamic and efficient remobilization of N. These leaf and N dynamics result in seasonal variation in photosynthetic rates (Chris Maier, pers. comm.) and hence canopy quantum efficiency. Introducing these changes into the 3-PG code can be expected to improve the accuracy with which the model simulates the growth of loblolly stands.

To illustrate the use of 3-PG as a tool for evaluating potential growth and yield, we ran the model for 25 yr with high fertility (Figure 6), using the parameter values (with one adjustment-see below) established from the SETRES study. The weather data were also those used for the SETRES and SETRES2 analyses. These runs assume, as they all do, high quality management, which would apply particularly to weed control during the early stages of growth. We have not assumed irrigation, so there are some, relatively minor, reductions in growth during the summer months of each year. Final standing stem biomass of the hypothetical stand was about 180 Mg ha⁻¹ (about 450 m³). Using the North Carolina State University Plantation Growth and Yield Predictor (Smith and Hafley 1984, Buford 1991), this is equivalent to a site index of approximately 26 m (base age 25) which represents a very good site on the Upper Coastal Plain (Schultz 1997). These results indicate that 3-PG, as parameterized here, is producing biologically sound results, within and beyond the time-scale of the experimental data sets being used.

A**B**

Figure 6. Time course of stem mass (A) and L^* (B) calculated for a well-fertilized, unthinned, *P. taeda* stand under good management. The parameter values used to calculate these curves were the ones established for the SETRES site.

Although not evaluated here, 3-PG has features that may prove useful for assessing the biological potential of *P. taeda* in the Southeast by examining the consequences of different stem populations, thinning, additional fertilization, the influence of variation in soil moisture holding capacity, and in weather conditions (the model can be run using average weather conditions or real annual data). When sufficient data on the growth patterns and allometric relationships of different genotypes are available, 3-PG could also be used to scale up results and may aid in developing tree ideotypes (Martin et al. 2000).

Also not discussed in detail here, but worth noting, is the fact that the problem of estimating forest productivity over large areas has been addressed by adapting 3-PG so that it can be driven by satellite data. Specifically, the Normalized Difference Vegetation Index (NDVI) that can be calculated from signals provided historically by NASA Landsat and by NOAA satellites (the new generation of Earth Observing

Satellites will provide excellent measurements for this purpose) is used to obtain estimates of L^* or, more directly, of the proportion of incident radiation absorbed by forest canopies. These can be corrected for the slope and aspect of the land units (pixel size determines the smallest area that can be assessed). Combined with weather and soil information, the satellite measurements lead to direct estimates of NPP for the observed forests. Details can be found in Coops et al. (1998a, b). The procedure does not provide a measure of standing biomass. Given some ground truth/calibration, and serial observations (say twice yearly, each year) the model can provide excellent estimates of forest growth rates over any land area.

Taken overall, the results and analyses presented here indicate that the structure of 3-PG is sound. The model can be calibrated to reproduce the growth patterns of loblolly pine (this has also been demonstrated for other tree species—see Law et al. 1999, Waring 2000). The parameter values obtained from calibration at one site can be used to predict growth at other sites, and changes in input data allow simulation of changes in growth patterns. Extrapolation with any model leads to results that are necessarily uncertain, and uncalibrated prediction with 3-PG is no exception to this, primarily because of problems concerning soil fertility and its effects on tree growth. The exercise presented here has not included rigorous tests of 3-PG as a predictive tool, but the results indicate considerable potential in this respect, and as an analytical tool, with possible applications for site evaluation, yield prediction, and scenario analysis by managers.

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