The Productivity & Sustainability of Southern
Forest Ecosystems in a Changing Environment
Edited by Mickler and Fox

17. A Linked Model for Simulating Stand Development and Growth Processes of Loblolly Pine

V. Clark Baldwin, Jr., Phillip M. Dougherty, and
Harold E. Burkhart

Linking models of different scales (e.g., process, tree-stand-ecosystem) is essential for furthering our understanding of stand, climatic, and edaphic effects on tree growth and forest productivity. Moreover, linking existing models that differ in scale and levels of resolution quickly identifies knowledge gaps in information required to scale from one level to another, indentifies future research needs to fill these information gaps, and provides a test of the present state of modeling sciences for creating model systems for predicting responses to natural and human-based disturbances.

Today there is a need to assess how such interacting stressors as air pollutants, (e.g., carbon dioxide (CO_2), ozone, acid rain), and climate change will affect forest health (forest function), tree growth, and stand productivity. Standard growth and yield models usually operate at an annual or longer resolution level and assume environmental conditions remain constant over time. As such, they are of limited use for assessing the effects of changes in weather and atmospheric chemistry on forest functioning or growth. However, growth and yield models are our best tools for predicting tree morphology and stand structural characteristics as a function of stand density, age, and site quality. Conversely, process models operate at hourly or daily levels and are suitable for estimating the effects of annual regimes of air pollution or weather on individual tree functioning (net photosynthesis, respiration, allocation, growth), but require that tree and stand characteristics be provided as model inputs (Landsberg, 1986). Because of the large input data requirements, hourly time steps, and inability to account for morphological changes with age and competition, most present-day process models are not suitable for predicting forest functioning or growth over multiple years.

By linking a growth and yield model and a process model, it should be possible to first utilize the output of the growth and yield model (i.e., predicted morphological and structural characteristics of trees grown at a given stand density, on a given site, for a given length of time) as direct inputs into a process model. Next, the process model could be used to assess the expected impact of environmental changes on tree functioning and growth for a one- to three-year period. The resulting information could then be fed back into the growth and yield model to update future predictions through modification of, for instance, the site index (SI) function. Thus, the procedure would be to 1) use the growth and yield model to grow a stand to a given age and describe the stand and structural characteristics of the constituent trees, 2) use the tree-structure descriptions and the process model to assess forest function at that age, 3) feed back the resulting information to the growth and yield model to adjust its prediction equations, and 4) repeat steps 1 to 3 until the end of the rotation.

Applications

The distant-dependent individual tree growth and yield model, PTAEDA2 (Burkhart et al., 1987), and the biological process model, MAESTRO (Wang and Jarvis, 1990a) parameterized for loblolly pine (Jarvis et al., 1991), were selected for this linkage experiment. Preliminary results of the linkage were described in Baldwin et al. (1993). The initial linked model was successfully developed through computer program changes and modeling using both existing data and some newly developed equations. Outputs from PTAEDA2 were used as driver variables for MAESTRO. Since the time of the initial development, by combining additional new equations and procedures developed from data collected specifically to fit the selected models, the linked model has been developed to its present-day stage.

Summary of the Component Prediction Systems

The growth and yield prediction system, PTAEDA2 (Burkhart et al., 1987) can be used to either simulate a plantation of loblolly pine 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 generating an initial precompetitive stand, and the second developing the growth and dynamics of that stand.

When applying PTAEDA2 to simulate plantations from time of planting, SI at base age twenty-five is specified and trees are assigned x and y coordinate locations in an 'n' by 'n' dimensional simulation plot. The juvenile stand is then advanced to age eight at which time intraspecific competition is assumed to begin. At that point, predicted juvenile mortality is assigned at random. Individual tree dimensions are then generated for the residual stand. The diameter distribution is generated from a two-parameter Weilbull distribution; the parameters of the distribution are estimated as functions of plantation age (eight years), number of trees surviving (from a stand-level survival function), and average height of the dominant and codominant trees at age eight (from a SI equation). Total tree height and crown ratio are predicted for every tree. After assigning dimensions to each tree, the competition effect of neighboring trees is calculated for every tree; this competition index takes into account both the size of and the distance to neighboring trees.

After generation of the precompetitive stand, competition is evaluated, and simulated trees are grown individually on an annual basis. In general, the 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), and a random component is then added, representing microsite and genetic variability. 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.

The net carbon gain of an array of trees in a stand is estimated by the MAESTRO-system. A description of the model, including all environmental and tree characteristics required to operate it, is found in Wang and Jarvis (1990a). Two key input requirements are 1) the positions of all individual trees in the stand as specified by their x, y, and z coordinates, and 2) 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 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 is up to 120 subvolume grid points within each tree crown. For every tree, an estimate is made of the radiation at a 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, the CO_2 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 leaf respiration, 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.

The Linkage Process

Limitations to making the PTAEDA2–MAESTRO linkage are the same as those expected for any analogous model linkages, that is, most tree attributes needed to describe a tree for input into MAESTRO were not standard outputs of PTAEDA2. In addition to diameter at breast height (DBH), total height, crown ratio or crown length, and stem weight or volume, MAESTRO required crown width, crown shape or crown volume, the horizontal and vertical distributions of the foliage biomass or density (leaf area per unit volume of crown), as well as branch and bole surface area or weight.

The user was required by MAESTRO to input actual values of these key stand and tree structural variables, all of which vary interdependently according to age, stand density, and site quality. Thus, simulations over several years were prohibitive. There were only three options for describing crown shape, therefore, the same crown shape and horizontal and vertical foliage distributions were assumed for all trees in the stand. For an individual tree-process model, it is essential that an accurate description of the crown shape, physical characteristics (i.e., weight, surface area), and distribution of its components be provided. Therefore, in this linkage project it was deemed essential to not only accomplish the linkage but to also improve upon estimation of the key tree-structure characteristics that would optimize the functions of MAESTRO to produce accurate estimates of crown assimilation and net carbon gain.

Because foliage density within a crown of loblolly pine is largely a function of nutrient and water availability (Dougherty et al., 1990; Vose and Allen, 1988), it is not possible to predict foliage density using only growth and yield information. Models for predicting total stand leaf biomass and leaf area duration for all age classes of foliage as a function of climate, available water, and stand characteristics are being developed for loblolly pine (Dougherty et al., 1990; Dougherty et al., 1995). Furthermore, because it is not known if a changing environment (for example elevated levels of CO_2 in the atmosphere) will change crown allometry, for the present stage of development it is assumed that crown-shape characteristics will not change as a result of those factors.

The stand measurements and modeling needed for the initial linkage were reported in Baldwin et al., (1993). Recent improvements deemed essential by the authors included 1) development of a tree-specific crown-shape model consisting of a second degree polynomial function constrained to equal zero at the crown tip for the outer shape, in addition to a straight-line inner-shape function to describe the cone-shape inner defoliated area of a loblolly pine crown (Baldwin et al., 1995; Baldwin and Peterson, 1997), 2) improved prediction equations for both foliage (old and new) and branch-weight, 3) improved prediction equations for both vertical and horizontal foliage distribution (old and new foliage) that predict foliage weight at its actual vertical location in the vertical plane, and 4) improved surface-area distribution equations for new and old foliage, branch, and surface area that have the same properties as the improved prediction equations (Baldwin et al., 1996). The branch surface-area equations allow MAESTRO the option of predicting woody mass respiration by surface-area relationships rather than by weight. Details of the data collected and research procedures (field, laboratory), methods (data analysis and modeling), and final results pertaining to these improved prediction equations and other factors required for the one-way linkage of the models have also been reported in the publications cited.

The effects of stand- and tree-structure changes on trends of tree functions over time (from ten to forty years) were tested with the PTAEDA2–MAESTRO linked models for a selected codominant-dominant tree (CDtree) for each of four treatments. To follow the CDtrees through an entire simulated rotation, it was necessary to select each CDtree from the survivors at the end of the rotation for each treatment. The four trees, of about average DBH at forty years, were traced back through time to age ten. Their characteristics, and the stand characteristics for each treatment, at ages ten, twenty, thirty, and forty years, are reported for the following treatments:

1. A loblolly pine plantation planted at 1683 trees hectare (ha) (2.4 × 2.4 m) spacing on site index (base age twenty-five years) land of 16.8 m, and unthinned through age forty;
2. A loblolly pine plantation planted at 1683 trees/ha (2.4 × 2.4 m) spacing on site index (base age twenty-five years) land of 16.8 m, thinned selectively from below at ages fifteen and twenty-five to a residual basal area of 16.1 m^2/ha;
3. Same as (1), except a higher SI of 21.3 m;
4. Same as (2), except a higher SI of 21.3 m.

The physiological parameters for both aboveground and belowground loblolly pine tissues were based on laboratory and field measurements of loblolly pines in Athens, GA (Teskey et al., 1986) and the similar southern pine, *Pinus elliottii* (Gholz et al., 1986; Cropper and Gholz, 1991). The climatic data, used for the MAESTRO portion of these simulations, were 1988 hourly climate data from Athens, GA. In that year, mean monthly air temperatures ranged from 6.2 to 27.5 °C, and soil moisture was never a limiting factor.

Results

Combining the allometric functions with the growth and yield model PTAEDA2 and then coupling PTAEDA2 with MAESTRO permitted us the opportunity to examine the effects of SI and thinning on the trends in tree-structure components and their effects on carbon gain and carbon loss. In this study, we evaluated the trends in crown volume, crown length and width, leaf area amount, leaf area distribution, mean crown leaf area density, aboveground biomass, branch and bole weight and surface area, and the ratio of foliage to structural mass or surface area. The results of the model simulations for the branch, foliage, and entire crown (e.g., volume, biomass, surface area) of each CDtree for each treatment and age are summarized in Table 17.1. Corresponding and additional predicted stand

Table 17.1. Aboveground Example of Loblolly Pine Tree Values from Simulations by the PTAEDA2-MAESTRO System from Ages Ten to Forty Years

Treatment	Age	DBH (cm)	Height (m)	Foliated crown depth (m)	Crown radius (m)	Height of max. crown radius (m)	Crown volume (m³)	New foliage biomass (kg)	Old foliage biomass (kg)	Branch biomass (kg)	Bole biomass (kg)	Total woody biomass (kg)	New foliage surface area (m²)	Old foliage surface area (m²)	Branch surface area (m²)	Bole surface area (m²)	Total woody surface area (m²)	Leaf area index
Medium spacing, low site, unthinned	10	12.3	8.0	4.7	1.3	3.9	13.7	2.66	2.41	4.5	16.7	21.2	26.58	24.08	4.2	1.7	5.9	3.7
	20	18.4	15.1	5.4	1.6	11.3	25.1	4.19	3.38	9.8	78.1	87.9	41.87	33.77	6.8	4.7	11.5	3.0
	30	21.7	19.5	5.6	1.9	15.6	37.0	5.18	3.78	12.9	150.8	163.7	51.76	37.77	8.0	7.2	15.2	2.4
	40	23.1	21.7	5.7	2.3	17.7	53.1	5.70	3.85	13.8	204.8	218.6	56.96	38.47	8.2	8.5	16.7	1.8
Medium spacing, low site, thinned at ages 15 and 25	10	15.1	8.6	5.4	1.5	4.4	22.0	4.10	3.52	8.4	26.9	35.3	40.97	35.17	7.1	2.2	9.3	3.5
	20	22.3	15.9	6.4	2.0	11.6	43.2	6.42	4.99	18.4	120.1	138.5	64.15	49.86	11.6	6.0	17.6	2.6
	30	26.6	20.8	6.7	2.3	16.4	63.6	8.01	5.69	25.1	239.7	264.8	80.04	56.86	14.0	9.4	23.4	2.2
	40	28.8	23.3	6.9	2.7	18.7	88.0	8.98	5.94	28.1	339.1	367.2	89.73	59.36	14.9	11.4	26.3	1.7
Medium spacing, high site, unthinned	10	14.5	10.2	5.5	1.3	6.1	17.4	3.11	3.03	7.1	30.5	37.6	31.08	30.28	5.8	2.5	8.3	3.5
	20	20.2	18.6	5.8	1.5	14.9	23.8	4.38	3.74	12.4	120.3	132.7	43.77	37.37	7.9	6.4	14.3	3.4
	30	22.7	22.9	5.7	1.8	19.3	30.3	4.99	3.82	13.9	198.9	212.8	49.86	38.17	8.1	8.8	16.9	2.9
	40	25.1	26.7	5.8	2.1	23.0	42.5	5.71	4.08	16.4	306.2	322.6	57.06	40.77	9.0	11.4	20.4	2.3
Medium spacing, high site, thinned at ages 15 and 25	10	18.0	11.2	6.5	1.6	6.7	30.4	4.89	4.56	13.9	51.4	65.3	48.86	45.57	10.1	3.4	13.5	3.1
	20	26.6	20.9	7.4	2.0	16.4	53.3	7.63	6.35	29.8	233.5	263.3	76.24	63.45	16.1	9.4	25.5	2.6
	30	30.4	26.1	7.4	2.3	22.7	68.7	9.00	6.75	35.7	406.0	441.7	89.93	67.45	17.7	13.5	30.2	2.3
	40	33.5	30.2	7.5	2.7	25.6	90.5	10.26	7.20	41.9	614.6	656.5	102.52	71.95	19.4	17.2	36.6	1.9

characteristics for each treatment and age are found in Table 17.2. Various graphical techniques are used to illustrate the trends observed.

Predicted Crown Volume Trends

The trends predicted for crown volume of the CDtree in each of the four SI-thinning combinations considered are illustrated in Figure 17.1a, b. Crown volume increased with age in a linear manner for all SI-thinning combinations. Thinning permitted crown volume to increase at more than twice the rate of the CDtree in the unthinned regime. In the thinned regime, (Figure 17.1a) crown volume of the CDtree growing on high SI land was slightly greater than the CDtree on low SI land through age twenty. At age thirty and forty, the CDtrees in the thinned stand had about the same crown volume for both SI conditions.

In the unthinned stands, crown volume of the CDtree was also initially greater for the high SI condition than for the low SI regime (Figure 17.1b). However, from age twenty to age forty, crown volume was predicted to be larger for the low SI CDtree than for the high SI CDtree. These results were predicted because the high SI tree had only slightly greater crown length (Figure 17.1d), although the low SI tree had greater crown width (Table 17.1). The pattern of foliated crown depth was consistent in both thinned and unthinned stands; although, as would be expected, the length was greater in thinned stands (Figure 17.1 c and d).

Both thinned and unthinned trees develop a portion of the inner crown that is not foliated (Figure 17.2). The percentage of the crown volume that is unfoliated is actually very low; it ranges from about 4% of the total crown volume at age ten to about 3% at age forty. Also, the volume of crown that does not contain foliage is mostly in the lower half of the tree crown (Figure 17.2). The difference in crown shapes and inner defoliated volumes results in the leaf area being displayed in different manners for trees in the thinned and low and high SI combinations.

Trends in Total Leaf Area

The trends in total amount of leaf area per CDtree determined for the four growing regimes also varied. For CDtrees in thinned stands, leaf area increased in a curvilinear relationship with age from ten to forty years (Figure 17.3). Leaf area of the high SI CDtree in the thinned regime was 15% (age forty) to 25% (age ten) greater than on the low SI CDtree. Because of the thinnings at ages fifteen and twenty-five, leaf area index (LAI) in thinned stands was predicted to decline from age ten until age forty (Figure 17.4).

The trend in total leaf area for high and low SI CDtrees in the unthinned regime also increased in a curvilinear manner, but at a much slower rate, especially beginning at age twenty (Figure 17.3). Only slight differences in leaf area were predicted for these trees. When leaf area was projected to the stand level, LAI was found to increase until age twenty and then declined slowly until age 40 (Figure 17.4). It is probable that LAI actually peaked earlier than age twenty years, but no simulations were made between ages ten and twenty. The decline in LAI occurred at a more rapid rate for the high SI CDtrees than the low CDtrees with the largest difference in LAI between highland and low SI trees being at the intermediate ages.

Table 17.2. Aboveground Loblolly Pine Stand Structure Values from Simulation of the PTAEDA2-MAESTRO System from Ages Ten to Forty Years

Treatment	Age	Quadratic mean DBH (cm)	Mean stand height (m)	Mean dominant height (m)	Number of trees surviving (trees/ha)	Basal Area (m^2/ha)	Bole volume (m^3/ha)	Foliage biomass (t/ha)	Branch biomass (t/ha)	Bole biomass (t/ha)	Woody biomass (t/ha)	Leaf Area (m^2/ha)	Branch surface area (m^2/ha)	Bole surface area (m^2/ha)	Woody surface Area (m^2/ha)
Medium spacing,	10	11.9	7.8	8.4	1337	14.8	60.7	4.06	6.68	21.72	28.40	45691	5365	2082	7447
low/and site,	20	17.2	13.8	14.7	1223	28.3	203.6	5.96	11.78	80.25	92.03	63308	7729	4892	12621
unthinned	30	20.0	17.4	18.4	1030	32.5	291.3	5.98	12.47	122.85	135.32	61792	7562	6050	13612
	40	22.2	19.9	20.8	796	30.7	314.0	5.22	11.30	142.00	153.51	53025	6512	5931	12443
Medium spacing,	10	11.9	7.8	8.4	1337	14.8	60.7	4.06	6.68	21.72	28.40	45691	5365	2082	7447
low/and site,	20	20.5	15.2	14.7	628	20.7	164.9	4.47	9.93	60.77	70.69	47362	6119	3215	9335
thinned at ages 15	30	26.0	19.5	18.4	329	17.4	179.2	3.41	.52	70.54	79.06	35142	4688	2838	7526
and 25	40	28.4	22.3	20.8	294	18.6	228.9	3.53	9.17	96.64	105.82	35718	4786	3297	8083
Medium spacing,	10	13.4	9.5	10.2	1371	19.4	96.5	5.17	9.36	35.40	44.76	57619	7010	2941	9951
high/and site,	20	18.9	17.0	18.6	1221	34.4	304.0	6.89	14.61	123.55	138.16	72251	9007	6608	15614
unthinned	30	22.0	21.4	23.5	1001	38.0	420.6	6.61	14.56	183.07	197.63	67397	8356	7971	15328
	40	24.4	24.6	26.9	761	35.6	448.2	5.71	12.96	209.21	222.18	57197	7096	7735	14831
Medium spacing,	10	13.4	9.5	10.2	1371	19.4	96.5	5.17	9.36	35.40	44.76	57619	7010	2941	9951
high/and site,	20	24.3	19.1	18.6	445	20.7	207.0	4.35	10.91	78.52	89.42	45435	6144	3457	9600
thinned at ages 15	30	29.8	24.5	23.5	245	17.1	225.1	3.27	9.13	91.35	100.47	33245	4607	3085	7692
and 25	40	32.8	28.1	26.9	215	18.2	258.8	3.02	8.73	112.83	121.56	30134	4182	3236	7418

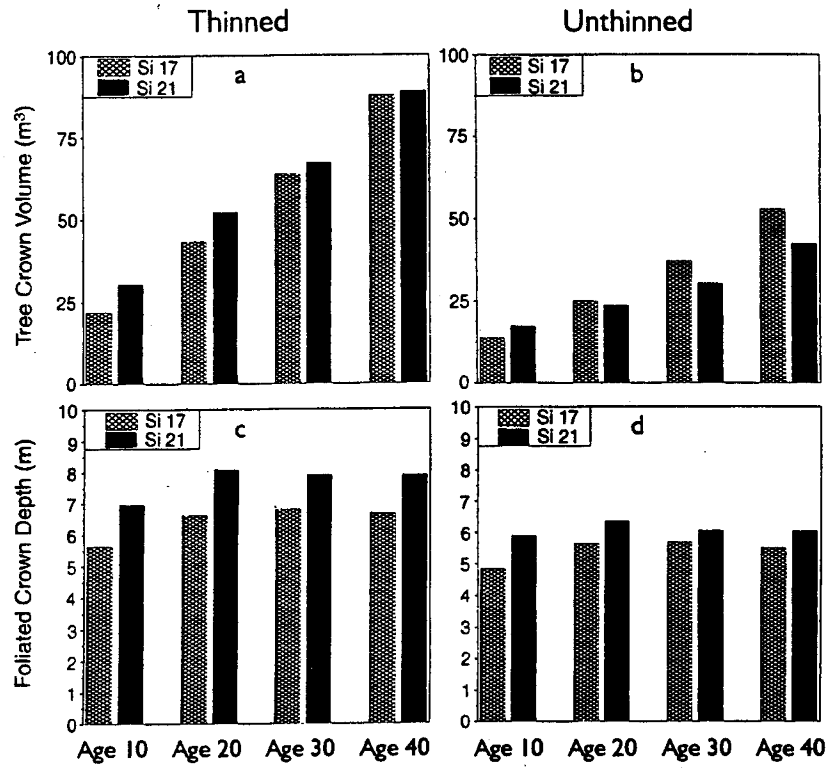

Figure 17.1. Predicted trends in crown volume and foliated crown length of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

Leaf Area Density

In general, because, high SI stands carry more leaf area than trees in low SI regimes (even though crown volume may be similar), leaf area density (LAD) has to be greater in high SI trees. The trends in CDtree LAD relative to crown volume are illustrated in Figure 17.5. Trees in thinned stands maintain a higher LAD than in unthinned stands at a given crown volume. High SI trees do have a slightly greater LAD than low SI trees, but the effect of stand density on mean tree LAD is greater than high or low SI effects on LAD at a specified crown volume.

For all SI-thinning combinations, CDtree LAD decreased with age (Table 17.1). The rate of decrease was greater in the unthinned stands. The distribution of CDtree LAD with age also changed and was different for thinned vs unthinned stands (Figure 17.6). For a given thinning regime, LAD decreased curvilinearly with age at all relative crown height positions. In the thinned regime, there were

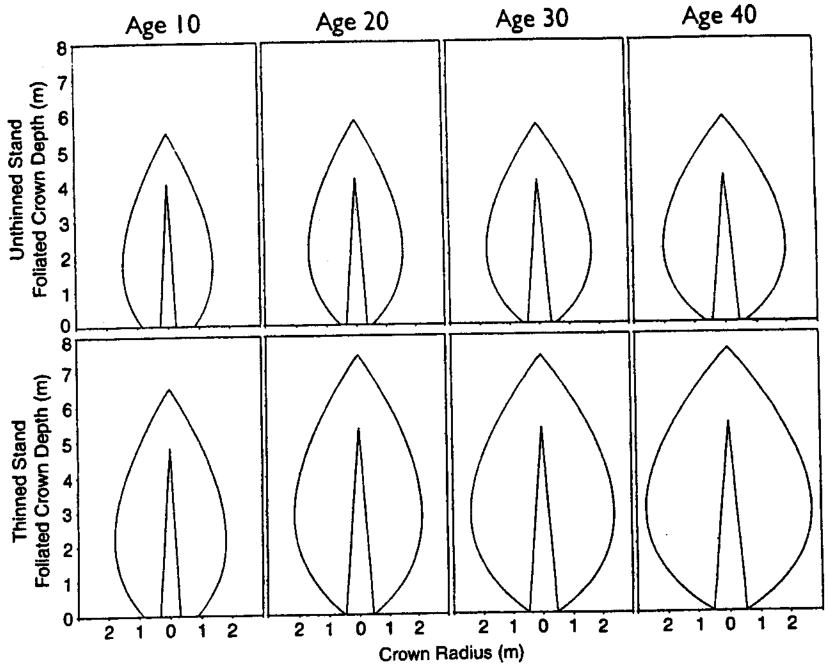

Figure 17.2. Predicted changes in crown shape over time of an example codominant-dominant loblolly pine tree in either a thinned or unthinned stand of site index equalling 16.8 m.

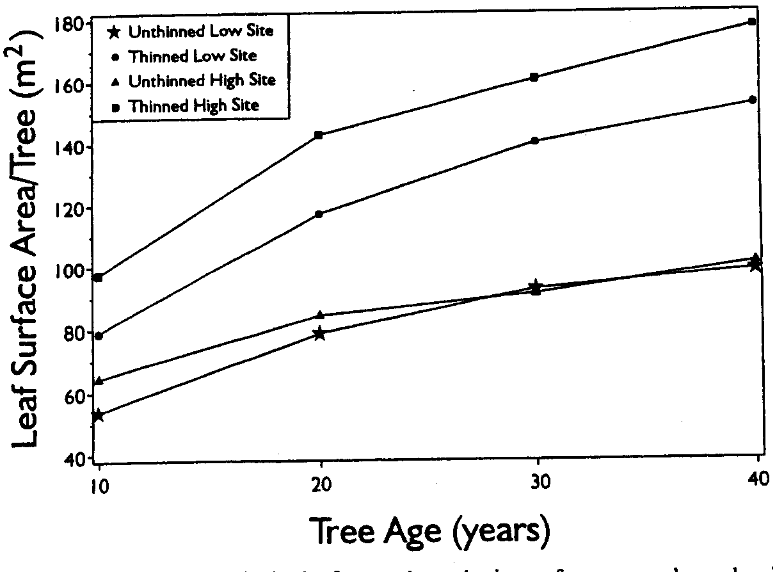

Figure 17.3. Predicted trends in leaf area through time of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

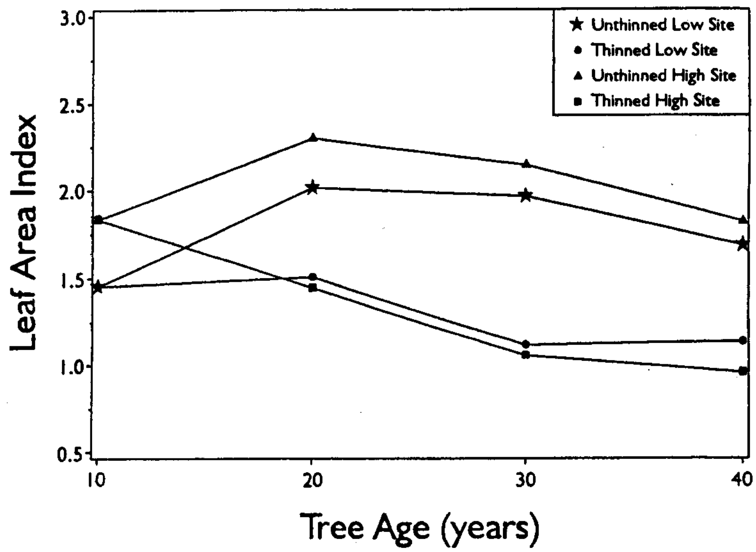

Figure 17.4. Predicted trends in stand leaf area index through time in loblolly pine stands of two site indices either thinned or unthinned.

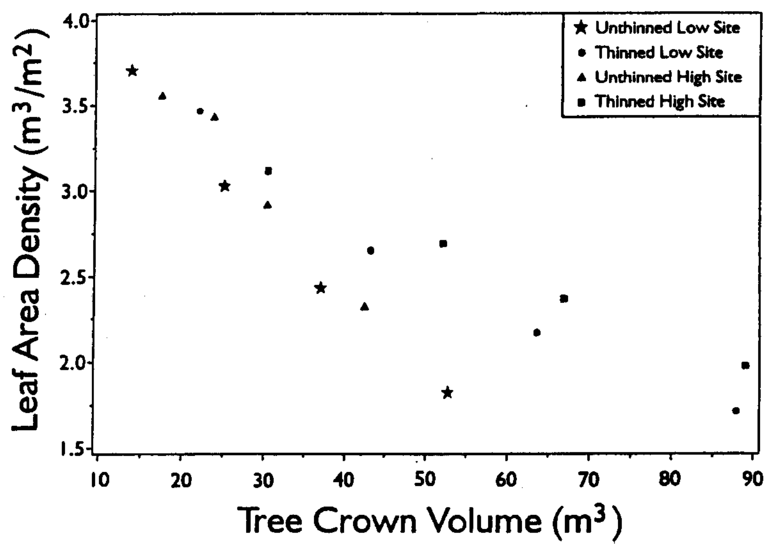

Figure 17.5. Predicted leaf area density compared to predicted tree crown volume at ages ten, twenty, thirty, and forty for an example comdominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

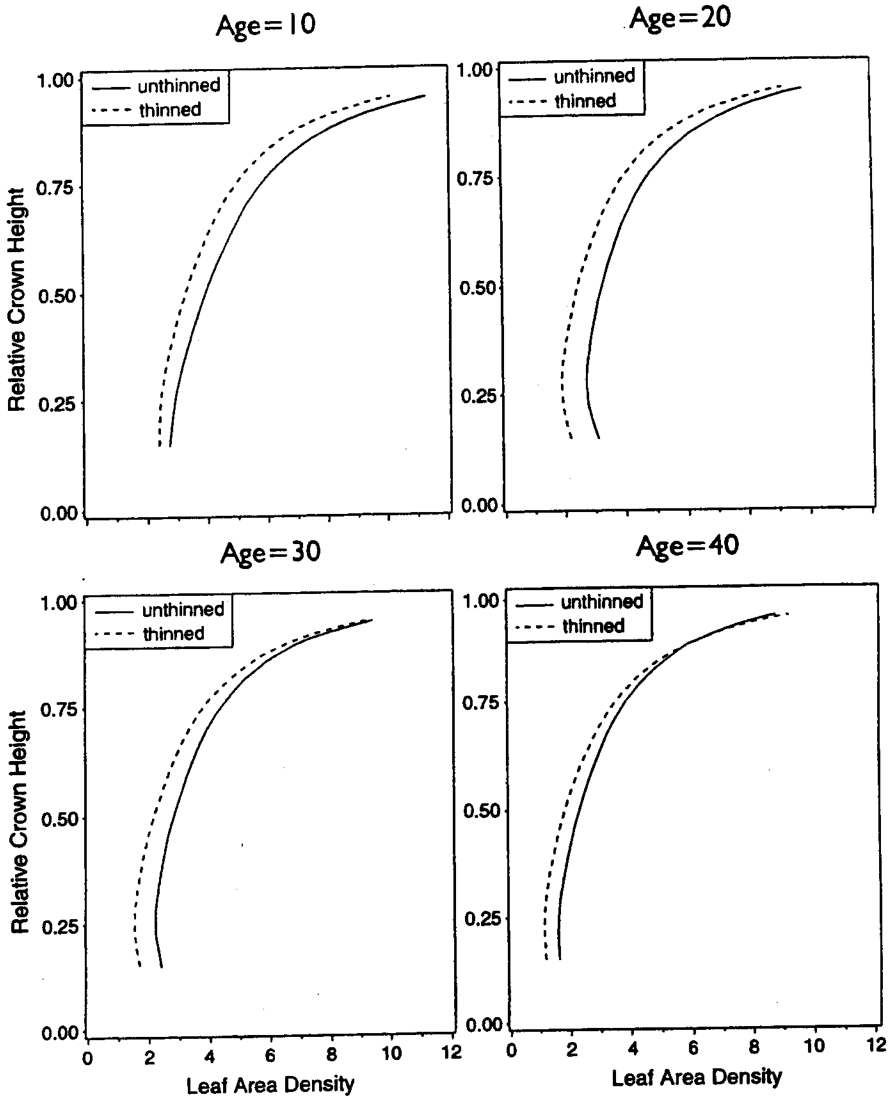

Figure 17.6. Predicted leaf area density for various relative crown heights at ages 10, 20, 30, and 40 of an example codominant-dominant loblolly pine tree in thinned or unthinned stands of site index equalling 21.3 m.

only small changes in LAD in the upper-crown after age ten; LAD in the upper-crown was approximately 10.3 m^2/m^3 at age ten and at age forty was still near 9.3 m^2/m^3. Near the lower one-quarter of the crown, LAD decreased from approximately 2.3 m^2/m^3 to about 1 m^2/m^3.

In the unthinned regime, LAD in the CDtree upper-crown changed more dramatically than in the thinned regime. Upper-crown LAD decreased from 11.5

m²/m³ at age ten (Figure 17.6) to 8.8 m²/m³ at age forty. However, LAD at the lower one-quarter relative crown height position decreased less than in the thinned regime. LAD at this crown position decreased from 2.8 m²/m³ to 1.7 m²/m³.

Trends in Branch and Bole Biomass and Surface Area

The range in branch biomass contribution to the total biomass (Figure 17.7a, b) across all four SI-thinned CDtree combinations considered was 19 to 24% at age ten. By age forty, the range in the percentage of the total biomass made up of branches was only 5 to 8%. This relationship indicates that on a biomass basis, branches are a minor component. However, this is not true on a surface area basis.

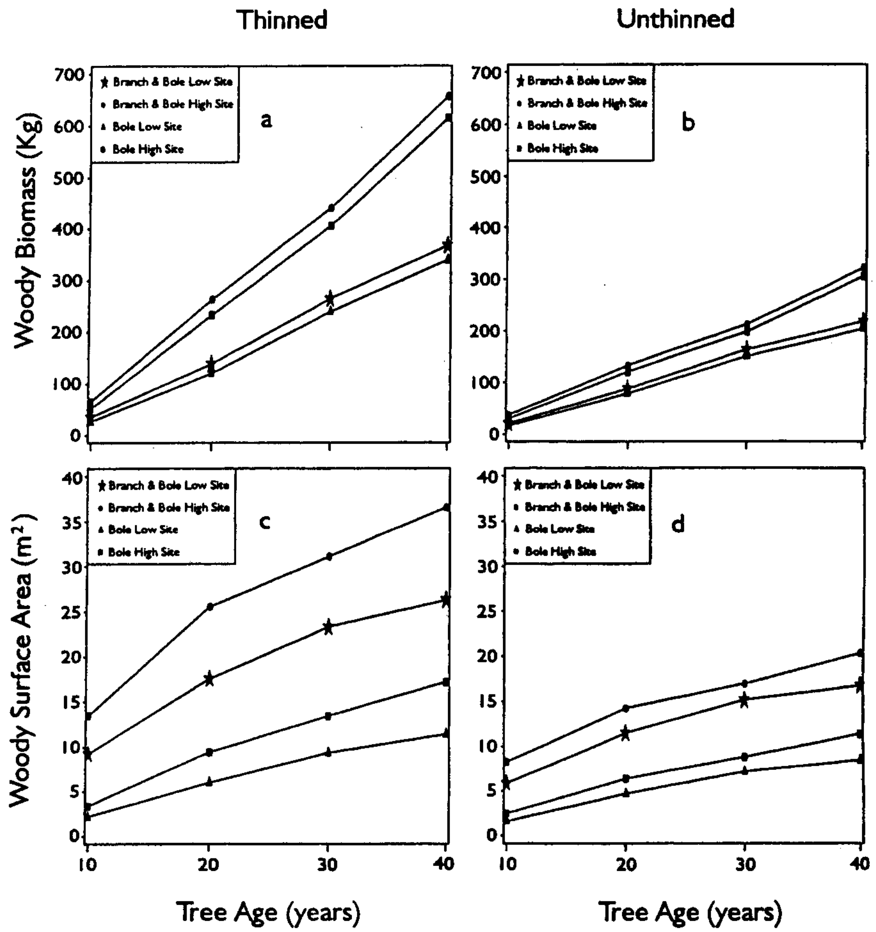

Figure 17.7. Comparison of predicted woody tissue weight and predicted surface area over time of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

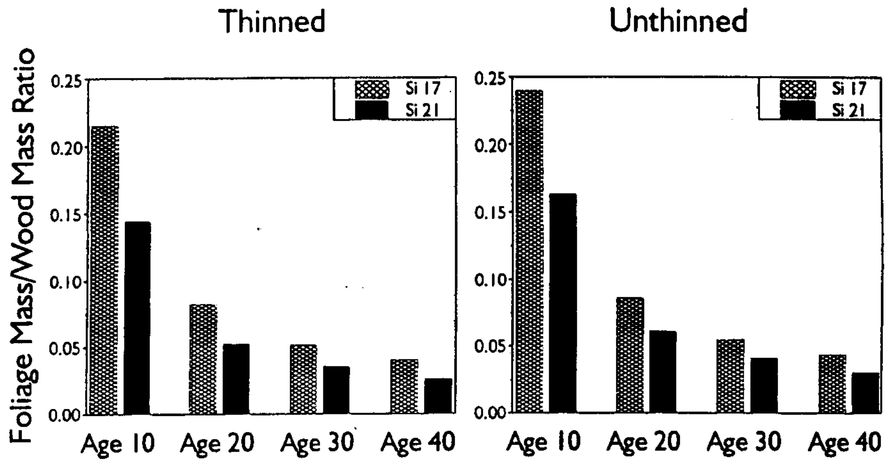

Figure 17.8. Trends over time of the ratio of predicted foliage biomass to predicted woody tissue biomass of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

The trends in CDtrees branch and bole surface areas are illustrated in Figure 17.7d, c. In the thinned regime at age ten, bole surface area constituted about 24 to 35% of the total CDtree aboveground woody tissue surface area (branch and bole) irrespective of SI class. By age forty, bole surface area was 43% (low SI) to 70% (high SI) of the total CDtree aboveground woody tissue surface area. Similar trends were predicted for the unthinned regime. However, bole surface area at all ages constituted a slightly greater percentage of the CDtree total surface area in unthinned stands. At age ten, the contribution of bole surface area to the total CDtree aboveground surface area was 4 to 6% greater in the unthinned than in the thinned regime and by age forty the difference was 8 to 9%. These predictions indicate a greater amount of branch material is developed and retained in the thinned regime.

Ratio of Photosynthetic Tissue to Woody Tissue

One of the greater differences between seedlings and trees is the ratio of foliage biomass to woody tissue biomass. At the seedling stage, this ratio is near 1.0. As can be seen in our simulations, this ratio changes rapidly with age (Figure 17.8). By age ten, the ratio of foliage biomass to woody tissue biomass is between .2 and .25 for the lower SI and approximately .15 for the high SI CDtrees. The rapid drop in the ratio of foliage biomass to woody biomass continued to age twenty and then decreased slowly thereafter. By age forty, this ratio was less than 5% in all cases.

Trends in the Ratio of Foliage Surface Area and Woody Tissue Surface Area

Similar trends to those observed for foliage weight to woody tissue biomass were also apparent for the trends in foliage surface area to woody surface area ratio

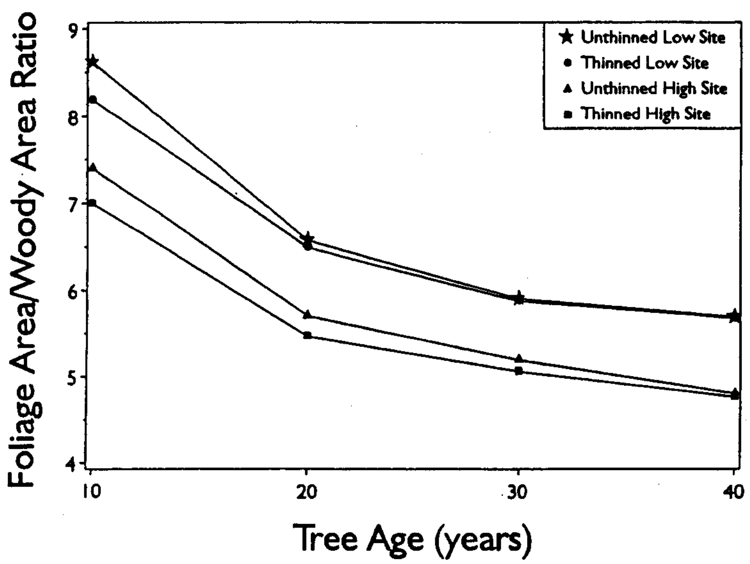

Figure 17.9. Trends over time of the ratio of predicted foliage surface area to predicted woody tissue surface area of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

(Figure 17.9). High SI CDtrees had slightly lower ratios than low SI CDtrees. One surprising difference in the surface area vs weight ratios is that the CDtrees in the unthinned stands appeared to maintain a greater "equilibrium" foliage surface area to woody surface area from age thirty to forty than the CDtrees in the thinned stand with unthinned trees having a ratio of only 4.8. This was apparently related to the larger size and perhaps greater number of developed branches on the thinned trees than on the unthinned trees.

Trends in Canopy Carbon Gain and Maintenance Respiration

The effects of the structural changes in trees related to age, SI, and thinning, on crown assimilation, total tree maintenance respiration, and net annual carbon gain (crown carbon gain minus total tree respiration) are shown in Figure 17.10a–f. Carbon gain increased at all ages for the CDtrees in the thinned scenario. Carbon gain of the CDtree in the high SI thinned regime had 40% greater carbon gain at age ten and 47% greater carbon gain at age forty than the low SI CDtree in the thinned regime. This gain occurred even though CDtree crown volumes in the thinned regime were actually greater for the low SI regime. However, total surface leaf area was 24% greater at age ten and 17% greater at age forty in the high SI vs low SI regime. Thus, LAD was greater in the thinned CDtree crowns (Figure 17.5) than in low SI CDtrees.

Crown assimilation in the unthinned regime increased with age for both the high and low SI CDtrees. Differences in crown carbon gain for high and low SI CDtrees in the unthinned regime were small (Figure 17.10b). This small differ-

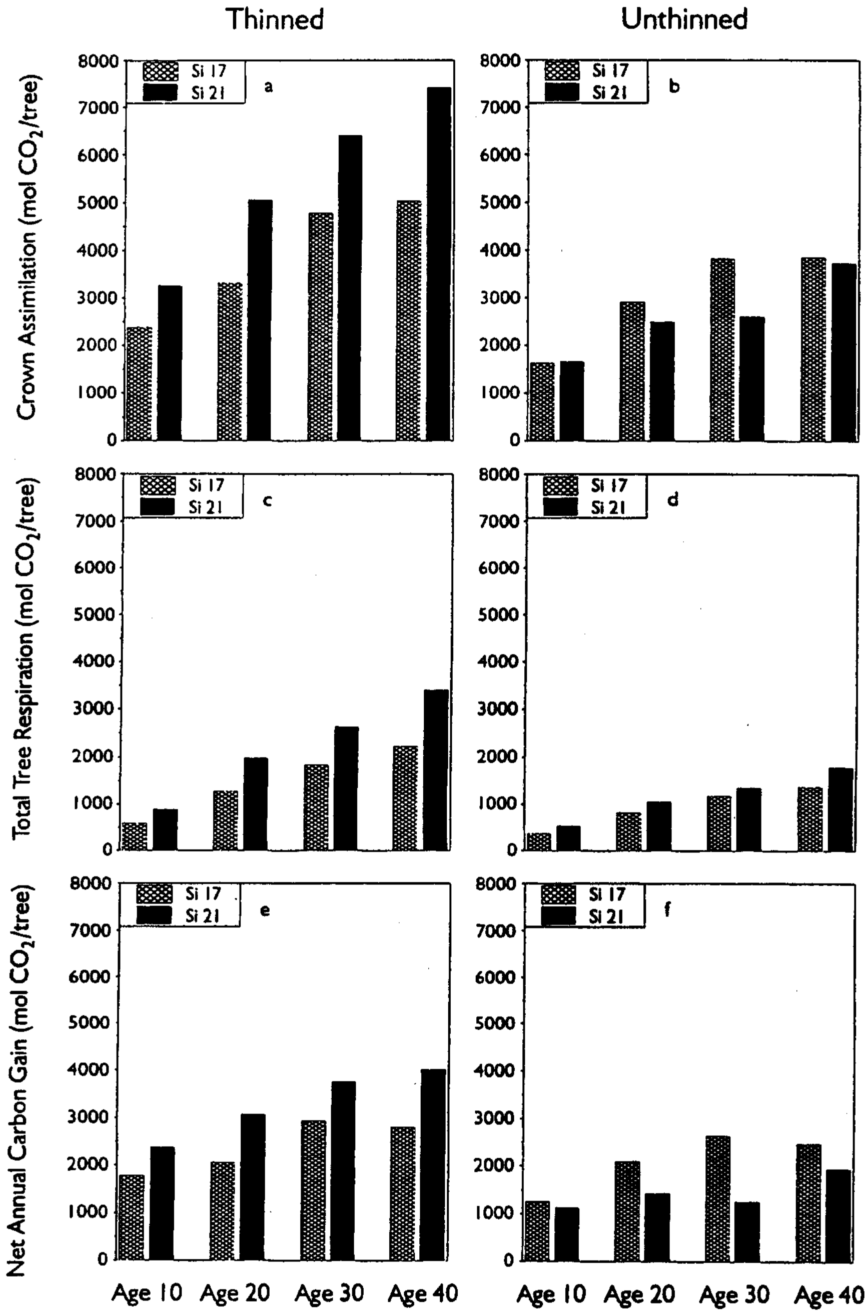

Figure 17.10. Predicted trends through time of total crown carbon assimilation, total tree maintenance respiration, and net annual carbon gain of an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

ence occurred because both the total leaf area per tree (Figure 17.3) and LAD (Figure 17.5) for unthinned trees was about the same, irrespective of SI class. Thus, the reduction in crown carbon gain as a result of not thinning was much greater for the CDtree in the high SI regime than in the low SI regime (contrast Figure 17.10a–c). Crown carbon gain per CDtree was about 50 to 57% more in the thinned regime than in the unthinned regime for the SI-50 CDtree, and 47 to 100% more in the thinned SI-70 CDtree than in the unthinned SI-70 CDtree. In fact, the thinned SI-50 CDtree was estimated to have greater crown assimilation than the unthinned SI-70 CDtree.

Trends in Total Tree Maintenance Respiration

Annual total CDtree maintenance respiration in the thinned regime increased almost linearly with age. The thinned SI-70 CDtree at all ages had higher respiration than the thinned SI-50 CDtree (Figure 17.7c, d). Total tree respiration in the unthinned plots was much lower than that in the thinned plots. The difference in respiration between the high SI CDtree and the low SI CDtree was also less than that determined for the similar trees in the thinned regime. At age ten, the total tree respiration for the CDtree in the SI-50 thinned regime was estimated to be 45% greater than the CDtree in the SI-50 unthinned regime. At age forty, this difference had increased to 63%. At age 10, total tree respiration of the thinned SI-70 CDtree was predicted to be 70% more than the unthinned SI-70 CDtree. This difference at age forty was estimated to be 91%. Thinning was clearly the major factor that influenced individual tree respiration cost.

Trends in Tree Net Annual Carbon Gain

The major factor that affected the trend in annual carbon gain was whether the stand was thinned or not. In the thinned scenario, the SI-70 CDtree maintained a more favorable annual net carbon gain than the SI-50 CDtree. In the unthinned regime, annual net carbon gain of the individual CDtrees in the high or low SI classes was not consistently different. This trend apparently resulted because at each age, foliage surface area of unthinned high and low SI trees were about the same (Figure 17.3) and the woody biomass component was predicted to be less for the low SI CDtree than for the high SI CDtree (Figure 17.7d). This combination of structural characteristics resulted in net carbon gain of the low SI CDtrees being about equal or slightly greater at most ages evaluated. In MAESTRO, the unit rates of photosynthesis and respiration do not vary by SI class.

Trends in Mean Annual Increment

To estimate mean annual increment (MAI) for the CDtrees in the four SI-thinning combinations, PTAEDA2 was used. In the thinned regime, SI had a large positive effect on MAI at all ages evaluated (Figure 17.11). CDtree MAI increased in the thinned scenario from age ten to age forty but only at a slow rate after age twenty. This result is important because crown volume, which is one of the major factors

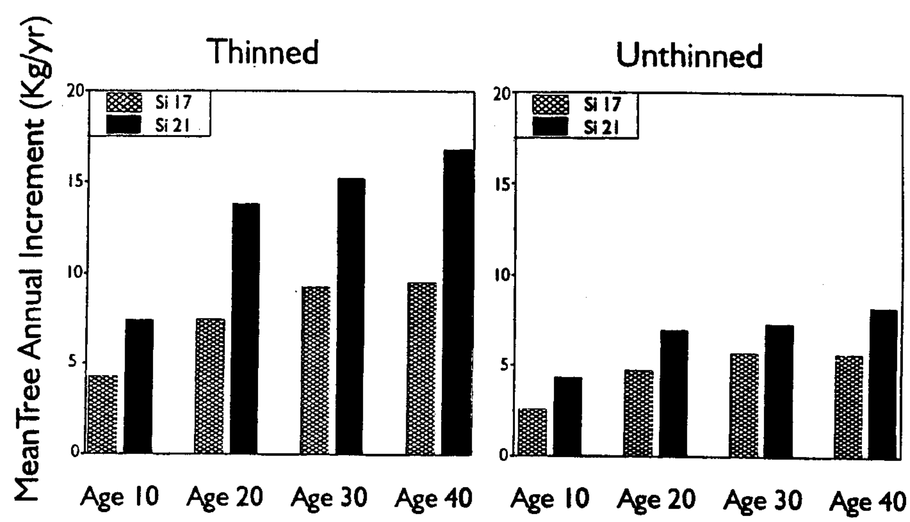

Figure 17.11. Trends of predicted mean annual woody biomass increment for an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned

that determines an individual tree's growth potential in PTAEDA2, increased linearly with age and was not very different for the high and low SI categories.

A similar trend in CDtree MAI was observed for the unthinned scenario as for the thinned scenario. However, MAI was about one-half of what is was in the thinned regime. Even though low SI CDtree crown volume was actually larger in the unthinned regime than for high SI CDtree, PTAEDA2 predicted that MAI would be greater for the high SI CDtree (Figure 17.11).

Relationship of Crown Annual Net Carbon Gain and Yield

If annual net carbon gain is allocated in a fixed ratio to stemwood production there should be a linear relationship between yield estimates made with PTAEDA2 and net carbon gain estimates made with MAESTRO. As shown in Figure 17.12, the relationship between yield and annual net carbon gain was linear. However, there was considerable variation in the relationship. This result suggests that a fixed allocation coefficient may not be correct.

Discussion and Conclusions

The objectives of this chapter were to show the value of linking a growth and yield model (PTAEDA2) with a process model (MAESTRO) to better understand the effects of tree and stand structure changes over time on tree and stand functioning. This objective was accomplished in two steps. First, by using stand-density man-

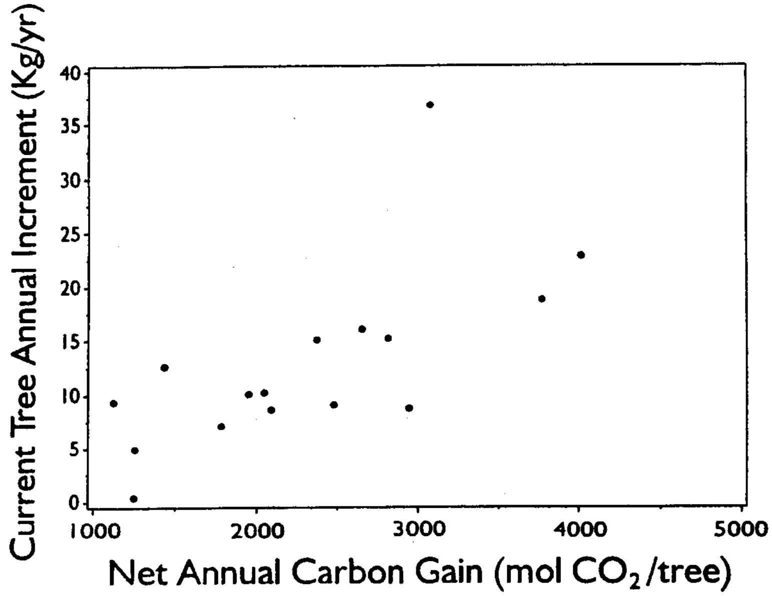

Figure 17.12. Predicted present-day annual woody biomass yield compared to predicted net annual carbon gain at ages ten, twenty, thirty, and forty for an example codominant-dominant loblolly pine tree in stands of two site indices either thinned or unthinned.

agement, the effects of stand structure changes on individual tree structure were predicted using PTAEDA2. Second, the effects of the resulting tree structure changes on various tree functions or physiological processes were presented. The results with a minimum of discussion all were presented in prior sections; several of these results are further discussed in this section.

This analysis showed that age, SI, and thinning affect many crown features that are important for predicting tree physiological functioning. Crown features altered by age, SI, and thinning include 1) total leaf area per tree, 2) mean crown leaf area density, 3) leaf area density distribution, 4) crown length, and 5) the nonfoliated fraction of the crown volume. In a prior study, Baldwin et al., (1993) demonstrated that vertical and horizontal leaf area distributions are affected both by age and stand density. Although some of these crown-structure changes may only have minor effects on net carbon gain, collectively the effect on light interception may be substantial. Cropper et al., (1996) evaluated potential effects of changing loblolly pine foliage distribution model from a Beta function to a truncated Weibull function that reflects the changes in the distribution parameters as a result of stand development (Baldwin et al., 1997). The impacts on annual net carbon assimilation varied by tree size—small trees exhibited a 9% reduction in carbon assimilation relative to that estimated with the Beta function. Larger trees exhibited a 30% increase in annual carbon assimilation with the new foliage distribution function relative to the Beta function. These results therefore demonstrate that having accurate descriptions of crown-structure characteristics is important.

Wang and Jarvis (1990b) used MAESTRO to evaluate the importance of various crown-structure properties of a Sitka spruce (*Picea sitchensis* (Bong.) Carr.) tree crown with respect to the absorption of photosynthetically active radiation, photosynthesis, and transpiration. Their results suggested that total tree leaf area and LAD are the crown-structure characteristics that have the greatest effect on light absorption. In the future, it is probable that accurate descriptions of crown structure with respect to potential carbon gain will be even more important, because under elevated levels of atmospheric CO_2 the potential for increased carbon assimilation will be greatly enhanced. However, the amount of enhancement appears to be closely related to the amount of photosynthetically active radiation that the foliage receives. Thus, more accurate descriptions of light distribution within the crowns of trees will be needed.

In temperate ecosystems, it is equally important to accurately describe tree-structure properties that affect maintenance respiration cost because maintenance respiration can consume more than 60% of gross primary productivity in pines (Ryan et al., 1994). This study clearly indicates that large differences in woody tissue maintenance respiration are apt to result if respiration is expressed as a function of woody surface area rather than as a function of woody biomass. The latter relationship increases in a linear fashion with age, whereas woody tissue surface area increases in a curvilinear manner (Figure 17.7a–c). Thinning also appears to substantially alter the ratio of foliage surface area to woody tissue surface area (Figure 17.9).

Maintenance respiration as a function of woody tissue surface area, foliage surface area, and root biomass is predicted by MAESTRO, but this system does not account for foliage, branch, and bole component variations in tissue nitrogen concentration, or that respiration rates may vary by two-fold depending on the nitrogen concentration of the tissue (Dougherty et al., 1996). Additionally, it is probable that all tissue components in high SI trees would have a higher nitrogen concentration than those of trees in a low SI stand. However, the combined effects of SI and thinning on woody tissue and photosynthetic tissue amounts and distribution ultimately determines the potential maintenance respiration cost, and carbon gain, and therefore, the net annual carbon gain and growth potential.

One important conclusion from this study is the overriding effect of thinning in determining annual net carbon gain. Thinnings were much more influential in the determination of individual tree annual net carbon gain than SI. This result was especially noticeable at the older ages evaluated, and should be considered seriously by those agencies responsible for maintaining "healthy forests."

It has been shown that as a research tool, the linked PTAEDA2–MAESTRO system allows those microeffects on stand structure and function to be considered that would have been impossible to predict using stand-process models. The ability of the linked model to predict changes in characteristics of individual trees was the desired objective of this system, even though hundreds of simulations and summarizations would be required to obtain stand averages. Several crown characteristics of loblolly pine needed as inputs to MAESTRO can now be predicted from PTAEDA2 for trees grown under a wide range of conditions. These changes replace the need for user input of several measures into MAESTRO and the linked model may now be used to assess the impacts of ozone, weather, or CO_2 regimes on carbon gain, respiratory demand, carbon storage, and growth trends. Some of these applications are demonstrated in the next chapter.

References

Baldwin VC Jr, Burkhart HE, Dougherty PM, Teskey RO (1993) Using a growth and yield model (PTAEDA2) as a driver for a biological process model (MAESTRO). Research Paper SO-276, US DOA, For Ser, South For Exper Sta. New Orleans, LA.

Baldwin VC Jr, Peterson KD (1997) Predicting the crown shape of loblolly pine trees. Can J For Res. 27:102–107.

Baldwin VC Jr, Peterson KD, Burkhart HE, Amateis RL, Dougherty PM (1997) Equation for estimating loblolly pine branch and foliage weight and surface area distributions. Can J For Res 27:918–927.

Baldwin VC Jr, Peterson KD, Simmons DR (1995) A program to describe the crown shape of loblolly pine trees. Compiler 13:17–19.

Burkhart HE, Farrar KD, Amateis RL, Daniels RF (1987) Simulation of individual tree growth and stand development in loblolly pine plantations on cutover, site-prepared areas. FWS-1–87, Virginia Polytechnic Institute and State University, School of Forestry and Wildlife Resources, Blacksburg, VA.

Cropper WP Jr, Gholz HL (1991) In situ needle and fine root respiration in mature slash pine (*Pinus elliottii*) trees. Can J For Res 21:1589–1595.

Dougherty PM, Hennessey TC, Zarnoch SJ, Stenberg PT, Holeman RT, Wittwer RF (1995) Effects of stand development and weather on monthly leaf biomass dynamics of a loblolly pine (*Pinus taeda* L.) stand. For Ecol Manage 72:213–227.

Dougherty PM, Oker-Blom P, Hennessey TC, Witter RE, Teskey RO (1990) An approach to modelling the effects of climate and phenology on the leaf biomass dynamics of a loblolly pine stand. Silv Carel 15:133–143.

Gholz HL, Vogel SA, Cropper WP Jr (1986) Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliottii*) in north Florida. Can J For Res 16:529–538.

Jarvis PG, Barton CVM, Dougherty PM, Teskey RO, Massheder JM (1991) MAESTRO. In Irving PM (Ed) *Acid deposition: state of science and technology. Vol. 3. Terrestrial, materials, health, and visibility effects.* National Acid Precipitation Assessment Program, Government Printing Office, Washington, DC.

Landsberg JJ (1986) *Physiological ecology of forest production.* Academic Press, London.

Ryan MG, Linder S, Vose JM, Hubbard RM (1994) Dark respiration of pines. In Gholz HL, Linder S, McMurtrie RE (eds) *Environmental constraints on the structure and productivity of pine forest ecosystems: a comparative analysis.* Ecol Bull (Copenhagen) 43:50–63.

Teskey RO, Fites JA, Samuelson LJ, Bongarten BC (1986) Stomatal and nonstomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. Tree Physiol 2:131–142.

Vose JM, Allen HL (1988) Leaf area, stemwood growth, and nutrition relationships in loblolly pine. For Sci 34:547–563.

Wang YP, Jarvis PG (1990a) Description and validation of an array model-MAESTRO. Agri & For Meteorol 51:257–280.

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