# Modeling intra-crown and intra-canopy interactions in red maple: assessment of light transfer on carbon dioxide and water vapor exchange

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**Summary** Daily and seasonal net photosynthesis ($A_{net}$), transpiration ($E$), absorbed photosynthetically active radiation ($Q_a$) and light-use efficiency ($\varepsilon_c$) in a red maple container nursery were simulated with MAESTRA, a three-dimensional canopy model. Effects of canopy heterogeneity were simulated by imposing changes in crown spacing. The light transfer sub-model, a distribution model of incident, direct, diffuse and scattered radiation within MAESTRA, was validated against field measurements of light interception on an intra-crown scale. In the container nursery, we found that a fiber-optic-based method of integrating photosynthetically active radiation ($Q$) was more suitable for crown-layer light transfer measurements and adjustments than either orthogonal line or individual quantum sensor measurements. The model underestimated intercepted $Q$ by 9.3, 18 and 11.1% for crown layers 1, 2 and 3, respectively; however, there were linear relationships between model estimates and observations made with each of the three measurement methods. We used the validated and parameterized light transfer model to assess intra-crown and intra-canopy light transfer on a layer, crown and canopy basis, and investigated effects of tree size ratio and tree spacing interactions on $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ in the container nursery. Heterogeneous crown and canopy photosynthesis were predicted to exceed values for a uniform canopy under space-limiting conditions. Tree size ratio had large effects on $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ when light to lower-canopy layers was limited by inadequate space between crowns. Increasing $Q_a$ at lower-crown layers had the largest impact on whole-crown and whole-canopy $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$. Increases in canopy productivity led to increased water use. Simulations of heterogeneous stands with adequate soil water indicated that light absorption is maximized under space-limiting conditions as a canopy crown moves toward heterogeneity. Nursery and plantation productivity per unit land area was optimized by tactical placement of trees of several sizes, but this was accompanied by increased canopy water use.

*Keywords: light interception, light-use efficiency, modeling.*

## Introduction

When water and nutrients are plentiful, light intercepted by the canopy is the primary factor limiting biomass production during the active growing period (Landsberg et al. 1996, Ong et al. 1996, Ceulemans and Daraedt 1999). Distances between crowns within a canopy can influence photosynthetically active radiation ($Q$) interception, photosynthesis ($A$) and transpiration ($E$) (e.g., Grace et al. 1987, Wang and Jarvis 1990*a*). Although it is known that competition for sunlight results in suboptimal growth under field conditions, much remains to be learned about the fundamental biophysical processes and interactions (Carter et al. 1989, Wang and Jarvis 1990*a*, Ong et al. 1996).

Various models have been developed to describe the interception of radiation by horizontally heterogeneous canopies. Detailed measurements of radiation interception are essential in order to parameterize such canopy models; however, the spatial and temporal variations of the radiation regime are difficult to measure during short time periods (Wang and Jarvis 1990*a*, Ong et al. 1996). The complex nature of crown structure has led to the use of simulation models for characterizing the responses of leaves, crowns and canopies to the environment (e.g., Wang and Jarvis 1990*b*, Knyazikhin et al. 1994, Baldocchi and Harley 1995, Rayment et al. 2002). Carbon and water exchange models have been verified at the leaf (Farquhar and von Caemmerer 1982, Collatz et al. 1991, Harley et al. 1992), individual tree (Wang and Jarvis 1990*a*, Bauerle et al. 2002) and canopy levels (Ogink-Hendriks 1995, Bosveld and Bouten 2001, Bauerle et al. 2002). Once validated, the next step in maximizing the productivity of agricultural and forest resources is to use models as a guide to ways of maximizing light-use efficiency and minimizing transpiration.

Although differing in canopy architecture from that of a heterogeneous forest stand, a container nursery provides a good system for validating and utilizing complex canopy models because it minimizes variation in canopy crown architecture.

For example, the use of trees in containers allows control over both their number and spacing at the outset and during an experiment, for example, to compensate for canopy development. Because the shapes of individual tree crowns are managed to conform to the requirements of the trade in ornamental nursery stock (e.g., ellipsoidal, paraboloidal, conical), container nursery canopies can be made up of trees with a specific and uniform crown shape. Furthermore, the space allocated between plants is predetermined and consistent (validating the assumption of a uniform stocking density), and the roots are contained, eliminating root interactions. Lastly, genetically similar plant material, or genetically identical clonal material, is grown within a nursery block, minimizing the effects of genetic control on canopy architecture and leaf angle distribution.

Despite the importance of maximizing resource capture and production in agro-ecosystems, there is little published information on the extent and consequences of crown interactions in nursery systems. There have been no studies on the use of a three-dimensional radiation transfer model under container nursery conditions or on the influence of controlled canopy heterogeneity within a managed nursery or plantation stand. Moreover, the influence of tree distribution on the light environment of a stand as a whole has not been studied extensively (Oker-Blom and Kellomäki 1983). We used the canopy model MAESTRA (Medlyn et al. 1999), an updated version of MAE-STRO (Wang and Jarvis 1990*a*, 1990*b*) incorporating the radiative transfer model of Norman and Welles (1983), which allows investigation of radiation interception through the canopy, and treats individual trees as discrete blocks. The model is suitable for intensively managed nurseries, where spacing is manipulated as much as three times annually and several sizes of plants exist within the same species at any one time.

Our objectives were to: (1) validate model estimates of $Q$ against measured values; (2) parameterize MAESTRA and analyze its ability to optimize $CO_2$ and $H_2O$ exchange in an *Acer rubrum* L. (red maple) container nursery; and (3) investigate intra-crown and intra-canopy interactions in a container nursery to test the hypothesis that heterogeneous distribution of crowns within a nursery block increases photosynthesis, water vapor exchange, absorption and efficiency in the use of $Q$ ($\varepsilon_c$). We also simulated the effects of distance and heterogeneity on intra-crown and intra-canopy net photosynthesis ($A_{net}$), $E$ and $\varepsilon_c$. Water vapor exchange model parameters were derived from substrate and leaf-scale measurements and validated against whole-plant flux data at ambient atmospheric $CO_2$ concentration (Bauerle et al. 2002). A fundamental understanding of how nursery systems utilize available sunlight is critical in determining optimal planting arrangements, tree densities and management strategies. In addition, the form and function of a model system may prove useful for deriving inferences about managed forest systems, forest system functioning, and natural heterogeneous forest stands.

## Materials and methods

The study was conducted at the Clemson University Calhoun Field Laboratory site in Clemson, South Carolina, USA, during 2001–2002. A full description of the site is given in Bauerle et al. (2002). Here we describe the validation of the light transfer sub-model of MAESTRA and detail some simplifications and adjustments that were made before running MAESTRA.

### Fiber optic Q validation measurements

We validated the light transfer portion of the model by measuring crown light interception at each layer of the crown boundary with multimode fiber optic bundles as described by Bauerle and Bowden (2004). To measure $Q$ interception with fiber optics, three trees were each fitted with a Corning optical cable. Four sets of 12 micro-fibers per cable were placed at the boundary edge of each of the three crown layers per tree in a spherical leaf angle orientation and fanned out to face each cardinal direction. Each micro-fiber was fastened to, and supported by, a 7-mm-diameter wooden dowel secured to the main stem with plastic fasteners. In sum, this arrangement integrated irradiance at 48 interception points (each 62.5 μm in diameter) per crown layer. All sensors sampled every minute and logged a 15 min mean (CR7X, Campbell Scientific, Logan, UT).

The sub-model of Norman and Welles (1983) simulated $Q$ interception. The model calculates mean intercepted solar radiant energy per square meter in the $Q$ and near infrared (NIR) wave bands. The model accounts for radiation scattering, proportion of direct and diffuse incoming radiant energy and sun position. Outputs from the model are intercepted $Q$ and NIR, and $Q_a$ averaged over a grid of points on a canopy layer basis. Because photosynthetic rate is related to intercepted $Q$, we followed the methods of Grace et al. (1987); however, we estimated intercepted $Q$ from incoming $Q$ on a 15 min time scale. To determine the applicability of the model, intercepted $Q$ estimates were plotted against field measured fiber optic, quantum sensor and line sensor values (Figure 1). Field measurement techniques were similar to those described by Grace et al. (1987), but we also employed an orthogonal grid of line sensors and fiber-optic-integrated $Q$ measurement techniques as described in (Bauerle and Bowden 2004).

### Model structure and parameterization

We parameterized MAESTRA, a three-dimensional model for calculating $Q_a$, for the site of a red maple container nursery near Clemson, SC, USA (34°40′8″ N, 82°50′40″ W). Model structure and parameterization followed that of Luo et al. (2001) as modified by Bauerle et al. (2002), based on a 15-min time step. Briefly, the positions and dimensions of the trees surrounding those in which $Q$ interception was measured were used to calculate radiation extinction after passing through the neighboring tree canopies, where the canopy is represented by an array of ellipsoidal tree crowns that takes into account the total leaf area of neighboring sub-volumes and trees, and average leaf angle distribution and clumping. Intercepted and absorbed radiation were calculated for each crown in this study as described in Wang and Jarvis (1990*b*), where the crown was divided into three layers, resulting in 12 sectors of 30° with

each layer forming 36 equal sub-volumes. Specific to crown-level estimates of $Q$ interception, the model input radiation was $Q$, and NIR and thermal radiation were estimated from $Q$ as described by Wang and Jarvis (1990b).

In MAESTRA, leaf angle distribution is ellipsoidal (Campbell 1986). The crown was assumed to have a spherically symmetric leaf angle distribution (standard canopy) in all simulations. The extinction coefficients for both direct beam and diffuse radiation were accounted for by the zenith angle or angles of the sun for both direct and diffuse solar radiation. The path length of radiation reaching each grid point was calculated from the size and shape of the tree crowns through which the radiation passed, and the distribution of leaf area within them. Beer's Law was applied to each path length of either direct or diffuse radiation intercepted on a grid point. Direct and diffuse radiation were treated separately, where transmission of diffuse $Q$ was handled by the method developed by Norman (1979). Multiple scattering was calculated by the method of Norman and Welles (1983). We calculated $Q_a$ by summing the sub-volumes, and leaf reflectance and transmittance values were determined with an integrating sphere and used to parameterize for $Q_a$ (Bauerle et al. 2004). Canopy $\varepsilon_c$ was calculated as net photosynthesis ($A_{net}$) per unit $Q_a$ (Medlyn 1998):

$$\varepsilon_c = A_{net}/Q_a \qquad (1)$$

where $\varepsilon_c$ represents all of the photosynthetic and respiratory processes.

*Leaf physiological properties*  The physiological parameter values used in the model are listed in Table 1. We used the parameters for the Farquhar and von Caemmerer (1982) photosynthesis model determined by Bauerle et al. (2003a) and the red maple stomatal conductance parameters for the Ball-Berry model determined by Bauerle et al. (2002). Dark respiration

Table 1. The physiological parameters of the red maple leaves used in MAESTRA estimated at a leaf temperature of 25 °C. Maximum rate of carboxylation ($V_{cmax}$), estimates of the maximum rate of ribulose-1,5-bisphosphate (RuBP) regeneration ($J_{max}$), dark respiration ($R$), the curvature of the light response of RuBP regeneration (θ), day respiration ($R_{day}$), leaf transmittance ($T_{leaf}$) and leaf reflectance ($R_{leaf}$). The Ball-Berry model (Ball et al. 1987) parameters are stomatal conductance when the irradiance tends to zero ($g_0$) and the slope ($g_1$).

| Parameter | Value |
|---|---|
| $V_{cmax}$ ($\mu$mol m$^{-2}$ s$^{-1}$) | 77.3 |
| $J_{max}$ ($\mu$mol m$^{-2}$ s$^{-1}$) | 189.1 |
| $R$ ($\mu$mol m$^{-2}$ s$^{-1}$) | 1.7 |
| θ | 0.7 |
| $R_{day}$ ($\mu$mol m$^{-2}$ s$^{-1}$) | 1.0 |
| $T_{leaf}$ (%) | 5.1 |
| $R_{leaf}$ (%) | 9.2 |
| $g_0$ ($\mu$mol m$^{-2}$ s$^{-1}$) | 0.0 |
| $g_1$ | 5.5 |

rates were taken from Bauerle et al. (2003b) for wet-site red maple ecotypes.

MAESTRA requires that the canopy be described at the individual crown level, where photosynthetic radiation response of a "target crown" depends on crown structure and the distribution of irradiance over the crown. The position of each tree in the stand is known and accounted for by a Cartesian coordinate system. To integrate $Q_a$ over temporal and spatial distributions of irradiance, each crown layer is treated as unifacial and the assimilating leaf area is defined as a one-sided area. To investigate the photosynthetic crown layer response function ($P_l$) on an individual crown layer basis, we modified the Oker-Blom (1985) shoot photosynthesis equation to characterize a crown layer $P_l$,

$$P_l = 1/A_l \int_{A_1} P_n(Q(r))dr = \int_0^{Q_{max}} P_n(Q)dF_n(Q) \qquad (2)$$

where $A_l$ denotes total leaf surface area of the layer and $F_n$ is the distribution function of $Q$ over $A_l$. Hence, the $Q$ measurement strategies allowed us to parameterize the model on a crown layer basis and investigate intra-crown responses. To integrate over temporal and spatial distributions of irradiance, where response to irradiance is assumed an invariant photosynthetic response (Stenberg et al. 1995), mean rate of crown photosynthesis ($P_c$) during a time period ($T$) was expressed as:

$$P_c = \int_0^{Q_{max}} P_n(Q)dF_{n,T}(Q) \qquad (3)$$

where $F_{n,T}$ is the distribution function of $Q$ at the crown layer surface during the given time period. For our study, $Q_a$ at the crown layer is the basic operational unit in modeling crown photosynthesis and water vapor exchange.

*MAESTRA application*

All assumptions for our simulations are based on experiments with container-grown red maple under nursery conditions. The assumptions are: (1) mean transmittance and reflectance of red maple leaves are constant through the crown; (2) all trees are identical for a given size; and (3) crown shape is approximated by an ellipsoid. To account for the influence of neighboring trees, MAESTRA was applied to 10 target trees per simulation. The target trees were located close to the center of the plot to minimize potential boundary influences. All target trees were within a 100-tree nursery plot per simulation having various distributions of stocking density and tree size ratio (a tree's absolute size in relation to its nearest neighbor) with the following restrictions: the target crown had to be located within the center of the plot to prevent boundary effects in calculating light interception and absorption, the plot of trees was assumed to be evenly spaced in nursery drip-irrigated rows and substrate volumetric water content was equal to or greater than 0.30 m$^3$ m$^{-3}$ (Delta-T Devices, Cambridge, U.K.; data not shown). The percent increase in intercepted $Q$ per crown layer

is listed in Table 2. Mean crown shape of the 3-year-old stand of red maple is listed in Table 3. At the end of the study, leaves of all trees in the plot were harvested and their area measured with an LI-3100 leaf area meter (Li-Cor, Lincoln, NE). Leaf area index was assumed to be constant during each simulation. Unless otherwise noted, physiological parameter values are as in Bauerle et al. (2002).

*Statistical analysis*

For each canopy layer, changes in $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ ($y$ values) with crown spacing ($x$) and tree size ratio were characterized by one of two empirical models. One was the exponential function:

$$y(x) = \alpha - \beta e^{-\lambda x} \qquad (4)$$

where response increases at an ever decreasing rate, according to the shape parameter $\lambda$, toward asymptotic value $\alpha$ as $x \to \infty$, and parameter $\beta$ shifts the location of the curve along the $x$-axis by determining the intercept $y(0) = \alpha - \beta$, which was characterized by $A_{net}$, $E$ and $Q_a$ for all three canopy layers and $\varepsilon_c$ for canopy layer 3. The other empirical model was the exponential function:

$$y(x) = \alpha + \beta e^{-\lambda x} \qquad (5)$$

where response declines at an ever decreasing rate toward the asymptotic value $\alpha$ as $x \to \infty$, and parameter $\beta$ shifts the location of the curve along the $x$-axis by determining the intercept

Table 2. Summary of percent of photosynthetically active radiation ($Q$) correction for individual crown layers of red maple. Intercepted $Q$ was increased proportionally per crown layer so that model values were equal to measured values. Values of $r^2$ represent the regression on all fiber-optically integrated intercepted $Q$ values versus MAESTRA estimated intercepted $Q$ per crown layer.

| Tree layer | $r^2$ | % $Q$ correction |
|---|---|---|
| 1 | 0.97 | +9.3 |
| 2 | 0.93 | +18.0 |
| 3 | 0.95 | +11.1 |

Table 3. Mean aboveground biometric characteristics of the 3-year-old containerized red maple stand grown in fertilized well-watered containers.

| Characteristic | Mean value |
|---|---|
| Tree height (m) | 2.6 |
| Crown length (m) | 1.66 |
| Crown width (m) | 1.3 |
| Leaf area (m$^2$) | 2.5 |
| Stem diameter (mm) | 30.14 |

$y(0) = \alpha + \beta$, which is characterized by $\varepsilon_c$ for canopy levels 1 and 2. The relationships were fitted by nonlinear least squares with an iterative process to obtain parameter estimates.

Response patterns for the tree size ratios of each canopy level were compared with the extra sum of squares principle (Draper and Smith 1966). Unconditional sum of squares error (SSE) and associated degrees of freedom (df) were obtained by fitting separate response curves for each tree size ratio. Comparison of specific tree size ratios required fitting a common response curve that produced a conditional sum of squares error (CSSE) and associated df. The difference in error sum of squares, CSSE-SSE, and df for common and separate curves provided the 'extra sum of squares' to test the hypothesis that responses for the specified tree size ratios are equivalent.

## Results

*Validation of crown light transfer*

The comparison of modeled intercepted $Q$ to both single point and integrated measurements is presented on a crown layer basis in Figure 1. We adjusted the light transfer model by com-
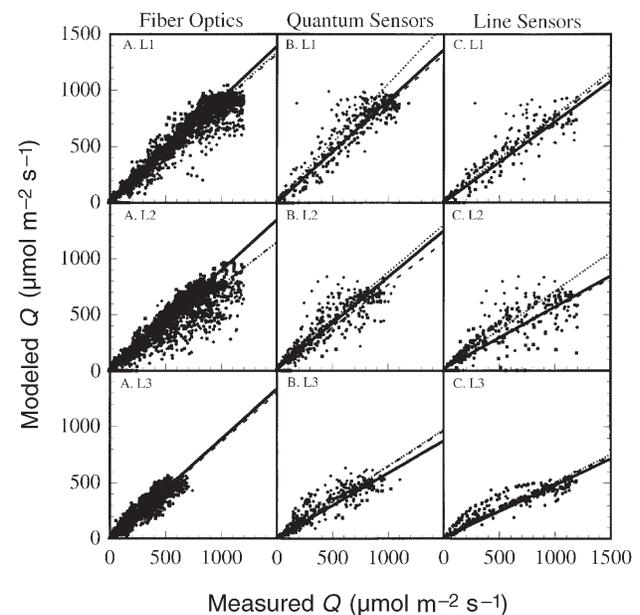


Figure 1. Comparison of model-estimated intercepted photosynthetically active radiation ($Q$) to measured $Q$ interception at three crown layers with three independent measurement techniques. Layers (L) are designated numerically (1, 2 and 3) for fiber optics (A), quantum sensors (B) and line sensors (C). Solid, dashed and dotted lines depict linear regressions on the three independent crowns at three layers within each crown. The mean of the three crowns per layer was used to adjust the model and the small variation between trees is only illustrated for comparative purposes with different symbols and line segmentation. Table 2 documents $r^2$ values and $Q$ percent correction at each layer.

paring mean $Q$ measured by fiber optic integration intercepted at three crown layers on three independent trees within the plot at a $Q \leq 1200$ µmol m$^{-2}$ s$^{-1}$ (up to the point of potential photoinhibition for red maple) (Bauerle et al. 2003$b$). The individual quantum sensor estimates (10 total) in the paired line and quantum sensor experiment were less suitable than the fiber optic measurements because the canopy was subject to sunflecks that could illuminate the within-crown quantum sensor. Therefore, we used the linear relationship between measured fiber optically integrated $Q$ and $Q$ estimated by the model on a crown layer basis to calculate $Q_a$ by incorporating reflectance and transmittance and proportionally increasing the intercepted $Q$ as described by LeFèvre et al. (2000) (Figure 1A). The model values were then equal to measured values. Figures 1A–C compare results obtained with a fiber optic integration method, which provided a continuous measure at each crown layer, to results obtained with line and quantum sensors, which for reasons of cost, had to be moved to each canopy layer manually, thus limiting the ability to capture within- and inter-crown variation.

The light transfer model within MAESTRA, which was originally validated and developed for coniferous trees, is known to underestimate light distribution in deciduous trees (LeFèvre et al. 2000). We found that the model underestimated the transfer of $Q$ within a deciduous tree crown by 9.3 to 18%.

*Intra-crown interactions of light absorption, photosynthesis, light-use efficiency, and transpiration*

Figure 2 illustrates relationships between $A_{net}$, $E$, $Q_a$, and $\varepsilon_c$ and crown spacing at different tree size ratios on a crown layer basis. Varying tree size ratio from 4:4 (uniform: equal crown length and width of the nearest adjoining neighbors) to 4:1 (heterogeneous: crown length and width are one fourth of that of the nearest adjoining neighbors) and tree spacing from 0.50–3 m$^2$ simulates different tree size ratios at a range of spacings. The spacing range represents the span of tree spacing and tree size ratios found in most USA red maple ornamental nurseries (L.P. Parsons, Jr., Parsons Nursery, Georgetown, SC, personal communication).

We compared the different tree size ratios by contrasting the exponential response patterns obtained with a fitting Equation 4 or 5. The extra sum of squares principle provided information for hypothesis testing, and distinct response patterns were detected ($P < 0.05$) for each of the tree size ratios in all cases except in Layer 3, where similar transpiration patterns were observed for the 4:4 and 4:3 size ratios. Response patterns for each tree size ratio changed across canopy layers (Figure 2). For Layer 1 (upper third of the crown), few interactions existed between $A_{net}$, $E$, $Q_a$, and $\varepsilon_c$ and tree size ratio as space between crowns increased. Only the most heterogeneous size ratio, 4:1, indicated any interactions (Figure 2, Layer 1). For Layers 2 and 3, however, interactions between $A_{net}$, $E$, and $Q_a$ and size ratio were observed. When space was limited (crown stems $\leq 1$ m center to center), trees with heterogeneous ratios absorbed more $Q$ and had higher $A_{net}$ and $E$ than when space between crowns was less limited for light transfer (crown stems
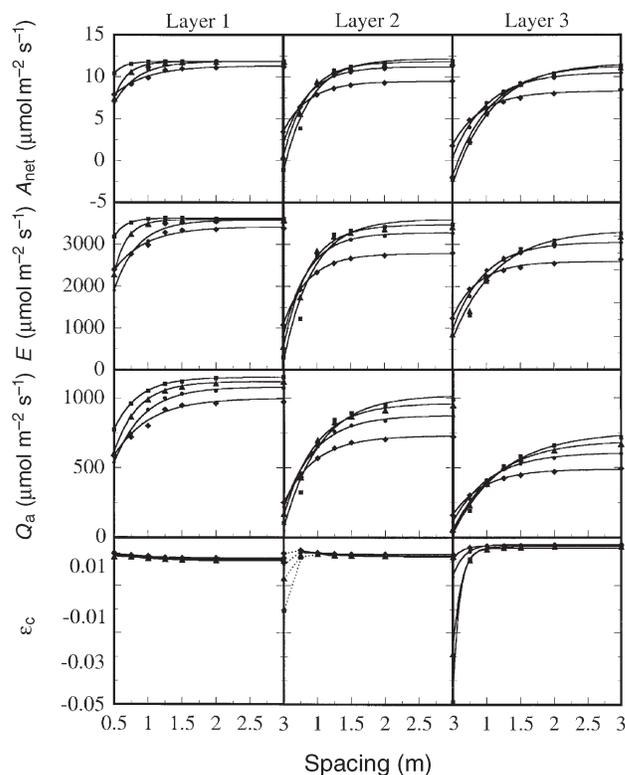


Figure 2. Intra-crown interaction between spacing and net photosynthesis ($A_{net}$), transpiration ($E$), absorbed photosynthetically active radiation ($Q_a$), and light-use efficiency ($\varepsilon_c$) at four tree size ratios and three canopy layers. Symbols are the means of 10 trees per layer at solar noon on a sunny day in June. Symbols illustrate the tree size ratios where (♦) is 4:1, (●) is 4:2, (▲) is 4:3 and (■) is 4:4. The broken line in Layer 2 $\varepsilon_c$ values is a connected line, whereas all solid lines are best fits.

$\geq 1$ m center to center). Light saturation per size ratio was similar among layers, and as spacing exceeded 1.5 m, the increase in $A_{net}$, $E$ and $Q_a$ began to plateau. Layer 1 had similar $\varepsilon_c$ values at all ratios and spacing combinations. Layers 2 and 3, however, had higher $\varepsilon_c$ values when space limited light transfer, and when space did not limit light transfer, $\varepsilon_c$ values became similar. Even at greater spacing, $\varepsilon_c$ was slightly higher in heterogeneous arrangements.

Figure 3 illustrates the interaction of $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ in relation to tree size ratio and crown spacing on a crown layer basis at solar noon on a sunny day in June. Among parameter estimates, spacing had a larger impact at Layers 2 and 3 than at Layer 1 (Figure 3). The ellipsoidal crown shape of ornamental red maple crowns places 50% of the foliage at Layer 2. The data in Figure 3 indicate that substantial increases in $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ can be obtained at Layers 2 and 3 by staggering trees of the same species having different size ratios. Three-fourths of the leaf area per crown receives more light as a result of a staggered arrangement of tree sizes, which increases $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ per m$^2$ of foliage. In addition, severe shading within a uniform crown arrangement (size ratio 4:4) can cause negative
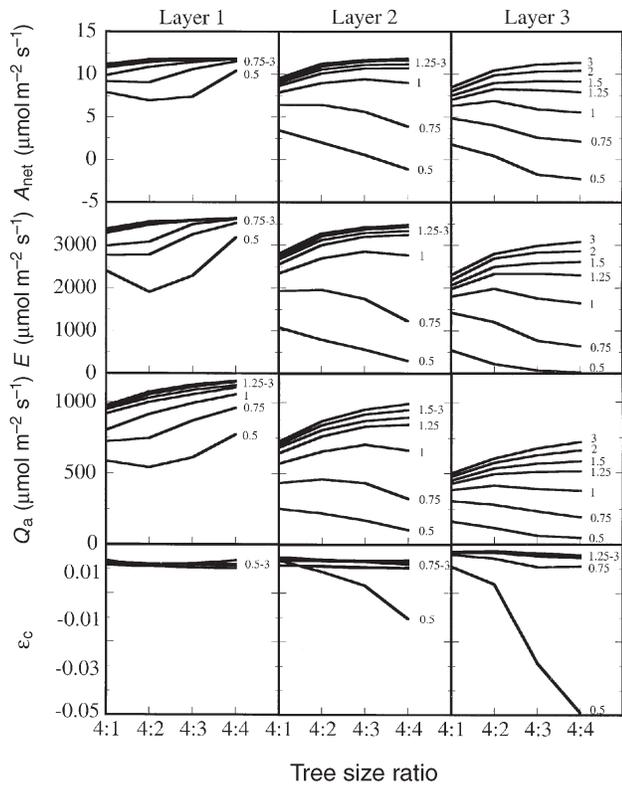
Figure 3. Comparison of intra-crown net photosynthesis ($A_{net}$) and transpiration ($E$) to absorbed photosynthetically active radiation ($Q_a$) and light-use efficiency ($\varepsilon_c$) at solar noon on a sunny day in June. Lines are the mean of 10 tree crowns at four tree size ratios (4:1, 4:2, 4:3 and 4:4). Spacing (m) is indicated to the right of the line.

Figure 4. Comparison of intra-canopy daily net photosynthesis ($A_{net}$), transpiration ($E$), absorbed photosynthetically active radiation ($Q_a$) and light use efficiency ($\varepsilon_c$) on a sunny day in June. Lines are means of 10 tree crowns at four tree size ratios (4:1, 4:2, 4:3 and 4:4). Spacing (m) is indicated to the right of the line.

$A_{net}$ and $\varepsilon_c$ at lower crown layers. Once lower crown layers received adequate illumination as a result of increased space between crowns, the benefits of staggering tree sizes diminished, especially at lower crown layers that were not light saturated.

Figure 4 illustrates the integrated interaction of $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ in relation to tree size ratio and crown spacing over an entire day. A 4:4 size ratio has an overall negative $A_{net}$ and $\varepsilon_c$ at limited crown space ($\leq 0.5$ m). Staggering trees of different sizes created a heterogeneous canopy, and increased $Q_a$, $\varepsilon_c$ and whole-crown carbon gain in absolute terms and per unit of land area.

*Intra-canopy interactions of light absorption, photosynthesis, light-use efficiency and transpiration*

To incorporate seasonal fluctuations (e.g., cloudy and sunny days), Figure 5 illustrates the accumulated amounts of $A_{net}$, $E$, $Q_a$ and $\varepsilon_c$ in relation to tree size ratio and crown spacing over the main 90-day portion of the growing season (June 5–September 2, 2002). When all weather patterns are considered, the overall outcome was similar to that of a single sunny day (Figure 4). On a unit area of foliage basis, accumulated $A_{net}$ and $E$ were highest when space was limiting and the tree size ratio was highest (4:1). Light-use efficiency below the point of
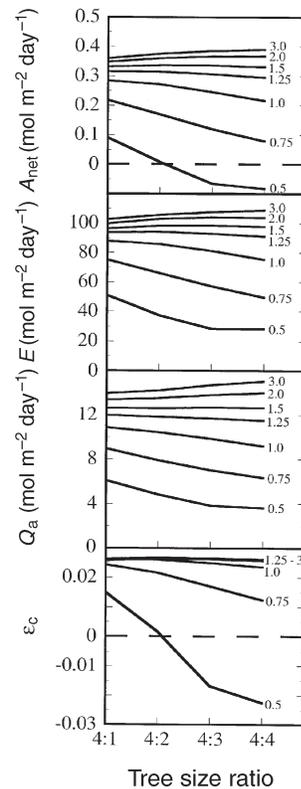
space limitation increased as tree size ratio moved toward greater heterogeneity (4:1).

## Discussion

In semi-natural forests, such as intensively managed plantations and nurseries, trees are often widely spaced and hence, more light is available for photosynthesis by lower crown layers. For the tree size ratios considered in this study, the results indicate that, as crown space becomes limiting, canopy heterogeneity results in elevated $A_{net}$, $Q_a$, $E$ and $\varepsilon_c$ relative to a uniform stand. Moreover, the model indicates that daily and seasonal $A_{net}$, $Q_a$, $E$ and $\varepsilon_c$ per $m^2$ of leaf area increase as a result of the creation of a heterogeneous stand of trees. Because the position and dimensions of each tree are specified in MAESTRA, the model predicts the effects of light transfer on alternative tree size ratios at both the individual tree and stand level. The MAESTRA simulations indicate that tactical placement of several annual tree sizes allows ellipsoidal crowns to achieve higher light-use efficiencies in dense multistoried canopies.

It is well known that the physiological response of a plant to a canopy gap can affect photosynthesis, respiration and sto-
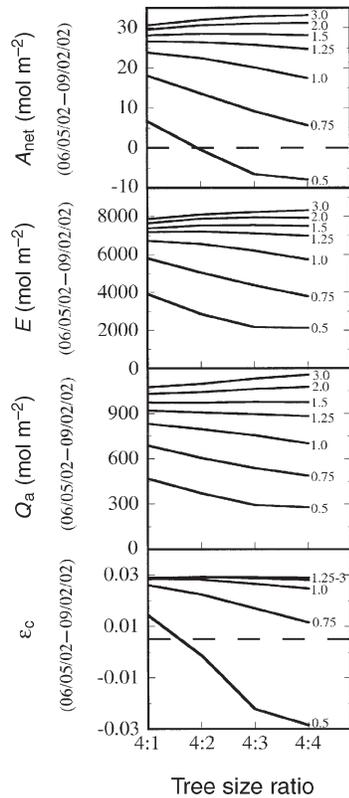
Figure 5. Comparison of intra-canopy seasonal net photosynthesis ($A_{net}$), transpiration ($E$), absorbed photosynthetically active radiation ($Q_a$) and light-use efficiency ($\varepsilon_c$) for the main portion of the growing season (June 5–September 2, 2002). Lines are the means of 10 tree crowns at four tree size ratios (4:1, 4:2, 4:3 and 4:4). Spacing (m) is indicated to the right of the line. Values are totals that incorporate all weather patterns during the 90-day period.

matal conductance (Ryel and Beyschlag 2000), and competition among plants is a complex process that warrants quantitative analysis (Beyschlag et al. 1990). Simulating the radiation regime within the tree crown is necessary to calculate individual crown and canopy photosynthesis (Jarvis et al. 1985). The physiological response of crown photosynthesis to light transfer provides a way of assessing canopy optimization potential of various configurations, spacings, tree size ratios and their interactions. In Sitka spruce (*Picea sitchensis* (Bong.) Carr.), Wang and Jarvis (1990*a*) identified crown shape as the least important structural property for $Q_a$, $A$ and $E$. In contrast, Kuuluvainen (1988) found that crown shape influenced stem production of Norway spruce (*Picea abies* (L.) Karst.). We expanded on these studies by considering the effects of canopy heterogeneity on a tree crop ecosystem and showed that canopy heterogeneity in dense ellipsoidal shaped crowns supports the hypothesis of Terborgh (1985) whereby high sun angles and dome-shaped crowns allow sunflecks to penetrate gaps and support multistoried canopies.

Seedlings and saplings respond to increased irradiances through enhanced photosynthetic rates leading to higher

growth rates (Ryel and Beyschlag 2000). When crown heights are discontinuous, light penetration to lower crown layers is increased (e.g., Kruijt et al. 1999), indicating that distribution of light through a canopy is a key factor in determining $A_{net}$ responses. Moreover, studies by Kellomäki et al. (1984, 1985) indicate that dense stands with minimal gap and overlap between crowns absorb $Q$ with high efficiency. However, Kuuluvainen and Pukkala (1987) point out that a contributing factor could be the large influence of broad crowns on the competition for light. In addition, trees may adjust their growth allometry in a way that tends to lessen the risk of being overtopped by competitors (Ritchie 1997).

Within-canopy $Q$ sampling requires more than a single sensor to characterize the large spatial variations (Anderson 1966, 1971). The number of sensors necessary to sample within 5% of the population mean can be in excess of 800 when the coefficient of variation is large (Baldocchi and Collineau 1994). Spatial averaging can be done with 1-m-long line sensors, but cost can be prohibitive where canopy heterogeneity necessitates the use of many sensors. Moreover, taller canopies can exceed the spatial sampling ability of line sensors (Pearcy 1989). We used orthogonal line sensors, quantum sensors and a fiber-optic-based $Q$ measurement system to compare measured incident $Q$ to that of model estimates. Unlike individual quantum sensors or line sensors, the fiber optic system integrated light at 48 light interception points into one $Q$ reading per layer, which reflected canopy geometry. A detailed analysis of the comparison among methods is presented in Bauerle and Bowden (2004). Based on these results, and in view of the importance of understanding how the quantity of light integrates over an individual crown and canopy layer, the integrated fiber optic system was used to parameterize the light transfer sub-model of MAESTRA.

Although all three independent measurement techniques indicated that modeled light transfer estimates were lower than measured values (Figure 1), our intercepted estimates were in general in agreement with the findings of LeFèvre et al. (2000) for a deciduous beech *Fagus sylvatica* (L.) forest. More importantly, the effect of creating a heterogeneous canopy by exploiting variation in tree size ratio is independent of the merits of the different sensors and the results would be evident regardless of the success of efforts to accurately parameterize the radiation transfer model within MAESTRA.

We attempted to quantify and analyze productivity in terms of resource capture and use in a container nursery. A fundamental understanding of resource utilization is crucial for selecting optimum management strategies, tree densities, species combinations and planting arrangements (Ong et al. 1996). Depending on the intra-canopy space limitations, canopy heterogeneity represents disorder and it may decrease the competition for radiation at the intra-crown scale. At the intra-crown and intra-canopy scale, fluxes of carbon and water exchange increase when canopy heterogeneity is maximized under space limiting conditions. The results have relevance to nursery and plantation management practices. Moreover, production potential per unit foliage area can be improved when

plants of different sizes are placed in a staggered arrangement to create a canopy of predetermined heterogeneity. Lastly, the quantification of resource capture and use through spatial heterogeneity was resolved in the vertical and horizontal planes with a three-dimensional biological process canopy model. The model estimates show that there are occasions when manipulation of canopy architecture is important. Spatially explicit process based models, such as MAESTRA, may allow exploitation of this observation and thereby improve plantation and nursery management strategies.

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## References

Abrams, M.D. 1998. The red maple paradox. Bioscience 48:355–364.

Anderson, M.C. 1966. Some problems of simple characterization of the light climate in plant communities. *In* Light as an Ecological Factor. Eds. R. Bainbridge, G.C. Evans and O. Rackman. Blackwells, Oxford, pp 77–90.

Anderson, M.C. 1971. Radiation and crop structure. *In* Plant Photosynthetic Production Manual of Methods. Eds. Z. Sestak, J. Čatský and P.G. Jarvis. Junk, The Hague, pp 412–467.

Baldocchi, D. and S. Collineau. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal attributes. *In* Exploitation of Environmental Heterogeneity by Plants. Physiological Ecology. Eds. M.M. Caldwell and R.W. Pearcy. Academic Press, San Diego, CA, pp 21–64.

Baldocchi, D.D. and P.C. Harley. 1995. Scaling carbon dioxide and water vapour exchange from leaf to canopy in a deciduous forest. II. Model testing and application. Plant Cell Environ. 18: 1157–1173.

Ball, J.T., I.E. Woodrow and J.A. Berry. 1987. A model predicting stomatal conductance and its contribution to the control of photosynthesis under different environmental conditions. *In* Progress in Photosynthesis Research, Vol. 4. Ed. J. Biggins. M. Nijhoff, Dordrecht, The Netherlands, pp 5.221–5.224.

Bauerle, W.L. and J.D. Bowden. 2004. A fiber optic-based system for integrating photosynthetically active radiation in plant canopies. HortScience. In press.

Bauerle, W.L., C.J. Post, M.F. McLeod, J.B. Dudley and J.E. Toler. 2002. Measurement and modeling of the transpiration of a temperate red maple container nursery. Agric. For. Meteorol. 114:45–57.

Bauerle, W.L., J.B. Dudley and L.W. Grimes. 2003*a*. Genotypic variability in photosynthesis, water use, and light absorption among red and Freeman maple cultivars in response to drought stress. J. Am. Soc. Hortic. Sci. 128:337–342.

Bauerle, W.L., T.H. Whitlow, T.L. Setter, T.L. Bauerle and F.M. Vermeylen. 2003*b*. Ecophysiology of *Acer rubrum* L. seedlings from contrasting hydrologic habitats: growth, gas exchange, tissue water relations, abscisic acid and carbon isotope discrimination. Tree Physiol. 23:841–850.

Bauerle, W.L., D.J. Weston, J.D. Bowden, J.B. Dudley and J.E. Toler. 2004. Leaf absorptance of photosynthetically active radiation in relation to chlorophyll meter estimates among woody plant species. Sci. Hortic. In press.

Bosveld, F.C. and W. Bouten. 2001. Evaluation of transpiration models with observations over a Douglas-fir forest. Agric. For. Meteorol. 108:247–264.

Campbell, G.S. 1986. Extinction coefficients for radiation in plant canopies calculated using ellipsoidal inclination angle distribution. Agric. For. Meteorol. 36:317–321.

Carter, G.A., K. Paliwal, U. Pathre, T.H. Green, R.J. Mitchell and D.H. Gjerstad. 1989. Effect of competition and leaf age on visible and infrared reflectance in pine foliage. Plant Cell Environ. 12: 309–315.

Ceulemans, R. and W. Deraedt. 1999. Production physiology and growth potential of poplars under short-rotation forestry culture. For. Ecol. Manage. 121:9–23.

Collatz, G.J., J.T. Ball, C. Grivet and J.A. Berry. 1991. Regulation of stomatal conductance and transpiration: a physiological model of canopy processes. Agric. For. Meteorol. 54:107–136.

Draper, N.R. and H. Smith. 1966. Applied regression analysis. John Wiley & Sons, New York, pp 67–69.

Farquhar, G. and S. von Caemmerer. 1982. Modelling of photosynthetic response to environmental conditions. *In* Physiological Plant Ecology. II. Encyclopedia of Plant Physiology, New Series. Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler. Springer-Verlag, Berlin, pp 549–588.

Grace, J.C., P.G. Jarvis and J.M. Norman. 1987. Modelling the interception of solar radiant energy in intensively managed stands. N.Z. J. For. Sci. 17:193–209.

Harley, P.C., R.B. Thomas, J.F. Reynolds and B.R. Strain. 1992. Modeling photosynthesis of cotton grown in elevated $CO_2$. Plant Cell Environ. 15:271–282.

Jarvis, P.G., H.S. Miranda and R.I. Muetzelfeldt. 1985. Modelling canopy exchange of water vapor and carbon dioxide in coniferous forest plantations. *In* The Forest–Atmosphere Interaction. Eds. B.A. Hutchison and B.B. Hicks. Reidel, Dordrecht, pp 521–542.

Kellomäki, S., P. Oker-Blom and T. Kuuluvainen. 1984. The effect of crown and canopy structure on light interception and distribution in a tree stand. *In* Crop Physiology of Forest Trees. Eds. P.M.A. Tigerstedt, P. Puttonen and V. Koski. Helsinki University Press, Helsinki, pp 107–115.

Kellomäki, S., T. Kuuluvainen and O. Kurttio. 1986. Effect of crown shape, crown structure and stand density on the absorption of light in a tree stand. *In* Crown and Canopy Structure in Relation to Productivity. Eds. T. Fujimori and D. Whitehead. Proc. Int. Workshop. Forestry and Forest Products Research Institute, Ibaraki, Japan, pp 339–358.

Knyazikhin, Y., A. Marshak, D. Schulze, R.B. Myeni and G. Gravenhorst. 1994. Optimization of solar radiation input in forest canopy as a tool for planting/cutting of trees. Transport Theory Stat. Phys. 25:671–700.

Kruijt, B., C. Barton, A. Rey and P.G. Jarvis. 1999. The sensitivity of stand-scale photosynthesis and transpiration to changes in atmospheric $CO_2$ concentration and climate. Hydrol. Earth Syst. Sci. 3:55–69.

Kuuluvainen, T. 1988. Crown architecture and stemwood production in Norway spruce (*Picea abies* (L.) Karst.). Tree Physiol. 4: 337–346.

Kuuluvainen, T. and T. Pukkala. 1987. Effect of crown shape and tree distribution on the spatial distribution of shade. Agric. For. Meteorol. 40:215–231.

Landsberg, J.J., S.D. Prince, P.G. Jarvis, R.E. McMurtrie, R. Luxmoore and B.E. Medlyn. 1996. Energy conversion and use in forests: the analysis of forest production in terms of radiation utilization efficiency. *In* The Use of Remote Sensing in the Modelling of Forest Productivity at Scales from the Stand to the Globe. Eds. H.L. Gholz, K. Nakane and H. Shimoda. Kluwer Academic Publishers, Dordrecht, pp 273–298.

LeFèvre, F., E. Laitat, B. Medlyn, M. Aubinet and B. Longdoz. 2000. Carbon pools and annual carbon fluxes in the beech forest sub-plot at the Vielsalm pilot station. *In* Forest Ecosystem Modelling, Upscaling and Remote Sensing. Eds. R.J.M. Ceulemans, F. Veroustraete, V. Gond and J.B.H.F. van Rensbergen. S.P.B. Academic Publishing, The Hague, The Netherlands, pp 137–153.

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

Medlyn, B.E. 1998. Physiological basis of the light-use efficiency model. Tree Physiol. 18:167–176.

Medlyn, B.E., F.-W. Badeck, D.G.G. de Pury et al. 1999. Effects of elevated $CO_2$ on photosynthesis in European forest species: a meta-analysis of model parameters. Plant Cell Environ. 22: 1475–1495.

Norman, J.M. 1979. Modification of the aerial environment of plants. ASAE, St. Joseph, MI, 538 p.

Norman, J.M. and J.M. Welles, 1983. Radiative transfer in array of canopies. Agron. J. 75:481–488.

Ogink-Hendriks, M.J. 1995. Modelling surface conductance and transpiration of an oak forest in The Netherlands. Agric. For. Meteorol. 74:99–118.

Oker-Blom, P. 1985. Photosynthesis of a Scots pine shoot: simulation of the irradiance distribution and photosynthesis of a shoot in different radiation fields. Agric. For. Meteorol. 34:32–40.

Oker-Blom, P. and S. Kellomäki. 1983. Effect of grouping foliage on the within-stand and within-crown light regime: comparison of random and grouping canopy models. Agric. For. Meteorol. 28: 143–155.

Ong, C.K., C.R. Black, F.M. Marshall and J.E. Corlett, 1996. Principles of resource capture and utilization of light and water. *In* Tree–Crop Interactions: A Physiological Approach. Eds. C.K. Ong and P. Huxley. CAB International, Wallingford, U.K., pp 73–158.

Pearcy, R.W. 1989. Radiation and light measurements. *In* Plant Physiological Ecology: Field Methods and Instrumentation. Eds. R.W. Pearcy, J. Ehleringer, H.A. Mooney and P.W. Rundel. Chapman & Hall, New York, pp 97–116.

Rayment, M.B., D. Loustau and P.G. Jarvis. 2002. Photosynthesis and respiration of black spruce at three organizational scales: shoot, branch and canopy. Tree Physiol. 22:219–229.

Ryel, R.J. and W. Beyschlag. 2000. Gap dynamics. *In* Leaf Development and Canopy Growth. Eds. B. Marshall and J.A. Roberts. CRC Press, Boca Raton, FL, pp 251–279.

Ritchie, G.A. 1997. Evidence for red:far red signaling and photomorphogenic growth response in Douglas-fir (*Pseudotsuga menziesii*) seedlings. Tree Physiol. 17:161–168.

Stenberg, P., E.H. DeLucia, A.W. Schoettle and H. Smolander. 1995. Photosynthetic light capture and processing from cell to canopy. *In* Resource Physiology of Conifers: Acquisition, Allocation, and Utilization. Eds. W.K. Smith and T.M. Hinckley. Physiological Ecology, Academic Press, San Diego, CA, pp 3–38.

Terborgh, J. 1985. The vertical component of plant species diversity in temperate and tropical forests. Am. Nat. 126:761–776.

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

Wang, Y.P. and P.G. Jarvis. 1990*b*. Description and validation of an array model—MAESTRO. Agric. For. Meteorol. 51:257–280.