

Vertical variation in canopy structure and CO₂ exchange of oak–maple forests: influence of ozone, nitrogen, and other factors on simulated canopy carbon gain

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Summary

Stand-level and physiological measurements were made for oak and maple species common in Wisconsin forests. Scaling relationships were identified to allow the development of a model for estimating net carbon exchange at the levels of a leaf, canopy stratum, and whole canopy. Functional relationships were determined between tissue gas exchange rates and perceived controlling variables. Vertical variation in leaf properties and in the distribution of foliage by weight, area, and species were characterized for several closed canopy forests. Forest canopies were divided into four horizontal strata to develop predictive models for canopy gas exchange. Leaf and canopy layer carbon dioxide exchange rates were predicted using leaf nitrogen concentration, leaf mass per area, ozone exposure, predawn leaf water potential, photosynthetically active radiation, and vapor pressure deficit as driving variables. Direct measurements of leaf gas exchange were used to validate the components (subroutines) of the model. Net carbon dioxide exchange was simulated for canopy layers at 5-min intervals over a diurnal time course. Simulations of canopy CO₂ exchange were made for a 30-m tall, mixed oak–maple forest under hypothetical ambient and greater-than-ambient ozone pollution regimes. Daily canopy net CO₂ exchange was predicted for seven forest stands and compared with estimates of aboveground net primary production, N availability, leaf area index, and canopy N.

Introduction

There is increasing concern about the impacts on forests of atmospheric pollution, potential climate change, and long-term changes in site productivity caused by timber harvesting. These impacts must eventually be addressed at the stand, ecosystem, and global scales. Unfortunately, they are difficult to evaluate solely from a physiological perspective because of the large size and complexity of the systems (Jarvis and McNaughton 1986). They may also be difficult to assess at the ecosystem-level, because of the difficulty of finding forests differing only in the variable of interest. Certain environmental treatments may be imposed on otherwise uniform forest stands, e.g., fumigation with atmospheric pollutants, but this is rarely feasible because of logistic problems and extremely high costs. Thus, simulation modeling may provide a valuable approach when applied in concert with controlled physiological studies (e.g., Reich 1983) and comparative field studies (e.g., Oleksyn 1983).

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The approach that we have taken is a hybrid of the "top-down" and "bottom-up" approaches (Jarvis et al. 1985). Our goal is to use functional or scaling relationships, or both, at large scales, with the first priority being to identify appropriate scales for different predictive relationships. Inasmuch as our target model systems are the north central forests of the United States, we have developed models that are as general as possible across species, sites, and time frames rather than focusing on a particular system. Thus, our approach has been to build the simplest model that can approximate reality and then make it more complex, in accordance with the goals of the particular modeling exercise. Implicit in this approach is the desire to develop driving variables that are easy and inexpensive to measure, so that the model may be broadly applied. A related approach has been described by Running and Coughlan (1988) and Grace (1990) who developed models that compromise between mechanistic detail and simplifying generality.

Our goals in the present study were to: (1) describe functional relationships affecting net carbon balance at the leaf level for several hardwood species of oak–maple forests; (2) characterize vertical variation in select canopy properties for these stands; (3) determine scaling relationships between canopy properties and physiological processes for these stands; and (4) use these relationships to develop predictive models for simulating the carbon balance of a forest canopy in response to resource availability and stress. In this paper we describe our approach for linking leaf- and stand-level measurements; present examples of the types of relationships determined to date; describe the assumptions and structure of a predictive model; test aspects of the model; and discuss several simulations of stand-level canopy carbon dioxide exchange.

One simulation considered the relative contributions of different stratified canopy layers to whole-canopy carbon gain in a 30-m tall, mixed oak–maple forest, as well as the relative contributions of the two dominant species. We then simulated the response of this stand to several ozone pollution regimes. Because most of our knowledge about tree response to this pollutant is based on studies with small seedlings grown in high light (Reich 1987), we simulated the response of an entire canopy to chronic ozone exposure, assuming that ozone concentrations are similar throughout the canopy. However, because it is possible that ozone concentrations are lower in the understory or lower canopy than in the upper canopy due to the filtering action of the canopy itself, we also simulated canopy response to ozone using several different scenarios of vertical ozone extinction in the canopy.

We also determined whether canopy net carbon gain is related to N availability or to stand-level measurements of aboveground productivity and leaf area index among northern hardwood forests by simulating canopy carbon gain with stand-level indices for seven forest stands in south central Wisconsin.

The model

Our carbon gain model, which was developed using a microcomputer software package called STELLA (High Performance Systems, Lyme, NH) (Bogen 1989), has

two main components: stand structure and photosynthetic rates (Figure 1). The first component involves the division of the canopy foliage into four horizontal layers or classes: (1) emergent, clearly above the main level of the canopy, hereafter referred to as "upper canopy;" (2) upper codominant, sunlit portions of the main canopy, hereafter "middle canopy;" (3) lower codominant, shaded portions of the main canopy, hereafter "lower canopy;" and (4) subcanopy/understory, foliage clearly below the main level of the canopy, hereafter "understory." The model requires input of several relatively simple indices of canopy structure and composition: leaf area index (LAI), mean leaf nitrogen (N) concentration, and leaf mass to area ratio (LMA) for each canopy layer and species. For the deciduous stands simulated in this study, there was no significant difference in mass-based leaf N concentration per species among canopy layers (Fownes 1985), hence mean canopy leaf N values for each species could be used instead.

The second part of the model consists of a series of steps used to predict instantaneous rates of net photosynthesis (P) in 5-min increments during the day for each of the canopy layers and species. Photosynthesis was modeled using a set of environmental constraints imposed by leaf N, LMA, ozone, incident photosynthetic photon

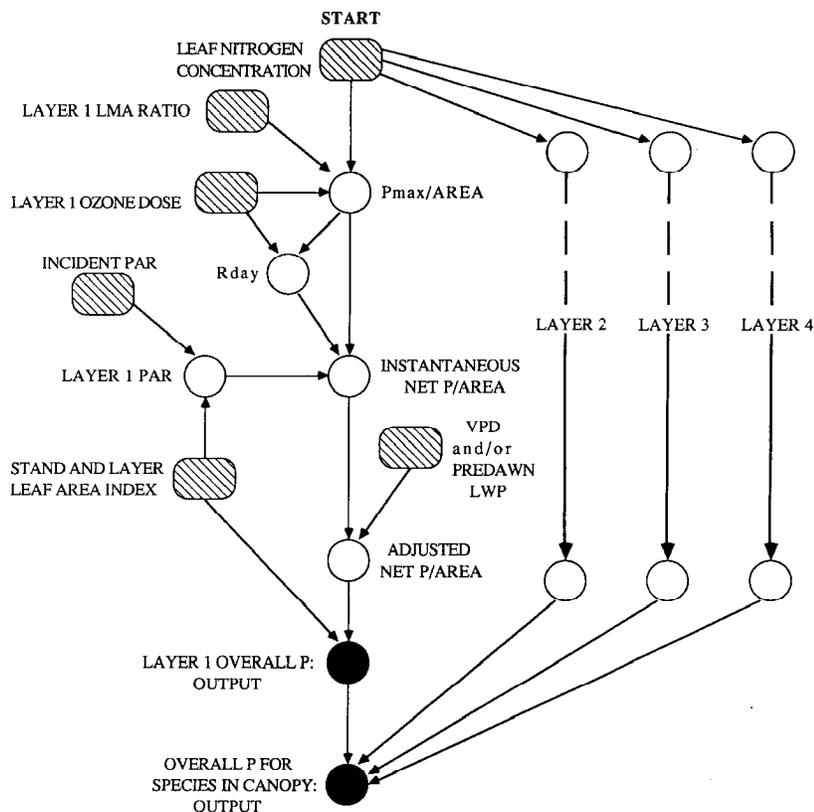


Figure 1. Model flow-chart as developed using the STELLA software package.

flux density (PPFD), predawn leaf water potential (LWP), and vapor pressure deficit (VPD) (Figure 1). An example of the types of relationships between each of these driving variables and net photosynthesis is given in Table 1. Where possible, species-specific relationships developed previously on other sites were used.

The light-saturated maximum photosynthetic rate at ambient CO_2 concentrations (P_{max}) was calculated for each canopy layer as a function of leaf N/area using leaf N and LMA. The present model is based on the assumption that N is the nutrient most limiting to photosynthesis (Field and Mooney 1986). Optimization models suggest that leaf N is partitioned within canopies on an area basis, and N/area has been observed to be highly correlated with maximum photosynthesis (DeJong and Doyle 1985, Hirose and Werger 1987). Although the mechanisms determining photosynthetic capacity can be more finely detailed at the biochemical level (von Caemmerer and Farquhar 1981), we believe that whole-leaf photosynthesis is an appropriate hierarchical level for modeling forest ecosystems. Furthermore, the relationship between leaf N and whole leaf photosynthetic capacity is a quasi-functional relationship that is well-suited for analyses involving multiple canopy layers, species, and stands of differing site qualities.

In the current version of the model, limitations to photosynthetic capacity due to ozone were incorporated before other environmental constraints, because the effect of ozone is primarily on the biochemical and photochemical processes of photosynthesis (Reich and Amundson 1985, Sasek and Richardson 1989). Ozone proportionally reduces net photosynthetic rates, depending on ozone concentration, a species' inherent leaf conductance, and other factors (Reich 1987).

We used equations based on Michaelis-Menten kinetics to model the steady-state response of photosynthesis to intercepted PPFD (Givnish 1988, Thornley 1976). For both oak and maple, the predominantly sunlit foliage (upper and middle canopy layers) was treated separately from the shaded foliage to differentiate between the effects of sun acclimation and shade acclimation on the characteristics of the light response curve (Teskey and Shrestha 1985, Givnish 1988). The slope of the photosynthetic light response curve (apparent quantum yield) is considered invariable among species under most natural conditions (Björkman and Demmig 1987), but the effect of ozone exposure was accounted for by the model (Reich 1983, Sasek and Richardson 1989). The intercept of the curve (daytime dark respiration, R_{day}) was calculated based on its relationship to photosynthetic capacity (Givnish 1988) with inclusion of an ozone effect on respiration independent of its effect on P_{max} (Reich 1983). Here we assume R_{day} to be ~50% lower for daytime (non-photorespiratory) than nighttime dark respiration (Azcón-Bieto and Osmond 1983, Brooks and Farquhar 1985, McCashin et al. 1988).

Total incoming PPFD can be input into the model from equations based on solar geometry and time of day (Gates 1980) or empirical data can be used (see Figure 4). For any 5-min interval, mean incident PPFD and VPD for canopy layers were estimated based on simple extinction relationships between these variables and the total LAI above each canopy layer. Although it is recognized that more complex models for light in canopies exist (Norman and Jarvis 1975), we used a general,

Table 1. Empirical relationships used in the STELLA canopy gain simulations.

Parameter	Driving variable	Parameter estimate	Reference
Layer PPFD	Total incoming PPFD, LAI above layer	$PPFD_{\text{Layer}} = PPFD_{\text{tot}} e^{-kLAI}$ broad-leaved forest $k = 0.6$	Jarvis and Leverenz 1983
$P_{\text{max}}/\text{AREA}$	% Leaf N, LMA	Oak: $P_{\text{max}} = -4.86 + 6.70 \text{ N LMA}$ Maple: $P_{\text{max}} = -1.60 + 5.62 \text{ N LMA}$	Reich et al. 1991 Reich et al. 1991
P/AREA	Ozone dose (ppm-h above background)	$P = P_{\text{max}}(1 - 0.01 [\text{O}_3])$	Reich 1987 Reich et al. 1986
R_{day}	P_{max}	$R_{\text{day}} = 0.0417 P_{\text{max}}$	Givnish 1988
Net P/AREA	$PPFD_{\text{Layer}}, k_m$ ($k_m = \text{half-saturation constant}$)	$P = P_{\text{max}} PPFD_{\text{Layer}} / (PPFD_{\text{Layer}} + k_m) - R_{\text{day}}$ Oak (sun, shade): $k_m = 310,180$ Maple (sun, shade): $k_m = 230,700$	Thornley 1976 Teskey and Shrestha 1985 Ellsworth and Reich unpublished observations Weber et al. 1985
Adjusted P/AREA	Predawn LWP (PD)	$P = P_{\text{max}}(1 + 0.37 (\text{PD} + 0.2) + 0.0367 (\text{PD} + 0.2)^2)$	Walters and Reich 1989 Dougherty et al. 1977
Adjusted P/AREA	VPD	Oak: $P = P (1 - 0.207 \text{ VPD})$ Maple: $P = P (1 - 0.216 \text{ VPD})$	Reich et al. 1990 Ellsworth and Reich unpublished observations

easily derived function which can be empirically verified using the LAI stratification data already required as input into the model. Moreover, it is possible that in closed canopy forests, crown shape and foliage inclination angles may only slightly affect whole canopy interception of radiant energy and net photosynthesis (Grace 1990). Transient responses of photosynthesis to rapid changes in environmental variables such as PPFD (e.g., sunflecks) were not included in the model.

Leaf conductance and photosynthesis usually decline during the day, even when incident PPFD is still saturating. It appears that the maximum conductance, or photosynthetic rate, observed on any given day is proportionally reduced during the day as a function of the maximum VPD (Fownes 1985, Ellsworth and Reich unpublished observations). Therefore, we used the average negative relationship between net photosynthesis and VPD to limit net photosynthesis over and above the limits imposed by leaf N, ozone, and PPFD. Because the model was designed for summertime conditions (June–September) when temperatures in Wisconsin are most favorable for photosynthesis, temperature was not considered in the current model, except for its influence on VPD. The model also does not consider diel variation in leaf water potential (LWP). Predawn LWP limits maximum daily leaf conductance, which in turn limits maximum daily net photosynthesis (Walters and Reich 1989, Reich and Hinckley 1990). Previous analyses suggest that predawn LWP and VPD account for sufficient variation in net photosynthesis that consideration of daytime LWP is unnecessary (Walters and Reich 1989). In the simulations presented here, predawn LWP was considered not limiting.

Methods

Physiological measurements

Measurements of net photosynthetic rate, photon flux density, leaf mass per area, leaf nitrogen concentration, leaf water potential, and other microenvironmental factors were made for several oak, maple, and other species from 1988–1990. The observations were made during the course of several studies at eight field sites in southern and central Wisconsin as well as in two controlled environment experiments (see Reich et al. 1990, 1991).

Leaf water vapor and CO₂ exchange were measured with a portable gas analyzer and cuvette system (Analytical Development Corporation, Hoddesdon, England), using a mass balance approach (Walters and Reich 1989). After making the gas exchange measurements, the leaves were collected and used for determinations of area, dry mass, and nutrient concentrations. Leaf areas were measured with a Li-Cor area meter (Li-Cor, Inc., Lincoln, NE). Foliar nutrient concentrations were analyzed by the Soil and Plant Analysis Laboratory, University of Wisconsin. Total leaf N concentrations were measured using microkjeldahl techniques. Leaf mass to area ratio (LMA) was calculated as the total leaf dry mass without petiole per leaf area when fresh.

Canopy structure

Vertical variations in leaf area, mass, and N were examined in seven deciduous forest stands in south central Wisconsin. Five of the stands are located at the University of Wisconsin Arboretum, Madison, WI and two are on Blackhawk Island, 70 km northwest of Madison. The stands are more than 35 years old and are dominated by oaks and maples. The vertical distribution of leaf area in these forests was measured in 1984 using a camera with a calibrated telephoto lens as a range-finder to find the distance above ground to individual leaves (Fownes 1985). The natural logarithm of the proportion of sight lines obstructed by leaves in 1-m height intervals estimated the proportion of total LAI in that interval (MacArthur and Horn 1969, Aber 1979). Species identification of each leaf sighted was used to estimate the proportion by species of leaf area in each of the four canopy layers, and litterfall mass was used to calculate canopy totals. Leaves from each canopy layer were sampled in August 1984 by shooting down small branches and LMA and percent N were determined by species for samples pooled within each of the four canopy layers. The camera technique for assessing total LAI and the proportion of total LAI in different species was validated against the litterfall method with good agreement (Fownes 1985). Data on litterfall, wood production (5-year average), and N availability have been published for the seven sites (Pastor et al. 1984, Lennon et al. 1985, Nadelhoffer et al. 1985, Fownes 1985).

Results and discussion

Subroutine validations

To validate subroutines of the model, predicted leaf-level photosynthesis was compared to measured photosynthesis under a variety of conditions. For example, we predicted diurnal trends in photosynthesis for *Prunus serotina* seedlings in southern Wisconsin in an open hedgerow and in a forest understory (Figure 2). Predicted values differed from measured values by about 5% on average with no tendency for either over- or underestimation except perhaps in early afternoon.

To test the ozone dose relationships of the model we compared predicted with measured photosynthesis for red spruce seedlings as reported by Taylor et al. (1986). The predicted values (in $\text{nmol g}^{-1} \text{s}^{-1}$) agreed closely with the measured values for both the polluted (predicted = 40.9 versus 39.3 = measured) and clean air (predicted = 41.9 versus 41.3 = measured) regimes. It would be interesting to test the model subroutine for plants showing greater ozone response (due either to greater dosage or greater sensitivity). However, we were unable to find other published information that included suitable measurements of photosynthesis for plants under known ozone dosage with known leaf N concentrations.

Simulations

The canopy structure of a 30-m tall northern red oak-sugar maple forest (SM2 in Pastor et al. 1984) on Blackhawk Island, Wisconsin, is shown in Figure 3. About

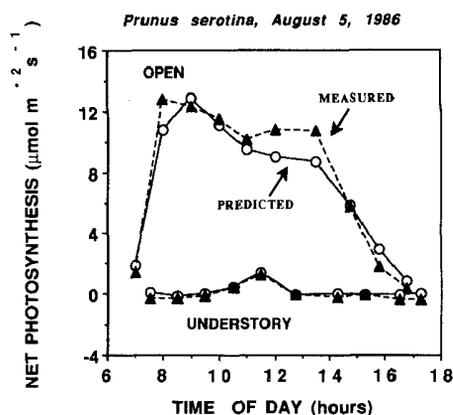


Figure 2. Predicted and measured net photosynthetic rates over the course of a summer day (August 5, 1986) for *Prunus serotina* seedlings/sprouts growing in an open hedgerow and in a forest understory in southern Wisconsin. Measured rates were the mean for four observations each on two individuals at each time interval. Measured data from Harrington et al. (1989).

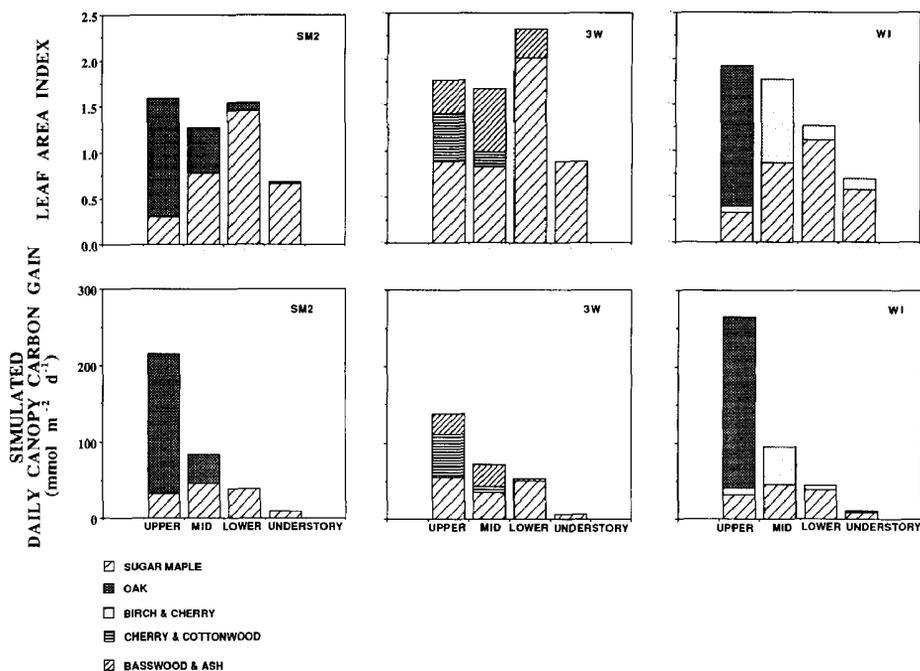


Figure 3. Vertical distribution of leaf area, by species, (top) and simulated daily carbon gain (bottom) in four horizontal layers of three deciduous forest stands in Wisconsin (see Figure 5 for stand information).

25–30% of total leaf area was present in each of the top three canopy layers and about 14% in the understory. The ratio of oak leaf area to maple leaf area declined from the top to the bottom of the canopy, shifting from 4/1 in the top layer to 0.6/1 in the middle canopy and less than 0.1/1 in the lower layer and understory. Leaf mass per

area (LMA) decreased significantly with height in both species and LMA was significantly greater in oak than in maple at all heights (data not shown). Mass-based leaf N concentrations did not vary with canopy height in either species (Fownes 1985).

Photon flux density in all four canopy layers was simulated for a typical summer day in Wisconsin with sunny conditions except for periodic cloudcover during the midday period (Figure 4). In the middle of the top layer of the canopy, PPF_D was between 700 and 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ between about 1000 and 1630 h (except for brief cloudy periods during midday). In the middle canopy strata, PPF_D was mostly between 300 and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ over the same time period, with irradiances between 100–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the lower canopy and less than 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$

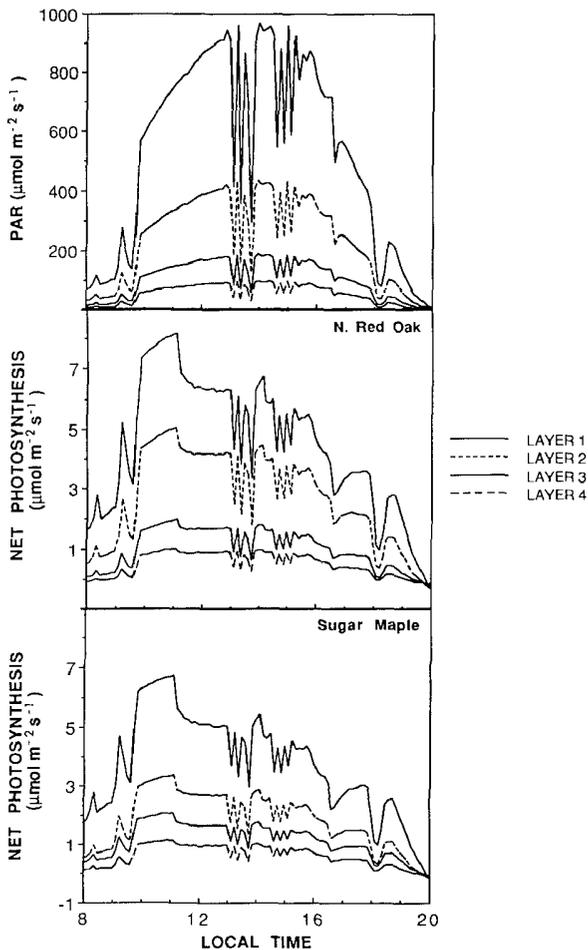


Figure 4. Simulated daily variation in photosynthetic photon flux density (PPFD) in the middle of four horizontal layers of a 30-m tall red oak-sugar maple forest (LAI = 5.1) on Blackhawk Island, Wisconsin for a representative summer day (August 17, 1989) (top); simulated daily variation in area-based net photosynthesis, by species, in the same four layers (middle and bottom).

in the understory.

Mean photosynthetic rates were simulated by species for each layer of the canopy (Figure 4). Photosynthetic rates on a leaf area basis decreased in both species with decreasing height in the canopy. The maximum simulated rates for the upper canopy were about 8 and 6.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for red oak and sugar maple, respectively. In the upper canopy in both species, maximum rates occurred about 1100 h and then declined during the remainder of the day. Examination of the simulation program indicated that the decline after 1100 h was largely the result of the effect of VPD on photosynthesis, with the remaining variation due to low irradiance during brief cloudcover.

The simulated daily pattern suggests that, on sunny days, the majority (> 60%) of photosynthesis in stand SM2 would occur in the upper layer of the canopy, with 86% occurring in the upper and middle layers combined (Figure 3). This distribution of carbon gain to the top of the canopy was almost entirely due to light extinction at lower layers. These results are consistent with estimates made for broad-leaved oak macchia vegetation in Portugal (Caldwell et al. 1986). In that study, 30% of the canopy (LAI of 5.4) was unshaded, and on a sunny summer day the unshaded portion of the canopy contributed two thirds of the total canopy carbon gain. In the Wisconsin forest with an LAI of 5.1, the upper canopy layer comprised 31% of the total canopy and contributed 62% of the total canopy carbon gain. Red oak was responsible for most of the net photosynthesis in the upper two layers of the canopy with sugar maple almost entirely responsible for positive photosynthesis in the lower canopy and understory.

Total canopy photosynthesis was simulated by summing integrated net photosynthesis of each canopy layer. Despite having less than two thirds the total leaf area of sugar maple, the contribution of red oak to total canopy photosynthesis (per unit ground area) was almost double that of maple. Two trends can largely account for this. First, and most important, red oak foliage was proportionally distributed in the canopy at greater heights than sugar maple. Second, red oak has greater LMA and leaf N concentration than sugar maple, both of which lead to greater photosynthesis for a given leaf area under the current model assumptions, even for identical canopy distributions.

Canopy structure and simulated canopy carbon gain are also shown in Figure 3 for two other stands. Although the vertical distributions of LAI in these stands differed from that in stand SM2, the vertical distribution of simulated canopy carbon gain was similar. In all three stands, sugar maple made a proportionally greater contribution to lower canopy and understory photosynthesis than to the LAI of the respective layers (Figure 3).

Ozone

Simulations of canopy photosynthesis were made for forest stand SM2 using an idealized radiation regime (see Methods) under four hypothetical ozone regimes. In each case, it was assumed that the forest was previously exposed for 12-h per day for 90 consecutive days to ozone, with mean exposure concentrations of either 0.035,

0.050, 0.065, or 0.080 ppm. The lowest ozone concentration was chosen to represent the concentration in unpolluted air under Wisconsin climatic conditions, with the other three concentrations representing more or less the range in mean summertime ozone concentration across much of humid North America (Reich 1987). The three higher ozone concentrations thus represent increases of 16.2, 32.4, and 48.6 ppm-h, respectively, in total dose above background. It was assumed that ozone concentrations on average are similar throughout the canopy (although the model was later altered to evaluate how ozone extinction in the canopy would affect canopy response; see Table 2). Two different simulations were run to predict "best-case" and "worst-case" scenarios. In one simulation, the effects of ozone exposure on photosynthetic capacity were treated as a linear function of cumulative dose (Reich 1983, 1987), whereas in the other simulation they were treated as a linear function of mean exposure concentration, as observed for sugar maple (Reich et al. 1986). In the former case, the influence of ozone exposure would become progressively greater over the hypothetical 90-day period, whereas in the latter scenario, the ozone effect would be relatively stable over time. Despite the importance of leaf conductance to ozone uptake and hence sensitivity (Reich 1987), in the present version of the model we chose to treat ozone response as a function of dose rather than uptake, because

Table 2. Simulated daily net carbon balance per unit ground area ($\text{mmol m}^{-2} \text{day}^{-1}$) for canopy layers in a 30-m tall oak-maple forest under several ambient ozone regimes and as affected by potential ozone extinction in the canopy (oak and maple data pooled).

Scenario	Under-story	Lower canopy	Middle canopy	Upper canopy	Total canopy	Percent change
<i>Background O₃</i> (0.035 ppm)						
	1.3	30.0	69.2	244.2	344.8	
<i>No O₃ extinction in canopy</i> (0.05 ppm)						
Dose-dependent	0.9	23.9	55.7	198.6	279.2	-19.0
Dose-independent	1.2	28.5	65.9	233.0	328.7	-4.7
<i>(0.65 ppm)</i>						
Dose-dependent	0.6	17.9	42.2	152.9	213.7	-38.0
Dose-independent	1.1	27.0	62.6	221.8	312.5	-9.4
<i>(0.08 ppm)</i>						
Dose-dependent	0.3	12.0	28.8	107.4	148.4	-57.0
Dose-independent	1.0	25.5	59.2	210.5	296.3	-14.1
<i>O₃ extinction vertically through canopy</i> (0.08 ppm)						
Dose-dependent	1.3	23.9	42.2	107.4	174.8	-49.3
Dose-independent	1.3	28.5	62.6	210.5	302.9	-12.2
<i>Total O₃ extinction below upper canopy layer</i> (0.08 ppm)						
Dose-dependent	1.3	30.0	69.2	107.4	207.9	-39.7
Dose independent	1.3	30.0	69.2	210.5	311.1	-9.8

this does not require consideration of leaf conductance and the model also does not require estimation of this parameter. Effects on dark respiration rate (Reich 1983, Amthor and Cummings 1988) were a function of current and recent exposure concentrations.

Simulated chronic ozone pollution had different effects on the total daily carbon balance of the four canopy layers (Table 2). Under the "worst-case" dose-dependent scenario, simulated chronic exposure to 0.08 ppm ozone reduced total daily canopy net carbon gain by 57%, whereas under the dose-independent scenario, total carbon gain was reduced by 14%. Under either scenario, reductions in net photosynthesis in the top layer of the canopy were responsible for 70% of the decrease, with lower carbon gain in the middle and lower layers accounting for 20 and 10% of the total decrease, respectively. This reflects the importance of the higher canopy layers to total net carbon gain rather than a difference in ozone response between canopy layers.

It is unknown at present to what extent ozone concentrations vary vertically in tall forest canopies. If canopy foliage acts as an efficient "filter" for ozone, while substantially reducing air movement into the lower canopy, it is possible that ozone concentrations in the lower canopy and understory could be significantly lower than in the air above or at the top of the canopy. To determine how such an ozone extinction might affect canopy photosynthetic response to ozone, we ran simulations in which ambient ozone averaged 0.080 ppm and either all ozone above background was 100% depleted below the upper canopy layer or ozone was gradually depleted, so that concentrations were 0.080, 0.065, 0.050, and 0.035 ppm in the upper, middle, lower, and understory layers, respectively. If ozone extinction occurs, we believe the latter scenario is the more likely of the two. Again, because of the predominance of the upper canopy layer on total daily carbon balance, simulated ozone extinction had a relatively modest impact on total daily carbon balance (Table 2). Gradual ozone depletion in the canopy would reduce the adverse impact of chronic 0.08 ppm ozone on total canopy carbon balance from -57 to -49% under the dose-dependent scenario and from -14 to -12% under the dose-independent scenario.

From these simulations we offer the following predictions about the interaction of canopy position and ozone exposure. (1) Because of the importance of the upper and middle canopy to the carbon balance, ozone effects on total canopy carbon balance will predominantly result from its effects on the upper canopy layers, and (2) for plants in the understory or lower canopy (such as seedlings, saplings, and understory dominant shrubs and trees), ozone can still have significant effects on carbon balance.

Multiple stand comparison

Estimated leaf area indices (LAI), totalled and by species, for seven south-central Wisconsin hardwood stands are shown in Figure 5. The seven stands varied in LAI from 4.5 to 6.8. In all stands, oak-maple species represented at least 60% of LAI. Total daily canopy carbon gain was simulated from the four canopy layers and expressed on a per unit ground area basis. In all seven stands, the upper and middle

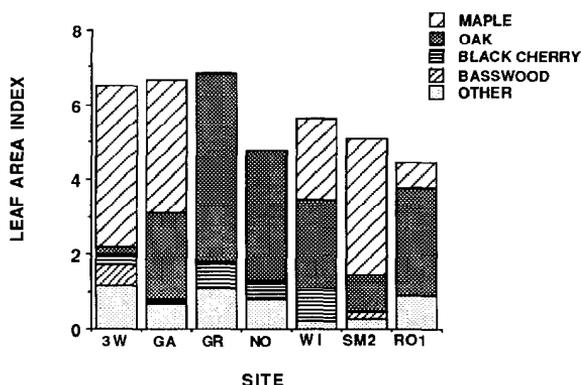


Figure 5. Total leaf area index and contribution by species for seven forest stands in Wisconsin. Labels after Fownes (1985); SM2, Sugar Maple 2, Blackhawk Island; 3W, Beltline Sugar Maple, U.W. Arboretum; GA, Gallistel Woods, U.W. Arboretum; GR, Grady Tract, U.W. Arboretum; NO, Noe Woods, U.W. Arboretum; WI, Wingra Woods, U.W. Arboretum; RO1, Red Oak 1, Blackhawk Island.

canopy layers accounted for between 78–86% of total canopy net photosynthesis (Figure 3 and data not shown). Variation in total canopy daily carbon gain was positively linearly correlated ($r^2 = 0.55$) with N availability (Figure 6). Neither canopy carbon gain nor total aboveground net primary production (ANPP) were significantly related to either total LAI, total canopy leaf mass, or total canopy N (data not shown). However, simulated daily canopy carbon gain was correlated with the total N in the upper canopy layer ($r^2 = 0.68$, Figure 6). Total aboveground net primary production was well correlated with both total N in the upper canopy layer and with simulated canopy carbon gain ($r^2 \geq 0.90$ in both cases, Figure 7). Wood production alone was also linearly correlated with simulated canopy carbon gain ($r^2 = 0.71$, data not shown). Because fine root production (using an N budget method) and ANPP in 11 Wisconsin forest stands (including several of those included in our

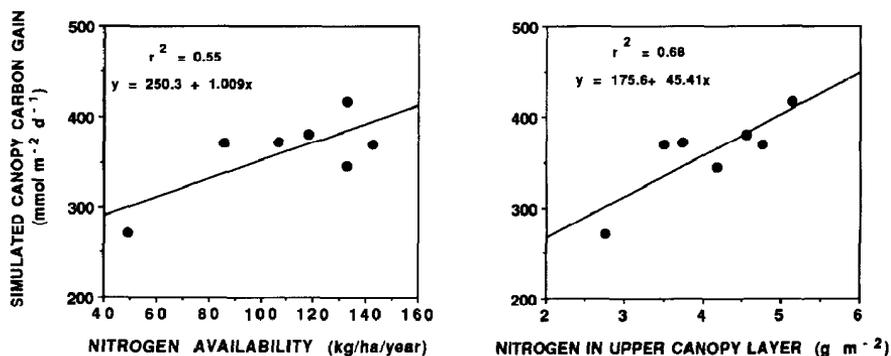


Figure 6. Simulated daily canopy carbon gain for a representative summer day in relation to N availability (left) and total N in the upper canopy layer (right) for seven deciduous forest stands. Data on N availability from Pastor et al. (1984), Lennon et al. (1984), Nadelhoffer et al. (1985) and Fownes (1985).

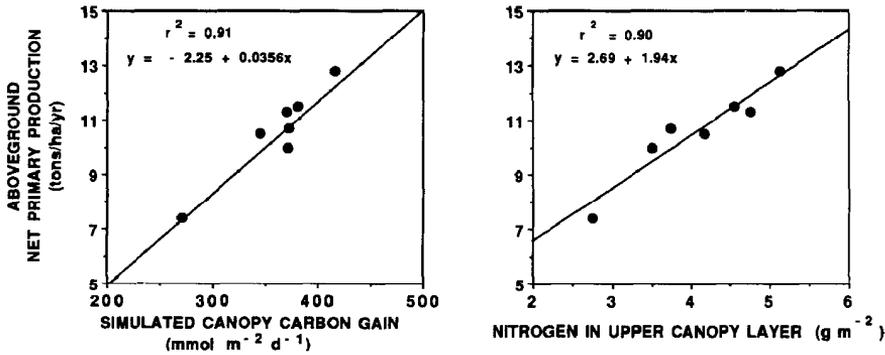


Figure 7. Aboveground net primary production ($\text{Mg ha}^{-1} \text{ year}^{-1}$) in relation to simulated daily canopy carbon gain (left) and total N in the upper canopy (right) for seven deciduous forest stands.

study) both increase with N availability (Aber et al. 1985), largely in parallel, this suggests that total net primary production is also likely to be correlated with both canopy carbon gain and N in the upper canopy layer.

Why are total canopy LAI, leaf mass, and leaf N not correlated with either simulated canopy carbon gain or estimated ANPP among the seven oak–maple stands? Leaf area index has been correlated with ANPP when comparisons of widely divergent forests are made (Gholz 1982), and with stemwood production in loblolly pine (Vose and Allen 1988). Similarly, ANPP was linearly correlated with leaf biomass for 16 loblolly pine stands across a range of sites, ages, and locations (Teskey et al. 1987). In our study, total LAI may be poorly related to either the short- (simulated daily canopy carbon gain) or long-term (ANPP) indices of aboveground productivity for at least two reasons.

(1) For a given LAI in a given canopy layer, different species (e.g., oak *versus* maple) have substantially different leaf mass and leaf N concentration, which may influence photosynthetic production. For example, for maple and oak species in the upper canopy, within or among stands, greater LMA and percent leaf N in oak result in roughly 30–100% greater leaf N/area. Because area-based net photosynthetic capacity is linearly related to area-based leaf N in these species (Reich et al. 1991), this results in a roughly 30–100% greater net photosynthetic capacity in oak as well. Also, on an individual tree basis, ANPP was greater per unit leaf area in red oak than sugar maple (Chapman 1990). Thus, for a given LAI in the upper canopy, a stand dominated by oak may have greater net photosynthesis or ANPP than one dominated by maple (Figure 3).

(2) Vertical distribution of LAI within canopies can vary because of site history, succession, stand age, and other factors in a fashion that confounds possible relationships between LAI and production, such as occur for stands of similar history, age, stocking, etc. An example of this might be a site with a high LAI in the lower canopy and understory, such as stand 3W. Despite a total LAI 1.4 times greater than stand SM2 (Figure 3), both ANPP and simulated canopy carbon gain were less in stand

3W. Moreover, because leaf biomass was not correlated with ANPP or canopy carbon gain for the seven oak-maple sites, this suggests that variation in leaf N concentration among species coupled with variation in vertical distribution of foliage may partially explain the lack of relationship of whole canopy foliar indices with simulated canopy photosynthesis or ANPP.

The strong correlations between estimated ANPP, upper canopy N pool, and simulated canopy carbon gain suggest that the amount of N in the sunlit part of the canopy determines canopy photosynthesis and ANPP. Such a mechanism may be widespread or it may be restricted to N-demanding systems such as the oak-maple forests in this study.

The exercises undertaken with this first version of the model were valuable in suggesting that components of the model were successful in predicting photosynthesis under several scenarios, in providing a quantitative means for developing hypotheses about ozone effects on forest canopies, and in providing a means for comparing canopy net CO₂ exchange capacities with other measures of stand productivity and resource availability. Stand modeling could provide an important basis for forest management decisions at the stand and landscape scales as well as providing insight into environmental problems.

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