Simulating the response of mature yellow poplar and loblolly pine trees to shifts in peak ozone periods during the growing season using the TREGRO model

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Summary  Multiple TREGRO simulations were conducted with meteorological data files containing different growing season peak ozone (O₃) episodes at O₃ exposures of 1.0 and 2.0× ambient O₃ to assess the relationship between O₃ response and the phenology of mature yellow poplar (Liriodendron tulipifera L.) and loblolly pine (Pinus taeda L.) trees. Regardless of O₃ exposure and peak O₃ episode occurrence, a peak O₃ episode in August caused the greatest reduction in carbon (C) gain in yellow poplar, whereas a peak O₃ episode in July caused the greatest reduction in C gain of loblolly pine. In both species, timing of the greatest simulated O₃ effect corresponded with the completion of the annual foliage production phenophase.

Simulated C gain of yellow poplar (total tree, coarse root, and total nonstructural carbohydrate) was reduced by O₃ to a greater extent than the corresponding compartments in loblolly pine, but the opposite was true for fine roots. This differential sensitivity to O₃ reflects the fact that both C assimilation and the O₃ response of the species were parameterized according to observed field measurements of each species. The differential sensitivity to O₃ of these species may have long-term implications for species composition in southeastern USA forests.

Keywords: air pollutants, Liriodendron tulipifera, phenology, Pinus taeda, total nonstructural carbohydrates.

Introduction

Industrial activity resulting in the release of ozone (O₃) precursors over the past century has increased the background O₃ concentrations from 20–40 to 40–60 ppb, a trend that is expected to continue into the next millennium (National Academy of Science 1992). Although O₃ production is centered in industrial areas, prevailing wind can transport O₃ to remote agricultural and forest ecosystems. Currently, O₃ is estimated to cause in excess of 3 billion dollars per year in agricultural crop losses (Heck et al. 1991), but the long-term effects of O₃ on forest species and ecosystems are less clear (Taylor et al. 1994).

Patterns of tropospheric O₃ concentration typically display an annual cycle in which the lowest O₃ concentrations occur during winter and the highest concentrations occur during summer. In the southeastern United States, summer climatic conditions of elevated temperatures, stagnant air masses, and high concentrations of NOₓ and volatile organic carbon compounds originating from natural and anthropogenic sources (Fehsenfeld et al. 1994) can elevate tropospheric O₃ concentrations fourfold over those occurring during the winter. In addition to environmental conditions that favor the production of tropospheric O₃, there are also intra- and inter-seasonal variations caused by variations in the concentrations of O₃ precursors and their proximity to the measuring station (Fehsenfeld et al. 1994). A consequence of the variability in O₃ formation is the difficulty in examining the relationship between growing season O₃ exposure (especially periods of peak O₃ episodes) and its effect on growth of forest tree species.

Total pollutant exposure is frequently described as the product of pollutant concentration and duration of exposure. However, because the primary avenue for O₃ entry into the plant is through the stomata (Rubin et al. 1996), O₃ injury is probably related to the product of stomatal conductance, leaf area, and O₃ exposure concentration. Therefore, the phenology of leaf area, conductance, and O₃ play a major role in determining injury. Experimental studies with Phaseolus vulgaris L. have shown that O₃ exposure profiles containing peak events result in greater injury than exposures with uniform profiles (Musselman et al. 1983, 1994), indicating that experimental exposures lacking peak episodes may underestimate the effects of O₃ on plant growth. Although the importance of peak events has been documented (Musselman et al. 1983, 1994), the interaction between peak events and phenology is unclear.

Two important forest tree species in the southeastern USA are yellow poplar (Liriodendron tulipifera L.) and loblolly pine (Pinus taeda L.). Both species are sensitive to O₃ in experimental studies (Chappelka et al. 1985, Chappelka et al...
1988, Sasek et al. 1991, Tjoelker and Luxmoore 1992, Cannon et al. 1993, Dizengremel et al. 1994, McLaughlin et al. 1994, Taylor 1994). Yellow poplar is a broadly distributed hardwood species with indeterminate leaf growth, whereas loblolly pine is a widely planted coniferous species that exhibits determinate foliar growth and is found together with yellow poplar on moist well-drained sites (Baker and Langdon 1990). Both species grow rapidly, are found in early successional environments, and may compete directly for available resources.

Because the interaction between tree phenology, growth habit, and episodic peak O\textsubscript{3} events is unclear, we examined how yellow poplar and loblolly pine would respond to variations in the occurrence of growing season peak O\textsubscript{3} episodes. We hypothesized that the contrasting phenology and growth habits of these species differentially affects their sensitivity to variations in the timing of a peak O\textsubscript{3} episode during the growing season. Because studies of this nature on mature trees in the field are difficult and expensive to conduct, we used the simulation model TREGRO (Weinstein et al. 1991) to assess: (1) whether there is a critical exposure period during the growing season that will result in increased O\textsubscript{3} response, and (2) what role phenology plays in the O\textsubscript{3} response of these species.

Materials and methods

TREGRO description

TREGRO is a physiological simulation model of the carbon (C), water, and nutrient fluxes of an individual tree that was developed to analyze the responses of trees to multiple environmental stresses. In the model, the tree is divided into compartments: a canopy of leaves grouped by age class, branches, stem, and coarse and fine roots in three soil horizons. In each compartment, the model keeps track of three C pools: structure (living, respiring tissue); wood (the non-respiring tissue); and total nonstructural carbohydrate (TNC). The model uses the Farquhar equations (Farquhar et al. 1980) to calculate C assimilation of the entire tree each hour as a function of ambient environmental conditions and the availability of light in the canopy, water, and nutrients. Carbon is redistributed daily within the plant for respiration, growth, storage, and replacement of senescent tissues. Priority for the C varies inversely with the distance between source and sink and varies directly with relative sink strength.

In TREGRO, the interaction between tree growth and the environment is achieved through the linkage of separate data files. The parameter file defines species-specific characteristics including (but not limited to): maximum photosynthetic rate, rates of maintenance and growth respiration, specifics of nutrient uptake kinetics, phenological patterns of growth, growth rates of individual tree compartments, photosynthetic response to O\textsubscript{3}, initial patterns of C allocation among compartments, and C partitioning within compartments among living structure, dead wood, and C reserves (TNC). The meteorological file defines the site-specific hourly environmental conditions including air temperature (°C), relative humidity (%), rainfall (mm), photosynthetic photon flux density (µmol m\textsuperscript{-2} s\textsuperscript{-1}), and O\textsubscript{3} concentration (ppb). In the present study, all TREGRO simulations were 3 years in length and used a meteorological data file collected on-site at Oak Ridge, TN, in 1989; for each subsequent year of simulation, the 1989 conditions were repeated.

TREGRO parameterization

The biomass and C allocation of the initial yellow poplar and loblolly pine trees were set in the TREGRO model. The simulation target was to grow a yellow poplar tree and a loblolly pine tree with three annual biomass increments. For the yellow poplar target tree, we set the annual diameter at breast height (dbh) increment at 0.30 cm year\textsuperscript{-1} and the height increment at 23 cm year\textsuperscript{-1} (Beck 1990). For the loblolly pine target tree, we set the annual dbh increment at 0.61 cm year\textsuperscript{-1} (Clark 1992). Biomass gain of all other tree compartments was estimated from the stem biomass (yellow poplar) or dbh increment (loblolly pine) assuming that no change occurred in the allometric relationships during the simulation period (Tables 1 and 2) (Clark and Schroeder 1977, Van Lear et al. 1986, Vogt 1991).

Initial tree biomass

The initial yellow poplar tree was estimated to be approximately 30 m tall, 41 cm in dbh, and 50 years old (Clark and Schroeder 1977, Beck 1990), with a mean crown radius of approximately 4.2 m (Trimble and Tryon 1966). Total tree biomass in midsummer was allocated at 1.91% foliages, 17.84% branch, 62.14% stem, 13.57% coarse root, and 4.53% fine root (Clark and Schroeder 1977, Vogt 1991). Leaf area was calculated from specific leaf area (Kolb and Steiner 1990) and foliar biomass. Tree biomass in each component was further partitioned into TNC, structure, and wood (in woody tissue). The proportion of wood in the initial tree’s stem, branches, and coarse (woody) roots (36.6%) was set to that reported for the stem by Panshin and de Zeeuw (1980). The remainder of the initial biomass was divided between TNC and structure. The TNC represented 30% of structure in the stem, branch, and coarse roots and 20% of structure in the foliage based on reported starch concentrations in roots (Jensen and Patton 1990) and TNC concentrations in foliage (Wullschleger et al. 1992) of yellow poplar trees.

Biomass of the initial loblolly pine tree was based on the dbh (25 cm) of dominant and codominant loblolly pine trees growing in South Carolina (latitude 34°). A tree of this dbh is approximately 40 years old and 21 m in height (Van Lear et al. 1986) with a mean crown radius of approximately 3.2 m (Smith et al. 1992). Initial biomass of individual tree components (foliage, branch, stem, and coarse and fine root) was calculated from dbh-based allometric equations derived from loblolly pine trees originally growing in South Carolina (Van Lear et al. 1986). The root component was further partitioned into 89 and 11% in coarse and fine roots, respectively (Van Lear and Kapeluck 1995). Foliage biomass was divided into four classes as described by Higginbotham (1974). Leaf area and specific leaf area were calculated from foliar biomass by regression equations from measurements of Blanche et al. (1985). Tree biomass in each component was further parti-
Table 1. Initial and final biomass and 3-year C gain values from literature allometric data and the resulting TREGRO model 3-year C gain and the percent estimate for a simulated 50–53-year-old yellow poplar tree.

<table>
<thead>
<tr>
<th>Component</th>
<th>Values from allometric equations (g C)</th>
<th>Model C Gain (g C)</th>
<th>% Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial biomass</td>
<td>Final biomass</td>
<td>3-Year C gain</td>
</tr>
<tr>
<td>Stem</td>
<td>395254</td>
<td>421759</td>
<td>26505</td>
</tr>
<tr>
<td>Branch</td>
<td>113475</td>
<td>121084</td>
<td>7609</td>
</tr>
<tr>
<td>Foliage</td>
<td>12149</td>
<td>12964</td>
<td>815</td>
</tr>
<tr>
<td>Root total</td>
<td>115128</td>
<td>122848</td>
<td>7720</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>86314</td>
<td>92102</td>
<td>5788</td>
</tr>
<tr>
<td>Coarse root total</td>
<td>43157</td>
<td>46051</td>
<td>2894</td>
</tr>
<tr>
<td>Coarse root A</td>
<td>43157</td>
<td>46051</td>
<td>2894</td>
</tr>
<tr>
<td>Coarse root B1</td>
<td>28814</td>
<td>30746</td>
<td>1932</td>
</tr>
<tr>
<td>Fine root total</td>
<td>14407</td>
<td>15373</td>
<td>966</td>
</tr>
<tr>
<td>Fine root A</td>
<td>14407</td>
<td>15373</td>
<td>966</td>
</tr>
<tr>
<td>Fine root B1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Fine root B2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total tree</td>
<td>636006</td>
<td>678655</td>
<td>42649</td>
</tr>
<tr>
<td>Total aboveground</td>
<td>520878</td>
<td>555807</td>
<td>34929</td>
</tr>
</tbody>
</table>

3-Year C gain = final biomass – initial biomass.
% Estimate = ((model C gain – 3-year allometric C gain)/3-year allometric C gain)100.
Values represent g C (mass = 2 times g C).
Root total = coarse root total + fine root total.
Coarse root total = coarse root A + coarse root B1.
Fine root total = fine root A + fine root B1 + fine root B2.
Total tree = stem + branch + foliage + root total.
Total aboveground = stem + branch + foliage.

Table 2. Initial and final biomass and 3-year C gain values from literature allometric data and the resulting TREGRO model 3-year C gain and the percent estimate for a simulated 41–44-year-old loblolly pine tree.

<table>
<thead>
<tr>
<th>Component</th>
<th>Values from allometric equations (g C)</th>
<th>Model C Gain (g C)</th>
<th>% Estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Initial biomass</td>
<td>Final biomass</td>
<td>3-Year C gain</td>
</tr>
<tr>
<td>Stem</td>
<td>116267</td>
<td>140421</td>
<td>24154</td>
</tr>
<tr>
<td>Branch</td>
<td>13181</td>
<td>18165</td>
<td>4984</td>
</tr>
<tr>
<td>Foliage</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Class 1</td>
<td>1391</td>
<td>1742</td>
<td>351</td>
</tr>
<tr>
<td>Class 2</td>
<td>1844</td>
<td>2310</td>
<td>466</td>
</tr>
<tr>
<td>Root total</td>
<td>33225</td>
<td>40869</td>
<td>7644</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>29570</td>
<td>36373</td>
<td>6803</td>
</tr>
<tr>
<td>Coarse root total</td>
<td>23360</td>
<td>28735</td>
<td>5375</td>
</tr>
<tr>
<td>Coarse root A</td>
<td>6210</td>
<td>7638</td>
<td>1428</td>
</tr>
<tr>
<td>Coarse root B1</td>
<td>3654</td>
<td>4496</td>
<td>842</td>
</tr>
<tr>
<td>Fine root total</td>
<td>2595</td>
<td>3192</td>
<td>597</td>
</tr>
<tr>
<td>Fine root A</td>
<td>694</td>
<td>854</td>
<td>160</td>
</tr>
<tr>
<td>Fine root B1</td>
<td>365</td>
<td>450</td>
<td>85</td>
</tr>
<tr>
<td>Fine root B2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total tree</td>
<td>165908</td>
<td>200507</td>
<td>37599</td>
</tr>
<tr>
<td>Total aboveground</td>
<td>132683</td>
<td>162638</td>
<td>29955</td>
</tr>
</tbody>
</table>

3-Year C gain = final biomass – initial biomass.
% Estimate = ((model C Gain – 3-year allometric C gain)/3-year allometric C gain)100.
Values represent g C (mass = 2 times g C).
Root total = coarse root total + fine root total.
Coarse root total = coarse root A + coarse root B1.
Fine root total = fine root A + fine root B1 + fine root B2.
Total tree = stem + branch + foliage + root total.
Total aboveground = stem + branch + foliage.
tioned into TNC, structure, and wood (in woody tissue). The proportion of wood in the initial tree’s stem, branches, and coarse (woody) roots (57%) was set to that reported for the stem by Blanche et al. (1985). The remainder of the initial biomass was divided between TNC and structure. The TNC represented 30% of structure in the stem, branch, and coarse roots and 20% of structure in the foliage based on reported TNC concentrations in coarse roots, stem, and foliage of loblolly pine trees (Friend et al. 1992).

Soil parameters
The soil rooting area of yellow poplar and loblolly pine (55.9 and 31.7 m², respectively) was defined to be identical to the projected crown area, assuming a crown radius of 4.2 and 3.2 m (Trimble and Tryon 1966, Smith et al. 1992) and a uniform circular-shaped crown (cf. Retzlaff et al. 1996).

Depths of the A, B1, and B2 soil horizons were set to 0.2, 0.2, and 0.3 m, respectively, based on average measured soil depths in southeastern loblolly pine stands (Harris et al. 1977). Soil water and nutrient conditions were set to be nonlimiting in all of the simulations.

Seasonal phenology
Initial seasonal foliage growth of mature yellow poplar trees begins in mid-April and the majority (> 80%) of foliage is produced by mid-July (Lamb 1915, Kienholz 1941). The remainder (=20%) of the foliage biomass is produced during the latter part of the growing season when conditions are favorable. Height and radial growth begin in mid-May (Kienholz 1941, Morrow and McKee 1963, Mowbray and Oosting 1968) and continue until approximately mid-September (Morrow and McKee 1963, Lieth and Radford 1971). Root growth occurs from spring to fall when conditions are favorable (Harris et al. 1977). Foliage senescence occurs during the second week in October (Lamb 1915). Yellow poplar trees senesce all current foliage.

Mature loblolly pine trees produce two cohorts of foliage per year with bud break of the first flush of foliage occurring in early spring (Higginbotham 1974). The first flush ends in early May and the second foliage flush initiates in mid-May and continues until mid-June (Higginbotham 1974). Height and radial growth begin soon after bud break of the first flush of foliage and continue until late July (Miller et al. 1987). Root growth occurs from spring to fall when conditions are favorable (Harris et al. 1977, Baker and Langdon 1990). Foliage senescence occurs late in the season with needle-cast occurring at the end of the growing season (approximately mid-November–early December) (Higginbotham 1974). Loblolly pine trees senesce all 2-year-old foliage, retaining only current-year foliage over winter.

Carbon assimilation
Yellow poplar net C assimilation for a midsummer 11-day period at high irradiance (1000 µmol m⁻² s⁻¹; 25–30 °C) was set to be approximately 0.0192 g C g⁻¹ C_leaf h⁻¹, based on values recorded by Cannon et al. (1993), Chappelka et al. (1988), Gunderson et al. (1993), Neufeld et al. (1985), Norby and O’Neill (1991), Tjoelker and Luxmoore (1992), and Wullschleger et al. (1992). Leaf respiration was set at 22% of net C assimilation (Wullschleger et al. 1992, Cannon et al. 1993).

Loblolly pine net C assimilation for a midsummer 11-day period at high irradiance (1000 µmol m⁻² s⁻¹; 25–30 °C) was set to be approximately 0.0035 g C g⁻¹ C_leaf h⁻¹ (Cregg et al. 1993). Leaf respiration was set at 25% of net C assimilation (Samuelson et al. 1992).

The final TREGRO simulated trees were calibrated by adjusting tissue growth rates and senescence rates in fine roots until two conditions were met: (1) when the simulated C gain of each of the tree components (foliage, branch, stem, and coarse and fine roots) and the total tree C gain was within 10% of the value for projected C gain from the literature-based allometric relationships (Tables 1 and 2), and (2) when the proportion of TNC and the ratio of structure to wood in each of the tree components at the end of a simulation matched that parameterized for the tree at the beginning of the simulation. Fine root senescence was set to approximate one complete root turnover per year for both species based on field measurements (Harris et al. 1977).

Ozone simulations
In TREGRO, effects of O₃ are simulated through a cumulative effect of the pollutant on the maximum rate of photosynthesis, V₃₃₃. The magnitude of the O₃ effect is controlled by a threshold of cumulative O₃ uptake, below which there is no effect on V₃₃₃ and a linear decrease in V₃₃₃ above this threshold with increasing cumulative uptake of O₃. Although O₃ does not accumulate in the leaf tissue, the effect of cumulative O₃ uptake is proportional to the sum of the hourly O₃ concentration times the foliar rate of O₃ conductance, because the primary avenue for O₃ entry is through the stomata (Rubin et al. 1996).

To evaluate the effect of the maximum O₃ response possible, we assumed that V₃₃₃ began decreasing as soon as any O₃ uptake occurred in the leaves (i.e., the O₃ threshold was zero). As the total amount of cumulative O₃ uptake increased during the growing season, we assumed a proportional decrease in V₃₃₃. The slope of the described response was set so that the reduction in photosynthesis observed at the end of the open-top chamber experiments matched the simulated reduction after a similar cumulative uptake of O₃ had occurred.

The yellow poplar response to O₃ was set in the parameter file according to the data of Cannon et al. (1993) (Figure 1), who measured a 10% reduction in net photosynthesis of seedlings relative to charcoal-filtered air after a total cumulative O₃ uptake of 0.0044 g g⁻¹ C_leaf. The loblolly pine response to O₃ was set in the parameter file according to the data of Sasek et al. (1991) (Figure 1), who measured a 24% reduction in current leaf net photosynthesis relative to that of seedlings in charcoal-filtered air after a total cumulative O₃ uptake of 0.0136 g g⁻¹ C_leaf.

In the simulation experiment, one short-term (8 day) peak O₃ episode was used in which O₃ concentrations increased and...
decreased in a normal diurnal pattern (for Oak Ridge, TN, 1989), with maximum O$_3$ concentrations of 125 ppb for between 3 and 8 h per day (Figure 2). All meteorological data in the Oak Ridge meteorological file, including the O$_3$ concentrations, were used to create the 8-day O$_3$ peak episode profile. The peak O$_3$ episode was placed in seven different (Oak Ridge, TN, 1989) meteorological files to produce peak O$_3$ exposures centered on the first day of each month between April 1 and October 1. To insert the peak O$_3$ episode, we simply substituted all the existing meteorological data during the insertion period with the peak meteorological data thereby avoiding the problem of mismatching environmental and O$_3$ data. However, because the overwritten areas at different times of the year do not contain identical recorded O$_3$ concentrations, there is slight variation (up to 3.7%) in the sum00 (sum00 = cumulative sum of hourly O$_3$ values during the growing season) O$_3$ exposure among files between the highest (123402 ppb-h) and lowest (118975 ppb-h) sum exposure. During the 1989 growing season, in the absence of our artificial O$_3$ peak, there were no episodic periods of highly elevated O$_3$ concentration (maximum recorded hourly concentration 88 ppb O$_3$); however, O$_3$ concentrations (up to 132 ppb) were measured at Oak Ridge, TN, in 1988. Model simulations (3-year duration) were performed with each of these altered meteorological files using O$_3$ concentrations of 0.0 (base case), 1.0, and 2.0 times the measured (1989) Oak Ridge, TN, ambient O$_3$ concentrations (3 O$_3$ concentrations × 7 meteorological files = 21 total simulations). Use of a 0.0 × O$_3$ exposure, although unrealistic in a field study, permitted determination of the maximum O$_3$ response possible.

Results and discussion

Matching phenology to reported values

We matched phenology parameters in the base TREGRO trees with those reported in the literature for both tree species. For instance, mature loblolly pine trees produce two cohorts of foliage per year with bud break of the first flush of foliage occurring in the early spring (Day of Year (DOY) 60) and ending on approximately DOY 135 (Higginbotham 1974). The second foliage flush initiates on approximately DOY 135 and continues until DOY 184 (Higginbotham 1974). Further, initial seasonal foliage growth of mature yellow poplar trees begins on DOY 99 and the majority (> 80%) of the foliage is produced by DOY 206 (Lamb 1915, Kienholz 1941). The remainder (< 20%) of the foliage biomass is produced during an additional period (DOY 207 to 246) of shoot growth. By setting the initial base-tree parameters using this and other phenological information, we were able to reproduce these demographic patterns accurately with TREGRO (Figure 3).

Phenological development is a complex phenomenon governed by a suite of environmental cues. TREGRO duplicates this process as controlled by the accumulation (from the start of simulation) of heat degree-days above 0°C. Therefore, we were able to parameterize mature yellow poplar and loblolly pine trees in TREGRO, simulate growth for a period of 3 years.
and duplicate the dynamics of phenological processes that are currently reported in the literature for individual yellow poplar and loblolly pine trees. Accurate simulation of dynamic phenological processes with TREGRO permitted investigation of the interaction between phenophase and episodic environmental (O₃) stress.

**Ozone simulations**

In our simulations, the presence of atmospheric O₃ (1.0 or 2.0 × ambient), regardless of timing of the peak O₃ episode, reduced total tree C gain (Figure 4), coarse root C gain (Figure 5), and tree TNC compartments (Figure 6) compared to the control trees of both species. Carbon gain of fine roots of both species was not affected at 1.0 × ambient O₃ (Figure 7). Additionally, as the O₃ concentration increased (to 2.0 × ambient), the O₃ effects (reflected by additional reductions in total tree, coarse root, fine root, and TNC C gain) became more pronounced. Negative C gain of the coarse roots, TNC and fine roots compartments reflects utilization of previously stored TNC and root turnover without replacement, respectively. It is known from field-exposure experiments that seedlings and saplings of both species, and branches of mature loblolly pine trees are sensitive to O₃ (Chappelka et al. 1985, Chappelka et al. 1988, Sasek et al. 1991, Tjoelker and Luxmoore 1992, Cannon et al. 1993, Dizengremel et al. 1994, McLaughlin et al. 1994). However, the simulation experiment represents the first time that the O₃ responses of whole mature trees of these species have been examined. McLaughlin and Downing (1995) studied changes in loblolly pine stem diameter during a 5-year period in the Oak Ridge, TN area, which included the 1989 conditions used in our modeling study, and found that ambient exposure in the field in combination with elevated temperature or low rainfall was associated with reduced stem increment. We do not know whether our simulated estimates of physiological responses accurately reflect the O₃ response that would occur in mature forest-grown trees. Hanson et al. (1994) have shown that gas exchange of mature red oak (Quercus rubra L.) trees exposed to O₃ is affected more by O₃ than similarly exposed red oak seedlings, indicating that caution

**Figure 4.** Change in tree mass following a 3-year TREGRO simulation of mature loblolly pine and yellow poplar trees with no O₃ exposure and monthly peak O₃ episodes. The response illustrated for the October peak O₃ episode was identical to a 1.0 and 2.0 × ambient exposure at this site with no peak O₃ episode; therefore, values representing O₃ exposure without a peak episode are not shown.

**Figure 5.** Change in coarse root mass following a 3-year TREGRO simulation of mature loblolly pine and yellow poplar trees with no O₃ exposure and monthly peak O₃ episodes. Negative values reflect utilization of previously stored TNC.

**Figure 6.** Change in total nonstructural carbohydrate (TNC) following a 3-year TREGRO simulation of mature loblolly pine and yellow poplar trees with no O₃ exposure and monthly peak O₃ episodes. Negative values reflect utilization of previously stored TNC.
should be used when extrapolating the results of seedling exposure experiments to mature trees. However, the nature of our simulated responses (reduced root growth and TNC content of yellow poplar and loblolly pine trees) matches those proposed in a conceptual model of O₃ response (Cooley and Manning 1987), observed in O₃ experiments with woody plants (see Tingey et al. 1976, Mortenson and Skye 1990, Retzlaff et al. 1992), and predicted in other simulation exercises (Retzlaff et al. 1996).

Carbon gain of yellow poplar (total tree, coarse root, and TNC) was reduced by O₃ to a greater extent than the corresponding compartments in loblolly pine, reflecting the fact that we parameterized the C assimilation (e.g., yellow poplar: Wullschleger et al. 1992 and loblolly pine: Cregg et al. 1993) and the O₃ (e.g., yellow poplar: Cannon et al. 1993 and loblolly pine: Sasek et al. 1991) response parameters of the two species according to field measurements (Figure 1) (i.e., we parameterized yellow poplar to be more sensitive to O₃). This differential sensitivity to O₃ has implications for the competition between these two species as they co-occur and are exposed to elevated concentrations of tropospheric O₃ in the forest ecosystems in the southeastern USA.

**Phenological O₃ response**

The simulated response illustrated for the October peak O₃ episode was identical to a 1.0 and 2.0 × ambient exposure at this site with no peak O₃ episode; therefore, values representing O₃ exposure without a peak episode are not shown. Thus, the presence of peak O₃ episodes differentially altered C gain (Figure 4), and the growth of individual tree compartments (Figures 5–7) independently of the atmospheric O₃ concentration. Additionally, as the O₃ concentration increased to 2.0 × ambient, the effects corresponding to the timing of the peak O₃ episode became more pronounced. In our simulations, the peak O₃ episode in August caused the greatest reduction in C gain in yellow poplar, whereas the peak O₃ episode in July caused the greatest reduction in C gain of loblolly pine. Timing of the greatest simulated O₃ effect corresponded with the completion of the annual foliage production phenophase (and therefore maximum C assimilating foliage area) on each of these tree species (Figure 3). At the time of the July peak O₃ episode, the simulated loblolly pine tree had reached the seasonal maximum photosynthetic foliage biomass. At the time of the August peak O₃ episode, the simulated yellow poplar tree had produced approximately 90% of the seasonal maximum photosynthetic foliage biomass.

Similar seasonal sensitivity responses have been noted previously for annual crops exposed to water stress (Eck et al. 1987, Halim et al. 1989, Stirling et al. 1989) and O₃ (Blum and Heck 1980, Kohut and Laurence 1983, McLaughlin and Conathy 1983, Younglove et al. 1994). All of these studies demonstrate sensitivity (e.g., reduced biomass and crop yield) to the timing of the environmental stress, particularly when the stress corresponds with critical phenological stages. Our simulation is the first study to link peak O₃ episodes to a specific phenophase in mature trees.

Our simulations of peak O₃ episode events did not alter the phenology of the two tree species. Date of initiation, patterns, and durations of stem and fascicle elongation of loblolly pine seedlings were not affected by O₃ treatment (cf. Mudano et al. 1992). However in another study, loblolly pine seedlings exposed to 2.0 × ambient O₃ exhibited a delay in fine root production (Edwards et al. 1992). Atmospheric O₃ will not normally alter the timing of phenological events directly in TREGRO because the timing of the occurrence of phenological events is driven by the accumulation (from the start of simulation) of heat degree-days above 0 °C, a model feature that is unrelated to O₃ exposure. However, in our TREGRO simulations, phenology could have been altered if sufficient reductions in available C (current assimilate or stored TNC) had occurred, thereby making C unavailable at the start of a phenophase, or available C supplies were exhausted before phenophase completion.

The TREGRO simulations demonstrate that there is a critical peak O₃ exposure period for yellow poplar and loblolly pine that is linked to the phenology of these two species. We observed maximum O₃ response when the peak O₃ episode occurred at or near the completion of the annual foliage production phenophase. Such simulation studies are useful in identifying physiological responses to environmental stress heretofore unavailable because of cost and other limitations. Recent re-analysis of data from four field crop-loss yield trials identified that growth-stage-dependent phenological weighting of pollutant exposure may result in more effective predictions of O₃ exposure resulting in yield reductions (Younglove et al. 1994). Results from similar studies could be used to
elucidate further the mechanism(s) of the phenological response of plants to environmental stress.

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