PREDICTING THE EFFECTS OF TROPOSPHERIC OZONE ON FOREST PRODUCTIVITY IN THE NORTHEASTERN U.S.

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Abstract: It is widely believed that tropospheric ozone presents a significant anthropogenic stress on forest ecosystems. Although much information has been collected regarding ozone effects at the seedling and leaf level, we do not have a reliable means of estimating the effect on mature, native forests. For the present study, we incorporated leaf-level ozone response information into an ecosystem model of forest production known as PnET-II in order to make whole-forest predictions that account for factors such as light attenuation, canopy ozone gradients and water stress. We ran the model using ambient ozone data from 64 locations across New York and New England. Predictions indicate reductions in annual NPP of from 2 to 17 percent under mean ozone from 1987-1992. Reductions were greatest in southern portions of the region on soils where drought stress was absent.

INTRODUCTION

The formation of ozone in the lower atmosphere poses a serious threat to forest growth in industrialized regions. Controlled exposure studies have shown that concentrations observed in ambient air cause substantial reductions in plant productivity. Observed effects include decreased photosynthetic rates (Reich and Amundson 1985, Pell *et al.* 1992), impaired stomatal function (Reich and Lassoie 1984), decreased biomass production (Shafer 1987, Wang *et al.* 1985), visible foliar injury (Hill *et al.* 1970), and accelerated foliar senescence (Swank and Vose 1991).

Data from these studies have been used to establish response relationships whereby reductions in photosynthesis are related to ozone exposure levels (Reich 1987). However, these relationships by themselves are insufficient for predicting whole-forest growth effects. Factors such as light availability, photosynthetic capacity and ozone concentrations vary within a forest canopy, but the outcome of these interactions cannot be estimated from studies conducted on seedlings or individual branches alone (Pye 1988).

The purpose of this study was to combine leaf-level ozone response data with a physiologically-based forest ecosystem model known as PnET-II in order to allow ozone response relationships to interact with important canopy-level factors. Our approach was to summarize the effects of ozone on net photosynthesis at the leaf interior by relating reductions in net photosynthesis to ozone uptake, as opposed to external dose or concentration. This is important since factors affecting leaf conductance can greatly alter plant response to a given external dose. The resulting equations were built into the PnET-II model and applied to individual canopy layers in order to calculate integrated, whole-canopy responses.

MODEL DEVELOPMENT

PnET-II

PnET-II is a monthly time step canopy- to stand-level model that is built on the following relationships: 1) maximum leaf photosynthetic rate is a linear function of foliar nitrogen content, each expressed on a mass basis

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(Aber and Federer 1992, Reich *et al.* 1995), and 2) water use efficiency is inversely proportional to vapor pressure deficit (Aber and Federer 1992). The simulated forest canopy is divided into multiple, even-mass layers to account for vertical variation in available light and specific leaf weight (Ellsworth and Reich 1993). The model has been successfully validated for forest production and CO_2 exchange at diverse locations across North America (Aber and Federer 1992, Aber *et al.* 1995a, 1995b).

Ozone response relationships

Data from ozone fumigation experiments indicate a strong relationship between cumulative ozone dose and reductions in net photosynthesis (Reich 1987). This impact varies greatly between species, although much of the variation can be explained by differences in stomatal conductance (Guderian et al. 1985, Reich 1987). Because conductance is the most important regulator of ozone uptake under a given external concentration (Taylor *et al.* 1994, Munger *et al.* 1994), this suggests that ozone effects on net photosynthesis can be expressed largely as a function of how much ozone reaches the leaf interior.

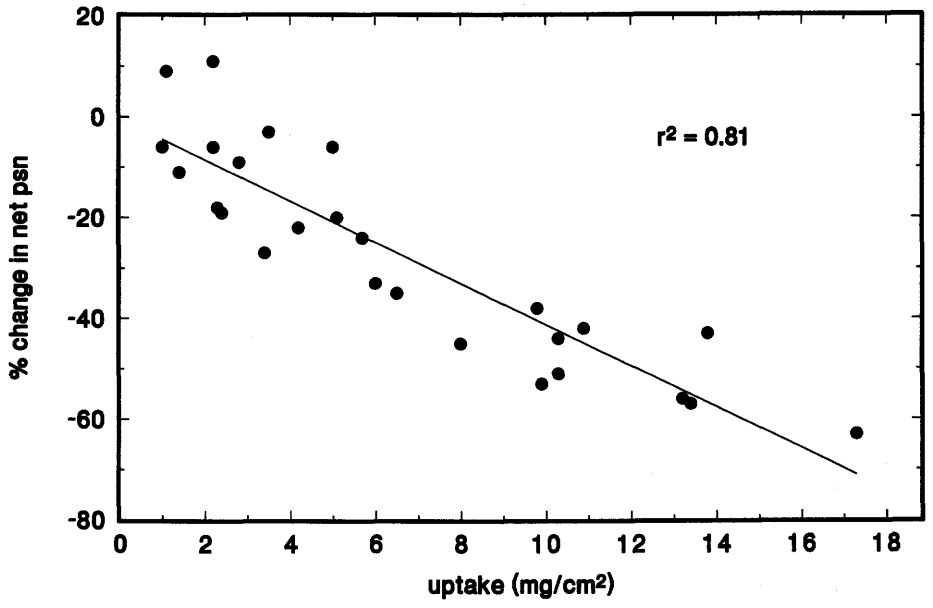

Figure 1. Percent reduction in net photosynthesis in relation to ozone uptake for hardwoods. From Reich 1987.

It follows that across species, declines in net photosynthesis should be better correlated with ozone uptake than with external concentration or dose. Figure 1 shows this relationship using data from independent studies conducted over periods of several days to several months on a wide variety of hardwood seedlings (from Reich 1987). Tjoelker *et al.* (1995) obtained similar results from mature sugar maple leaves in a partial-canopy, open-air fumigation study conducted over a period of three months. Using pooled data from figure 1 and Tjoelker *et al.* (1995), we have derived the following response equation:

1) $\quad dO_3 = 1 - (.0026 * g * D40)$

where dO_3 is the ratio of ozone-exposed to control photosynthesis, g is mean stomatal conductance (in mm/sec) and D40 is the cumulative ozone dose (in ppm-h) above a threshold concentration of 40 ppb, calculated as the sum of all hourly values > 40 ppb after subtracting 40 from each. We use this threshold because 40 ppb is approximately the level at which negative impacts begin to appear in the pooled data set. Several other studies have also found 40 ppb to be the threshold beyond which negative growth effects begin to occur (Fuhrer 1994, McLaughlin and Downing 1995).

Canopy ozone gradients

We evaluated ozone gradients within a forest canopy using data from Munger *et al.* (1994), which includes three years of measurements along a vertical profile through a mixed hardwood forest at the Harvard Forest in central Massachusetts. For all months of the growing season we calculated the D40 value at each canopy level and plotted the resulting gradients. Figure 2 shows these gradients for May and July of 1992, during which times, ozone below the canopy decreased to 72 and 18 percent of the above-canopy D40, respectively. The shape of these patterns is such that, even during months of substantial canopy depletion, ozone levels remain high in the upper canopy layers where light levels and photosynthetic rates are greatest. For all three years, canopy ozone depletion increased from spring through midsummer and declined at the end of the growing season. These trends can be described by the equation:

2) $$dD40_{level} = 1 - (level * a)^3$$

where $dD40_{level}$ is the proportion of the above-canopy D40 at a given canopy level, *level* is the normalized canopy level from 0 at the ground to 1 at the top of the canopy, and a is the ozone extinction coefficient that is determined for each month from mean monthly D40 values. Table 1 shows mean values of a along with the corresponding absolute canopy gradient in D40 for each month of the growing season from 1991 to 1993.

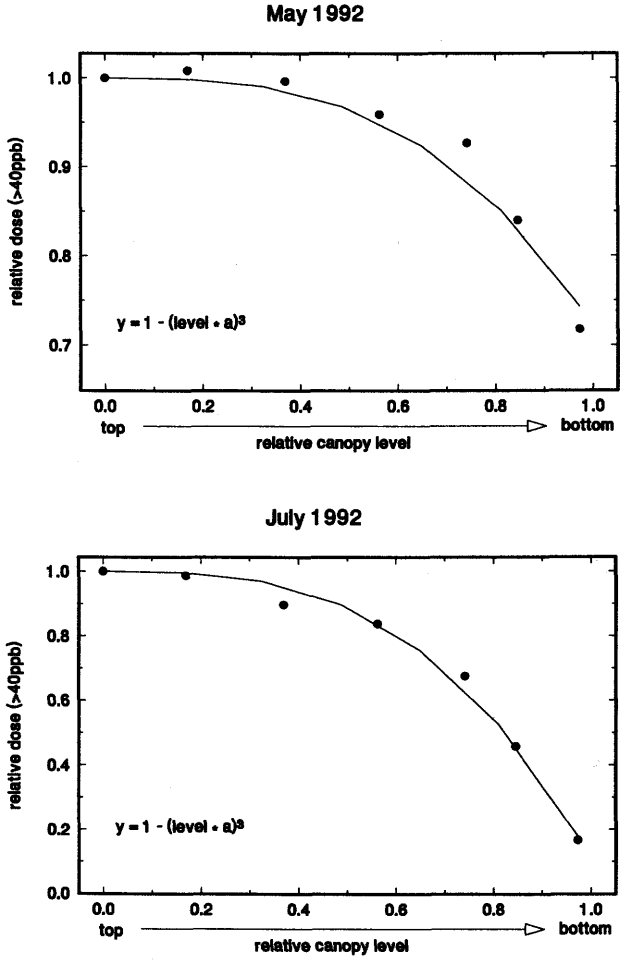

Figure 2. Ozone dose > 40ppb in relation to canopy position at the Harvard Forest in Central Massachusetts. Both axes have been normalized to a scale of 0 to 1. Data are from Munger *et al.* 1994.

Table 1. Solutions to equation 2, showing mean canopy depletion of ozone D40 between 1991 and 1993.

Month	*a* (from eq. 2)	R^2	% decrease from above to below canopy
May	.6776	.96	31
June	.8388	.94	61
July	.9310	.98	75
August	.9243	.96	75
September	.9449	.98	77
October	.8333	.94	61

Incorporation of ozone effects into PnET-II

For the prediction of ozone effects on whole-forest growth, equation 1 has been built into the PnET-II model's photosynthesis routine at the level of individual canopy layers. For each layer, leaf conductance is calculated as a function of potential net photosynthesis, and is thus affected by available light at that layer, foliar nitrogen content, and temperature. Monthly D40 values are estimated for each canopy layer by combining ambient concentrations with the mean 1991-93 ozone depletion profiles (from equation 2 and table 1). Ozone effects are determined from May through October and are calculated cumulatively for each layer.

Conductance (g) is calculated as a linear function of net photosynthesis, based on a strong relationship ($r^2 = 0.93$) between the two among data in the literature (Abrams *et al.* 1990, Amthor *et al.* 1990, Aubuchon *et al.* 1978, and Hinckley *et al.* 1978). In equation 1, ozone uptake is approximated by the product of g and D40. Because g represents conductance to water vapor, calculating actual uptake rates would require inclusion of the diffusivity ratio of water vapor to ozone. However, because this ratio is a constant, it's inclusion in the derivation and application of equation 1 would have no effect on the resulting predictions. For simplicity we have left it out of the equation.

Given the relationship between conductance and net photosynthesis, ozone exposure might be expected to cause conductance to decline along with photosynthesis, resulting in a reduction of subsequent ozone uptake. Reduced leaf conductance has been observed in many studies, although the effect is often minimal with respect to the photosynthetic response (e.g. Pell *et al.* 1992), or reversed under certain light regimes (*e.g.* Reich and Lassoie 1984, Volin *et al.* 1993). In one of the only open-air exposure studies performed on a mature tree canopy under field conditions, there was virtually no change in conductance (and hence ozone uptake) despite large reductions in photosynthesis (Tjoelker *et al.* 1995). This lack of a response suggests impairment of stomatal function, as the net effect is an uncoupling of the normal relationship between photosynthesis and conductance (Volin *et al.* 1993, Tjolker *et al.* 1995).

In the absence of consistent and predictable changes in conductance, we have not included any such feedback in the present modeling exercise. Inconsistencies in observed stomatal response indicate a lack of understanding of how ozone affects leaf conductance, but because photosynthetic responses are generally much greater than, and typically precede changes in conductance (when such changes have been observed), this should not be a crucial issue in predicting ozone effects on whole-forest productivity.

Interactions between ozone and drought

For each canopy layer, the model tracks photosynthesis with and without ozone in order to determine the potential, whole-canopy ozone effect and to allow interaction with drought stress, which is calculated for the entire canopy as opposed to individual leaf layers. After the calculation of potential canopy photosynthesis (without ozone or water limitations), the PnET-II model's water balance routine determines potential transpiration and performs a comparison

with the amount of available soil moisture. If soil moisture is not adequate to meet the transpirational demand, water stress ensues and canopy photosynthesis is reduced.

Because the primary physiological response to water limitation is stomatal closure and ozone effects are linearly related to stomatal conductance, the potential (no water limitation) whole-canopy ozone effect is reduced proportionally to the degree of water stress. For example, if water stress causes a 20 percent reduction in potential photosynthesis (dWater = 0.8), and the potential whole-canopy ozone effect is also a 20 percent reduction, the final ozone effect is reduced by a factor of 0.8 to 16 percent ($dO_3 = 0.84$).

MODEL APPLICATION

We have run the model for hardwood forests across the northeastern U.S. using ozone data obtained from the U.S. Environmental Protection Agency's Aerometric Information Retrieval System (AIRS) between 1987 and 1992. For each collection station, we used raw, hourly data to determine the monthly dose above 40 ppb. We only considered measurements from between 7AM and 7PM to exclude unusually high nighttime concentrations. To minimize error caused by missing data, a 90 percent completeness criterion was imposed whereby any month containing less than 90 percent of the expected number of observations was not used in calculating long-term monthly means. The resulting data set included 64 sites with average monthly values determined from 3 to 7 years of data (figure 3). In computing long-term mean values, some bias between sites may result from differences in the years for which data were available.

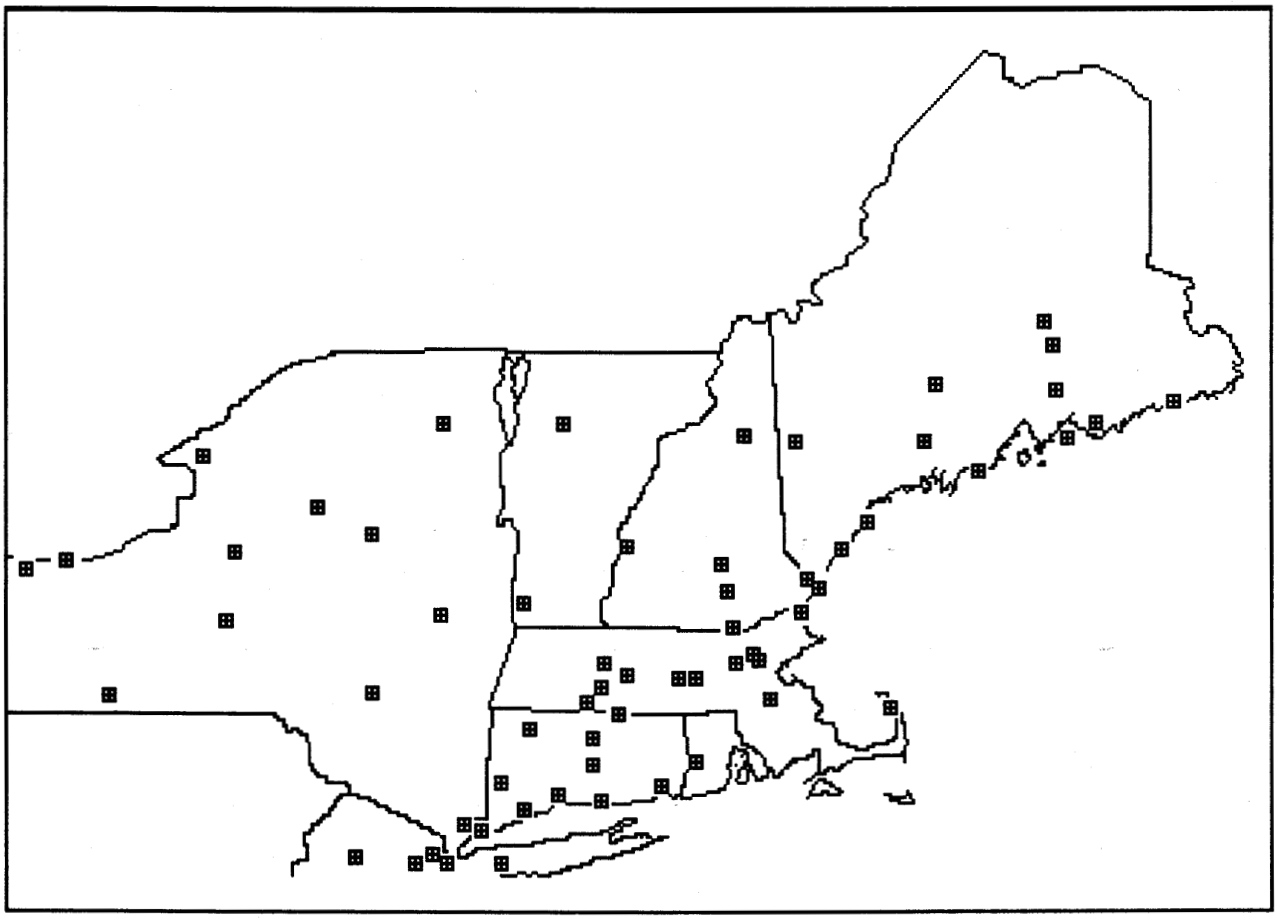

Figure 3. Locations of EPA ozone monitoring stations.

Climate data required by the PnET-II model were calculated for each of the 64 ozone data sites using a statistical climate model derived for the region from 30 year mean weather station data (Ollinger *et al.* 1995). We used a foliar nitrogen value of 2.2 percent, based on values measured at the Harvard Forest (Martin and Aber 1995). In the absence of soil water holding capacity (WHC) data from each site, we have run the model under several conditions ranging from high to low WHC.

RESULTS AND DISCUSSION

Results of initial model runs indicate decreases in annual net primary production (NPP) of from 2 to 17 percent as a result of mean ozone levels from 1987-1992 (figure 4) with greatest reductions in southern New York and New England where ozone levels and potential photosynthesis were greatest. The predicted decrease was negatively correlated with latitude, following a trend of decreasing ozone from south to north across the region. Predictions varied significantly across the range of soil WHC values used (2-36 cm.), although ozone-induced growth reductions were substantial even on soils with low WHC (figure 4).

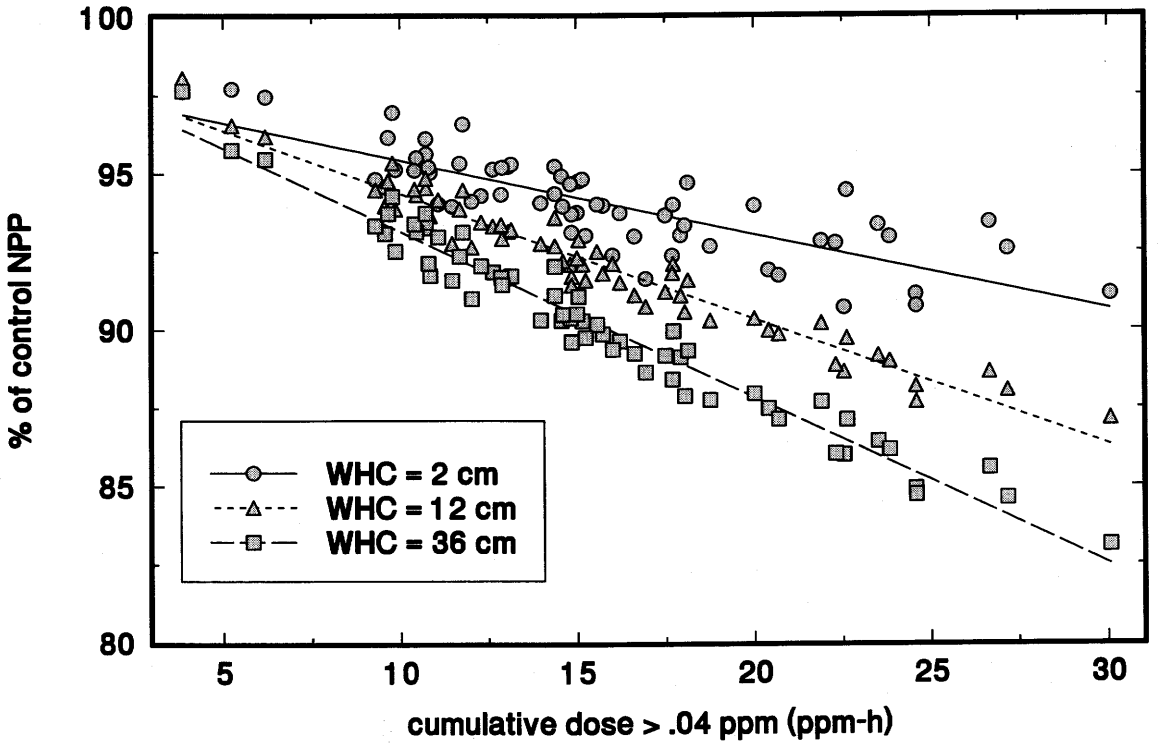

Figure 4. Predicted change in annual NPP at 64 sites across the study region in response to mean ozone levels from 1987-1992. Predictions are shown for three levels of soil water holding capacity to show how the response changes from well-watered (WHC = 36) to drought-stressed (WHC = 2) conditions.

Table 2 shows means and ranges of predicted NPP for the 64 sites under all soil WHC values used. At WHC = 36 cm, all predicted drought stress was eliminated, so these values can be used as a reference in estimating drought effects resulting from other moisture conditions. Under all but the two wettest conditions, drought stress caused greater growth reductions than ozone. At WHC = 12 cm, which represents a typical well-drained till soil, ozone effects on NPP were roughly 25 percent less than what was predicted in the absence of drought stress.

Table 2. Mean predicted NPP (g/m^2yr) across the 64 study sites with and without ozone effects at 5 levels of soil water holding capacity (cm).

Soil WHC	NPP without ozone mean	NPP without ozone range	NPP with ozone mean	NPP with ozone range	mean % reduction
2	723	640-776	680	591-734	5.9
6	1136	991-1230	1048	915-1151	7.7
12	1354	1187-1475	1247	1190-1372	7.9
24	1732	1574-1846	1573	1411-1699	9.2
36	1840	1645-1993	1659	1527-1807	9.8

We consider these predictions to be conservative in that ozone effects are based solely on reductions in photosynthesis. Although this is generally accepted as the major physiological effect of ozone, other responses may also be important, particularly under circumstances such as unusually high concentration events. Nevertheless, current predictions do suggest substantial declines in NPP among forests across the northeast region. Although we have not addressed ozone effects on wood production, we expect wood to be affected to a greater extent than NPP because wood is a relatively low priority in tree carbon allocation.

In addition to ozone, other factors such as land use and atmospheric nitrogen deposition can have substantial impacts on ecosystems. Determining the net effect of human activities on forest growth thus requires consideration of all these factors taken together, rather than any one on its own. Although the outcome of these interactions remains largely unknown, this study suggests that concern over ozone as a cause of ecological and economic degradation is warranted.

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