

Ecological Effects of Tropospheric Ozone: A U.S. Perspective - Past, Present and Future

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ABSTRACT

Understanding the effects of tropospheric ozone on vegetation, as called for in the U.S. Clean Air Act, has involved collection of experimental data at the species level and, in particular, at the level of the individual and populations. Frequently the studies have been regression designs involving single species and single pollutants resulting in quantitative exposure-response functions that characterize the effects on biomass or reproduction (crop yield). Recently, the 1996 EPA Oxidant Criteria Document reviewed the published research on oxidant effects on crops, forests, and ecological resources, and concluded that the current secondary National Ambient Air Quality Standard (NAAQS) for ozone is neither protective or appropriate. The subsequent discussion and decision on what is an appropriate form and level of the secondary NAAQS utilized results from single pollutant and single species studies. To estimate concentrations causing effects composite response-functions for crops and trees from a large number of species were developed, predicting crop yield loss or annual biomass loss in seedlings. This approach is useful based on available quantitative data on biological effects; however it assumes that individual plant response does not change in the presence of other stresses or in natural systems which are considerably more complex (e.g. species' assemblages and competition for resources). For example, the importance of biological complexity is illustrated when we examine the below-ground ecosystem, an often overlooked portion of the ecosystem. We have found that incorporating natural biological complexity into potting soils can result in carbon fluxes opposite those predicted from individual plant studies using artificial media lacking natural soil foodwebs. A future research approach to understanding O₃ effects on ecosystems is required that will develop the necessary linkages to extrapolate experimental data taken at the individual level, often in artificial conditions, to predict changes on individuals or populations in more complex native environments. We will present experimental and modelling activities from our laboratory that show how we are beginning to address the problems of scale, complexity, and multiple stresses in forested ecosystems exposed to ozone stress. Questions frequently posed in

ecological risk assessments.

1. INTRODUCTION

The Clean Air Act mandates the protection of ecological resources from adverse effects of air pollutants through setting a secondary National Ambient Air Quality Standard (NAAQS). Ecological resources are part of public welfare and include crops, forests, soils, ecosystems. As part of the standard setting process, EPA critically reviews all the pertinent literature every 5 years, and presents the conclusions in the Ozone and other Photochemical Oxidants Criteria Document (U.S. EPA, 1996). This document is scientifically peer-reviewed and reviewed by the Clean Air Science and Advisory Committee (CASAC). The revised and approved document then provides the scientific basis for EPA's decisions regarding the NAAQS for ozone.

The most recent Oxidant Criteria Document was completed in 1996 (U.S. EPA, 1996), and concluded that the general conclusions of the previous 1986 Criteria Document and the 1992 Supplement were not altered. The general conclusions were (a) current ambient ozone concentrations in many areas of the country were sufficient to impair growth and yield of plants; (b) effects occur with only a few hourly occurrences above 0.08 ppm; (c) several species exhibited growth and yield effects when the mean ozone concentration exceeded 0.05 ppm for 4-6 hr/day for at least 2 weeks; (d) regression analyses of the National Crop Loss Assessment Network (NCLAN) data developing exposure-response functions for yield loss indicated that at least 50% of the crops were predicted to exhibit a 10% yield loss at 7-hr seasonal mean ozone concentrations of 0.05 ppm or less; (e) European crop yield loss studies substantiated the effects observed in this country; and (f) studies of forest tree seedlings substantiated pre-1986 studies indicating the sensitivity of a number of species, at least as seedlings. The experimental studies showed that tree seedling growth is altered at ozone concentrations observed in many areas of the U.S.

The 1996 Oxidant Criteria Document also reported that the conclusions of the 1992 Supplement were still valid: (a) The current 1 hour form of the standard (120 ppb) is not protective nor is it an appropriate air quality indicator for plants; (b) the 7- and 12-hr seasonal mean was also not appropriate because of it treats all concentrations equally, and does not consider exposure duration; and (c) the experimental studies suggest the indicator of air quality for a secondary NAAQS should cumulate all hourly concentrations during the daylight hours and weight the higher concentrations (the 'best' weighting scheme or the relative importance of concentration ranges is not known; however, concentrations above 60 ppb are generally considered important in causing effects)

As a result of the scientific data, EPA has concluded that the current secondary NAAQS is not protective of ecological resources, in particular protecting crops and forests in the U.S. The proposal for an alternative secondary NAAQS consists of 2 options for consideration. (1) Set the secondary NAAQS equal to the newly proposed alternative primary NAAQS (8 hr maximum of 80-90 ppb with 1-5 exceedances). While this proposal is based on air quality analyses, and is not biologically related to plant response, the attainment of the alternative proposed primary NAAQS would result in a reduction in ozone

concentrations harmful to plant growth.; or (2) set the secondary as a 3 month, 12 hr SUM06 of 26.4 ppm hr. This air quality indicator is based on current biological response data and would prevent tree seedling biomass losses and crop yield losses greater than 10% in 50% of the species. The decision regarding which proposal to adopt is still pending.

The process of assembling the Criteria Document also reveals the scientific gaps in our knowledge of ozone effects on plants. Primary among these are (a) the problems associated with relating 2-4 year-old tree seedling response to ozone over 1-3 seasons to the response of large, mature trees over a 40-200 year life cycle; (b) the problems associated with extrapolating responses developed on individuals and relating it to the response of a forest stand; (c) how little we know about natural system complexity, wherein the interaction of species, genotypes, and the multitude of past and present environmental influences dictate the eventual response of the species or community in question. We will provide a brief overview of approaches we are taking to address these major areas of uncertainty.

2. PROBLEM: *Predicting Effects of Ozone on Long-lived Species over time, across varied environments, and in assemblage with other species.*

The knowledge gaps pointed out in the 1996 Criteria Document represent the source of much of the uncertainty in any risk characterization for any atmospheric pollutant, i.e. the ability to predict effects over long time periods, across diverse regions, and across scales of biological organization. Fig. 1 illustrates three important considerations when extrapolating data: (1) the influential role of *size and ontogeny* : seedlings to mature trees; (2) *complexity of the environment* , including belowground processes and trophic groups, species diversity and stand structure: chambers to forests; and (3) the role of *time* : single season to multiple years. The whole tree in Fig. 1, including the aboveground and belowground tissues, is the experimental subject. Experimental studies have developed quantitative exposure-response functions to a single pollutant, for a single species at the individual to population level, of a given age, size and phenotypic stage, over a single season, and growing in a defined environment, either artificial or natural (lower left hand corner of the triangle). The information gained from each of these exposure experiments is then invariably used in risk characterizations for prediction of the effect along one or more of the lines of the triangle, i.e. mature trees, forests, and multiple years. Areas where the experimental data is limited. The prediction of risk to forests over multiple years requires an understanding of all the components of a forest, including the belowground component, species assemblages and age structure, as well as the spatial and temporal factors, in order to make inferences as to how a forest will respond to a given level of pollutant over time. The first concern is the significant limitations in extrapolating effects at the individual level. Changes in physical size as the tree ages, as well as changes in processes that occur with maturation need to be accounted for in making inferences beyond the experimental. For example, forest tree seedlings that range 1-10 ft in height are studied and potential effects are inferred on mature trees that will attain heights of 150 ft. Because of differences in resource utilization in trees of different size and age (Wareing, 1993; Hinckley et al., 1997), we anticipate there being differences in both the

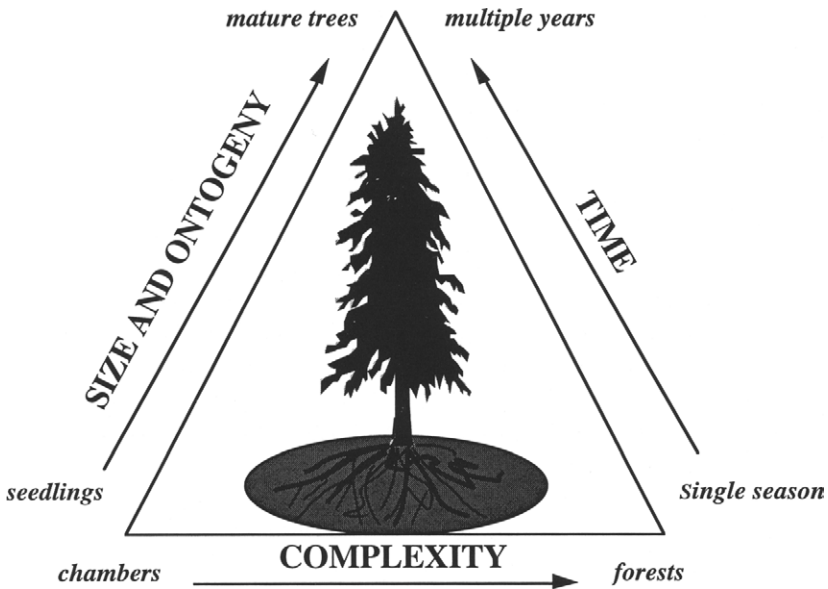


Figure 1. Extrapolation of stressor effects data (e.g. exposure response functions) across: (1) **SIZE AND ONTOGENY** of species, e.g. from seedlings to mature trees; (2) **TIME**, including the duration of the stress exposure, season of exposure, year-to-year variation of exposure, phenology and life span of species; and (3) **COMPLEXITY**, from experimental chamber studies to ‘real-world’ conditions, artificial soils to native soils with inclusions of intact soil food webs, or single individuals to communities to landscapes

uptake of ozone, as well as the ultimate effect on growth, to result from age and size differences. A few studies have indicated such differences in response and attributed those differences to uptake of ozone (Grulke et. al., 1989; Samuelson and Edwards, 1993; Fredericksen et al., 1996).

In addition to these age/size limitations, the spatial and temporal distribution of environmental and exposure factors influencing the response to a pollutant need to be considered in the extrapolation. Water and nitrogen availability is of particular importance in understanding response to a pollutant over the species’ range. The ozone exposure varies from year to year with weather and emissions. The year-to-year variation of exposure is not accounted for in most experimental data. How to appropriately use available data in risk characterizations is a question for future activity, as well as conducting new research to address questions of the influence biological scale and multiple environmental factors on the effect of ozone.

3. RESEARCH APPROACH - *How to address the shortcomings in existing data and reduce uncertainty in extrapolations needed for risk characterization*

A multifaceted, interactive research approach is required, including experimental and modelling components, with each informing the other. The objective is a mechanistic understanding of each of the lines of extrapolation illustrated in Fig. 1.

Plants are exposed to a wide range of spatially distributed environmental extremes, including anthropogenic stressors (Taylor et al., 1994). Plants utilize available resources in order to optimize growth and reproductive outputs under constantly changing conditions. Air pollution represents a stress similar to other stresses in that plant response is the result of both avoidance and tolerance mechanisms (Ariens et al., 1976; Tingey and Andersen 1991). Avoidance factors include factors that restrict the pollutant from reaching the target site, e.g., stomatal closure. Tolerance factors include physiological shifts that result when the stress reaches the target site and causes a metabolic change. Despite the nature of tolerance mechanisms, plant response to a stress involves a shift from one metabolic condition to another, and therefore represents a stress response.

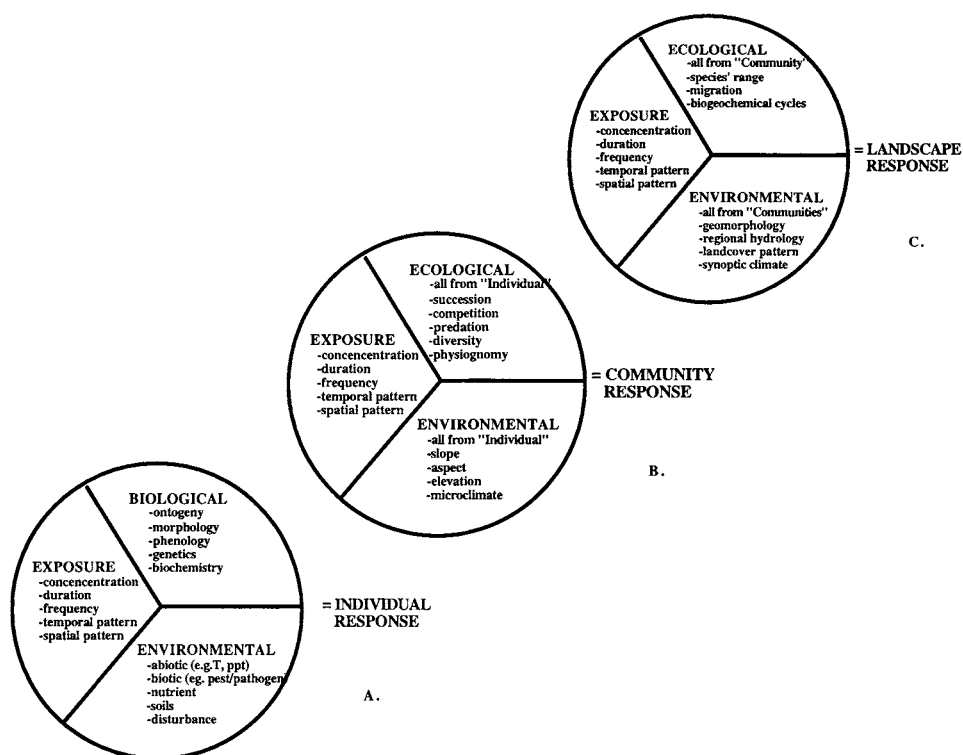


Figure 2. Factors influencing plant response to stress at the Individual/Population level (A) or Community/Stand level (B) or the Landscape level (C)

There are several factors that affect the magnitude of plant response to ozone stress (Hogsett et al., 1988), and Figure 2 shows a list of important factors at each spatial scale of interest. Figure 2a provides a list of factors influencing individual plant response to ozone, including (1) the past and present environmental milieu, including daily and seasonal weather conditions, soil fertility and water holding capacity, soil food web, and disturbances of various kinds (pest infestations, wildfire, floods, land-use, and so on); (2) biological factors, including genetic variability and constraints, seasonal phenology, limits to biochemical responses and (3) components of stressor exposure, including concentration of pollutants, frequency and duration of exposure, and daily, seasonal and annual patterns of exposure. All of these factors need to be considered to extrapolate the individual plant's response across temporal and spatial scales.

Understanding the factors that influence response to ozone stress is considerably more complex at the level of communities (Fig 2B) than at the level of the individual (Fig 2A). Predicting behavior of individuals growing in mixed age, mixed species stands includes all of the factors that influence individual responses, plus such factors as variations in elevation, steepness of slopes, and aspect, and the predictable characteristics of climate near the ground (microclimate). In addition, ecological processes (plant succession from least to most shade tolerant species; competition for sunlight, nutrients, and soil moisture; effects of biodiversity and the physiognomy of vegetation) cannot be derived directly from knowledge of the biological attributes inherent in individual plants. Yet, these processes play a critical role in determining individual plant response to stressors as they form groups of species (populations). Indeed, exposure to stressors must now include a careful review of plant spatial distribution as controlled by the environmental variables included in Figure 2B.

The shift from consideration of relatively uniform stands of vegetation gathered into communities, to highly diverse ecosystems gathered into watersheds and landscape units involves additional processes that modify response to stressors (Fig 2C). Environmental effects of geomorphology (landforms, geology, drainage patterns) and regional hydrology (seasonal movement of moisture in soils, into streams and the atmosphere) combine with synoptic climate variables (air mass frequencies, teleconnected patterns such as *el niño*) to generate a regional response which will not equal the average response of populations in the region. Land uses create varying sizes and connectivities of wildlands, each of which functions differently. Related ecosystem processes become significant at this dimension. For example, they define the geographic ranges of animal and plant species distribution, and the daily and seasonal movements (animal migrations) or long-term changes in their boundaries (plant migration). Although the exposure variables at the landscape level are mostly those useful at the level of individual plants, the converse is not true: the landscape-level phenomena can be predicted without much consideration of individual plant characteristics or their environmental constraints.

The extrapolation from individual to community to landscape and on to the biome level requires multiple steps (Hinckley et al., 1997). Typically, one works with empirical information generated at one level of organization, using it to model and validate at the next level of organization, and subsequently using that information (model) to predict (implications) at a third level of organization. The complexity characteristic of each level of

hierarchy precludes extrapolation beyond 2 or 3 levels of scale. For the purposes of studying ozone effects, it is necessary to bridge scales across each of several levels of complexity: cells-organs-individuals; organs-individuals-stands; individuals-stands-ecosystems; stands-ecosystems-landscapes.

Ideally, the complexities described above for each level of scale could be addressed experimentally using experimental designs that are quantitative and enable prediction of effects over a range of concentrations, including the variation in that response (Hogsett et al. 1988). Due to logistical problems, exposure studies over several years are not easily accomplished on whole forests, or even whole trees. Therefore, extrapolation from smaller scaled exposure studies is necessary. To accomplish the extrapolations, we use a combination of process-based and stand-level model simulations. Models can be parametrized for large trees or stands that simulate the interaction of multiple factors in response to ozone based on the experimental studies of the multiple interactions, such as those illustrated in Figure 2.

Models are essential components of any risk characterization of ecosystems response to natural and anthropogenic stressors (Rastetter, 1996). Driving forces such as temperature, precipitation, nutrient inputs, topography, soil moisture, and soil biota make it impossible to predict future response to ozone based on single-factor experiments alone (Rastetter et al., 1996). Process-based models at the individual or the stand level can provide a self-consistent synthesis of the results of many experiments. The synthesis provided by these models includes the interactions among physiological and ecological processes that give rise to the synergistic responses to multiple environmental factors and stresses (Rastetter et al., 1996).

Coupled with modelling efforts, correlative, observational studies can be carried out in forested areas along pollution gradients where monitoring is concurrent and other environmental gradients (e.g. water availability) are present. These studies are possible in some regions of the U.S. (Miller et al., 1982;1989), and will be useful in helping us understand population-level responses as well as validating model simulations.

As a way to illustrate how we are combining experimental and modelling efforts, several examples of our current research activity in Corvallis are discussed. We have associated each example with a particular level of biological organization, i.e., individual/population, community, and landscape; however, there is overlap among the levels both in the experimental information obtained and its subsequent use.

3.1. Individual/Population

3.1.1. Extrapolation of effects on a few species to reflect the effect on all species

A major portion of the research activity over the past decade has been directed at developing exposure-response functions for both crops and forest tree species (Heagle et al., 1988; Fuhrer et al., 1989; Hogsett et al., 1989; Tingey et al. 1991; Neufeld et al., 1995; Karnosky et al., 1995.). Many of the studies were designed to predict growth and yield effects at the individual and population level at a range of ozone concentrations. The primary means of exposing plants during the last 15 years has included the use of the open top chamber methodology for developing the empirical database of ozone effects on crop and

tree species (Heagle et al., 1988; Taylor et al., 1994). Open-top chambers provide a sufficient range of ozone treatments for quantifying effects (i.e. exposure-response functions), and still provide growing conditions that closely match those in the plants' natural growing environment. In addition, the multitude of chamber sites has permitted adequate replication of studies from year to year. Examples of these studies include the National Crop Loss Assessment Network (NCLAN) (Heck et al, 1991), the European Open-Top Chamber studies (Weigel et al., 1987), and several studies of tree species (Hogsett et al., 1989; Matyssek et al., 1993; Neufeld et al., 1995; Karnosky et al., 1995; Rebbeck, 1996). The studies included a wide range of response functions illustrating that ozone response is species dependent. For the first few years of the our project studying forest tree species, we developed exposure response functions for 11 forest tree species during 1-2 year exposure seasons using open-top chambers at locations across the U.S. (Table 1). Sites were selected in different regions of the U.S. where the species of interest were indigenous. A common research protocol was used at each site, and several of the species were examined at more than one site.

Table 1. Tree Species: Locations and exposure durations used to construct composite exposure response function.

Species/family	Site	Exposure duration (days)
Aspen—wild	Oregon	112
	Michigan	98
Douglas fir	Oregon	234
	Oregon	234
Ponderosa pine	Oregon	230
	Oregon	280
Red alder	Oregon	118
	Oregon	112
Black cherry	Smokey Mtn Nat'l Park	76
	Smokey Mtn Nat'l Park	140
Red maple	Smokey Mtn Nat'l Park	55
Tulip popular	Smokey Mtn Nat'l Park	184
	Ohio	222
Virginia Pine	Smokey Mtn Nat'l Park	98
Loblolly	Alabama	555
Sugar Maple	Michigan	180
	Ohio	222
E. white pine	Michigan	180
	Ohio	222

Figure 3 shows examples of exposure-response functions for total biomass (foliage, stem and root) after one growing season. Douglas-fir (*Pseudotsuga menziesi* (Mirb.) Franco) seedlings were relatively insensitive to ozone (Fig. 3a), while ponderosa pine (*Pinus ponderosa* Laws.) (Fig 3b) and quaking aspen (*Populus tremuloides* Michx.) (Fig. 3c) were relatively sensitive to ozone. The response of the other 7 species varied from insensitive (e.g. Virginia pine, *Pinus virginiana* Mill.) to moderately sensitive (e.g. Sugar Maple, *Acer saccharum* Marsh.) to sensitive (e.g. Black cherry, *Prunus serotina* Ehrh.). Given the range in response among species, it is difficult to generalize or extrapolate an effect across all species in order to provide information for decision making regarding risk characterization and standard setting. However, one approach to accomplishing such a task is to develop a composite exposure-response function for tree species and one for crops. Figure 4 shows the composite functions for crops and tree species. The percentile distributions illustrate the range of predicted relative biomass loss as a result of ozone exposure. At 30 ppm-hr ozone, the predicted biomass loss of tree seedlings ranges from 0-20%.

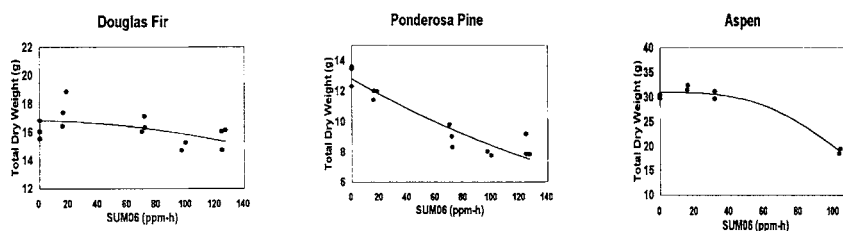


Figure 3. Exposure-response functions for Douglas-fir, Ponderosa Pine and Aspen. Total biomass response after one season of exposure. Exposure is expressed as SUM06 (sum of all hourly values equal to or greater than 60 ppb during the daylight hours (12 hr) over the growing season)

The Weibull or linear exposure-response model was used to relate final harvest biomass and exposure, expressed as the 12-h SUM06 index for 31 NCLAN crop studies (Fig 4A) and 26 tree seedling studies (Fig 4B). Separate regressions were calculated for studies with multiple harvests or cultivars, resulting in a total of 54 individual equations from the 31 NCLAN studies and 56 equations from the 26 seedling studies. For crops, each equation was used to calculate the predicted relative yield loss at 10, 20, 30, 40, 50, and 60 ppm-h, and the distributions of the resulting loss were plotted (Fig 4A).

For seedlings having been exposed to ozone for one or multiple exposure seasons of varying durations, each equation was used to calculate the predicted biomass loss at 10, 20, 30, 40, 50, 60, and 70 ppm-h per 92 days a year, and the distributions of the resulting loss were plotted (Fig 4B).

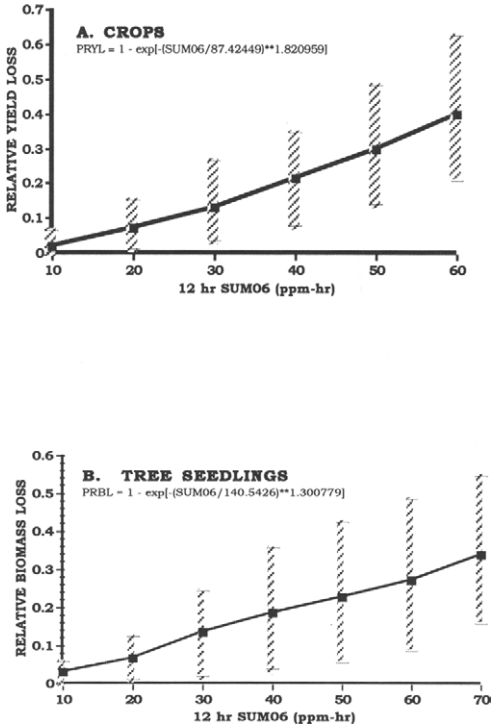


Figure 4. Composite exposure response functions for crops (A) and tree seedlings (B). Median response (50th percentile) is illustrated with solid line and weibull model given in each figure. 25th and 75th percentile shown with shadowed bars at each exposure value.

At each SUM06 value, the median (50th percentile) response was used to characterize the typical plant response to ozone across studies. The composite curve for crops or seedlings is the calculated Weibull model fit to the median response points.

Using these composite functions which composite species response, one can select an ozone concentration for a standard that is protective of trees or crops, depending on the level

of protection sought. The line represents the Weibull curve that describes the response in 50% of the seedlings or crops. Using this as an estimation of the mean response in tree species, concentrations can be determined that are protective against 10, 20, or 30% biomass losses (or crop yield losses), in 50% of the species. Although this approach provides some means to estimate the impact of ozone on crop and forest species, it includes large uncertainties because of the species-dependence of the response, and it does not account for the variation in the response resulting from different growing environments, exposure or other biological/ecological considerations (Fig. 2).

3.1.2. Extrapolation of effects along the line of increasing complexity

As controlled experimental studies begin to incorporate the multitude of factors typical of natural systems, (e.g. temporal and seasonal variation in exposure concentrations, variation in availability of water and nitrogen, presence of intact soil food web and rhizosphere biota, presence of competing species, etc), an understanding of both the direction and the magnitude of the modification by these influences on the exposure-response will result. The information can be used to reduce uncertainty in risk assessments, as well as improving process-based models simulating long-term effects of ozone on forest communities. Many earlier studies have examined the influence of these factors, including water stress on crops (e.g. Tingey & Hogsett, 1985; Miller et al. 1989; Temple et al 1988.), relative humidity (McLaughlin & Taylor, 1980), nutrient status (e.g. Tjoelker & Luxmore 1991; Bytnerowicz et al, 1990), exposure components (Walmsley et al., 1980; Musselman et al., 1983; 1986; Hogsett et al., 1985; 1988; Hogsett and Tingey, 1991).

Three examples of ongoing studies at our lab looking at this question from the perspective of the individual, community (Sec. 3.2.1), and landscape (Sec. 3.3) (Fig 2) are presented.

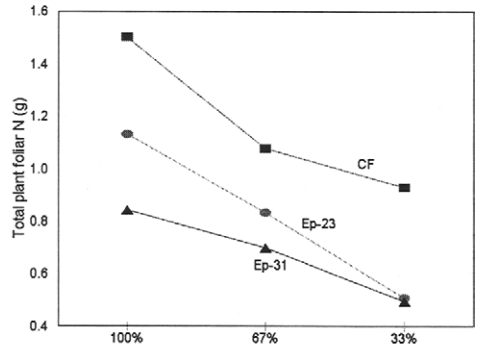
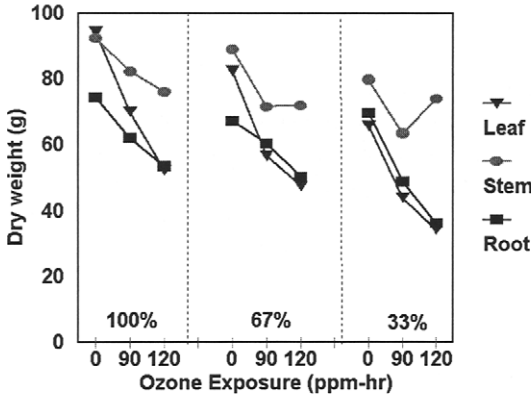
Nitrogen Status:

In a study of the influence of nitrogen supply on the response of ponderosa pine to ozone, we have measured both an individual response and a 'system' level response (Andersen and Scagel, 1997). Three levels of nitrogen- full, 2/3 or 1/3 rate was provided the year prior to exposure and continued through the year of exposure. The exposures were continued for 2 years. Figure 5 shows the response in biomass and foliar nitrogen content after one year of ozone exposure as not obviously different with varying nitrogen. The observed response suggests there is not a significant influence of nitrogen status on the growth response to ozone, and thus it may be appropriate to extrapolate exposure-response functions describing biomass at the level of the individual across regions differing in nitrogen availability. One measure of system level response, however, CO₂ flux from the soil, did indicate an influence of nitrogen status. Figure 5 shows a more pronounced response to ozone at the low nitrogen level, suggesting a possible interaction. The low nitrogen status may influence the ability to maintain roots and increased root mortality may be contributing to increased metabolic activity of soil biota and thus account for the increased CO₂ flux from soil. These studies are not completed and are not thoroughly analyzed, but do suggest

possible implications in our ability to extrapolate exposure response functions spatially as a result of available nitrogen. The measured response, biomass loss or CO₂ flux from soil, are both valid and provide critical data for risk characterization. However, from this study two different conclusions might be drawn on the role of nitrogen depending on whether the endpoint for assessment was at the level of the individual, or at the system level.

A. BIOMASS - LEAF, STEM & ROOT

B. FOLIAR NITROGEN



C. SOIL CO₂ FLUX

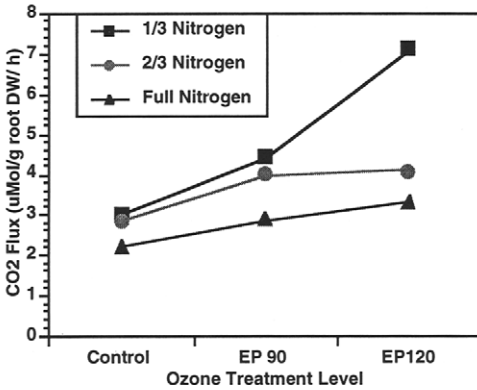


Figure 5. Response of ponderosa pine to 3 levels of ozone (Episodic [Ep] regimes having a SUM0 of 90 & 120 ppm hr and charcoal filtered[CF]) under 3 levels of nitrogen (100%, 67% & 33% of precribed application) in native soils. (A) biomass response after one season. (B) Total foliar nitrogen after one season. (C) Soil CO₂ flux after one season.

3.1.3. Extrapolation of effects from seedlings to mature trees:

Understanding the role of size and age in determining tree response to ozone is very important. As discussed above, much of the data we have today was obtained on various species of trees in the seedling stage, usually 1-5 years of age. As a result, the uncertainty in using this data to extrapolate the effects on large mature trees is very significant for any risk assessment. How maturation (ontogeny) effects tree response to air pollution is not known. It is thought that changes in pollutant uptake may occur with size, as well as differences in carbon sink sizes, the size of respiratory pools, and priorities (such as growth versus maintenance respiration) may affect the way the tree responds to ozone. Very few studies have addressed this question due to the technical difficulties of exposing large trees to ozone (Samuelson and Edwards, 1993; Grulke et al., 1989; Fredericksen et al., 1995).

Studies in Corvallis are planned focusing on resource utilization (C, N, H₂O) by trees (e.g. Ponderosa pine) as a function of size and age. The research will develop a mechanistic basis for scaling (Wareing, 1993), and will provide data to parametrize models that will incorporate age differences in resource utilization (Hinckley et al., 1997) affected by ozone, as well as incorporating gas exchange differences which effect ozone uptake.

3.2. Community

3.2.1. Extrapolation of effects along the lines of complexity:

Presence of other species and the soil food web:

In the second example, studies at Corvallis have indicated the influence of intact soil food webs and the importance of including belowground complexity in when studying tree response to ozone. Mesocosms in open-top chambers were planted with varying densities of blue wild rye (*Elymus glaucus* Buckl.) (a natural competitor of ponderosa pine seedlings) and a single ponderosa pine seedling in soil from a ponderosa pine forest (Andersen, et al. 1997). The response to ozone exposure was measured as changes in carbon dynamics, including allocation in individuals (species) and soil respiration as CO₂ flux, over 3 years. This was not a true competition study design because it lacks the necessary permutations, however, it does indicate the influence of increasing complexity of the environment on the exposure response. The preliminary data would suggest that there is not an interaction between plant density and ozone. Figure 6 shows an increase in CO₂ flux and soil organic matter as grass density and ozone concentration increases. However, what we are learning from this study is the importance of an intact soil food-web, which was included here with the native ponderosa pine forest soil. Earlier exposure studies of carbon allocation belowground, both from our lab and results from other laboratories, showed a decrease in allocation of carbon belowground with ozone exposure (Gorissen and van Veen, 1988; Spence et al. 1990; Andersen and Rygiewicz, 1995).

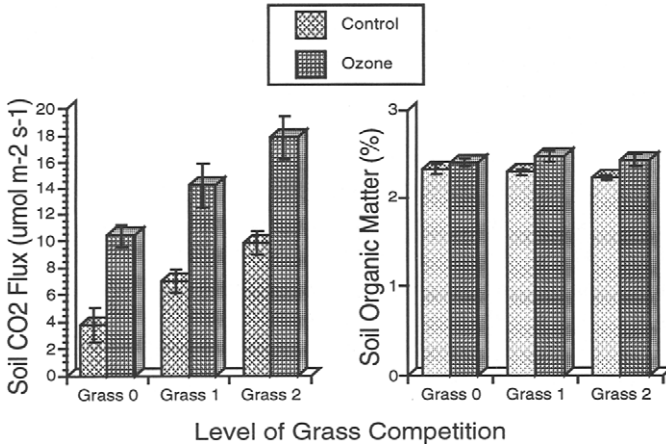


Figure 6. Soil CO₂ flux (A) and Soil organic matter (B) following exposure to ozone for 1 year in mesocosms containing pine seedling and blue stem rye grass at 3 increasing densities (“Grass 0,1,2”). Bars indicate 95% confidence interval. Differences were significant at the 5% level

From these individual plant studies we would have predicted that ozone exposure would decrease CO₂ flux from soil due to less allocation of carbon belowground, rather than increase it as shown in Figure 6. The increase in both soil organic matter and soil CO₂ flux may be the result of increased root turnover and subsequent degradation by soil organisms in ozone exposed systems, which could increase total soil CO₂ flux. If this is the case, perhaps with time a decrease in flux will be observed as the seedlings get older and the total root system size decreases. Exactly how this information can be included in extrapolation of results for risk characterization is not known, however it does indicate that when studies are accomplished in simple systems and over short time frames (1-3 years), some degree of uncertainty should be included.

3.3 Landscape level

We have employed an approach for extrapolating tree biomass and crop yield response functions across each species' range to determine the extent and magnitude of possible ozone risk to ecological resources in the U.S. (Hogsett et al., 1997). The approach uses a geographical information system (GIS) to integrate all the necessary data in a spatial context., including (1) estimated exposure over a growing season, (2) characteristics of the growing environment (e.g. precipitation, temperature, soil water, soil nitrogen levels, etc), (3) species' distribution, (4) species' inventory data (e.g. standing biomass, productivity) and (5) landscape features (e.g. elevation) (Figure 7).

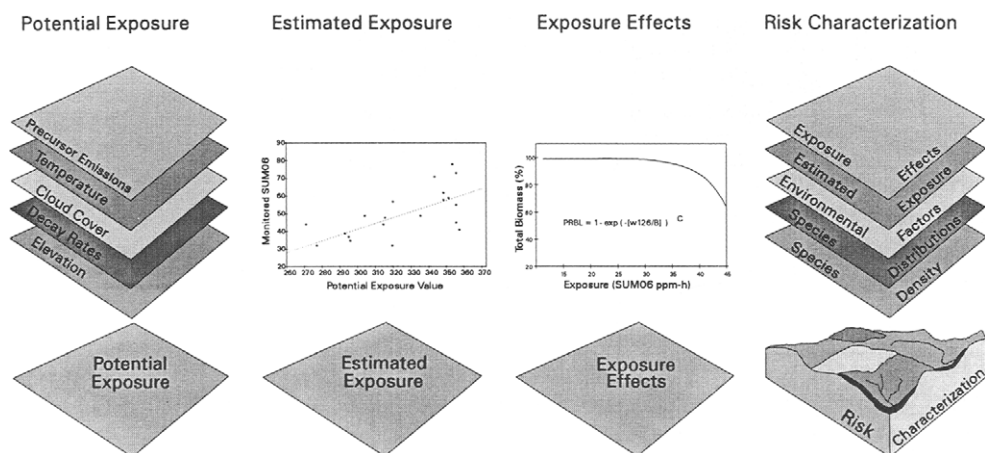


Figure 7. The GIS data layers for characterizing risk of ozone to tree species, including GIS-based estimation of ozone exposure in non-monitored areas for a given year, seedling or model-simulated tree exposure response functions for each species, and the spatial data on environmental factors such as precipitation, and species density. The combination of these layers results in a new map of risk.

The approach is useful for distributing experimentally-derived exposure-response functions from previous crops or tree seedling exposure studies, as well as extrapolating process-based whole-tree model simulations of large trees using TREGRO (Weinstein et al. 1991) over a 3 year time period incorporating the role of environmental influence such as water or nitrogen, or stand-level model simulations of community structure (ZELIG) incorporating very long-term effects (100 years) as a result of ozone, climate, soil, water and nutrient availability. These extrapolation are based on the spatial and temporal distribution of ozone exposure and climate variables, e.g., precipitation and temperature that are present across the species' range or the region of the forest-type. The results of spatially distributing seedling exposure-response functions and then area-weighting that response is given in Figure 8. A sensitivity-ranking based on ozone sensitivity of each species and the potential area of the species impacted can be made (Hogsett et al 1997).

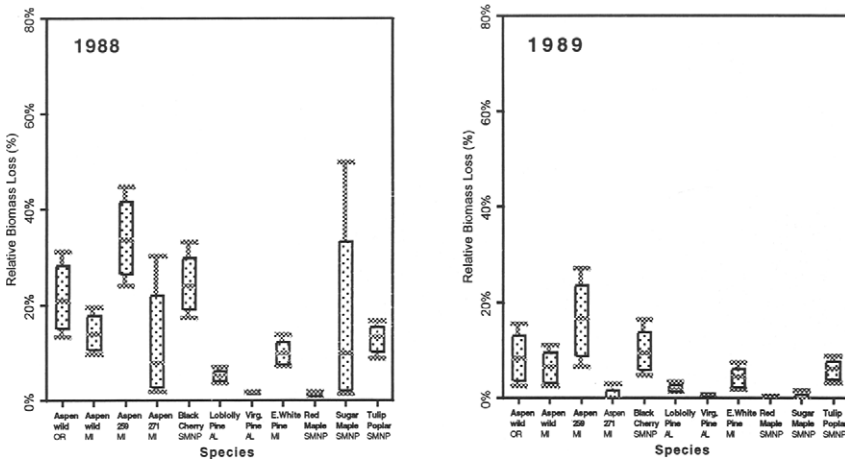


Figure 8. Area-weighted annual biomass loss in seedlings from 1988 and 1989 ozone exposure. Percentile distributions of species' area is shown for 10th, 25th, 50th, 75th and 90th percentile. The response for 50% of the species' area is shown as the midline in the shadowed box. The 25 and 75% of the area are the ends of the shadowed box.

To illustrate the process-based model simulation approach, Figure 9 shows the response in loblolly pine biomass after 3 years of exposure. We compared a hot, dry year having relatively high ozone concentrations (1988) to a cooler, wetter year having relatively low ozone concentrations (1989). TREGRO was parametrized from available literature on

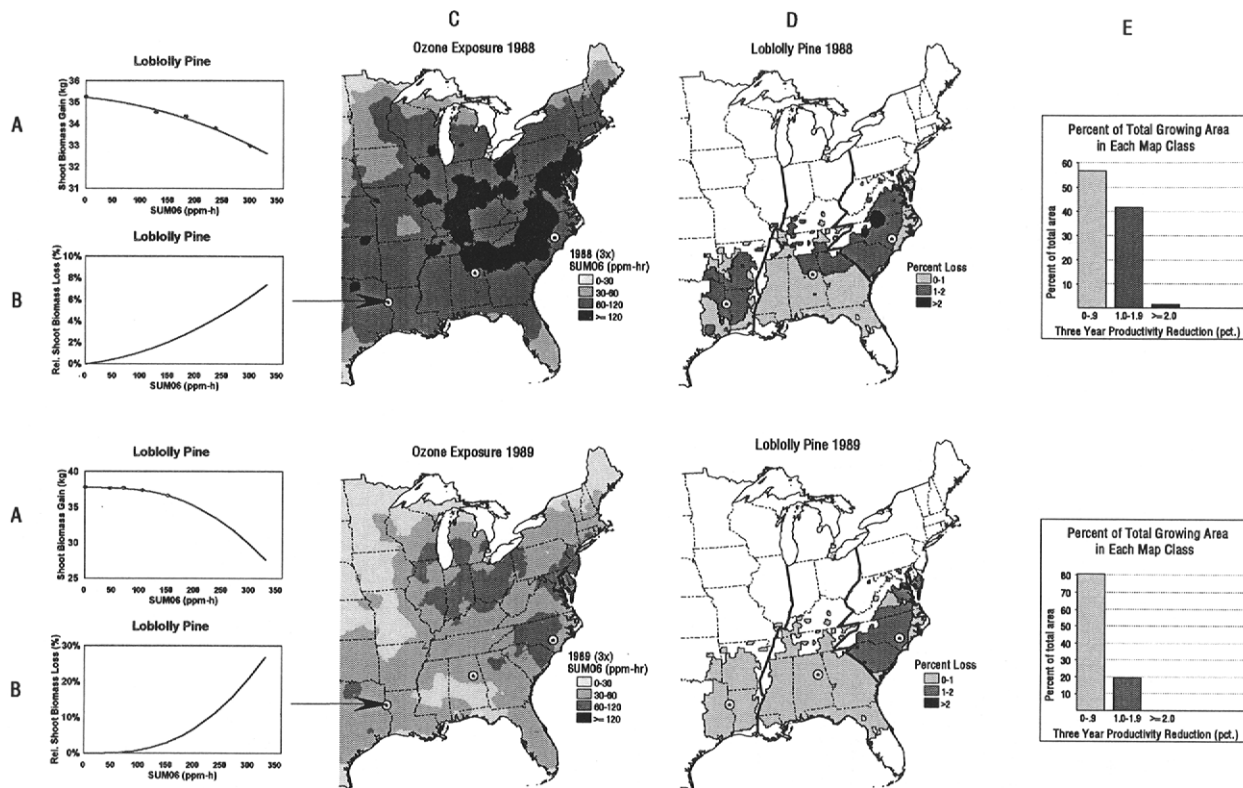


Figure 9. Regional extrapolation of TREGRO-generated aboveground biomass response functions. Two ozone exposure years were compared to illustrate response to a year of high ozone exposure (1988) and a more typical year of ozone exposure (1989) (C). Simulations were for 3 years with the model parametrized for a 30 year-old loblolly pine. The range of response possible across the region of loblolly was accomplished using climate data from 3 sites: a relatively wet area (Cumberland Co., NC), a relatively dry site (Cado Parish, LA), and an average site (Shelby Co., AL). From the response functions generated for each of these 3 sites (A), biomass loss functions were derived (B) and combined with estimated ozone exposures for 1988 or 1989 (C) and the loss interpolated across a region expected to have the same climate (D). Histograms (E) illustrate the area of loblolly experiencing 0→2% loss over the 3 year simulation.

large mature loblolly pines and used meteorological and ozone exposure data from 3 sites across the range of loblolly. The sites represented a relatively drier region (Cado Parish, Louisiana), a relatively wetter region (Cumberland Co. North Carolina) and an average site (Shelby Co., Alabama) based on a 10 year average of all met sites in this region. Using 3 sites for the simulations allows a means to demonstrate the range of response to ozone across the species' range based on the meteorological variables of precipitation and temperature. The biomass response functions resulting from the 3 year runs (1988-1988-1988 and 1989-1989-1989) for each met site are interpolated over the region that is thought to be experiencing the same climate. Cado Parish response functions for the two 3-year scenarios are shown in Figure 9A. The biomass loss function (Fig 9B) is derived from the shoot biomass response function (Fig 9A) and is applied across the appropriate region with the estimated ozone exposure (Fig 9C) and the resulting biomass loss maps are generated (Fig 9D). The histograms (Fig 9E) show the area of loblolly predicted to experience various reductions in growth over the 3 year period. Clear differences are apparent comparing the higher ozone exposures of 1988 to the 1989 scenario of relatively low ozone. Sixty percent of the loblolly area is predicted to experience 1-2% reductions in productivity over the three years of 1988 ozone, compared to 20% of the area when 1989 exposure scenarios are used.

The TREGRO response function generated using the climate data for the relatively wet year of 1989 compared to the function generated using the relatively dry year predicts changes in growth at less ozone concentration (150-200 ppm-hr for 3 year exposure) than that from the dry year of 1988 (250-300 ppm-hr for 3 years) (Fig 9A) suggesting the role of precipitation in the response to ozone. In the drier year, the reduced conductivity would result in less ozone being taken up and thus higher exposures are needed to cause effects. To illustrate the effect of precipitation on the biomass loss across the region of loblolly pine, the response function from 1989 is used with the estimated ozone exposures of 1988 and 1989 (Figure 10). With the higher ozone exposure of 1988 and the greater ozone response simulated using the higher precipitation there is a greater loss exhibited than when this same response function is used with the 1989 estimated ozone exposure (Fig 10D). If the same ozone exposure year (1988) is compared using the 3 year 1988 and 3 year 1989 generated response function, there is substantially more area experiencing greater than 2% productivity loss with the wet year (1989)-generated response function (Fig 9D and 10D). This simulation is in keeping with experimental data demonstrating the reduced effect of ozone under drought conditions (Tingey and Hogsett 1985). Although there are higher exposures in 1988, because of the higher temperatures, and less precipitation, there is presumably less ozone uptake due to stomatal closure. The model simulated response function demonstrated this. These results also suggest a possible weighting scheme as year to year variation in exposure is taken into consideration for exposure-response functions and developing air quality indices. The result of such an analysis in a risk characterization is that less weight would be given to warm years where precipitation is low compared to cooler, wetter years (even though less ozone exposure would be anticipated).

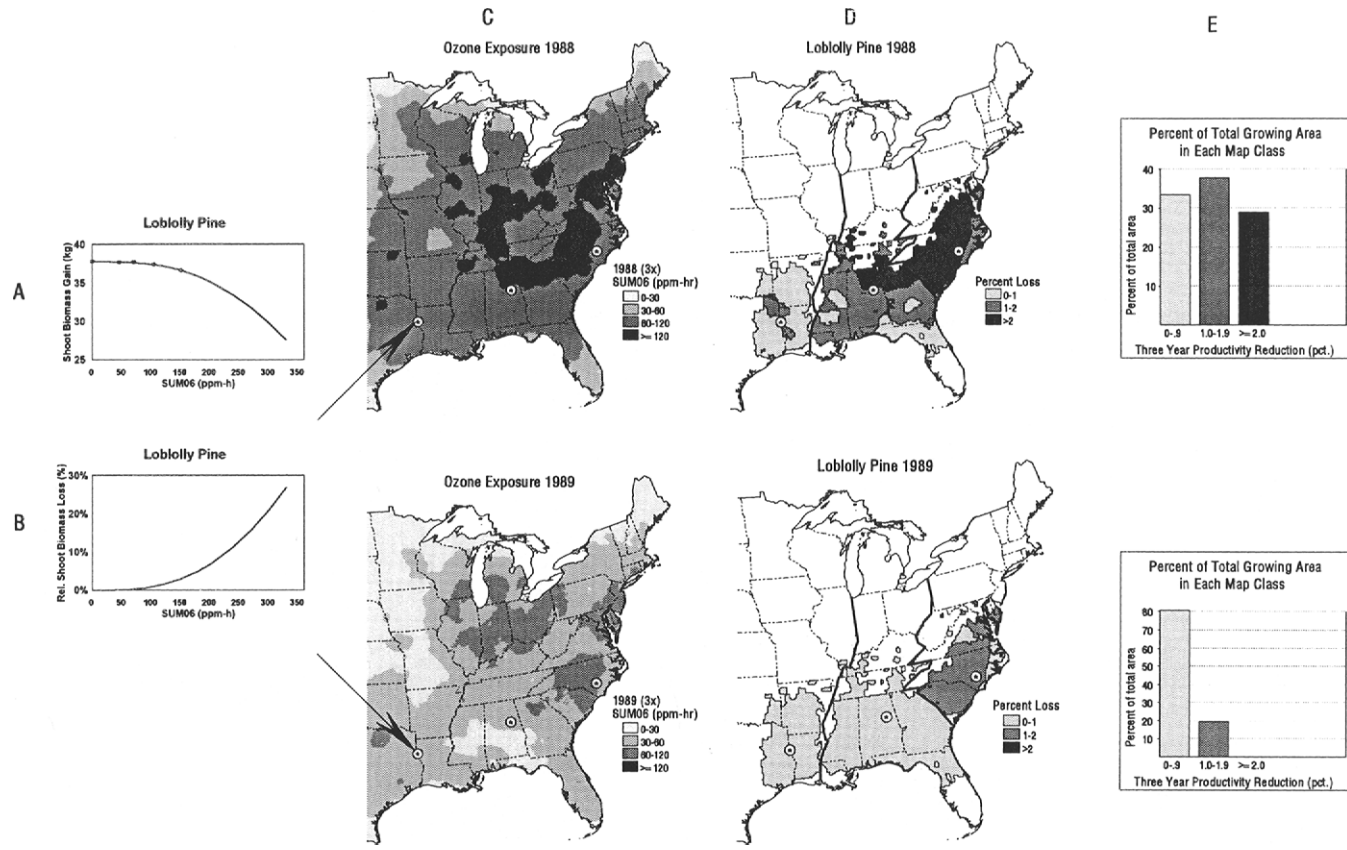


Figure 10. The role of Precipitation in aboveground biomass response to ozone. TREGRO generated response function of shoot biomass response for a relatively wet year of 1989 (A) was used to derive a biomass loss function (B) and that was applied to 1988 and 1989 estimated ozone exposure (C) across the region of loblolly using the GIS. The loss was interpolated across the region expected to have the same climate to produce maps (D) and from the maps, histograms reflect the area of loblolly predicted to experience various reductions in productivity over 3 years (E).