Disturbance Effects

INDIVIDUAL TREE FIVE-YEAR BASAL AREA AND CROWN DIAMETER GROWTH IN APPALACHIAN HARDWOOD STANDS AS INFLUENCED BY THINNING AND GYPSY MOTH DEFOLIATION

Kurt W. Gottschalk[1]

Abstract—I evaluated silvicultural treatments to minimize gypsy moth effects on forests in experimental plots on the West Virginia University Forest. Two treatments, presalvage thinning and sanitation thinning, were used. As part of the evaluation, I measured individual tree basal area growth and crown diameter growth over a five-year period. This period began with pretreatment measurements of stem dbh and crown diameter in 1989 before thinning and defoliation. Thinnings were installed during the winter of 1989-1990 and had paired control stands that were not thinned with four replicates of each treatment and control. Gypsy moth defoliated six of the 16 stands in 1990 and 1991. Mortality resulting from the defoliation-induced stress along with drought stress in 1991 occurred over the following three years. At the end of this period of stress and mortality, stem dbh and crown diameter were remeasured for all living trees. Stem dbh was converted to basal area. Basal area growth and crown diameter growth (or shrinkage in some cases) were calculated by taking the difference between the two measures.

Mean change in crown diameter was 3.5 feet and was normally distributed. About 35 percent of the trees had a reduction in crown diameter due to dieback. The range of crown diameter changes was -28 to +31 feet. Crown diameter change was significantly correlated with species, treatment (control, control+defoliation, thinning, thinning+defoliation), and the pretreatment crown class, but was not correlated with the pretreatment crown vigor nor the number of sides released. Despite the significance of the correlated variables, they explained very little of the variation in crown diameter change.

Mean change in basal area growth was 0.07 square feet and had a skewed distribution. Less than 1 percent of the trees had a decrease in basal area and 65 percent had only small increases in basal area (0.0 to 0.1 ft^2). The distribution dropped in an exponential pattern up to the maximum change of 1.28 square feet. Basal area change was significantly correlated with species, treatment, pretreatment crown class, pretreatment crown vigor, number of sides released, and crown diameter change. In a forward stepwise regression, the first and most important variable was pretreatment crown class. It was then followed by crown diameter change, species, and pretreatment crown vigor but all of the variables explained only a small portion of the additional variation.

Evaluation of treatment effects on crown diameter change showed that defoliation reduced crown diameter growth regardless of thinning treatment and thinning treatment increased crown diameter growth regardless of defoliation. Mean crown diameter growth (in feet) by treatment was:

Control + defoliation	2.5a
Thinned + defoliation	2.9ab
Control	3.2b
Thinned	4.7c

Evaluation of treatment effects on basal area change showed that thinning treatments increased growth regardless of defoliation and defoliation actually increased growth of surviving trees but less so in thinned stands than in control stands. Mean basal area growth (in square feet) by treatment was:

Control	0.055a
Control + defoliation	0.073b
Thinned + defoliation	0.084c
Thinned	0.084c

The positive effects of thinning on crown diameter and basal area growth trends especially when defoliated along with information on the mortality rates in the thinned versus unthinned stands support the use of thinning before gypsy moth defoliation as an useful technique to minimize gypsy effects on forests.

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Citation for proceedings: Stringer, Jeffrey W.; Loftis, David L., eds. 1999. Proceedings, 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 293 p. [Oral presentation abstract].

INDIVIDUAL TREE MORTALITY PREDICTION FUNCTIONS FROM GYPSY MOTH DEFOLIATION AS WELL AS TREE, STAND, AND SITE VARIABLES

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Abstract—Stands from central Pennsylvania were followed for fifteen years to provide records of plot slope, position, aspect, site index, land capability class; tree species, diameter, crown class, vigor or health, as well as annual gypsy moth defoliation. These data are used to create individual tree mortality prediction models for species and species groups under various degrees of defoliation. These models are tested against independent data and compared to previously published models for predicting tree mortality in similar situations. These results are then compared to log-odds-ratio analysis of variance results for these same data to provide further understanding of utility of these models and their precision for use in long term predictions of forest stand conditions. While analysis of variance provides a very useful characterization of mortality over these data, the difference in utility of the individual tree mortality models is demonstrated for predicting continuing impacts of defoliation over a wider range of defoliation histories and tree conditions. It is demonstrated how individual tree mortality models utilize defoliation history on individual trees and can account for the cumulative effects of defoliation over a number of years while other analytic procedures account for a effects associated with a prescribed pattern of defoliation over a fixed time interval.

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Citation for proceedings: Stringer, Jeffrey W.; Loftis, David L., eds. 1999. Proceedings, 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 293 p. [Oral presentation abstract].

CHARACTERISTICS OF THE CHESTNUT BLIGHT FUNGUS ISOLATED FROM SCARLET OAK IN PENNSYLVANIA

D.D. Davis and M.L. Torsello[1]

Abstract—More than 100 isolates of the chestnut blight fungus, *Cryphonectria parasitica* (=*Endothia parasitica*), were collected during a survey across Pennsylvania from infected scarlet oaks (*Quercus coccinea*) suffering from basal Cryphonectria cankers. Comparisons were made among isolates, as well as to a standard virulent (relative to American chestnut) and standard hypovirulent isolate in terms of linear growth on agar, lesion area induced in apple fruit, and canker area induced on American chestnut saplings. A ranking test indicated that growth on agar, lesion area induced in apple, and canker size induced on American chestnut were correlated. Most isolates grew on agar, infected apple fruit, and infected chestnut stems in a manner similar to that of the standard virulent isolate. A reservoir of virulent inoculum from scarlet oaks may confound efforts at biological control of chestnut blight on American chestnut. The possibility that a small number of isolates from scarlet oak may be hypovirulent on American chestnut should be investigated because one isolate had characteristics similar to the known hypovirulent isolate.

INTRODUCTION

Cryphonectria parasitica (Murrill) Barr (=*Endothia parasitica* (Murrill) P.J. Anderson & H.W. Anderson), virtually eliminated the American chestnut (*Castanea dentata* (Marsh.) Borkh.) as a forest tree throughout its range in the USA in the early 1900s (Roane and others 1986). Recently, there has been renewed interest in control of chestnut blight on American chestnut through the use of biocontrol (Nuss 1992). However a confounding factor in this biocontrol effort is that the surviving sprouts of American chestnut often grow in the understory of oak forests, and many of companion oak species, including scarlet oak (*Quercus coccinea* Muenchh.), also are susceptible to *C. parasitica* (see review in Torsello and others 1994). Working with oaks in southeastern USA, Nash and Stambaugh (1982) suggested that infected oaks could serve as reservoirs of virulent *C. parasitica* inoculum, especially in forest stands where American chestnut has been eliminated They also indicated that the virulence of some of the southeastern oak isolates, when placed into American chestnut, was equal to or greater than those isolates originally obtained from American chestnut (Nash and Stambaugh 1987).

In addition to harboring these virulent isolates of the chestnut blight fungus, scarlet oak may also contain less virulent, or hypovirulent, strains of the fungus. In fact, some biocontrol efforts in controlling chestnut blight in American chestnut are based on the use of this hypovirulence (Nuss 1992). Although hypovirulent isolates of *C. parasitica* have not been reported from hosts other than American chestnut, infected oaks may represent a potential, unstudied reservoir of hypovirulence for use in this biocontrol effort. Determination of isolate virulence with respect to American chestnut involves inoculation and evaluation of canker development on chestnut stems in the field (Elliston 1982, 1985; Scibilia and Shain 1989). However, such field trials are time consuming, and the limited number of uninfected chestnut stems present in some forest stands may not allow studies involving large numbers of isolates. Therefore, Elliston (1982, 1985) suggested inoculation of apple fruit as a rapid and efficient means to initially screen large numbers of isolates of *C. parasitica* to estimate virulence. Fulbright (1984) reported that the rate of colonization of "Granny Smith" apple fruit infected by *C. parasitica* isolates obtained from American chestnut might be used to estimate relative virulence of the same isolates in chestnut. In addition, Bedker (1989) suggested that linear growth rate in culture might be used to estimate the virulence of *C. parasitica* isolates in chestnut.

Linear growth in culture and ability to colonize apple fruit, in conjunction with chestnut stem inoculations to evaluate virulence, have not been examined for isolates of *C. parasitica* from scarlet oak. If successful, estimation of potential virulence of isolates based on linear growth in culture and/or apple colonization would allow a quick identification of source material for further studies dealing with virulence of *C. parasitica*. Also, inoculation of American chestnut stems under field conditions may yield insights into the possible role of inoculum from oaks on biological control of chestnut blight.

The objective of this study was to compare isolates of *C. parasitica* from scarlet oak growing in Pennsylvania, in terms of linear growth in culture, lesion size produced in apple fruit, and canker size induced on American chestnut stems. Comparisons were also made to known virulent or hypovirulent isolates.

METHODS

Linear Growth in Culture

During a survey across Pennsylvania, we collected 102 isolates of *C. parasitica* from cankered scarlet oak (SO);

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Citation for proceedings: Stringer, Jeffrey W.; Loftis, David L., eds. 1999. Proceedings, 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 293 p. [Peer-reviewed paper].

detailed methods regarding isolation and culturing have been presented (Torsello and others 1994). Initial isolations were cultured on acidified Difco potato dextrose agar (aPDA, 1 ml of 85 percent lactic acid per liter of potato dextrose agar). Subsequent cultures were maintained on acidified PDA containing methionine (100 mg/l) and biotin (1 mg/l) (PDAmb) (Anagnostakis and Aylor 1984). Occasionally, more than one SO isolate was obtained from a single canker. Since several vegetative compatibility types can occur in a single canker (Nash and Stambaugh 1989), each isolate was treated as a distinct entity. The linear growth of the 102 SO isolates was compared to the linear growth of EP155 and EP713, two *C. parasitica* isolates of known virulence. EP155 is a "standard" (Anagnostakis 1992) virulent isolate, American Type Culture Collection (ATCC) #38755, and has a normal phenotype. EP713 is a slow-growing, hypovirulent isolate (ATCC #52571) (Anagnostakis 1992). EP155 was obtained from W. MacDonald, West Virginia University, and EP713 was obtained from S. Anagnostakis of The Connecticut Agricultural Experiment Station.

One 7-mm diameter plug of PDAmb with mycelium was removed from each 7-day-old SO isolate, as well as EP155 and EP713, and placed on PDAmb against the wall of a petri plate. Four sets of each isolate were grown upside down in petri plates to minimize moisture accumulation on the agar surface. Plates were maintained in darkness at 21°C on four shelves in a controlled environment room utilizing a randomized block design with two replications. Shelves located perpendicular to a possible vertical temperature gradient in the room were considered as blocks. Each block consisted of a complete set of 102 SO isolates, EP155, EP713, and a control. After 7 days, the morphology of each colony was described and the growth of each isolate measured by taking two linear measurements per plate, from the edge of the plug to the distal edge of the colony, and averaged.

The 102 SO isolates, EP155 and EP713 were ranked in order of linear growth produced after 7 days (Minitab 1991). Growth data also were analyzed using ANOVA and Tukey's Honestly Significant Difference (HSD) multiple comparison procedure (p=0.05) to determine if significant differences in growth occurred among isolates (SAS 1985).

Apple Inoculations

One isolate from the linear growth study failed to grow. Therefore, 101 SO isolates, EP155, and EP713, plus a sterile PDAmb plug as a control were used to inoculate apple fruit. Fruit of the apple cultivar "Granny Smith" were sorted for uniformity, washed with sterile distilled water and detergent, wiped with 65 percent ethanol, and placed in a laminar flow hood. Each fruit was labeled with a waterproof marker and inoculated with three isolates. Each apple was inoculated with EP155 as a standard; the remaining two inoculations per apple were either SO isolates, EP713, or the control. A 7-mm diameter plug was removed from each fruit using a sterile cork borer, and a 7-mm plug of PDAmb containing the isolate, or sterile PDAmb agar as a control, was placed into the hole. Non-absorbent cotton was placed over the plug and the apple was wrapped with a strip of parafilm to minimize evaporation. Apples were placed on five vertically arranged shelves in a randomized complete block design. Shelves were considered as blocks against a possible vertical temperature gradient. Inoculated apples were incubated in the dark in a controlled-environment room set at 22°C. Temperature was recorded daily on shelves using glass thermometers.

Isolates, except for EP155, were randomly selected for inoculation of each apple within a block. Inoculated fruits were then randomized with respect to shelf position. Lesion length (mm) and width (mm) on each fruit were measured on the 12th day after inoculation. The experiment was terminated after 12 days since isolate interactions within individual fruits became a possibility as the lesions enlarged. Lesion area was determined and standardized by dividing the lesion area induced by each test isolate by the lesion area induced by the standard EP155 on the same apple.

The 101 SO isolates, as well as EP155 and EP713, were ranked in terms of lesion area induced (Minitab 1991). Data also was subjected to General Linear Model (GLM) analysis and Tukey's HSD mean comparison test (p=0.05) was used to test for differences in mean lesion areas induced by the various isolates (SAS 1985).

Chestnut Inoculations

Eighteen American chestnut sprouts growing in a 10-year-old clearcut in the Savage River State Forest, New Germany, Maryland were selected for inoculation. Sprouts selected did not have *C. parasitica* cankers within the proposed inoculation height on the main stem (0.5m to 3.0m), nor any other obvious large cankers on the stem. Due to the limited number of suitable stems available, all isolates could not be tested. Five of the *C. parasitica* isolates which induced the largest lesions on apple fruit(SO isolates 9, 31, 57, 77, and 86), and five of the isolates which induced the smallest lesions (SO isolates 12, 17, 39b, 69 and 99) were selected, along with the standard virulent EP155, hypovirulent EP713, and a PDAmb agar control.

On May 17, 1991, four inoculation wounds per stem were made by removing circular areas of bark with a sterile, 7-mm diameter core borer. Plugs of inoculum from 7-day-old cultures of *C. parasitica* on PDAmb, or sterile agar plugs as controls, were placed in the wound (mycelium towards the pith) and covered with parafilm. Each chestnut sprout was inoculated with the standard virulent isolate EP155. The remaining three wounds on each stem received the SO isolates, the hypovirulent EP713, or the control in a random distribution. Three repetitions of each isolate, other than EP155, were used. Inoculation wounds were not placed directly beneath one another on the same stem to minimize the possibility of conidia spread by stemflow from one inoculation point to another. Inoculation points were spaced at maximum allowable distances to minimize over-lapping canker growth between or among isolates.

Length (mm) and width (mm) of each canker was measured on August 29, 1991, 104 days after inoculation.

Field observations during canker development indicated that this time period was sufficient to assure that cankers were well established, yet not so large as to girdle the stem or overlap. The linear length and width measurements were converted to area prior to analysis. Since stems were variable in size and shape, lesion area was standardized by dividing the area induced by each isolate by the area induced by EP155 on the same stem, and ranked (Minitab 1991). The ranking was compared to the rankings for linear growth in culture, as well as the ranking for lesion size induced in apple fruit, and tested using Spearman's rank correlation (Minitab 1991). Data also were subjected to GLM analysis and Tukey's HSD mean separation test (p=0.05) (SAS 1985).

RESULTS

Linear Growth in Culture

There was no significant difference in linear growth among blocks (shelves in the incubator), but mean growth between the two replications was significantly different. However, in replication 2, growth of most isolates was poor and erratic, apparently due to laboratory techniques. Therefore, only data from replication one is presented in this paper (see Torsello (1992) for data from replication two).

Few significant differences in linear growth were observed among isolates; complete datasets for all 102 SO isolates are not presented, but have been reported elsewhere (Torsello 1992). Only isolate 68a of the 102 SO isolates grew significantly greater than that of the standard virulent strain EP155. Isolates 81 and 99, as well as the hypovirulent EP713, grew significantly less than EP155. The linear growth of SO isolate 99 and the hypovirulent EP713 were similar and were significantly less than all other isolates. There were no significant differences in growth among the remaining SO isolates.

The general culture morphology of all isolates, except for SO isolate 99, was similar to that of EP155, the standard virulent isolate. The morphology of isolate 99 was similar to that of the known hypovirulent EP713.

Lesion Induction in Apple

Monitoring with thermometers within the controlled environment room revealed no temperature gradient. However, apples on block 2 (shelf 2) had a slightly, but significantly, greater mean lesion area as compared to block 4 (shelf 4). Other comparisons among blocks were non-significant. Scarlet oak isolate 99 induced significantly smaller lesions on the fruit compared to all other isolates, including the standard hypovirulent EP713 and the standard virulent isolate EP155. Only SO isolates 22 and 47 induced significantly larger lesions than the hypovirulent EP713, but the lesions were not significantly different in size from those induced by EP155 (Torsello 1992). Other isolates induced lesions on apples not significantly different from those induced by EP155. The sterile agar plug resulted in minimal browning around each inoculation wound.

Canker Induction in Chestnut

Data from one stem were eliminated due to failure of EP155 to induce lesions, which precluded standardization. Considerable variation in canker size was noted, even among repetitions of the same isolate. Six isolates induced lesions larger than the standard EP155, and five isolates induced cankers smaller than EP155, but differences in lesion area among replications, individual stems, or isolates were not significant (data not presented). Isolate 99 induced the smallest lesion of all isolates. The sterile agar plug resulted in minimal, but measurable, browning around some inoculation wounds.

Ranking of Isolates

The relative ranking, standardized with reference to EP155, of canker size induced on American chestnut by 10 isolates and hypovirulent strain EP713 is shown in Table 1. Rankings from the apple fruit inoculations were very similar to the rankings derived from the chestnut stem inoculations, with a significant (p=.01) Spearman's rank correlation coefficient of 0.874. Likewise, the rankings from the first replication of the linear growth study correlated significantly (r=0.877, p=.01) with the rankings from the chestnut inoculations. However, rankings from the second replication of the linear growth study were not correlated (r =-.009, p=non-sig.) with rankings derived from the chestnut inoculations.

DISCUSSION

In terms of linear growth on agar, there were few differences among the 102 SO isolates of *C. parasitica* (See Torsello 1992 for complete dataset). Only scarlet oak isolate 99 (SO99) and the known hypovirulent EP713 (Anagnostakis 1992) grew significantly less than the standard virulent EP155 in both replications. The general culture morphology of all isolates except SO99 was similar to the phenotype of EP155 in both replications. SO99 exhibited submerged hyphae, reduced fruiting, and a mycelial morphology similar to that of some hypovirulent strains (Anagnostakis 1990). Based on linear growth in culture, we conclude that most of the SO isolates to be more similar to the virulent than to the hypovirulent strains, with the exception of SO99.

With regard to apple fruit, most of the 102 SO isolates induced lesions similar in size to those caused by the standard virulent isolate EP155. However, SO99 induced significantly smaller lesions on the fruit compared to all other isolates, including the standard hypovirulent EP713 and the standard virulent isolate EP155, again indicating characteristics of possible hypovirulence (Fulbright, 1984).

On the stems of American chestnut, considerable variation in canker size was noted, even among repetitions of the same isolate. Six isolates induced lesions larger than the standard EP155, and five isolates induced cankers smaller than EP155 (Table 1), but differences in lesion area among replications, individual stems, or isolates were not significant (Torsello, 1992). The lack of significance in the chestnut stem canker data is attributed in part to a severe drought that occurred during canker development, arresting growth of some inoculated saplings and causing mortality

Table 1—Relative ranking of growth of the 12 *C. parasitica* isolates which were common to all studies, in terms of canker size (ratio) produced on American chestnut, lesion size (ratio) induced in apple fruit, and linear growth (mm) in culture

Chestnut stem			Apple fruit		Linear growth	
ID	Area	Rank	Area	Rank	mm	Rank
99	0.450[a]	1	0.216[b]	1	7.00[c]	1
69	0.508	2	0.716	6	39.25	7
713[d]	0.523	3	0.608	2.5[e]	14.00	2
12	0.585	4	0.618	4	38.75	5
17	0.642	5	0.608	2.5	37.50	3
155[d]	1.000	6	1.000	7	39.00	6
39b	1.126	7	0.638	5	38.00	4
77	1.399	8	1.236	10.5	41.50	8.5
9	1.702	9	1.222	9	44.50	12
86	5.078	10	1.236	10.5	41.50	8.5
31	5.225	11	1.198	8	43.75	11
57	6.252	12	1.300	12	43.00	10
Correlation coefficient:			0.874[f]		0.877	

[a] Ratio of (canker area induced by each isolate) / (canker area induced on the same stem by EP155) 104 days after inoculation.
[b] Ratio of (lesion area induced by each isolate) / (lesion area induced on the same apple fruit by EP155) 12 days after inoculation.
[c] Linear growth (mm) after 7 days on PDAmb.
[d] 155 is the standard virulent isolate (EP155) and 713 is a known hypovirulent isolate (EP713).
[e] The same number (ending in .5) appearing within a column indicates equal ranking.
[f] Spearman's rank correlation coefficient comparing the relative ranking of respective columns to the results of the American chestnut inoculations.

of others, thus reducing the sample size and introducing variability. This variability confounded the critical comparison between the stem inoculation results with the linear growth and/or apple inoculation results, since stem canker production is the ultimate test for hypovirulence. However, it is important to note that, of all the isolates studied, SO99 induced the smallest lesion on American chestnut.

The relative rankings (Table 1) also reveal that the virulence ranking based on apple fruit inoculations were very similar to the rankings derived from the chestnut stem inoculations. Also, the rankings from the first replication of the linear growth study correlated significantly with the rankings from the chestnut inoculations. However, rankings from the second replication of the linear growth study were erratic, and not correlated with rankings derived from the chestnut inoculations, thus confounding any comparisons of our results with those of Bedker (1989). The rankings do support the use of inoculation of apple fruit as a possible means to initially screen large numbers of isolates of *C. parasitica* to estimate virulence (Elliston (1982, 1985; Fulbright, 1984). However, because of the results of replication 2 of the linear growth study, these results do not necessarily support those of Bedker (1989) who suggested that linear growth rate in culture might be used to estimate the virulence of *C. parasitica* isolates in chestnut.

Isolate SO99 should be investigated for the presence of viruses conferring hypovirulence. Hypovirulent isolates of *C. parasitica* have not been reported from hosts other than chestnut. However, results from this study indicate that only a small percentage of the isolates (perhaps 1 percent) from scarlet oak have characteristics of those known to be hypovirulent. If hypovirulence is present within *C. parasitica* on scarlet oaks, even in a small percentage, this population should be considered when formulating biocontrol efforts of chestnut blight on American chestnut involving use of hypovirulence.

However, most of the isolates collected from scarlet oaks across Pennsylvania had characteristics similar to the known virulent isolate, EP155. We concur with Nash and Stambaugh (1982), who found that cankered oaks in the southeastern USA may serve as important reservoirs of virulent *C. parasitica* inoculum, and that virulence (in

American chestnut) of some oak isolates is equal to or greater than that of isolates originally obtained from American chestnut.

ACKNOWLEDGMENTS

We gratefully acknowledge financial support from the Cooperative Education Program of the U. S. D. A. Forest Service, and cooperation from the Bureau of Forestry of the Pennsylvania Department of Environmental Resources. Department of Plant Pathology Contribution No. 2058.

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THE EFFECT OF SOIL MANGANESE ON JAPANESE LARCH (*LARIX LEPTOLEPIS* SIEB. AND ZUCC.) SEEDLINGS IN THE GREENHOUSE

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Abstract—Preliminary analysis of 9 year old Japanese larch trees and soil subjected to applications of triple ambient annual nitrogen (N) and sulfur (S) deposition revealed elevated available soil and foliar manganese (Mn) levels and decreased growth compared to controls. A greenhouse study was conducted in which Japanese larch seedlings were grown in field collected soil amended with 0, 100, 500, and 1000 mg of Mn as $MnCl_2$ per 8352 cm^3 of soil to determine the role of Mn in these growth differences. Growth was measured for 73 days. Soil samples were analyzed for magnesium (Mg), Mn and pH and foliar samples collected on day 73 were analyzed for Mn. Total chlorophyll concentrations were also determined. Control Japanese larch seedlings had significantly greater mean chlorophyll concentrations than treated seedlings. Japanese larch seedlings responded to increased Mn supply with increased uptake of Mn. Height and diameter growth were not significantly different ($\alpha \geq 0.05$) among the four treatments. However, overall height growth of Japanese larch was 10 percent less in the three treatments compared to the control. These results are supportive of the hypothesis that elevated available soil Mn may have contributed to the observed growth differences between control and treated Japanese larch in the field.

INTRODUCTION

Very little information exists about the potential phytotoxic role Mn may play with regard to forest health and tree nutrition. In the United States, deposition of anthropogenically produced N and S introduces strong mineral acids to the soil which influence soil chemistry. Deleterious effects to forest trees have been attributed primarily to soil changes, such as decreased levels of exchangeable base cations (especially calcium (Ca) and Mg), elevated hydrogen ion concentrations (lower soil pH) and higher levels of toxic aluminum (Joslin and others 1992; Thornton and others 1989). Manganese availability also is increased as a consequence of these soil changes, but has been given little attention (Elamin and Wilcox 1986). Gradual base cation depletion and low pH lead to soil Mn levels that may be detrimental to plant growth (Ohki 1984; Terry and others 1975). Excessive Mn has been associated with disruption of many physiological functions, such as reduced enzyme, hormone and chlorophyll production, inhibition of ATP formation, and reduced respiration (Elamin and Wilcox 1986).

Plant tolerance variations to excessive Mn are large (Kohno and others 1984; Simon and others 1986). Plant tolerance also has been associated with decreased transport of absorbed Mn from roots to leaves (Smith and others 1983). With some species, a reduction in chlorophyll content of the leaves sometimes accompanies the accumulation of toxic concentrations of Mn in the plant (Morgan and others 1976). Toxicity has been attributed to Mn induced Fe deficiency (Smith and others 1983).

Plants may differ considerably within and among species in Mn tolerance due to genetic characteristics and environmental factors such as nutrient availability in the soil. The presence of other ions including Fe, Ca, and Mg can modify Mn uptake (Goss and Carvalho 1992). Maas and others (1969) showed that Ca ions further enhanced the inhibition of Mn uptake by Mg. The mechanism responsible for selective uptake gave rise to the concept of carriers with varying affinities for the elements selectively accumulated. Because none of the effects between Ca, Mg, and Mn can be explained by mutual competition for the same transport site (Moore and others 1961), the regulatory action must result at a site other than the actual absorption site (Maas and others 1969). Manganese appears to function like Ca in maintaining membrane integrity (Maas and others 1968). Foy and others (1969) found increasing the Ca concentration in soil reduced Mn toxicity by reducing Mn uptake by roots or by reducing its transport to stems and leaves.

Ouellette and Dessureaux (1958) reported that excess Mn becomes detrimental only when enough of it moves from the roots to the above ground biomass. Therefore, Mn determination in leaves and stems provides a good indication of toxicity. Ohki (1974) defined critical Mn levels as the concentration in tissue associated with a 10 percent reduction in maximum growth and used this critical level to evaluate response in wheat to Mn. Kohno and others (1984) used the lowest Mn concentration level in the leaves at which toxicity symptoms developed as a more sensitive measure of plant tolerance to Mn. However, critical levels of Mn for various tree species have not been ascertained. If critical level data were available, the evaluation of foliar Mn status of field grown trees could be used as a guideline for diagnosing Mn toxicity.

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Citation for proceedings: Stringer, Jeffrey W.; Loftis, David L., eds. 1999. Proceedings, 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 293 p. [Peer-reviewed paper].

Analysis of Japanese larch foliage samples in 1993 taken from watershed 9, an 11.6 ha experimental watershed located 13 Km west of Parsons, West Virginia, revealed elevated Mn concentrations and reduced height growth as a result of annual treatments with 169 kg/ha of ammonium sulfate (Pickens and others 1995). The treatments began in 1987 four years after this watershed was clearcut and root raked and three years after it was planted with 2-0 Japanese larch seedlings at 1.8 x 1.8m spacing. Vegetation existent at the time of clearcutting consisted of mixed low grade hardwoods that had colonized abandoned agricultural fields.

Increased solubility of soil Mn was expected as a result of the ammonium sulfate treatments. The observed increased foliar Mn coupled with the sparse amount of information available on the potential effects of elevated soil Mn to trees prompted this investigation. Although Japanese larch is not now an important commercial tree species in the central hardwood region, it has been used extensively for strip mine reclamation plantings. Interest has also been expressed in converting low grade Appalachian hardwood stands to Japanese larch for fiber production. Watershed 9 where the initial observations of Mn response were made was converted to Japanese larch for this purpose (Kochenderfer and Helvey 1989). The study presented here was designed to evaluate Japanese larch seedling growth responses to various amounts of added Mn, and to determine whether or not Mn toxicity could explain the reduced growth of the treated Japanese larch observed in the field. In particular, we tested the following null hypotheses: (1) Japanese larch growth would not be reduced under the highest soil Mn levels; (2) Foliar Mn levels would not increase with increasing soil Mn levels; (3) Soil Mn levels could not be used to predict foliar Mn levels; (4) Elevated foliar Mn would not interfere with chlorophyll production.

MATERIALS AND METHODS

Soil Collection

Mineral soil obtained from Watershed 9, an experimental watershed operated by the USDA Forest Service in north central West Virginia, was collected on May 11, 1993 and used as the growth medium for the seedlings in this study. The soil was a Calvin channery silt loam (loamy skeletal, mixed, mesic Typic Dystrochrept weathered from the Hampshire sandstone formation (Losche and Beverage 1967). This soil had received 19 ammonium sulfate applications over the previous 7 years prior to collection. Under heavy acidic inputs, soils high in potentially available Mn release large amounts of this element (Kazda and Zvacek 1989). Manganese shows a strong association with Fe in rocks and soil, and is found adsorbed onto the surface of fine grained soil minerals. The Calvin channery silt loam used in this study was developed in uplands and weathered from sandstone and acid red shale (Losche and Beverage 1967). The pH of this soil was 4.22. The concentration of Mn in these sedimentary rocks has been reported to be in the range of 170-600 mg/kg. The average content of United States surface soils is 560 mg/kg (Gilkes and McKenzie 1988).

Soil was collected by extracting the A horizon mineral soil from three adjacent soil pits located on the northern boundary of watershed 9. The soil was mixed thoroughly and sieved to remove stones (> 1 cm^2), and placed into 48 clear, acrylic tube planters (45.2 cm tall x 15.2 cm in diameter). Each planter contained approximately 8352 cm^3 of soil. The bottom of each plastic planter was covered with nylon mesh fabric to allow drainage and covered with a porous polyethylene cap for additional support. Each planting cylinder was wrapped with aluminum foil to reduce soil heating and prevent algal growth.

Study Design

Seedlings were selected randomly for planting from a bundle of 200 2-0 stock Japanese larch seedlings (Saratoga Tree Nursery, New York DEC, Saratoga Springs, NY, seedlot 811, seed orchard #13). At planting, seedling heights (nearest 0.1 cm, meter stick) from root collar to tip of the dominant terminal and diameters (nearest 0.1 mm, Doall Electronic Digital caliper, Maxcal, USA) at 1 cm above the root collar were measured. All seedlings were breaking dormancy at the time of planting. All planters received 2 liter of distilled water at the time of planting. The planters were arranged in blocks of 12, placed in a greenhouse and the seedlings were allowed to grow from May 18 until July 8, 1993. Each block contained three planters of each treatment including controls. There were four treatment blocks in this randomized block design for each species. Dead or dying seedlings were replaced prior to July 8.

The soil in the planters was amended by adding 100 mg (treatment 2), 500 mg (treatment 3) and 1000 mg (treatment 4) of Mn in the form of $MnCl_2$ to each of three planters in each block (24 total planters per treatment) on July 8. An additional 24 planters served as controls. The $MnCl_2$ was dissolved in 1 liter of deionized water. The bottle used to add the Mn solution was rinsed three times with 50 ml (total) of deionized water and this water also was added to each planter. Each planter received 271 ml of water two times per week (2.97 cm/week). This amount was sufficient to keep soil moisture replenished. Growth measurements commenced on July 8 and ended on September 18. Seedling height and diameter data represent net growth during this 73 day period.

Twenty-four hours after treatment a soil sample was collected from the top 7-10 cm in each planter. Soil was collected in paper bags, air dried, and analyzed for 0.01 molar $SrCl_2$ extractable (Joslin and Wolfe 1989) Mg and Mn by atomic absorption spectrophotometry. Atomic absorption spectrophotometry analysis was performed within 48 hours of extraction. Soil pH was determined in 1:1 water/soil paste (Black 1964).

The experiment was terminated on September 18, 1993. Seedling heights and diameters were measured. Foliar samples for chemical analysis of Japanese larch were obtained by removing and compositing all needle whorls on two lateral branches on each seedling. All foliar samples were rinsed in deionized water, placed in paper bags, and oven dried at 105 °C for 24 hours. Samples were then

ground in a Wiley mill (Thomas Scientific, USA) fitted with a 20 um screen and submitted for ICP (Inductively Coupled Plasma Emission Spectroscopy) analysis to the Agricultural Analytical Services Laboratory (College of Agricultural Sciences, The Pennsylvania State University, University Park, PA 16802) to determine aluminum (Al), boron (B), Ca, copper (Cu), iron (Fe), potassium (K), Mg, Mn, sodium (Na), phosphorus (P), and zinc (Zn) (Dahlquist and Knoll 1978). Only Ca, Mg, Mn and Fe are reported here.

Quality assurance/control for all analysis included analytical duplicates and standard reference materials. Precision was determined by analyzing one duplicate soil and foliar sample with every 12 samples. Differences between the chemistry of the sample and its split were not significantly different from zero.

Total chlorophyll (chlorophyll a+b) concentration was measured on a randomly selected subsample of four Japanese larch trees for each of the four treatments. Preparation, extraction and determination of chlorophyll followed the method of Arnon (1948).

Data Analysis

All statistical analyses were performed using SAS statistical packages (SAS Institute 1985), following a randomized block design. Within a treatment, analysis of variance showed no significant differences for each chemical parameter among blocks, and values were then pooled by treatment. General linear regression was performed using treatment means of foliar and soil measurements.

RESULTS AND DISCUSSION

The height of Japanese larch seedlings was consistently reduced in the three treatments, but diameter growth was not (Figure 1). None of the changes was statistically significant, but a greater than 10 percent height growth decrease was observed, for all treatments which at least one author has considered important (Ohki 1985). Acceptance or rejection of null hypothesis one was thus somewhat uncertain. Statistical significance in height growth across treatments may have been achieved with a larger sample size.

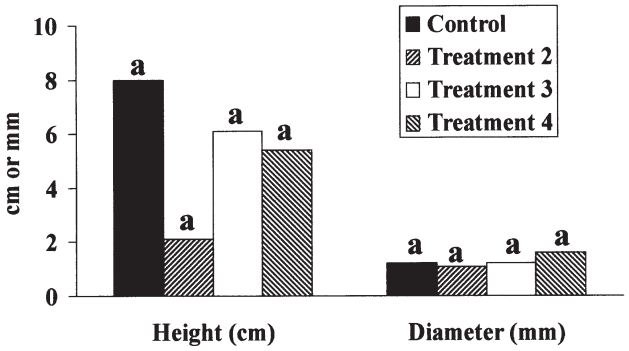

Figure 1—Mean height and diameter growth for Japanese larch from July 8, 1993 to September 18, 1993. Different letters above bars indicate significant differences at alpha = 0.05.

Control soil had significantly greater hydrogen ion concentration and significantly lower Mn compared to all other treatments (Table 1). Mn concentrations followed treatment 4 > treatment 3 > treatment 2 > control (all significantly different) for the soil Mn values. Soil Mg did not differ significantly among treatments.

Comparisons of foliar Mn for Japanese larch are given in Figure 2. All treatments were significantly different with the relative magnitudes of foliar Mn concentrations matching the treatment Mn additions. Japanese larch seedlings responded to increased Mn supply with increased uptake and foliar Mn concentrations. The relationship between initial soil Mn supply and foliar Mn concentration for Japanese larch is given in Figure 3. The relationship is significant (p=0.0001) and the two variables have an R^2 = 0.50. Thus, null hypotheses two and three were rejected.

The presence of other ions can modify the uptake of Mn from solution. In studying Mn toxicity to melons, Simon and others (1986) found that competition exists between Mg and Mn for specific binding sites. However, Maas and others (1969) explained the effects of Ca and Mg, on Mn as Mn absorption being non-competitively inhibited by Mg and stimulated by Ca. No differences existed for soil Mg among

Table 1—Initial soil sample mean concentrations (0.01 M $SrCl_2$ extractable Mn and Mg; pH in water) and statistical comparisons among treatments

Soil parameter	Control	Trt. 2	Trt. 3	Trt. 4
Mn (meq/100g)	0.012a	0.127b	0.374c	0.633d
pH (pH units)	4.22	4.01	3.95	3.83
pH (meq H^+/100g)	0.060a	0.098b	0.110b	0.148c
Mg (meq/100g)	0.074a	0.080a	0.085a	0.089a

Soil parameters with different letters indicate significant difference among treatments at $\alpha \leq 0.05$; n=24; pH was not tested.

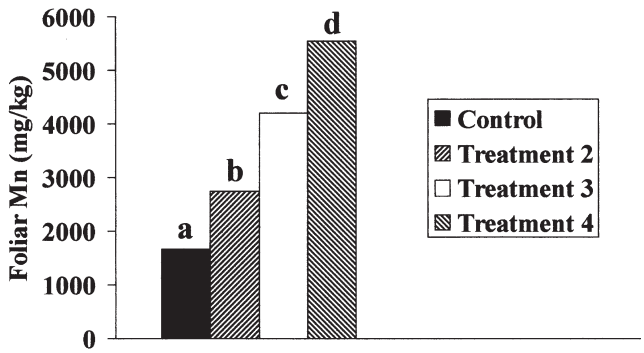

Figure 2—Japanese larch foliar Mn concentration comparisons among treatments. Different letters above bars indicate significant differences at alpha = 0.05.

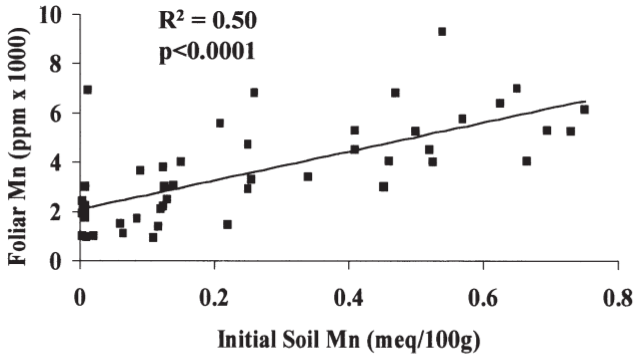

Figure 3—Regression relationship between initial soil Mn concentrations and Japanese larch foliar Mn at the end of the study for all treatments including control.

treatments in this study. For Japanese larch seedlings in this study, soil Mn concentrations and foliar Ca, Mg, and K were not consistently nor strongly correlated.

Foliar observations were recorded for all trees on June 15, July 28, August 18, and September 17, 1993. Japanese larch foliage did not exhibit any visual deficiency/toxicity symptoms regardless of treatment throughout the experiment.

Average chlorophyll concentrations (Figure 4) were greater in the control Japanese larch seedlings when compared to the other three treatments (reject null hypothesis four). Ohki (1985) found that excessive Mn in solution culture (500 mg/l) resulted in reductions of chlorophyll concentration in wheat. Others have reported chlorophyll synthesis inhibition by excessive Mn (Clairmont and others 1986; Csatorday and others 1984). The probable site of Mn inhibition is a Fe requiring step following the insertion of Mg in the tetrapyrrole ring of the chlorophyll molecule (Clairmont and others 1986). No correlations were found between soil Mn and foliar Fe, nor between foliar Mn and foliar Fe. There were no significant differences in foliar Fe among treatments.

Ohki (1985) defined the Mn critical toxicity level as the foliar concentration associated with a 10 percent growth

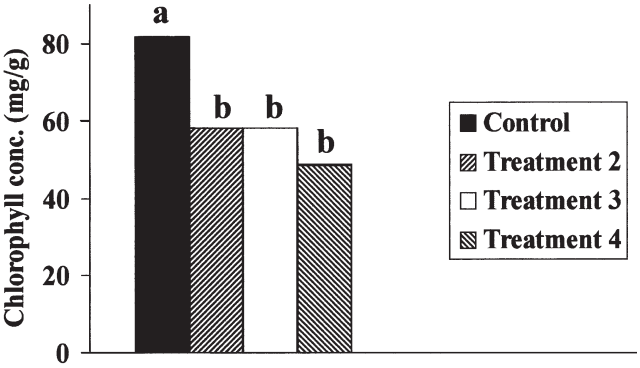

Figure 4—Japanese larch chlorophyll concentrations in mg/g. Different letters above bars indicate significant differences at alpha = 0.05.

reduction. Using the relative growth of the control as the maximum amount achievable for this experimental time period. A 10 percent reduction for Japanese larch would have resulted in a 7.2 cm height increase and a 1.1 mm diameter increase. Larch height growth in treatments 2, 3 and 4 all fell below this value, averaging 2.1 cm, 6.1 cm, and 5.4 cm, respectively. Diameter growth did not exhibit a response. These growth changes occurred in the absence of visual foliar symptoms. The critical toxicity level as defined by Ohki (1985) may have some merit in predicting growth changes in Japanese larch. Although no observed Mn symptoms in larch seedlings were recorded, the trends of decreasing growth and chlorophyll concentration along with significantly greater levels of foliar Mn with soil Mn additions suggested that some inhibitory effects to the photosynthetic process may have occurred.

SUMMARY AND CONCLUSIONS

Under acidic soil conditions, soil macronutrients such as Ca and Mg and potentially toxic micronutrients such as Mn become more mobile, enhancing their uptake by tree roots. Sensitivity of most forest trees to elevated Mn remains unknown. Under conditions of low soil pH and low soil-available Mg and Ca commonly found in extremely acidic forest soils, Mn toxicity could occur. Soil Mn levels were a good predictor of Japanese larch foliar Mn, at least for the range of Mn availability used in this study. The results of this study suggest that Mn toxicity and subsequent foliar chlorophyll reductions may play a role in the reduced height growth observed in the N and S acidified Japanese larch plantings reported by Pickens and others (1995) and Kochenderfer and others (1995) on an acidified watershed. Further investigation of the impacts of increasing Mn availability and toxicity to other tree species that commonly grow in relatively Mn rich, extremely acid edaphic environments in the central hardwoods region would seem to be prudent.

ACKNOWLEDGMENTS

This work is based on work supported by funds provided in part by the US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, under Cooperative Agreement 23-742, and in part by the School of Forest Resources, College of Agricultural Sciences, and the Environmental Resources Research Institute, The Pennsylvania State University. Any opinions, findings, conclusions or recommendations expressed in this publication are those of the authors and do not necessarily reflect the view of the Department of Agriculture. We thank Bryan Swistock for assistance in figure design and preparation.

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NORTHERN RED OAK GROWTH REPONSE TO CLIMATE AND INDUSTRIAL AIR POLLUTION IN WESTERN PENNSYLVANIA

J.R. McClenahen, D.D. Davis, and R.J. Hutnik[1]

Abstract—Northern red oak (*Quercus rubra* L.) radial growth response over time and space was examined along an inferred air pollution gradient on Laurel Ridge, a northeast - southwest anticlinal ridge, in relation to local and historically varying air pollutant emissions from coal-burning power generation and iron production within the greater Johnstown area (Conemaugh Gap) in west-central Pennsylvania. The specific objectives were to determine the effects, if any, of industrial air pollution (primarily sulfur dioxide) on: (1) the relationship of tree growth and climate, (2) tree growth as measured by basal area increment and, (3) the separate growth responses that may be related to long-term air pollution from Johnstown industry and more recent coal-burning power generation. On the east side of Conemaugh Gap, the city of Johnstown has been a major iron production center from the 1920's until 1977. Two power generating stations on the west side of Conemaugh Gap began operation in 1950 and 1970, respectively. We collected pairs of tree cores from at least 20 canopy northern red oaks in 11 mostly ridge top stands ranging from 11 km downwind to 34 km upwind of Conemaugh Gap. Indexed tree-ring chronologies for each stand were derived by standard dendrochronological techniques, and these chronologies were modeled with temperature and precipitation variables by stepwise multiple regression. The resulting growth-climate models indicated that growth of northern red oaks on Laurel Ridge most consistently and positively responded to July precipitation of the growth year, and warmer than normal summer temperatures in the preceding year. In general, upwind control stands showed the strongest relationship with climate, while growth in stands nearer to and downwind of Conemaugh Gap exhibited weaker or virtually no relationship with climate. The spatial patterns of basal area growth rates generally mimicked those of the growth-climate models; an increasing growth rate was evident with distance away from Conemaugh Gap. We conclude that growth of canopy northern red oaks on the upper slopes of Laurel Ridge near to, and downwind of, Conemaugh Gap exhibited anomalous long-term low growth rates and climatic decoupling. The most likely cause of this growth anomaly is historical industrial emissions from Johnstown, with little or no indication of an additional growth impact when the power generating stations went on-line. Whether red oak growth and climatic sensitivity recover in the Conemaugh Gap area as a result of improving air quality is under investigation.

INTRODUCTION

The health of forests and natural ecosystems is a major focus of public agencies and private forest owners. This focus has emerged from an awareness that native and introduced pests, air quality, changing land use patterns, forest management practices, climatic extremes, and many other potential stressors may be increasingly affecting forest health (Smith 1990). Measuring forest health is a major challenge in part because the concept lacks specific definition (Kolb and others 1994). There is no concensus about which critical indicators to measure and there is a deficiency of data about the normal range of many proposed health indicators. A further complication is the difficulty in identifying causal factors after forest or tree declines occur (Manion and Lechance 1992).

Tree growth variation, as manifested in annual ring widths, is one approach for identifying stress or declining vigor (McClenahen 1995). Some studies have shown marked changes in tree-ring response to climate and (or) growth reductions in a variety of species in the presence of high pollutant dose (Sutherland 1990, Thompson 1981, Fox and others 1986). A few instances of growth-climate decoupling or growth decreases have been reported in the absence of unusual mortality or decline symptoms (McClenahen and Dochinger 1985, Phipps and Whiton 1988, Puckett 1982, Tryon and others 1979). Further, dead or symptomatic trees may reveal anomalous tree-ring responses compared to healthy trees (McClenahen 1995), but means for detecting predisposing stress that may portend declining health have not been specifically developed.

This study focuses on the potentially interacting effects of climate variation and regional air pollution on tree growth. The research was conducted on Laurel Ridge in the vicinity of Johnstown, a major industrial city, in westcentral Pennsylvania, USA (Fig. 1).

Laurel Ridge affords partial isolation of pollutant emissions from industrial Johnstown to the east and two local power generating stations to the west. Periods of non-overlapping emissions from these two sources also provided a temporal isolation of emissions. Thus, a unique opportunity was available to study the separate and combined effects of air pollution from these two pollutant sources on tree growth.

We compared the regional patterns of tree growth-climate responses and growth rates of northern red oaks (*Quercus rubra* L.) across an inferred gradient of industrial emissions from Johnstown and the two power generating stations

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Citation for proceedings: Stringer, Jeffrey W.; Loftis, David L., eds. 1999. Proceedings, 12th central hardwood forest conference; 1999 February 28-March 1-2; Lexington, KY. Gen. Tech. Rep. SRS-24. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 293 p. [Peer-reviewed paper].

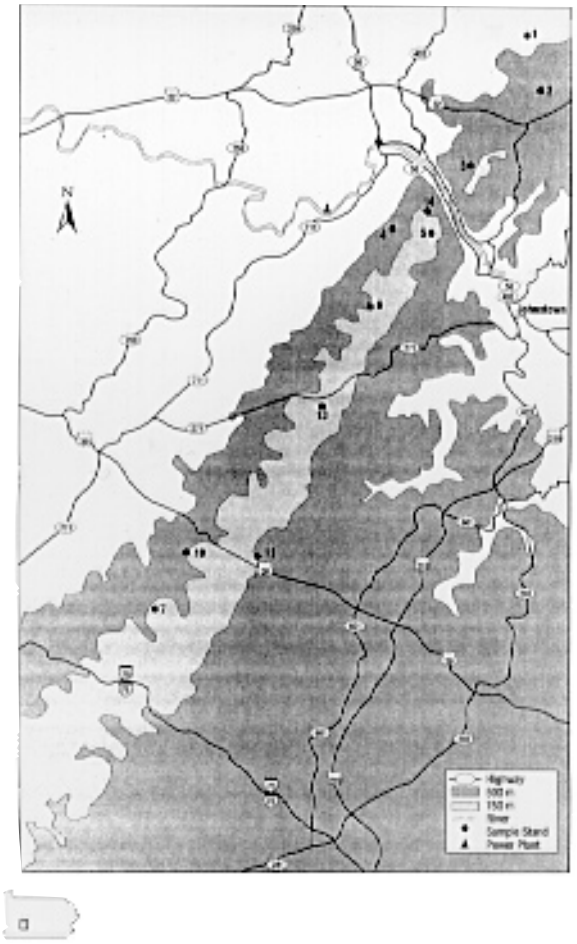

Figure 1—Study area and numbered sample stands. Scale is approximately 1 cm = 5 km.

(Fig. 1). The specific objectives of this study are to determine the effects, if any, of air pollution within the Conemaugh Gap (Greater Johnstown) industrial area on: (1) the relationship of tree growth to climate, (2) tree growth as measured by basal area increment and, (3) the separate growth impacts that may be related to long-term air pollution from Johnstown industry and more recent power generation from local coal-burning power stations.

METHODS

Study Area

Tree coring sites were located on Laurel Ridge, a NE to SW-oriented anticlinal ridge 700-800 m in elevation. The area lies within the Allegheny Plateaus Physiographic Province in portions of Cambria, Indiana, Westmoreland and Somerset Counties (Fig. 1). The climate is continental with a mean growing season temperature of 9.8°C and annual precipitation averaging 104 cm. Forests on Laurel Ridge are second and third growth mixed hardwoods. Oaks (*Quercus* spp.) dominate the ridgetops and drier slopes. Coves and moist slopes have mixtures of *Prunus serotina* Ehrh., *Acer rubrum* L., *Liriodendron tulipifera* L., *Quercus* spp., and others.

Historically, sulfur dioxide (SO_2) has been the primary air pollutant in the Conemaugh Gap area since the late 19th century (Fig. 2). On the southeast side of Laurel Ridge at the eastern side of Conemaugh Gap, Johnstown iron and steel production, and attendant coke plants, began operation in 1872, increasing exponentially from about the 1920's through the 1960's (Brown 1989). Beginning about 1977, a drastic decline in iron production and cleaner technology resulted in reduced SO_2 emissions (Brown 1989).

Two coal-fired power plants are located on the northwest side of Laurel Ridge near the western side of Conemaugh Gap (Fig. 1). The Seward plant began operation in 1950 with one 64 mw unit and a stack height of 70 m. A second unit added in 1957 increased generating capacity to 137 mw. Stack height was increased to 183 m in 1977. The Conemaugh station, with a stack height of 305 m, started one 850 mw unit in 1970 and a second unit of equal capacity in 1971. SO_2 emissions from two other large power stations to the northwest apparently do not appreciably impinge the area of this study (Hutnik and others 1989).

Sample Stands

Beginning in 1987, data were collected within 11 mostly ridge top or upper slope, mature, closed canopy, even-aged, northern red oak stands (1-10 ha). Ideally, stands lacking partial cutting were chosen, but many had received light thinnings as part of forest management practices. Stands 7, 10 and 11, to the southwest and upwind of pollutant sources, served as controls in regard to pollutant emissions from the power generating stations and Johnstown industries to the northeast (Fig. 1), although transport of sulfur and nitrogen from sources outside the region and subsequent deposition onto Laurel Ridge is well-recognized (e.g., Pierson and others 1989).

Soils on the study sites are well to moderately well drained, very stony loams and silt loams, predominantly Typic Dystrochrepts, occasionally including some Typic Hapludults and Aquic Fragiudults.

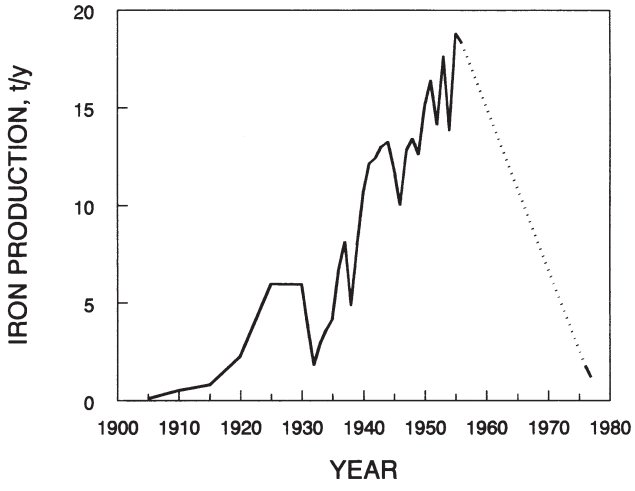

Figure 2—Historical iron production at Johnstown (Data from Brown, 1989).

Tree-Ring Sampling

Pairs of 5 mm diameter cores were extracted at 1.3 m height from boles of at least 20 dominant and codominant red oaks in each of the 11 stands. Trees without dieback or mechanical crown or bole injury were selected. Cores were air-dried, glued into wooden holders, and surfaced with successively finer sanding papers. Visual crossdating was performed, ring widths were measured to 0.01 mm precision, and crossdating was verified using computer program COFECHA (Holmes 1985).

Statistical Analyses

The ring-width series of each core within a stand was standardized to create stationary time series and to remove autocorrelated trend largely associated with age and competition. This was achieved by a double-detrending procedure followed by autoregressive modelling, using Cook's (1987) method and computer program ARSTAN. First, a linear or negative exponential trend line was fit to each series and indices were computed from the ratio of curve value to ring width. The second detrending was achieved by fitting a spline curve to the initial indices and recalculating. Lastly, an appropriate autoregressive (AR) model was fit to each detrended series, and to the mean stand chronology. This step yielded two types of mean stand chronologies: the mean indices after AR modeling of individual series (residual chronology), and the arstan chronology consisting of the residual chronology plus that portion of the original trend (persistence) common to most individual series. Thus, the residual chronology represents the mean "white noise" stand chronology. The arstan chronology additionally contains the common (pooled) persistence that may be associated with some exogenous factors affecting growth.

Stepwise multiple regression models were developed to relate red oak residual and arstan growth indices for each of the eleven stands to regional climate (objective one). Total monthly precipitation and mean monthly temperature data were each averaged from Historical Climatic Network database stations at Johnstown, New Castle and Uniontown (Boden 1987, Bradley and others 1985). A 17-month climate year (prior May through September of the growth year) comprised the 34 total variables in the stepwise regression analyses with residual and arstan indices for each stand. A common calibration period of 1920-1969 (51 years; pre-Conemaugh power station emissions) was used. Stepwise regression climate calibrations were performed using PRECON (Fritts and others 1991). A value of F = 4.00 was used for adding variables. The resulting models were evaluated in terms of lack of fit, Durbin-Watson statistic, variance inflation factors, and the residuals plots. A series of tests described by Cook and others (1987) were employed to verify the calibration models using independent climate data from 1970-1986, and to address objective three. Actual and predicted indices were examined for similarity of pattern by simple linear correlation, for significant predictive bias by t-tests of the residuals for difference from zero, and for indication of predictive skill by reduction of error (RE).

Annual basal area increment (BAI) was computed for each ring width series from core radii and the ring widths using computer program AREA (Phipps and Fields 1988). Radial growth trend differences among stands were examined by comparing the slopes of linear regressions fitted to the individual stand cumulative mean BAI data (objective two).

RESULTS

Chronology Characteristics

Chronology statistics were initially examined for indication of comparative stand growth disturbance histories (Table 1). Autoregression parameter differences, in terms of the model coefficients (Φ) and percent explained variation (R^2), between the mean of individual series models and the pooled model for all series imply a spatially varied disturbance history within the stand, while similar parameter values suggest spatially homogeneous disturbances (Cook 1988). In this regard, stands 1, 2, 10, and 11 show relatively heterogeneous disturbances by virtue of large differences in both R^2 and Φ. In fact, charred snags indicated the occurrence of fire in stand 1; stand 2 had a light partial cutting approximately 20 years earlier. However, growth disturbance histories appeared fairly uniform within most stands. In fact, the remaining seven stands were similar in common persistence (pooled R^2) and pooled AR coefficients (Φ) (Table 1). These stands had 30-45 pct common growth persistence, indicative of even-aged forests lacking significant heterogenous disturbances.

These chronologies portray the historic natural disturbances, stand development trends, and direct human interventions such as cutting and fire that partly molded present forests on Laurel Ridge, but they show no specific relationship to the Conemaugh Gap area.

Growth-Climate Models

Red oak growth relationships with climate varied considerably among stands, with the percentage of growth explained by climate variables ranging from 9.3 to 49.1. Mean monthly temperature variables entered the regressions more frequently than precipitation variables (Fig. 3). Growing season temperature, especially in the prior year, had a generally positive growth relationship, although the specific temperature variables were not very consistent among stands or between residual and arstan chronology models within stands. Some of these inconsistencies could be related to variation in site and tree ages, although sample tree ages were mostly similar among stands (Smith and Rennie 1995). The single most consistent and important climate variable appearing in models was July precipitation in the growth year, which was always positive in its relationship.

The strength of the climate relationships among stands, indicated by the percentage of explained variation (R^2(pct), adjusted for number of variables), revealed some striking spatial patterns (Fig. 4). Growth in the southernmost, upwind stands (control stands 7, 10, 11) was consistently and relatively strongly coupled with climate. This was reflected in both the residual and arstan chronology models. These three stands were originally selected as controls by virtue of their distance and upwind direction from the Conemaugh

Table 1—Red oak chronology statistics; Φ_1 and Φ_2 are the series mean or pooled autoregression (AR) coefficients for models up to AR(2); R^2 is the variation explained by autoregression averaged over individual series or from pooled autoregression

				Autoregressive model					
				Series means			Pooled		
Stand	Chron. length	No. series	AR order	Φ_1	Φ_2	R^2	Φ_1	Φ_2	R^2
	No. yrs.					*Pct.*			*Pct.*
1	103	40	1	.529	-	29.6	.409	-	16.7
2	114	40	1	.489	-	25.8	.431	-	18.6
3	73	40	1	.584	-	35.9	.604	-	36.5
4	107	40	1	.617	-	39.1	.675	-	45.6
5	91	40	2	.533	.064	36.7	.502	.184	40.0
6	141	46	1	.540	-	30.1	.549	-	30.2
7	141	42	3	.478	.047	31.5	.384	.122	33.8
10	132	31	1	.518	-	29.4	.434	-	18.8
11	129	42	1	.469	-	23.2	.394	-	15.5
13	140	40	2	.575	.034	37.5	.518	.158	39.3
14	75	40	1	.541	-	30.8	.537	-	28.9

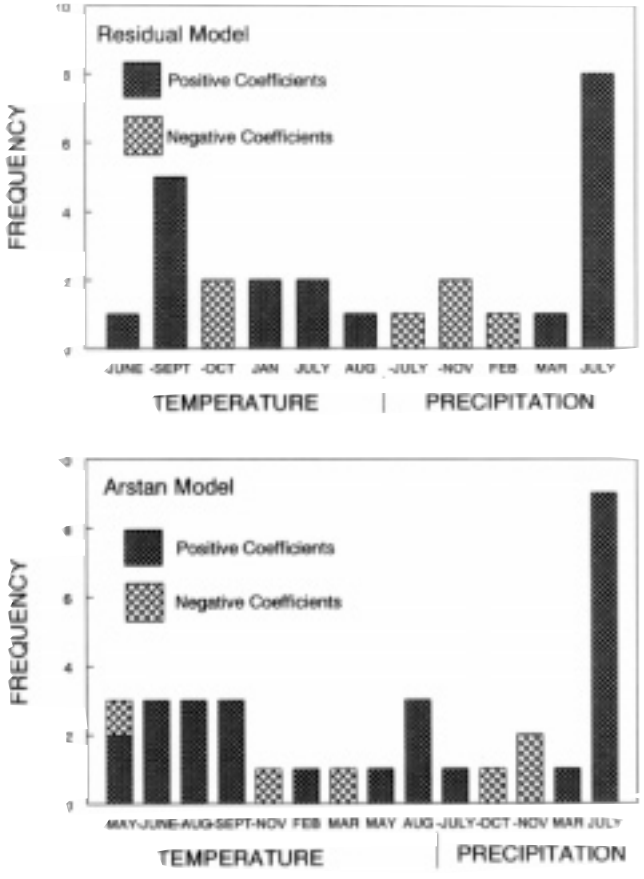

Figure 3—Frequencies of monthly mean temperature and monthly total precipitation variables appearing in calibration models of the eleven stands using residual and arstan chronologies. Numbers indicate stands. Negative signs preceding months indicate prior year.

Gap area. Compared to the control stands, residual chronology models of stands near Conemaugh Gap were notably weaker; while common (pooled) growth persistence in the arstan chronologies dramatically strengthened the growth-climate relationships in certain of these stands (viz., stands 1, 2, 4, 13). However, stands 5 and 6 exhibited virtually no growth response to climate variation.

Evaluation of the growth-climate calibration models for each stand indicated that all were significant in terms of correlated patterns of actual and predicted indices, and all exhibited some predictive skill (Table 2). However, these criteria revealed weaker models for stands 5 and 6 and, to a lesser extent, stands 1, 3 and 14.

The calibration model verifications using the period 1970-1986 showed uniformly poor predictive potential (Table 2). Although none had significant bias, there was no evidence that predicted indices correlated with observed indices, and no models exhibited predictive skill. Thus, although potentially useful calibration models were obtained for many of the stand chronologies, none were adequate for predicting growth in the post-1969 period. Further, calibrations based on the entire 1920-1986 period for each stand chronology yielded consistently lower percentages of explained variation than the 1920-1969 calibrations. Calibration of the control chronology (mean of stands 7, 10 and 11) with climate for the entire 1920-1986 period identified only two significant variables, July precipitation and prior April temperature, and it explained less than half of the growth variation (21.9 pct) explained by the 1920-1969 calibration model. These results portray a regionally

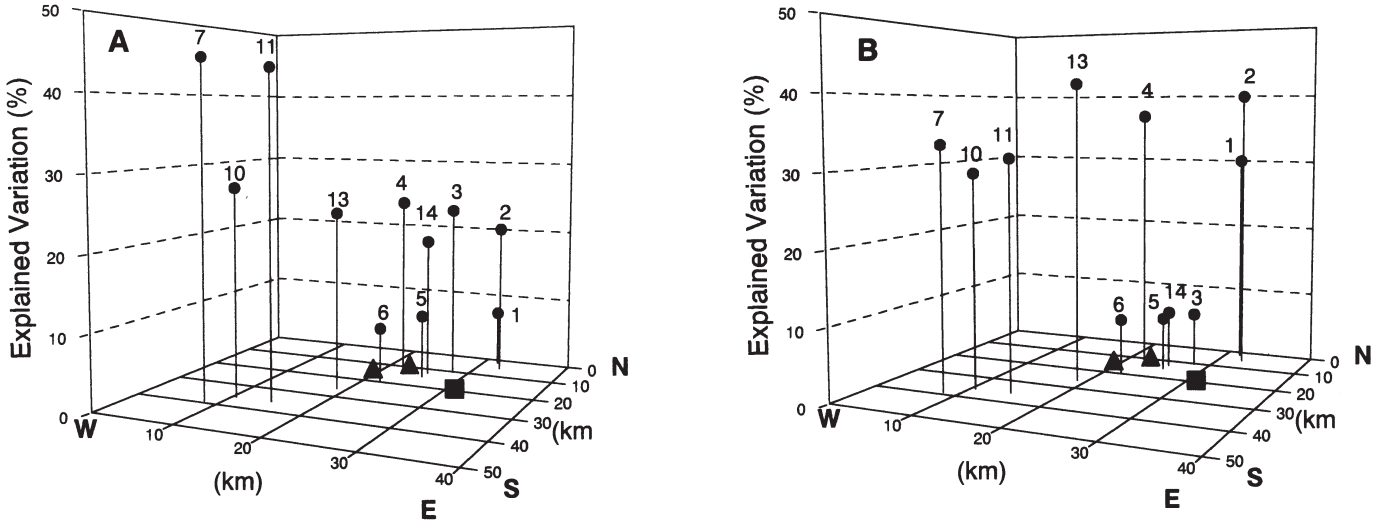

Figure 4—Geographical patterns of percentages of explained variation ($R^2_{adj.}$) for climatic calibration models based on (A) residual and (B) arstan tree-ring chronologies. Triangles indicate power station locations, the square indicates the location of Johnstown.

Table 2—Comparison of arstan and residual indices-based climate model performance for 1920-1969 (calibration period) and 1970-1986 (verification period); the simple correlation coefficient (r) measures the correspondence in pattern between actual and predicted indices; bias is the mean residual, with significant values an indication of over- or under-prediction; reduction of error (RE) >0 suggests predictive skill over using the mean index value (no significance test available)

		Residual			Arstan		
Stand	Period	r	Bias	RE	r	Bias	RE
1	Calib.	0.38*		0.09	0.60*		0.36
	Verif.	0.24	0.018	0.05	0.01	0.040	-0.84
2	Calib.	0.50*		0.25	0.69*		0.47
	Verif.	0.01	-0.001	-0.32	0.02	0.039	-0.41
3	Calib.	0.52*		0.27	0.32*		0.10
	Verif.	0.34	-0.058	-0.01	0.10	-0.056	-0.32
4	Calib.	0.53*		0.28	0.66*		0.43
	Verif.	0.16	-0.014	-0.05	0.10	-0.045	-0.63
5	Calib.	0.32*		0.11	0.31*		0.09
	Verif.	-0.20	0.032	-0.48	-0.12	-0.019	-0.19
6	Calib.	0.31*		0.09	0.31*		0.10
	Verif.	0.23	0.039	0.02	0.17	0.030	0.01
7	Calib.	0.70*		0.49	0.61*		0.37
	Verif.	0.12	0.020	-0.17	0.28	-0.057	-0.12
10	Calib.	0.63*		0.39	0.66*		0.44
	Verif.	0.08	-0.036	-0.11	0.06	-0.030	-0.63
11	Calib.	0.69*		0.48	0.60*		0.36
	Verif.	0.17	0.054	-0.07	0.21	0.038	-0.01
13	Calib.	0.54*		0.29	0.69*		0.47
	Verif.	0.13	0.022	-0.20	0.00	0.013	-1.43
14	Calib.	0.47*		0.22	0.31*	0.10	
	Verif.	0.26	-0.019	-0.01	0.07	0.008	-0.12

*Significant at $P \leq 0.05$.

unstable growth response to climate in addition to the spatial differences noted above.

Basal Area Growth

Linear regressions closely and accurately described the cumulative mean basal area increments between 1920 and 1986 for 10 of the 11 stands ($R^2 \geq 0.98$). Stand 14 had a curvilinear growth pattern (linear $R^2 = 0.90$) due to a growth release around 1955 and is excluded from the following discussion.

The spatial pattern of basal area growth rates (Fig. 5) generally mimics that of the growth-climate model strengths depicted in Figure 4. As a group, stands 2, 3, 5, 6 and 13 exhibited lower growth rates than stands 1, 4, 7, 10 and 11. These growth rates depict a generally increasing growth gradient away from the Conemaugh Gap area. An exception is stand 4 on the northwest base of Laurel Ridge near the power plants, which exhibited a growth rate comparable to stands remote from Conemaugh Gap despite its proximity to the power stations. The physiographic location of stand 4 would probably shield it from pollutants originating at Johnstown (Fig. 1). Stands 5 and 6 were notable for lacking a growth relationship with climate, and the mean sustained growth rates of these stands (and stand 2) implies a history of non-climatic growth stress. There was no physical evidence within these stands to indicate a possible explanation.

DISCUSSION AND CONCLUSIONS

The 1920-1969 climate response calibration models show that above normal July rainfall in the growth year, and warmer than normal summer temperatures in the preceding year, promote red oak growth in these stands. The arstan chronologies were generally better correlated with climate than the residual chronologies, indicating a general persistence in the effect of climate on growth that may be a physiological characteristic of the species. However, this persistence was especially evident in chronologies from the vicinity of Conemaugh Gap, suggesting the presence of additional exogenous environmental stress in that area.

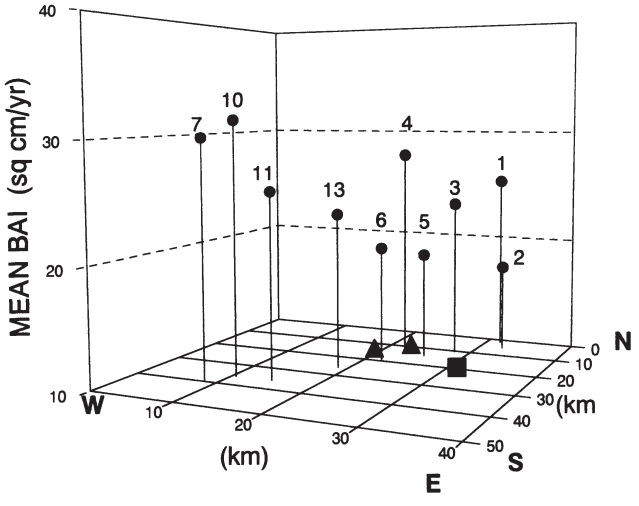

Figure 5—Geographical patterns of stand cumulative mean basal area increment (BAI) growth rates. Numbers indicate stands. Triangles show power station locations and the square indicates the location of Johnstown.

The climatic response is generally consistent with the ecophysiological nature of oak growth. Oaks tend to occupy relatively warm, dry habitats. Their ring-porous characteristic results in a dependency on stored energy from the previous year for earlywood formation, while latewood production relies more upon current season growing conditions. July precipitation is clearly the most critical climatic factor in growth of red oaks on Laurel Ridge.

Red oaks within the northeastern portion of the study area generally exhibited an anomalous uncoupling of the climate-growth relationship that generally predates the Conemaugh, Seward or other local power stations. Red oaks have also had notably low growth rates within this same locality during pre- and post-operational times. These findings raise the possibility that anthropogenic disturbances, perhaps including fire, destructive logging practices, and industrial emissions from Jownstown, may have strongly impacted red oak growth in the locality at least two decades prior to 1986.

Stands 5 and 6 show the most consistent lack of climatic growth response (and the lowest basal area growth rates), followed by stands 1, 2, 3 and 14. Notably, these appear to lie within the Johnstown airshed. In particular, stands 5 and 6 are situated on the ridge top directly above the city. Although geographically within the same general area, stands 1, 4, 13 and 14 were somewhat better correlated with climate. However, stands 1 and 13 are more remote from Johnstown, while stands 14 and 4 lie respectively on the mid-slope and at the base of the opposing side of Laurel Ridge from the city, and may have been relatively sheltered from Johnstown emissions. Although a similar sheltering effect might be true for stands 1, 2 and 3, Johnstown emissions could be carried to these stands through Conemaugh Gap by prevailing winds.

Evaluation of 1920-1969 growth-climate calibrations, and comparisons with models derived for 1920-1986, indicated that the relationship of red oak growth on Laurel Ridge has not remained stable. Precisely when this transition took place cannot be established from our analyses, but it is evident in the post-1969 period at all sites. Comparatively high frequencies of insect defoliations and droughts during 1970-1992 resulted in extensive red oak mortality on Laurel Ridge between 1990-1992 (McClenahen and others 1997). Comparisons of red oak and tuliptree chronologies indicate that relatively few oak defoliations occurred in the study area between 1930 and 1957, while the more recent, recorded defoliations were confirmed (unpublished data of the authors). These droughts and increasing defoliation events, a number of which fell within the chronology period 1969-1986, may have contributed greatly to the general red oak growth-climate uncoupling.

Summarizing these results: (1) the importance of common persistence in the arstan calibrations may reflect an interactive effect of climate and other environmental stress

within ridgetop and upper slope stands near the Conemaugh Gap during power plant pre-operational times, (2) there was a long-term depressed growth-climate relationship for most stands within the Conemaugh Gap area, especially on the ridgetop above Johnstown, (3) the comparative structures of the AR models mitigate against differences in endogenous disturbance histories as a sufficient explanation for these anomalous spatial patterns of growth-climate response and, (4) stands most likely exposed to Johnstown industrial emissions exhibited comparatively lower basal area growth trends.

We conclude that growth of canopy northern red oaks on the upper slopes of Laurel Ridge near to, and downwind of, Conemaugh Gap exhibited an anomalous long-term low growth rate and more pronounced climatic decoupling. The most likely cause of this growth anomaly is historical industrial emissions from Johnstown. There is little indication that sulfur emissions from local power stations established mostly in the late 1960's and early 1970's had an additional growth impact. Whether comparative red oak growth and climatic sensitivity recover in the Conemaugh Gap area as a result of improved air quality in Johnstown (and reduced power plant emissions) is presently under investigation.

ACKNOWLEDGMENTS

This study was supported by a contract from the Chestnut Ridge Energy Center. We gratefully acknowledge the technical contribution of Nikki H. McCarthy for assistance in collecting cores and developing the tree-ring chronologies. Robert P. Long contributed one of the red oak chronologies used in the study.

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