1-1-1998

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Recommended Citation

MacDonald, Neil W.; Witter, John A.; Reed, David R.; Burton, Andrew J.; Pregitzer, Kurt S.; and Liechty, Hal O., "Environmental Stress Effects on Vigor, Mortality, and Growth in Northern Hardwood Forests Along a Pollution-Climate Gradient" (1998). *Peer Reviewed Publications.* Paper 20.
http://scholarworks.gvsu.edu/biopeerpubs/20

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MICHIGAN ACADEMICIAN XXX, 27–471(1998)

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ABSTRACT

Concern exists over the effects of interacting environmental stresses on the ecological integrity of temperate forests. Coincidence of sensitivity to drought, increasing occurrence of defoliation, and elevated pollutant deposition has produced speculation that northern hardwood forests may be susceptible to the increased climatic stresses projected for the Great Lakes region. The objective of our study was to examine relationships among environmental stress factors, vigor, mortality, and growth in northern hardwood forests located along a pollution-climate gradient in the Great Lakes region. Between 1987 and 1993, we quantified climatic variables, pollutant deposition, insect defoliation, and tree vigor and growth at five sites along this gradient. Drought and defoliation occurred to varying degrees during the study period. Symptoms of chronic environmental stress, such as cankers and epicormic branching, were most pronounced at extreme ends of the gradient. Periodic diameter increments decreased for suppressed trees but increased for dominant trees from north to south, primarily related to climatic factors. Variation in annual diameter increments was strongly associated with moisture availability, with diameter growth being greatly reduced during episodic droughts at the more southerly sites. At one site that experienced both drought and defoliation in 1988, worsening crown condition, elevated mortality, and reduced growth were consistent with the effects of acute levels of environmental stress. While most northern hardwood forests in the Great Lakes region are currently healthy, our results provide additional evidence that these forests are sensitive to increased severity of environmental stress, and may experience alterations in mortality and growth if climate changes as some have predicted.

INTRODUCTION

Environmental stress factors that affect the growth and productivity of forest ecosystems include temperature and precipitation (Cook et al. 1987), drought and water deficits (Cook and Jacoby 1977), nutrient deficiencies or imbalances (Waring 1985), adverse soil physical or chemical properties (Hyink and Zedaker 1987), insect defoliation (Kulman 1971), and air pollution (Innes and Cook 1989). These stress factors often occur sequentially or are present simultaneously and may interactively affect individual trees or entire forest stands (Hain 1987; Mattson and Haack 1987; LeBlanc 1993). Symptoms of environmental stress include observable changes in tree vigor, decreases in tree growth, or increased mortality rates (Waring 1987; Franklin et al. 1987).

Concern exists over the effects of both atmospheric pollutant deposition (e.g., Schulze 1989) and climate change (e.g., Cook and Johnson 1989) on the composition, health, and productivity of temperate forests. Both pollutant deposition and climate change represent additional stresses on forest ecosystems that also may be nutrient limited, drought prone, and subject to episodic insect and disease outbreaks (Bernier et al. 1989; Witter et al. 1992; LeBlanc and Foster 1992). Forests in the Great Lakes region of North America are exposed to dual gradients of atmospheric pollutant deposition and climate (Burton et al. 1993). Because of their location between major ecotones or transition zones (Jones et al. 1994), forests in this geographic region may change dramatically over the next century if global climate changes as some have predicted (Pastor and Post 1988; Solomon and Bartlein 1992).

We began studying the effects of atmospheric pollutant deposition and climate on northern hardwood forest ecosystems at multiple sites in the Great Lakes region in 1987. Our research at these sites has been multidisciplinary, and has encompassed a variety of studies related to the interactive effects of pollutant deposition and climate on nutrient cycling, forest growth and productivity, carbon allocation, genetic diversity, and seedling recruitment (Witter 1991). For example, previous work has demonstrated that atmospheric pollutant deposition has affected nutrient cycling within these northern hardwood forests (Pregitzer at al. 1992; MacDonald et al. 1992; Liechty et al. 1993). Variation in growth of these forests over the past 50 years was strongly related to climate (Lane et al. 1993). While no significant differences in stand basal area or biomass increment among study sites were detected for a four-year period between 1988 and 1991, there was substantial year-to-year variability in growth within and among stands (Reed et al. 1994). The objective of the study reported here was to examine relationships between environmental stress factors and variation in tree vigor, mortality, and growth at five northern hardwood forests located along the Great Lakes pollution-climate gradient.

METHODS

Site selection and description

We selected analogous sites representing northern hardwood forests based on regional differences in pollutant deposition, similarity of overstory species composition and structure, stand age, physiography, soil properties, and recent stand history. Sites were selected from a list of 31 potential locations based on field visitations, statistical comparisons among potential sites, and subjective decisions based on the investigators' experience with the ecosystem type (Burton et al. 1991). Site locations (Table 1, Figure 1) span a region with pronounced gradients of climate and atmospheric pollutant deposition (MacDonald et al. 1992; Burton et al. 1993). Sites 2 to 5 represent regions

FIGURE 1. Locations of northern hardwood research sites in the Great Lakes region.

TABLE 1. Locations and Stand Characteristics† of Northern Hardwood Research Sites in the Great Lakes Region

	Site				
Variable#	2	3	4a	4b	5
Latitude (N)	46°52'	45°33'	44°23'	44°21'	43°40'
Longitude (W)	88°53'	84°52'	85°50'	85°42'	86°09'
Stand Density§ (trees ha^{-1})	696 (177)	759 (172)	811 (100)	644 (96)	907 (93)
Basal Area (m^2 ha^{-1})	33.4 (0.4)	30.7 (1.4)	31.8 (2.5)	31.5 (1.9)	32.2 (1.9)
Sugar Maple Basal Area (%)	86.5 (7.1)	85.0 (6.2)	81.8 (5.7)	76.7 (3.4)	73.3 (12.9)
Stand Age (yr)	85	79	80	82	84

† Stand characteristics as measured at end of 1993 growing season.

Values for stand characteristics presented as means with standard deviations in parentheses.

§ Stand density based on number of trees recorded as alive in 1993.

that have different pollutant deposition rates, increasing from north to south. Sites 4a and 4b represent different ecological conditions within an area of similar pollutant deposition, Site 4b having higher moisture and fertility status than 4a. Total stand basal areas and ages were selected to be as similar as possible while maximizing the sugar maple (*Acer saccharum* Marsh.) component (Table 1). All stands are even-aged, having regenerated following logging in the early 1900s, and are surrounded by similar deciduous forests. Soils at all sites are predominantly sandy, mixed, frigid Alfic and Typic Haplorthods (MacDonald et al. 1991).

Tree growth and vigor measurements

Three 0.09 ha (30 m x 30 m) measurement plots were established at each site. Plots were subjectively located within the 5 to 6 ha stands to maximize plot similarity in soil and overstory characteristics within and among sites. Each tree on the measurement plots was numbered and classified in suppressed, intermediate, codominant, or dominant crown positions following standard methods (Zedaker and Nicholas 1986). Diameter at breast height (1.37 m) of trees $\geq$ 5.0 cm in diameter was measured each fall between 1987 and 1993 after at least 50 % of leaf fall had occurred. Diameter of each tree was measured by two individuals who had to agree within ± 1 mm; this resulted in a standard error of $\leq$ 0.3 mm for individual diameter measurements as determined from 10% remeasurement. Periodic increments for individual living trees were calculated as the difference in diameter between 1993 and 1987. Annual diameter increments for individual living trees were calculated from annual measurements for each of the six growth years between 1987 and 1993.

Beginning in 1988, tree vigor and stress symptoms (crown condition, defoliation, frost cracks, cankers, sugar maple borer (*Glycobius speciosus* Say) damage, and epicormic branching) were quantified for each tree on the measurement plots using visual integer-scale rating classes (complete descriptions for ratings in each category are presented as footnotes in Tables 3 and 4 and Figure 3). Newly dead trees also were identified at this time. Each year, ratings at all sites were assigned between mid-July and mid-August. Ratings for each category were made after inspecting the crown and bole of the tree from several locations. Ten percent of the trees on each plot were reexamined to determine the deviation from initial rankings in each category. On average, less than five percent of rankings deviated from initial values in any category during any year of the study.

Environmental measurements

Precipitation amounts and atmospheric pollutant deposition have been monitored at each site since 1987 as described by MacDonald et al. (1992), Pregitzer et al. (1992), and Liechty et al. (1993). Beginning in 1989, air temperature, soil temperature, and soil moisture have been measured at the center of each plot from late March through mid-November at all sites with the exception of Site 4b. Air temperature is measured at a height of 2 m and soil temperature is measured at a depth of 15 cm using thermistors (Model ES-060-SW Temperature Probe, Omnidata International, Inc., Logan, UT). Soil moisture is recorded at depths of 15 and 75 cm using gypsum blocks (Model 5201, Soilmoisture Equipment Corp., Santa Barbara, CA). Sensors are not replicated within plots. Sensors are scanned at 0.5-hr intervals and average values are recorded every three hr on a data logger (Easylogger 800 Series, Omnidata International, Inc., Logan, UT). We estimated available water deficits (potential evapotranspiration – actual evapotranspiration) on a monthly basis for the period 1987–93 using the Thornthwaite water balance equation (Mather, 1978), basing available water holding capacity on the upper 75 cm of soil. Monthly precipitation and mean monthly temperature data from the nearest National Oceanic and Atmospheric Administration stations with complete records were used wherever site-specific information was unavailable during the period 1987–93. Degree days >5.6 °C were calculated from mean monthly temperatures as described by Tuhkanen (1980).

Statistical Analysis

Parametric one-way analyses of variance for climatic and mensurational data were conducted with sites considered a fixed effect. For one-way analyses of variance, years were treated as replications for climatic data, while mensurational measurements were replicated at the plot level. Repeated measures analyses of variance were used where we wished to incorporate multiple-year comparisons (annual water deficits, annual diameter increments). Mean separation for parametric analyses was accomplished using Tukey's multiple comparison test (Steel and Torrie 1980). Crown condition, defoliation, and environmental stress symptom ratings were compared using the Kruskal-Wallis non-parametric analysis of variance. Differences in ratings within or among sites were determined using a non-parametric multiple comparison procedure described by Conover (1980). Within-site correlations involving annual defoliation or crown condition ratings were based on plot means (n=18). Across-site correlations between environmental factors (growing degree days, water deficits, pollutant deposition) and periodic diameter increments were based on site means (n=5).

RESULTS AND DISCUSSION

The existence of parallel gradients in climate and pollutant deposition are viewed by some as complicating factors (e.g., Lucier and Stout 1988), but are a reflection of real world conditions, not an artifact of study design. In any environmental gradient analysis, the potential confounding effects of co-varying factors need to be recognized and controlled to the extent possible. Careful selection of analogous sites combined with the use of site-specific measurements and long-term records of both pollutant deposition and climatic conditions have allowed us to separate many of the effects of climate, edaphic factors, and pollutant deposition on forest ecosystem processes at these study sites (e.g., Pregitzer and Burton 1991; MacDonald et al. 1991; Pregitzer et al. 1992; MacDonald et al. 1992; Liechty et al. 1993; Burton et al. 1993; Lane et al. 1993; Reed et al. 1994). Burton et al. (1991) present a full discussion and evaluation of our approach to selecting and intensively studying a small number of similar sites to minimize confounding effects.

Environmental Stress Factors

Mean annual air temperatures, April to October soil temperatures, and growing degree days measured during the study period (1987–93) increased significantly from Site 2 to Site 5 (Table 2). Mean growing season (May to August) air temperatures followed this same trend, but means were not significantly different. Significant differences in annual precipitation were observed, but growing season precipitation was virtually identical across the five sites (Table 2). Available water deficits tended to increase from north to

TABLE 2. Climate+ and Pollutant Deposition at Northern Hardwood Research Sites in the Great Lakes Region.

	Site				
Variable	2	3	4a+4b	5	P#
			°C		
Degree Days	1551b	1689ab	1677ab	1907a	0.031
> 5.6 °C	(200)	(202)	(196)	(237)	
Annual Air	5.1b	6.2ab	6.1b	7.7a	0.001
Temperature	(1.0)	(1.0)	(1.0)	(1.0)	
May–August	16.2	16.8	16.8	17.9	0.123
Air Temperature	(1.3)	(1.3)	(1.3)	(1.4)	
April-October	10.3b	11.0b	11.3b	12.9a	0.001
Soil Temperature	(0.8)	(0.7)	(0.7)	(0.9)	
			cm		
Annual	78.3b	78.6b	99.6a	86.3ab	0.008
Precipitation	(10.3)	(7.3)	(14.2)	(13.9)	
May - August	31.1	26.6	31.8	30.0	0.729
Precipitation	(3.4)	(9.0)	(12.5)	(9.8)	
Available	7.7	11.9	10.6	13.6	0.395
Water Deficit	(3.2)	(6.9)	(7.2)	(7.4)	
			kg ha^{-1}		
H^+ Deposition	0.22	0.55	0.67	0.68	§
SO_4^{2-} Deposition	14.8	22.8	27.1	29.1	§
NO_3^- Deposition	17.0	25.8	34.4	33.8	§

+ Values for climatic variables represent annual means with standard deviations in parentheses for the period 1987-1993.

Significance probability of analysis of variance. Means without common letters differ significantly; letters compare means among sites.

§ Values for pollutant deposition variables represent mean annual total wet + dry deposition (from MacDonald et al. 1992). Means were not compared statistically because dry deposition estimates were not based on replicated measurements.

south, but means did not differ significantly. Pollutant deposition (H^+, SO_4^{2-}, NO_3^-) increased from Site 2 to Site 5 (Table 2), a gradient that has been extensively documented (Pregitzer et al. 1992; MacDonald et al. 1991, 1992; Liechty et al. 1993). Other research has shown that a gradient of ground-level ozone roughly parallels the acidic deposition gradient in the Great Lakes region (McLaughlin 1996), with an average two-fold increase in ozone concentrations from north to south (Witter 1991).

In contrast to the mean available water deficits, annual available water deficits were highly variable from year to year within and among sites (Figure 2). Periods of moderate drought (water deficits of 10 to 20 cm) were fairly common during the study period, but were most frequent at Sites 3 to 5. Severe drought (water deficits >20 cm) occurred during 1988 at Sites 4a, 4b, and 5, with a pronounced gradient in water deficit evident from Site 2 to Site 5. The 1988 drought was widespread and noted throughout the Midwest and upper Great Lakes region (Allen et al. 1992; Foster et al. 1992; LeBlanc 1993). Patterns in calculated monthly available water deficits corresponded well to patterns in soil moisture recorded on the plots by gypsum blocks (N. W. MacDonald, unpublished data).

Defoliation occurred at Sites 3, 4a, and 4b during the period of this study (Table 3). Defoliation at Sites 4a and 4b in 1988 and 1989 was caused by the forest tent caterpillar (*Malacosoma disstria* Hübner). Defoliation at Site 3 in 1990 was caused by forest tent caterpillar and greenstriped mapleworm (*Dryocampa rubicunda* Fabricius). Defoliation at Site 4b in 1992 also was caused by the greenstriped mapleworm. At Site 4a in 1992, we observed defoliation of all species by gypsy moth (*Lymantria dispar* L.). Defoliation was severe at Site 4b in 1988, with approximately 80% of the foliage consumed. Defoliation ratings in all crown positions at this site during the study period were positively correlated ($r = 0.84^{**}$ to 0.91^{**}) with current-year water deficits. Defoliation was not correlated with current-year water deficits at Sites 3 or 4a.

Measures of climatic factors that would favor tree growth on a regional basis (growing degree days, mean annual temperature, and to some extent mean annual precipitation) increased from north to south. Increased NO_3^- deposition from north to south co-varied with this trend and also could benefit growth through a fertilizer effect (Aber et al. 1989). However, environmental stress factors (water deficits, deposition of pollutants) also increased from north to south, and soils tended to become more drought-prone at the southerly sites as a result of lower silt plus clay contents (MacDonald et al. 1991). Superimposed on known trends in climate, pollutant deposition, and soils were unpredictable stresses such as insect defoliation and the occurrence of severe drought.

Environmental Stress Symptoms

Chronic stress symptoms, including frost cracks, cankers, epicormic branching, and sugar maple borer damage, were most pronounced at sites at the extreme ends of the gradient (Table 4). Frost cracks were most prevalent and

TABLE 3. Mean Defoliation Ratings+ for Northern Hardwood Research Sites in the Great Lakes Region

	Site					
Year	2	3	4a	4b	5	*P#*
1988	1.01c	1.00c	1.18b	3.98a	1.01c	<0.001
1989	1.03c	1.01c	1.21b	1.68a	1.00c	<0.001
1990	1.01b	1.76a	1.02b	1.01b	1.00b	<0.001
1991	1.01	1.02	1.02	1.01	1.00	0.200
1992	1.03c	1.03c	2.29a	1.15b	1.01c	<0.001
1993	1.02	1.02	1.01	1.01	1.00	0.288
n§	(196/184)	(234/205)	(235/219)	(194/170)	(284/245)	

+ Mean ratings calculated for all trees alive during the year indicated. Defoliation rating categories: 1 = 0-20%, 2 = 21-40% 3 = 41-60%, 4 = 61-80%, 5 = 81-100%.

Significance probability of Kruskal-Wallis non-parametric analysis of variance. Means without common letters differ significantly; letters compare defoliation ratings among sites within a single year.

§ Number of trees included in statistical analyses of defoliation ratings (1988/1993)

severe at Site 2 on codominant and dominant trees. Elevated sugar maple borer damage was exclusively limited to Site 2 on suppressed, intermediate, and codominant trees. Cankers were most severe on suppressed and intermediate trees at Site 2, but most severe on codominant and dominant trees at Site 5. Epicormic branching was consistently greatest on suppressed, intermediate, and codominant trees at the most southerly site (Site 5). Certain stress symptoms were clearly related to specific environmental stress factors, e.g., occurrence of frost cracks was associated with low winter temperatures at Site 2. In contrast, the occurrence and severity of cankers did not appear to be associated with a specific environmental stress since both Sites 2 and 5 had high canker ratings. Higher numbers of epicormic branches may be associated with the higher temperatures and increased frequency of drought at Site 5. The effect of elevated pollutant deposition and ozone exposure on occurrence and prevalence of these stress symptoms is uncertain, but pollutant-related stresses would be greatest at Site 5.

Crown condition ratings provide an integrated measure of tree vigor and are sensitive to major environmental stresses that adversely affect tree growth and mortality (Allen et al. 1992; Wilmot et al. 1995). For most years and sites, crown condition was significantly worse (higher rating) for suppressed trees as compared to intermediate, codominant, and dominant trees (Figure 3). In general, mean crown condition ratings of intermediate, codominant, and dominant trees indicate that these stands were reasonably healthy during the study period. This is consistent with the results from several monitoring

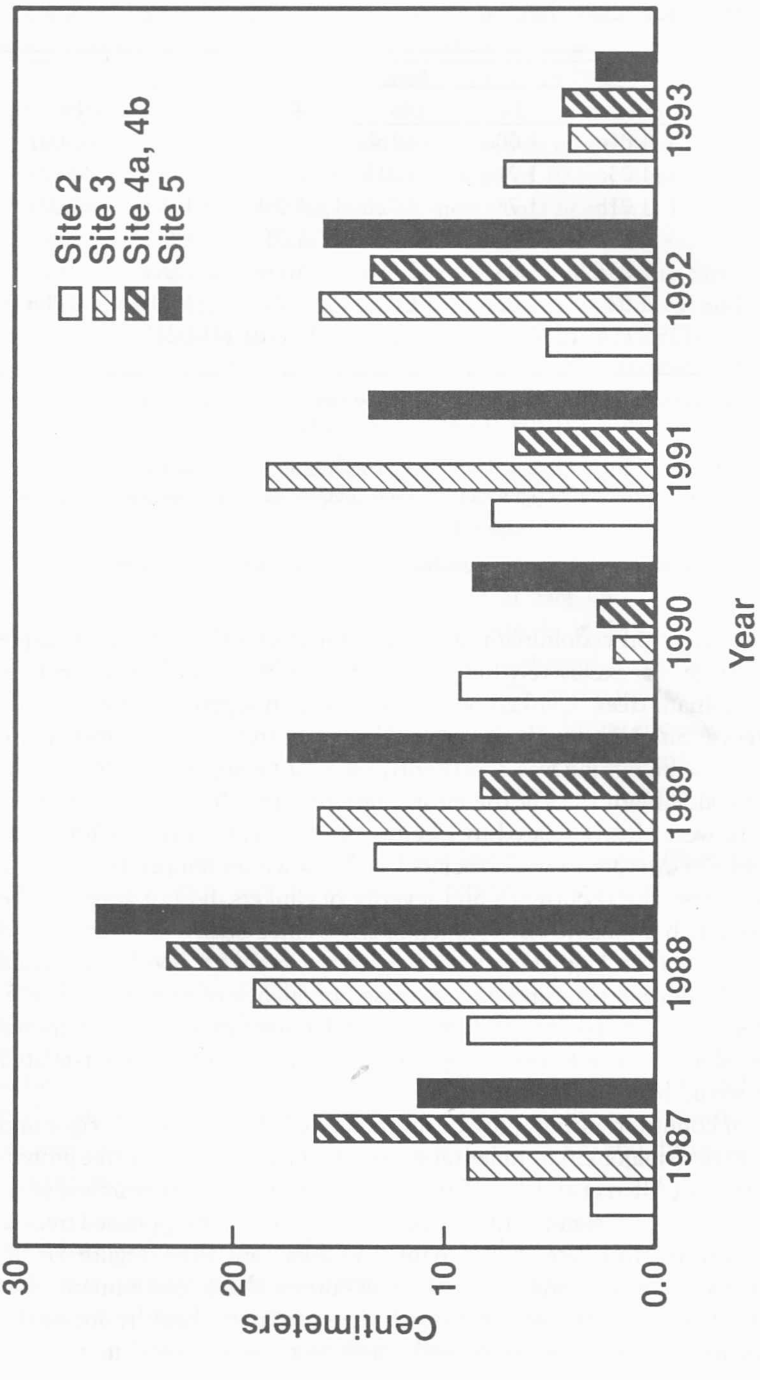

FIGURE 2. Mean annual available water deficits at northern hardwood research sites in the Great Lakes region, 1987-1993. Tukey's critical value (*w*0.05) = 3.6 cm for all comparisons.

TABLE 4. Mean Environmental Stress Symptom Ratings+ for Northern Hardwood Research Sites in the Great Lakes Region

Crown Position	Site 2	3	4a	4b	5	*P#*
			Frost Cracks§			
Suppressed	1.08	1.01	1.00	1.02	1.02	0.086
Intermediate	1.09	1.00	1.03	1.00	1.00	0.194
Codominant	1.21a	1.00b	1.04b	1.00b	1.05b	<0.001
Dominant	1.52a	1.04b	1.09b	1.03b	1.17b	0.001
			Cankers§			
Suppressed	2.39a	2.11cd	2.05d	2.20bc	2.24b	<0.001
Intermediate	2.33a	1.91c	2.10bc	1.58d	2.16ab	<0.001
Codominant	2.00b	1.94b	2.00b	1.66c	2.24a	<0.001
Dominant	2.15ab	1.88bc	1.91bc	1.70c	2.19a	0.021
			Epicormic Branching§			
Suppressed	2.12cd	2.01d	2.38b	2.25bc	2.79a	<0.001
Intermediate	1.97bc	1.78c	2.13b	1.79c	2.49a	<0.001
Codominant	1.48b	1.43b	1.51b	1.50b	1.81a	<0.001
Dominant	1.22	1.21	1.25	1.06	1.33	0.197
			Sugar Maple Borer Damage§			
Suppressed	1.17a	1.01b	1.00b	1.06b	1.00b	0.006
Intermediate	1.56a	1.00b	1.00b	1.00b	1.00b	<0.001
Codominant	1.65a	1.00b	1.00b	1.02b	1.00b	<0.001
Dominant	1.12	1.00	1.00	1.11	1.00	0.253

+ Means calculated using most recent data from all live trees rated between 1988-1993.

Significance probability of Kruskal-Wallis non-parametric analysis of variance. Means without common letters differ significantly; letters compare stress ratings among sites within a single crown position.

§ Environmental stress rating categories:

Frost cracks: 1 = no visible cracks in bole, 2 = small visible cracks, 3 = large visible cracks.

Cankers: 1 = no visible cankers on bole, 2 = small cankers visible, 3 = large cankers visible.

Epicormic branching: 1 = less than 3 epicormic branches on bole, 2 = relatively high numbers of epicormic branches present on bole above 3 m from ground, 3 = high numbers of epicormic branches present on bole above 2 m from ground, 4 = very high numbers of epicormic branches present covering much of the bole.

Sugar maple borer damage: 1 = no visible damage, 2 = light damage with only horizontal scars visible, 3 = moderate damage with one horizontal scar and one vertical scar visible, 4 = severe borer damage with more than one vertical scar visible.

networks, which showed that most forest stands in the region had relatively stable tree condition during the mid-1990s (McLaughlin 1996). Increased crown condition ratings for intermediate, codominant, or dominant trees at Sites 4a, 4b, and 5 (Figure 3c, 3d, 3e) between 1988 and 1989 reflect the impact of the 1988 drought on tree vigor at these sites, alone or in combination with defoliation. Similar effects of the 1988 drought on crown condition of sugar maple forests in Wisconsin were reported by Allen et al. (1992). The trend in crown condition ratings for dominant trees at Site 3 (Figure 3b) indicate a gradual improvement in tree vigor over time. In contrast, temporal trends in crown condition ratings of intermediate, codominant, and dominant trees at Site 4b (significantly correlated with year, $r = 0.63^{**}$ to 0.81^{**}) were consistent with a gradual decline in crown condition since 1987 at this site.

Mortality

Annual mortality differed among sites only for 1987-1988, when mortality at Site 4b was significantly greater than at all other sites (Table 5). This was the observed result of the extreme drought and severe defoliation experienced at this site in 1988, and is typical of episodic mortality in response to acute environmental stress (Franklin et al. 1987). Episodic mortality in response either to drought (Parshall 1995) or to the co-occurrence of defoliation by forest tent caterpillar and drought (Bernier et al. 1989; Gross 1991) has been reported in other sugar maple-dominated northern hardwood forests. Annual and cumulative mortality at all of our sites was predominantly confined to the suppressed and intermediate crown classes. Cumulative basal area mortality (1987–93) was greatest at Site 4b, largely a result of the significantly elevated mortality in 1987–88. In contrast, cumulative mortality was least at Site 2 where major environmental stresses (drought, defoliation, pollutant deposition) and numbers of suppressed trees were least.

Periodic Diameter Increment

Trends in periodic survivor diameter increment differed by crown position (Table 6). For suppressed trees, diameter increment decreased significantly from Site 2 to Site 5. Periodic diameter increment did not differ significantly among sites in either intermediate or codominant crown positions. In contrast to growth of suppressed trees, growth of dominant trees increased significantly from Site 2 to Site 5. Periodic increment of dominant trees at Site 4b was low compared to that at all other sites. The progressive worsening in crown condition, elevated mortality of suppressed trees, and lower growth of dominant trees are indicative of the unusual levels of environmental stress experienced at Site 4b during the study period. The episode of severe defoliation coupled with extreme drought at this site in 1988 appear to have initiated this period of increased mortality and diminished vigor and growth, similar to reports by Gross (1991) for sugar maple-dominated northern

TABLE 5. Annual and Cumulative Basal Area Mortality at Northern Hardwood Research Sites in the Great Lakes Region

	Site					
Year	2	3	4a	4b	5	*P*+
	$m^2\ ha^{-1}$					
87–88	0.14b	0.00c	0.16b	0.44a	0.05c	0.018
	(0.04)	(0.00)	(0.05)	(0.29)	(0.08)	
88–89	0.04	0.14	0.06	0.04	0.09	0.358
	(0.04)	(0.03)	(0.07)	(0.08)	(0.03)	
89–90	0.21	0.22	0.12	0.06	0.20	0.512
	(0.22)	(0.14)	(0.20)	(0.05)	(0.07)	
90–91	0.01	0.09	0.23	0.36	0.16	0.504
	(0.02)	(0.05)	(0.26)	(0.38)	(0.27)	
91–92	0.06	0.12	0.07	0.10	0.06	0.972
	(0.07)	(0.17)	(0.06)	(0.15)	(0.11)	
92–93	0.22	0.41	0.09	0.29	0.29	0.271
	(0.33)	(0.26)	(0.02)	(0.24)	(0.10)	
Cumulative Mortality 87–93	0.68b	0.98ab	0.73b	1.29a	0.84ab	0.022
	(0.31)	(0.11)	(0.24)	(0.16)	(0.07)	
Total *n*#	19	29	20	37	44	

+Significance probability of Kruskal-Wallis non-parametric analysis of variance (annual means) or parametric analysis of variance (cumulative 1987-1993 means). Means without common letters differ significantly; letters compare means across sites within a single year. Values represent means with standard deviations in parentheses.

#Total number of trees dying per site between 1987 and 1993.

hardwood forests in Ontario and by Bauce and Allen (1991) for a sugar maple forest in New York.

The observed trend across sites in periodic diameter increment of suppressed sugar maples was negatively correlated with mean growing season water deficits ($r=-0.88^*$), consistent with growth of suppressed trees being sensitive to differences in water availability among sites. Because of their competitive disadvantage, suppressed trees would be the first to display this type of response (Franklin et al. 1987; Waring 1987). Periodic increment of suppressed trees also was negatively correlated with deposition of H^+ ($r=-0.88^*$) and SO_4^{2-} ($r=-0.94^*$), consistent with pollutant deposition acting as an additional or interactive stress on suppressed trees at the more southerly

TABLE 6. Periodic (1987–1993) Survivor Diameter Increments at Northern Hardwood Research Sites in the Great Lakes Region

Crown Positions	Site 2	Site 3	Site 4a	Site 4b	Site 5	P+
	cm					
All Species Combined						
Suppressed	0.18a (0.05)	0.13ab (0.03)	0.11ab (0.04)	0.09ab (0.04)	0.04b (0.07)	0.040
Intermediate	0.36 (0.13)	0.27 (0.08)	0.26 (0.10)	0.34 (0.22)	0.28 (0.20)	0.901
Codominant	0.87 (0.14)	0.90 (0.08)	0.98 (0.18)	1.01 (0.04)	1.28 (0.31)	0.107
Dominant	1.43b (0.06)	1.72ab (0.26)	1.73ab (0.34)	1.30b (0.06)	2.06a (0.10)	0.008
Sugar Maple Only						
Suppressed	0.18a (0.05)	0.12ab (0.03)	0.10ab (0.04)	0.08ab (0.03)	0.03b (0.09)	0.043
Intermediate	0.37 (0.14)	0.28 (0.10)	0.26 (0.10)	0.36 (0.24)	0.29 (0.20)	0.894
Codominant	0.93 (0.19)	0.89 (0.06)	0.97 (0.16)	0.95 (0.12)	1.22 (0.38)	0.403
Dominant	1.47b (0.07)	1.38b (0.07)	1.44b (0.21)	1.20b (0.01)	1.91a (0.26)	0.003

+Significance probability of analysis of variance. Means without common letters differ significantly; letters compare means across sites within a single crown position. Values represent means with standard deviations in parentheses.

sites. Lack of differences among sites in growth of intermediate and codominant trees also may be related to increasing environmental stress if growth at southerly sites is being constrained by water availability, as suggested by Lane et al. (1993).

Periodic diameter increments of codominant and dominant trees (all species combined) were positively correlated with mean growing degree days (r=0.81, P <0.1, to 0.94*), consistent with growth of codominant and dominant trees being primarily dependent on growing season length. Similar relationships between forest growth and climate were previously noted by Graumlich (1993) in the western upper Great Lakes region. Trends in periodic increment of codominant and dominant trees at Sites 2, 3, 4a, and 5 were consistent with documented increases in foliage and litterfall biomass

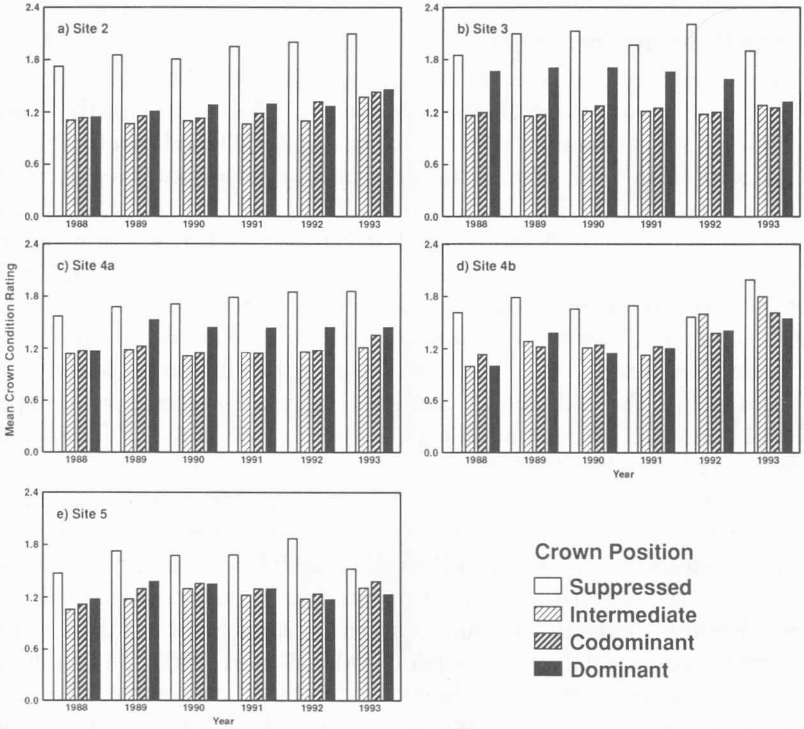

FIGURE 3. Mean annual crown condition ratings by crown position at five northern hardwood research sites in the Great Lakes region. Crown condition rating categories: 1 = healthy crown with few dead twigs, branches, or branch stubs; 2 = crown with occasional large dead branch in upper portion, below normal foliage density, some small dead twigs at top of crown, and a few large branch stubs on upper bole; 3 = crown with moderate dieback, several large dead branches in upper crown and bare twigs beginning to show, several branch stubs on upper and mid bole; 4 = approximately one-half of crown dead; 5 = over one-half of the crown dead. Differences between mean crown condition ratings ≥ 0.3 units are significant at $P \leq 0.05$ for all comparisons.

from Site 2 to Site 5 (Pregitzer et al. 1992; Burton et al. 1993). Observed growth differences among sites do not appear to be related to differences in soil fertility, as foliar analyses revealed no nutrient deficiencies or toxicities at any of the study sites (Burton et al. 1993). Soil variables associated with water-holding capacity (e.g., organic C, silt) did serve as significant predictors of periodic diameter increment when combined in multiple regression equations with climatic variables (N. W. MacDonald, unpublished data). While elevated NO_3^- deposition could contribute to enhanced growth at the southern sites (Abet et al. 1989), NO_3^- deposition was not a significant predictor of periodic increment.

Annual Diameter Increment

Annual survivor diameter increment was highly variable at all five sites (Fig. 4), consistent with a high degree of climatic influence on growth (Bauce and Allen 1991; Graumlich 1993). Lane et al. (1993) found that for the 50-yr period prior to 1990, precipitation increased in importance as a determinant of growth at the southern study sites. In our study, variability in annual diameter increments was pronounced at Sites 4a and 5, where diameter increment was greatly reduced by drought in certain years (e.g., 1988, 1989), but was substantially higher during years when moisture was abundant (e.g., 1990, Figure 4). Variability in annual diameter increments was even more pronounced at Site 4b, which experienced severe defoliation in concert with drought early in the study period. Sensitivity of growth of forests in the upper Great Lakes region to extreme climatic events also was noted by Foster et al. (1992) and Graumlich (1993).

Our study sites span a geographic region where forests are expected to experience increasing climatic stress over the next century as a direct result of global climate change (Reed and Desanker 1992; Jones et al. 1994). Results of our study showed that the trees at the majority of our sites were predominantly healthy, similar to the results of several regional forest health monitoring programs during the same time period (McLaughlin 1996). The results of our study, however, also support the contention that the vigor, mortality, and growth of northern hardwood forests are extremely sensitive to changes in climatic conditions, and response to changes in climatic conditions is rapid. In comparison, the effects of pollutant deposition on vigor, mortality, and growth are subtle and masked by the overriding effects of climate, as previously concluded by other researchers (LeBlanc et al. 1987; Allen et al. 1992; LeBlanc 1993; Brooks 1994).

One of the postulated effects of global warming is that there will be an increase in the frequency of drought in the Great Lakes region (Pastor and Post 1988; Solomon and Bartlein 1992). Predicted impacts of stressful climatic conditions include reduced radial growth and changes in stand composition and structure in forests susceptible to these environmental stresses (LeBlanc and Foster 1992; Graumlich 1993; Jones et al. 1994; Parshall 1995). Drought also coincides with climatic conditions that allow populations of certain defoliator insects to attain outbreak levels (Ives 1981). The frequency of defoliation of forests in the Great Lakes region is expected to increase as a result of invasion by the gypsy moth and other exotic forest pests (Liebhold et al. 1995). The strong links among drought, air pollution, and susceptibility to insect defoliation (Mattson and Addy 1975; Hain 1987; Mattson and Haack 1987) suggest that sites currently occupied by northern hardwood forests in the Great Lakes region are susceptible to environmental stresses and declines in growth and vigor in the future if climate changes as predicted (Reed and Desanker 1992; Jones et al. 1994). In our study, the occurrence and

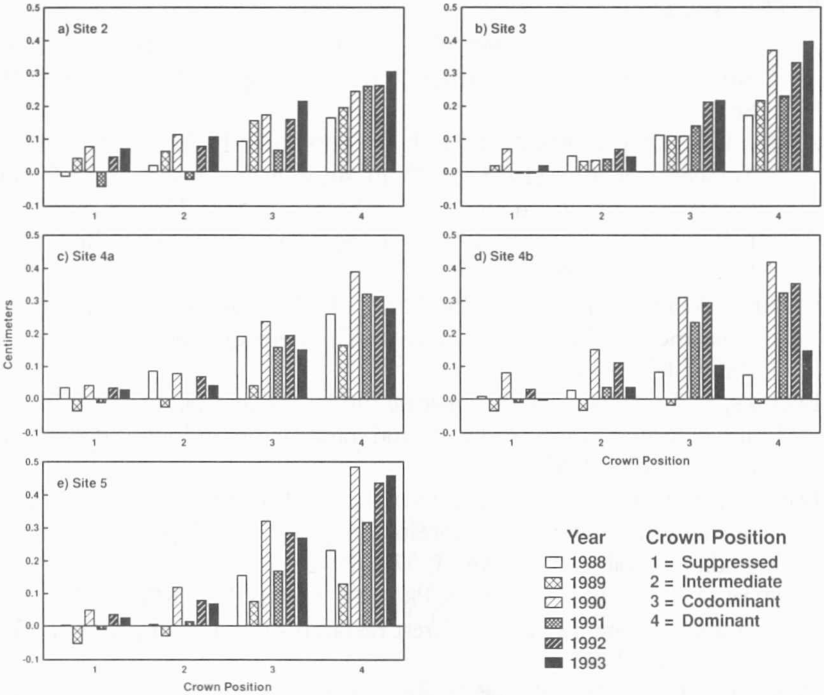

FIGURE 4. Mean annual survivor diameter increments (all species combined) by crown position at five northern hardwood research sites in the Great Lakes region. For all comparisons, Tukey's critical value (*w*0.05) = 0.16 cm at Site 2, 0.14 cm at Site 3, 0.15 cm at Site 4a, 0.12 cm at Site 4b, and 0.18 cm at Site 5.

distribution of stress symptoms, the sensitivity of growth at the southern sites to drought, the reduced growth of suppressed trees at the southern sites, and elevated mortality of suppressed and intermediate trees at one site in response to drought and defoliation are additional indications of the susceptibility of these forests to increased severity of environmental stress.

ACKNOWLEDGEMENTS

The authors especially acknowledge the late Peter Greaney for his unique and invaluable contributions during the early stages of this study. This research was supported by the Northeastern Forest Experiment Station, Eastern Hardwoods Research Cooperative, within the joint USEPA-USDA Forest Service Forest Response Program; the USDA Forest Service Northern Global Change Program; and the McIntire-Stennis Program. This paper has not been reviewed by funding agencies and should not be construed to represent the policies of these agencies.

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