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PRODUCTION DYNAMICS AND CLIMATE IN FOUR NORTHERN HARDWOOD STANDS LOCATED IN MICHIGAN

By

Shannon E. Brown

A DISSERTATION

Submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

(Forest Science)

Michigan Technological University

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This dissertation, "Production dynamics and climate in four northern hardwood stands located in Michigan," is hereby approved in partial fulfillment of the requirements for the degree of DOCTOR OF PHILOSOPHY in the field of Forest Science.

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Date

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ABSTRACT

Studies have linked changes in climate to changes in forest production. To address the impact of climate on above- and belowground production, estimates of root respiration and measurements of canopy dynamics and aboveground woody production were recorded in four northern hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.) over ten years (1989-1998). The stands extend along a 500 km latitudinal gradient from northern to southern Michigan and have similar soils, physiography, stand structure, and species composition. Rates of fine root respiration were estimated using climatic data collected from these stands. Over the lifetime of the root, assuming no acclimation to higher temperatures, the fine root system becomes a significant sink for carbohydrates during warm, wet periods. However, results illustrate how little is known about the environmental controls regulating root maintenance costs and mortality rates. Relationships among climate, leaf duration, litter production, and aboveground woody growth were also examined for these forests. Year-to-year differences in climate appear important in controlling shoot dynamics, especially leaf duration. However, aboveground woody production across years and sites was not strongly related to any aspect of climate or canopy dynamics, and was too variable to be predicted by any combination of these variables. This variability in aboveground woody production suggests that it is unlikely that changes in production at these sites will be predicted using models incorporating climate change scenarios.

INTRODUCTION

The Michigan Gradient Study is a long-term project looking at various environmental impacts on ecological processes within four northern hardwood stands dominated by sugar maple (*Acer saccharum* Marsh.). The stands extend along a 500 km latitudinal gradient from northern to southern Michigan and are similar in age, basal area, species composition, soils, physiography, and stand structure.

This dissertation describes how above- and belowground production may be affected by climate over time (1989-1998). Unfortunately, due to the removal of data-loggers and occasional equipment failure, climate data were not complete across the entire time period (1989-1998). In order to address how climate could impact production in these forests, methods had to be derived to complete the climate data set. Chapter 1 describes a method to fill-in missing soil temperatures using air temperature and Julian date as independent variables. Appendices A and B also address missing climate data. Appendix A includes a table of equations and NOAA Stations used to fill-in missing air temperature data. Appendix B describes a method to fill-in missing weekly soil matric potential using potential evapotranspiration and precipitation. The resulting data sets (merged observed and predicted climate) were used in the analyses for Chapters 2 and 3. Chapter 2 addresses how estimated root respiration can vary with climate over time. The question of acclimation to both soil temperature and matric potential is addressed. Also, the possible consumption of different percentages of non-structural carbohydrates during root respiration is estimated. Chapter 3 examines the relationships among climate, canopy dynamics, and aboveground production. The overall objectives of this thesis are to understand

how aboveground and belowground production has changed in these forests during the last ten years (1989-1998), and the role climate has played in affecting these changes.

CHAPTER 1

Predicting daily mean soil temperature from daily mean air temperature in four northern hardwood forest stands[1]

ABSTRACT

Soil temperature is very important in regulating ecosystem processes, yet it is often difficult and costly to measure. Most models that have endeavored to predict soil temperature have either a long time step or several complicated independent variables. Daily mean air and soil temperatures were measured from 1989-1997 in four northern hardwood sites along a 500 km latitudinal gradient in Michigan. These data were used to derive a simple method to predict daily mean soil temperature (depth of 15 cm) using the daily mean air temperature from the previous day and a cosine function of Julian date ($R^2 = 0.93$-0.96; SEM = 0.98 -1.40 °C). Predicted values were compared with actual recorded soil temperatures from 1997 at each of the sites, and the average difference between the observed and predicted values ranged from 0.11 to 0.39 °C. Different coefficients were estimated for each of the sites, however this general method of predicting soil temperature appears applicable to any site. Once calibrated for a given site, soil temperature may be simply estimated, thus reducing the need for extended monitoring efforts. This method also allows the reconstruction of soil temperature records beyond the monitoring period. Projecting long-term trends in soil temperature may help to further elucidate several ecosystem processes and also may provide more information on how a changing global climate will impact forest ecosystems.

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[1] Chapter accepted as paper for Forest Science, October 26, 1999.

INTRODUCTION

Soil temperature is a very important climatic variable affecting ecosystem processes, especially those occurring below-ground. Changes in soil temperature have been linked to changes in soil properties such as pH and ion concentrations (Tomlinson 1993). Likewise, changes in soil temperature can impact various components of soil respiration (Boone et al. 1998, Kirschbaum 1995, Raich and Schlesinger 1992), microbial decomposition and mineralization (MacDonald et al. 1995, Bonan and Van Cleve 1992, Van Cleve et al. 1990), and fine root respiration and turnover (Burton et al. 1998, Zogg et al. 1996, Hendrick and Pregitzer 1993). These types of changes could have profound impacts on the carbon balance of forest ecosystems (Bonan and Van Cleve 1992)

The impact of soil temperature on processes such as fine root respiration is often exponential rather than linear (Burton et al. 1998). Therefore, models based on monthly or annual time steps may not accurately predict the dynamic changes in such below-ground processes. Although it is important to have site-specific measurements of daily soil temperature, it is often difficult and costly to monitor soil temperatures for extended periods of time. Continual monitoring also requires continuous maintenance; equipment failure can lead to missing data. Missing climatic data can be approximated using data from a nearby permanent weather station (Kuuseoks et al. 1997, Lane et al. 1993). However, although many of these stations record daily air temperature and precipitation, the majority do not record daily soil temperatures. Deriving a method to predict daily mean soil temperature from daily mean air temperature could decrease the amount of time and cost necessary for on-site monitoring of soil temperature. In addition, linking soil temperature with daily air temperature from permanent weather station data could allow researchers to explore historic trends in soil temperature data beyond the period of actual on-site monitoring.

Models do exist to predict soil temperature. However, many of these models are based on monthly time steps (Yin and Arp 1993, Toy et al. 1978), which, as stated above, may be not be sufficient to accurately estimate ecosystem processes. Other models require several parameters such as solar radiation, soil thermal diffusivity, soil surface energy balance, and wind speeds (Levine and Knox 1997, Thunholm 1990, Nobel and Geller 1987, Parton 1984). Although these methods may be accurate and precise, they require data that may be difficult and/or costly to monitor on-site. Likewise, historical data sets probably would not include all the necessary data. Therefore, the objective of this study was to develop a simple method to predict daily mean soil temperature (depth of 15 cm) from daily mean air temperature in four northern hardwood forests located along a 500 km latitudinal gradient.

METHODS

Daily mean air temperatures at 2 m above the ground and daily mean soil temperatures at a depth of 15 cm were recorded in four northern hardwood stands from 1989 through 1997. The four stands extend along a 500 km latitudinal gradient from northern to southern Michigan (Figure 1.1). These sites are second-growth forests dominated by sugar maple (*Acer saccharum* Marsh.) and are similar in age, basal area, species composition, soils, physiography, and stand structure (Table .1.1; Burton et al. 1991*a*). Yearly precipitation is fairly consistent among the sites (810-870 mm), however the mean annual temperature (7.6-4.3 °C) decreases from the southern to northern sites (Burton et al. 1991*b*).

Air temperatures at three different locations within each site were recorded at 2 m above the ground every 30 minutes using Thermistors (Model ES-060-SW, Omnidata, Logan, Utah USA). Averages were recorded every three hours by data loggers (Model 925, Omnidata, Logan, Utah USA), and these three-hour averages were then used to calculate the average daily air temperature for each location. The average daily temperature for a site was calculated using the average of the three sampling locations. Air temperatures for approximately 15 % of the total number of days were missing due to occasional equipment failure. Regression equations and coefficients derived by Kuuseoks et al. (1997) that utilized data from nearby NOAA stations were used to estimate missing air temperatures.

Soil temperatures were measured near the same three locations as air temperature at each of the sites. These temperatures were recorded at a depth of 15 cm using Thermistors (Model ES-060-SW, Omnidata, Logan, Utah USA). Soil temperatures were recorded every 30 minutes. The average daily soil temperature for each location was calculated from these 30-minute averages, and the average daily soil temperature for each site was calculated as the average of the three locations. Similar to air temperature, approximately 15 % of the total number of days were missing due to occasional equipment failure. Some missing values could be filled in using soil temperature data from nearby plots within the same site, however the following method had to be used to fill in most of the data.

The complete air temperature and soil temperature data sets for each site from 1989 through 1997 were used to formulate a regression equation to predict missing soil temperatures from air temperature. Several different estimations of air temperature were tested: daily mean air temperature, mean air temperature from the previous day, and 3-day, 5-day, 7-day, 10-day, 14-day and 20-day running mean air temperatures. Air temperature increases faster than soil temperature in the spring and decreases faster than soil temperature at the end of the growing season. A second variable, cosine ((JD-220)/220), incorporating Julian date (JD) and the JD at which the average high soil temperature was reached (JD 220) was used to remove the seasonal trend in over- and under-estimation of soil temperature. Hence the following general equation was generated to predict soil temperature (ST):

$$ST = \beta_0 + \beta_1 * \phi + \beta_2 * \gamma + \varepsilon; \qquad (1)$$

where ϕ = daily mean air temperature of the previous day and γ = cosine ((JD-220)/220).

Different coefficients were calculated for each site. Daily mean soil temperatures recorded at each of the sites during 1997 were compared to predicted soil temperatures to validate the above equation. Only JD 91 through JD 334 (April 1 through November 30; the growing season plus some time at either end of the season) were considered in the models. Since all of these sites experience snow coverage during the winter months and the observed soil temperatures did not change during this winter period, these starting and ending dates were chosen based on the average dates at which soil temperature began fluctuating in the spring and stopped changing in the fall. Also, descriptive statistics were calculated for annual air and soil temperatures, and daily mean air and soil temperatures for JD 91 through JD 334.

RESULTS

Air temperatures predicted using coefficients and algorithms developed by Kuuseoks et al. (1997) were deemed accurate at a particular site for any given date. The comparison of actual temperatures and predicted values for these dates indicated that the equations accounted for 96 to 99% of the variation in air temperature and were consistent with the performance recorded by Kuuseoks et al. (1997). Therefore, missing air temperature data were replaced using the equations from Kuuseoks et al. (1997) in conjunction with records from nearby NOAA stations, and the complete air temperature data (observed merged with predicted) was used in these analyses.

Equation (1) was used to predict soil temperatures for individual sites across an entire season. The use of the cosine function eliminated seasonal over- and under-estimation of soil temperatures associated with using air temperature alone. For example, increases in soil temperature in the spring and decreases in the fall lagged behind the changes in air temperature (note the range of air temperatures with soil temperatures <5°C in Figure 1.2). Although many expressions of air temperature were tested, daily mean air temperature from the previous day yielded the best empirical fit. This, along with the cosine function of JD in Equation (1), successfully predicted daily mean soil temperature for 1997 ($R^2 = 0.93$ to 0.96; SEM = 0.98 -1.40 °C) for each of the sites (Figure 1.3). Equations developed using the other expressions of air temperature did not predict daily soil temperatures as successfully (maximum $R^2 = 0.88$ to 0.90 using the 3-day running mean air temperature, for example). Thus the previous day air temperature, along with the cosine of JD, was used to predict daily mean soil temperatures.

Different coefficients were derived for each site. These coefficients in the equations for each of the sites varied consistently with latitude (Figure 1.3). For example, β_0 and β_2 decreased from north to south, whereas β_1 increased from north to south. This latitudinal relationship is also reflected in the descriptive statistics, which showed an increase in the annual and seasonal daily mean air and soil temperatures from north to south (Table 1.2). This, not surprisingly, implies that latitude may be significant in the relationship between air and soil temperature. Latitude was tested as both a separate independent variable and as an interaction term with air temperature and the cosine function of JD. However, adding latitude to Equation (1) did not increase its predictive ability. Therefore, it was not used in the final equation predicting daily mean soil temperature.

DISCUSSION

Use of air temperature from the previous day and a cosine function of JD to predict soil temperature was as accurate and, in some cases, more precise than predictions from studies that used a greater number of meteorological parameters (Levine and Knox 1997, Zheng et al. 1993). Thus, this general empirical method could lead to reasonable estimates of soil temperature without constant on-site monitoring or calculation of many variables. Using fewer variables increases the probability that necessary information will be available to estimate missing values.

An important consideration is the estimation of winter soil temperature. Equation (1) predicts temperatures for the months of May through November. Winter soil temperatures did not change at these sites. Therefore, a constant soil temperature could be reasonably used during the winter months. However, the success of using a constant temperature during the winter for other areas will depend on the specific length and characteristics of the winter period.

Another important consideration is the latitudinal differences in the constants and coefficients derived for the different sites using Equation (1). These differences suggest that these particular coefficients are only applicable to these sites. Likewise, the JD of the mean peak soil temperature (JD 220 in this study) may change with major shifts in latitude. Although this general method is likely applicable for most sites, individual coefficients and constants will have to be calculated for each site. Moreover, changes in the amount and type of vegetative cover can cause differences in soil thermal regimes (Balisky and Burton 1993, Flerchinger and Pierson 1991). Different species assemblages can have different canopy architectures, which can impact the amount of radiant energy reaching the forest floor (Balisky and Burton 1993). Also, the removal of the canopy during a disturbance such as clear-cutting can change the thermal dynamics of the soil (Liechty et al. 1992). It is important to consider these elements when deriving coefficients for different sites; both soil and air temperatures will need to be monitored for a period of time and compared in order to derive the correct coefficients for a particular site.

Once coefficients for Equation (1) are derived for the sites of interest, soil temperature may no longer need to be monitored on these sites. This will decrease cost and equipment maintenance. Likewise, air temperature data from historical sources could be used to estimate trends in soil temperature over longer periods of time. This could prove invaluable in research addressing trends in ecosystem processes, especially those integrally linked with soil temperature. However, long-term extension of the soil temperature record in this way would assume that vegetative thermal cover was constant over time. This may be appropriate for short time periods, but over longer time periods changes in the vegetative community might upset the relationship between air temperature at 2 m and soil temperature. However, this type of effect could be documented through further field investigation.

The ability to estimate soil temperatures could be important in studies addressing global warming. Projected increases in global air temperatures have been linked to possible forest decline through decreases in forest productivity and changes in forest composition (Jones et al. 1994, Jones et al. 1993, Tomlinson 1993). Predicting how soil temperature will fluctuate with changing air temperature could further explain how ecosystem processes may be impacted by a changing global climate.

CONCLUSIONS

Soil temperature, although integral in many ecosystem processes, is often difficult and costly to observe. The approach in this study provides a simple method to estimate soil temperature using daily air temperature from the previous day and a cosine function of Julian date. Although the coefficients and constants were estimated for each of the sites in this study, this general method of estimating soil temperature appears applicable to any site once the relationship between air and soil temperature is initially established. In contrast to other models, this approach reduces the number of variables needed to predict soil temperatures. It also decreases the impact of equipment failure and makes it more likely that needed information will be available from other sources, such as permanent weather stations. Successful prediction of soil temperature can lead to a decrease in the time, cost, and equipment maintenance necessary for on-site monitoring and allow researchers to use data from other sources. Projecting long-term trends in soil temperature may help to elucidate ecosystem processes, and clarify how these processes may be affected by changes in climate.

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Table 1.1: Location and stand characteristics of the four sites used in this study. Stand characteristics are based on measurements made in 1993. Values for stand characteristics presented as means with standard deviations in parentheses.

	Site A	Site B	Site C	Site D	Literature source
Latitude	46°52'N	45°33'N	44°23'N	43°40'N	
Longitude	88°53'W	84°51'W	85°50'W	86°09'W	
Stand density (tree ha^{-1})	696 (177)	759 (172)	811 (100)	907 (93)	MacDonald et al. (1998)
Basal area (m^2 ha^{-1})	33.4 (0.4)	30.7 (1.4)	31.8 (2.5)	32.2 (1.9)	MacDonald et al. (1998)
Soil families	sandy, mixed, frigid Alfic & Typic Haplorthod	sandy, mixed, frigid Alfic & Typic Haplorthod	sandy, mixed, frigid Alfic & Typic Haplorthod	sandy, mixed, mesic Typic Haplorthod	MacDonald et al. (1994)
Soil texture	loamy sand	sand	sand	sand	MacDonald et al. (1992)
pH	4.4	4.7	4.3	4.3	MacDonald et al. (1995)

Table 1.2: Descriptive statistics for: annual air temperature, air temperature for JD 91-334 (April 1 - Nov. 30), annual soil temperature, and soil temperature for JD 91-334.

	Site A 46°52'N, 88°53'W	**Site B** 45°33'N, 84°51'W	**Site C** 44°23'N, 85°50'W	**Site D** 43°40'N, 86°09'W
Annual air temperature (°C)				
N	9	9	8	8
Mean	4.224	5.473	6.302	7.106
Standard error	0.191	0.222	0.197	0.202
Minimum, Maximum	3.18, 5.06	4.60, 6.59	5.46, 7.37	6.31, 7.96
Air temperature (°C); JD 91-334				
N	9	9	8	8
Mean	9.814	11.004	11.405	12.176
Standard error	0.173	0.227	0.469	0.241
Minimum, Maximum	9.15, 10.58	10.08, 12.16	10.86, 12.03	11.17, 13.16
Annual soil temperature (°C)				
N	9	9	8	8
Mean	6.373	6.919	7.607	8.327
Standard error	0.114	0.112	0.100	0.165
Minimum, Maximum	5.76, 6.75	6.27, 7.49	7.24, 8.11	7.69, 9.09
Soil temperature (°C) JD 91-334				
N	9	9	8	8
Mean	9.285	10.095	10.754	11.746
Standard error	0.150	0.181	0.140	0.690
Minimum, Maximum	8.52, 9.94	9.22, 10.95	10.27, 11.30	10.75, 12.84

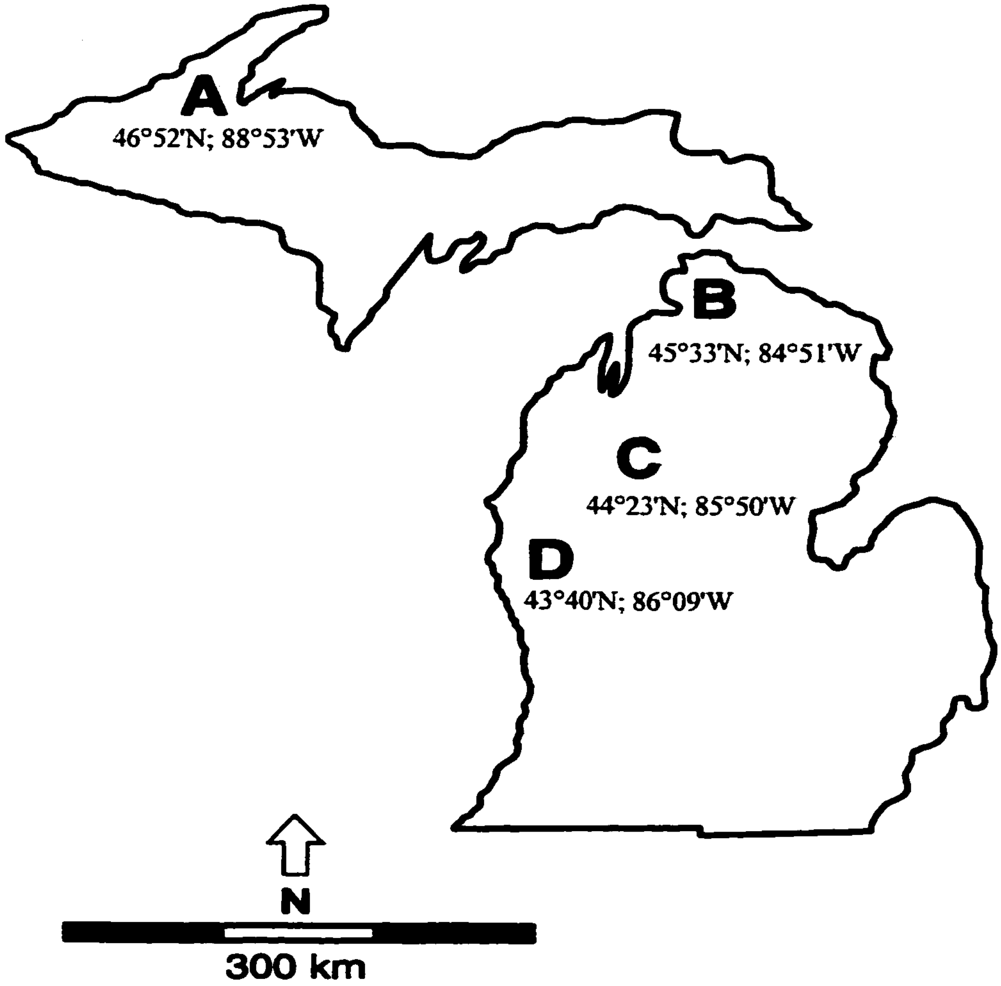

Figure 1.1: Locations of study sites extending along a 500 km latitudinal gradient within Michigan (after Burton et al. 1991*a*).

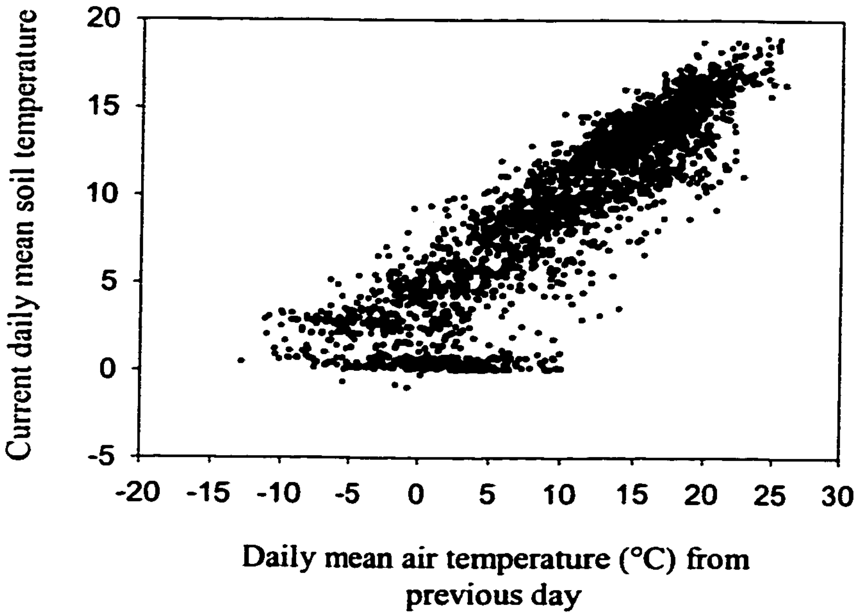

Figure 1.2: Relationship between daily mean soil temperature at time t and daily mean air temperature from the previous day (t – 1) recorded at site A from 1989-1997. Increases in spring soil temperatures and decreases in fall soil temperatures lag behind changes in air temperature.

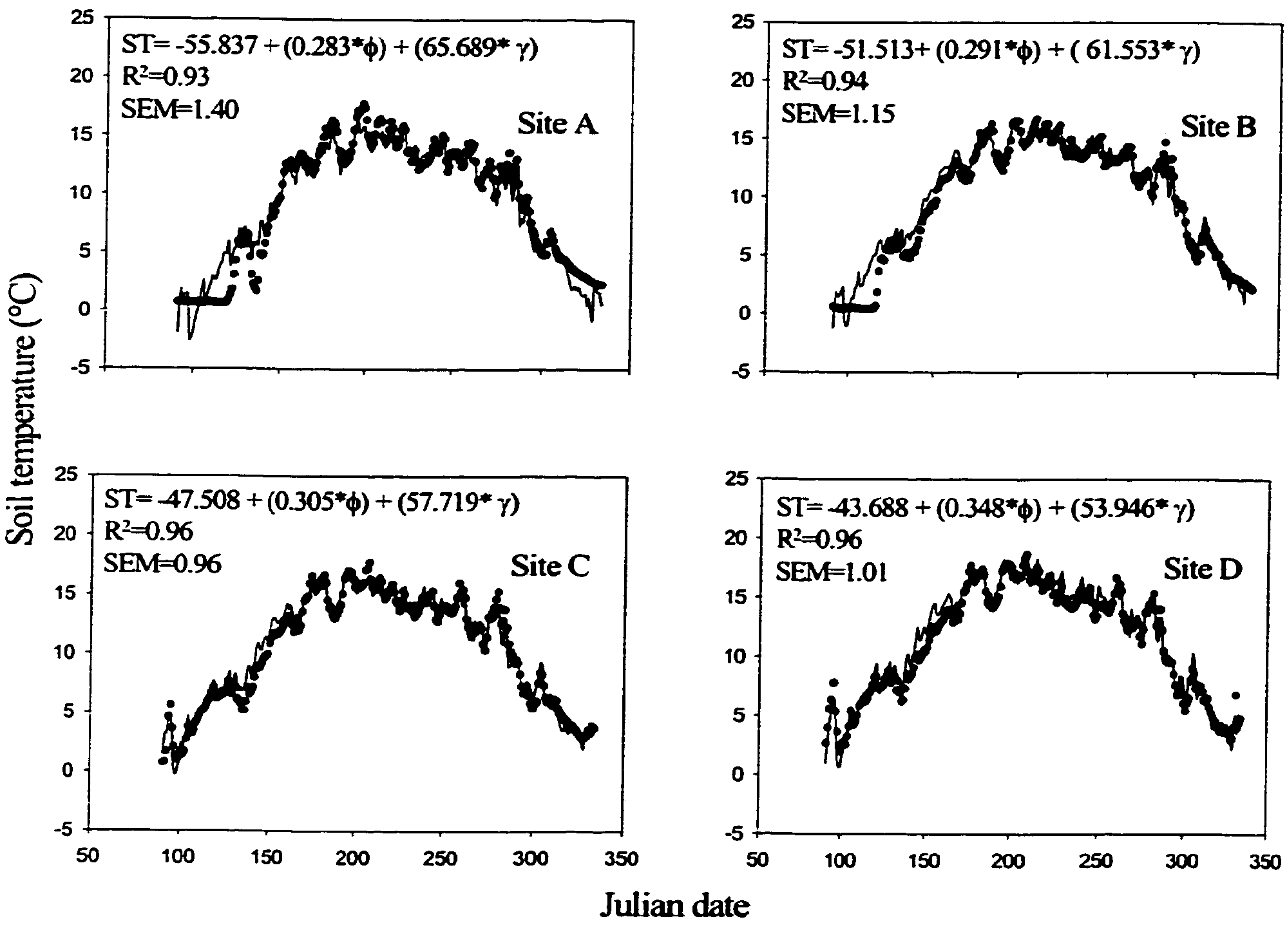

Figure 1.3: Recorded and predicted daily mean soil temperatures from April 1 through Nov. 30, 1997 for four sites along a latitudinal gradient in Michigan. Each graph contains a series of dots depicting the recorded daily mean soil temperatures, and a line depicting the predicted daily mean soil temperatures. The general equation used to predict soil temperature is as follows: $ST = \beta_0 + \beta_1 * \phi + \beta_2 * \gamma$; where ϕ = daily mean air temperature at time t-1, and γ = cosine ((JD-220)/220). The specific equation, coefficients of determination (R^2) and standard error of the estimates (SEM) are given for each site.

CHAPTER 2

Effects of soil temperature and matric potential on rates of estimated fine root respiration

ABSTRACT

Fine roots constitute an important part of the carbon cycle in forested ecosystems. In this study, rates of fine root respiration were estimated using climatic data collected from 1989 through 1998 in four northern hardwood forest stands located along a 500-km latitudinal gradient in Michigan. Also, the rate of depletion of existing non-structural carbohydrates was modeled for roots based on soil and root conditions during 1998. Estimates of root respiration varied within and among years and with latitude, and were highly correlated with soil temperature except during periods of moisture stress when estimated respiration rates dropped considerably. Assuming no additional allocation of nonstructural carbohydrates to individual roots, fine roots were predicted to exhaust existing reserves within 1.5-3.5 weeks. Over the lifetime of the root, maintenance respiration was a significant carbon cost. Assuming no acclimation to higher temperatures, the fine root system becomes a significant sink for carbohydrates during warm, wet periods. The question of acclimation to higher temperatures and temperature-induced mortality were not specifically addressed. However, results illustrate how little is known about the environmental controls regulating root maintenance costs and mortality rates.

INTRODUCTION

One important component of carbon (C) dynamics in forested ecosystems is below-ground. Although much is still unknown about below-ground processes and their contribution to the global carbon cycle, soil organic carbon may actually constitute the greatest pool of terrestrial C storage (Schimel et al. 1994). Fine root production can be twice as high as leaf production (Fahey and Hughes 1994), and the amount of C returned to the soil from the turnover of fine roots within northern hardwood ecosystems could equal or exceed that from leaf litter (Hendrick and Pregitzer 1993).

Fine root dynamics are significantly affected by temperature (Burton et al. 1996, Zogg et al. 1996, Burton et al. 1998), nitrogen (N) availability (Zogg et al. 1996, Burton et al. 1998), and moisture (Bryla et al. 1997, Burton et al. 1998). In order to model the maintenance respiration of fine roots in northern hardwood forests dominated by sugar maple (*Acer saccharum* Marsh.), Burton et al. (1998) developed an equation that incorporated soil temperature, soil matric potential, and root N concentration. They demonstrated that 90% of the variation in root respiration was due to changes in soil temperature and found no evidence for acclimation in respiration to higher temperatures. Burton et al. (1998) also showed that maintenance respiration declined during moisture stress, and drought could reduce root respiration in relation to the amount of C allocated below-ground. How roots respond to fluctuating environmental conditions is crucial in understanding overall forest C dynamics.

Sugar maple fine root production and mortality occur simultaneously throughout the year (Hendrick and Pregitzer 1992, 1993), and rates of root mortality may also increase with elevated temperatures (Hendrick and Pregitzer 1993, King et al. 1999).

Most fine roots are produced during the growing season (April-August) with the greatest production occurring during the spring (April-June; Hendrick and Pregitzer 1996). The majority of these fine roots live approximately one year (Hendrick and Pregitzer 1992, Burton et al. unpublished data). After they are constructed, respiration measured on a cohort of roots would be due primarily to the maintenance costs of keeping individual roots alive and functioning. Others have demonstrated that maintenance respiration constitutes the majority of total root respiration (Mata et al. 1996), and can be as great or greater than the cost of construction over the lifetime of the root (Eissenstat and Yanai 1997). The objectives of this study were to: (1) expand estimates of root respiration to encompass several years of actual climatic data using the equation derived by Burton et al. (1998) in order to understand the potential magnitude of annual variation in root maintenance respiration and how that relates to annual variation in climate; and (2) simulate the relative rate at which non-structural carbohydrates (TNC) are exhausted using actual soil temperature, soil matric potential, and root nitrogen (N) concentration, and a range of nonstructural carbohydrate concentrations.

METHODS

Daily mean air temperatures at 2 meters above the ground, daily precipitation, daily mean soil temperatures (depth 15 cm), and daily mean soil moisture levels (depth 15 cm) were recorded in three 30 X 30m plots within four northern hardwood stands from 1989 through 1997. The four stands extend along a 500 km latitudinal gradient from northern to southern Michigan (see Figure 1.1, Chapter 1). These sites are second-growth forests dominated by sugar maple (*Acer saccharum* Marsh.) and are similar in age, basal area, species composition, soils, physiography, and stand structure (Burton et al. 1991*a*). Yearly precipitation is fairly consistent among the sites, however the mean annual air temperature decreases from the southern to northern sites (Burton et al. 1991*b*).

Climate data for approximately 15 percent of the total number of days were missing due to occasional equipment failure. Daily air temperatures and weekly precipitation values were filled-in using methods derived by Kuuseoks et al. (1997) utilizing data from nearby National Oceanic and Atmospheric Administration (NOAA) weather stations (see Appendix A). The only exception to this approach was the use of data from the University of Michigan Biological Station to fill-in missing precipitation values for Site B. These data were considered more representative of data measured on site (Burton, personal observation). The missing soil temperatures and soil matric potentials were approximated using regression methods. Soil temperatures were predicted from air temperature and Julian date (Brown et al. 1999; see Chapter 1), and soil matric potentials (MPa) were estimated using the difference in weekly precipitation and potential evapotranspiration (calculated using Thornthwaite and Mather 1957) summed over the previous 4 weeks (see Appendix B for methodology).

From 1994-1996, Burton et al. (1998) periodically measured root respiration on excised fine roots (<1 mm in diameter) collected from 10 m wide buffer strips surrounding each plot (see Burton et al. 1998 for complete description of methodology). Respiration was measured at 6°, 18°, and 24° C within 3 hours of sample collection. Subsamples of roots were also dried and analyzed for nitrogen (Burton et al. 1998). Burton et al. (1998) compared root respiration data across all sites, and used linear and nonlinear procedures to determine the effects of soil temperature (depth 15 cm), soil matric potential (depth 15 cm), and root N concentration on root respiration. Respiration is exponentially related to temperature, and linearly related to N concentration and soil matric potential (Burton et al. 1998). They gave the following empirical relationship:

$$R_{CO_2} = (0.058N + 0.622M)e^{0.098T} \quad (1)$$

$(R^2 = 0.93, p < 0.001$, Standard error of the estimate, SEM = 1.08)

where R_{CO_2} is the respiration in nanomoles of CO_2 per gram fine root biomass per second, N is the root nitrogen concentration in grams per kilograms, M is soil matric potential in megapascals (MPa), and T is soil temperature at 15 cm (Burton et al. 1998). The relationship presented in equation 1 accurately represented root respiration across all four sites, and there was no evidence for temperature acclimation (Burton et al. 1998).

This equation was used to estimate weekly root respiration using complete data sets of weekly climate data for Sites A-D for the years 1989-1998. The values were multiplied by a correction factor (0.00726) to convert respiration from CO_2/gram dry weight/sec. to mean weekly number of grams of carbon respired per gram of dry weight of root. The average N concentration of the roots was held constant throughout the calculations, and N concentrations were based on measurements of roots collected at each study site (Site A=17.4 g N/kg, Site B=18.8 g N/kg, Site C=18.6 g N/kg, Site D=17.4 g N/kg; Burton et al. 1996). Mean root nitrogen content was not measured on a weekly basis, and Burton et al. (1998) concluded that fine-root respiration was likely independent of seasonal changes in N concentrations. The average weekly respiration values were summed for each year to determine the estimated amount of carbon respired each year, and this estimate of total respiration was compared across sites using ANOVA and the Student-Newman-Keuls (SNK) test (Zar 1974).

The estimated values of respiration (g C/g dry weight/wk) from 1998 were also used to determine the relative rate of consumption of carbon in the form of existing TNC (starches + sugars) by individual roots during maintenance respiration. The amount of total carbon in the root was assumed to be 0.5 g/g dw^{-1} (Pregitzer et al. 1997), and the amount of this carbon hypothetically dedicated to TNC was calculated in one-percent increments from 1-15% based on data from the literature (Table 2.1). A root was considered 'dead' once the grams of C expended via respiration equaled or exceeded the carbon available from TNC; this exercise assumes no translocation of "new" TNC into fine roots. This analysis was conducted in an attempt to understand how long fine roots could function without the import of C from other sources within the tree. The potential weekly use of existing TNC by respiring roots was calculated for each of the sites using estimated respiration values starting at 3 different times during 1998 (week 1, January 1; week 18, May 1; and week 32, August 7).

RESULTS

In general, the estimates of mean annual root respiration for 1989-1998 and total annual root respiration across years increased from north to south (Table 2.2) and corresponded directly to changes in soil temperature (Figure 2.1). However, estimated respiration does drop during periods of moisture stress, such as the one observed in 1998 (Figure 2.1). For example, during 1998 average matric potential was one of the lowest values, and average soil temperature was one of the highest values recorded for all of the sites during the period of record (1989-1998). As a result of the higher soil temperatures, the estimate of total annual root respiration in 1998 was very high for most of the sites. However, these estimates were not the highest estimated values of annual root respiration at Sites A, B, and D (Table 2.2). This was likely due to the more negative matric potential recorded during the summer of that year, which caused a drop in the estimated amount of carbon respired (Figure 2.1; Table 2.2). These types of results were observed across all sites and years due to the approach that was used to estimate respiration, which assumed acclimation to changes in soil moisture, but not soil temperature.

Once the amount of carbon respired by the fine roots was estimated, the relative consumption of existing non-structural carbohydrates (TNC) by a root was calculated based on respiration values beginning at three different times during 1998. Roots that contain 1-2% TNC only "lived" a maximum of 1.5 weeks before all their carbon was expired (Table 2.3). This was observed at all times during the year. However, as the percentage of carbon in TNC increased, the estimated time a root could survive solely on existing TNC also increased (Table 2.3). This was expected, and roots with 15% TNC could potentially respire up to 10.5 weeks during the winter before the existing TNC were completely exhausted (Table 2.3). However, during the spring and summer, this time decreased across all sites and percentages of TNC (Table 2.3); 15% TNC is clearly the largest amount of TNC reported in the literature, and such high concentrations are probably unrealistic for any time during the growing season (Table 2.1). At Sites C and D, only those roots with greater than 8% TNC were estimated to be able to survive longer than 1 week on existing TNC during August 1998 (Table 2.3).

DISCUSSION

Root respiration estimated for these northern hardwood stands from 1989-1998 differed among sites and varied across years within an individual site. Mean estimated rates of annual respiration and estimates of annual total respiration exhibited latitudinal gradients (Table 2.2). Annual totals only varied an average of 8% across years among sites A - D (Table 2.2). Likewise, within a given site, mean estimated rates of respiration varied annually anywhere from 2 to 16% in subsequent years (Table 2.2). Soil temperatures and soil matric potential vary similarly along the latitudinal gradient and across years (Table 2.2). The results of this study suggest that the potential variation in the magnitude of fine root maintenance respiration for these forests is relatively small, not more than 20%.

The exponential effect of soil temperature on maintenance respiration is evident throughout the data set. Across sites, years that experience higher average soil temperatures consistently have higher estimates of C utilized for respiration (Table 2.2). Other studies have also established this type of relationship between fine root respiration and temperature (Burton et al. 1996, Simmons et al. 1996, Zogg et al. 1996, Bouma et al. 1997). Minchin et al. (1994) showed that exposing barley roots to 38% higher temperatures increased the rates of respiration 35%, and cooling roots 38% caused a 20% decrease in respiration. Also, changes in soil temperatures may actually change the sink strength of roots. Minchin et al. (1994) concluded that the increase in temperature of roots caused an increase in the metabolic rates of roots and the rate of C import into the roots. This implies sink-limited growth of roots and that temperature can change the C sink strength. Obviously, if acclimation to higher temperatures does not occur, root longevity is tightly linked to C supply during the warmer, summer months.

Equation 1 assumes that respiration is consistently and exponentially related to soil temperature unless a drought occurs (Burton et al. 1998). It does not incorporate the possibility of fine root respiration acclimating to varying temperatures. Acclimation could be important in determining the response of ecosystems to environmental changes (Ryan 1991) and should be addressed in models estimating forest C processes. For example, similarities in rates of respiration can result from a combination of adaptation and acclimation processes (Amthor 1994). Different species of alpine plants have exhibited acclimation and thereby decreased C losses during leaf dark respiration at higher temperatures (Larigauderie and Körner 1995, Arnone III and Körner 1997). The roots of some tree and grass species also appear to acclimate to changing temperatures (King et al. 1996, Bryla et al. 1997, Fitter et al. 1998). Fitter et al. (1998) observed no seasonal pattern in temperature sensitivity of respiration of roots growing at cooler temperatures and suggested that the rate of root respiration was unrelated to temperature. The acclimation of roots to changing temperatures could decrease the cost of maintenance respiration of roots (Bryla et al. 1997) and thereby decrease the C cost of maintenance respiration during periods of higher temperatures. However, many experiments documenting acclimation have measured respiration under laboratory conditions during which temperature was held constant for long periods of time (Bryla et al. 1997, Larigauderie and Körner 1995, Arnone III and Körner 1997). This does not accurately reflect field conditions, especially during the growing season when soil temperatures can fluctuate considerably over short periods of time. For example, daily mean soil temperatures fluctuated 0.1 to 4°C during the growing season of 1998. Even within one day, hourly soil temperature can vary considerably (Burton, personal observation). Yet, the dichotomy in the reported response of plants to varying temperatures still suggests that several factors may be important in determining how root respiration responds to a changing climate, and that this response may be species-specific and/or site-specific (Larigauderie and Körner 1995, Self et al. 1995). Clearly, more work needs to be done to determine the degree to which fine roots may or may not acclimate to changing temperatures.

Another important consideration in the relationship of respiration to temperature is the impact of moisture stress. Equation 1 assumed a linear relationship between respiration and matric potential. Therefore, when moisture stress occurs, such as that observed at the sites in 1998, estimates of respiration can drop to almost zero (Figure 2.1), and years that experienced more frequent and/or severe moisture deficits showed a marked drop in estimated respiration rates throughout the data set (Table 2.2). Other studies have established that roots reduce respiration rates during droughty conditions (Santantonio and Herman 1985, Hall et al. 1990, Bryla et al. 1997), even during periods with higher soil temperatures (Hall et al. 1990). However, in a pattern similar to soil temperature, not all studies have demonstrated that respiration is affected by changes in soil moisture. Bouma et al. (1997) found that although respiration was related to temperature in citrus species, it seemed unaffected by the soil moisture content. Kosola and Eissenstat (1994) demonstrated that less photosynthate was allocated to fine roots during soil drying, which could lead to lower rates of respiration. The response of roots to declining soil moisture could also vary among species and/or sites. This suggests that other factors besides changing temperatures and moisture conditions may impact fine root maintenance respiration.

It is possible that source-sink relations within plants and forest stands could be more important in determining root growth than differences in respiration due to dominant environmental factors such as changing temperatures and/or moisture conditions (Fitter et al. 1998). Horwath et al. (1994) determined that the maximum specific activity of below-ground respiration in July and September occurred 2 days after $^{14}CO_2$ was assimilated by the canopy of a young *Populus* forest. The study by Horwath et al. (1994) and this study both suggest fine roots need a continual source of C during the summer and probably will not survive long without an influx of new C. A tight relationship could exist between root longevity and whole-tree C source-sink relationships during much of the growing season.

The initial size of the TNC pool, along with the strength of various sinks, impacts fine root longevity or turnover rate. The roots of some species, such as citrus, can live from 16 to 152 days (Eissenstat and Yanai 1997), and the roots of northern hardwood species such as sugar maple (the dominant species at all four of our study sites) can live for a year or more (Hendrick and Pregitzer 1992, Fahey and Hughes 1994, Burton et al., unpublished data). Using the 1998 rates of respiration, a gram of root that lives for a year will use an estimated of 0.80 to 0.94 g of TNC per g biomass for maintenance respiration across the four sites. Even roots constructed in June that die 2 weeks later use approximately 0.038 - 0.048 g of TNC per g biomass for maintenance. Assuming that one gram of root has approximately 0.5 g of C (Pregitzer et al. 1997) and an average of 8% of this is comprised of TNC (0.04 g C), these roots would have respired all of this existing TNC within 2 weeks and over 200% of the existing TNC if they lived one year, the average life expectancy of an individual root. Fine roots must be a strong C sink, especially during the summer and fall when temperatures are the high, and the maintenance of these roots is important for water and nutrient uptake. It is possible that fine roots continually receive a recharge of TNC throughout the season and/or at the end of the growing season (Nguyen et al. 1990, Wan and Sosebee 1990, Li et al. 1996). Therefore, understanding the TNC costs of maintaining roots throughout the year and the source-sink relationship between roots and other parts of the tree could help clarify processes controlling overall C allocation and cycling within forests.

CONCLUSIONS

This study demonstrates how root respiration and C costs potentially vary among years and with latitude if acclimation to higher temperatures does not occur. Estimated use of TNC was higher at the southernmost site and during the late summer when soil temperatures were high. Assuming no acclimation, the annual rates of fine root maintenance respiration varied by 1 to 20% within and among years and sites. Acclimation of roots to temperature was not addressed, but is critical in determining the degree to which trees will respond to changing temperature. Results suggest roots must be tightly linked to C supply from the canopy during the growing season. This implies whole tree source-sink relationships are critical in determining fine root longevity.

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Table 2.1: Percentage of non-structural carbohydrates (TNC) in fine roots from various sources. Location of samples and timing of sampling (in parentheses) from each study is included.

Approximated percentage of TNC (starches + sugars)	Fine root diameter	Species	Location	Literature source
~8-14% (visually estimated from Figure 2.1)	< 1 mm	*Pinus taeda* (L.)	NC, OK, AK (autumn-winter)	Hallgren et al. (1991)
4-6%	≤ 1mm	*Populus tremuloides* (Michx.) *Betula alleghaniensis* (Britton)	Northern WI (autumn)	King, personal communication
1.6-8.5%	≤ 0.05 mm	*Populus spp.*	Clones grown in MI (autumn)	Nguyen et al. (1990)
8.5-15%	0.05-1 mm	*Populus spp.*	Clones grown in MI (autumn)	Nguyen et al. (1990)
~2.5-4.0% (visually estimated from healthy stand values in Figure 2.1)	≤ 2 mm	*Acer saccharum* (Marsh.)	VT (spring & autumn)	Liu and Tyree (1997)
~3.5-6% (visually estimated from unpruned values in Figure 2.1)	< 2 mm	*Citrus sinensis* (L.) Osbeck	FL (autumn, winter, & spring)	Eissenstat and Duncan (1992)

Table 2.2: Mean weekly air temperature, weekly soil temperature, and weekly soil matric potential with standard errors (in parentheses) for individual years and across all years (1989-1998). Total annual root respiration (g C/g dry weight/wk) estimated for each year and across years is also included. Row means with different letters differ ($p<0.05$).

	Site A 46°52'N, 88°53'W	**Site B** 45°33'N, 84°51'W	**Site C** 44°23'N, 85°50'W	**Site D** 43°40'N, 86°09'W
Weekly air temperature (°C)				
1989	3.69 (1.55)	4.84 (1.54)	–	–
1990	5.10 (1.29)	6.42 (1.26)	7.40 (1.17)	–
1991	4.85 (1.44)	6.63 (1.39)	–	–
1992	4.25 (1.25)	5.23 (1.22)	–	–
1993	4.01 (1.37)	5.24 (1.36)	6.26 (1.30)	6.96 (1.30)
1994	4.79 (1.49)	5.52 (1.50)	6.44 (1.36)	7.15 (1.38)
1995	4.51 (1.50)	5.74 (1.45)	6.64 (1.40)	7.32 (1.42)
1996	3.30 (1.55)	4.74 (1.45)	5.55 (1.41)	6.39 (1.39)
1997	4.45 (1.38)	5.49 (1.34)	6.16 (1.25)	6.73 (1.25)
1998	6.71 (1.33)	7.90 (1.27)	8.68 (1.21)	9.46 (1.22)
Across all years	4.54 (0.29)	4.38 (0.31)	6.73 (0.39)	7.34 (0.45)
Weekly soil temperature (°C)				
1989	6.62 (0.83)	7.21 (0.82)	–	–
1990	6.59 (0.77)	7.39 (0.83)	7.34 (0.88)	–
1991	6.78 (0.80)	7.61 (0.85)	–	–
1992	5.92 (0.71)	6.53 (0.73)	–	–
1993	6.15 (0.78)	6.97 (0.81)	6.95 (0.96)	8.28 (0.87)
1994	6.69 (0.79)	7.37 (0.80)	7.11 (1.00)	8.60 (0.84)
1995	6.72 (0.89)	7.29 (0.84)	7.63 (0.95)	8.69 (0.93)
1996	6.18 (0.84)	6.86 (0.81)	7.39 (0.80)	7.96 (0.86)
1997	6.63 (0.81)	6.78 (0.81)	7.46 (0.79)	8.05 (0.82)
1998	7.58 (0.82)	8.07 (0.83)	9.13 (0.81)	9.75 (0.85)
Across all years	6.59 (0.14)	7.21 (0.14)	7.58 (0.27)	8.29 (0.37)
Weekly matric potential (MPa)				
1989	-0.129 (0.023)	-0.150 (0.036)	–	–
1990	-0.095 (0.016)	-0.075 (0.008)	-0.073 (0.001)	–
1991	-0.071 (0.004)	-0.169 (0.042)	–	–
1992	-0.067 (0.003)	-0.122 (0.032)	–	–
1993	-0.071 (0.005)	-0.060 (0.001)	-0.077 (0.002)	-0.075 (0.002)
1994	-0.064 (0.001)	-0.059 (0.001)	-0.090 (0.011)	-0.117 (0.020)
1995	-0.063 (0.001)	-0.122 (0.018)	-0.185 (0.033)	-0.193 (0.035)
1996	-0.064 (0.001)	-0.114 (0.026)	-0.135 (0.018)	-0.127 (0.020)
1997	-0.065 (0.001)	-0.099 (0.013)	-0.130 (0.023)	-0.091 (0.007)
1998	-0.119 (0.019)	-0.229 (0.052)	-0.176 (0.044)	-0.197 (0.041)
Across all years	-0.081 (0.008)	-0.120 (0.017)	-0.124 (0.017)	-0.133 (0.021)

Table 2.2 (cont.)

Annual total root respiration (g C/g/year)				
1989	0.768	0.858	–	–
1990	0.779	0.953	0.963	–
1991	0.827	0.875	–	–
1992	0.737	0.802	–	–
1993	0.773	0.926	0.953	0.984
1994	0.821	0.953	0.952	0.948
1995	0.864	0.902	0.899	0.940
1996	0.801	0.866	0.883	0.889
1997	0.827	0.875	0.885	0.929
1998	0.846	0.853	0.999	0.971
Across all years	0.804 (0.013) *a*	0.886 (0.015) *b*	0.934 (0.017) *cd*	0.943 (0.014) *d*

Table 2.3: Average weekly soil temperature (°C) and expected time before the C content of the roots is exhausted (weeks) if the only carbon source for maintenance respiration is existing non-structural carbohydrates (starches + sugars; TNC). Rates of respiration (g C/g dry weight/week) starting week 1 (January 1, 1998), week 18 (May 1, 1998), and week 32 (August 7, 1998) were used. Different percentages of non-structural carbohydrates based on literature (Table 2.2) were used to estimate the number of grams of carbon contributed by non-structural carbohydrates to the total number of grams of carbon available to the root (0.5 g/g root; Pregitzer et al. 1997).

	Site A 46°52'N, 88°53'W			**Site B** 45°33'N, 84°51'W			**Site C** 44°23'N, 85°50'W			**Site D** 43°40'N, 86°09'W		
	Week 1	Week 18	Week 32	Week 1	Week 18	Wee k 32	Week 1	Week 18	Week 32	Week 1	Week 18	Week 32
Average weekly soil temperature (°C)	1.28	8.6	16.96	0.43	8.69	17.3	1.61	10.03	18.3	2.07	11.06	18.76
	Approximate time before C supply of roots is exhausted (weeks)											
Percentage TNC												
1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1	<1
2	<1	<1	<1	1	<1	<1	<1	<1	<1	<1	<1	<1
3	1.5	<1	<1	1.5-2	<1	<1	1-1.5	<1	<1	1.5	<1	<1
4	2	<1	<1	1.5-2	<1	<1	1.5-2	<1	<1	1.5-2	<1	<1
5	2.5	1	<1	2.5-3	1-1.5	<1	2-2.5	1	<1	2-2.5	<1	<1
6	3	1-1.5	<1	3	1.5-2	1-1.5	2.5-3	1-1.5	<1	2.5-3	1-1.5	<1
7	3.5	1-1.5	<1	3.5-4	1.5-2	1-1.5	3-3.5	1-1.5	<1	3-3.5	1-1.5	<1
8	4	1.5-2	<1	4	1.5-2	1.5-2	3.5-4	1.5-2	<1	3.5-4	1.5-2	<1
9	4.5	2	1-1.5	4.5-5	1.5-2	1.5-2	4-4.5	1.5-2	<1	4-4.5	1.5-2	<1
10	5	2-2.5	1-1.5	5	2	1.5-2	4.5-5	1.5-2	1-1.5	5	1.5-2	<1
11	5.5	2.5-3	1.5-2	5.5-6	2-2.5	2	5-5.5	2	1-1.5	5.5-6	1.5-2	<1
12	6	2.5-3	1.5-2	6	2-2.5	2-2.5	5.5-6	2-2.5	1-1.5	6-6.5	2-2.5	1
13	6.5	2.5-3	1.5-2	6.5-7	2-2.5	2-2.5	6	2-2.5	1-1.5	6.5-7	2-2.5	1-1.5
14	7-7.5	3-3.5	1.5-2	7	2.5	2.5	6.5-7	2.5-3	1-1.5	7-7.5	2-2.5	1-1.5
15	7.5-8	3-3.5	2-2.5	7.5-8	2.5-3	2.5-3	7	2.5-3	1.5-2	7.5-8	2-2.5	1-1.5

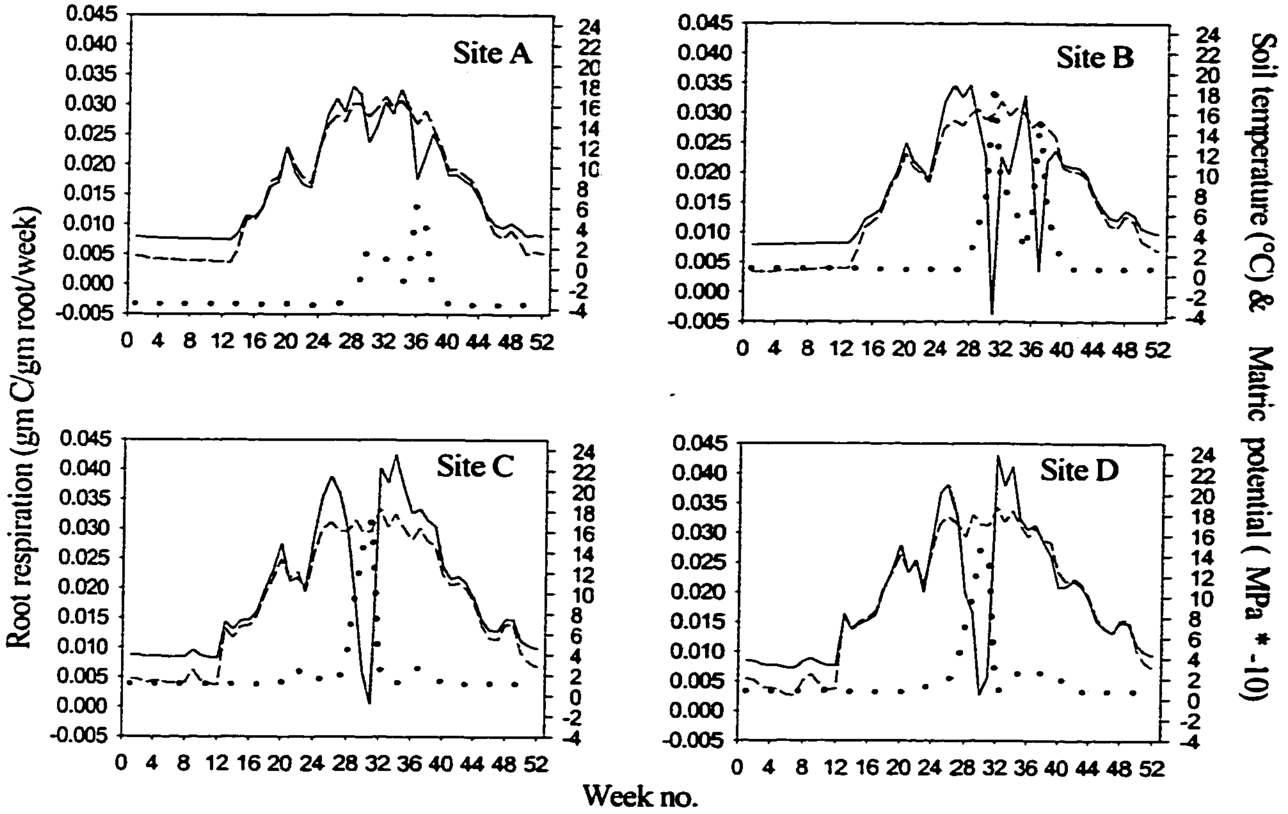

Figure 2.1: Weekly mean soil temperature (°C), soil matric potential (MPa), and rates of fine root respiration (g C/g dry weight/wk) recorded during 1998 for four sites along a latitudinal gradient in Michigan. Each graph contains a line depicting estimated weekly mean root respiration, a dashed line depicting mean weekly soil temperature, and a dotted line depicting mean weekly soil matric potential (MPa * -10). Root respiration was calculated using the equation derived by Burton et al. 1998 and converted to g C/g dry weight/wk.

CHAPTER 3

Relationships among climate, canopy dynamics, and aboveground woody growth in northern hardwood forests

ABSTRACT

Relationships among climate, leaf duration, litter production, and above-ground woody growth were examined for four northern hardwood forest stands located along a 500 km climatic gradient in Michigan for the period 1989-1998. Leaf duration was estimated using the Julian dates (JD) of 50% leaf expansion and leaf off and was progressively longer from north to south. The mean JD of leaf expansion differed among the sites ($p<0.001$), however the cross-site mean heat sum for leaf expansion (214.6 growing degree days > 4°C, GDD) did not. Yearly variation in leaf duration could be predicted by subtracting the JD the cross-site mean photoperiod (11.24 hours) was reached from the JD the mean GDD was reached ($R^2=0.68$; standard error of the estimate = 6.2 days). Total litterfall (foliar + reproductive litter) increased from north to south and differed among the sites ($p<0.05$). Total litter during any given year was linearly related to the number of GDD accumulated by the previous year's JD of leaf off ($r^2 = 0.36$; $p <0.001$, standard error of the estimate = 44.3). In contrast to leaf duration and litter production, aboveground woody growth did not differ among the sites and did not display latitudinal trends. Aboveground woody survivor growth was somewhat positively related to total litter mass ($r=0.37$, $p<0.05$) and leaf duration ($r=0.43$, $p<0.05$), and negatively related date of leaf on across sites ($r=0.45$, $p<0.05$). However, this relationship is not consistent among sites and does not explain decreased growth associated with longer leaf duration observed in 1998. Year-to-year differences in climate appear important in controlling shoot dynamics. However, aboveground woody production across years and sites was not strongly related to any aspect of climate or canopy dynamics, and was too variable to be predicted by any combination of these variables.

INTRODUCTION

Shoots are the production modules of the tree and greatly impact the carbon cycle within the tree. Factors that affect aspects of shoot growth, such as leaf duration, will likely impact the carbon dynamics within a tree (Barnes et al. 1998). For example, the carbon-sink strength of shoots of different species and genotypes can be correlated with the time of bud break, rate of shoot growth, and duration of shoot growth (Kozlowski et al. 1991). One of the most important aspects of shoot growth in deciduous species is the duration of time the shoots are able to fix carbon. Leaf area, leaf duration, and rates of photosynthesis per unit of leaf area control primary production, and leaf duration during the growing season could be an important indicator of overall forest productivity.

Spring flushing, or leaf expansion, is the beginning of vegetative growth in the spring and is highly correlated to temperature (Barnes et al. 1998; Cannell et al. 1985). For trees in northern climates, leaf expansion usually occurs once a certain heat sum above a given threshold temperature has been reached (Barnes et al. 1998; Owens et al. 1977). This heat sum is usually expressed as an estimate of the number of growing degree days accumulated prior to expansion (Perala 1985). Strategically, flushing at a certain cumulative heat sum increases growth while reducing the potential for frost damage (Cannell 1997; Cannell et al. 1985). Genotypes originating further north usually flush at a later date than trees further south (Barnes et al. 1998), and this delay in leaf development influences leaf duration.

Leaf off is likely related to photoperiod, which is a function of latitude (Barnes et al. 1998; Cannell and Willett 1975). For example, night length in the fall accurately predicted the cessation of shoot growth for northern trees (Hänninen et al. 1990), and the date of bud set for Scots pine (*Pinus sylvestris* L.) varied latitudinally (Hurme et al. 1997). Genotypes originating at higher latitudes cease growth sooner than those further south (Barnes et al. 1998; Hurme et al. 1997; Morgenstern 1996), suggesting that the critical photoperiod for growth cessation in genotypes from more northern latitudes is longer than that required by plants found at southern latitudes (Junttila 1982). Similar to the timing of budburst in spring, the entrance into dormancy in the autumn is another mechanism to avoid damage caused by an early frost (Barnes et al. 1998).

In temperate and boreal forests, bud burst and leaf abscission control leaf duration during the growing season (i.e. the potential duration of carbon gain). Therefore, explaining the mechanisms that drive both phenological events and developing the ability to predict the dates for each event would provide a more accurate understanding of the leaf duration for a species and/or forest stand. However, leaf duration in deciduous forests has not been extensively studied. Most studies have only addressed the factors contributing to budburst in the spring and/or those controlling growth cessation in the fall; the majority of previous studies were primarily provenance studies of conifer species (Hurme et al. 1997; Hänninen et al. 1990; Cannell et al. 1985).

Shoot growth of deciduous species such as sugar maple (*Acer saccharum* Marsh.) can be very deterministic (Kramer and Kozlowski 1979), and therefore shoot dynamics, such as total foliar production in the current year, could be impacted by climate during the previous year (Kozlowski 1964; Barnes et al. 1998). Also, total foliage mass, leaf area index, and specific leaf area can be correlated to leaf longevity (Gower et al. 1993; Reich 1993). Environmental conditions, along with heredity, operating through a physiological process such as shoot growth can regulate the overall growth patterns of woody plants (Kramer and Kozlowski 1979; Kozlowski and Pallardy 1997). Unfortunately, it is often difficult to quantify the impact of single environmental factors on growth because plant growth involves integrated responses to numerous ontogenetic and environmental events, and the relative importance of environmental stresses on growth can change with time and may or may not be immediately obvious (Kozlowski et al. 1991).

Many studies that have addressed the long-term impact of climate on tree growth have used some form of tree-ring analyses and compared the results of these analyses to simulated and/or historical climate data (Hessl et al. 1996; Heisey 1995; Parshall 1995; Volk and Fahey 1994; Yin et al. 1994; Liu and Muller 1993). However, although these studies can show how tree growth may be affected by climate, they often do not use actual climate data from the stand they are studying, even though the conditions of the local site can be very important in determining the time and duration of growth (Barnes et al. 1998). Also, although diameter (Burton et al. 1991*a*) or cross-sectional area (Chapman and Gower 1991) may be used to predict foliar biomass, it can be difficult to link actual and specific canopy dynamics, such as periodic reproductive production, with deciduous tree growth and/or climate using diameter growth alone.

In order to assess how climate affects the various components of tree growth, this study incorporates 10 years of climate data, leaf duration data, canopy dynamics, and aboveground woody growth for four northern hardwood stands located along a 500 km latitudinal gradient. The objectives of this study were to: 1. Quantify the relationship between leaf on and growing degree-days; determine the relationship between leaf off and photoperiod; and use these relationships to predict leaf duration in these four northern hardwood stands; 2. Compare year-to-year variability in total, foliar, and reproductive litter across and within the four stands; and 3. Compare year-to-year variability of aboveground woody biomass and basal area production and mortality; 4. Examine relationships among leaf duration, litter production, and aboveground woody growth at each site and across all four sites and compare these aspects of tree growth to climatic data measured at each site.

METHODS

The four hardwood stands used in this study extend along a 500 km latitudinal gradient from northern to southern Michigan (see Figure 1.1). These sites are second-growth forests dominated by sugar maple (*Acer saccharum* Marsh.) and are similar in age, basal area, species composition, soils, physiography, and stand structure (Burton et al. 1991*b*).

Climate

Daily mean air temperatures at two meters above the ground and daily precipitation were recorded within the four stands from 1989 through 1998. Air temperatures at two meters above the ground were recorded every 30 minutes within three, 30m X 30m plots at each of the four sites using thermistors (Model ES-060-SW, Omnidata, Logan, Utah, USA). Data loggers (Model 925, Omnidata, Logan, Utah, USA) recorded averages every three hours. The three-hour averages then were used to calculate the average daily temperature for each plot and site. Precipitation was measured daily and summed weekly. Samples were collected in a Belfort weighing rain gauge located in open areas near each site (within 10 km).

Climate data for approximately 15 percent of the total number of days were missing due to occasional equipment failure and removal of the dataloggers from the field during the first three winters of the study. Daily air temperatures and weekly precipitation values were filled-in using methods derived by Kuuseoks et al. (1997), utilizing data from nearby National Oceanic and Atmospheric Administration (NOAA) weather stations. The only exception to this approach was the use of data from the weighing rain gauge at the University of Michigan Biological Station to fill-in missing precipitation values for Site B. These data were considered more representative of data measured on site than the nearest rain gauge (Burton, personal communication).

Weekly average air temperature (calculated from daily air temperatures) and weekly total precipitation were used to estimate weekly potential evapotranspiration (PET) and actual evapotranspiration (AET; Thornthwaite and Mather 1957); the seasonal (May-September) PET, AET, and available water deficit (PET-AET) were calculated from these data. Mean air temperature and total precipitation also were calculated for May - September of each year. Species such as maple, birch, and oak can form wood from May until early September in this region (Barnes et al. 1998). Therefore these climate data were considered reasonable estimates of the growing season climate.

Leaf duration

Dates of leaf expansion and leaf off for the four stands were recorded from 1989 through 1998. The number of growing degree days (GDD) was calculated for each site for each year beginning February 1 (Julian date 32) and continuing to the date of leaf expansion. The critical Julian date (JD) of leaf expansion was defined as the date when greater than 50% expansion had occurred. These dates were observed by visiting each site several times during the spring of each year (every one to two weeks) and visually estimating leaf expansion. The threshold value used in the calculation of GDD was 4°C, therefore any days after Feb. 1 with mean temperatures above this threshold contributed to the accumulation of degree days. Growing degree days were calculated as:

$$GDD = \left[\sum_{i=32}^{N} (T_i - 4°C) \right] \qquad (1)$$

N = Julian date of >50% leaf expansion.

Ti = the average daily temperature (°C)

Growing degree days to leaf expansion were then compared across sites and years (1989 through 1997) using ANOVA and the Student-Newman-Keuls test (Zar 1974). The JD of leaf expansion was also compared across sites and years using these same procedures. Temperature data from 1998 were withheld from the calculation of the mean site and cross-site mean GDD. This was done to test if the date at which the cross-site mean GDD was reached reliably predicted the JD of leaf expansion for each site. This was accomplished by comparing the actual JD of leaf expansion in 1998 to the JD when the cross-site mean GDD was reached or exceeded.

Leaf off was arbitrarily defined as the date when less than 75% of the canopy remained. This also was assessed visually when visiting each site during the autumn of each year (at least weekly), and these assessments were verified based on biweekly measurements of leaf litter fall mass made each autumn. Photoperiod (hours) on the date of leaf off was calculated using the Navy military web site (U. S. Naval Observatory, Astronomical Applications Dept. 1998). The photoperiod and JD of leaf off for 1989 through 1997 were compared across all sites for all years using ANOVA and the Student-Newman-Keuls test (Zar 1974). Data from 1998 were withheld from these analyses to test if leaf duration could be predicted using the across-site mean photoperiod (see below).

Leaf duration (days) was calculated as the difference between the JD of leaf off and JD of leaf expansion. Leaf duration was then compared across all sites and years using an ANOVA and Student-Newman-Keuls test (Zar 1974). The cross-site mean photoperiod of leaf-off and the cross-site mean GDD of leaf on for 1989-1997 were used to derive an equation for predicting leaf duration in the form:

$$\text{Leaf duration} = \text{JD of mean photoperiod} - \text{JD of mean GDD} \qquad (2)$$

Data from 1998 were used to determine how accurately leaf duration was predicted using this equation.

Total, foliar, and reproductive litter

Leaf litter biomass and leaf area indices (LAI) were calculated for each of the plots within a site using the litterfall method (Burton et al. 1991*a*). To determine LAI and biomass using the litterfall method, eight 0.5 m^2 litter traps were established on each plot. Material from these traps was collected monthly during the growing season and biweekly during the fall from 1989-1997. Litter was separated into leaves by species, wood, insect frass, and other material, primarily reproductive parts. In order to estimate biomass of both foliar and reproductive litter, the fraction of each litter component was determined for 25-50% of the litter traps. All litter samples were dried at 70°C for 48 hrs prior to weighing.

One-half of the litter from one trap on each plot was maintained in fresh condition to measure the leaf area (one side). After leaf area was measured, the samples were dried and weighed in order to determine the specific leaf area (SLA) of the litter. Leaf area indices were estimated by multiplying the leaf litter weight of a species by its SLA and summing for all the species at one site. Mean annual total litter, foliar litter, and reproductive litter were estimated for each year within a site by averaging the data collected from the three plots, and these data were compared across all years and sites using ANOVA and Student-Newmann Keuls tests (Zar 1974).

Aboveground woody production

Within each of three 30 X 30 meter plots established within each site, the diameter at breast height (dbh; 1.37 m) was measured for individual surviving trees (trees that were living at the beginning and end of the year) with a dbh greater than 5 cm. Measurements were made in the fall of each year (1988-1998) after at least 50% of leaf fall had occurred. The heights of each tree were measured in the fall of 1987, 1992, and 1998. These were measured by two individuals using clinometers in order to insure agreement within ± 1 meter. Height increments were interpolated between the measured years and used to estimate heights of individual trees during the years not measured.

Survivor standing crop and growth (i.e. the production of new woody biomass) were calculated across all years. The basal area of each tree alive at the beginning and end of a year was calculated using the standard mensurational formula (Avery and Burkhart 1983). This was summed annually by species and by plot and converted to a per hectare basis. Survivor basal area increment between successive years was then calculated from the yearly total survivor basal area from each of the three plots within a site, and these values were averaged to estimate a mean increment for each site.

Survivor growth of aboveground woody biomass (bole plus branches) for individual trees within each plot at each site was also calculated using the individual tree height and dbh measurements. These height and dbh measurements were incorporated into biomass equations for Lake States forest species assembled by Host et al. (1989). For trees that died between height measurements, either a height increment of zero was used (for years 1989-1992) or the previous annual height increment from 1988-1992 was used (for years 1992-1998) until mortality occurred. The biomass of individual trees was summed within each plot for each year at each of the four sites. Yearly totals were calculated for each plot, and converted to a per hectare basis. These biomass values per hectare were averaged across the three plots to derive an average site biomass value. Survivor biomass increment was calculated from the annual survivor biomass for each site.

Mortality and ingrowth were determined each year for plots at each of the sites and totaled across plots to get an estimate of both within a site during an individual year. Individuals that were dead when the diameters were measured in the fall were included in the estimates of mortality for that year. Ingrowth occurred when a tree reached a dbh of 5cm or greater in a given year.

Net biomass and basal area (equal to survivor growth + ingrowth – mortality) of the standing crop was also calculated for each site. Net biomass and basal area increments were calculated similarly to survivor growth variables.

Descriptive statistics were computed for biomass, basal area, biomass increment, and basal area increments. These values were compared across all years and across all four sites using ANOVA and the Student-Newman-Keuls procedure (Zar 1974).

Leaf duration data, aboveground litter data, and aboveground woody production were compared with each other and with annual and growing season climate using Pearson's Correlation and linear regression analyses.

RESULTS

Climate

The average growing season (May-September) temperature and annual air temperature (1989-1997) decrease from the southern to northern sites, but yearly and growing season precipitation did not differ among the sites (Table 3.1). Average potential evapotranspiration (PET) and available water deficit from May-September did not differ among sites (Table 3.1).

Leaf duration

The mean GDD on the date of leaf expansion was quite variable from year to year within individual sites. However, the cross-year mean GDD days to the JD of leaf expansion did not differ among the sites ($\alpha = 0.05$; Table 3.2). In contrast, the average JD of leaf expansion did differ among the sites for the years 1989 to 1997 ($p<0.0001$). This difference showed a north-south pattern with the date of leaf expansion occurring later at Site A than the rest of the sites (Table 3.2), despite no difference in the mean GDD on the JD of leaf on.

The cross-site mean GDD (214.6 GDD) was used to predict the JD of leaf expansion for 1998. In contrast to most years, the spring of 1998 was unusually warm.

Therefore the required number of GDD for leaf expansion at each site was reached from 9 to 27 calendar days earlier than other years in this data set (Figure 3.1). Nonetheless, using the cross-site mean value of 214.6 GDD, leaf expansion in 1998 was still predicted within four days of the actual JD for every site (Table 3.3; Figure 3.1).

In contrast to growing degree days, the mean photoperiod on the date of leaf off was relatively invariant for each site (Table 3.2). Likewise, the actual date of leaf off at each site was similar from year to year. However, photoperiod and leaf off date differed among the sites ($p<0.001$). For both variables, the northern most site, Site A, had an earlier leaf off date with a corresponding longer photoperiod than the other three sites (Table 3.2).

Differences in leaf duration among the sites followed a similar pattern to that of growing degree days, with Site A having significantly shorter leaf duration than Sites B, C, and D (Table 3.2). Leaf duration was more variable than the JD of leaf expansion or leaf off (Table 3.2). Using the dates of the cross-site mean photoperiod (11.24 hrs) and cross-site mean GDD (214.6), leaf duration in 1998 for Sites A-D was predicted by Equation 2 within six days (Table 3.3).

Total, foliar, and reproductive litter

Mean annual total litter mass, foliar litter mass, and LAI exhibited a latitudinal trend similar to that of leaf duration and the JD of leaf on, increasing from north to south (Table 3.4). Sites differed in the amount of total litter mass across the years, with 6-19% less total litter measured at Sites A and B compared to the rest of the sites. Site A also had 11-20% lower annual foliar litter compared to Sites C and D (Table 3.4). However, these latitudinal trends in total litter, foliar litter, and LAI were not always consistent within individual years across sites, and these data could vary considerably year-to-year within sites. Specific leaf area (SLA) did not differ among the sites (Table 3.4).

In contrast to total and foliar litter, reproductive litter did not display a latitudinal trend and did not differ among the sites (Table 3.4). The total reproductive litter observed at any particular site varied greatly among individual years. However, with some exceptions (especially at Site D), years with larger reproductive crops were consistent across sites.

The relationships among these litter variables often varied within individual sites. For example, although total litter and foliar litter increased together across sites ($r=0.67$; $p<0.05$), this was not always the case for individual sites. Total litter and foliar litter were not correlated at Sites A, C, and D, and only somewhat correlated at Site B ($r=0.63$, $p=0.07$). Likewise, although total foliar litter generally decreased with increases in total reproductive litter across sites ($r=0.35$, $p<0.05$), individual sites displayed different results. Site A, which usually had the highest reproductive litter crop for any given year, was the only site that had a negative relationship between foliar and reproductive litter ($r= -0.75$, $p<0.05$). Total foliar litter also decreased in response to increased defoliation at both sites where defoliation was observed ($r=0.62$, $p=0.10$; $r=0.84$, $p<0.05$, for sites B and C, respectively).

Aboveground woody production

Unlike leaf duration and litter data, estimates of aboveground woody production did not exhibit latitudinal trends among the sites (Table 3.5). Net and survivor biomass increments and net and survivor basal area increments were extremely variable, and did not differ among sites (Table 3.5; Figure 3.2). Negative net basal area increments were observed during some years within individual sites due to mortality within a given year. Mortality did not vary among the sites, but was extremely variable among years within an individual site and also across sites (Table 3.5). Despite occasional high levels of annual mortality, mortality was primarily restricted to trees less than 15 cm dbh, and all sites and the majority of species within each site did increase in basal area from 1989 to 1998 (Table 3.6). Ingrowth did occur at two of the sites, but was restricted to one tree at each site and had a negligible effect on the overall calculations of average biomass and basal area production.

Relationships among climate, leaf duration, aboveground litter, and aboveground woody production

The relationships observed among production variables and between production variables and climate were extremely varied across sites. Although some general trends were observed, these relationships did not always occur within individual sites. For example, across sites and years, total litter during any given year was linearly related to the previous year's GDD to leaf off [total litter = 138.9 + (0.166*GDD); $r^2 = 0.36$; $p < 0.001$, SEM = 44.3; Figure 3.3]. In general, mean annual total litter increased with mean annual GDD from north to south (Figure 3.3). Using this relationship, the total litter in 1998 for each site using the number of GDD from 1997 predicted total litter fall within 21-81 g/m^2. However total litter was not related to GDD from the previous year within any particular site. Similarly, other measures of the previous year's growing season climate were related to total litter across sites. The current year's total litter increased with both mean temperature and PET from the previous May-September ($r=0.61$, $p<0.05$; $r=0.58$, $p<0.05$, respectively), however this relationship was not observed within any individual site. Instead, total litter was not related to any measurement of climate at Sites A, B, or D and only to the current year's total May-September precipitation at Site C.

Total foliar litter was also inconsistently related to climate across and within sites. Across years, mean total foliar litter was positively related to the mean air temperature observed from May-September ($r=0.40$, $p<0.05$). However, at any given site, it was not related to any climate or aboveground woody production variables. In contrast, the relationship of reproductive litter to climate within and across sites was more consistent. Across sites and within Sites B and C, reproductive litter increased with higher mean temperatures recorded during the previous growing season ($r=0.59$, $p<0.05$ across sites).

Another important relationship that demonstrates differences among individual sites is between survivor basal area increment and leaf duration. In general, survivor basal area increment increases with leaf duration ($r=0.32$, $p<0.05$; Figure 3.4). However, this relationship is not observed within any individual site across years, and does not explain growth in 1998. Leaf duration during 1998 was considerably longer than average leaf duration across years at all the sites, but survivor basal area increments at three of the sites in 1998 were 38-51% lower than average, and the same as the average increment across years at the fourth site. Similar relationships exist between survivor biomass increment and leaf duration ($r=0.43$, $p<0.05$) and between survivor biomass increment and total litter ($r=0.37$, $p<0.05$), but these relationships are also not observed within any individual site across years.

Both net and survivor growth at individual sites were related to different climatic variables, however there were no significant relationships between climate and aboveground production across sites. For example, growing season precipitation was not related to aboveground production across sites ($r=0.10$, $p>0.05$; Figure 3.5). This type of relationship was observed between all current and previous year's climatic variables and measures of aboveground woody production. Aboveground woody production was related to some aspects of climate within Sites A and D. This was especially evident at Site A, where survivor woody growth is more related to the temperature and precipitation during the current year's growing season. Survivor basal area increment was related to annual precipitation at Site D ($r=0.81$, $p<0.05$); survivor growth at Sites B and C were not related to any measure of climate.

DISCUSSION

Leaf duration

The number of growing degree days to 50% leaf expansion did not vary among the sites, but the Julian date did differ; the date of leaf expansion was considerably later at the northernmost site, Site A. This is consistent with other studies that have shown that genotypes at northern latitudes flush later than those at southern latitudes (Barnes et al. 1998). Cannell and Smith (1986) also found that the date of budburst for Sitka spruce (*Picea sitchensis* Bong.) was positively correlated with the date at which a certain number of degree days above a threshold of 5°C were achieved. Our results suggest that the species in these stands (primarily sugar maple) reach 50% leaf expansion when a site has reached a specific number of degree days. This conclusion is further validated by our ability to use the date at which this GDD value was reached to predict the leaf expansion dates within five days for 1997 and within four days for 1998.

However, the variability in the mean GDD within and among the stands from 1989 to 1997 also implies that factors other than GDD may influence the timing of leaf expansion. For example, some studies have suggested that the length of winter chilling before budburst could control the release from dormancy in some species (Cannell 1997; Murray et al. 1989; Perala 1985; Worrall 1983; Kramer and Kozlowski 1979). Other factors to consider are the observations used to define both leaf expansion and GDD. Leaf expansion was defined as the JD the trees had >50% leaf expansion; this may not be the most appropriate point in shoot development at which to define expansion. A more ecologically relevant date may be when the buds first flush or when the leaves are more completely expanded. Also, the sites were not visited daily; the JD of leaf expansion was calculated using visual observations of leaf expansion recorded weekly. Therefore, there is an element of measurement error contributing to the variability in dates reported here. Another important consideration is the threshold temperature used for the calculation of GDD; 4°C could be less than optimum for these forest stands. However, analyses showed that altering the threshold value did little to alleviate the variation found in the calculation of mean GDD for the sites across years. This is consistent with the conclusion of Thomson and Moncrieff (1982) who determined that although different threshold values can be used to calculate GDD, the relationship between the number of GDD and the timing of bud burst/leaf expansion would not be greatly altered. Although other factors may be impacting bud burst and leaf expansion, the results from this study suggest that GDD are strongly related to leaf expansion and can be reliably used to predict leaf expansion even in very unusual years (e.g. 1998; Figure 3.1).

The Julian date of leaf off and the photoperiod did not differ among the sites with the exception of the northernmost site, Site A. Also, the length of photoperiod on the date of leaf off for each individual site across years was relatively invariant. However, the photoperiod at leaf off was longer at Site A. Junttila (1982) also found that northern areas had a higher value for photoperiod at leaf off, and Hurme et al. (1997) reported that the date of bud set varied up to three weeks between the northernmost and southernmost seedlings along a latitudinal gradient of 60-67°N. This suggests that photoperiod (or night length) is a primary factor controlling growth cessation (Barnes et al. 1998; Hänninen et al. 1990; Juntilla 1982; Cannell and Willett 1975). As with the date of leaf on, the date of leaf off could be influenced by factors other than photoperiod. Hänninen et al. (1990) suggest that the temperature sum to leaf off, along with night length, could impact the timing of the cessation of shoot growth in northern woody plants. However, they also found that a model using just night length was the most effective in predicting the end of the growing season. The date of leaf off in this study was defined as the date at which less than 75% of the canopy remained and was determined from weekly observations. At this time, little or no green foliage remained in the canopy. This may not be the most appropriate method for determining the actual date of leaf off, however, it seems unlikely that changing the definition of leaf off (e.g. to a smaller or larger percentage of canopy loss) would greatly change the relationship between photoperiod and date of leaf off. Photoperiod is likely the driving factor controlling the entrance of these species into dormancy (Barnes et al. 1998; Morgenstern 1996), which is evidenced by the invariance in the JD of leaf off observed in this study.

Leaf duration could be predicted using just the latitude of the site as the independent variable (Leaf duration = 475.93 – (7.46 * Latitude); r^2 =0.63; standard error of the estimate=6.7 days). However, these relationships of latitude to leaf duration can only indicate general trends in leaf duration and did not describe the year-to-year variability observed within sites. Yearly differences in leaf duration could be more reasonably predicted using Equation 2. This relationship, which estimated duration better than latitude in 1998 (within 6 days compared to within 22 days using latitude), indicates that much of the variability among sites and between years in leaf duration can be explained by the GDD to leaf on and photoperiod at leaf off (r^2 = 0.68; standard error of the estimate=6.4 days). The photoperiod in the autumn is invariant, but the JD at which the GDD for leaf on is attained varies according to differences in spring temperatures. Leaf duration was predicted more accurately when we accounted for differences in spring temperatures during individual years, such as the warmer than average temperatures in 1998. However, both the relationship of leaf expansion to GDD and the relation of photoperiod to leaf off has been reported to be either regionally and/or species specific (Barnes et al. 1998; Cannell and Willett 1975). Although this specific relationship should not be used for other regions and/or species, it is likely that a similar methodology could be used to explain leaf duration in another region or for another forest type.

Total, foliar, and reproductive litter data

Similar to leaf duration, latitudinal gradients existed for both total and foliar litter production. Other studies done at these sites found similar results (Burton et al. 1993; Burton et al. 1991*a*). This may be due to the latitudinal differences in climate as emphasized by the general linear relationship between total litterfall and the number of GDD to the previous JD of leaf off (Figure 3.2) and could explain differences in litter production among the sites. This relationship between total litterfall and the climate during the previous growing season is not surprising given the often very deterministic nature of sugar maple shoot development (Kramer and Kozlowski 1979). Favorable climate during the year the bud is formed results in the formation of large buds with larger carbohydrate reserves, which can produce longer shoots with more leaves the following year (Kozlowski et al. 1991), strongly affecting the initial spring growth of buds of deciduous species, such as sugar maple (Kramer and Kozlowski 1979). Thus, the climate from the previous year will likely determine the extent of carbohydrate reserves for shoot development during the following growing season. However, this relationship between the previous year's climate and total litterfall was not consistent across years within individual sites. Although total litter fall was related to the average air temperature and PET from the previous growing season at Site B, this was not the case at the other sites. Total litterfall at Site C, for example, was more related to precipitation, which was also demonstrated by Grier and Running (1977) in coniferous forests. Also, total litter estimates within and among sites were extremely variable, which could suggest that production at these sites varies considerably.

One important consideration in the estimation of total litter is the occurrence of periodic defoliation events. At the sites where defoliation occurred, foliar litter mass declined (Table 3.3). Defoliation by insects such as the gypsy moth can affect individual trees by reducing growth and leaf area (Witter and Stoyenoff 1992). Defoliation can also change foliage quality (Witter and Stoyenoff 1992), and after defoliation, there are usually fewer and smaller replacement leaves (Wargo 1981). Decreases in foliar mass associated with defoliation events at Sites B and C are likely caused by decreased leaf area and are impacting total litter estimates during those years that defoliation occurred.

Differences in total litterfall could also be due to differences in the factors controlling foliar and reproductive litterfall. In general, total litter estimates increased with foliar litter. However, the relationship between total and foliar litter could be influenced by the development of periodic large reproductive crops. Reproductive structures can be a strong carbon sink (Kozlowski 1992), and the production of large periodic reproductive crops within a site often had a negative impact on the amount of foliar litter, especially at Site A. Pregitzer and Burton (1991) also demonstrated that foliar and reproductive litter production were negatively correlated at these sites and suggest a direct trade off in biomass between the two.

In general, reproductive litter was related to the previous year's climate, however foliar litter totals were more related to mean temperatures and leaf duration during the current year's growing season. This suggests a more favorable growing season could cause an increase in foliar production, and a longer growing season may enable trees to support a greater foliage mass (Chabot and Hicks 1982). Gower et al. (1993) also found a positive relationship between foliar biomass and leaf longevity and between stand-level-values of leaf area and leaf longevity in both conifer and deciduous species in Wisconsin.

The differences in foliar and total litter among sites implies that shoot elongation can depend on weather conditions both when the terminal bud is formed and early in the growing season during bud elongation (Kramer and Kozlowski 1979). For example, sugar maple dominates all four stands, and although sugar maple shoots are largely deterministic, it is possible that shoots can consist of two types (Powell et al. 1982). Most sugar maple shoots expand their preformed leaves and then develop a terminal bud (Kozlowski and Pallardy 1997). However, some sugar maple shoots may also develop several pairs of neoformed leaves after the expansion of preformed leaves and before the development of terminal buds (Kozlowski 1992; Powell et al. 1982; Gregory 1980). Therefore, it is possible that sugar maple shoots could expand for a longer time under favorable conditions (Kozlowski 1992). This ability may explain the variability in foliar litter seen within individual sites. Another important consideration is the impact of drought. This study did not show any relationship between foliar production and precipitation, however decreases in moisture at the time of formation can reduce both the size and number of leaves (Kozlowski and Pallardy 1997). The differential responses of both foliar and reproductive litter to different aspects of climate within sites and/ or years could explain some of the variability in aboveground litter measurements. However, in general, yearly litter (total, foliar, and reproductive) production seems to be primarily related to changes in growing season temperatures both during the previous and current years. Thus, it is possible that changes in climate conditions that lead to warmer temperatures will influence shoot dynamics, in particular increases in both leaf duration and litter production in temperate deciduous forests. However, it is likely that individual differences among sites and/or species may moderate specific site responses to differences in climate.

Aboveground woody production

Aboveground woody growth did not differ among the sites across years and did not consistently relate to any measurement of climate or canopy dynamics. Tree-ring studies and other short-term studies done at these same sites also did not find uniform patterns in recent growth trends across sites (Lane et al. 1993, Reed et al. 1994). Reed et al. (1994) were unable to find differences in increment due to regional climate or site characteristics and suggested longer-term studies were needed.

Other studies have demonstrated variations in radial growth have been associated with differences in the amount of foliage (Braekke and Kozlowski 1975) and have used diameter (Burton et al. 1991*a*) or cross-sectional area (Chapman and Gower 1991) to predict foliar biomass. However, this study did not demonstrate any strong correlations between leaf duration and/or foliar litter production and aboveground woody production. Although survivor basal area increment was positively related to leaf duration, this relationship did not explain the decrease in survivor basal area growth in 1998, despite the much longer leaf duration. The relationships between aboveground woody growth and canopy dynamics were not consistent among sites, and unlike leaf duration and litter production, woody increments did not display a latitudinal gradient.

Differences in annual woody growth across sites also were not related to annual or growing season climate. Several other studies have demonstrated this change in the growth in deciduous species associated with differences in air temperatures (Yin et al. 1994; Lane et al. 1993; Braekke and Kozlowski 1975) and mean number of growing degree days (MacDonald et al. 1998). Also, Lane et al. (1993) demonstrated through tree-ring width studies that temperature conditions lengthening the previous growing season in the fall were positively correlated to current ring width, which was probably due to an associated increase in carbohydrate reserves. However, this long-term field study does not reflect these results, which suggests that changes in annual and/or growing season temperatures are not impacting aboveground woody production during this time period.

Another important consideration is moisture availability. Drought may cause decreases in growth (Liu and Muller 1993; Ibrahim et al. 1997). Using these same sites, MacDonald et al. (1998) found from 1989-1993, Sites C and D had higher variability in annual diameter increments, and reported reductions in dbh increment associated with drought events during certain years at these two sites. This higher variability in increment during more droughty years may reflect higher competitive stress during those years at these sites. Lane et al. (1993) also demonstrated that precipitation was important at the same southern sites even though growth at these sites was most sensitive to temperature. This study also did not find any consistent relationship between woody growth and precipitation or between woody growth and available water deficit at any of the sites, but individual years that experienced lower survivor growth were also drier years. However, not all drier than average years had lower than average survivor growth. It is possible that differences in precipitation and available water deficits could be mediating the response of woody growth to changes in temperatures, however differences in woody growth could not be adequately explained across or within sites using a single combination of climate and/or canopy variables.

Many models addressing how global climate change may or may not impact forest use variations in climate to drive changes in forest production (Korol et al. 1991; LeBlanc and Foster 1992; Aber et al. 1995; Korol et al. 1996). For example, the Osnabruck Model (OBM) uses a single factor limitation and assumes that temperature or precipitation limits productivity (McGuire et al. 1993). Models such as the Terrestrial

Ecosystem Model (TEM; McGuire et al. 1993) and PnET-II (Aber et al. 1995) predict an increase in net primary productivity in northern forests with an increase in temperature (McGuire et al. 1993). Quantifying the impact of a single environmental factor on growth is often complicated because plant growth involves integrated responses to numerous ontogenetic and environmental events; also the relative impact of environmental stresses on production can change over time and may or may not be immediately obvious (Kozlowski et al. 1991). Our study incorporates many years of actual climate and production data and includes enough variability across years to encompass many of these climate change scenarios. However, aboveground productivity or changes in foliar biomass could not be precisely predicted using any combination of temperature or moisture data. This suggests that models such as those described above will not adequately predict changes in forest production across these sites, and it is possible that changes in climate could have little or no effect on aboveground woody production at these sites.

CONCLUSIONS

Differences in canopy dynamics in these four northern hardwood sites are associated, in part, with differences in air temperature before shoot expansion, during the growing season, and to the date of leaf drop. For example, the date of leaf expansion was strongly related to the accumulation of a certain number of growing degree days (i.e. cumulative heat sum) in the spring, and variation in leaf duration appears to be mostly due to the changes in the date of shoot development in the spring. Air temperature could also be used to reasonably estimate total litter fall across the gradient. This long-term implies that warm spring temperatures can have an impact on leaf duration and also total litter production across these hardwood forests.

In contrast, aboveground woody growth did not differ among these sites across years and was not consistently related to any measurement of climate or canopy dynamics. Differences among the sites and across years also suggest that canopy dynamics and aboveground woody growth at these sites integrate numerous other variables and interactions among variables not accounted for by this study. This is also reflected in the low correlation coefficients derived for many of the tested relationships. However, the variability in aboveground woody production suggests that it is unlikely that changes in production at these sites will be predicted using climate change scenarios.

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Table 3.1: Location and climate data for study sites. Rows contain the mean and standard deviation from three plots located at each site. Means with different letters within a row differ ($p<0.05$).

	Site A	Site B	Site C	Site D
Latitude	46°52'N	45°33'N	44°23'N	43°40'N
Longitude	88°53'W	84°51'W	85°50'W	86°09'W
Annual air temperature (AT, °C)	4.22 (0.57) *a*	5.48 (0.66) *b*	6.30 (0.56) *c*	7.11 (0.57) *d*
Annual precipitation (ppt; cm)	79.55 (12.37)	82.44 (10.35)	89.38 (11.43)	77.26 (10.20)
May-September AT (°C)	14.81 (0.85) *a*	15.73 (0.95) *ab*	16.19 (1.08) *b*	16.77 (1.13) *b*
May-September ppt. (cm)	320.6 (45.5)	295.1 (86.5)	313.1 (83.8)	347.9 (56.3)
May-September potential evapotranspiration (PET; cm)	40.32 (1.62)	41.40 (1.80)	41.40 (1.98)	42.66 (2.34)
May-September available water deficit (PET-actual evapotranspiration; cm)	5.32 (3.98)	9.69 (6.58)	8.34 (4.65)	8.87 (4.58)

Table 3.2: Leaf duration data recorded from 1989-1997 at four northern hardwood sites located along a 500 km latitudinal gradient. Julian dates (JD) of leaf on (date when 50% of leaves expanded) and leaf off (date 75% of the leaves have dropped) are included. Growing degree days (GDD) to the dates of leaf on and leaf off also are presented. Across year means with standard deviations in parentheses are shown for each site. Row means with different letters are significant ($p<0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude Longitude	46°52'N 88°53'W	45°33'N 84°51'W	44°23'N 85°50'W	43°40'N 86°09'W
Leaf on (JD)	152 (4.93) *b*	143 (5.33) *a*	140 (6.78) *a*	137 (5.95) *a*
Leaf off (JD)	276 (3.66) *a*	285 (5.05) *b*	286 (3.59) *b*	286 (3.56) *b*
Photoperiod (hrs) at leaf off	11.57 (0.20) *b*	11.14 (0.26) *a*	11.12 (0.19) *a*	11.14 (0.17) *a*
GDD to leaf on	234 (43.34)	193 (24.14)	221 (3.59)	215 (31.98)
GDD to leaf off	1595 (107.93) *a*	1792 (122.57) *b*	1858 (76.51) *bc*	2019 (136.93) *d*
Leaf duration (days)	124 (6.76) *a*	143 (5.11) *b*	147 (5.95) *b*	150 (5.68) *b*

Table 3.3: Validation of the use of growing degree days (GDD) to predict leaf duration. The Julian date (JD) of leaf expansion for each site, the predicted date of leaf expansion using the JD each site reached the cross-site mean GDD (214.6 GDD) from 1989-1997, and predicted leaf duration for each site in 1998.

	Site A	**Site B**	**Site C**	**Site D**
Latitude	46°52'N	45°33'N	44°23'N	43°40'N
Longitude	88°53'W	84°51'W	85°50'W	86°09'W
1998				
Actual JD of leaf expansion	130	126	124	121
Predicted JD of leaf expansion	134	129	125	121
Difference in days between actual and predicted JD of leaf expansion	4	3	1	0
1998				
Actual leaf duration	148	160	163	169
Predicted duration	142	157	164	169
Difference in days between the actual and predicted leaf duration	6	3	1	0

Table 3.4: Annual total litter (kg/ha), foliar litter (kg/ha), reproductive litter (kg/ha), leaf area index (LAI, m^2/m^2), and specific leaf area (SLA, g/cm^2) recorded from 1989-1997. Across-year means and standard deviations (in parentheses) from three plots are supplied for each site. Row means with different letters differ ($p < 0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude Longitude	46°52'N 88°53'W	45°33'N 84°51'W	44°23'N 85°50'W	43°40'N 86°09'W
Total litter (g/m^2)	399.6 (29.9) *a*	423.6 (60.3) *a*	475.8 (36.1) *b*	492.3 (35.6) *b*
Foliar litter (g/m^2)	327.1 (36.7) *a*	366.6 (50.9) *ab*	388.6 (47.6) *b*	406.9 (26.3) *b*
Reproductive litter (g/m^2)	42.3 (45.3)	30.8 (32.2)	31.6 (17.8)	35.0 (12.3)
LAI (m^2/m^2)	6.5 (0.8) *a*	7.2 (1.4) *ab*	7.4 (1.2) *ab*	8.0 (0.7) *b*
SLA ($cm^2\ g^{-1}$)	197.3 (12.9)	194.1 (18.1)	189.9 (14.6)	197.1 (11.0)
% Defoliation	None observed.	3.3	7.6	None observed.

Table 3.5: Aboveground woody data recorded from 1989-1997. Mean net biomass (metric tons/ha), basal area (m^2/ha), mean survivor biomass, survivor basal area, and increments are presented with standard deviations in parentheses. Mortality (number of stems/ha) for individual sites is included. Across-year means and standard deviations for each variable are supplied for all the sites. Row means with different letters differ ($p < 0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude Longitude	46°52'N 88°53'W	45°33'N 84°51'W	44°23'N 85°50'W	43°40'N 86°09'W
Net biomass (metric tons ha^{-1})	287.1 (13.1) *a*	281.8 (9.9) *a*	303.6 (12.7) *b*	271.9 (16.5) *a*
Net basal area (m^2 ha^{-1})	33.4 (0.8) *c*	30.7 (0.5) *a*	31.7 (0.8) *b*	32.2 (1.2) *b*
Net biomass increment (metric tons ha^{-1})	4.7 (0.8)	3.5 (1.7)	4.2 (1.7)	5.5 (2.3)
Net basal area increment (m^2 ha^{-1})	0.31 (0.10)	0.19 (0.22)	0.24 (0.22)	0.37 (0.30)
Survivor biomass (metric tons ha^{-1})	287.6 (13.2) *b*	283.4 (10.8) *b*	304.9 (13.7) *b*	273.0 (17.3) *a*
Survivor basal area (m^2 ha^{-1})	33.5 (0.9) *a*	30.9 (0.6) *b*	31.9 (0.9) *b*	32.4 (1.3) *b*
Survivor biomass increment (metric tons ha^{-1})	6.0 (1.1)	6.1 (1.0)	7.5 (2.3)	7.2 (1.8)
Survivor basal area increment (m^2 ha^{-1})	0.40 (0.10)	0.42 (0.12)	0.42 (0.13)	0.55 (0.22)
Mortality (basal area; m^2 ha^{-1})	0.09 (0.08)	0.23 (0.19)	0.18 (0.21)	0.18 (0.21)

Table 3.6: Average basal area (m^2/ha) for each species and average basal area per site in 1988 and 1998.

	Site A 46°52'N, 88°53'W		**Site B** 45°33'N, 84°51'W		**Site C** 44°23'N, 85°50'W		**Site D** 43°40'N, 86°09'W	
	1988	1998	1988	1998	1988	1998	1988	1998
Acer saccharum	27.5	30.0	25.4	26.5	24.9	26.1	22.5	23.7
Abies balsamea	0.06	0	–	–	–	–	–	–
Acer rubrum	1.4	1.6	–	–	2.4	2.9	4.1	5.12
Betula alleghaniensis	2.3	2.4	–	–	–	–	–	–
Fagus grandifolia	–	–	0.9	0.9	0.03	0.03	0.5	0.6
Fraxinus americana	–	–	2.4	3.2	–	–	–	–
Ostrya virginiana	0.06	0.01	0.06	0.06	–	–	0.06	0.04
Prunus serotina	–	–	–	–	1.5	1.7	2.2	2.7
Quercus rubra	–	–	–	–	1.4	1.7	0.74	1.1
Tilia americana	0.5	0.6	0.9	0.6	–	–	–	–
Total basal area	31.9	34.6	29.6	31.4	30.2	32.5	30.1	33.2

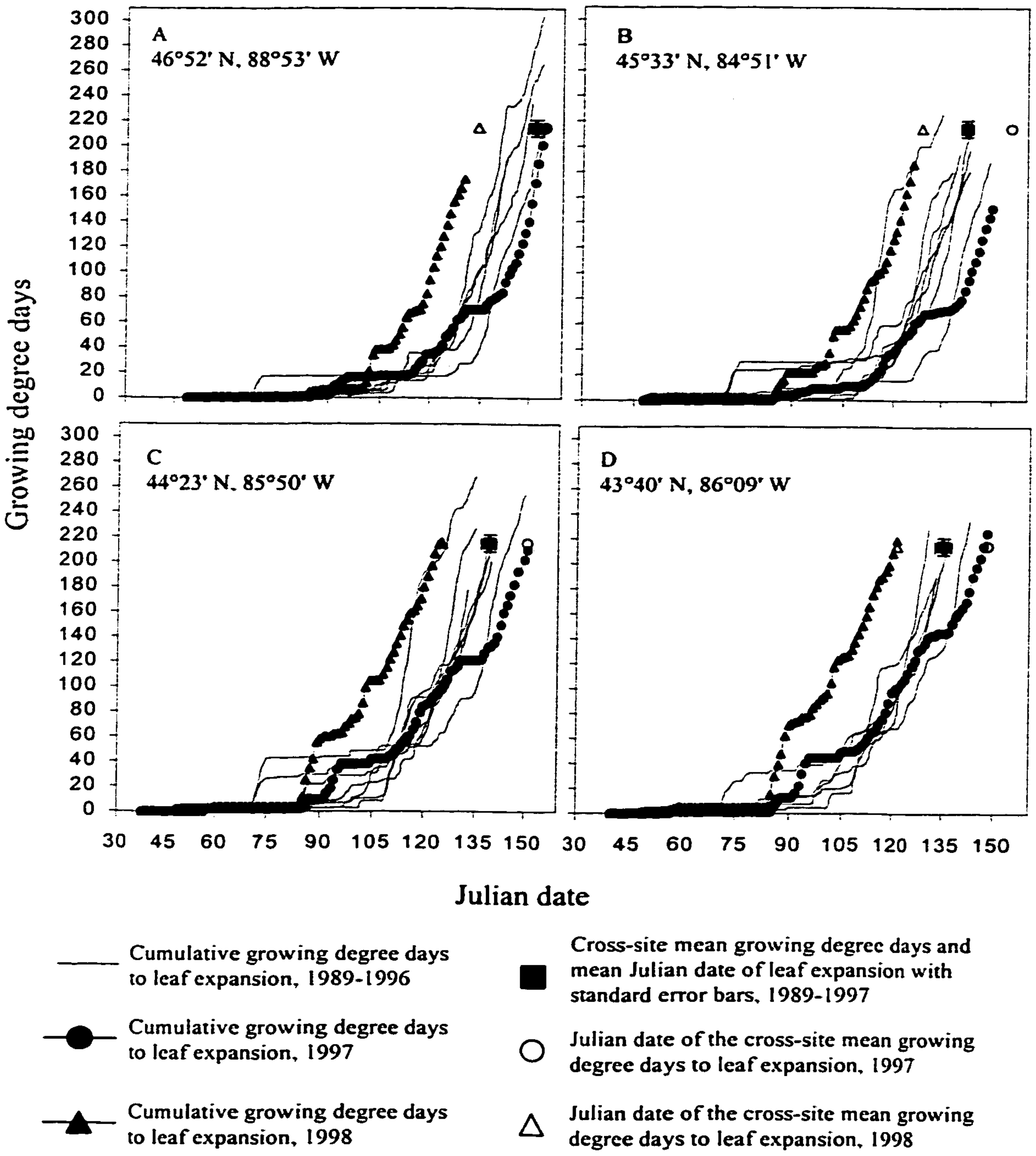

Figure 3.1: Growing degree days (GDD) for 1989 through 1998 for Sites A-D. The years between 1989 and 1996 with a complete record are in solid black lines. The square with standard error lines signifies the mean Julian date (JD) of leaf expansion and the cross-site mean GDD on the date of leaf expansion (214.6 GDD). The line with filled circles refers to the accumulation of GDD to leaf expansion during the spring of 1997, a cooler than average spring. The line with filled triangles refers to the accumulation of growing degree days in the spring of 1998, a very warm spring. The open circle and triangle refer to the Julian date the cross-site mean GDD was reached during the spring of 1997 and 1998, respectively.

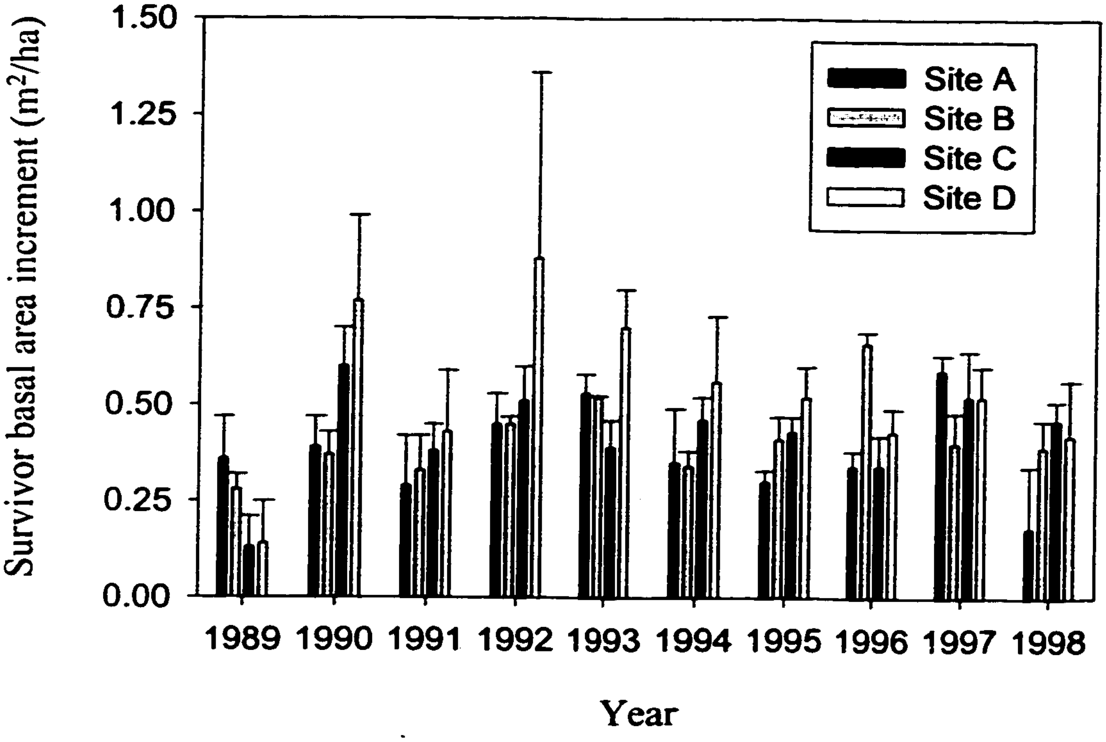

Figure 3.2: Survivor basal area increment for individual sites from 1989-1998. Bars reflect +1 standard deviation.

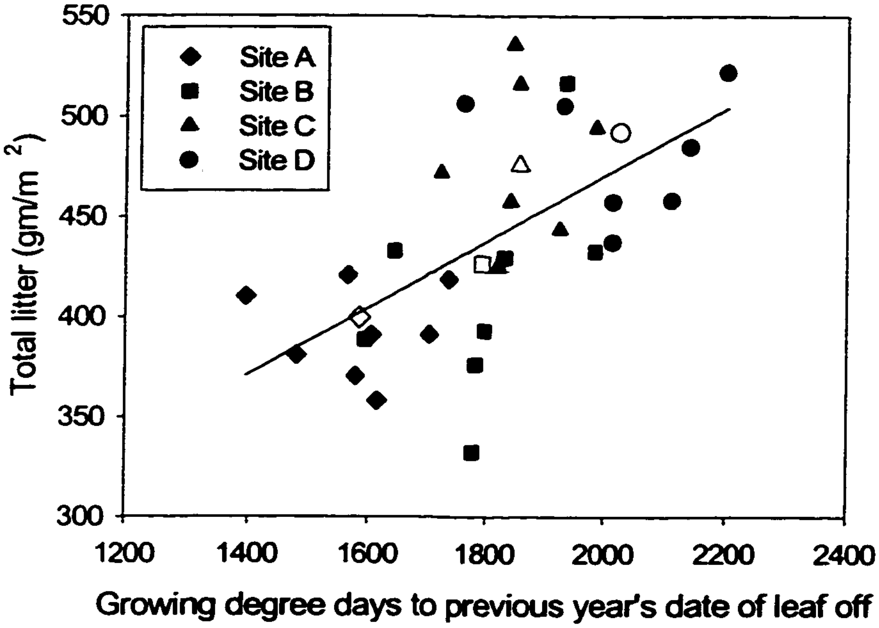

Figure 3.3: Relationship between the growing degree days (GDD) to the previous year's date of leaf off and total litter (kg/ha) from 1989-1997. A scatter plot of individual sites across years is presented with a solid line representing the regression line that incorporates data across all sites [total litter = 138.9 + (0.166*GDD); $R^2 = 0.36$; $p < 0.001$, SEM = 44.3]. Open symbols represent the mean total litter and GDD to previous leaf off across all years for each site.

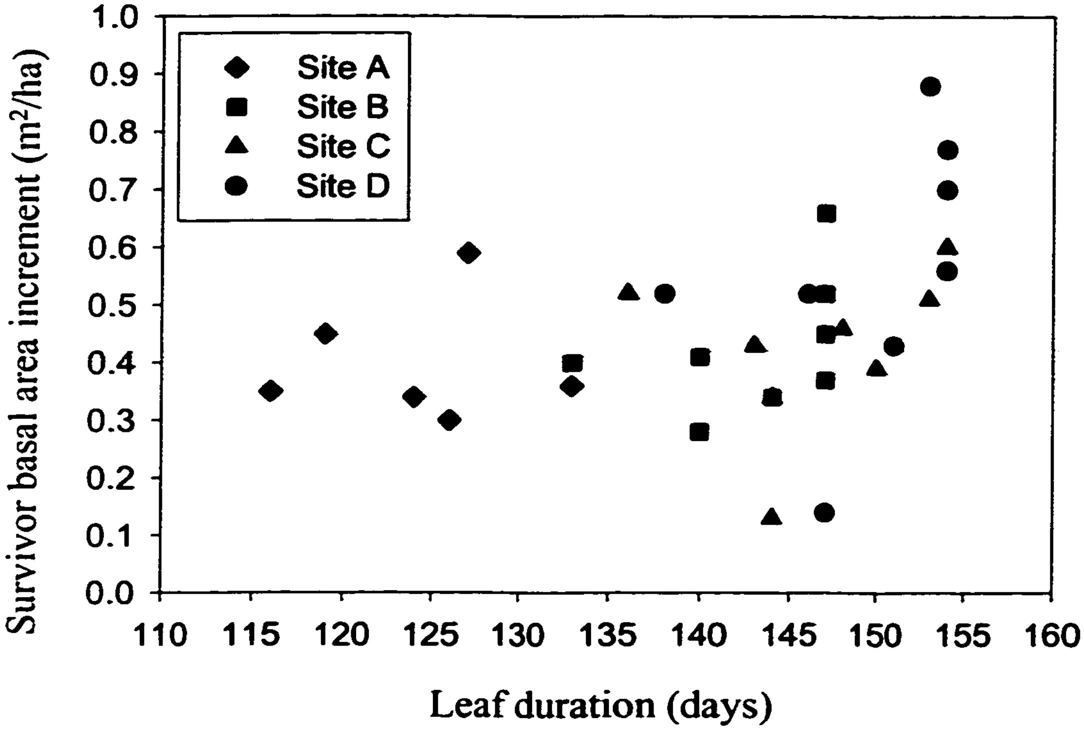

Figure 3.4: Relationship between the leaf duration and survivor basal area increment (m^2/ha) within individual sites from 1989-1997.

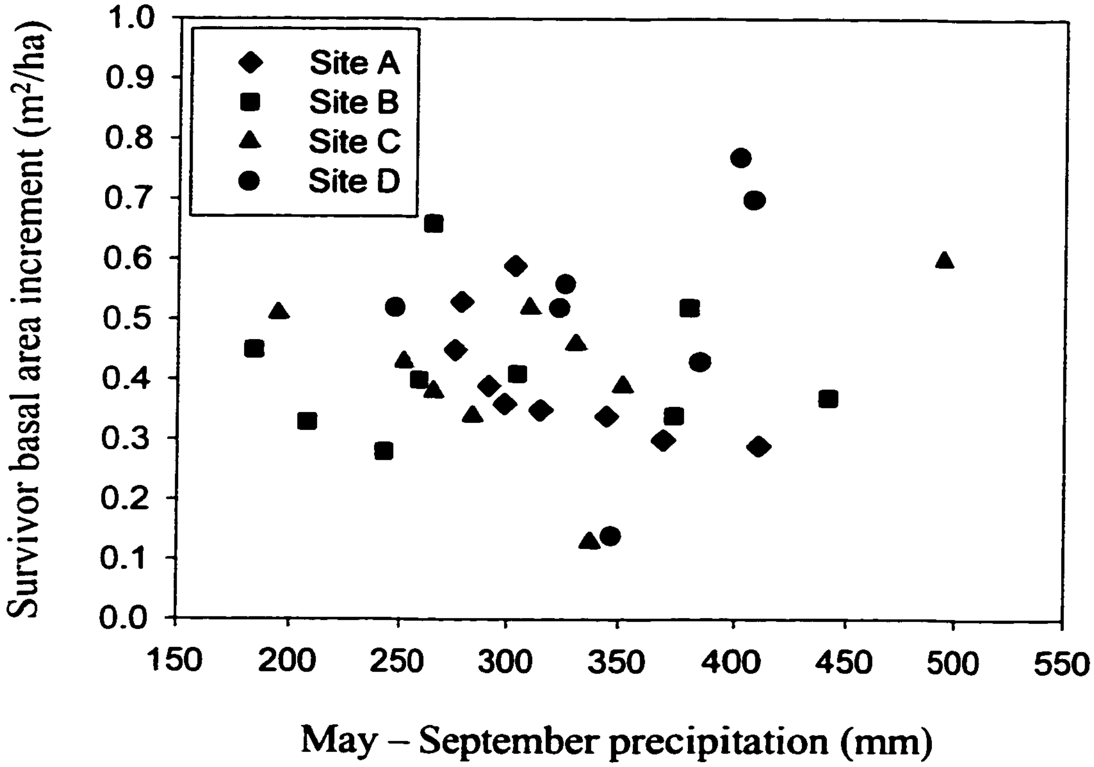

Figure 3.5: Relationship between the growing season precipitation and survivor basal area increment (m^2/ha) within individual sites from 1989-1997.

CONCLUSIONS

In conclusion, this dissertation demonstrates how climate may be impacting both below- and aboveground production dynamics over long periods of time. However, much work still needs to be done to determine the variables potentially driving production at these sites. For example, it is likely that other factors besides changing temperatures and moisture conditions may impact fine root maintenance respiration, and that roots must be tightly linked to C supply from the canopy during the growing season. Clearly, more research needs to be conducted to determine how environmental controls regulate root maintenance costs and mortality rates. Likewise, differences in canopy dynamics in these four northern hardwood sites are associated, in part, with differences in air temperature before shoot expansion, during the growing season, and to the date of leaf drop. However, canopy dynamics and aboveground woody growth were not consistently related to any measurement of climate. Individual site differences suggest that few general conclusions about the relationships among growth and climate variables can be made across an ecosystem. Individual sites likely will respond differently to a changing climate, however it is difficult to quantify the impacts of individual aspects of climate on growth because of the variability in production across sites and years.

APPENDICES

APPENDIX A

Equations used by Kuuseoks et al. (1997) to predict air temperatures for the sites using NOAA Station air temperature data.

Table A1: Equations used by Kuuseoks et al. (1997)[1] to predict air temperatures (AT) for the sites using NOAA Station AT data. The general equation is as follows: $AT = \beta_0 + \delta * \beta_1 + \gamma * \beta_2$; where β_1 and β_2; = AT from each NOAA Station and δ and γ are the coefficients unique to the first and second NOAA Station, respectively.

Site	NOAA Stations used as independent variables	Equation	R^2 (MSE) reported by Kuuseoks et al. (1997)
Site A	Houghton FAA Airport Herman	$AT = 0.21 + 0.56 * \beta_1 + 0.38 * \beta_2$	0.97 (1.29)
Site B	Pellston Airport Cross Village	$AT = -0.64 + 0.60 * \beta_1 + 0.40 * \beta_2$	0.97 (1.12)
Site C	Traverse City FAA Airport Baldwin	$AT = -0.15 + 0.68 * \beta_1 + 0.25 * \beta_2$	0.97 (1.58)
Site D	Montague Big Rapids	$AT = 0.15 + 0.29 * \beta_1 + 0.67 * \beta_2$	0.98 (0.74)

[1] Kuuseoks, E., H. O. Liechty, D. D. Reed, and J. Dong. 1997. Relating site-specific weather data to regional monitoring networks in the Lake States. Forest Science 43: 447-452.

APPENDIX B

Method to predict matric potential using daylength, air temperature, and precipitation.

Method to predict soil matric potential using daylength, air temperature, and precipitation

Soil matric potential was measured in three plots within each of the sites. Single gypsum blocks (Model 5201, Soilmoisture Equipment Corporation, Santa Barbara, California, USA) were buried at 15 cm in each of the plots. Omnidata EasyLoggers (Model 824, Data Loggers Inc., Logan Utah, USA) recorded resistance every 30 minutes at each plot and recorded average readings every 3 hours. The average daily matric potential for each site was calculated as the average of the three plots. Relationships from moisture blocks put in intact soil cores from each of the plots and equilibrated on soil moisture plates (potentials ranged from –0.01 to –1.5 MPa) were used to convert the resistance readings (ohms) from the moisture blocks to matric potential (megapascals). Similar to both air and soil temperatures, approximately 15 percent of the total number of days were missing due to occasional equipment failure. Weekly average matric potential was calculated for the existing data. Similar to soil temperature, some of the missing values could be filled-in using data from nearby plots within the same site. However, another procedure needed to be developed to fill-in most of the missing data.

Weekly average daylength, weekly average air temperature, and total weekly precipitation from each of the sites were used to derive a method to fill-in missing average weekly soil matric potential. Daily matric potential was not considered; it could not be confidently predicted due to the inherent lag in the absorption by the moisture blocks. Weekly average daylength (U. S. Naval Observatory, Astronomical Applications Dept. 1998) and with weekly mean air temperature were used to derive weekly potential evapotranspiration (PET) using Thornthwaite's equation (Thornthwaite and Mather 1957). Weekly PET was subtracted from weekly total precipitation, and these differences were summed over 4 weeks. Any 4-week sum greater than zero was considered zero because soils have a measurable field capacity, beyond which they can hold no more water against gravity. This puts an upper limit on their matric potential, thus any predictor for matric potential also needs to have an upper limit. In order to predict matric potential, regression equations were derived to predict soil moisture deficits (megapascals, MPa) from the difference in weekly precipitation and potential evapotranspiration (PET) summed over the previous 4 weeks. The regression equation had the following general format:

$$MPa = \beta_0 + \beta_1 * \delta; \qquad (1)$$

where δ = the summed difference of precipitation and PET (values < 0) from the previous 4 weeks. Different constants and coefficients were calculated for individual sites. These predicted values of soil matric potential were compared to actual values of mean weekly matric potential from 1998 to validate the above method.

Soil matric potential (MPa) was estimated using precipitation and Thornthwaite and Mather's estimate of PET (Equation 1). Summing the difference between precipitation and PET from the previous 4 weeks was the most successful method to predict matric potential. Other independent variables such as actual evapotranspiration, weekly soil temperature, weekly air temperature, weekly precipitation, weekly PET, and various combinations were tested, however the summed difference of precipitation and PET yielded the best empirical fit ($R^2 = 0.26 - 0.42$; $p < 0.001$; SEM = -0.83 to –0.204 MPa). Although this approach underestimates the magnitude of change in matric potential, the method successfully predicts when matric potential will change (Figure B1). Other studies have suggested that soil moisture data derived using equations developed by Thornthwaite and Mather (1957) are reasonable estimates of actual soil moisture (Huang et al. 1996; Pastor and Post 1986). Hence, this method of filling-in matric potential data was considered reasonably accurate for these sites.

LITERATURE CITED

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Pastor, J., and W. M. Post. 1986. Influence of climate, soil moisture, and succession of forest carbon and nitrogen cycles. Biogeochem. 2: 3-27.

Thornthwaite, C. W., and J. R. Mather. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology 10: 183-311.

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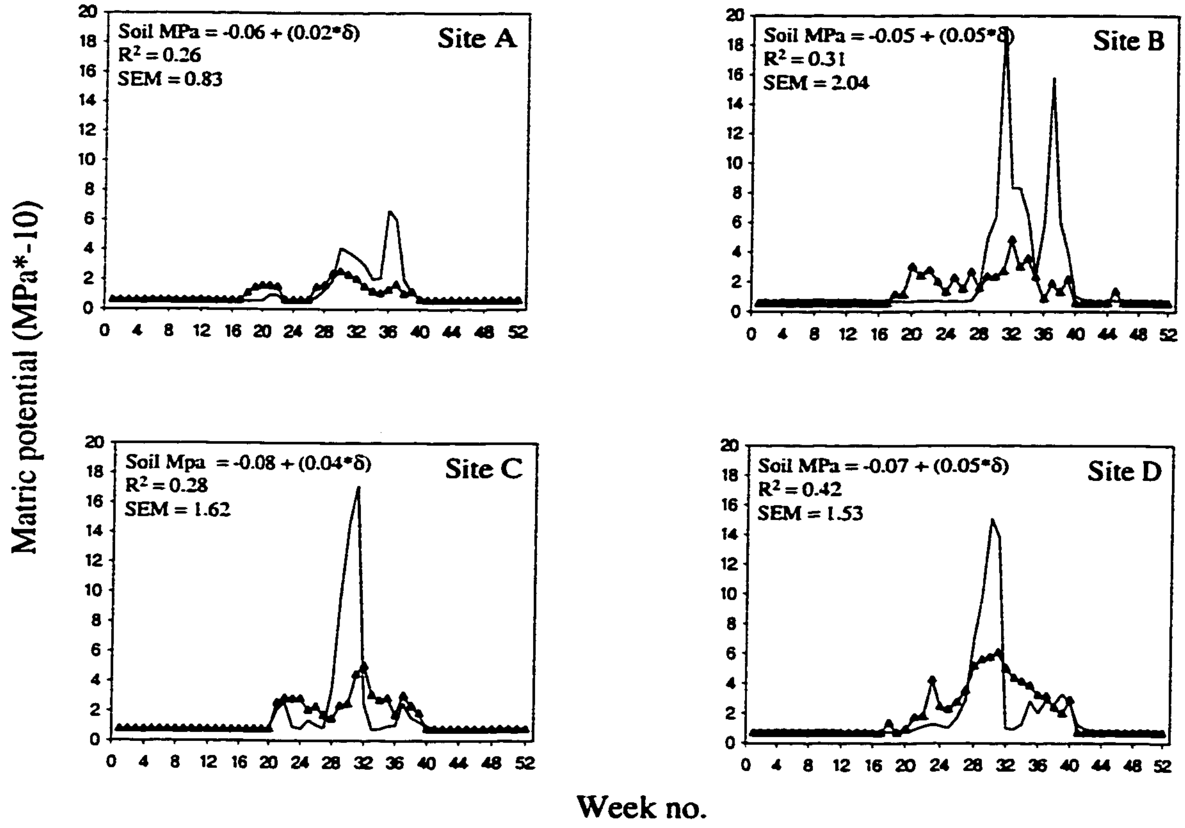

Figure B1: Recorded and predicted weekly mean soil matric potential (MPa) during 1998 for four sites along a latitudinal gradient in Michigan. Each graph contains a line depicting the recorded weekly mean soil matric potentials, and a line with triangles depicting the predicted weekly mean matric potential. The general equation used to predict matric potential is as follows: Soil MPa = $\beta_0 + \beta_1 * \delta$; where δ = the summed difference of precipitation and PET (values < 0) from the previous 4 weeks. The specific equation, coefficients of determination (R^2), and standard error of the estimates (SEM) are presented for each site.

APPENDIX C

Year-to-year variation in canopy and aboveground woody data within individual sites from 1989-1997.

Table C1: Leaf duration data recorded from 1989-1997 at four northern hardwood sites located along a 500 km latitudinal gradient. Julian dates (JD) of leaf on (date when 50% of leaves expanded) and leaf off (date 75% of the leaves have dropped) are included. Growing degree days (GDD) to the dates of leaf on and leaf off also are presented. Across year means with standard deviations in parentheses are shown for each site. Row means with different letters are significant ($p<0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude	46°52'N	45°33'N	44°23'N	43°40'N
Longitude	88°53'W	84°51'W	85°50'W	86°09'W
Leaf on (JD)				
1989	143	143	139	136
1990	--	135	135	135
1991	--	--	--	--
1992	154	140	133	133
1993	--	138	135	131
1994	154	144	139	133
1995	151	143	140	137
1996	156	149	150	137
1997	155	150	150	148
Across all years	152 (4.93) *b*	143 (5.33) *a*	140 (6.78) *a*	137 (5.95) *a*
Leaf off (JD)				
1989	276	283	283	283
1990	275	282	289	289
1991	274	278	281	283
1992	273	287	286	286
1993	278	285	285	285
1994	270	288	287	287
1995	277	283	283	283
1996	280	296	293	294
1997	282	283	286	296
Across all years	276 (3.66) *a*	285 (5.05) *b*	286 (3.59) *b*	286 (3.56) *b*
Photoperiod (hrs) at leaf off				
1989	11.57	11.23	11.27	11.28
1990	11.65	11.28	10.98	11.00
1991	11.70	11.52	11.38	11.30
1992	11.77	11.05	11.15	11.17
1993	11.45	11.12	11.15	11.18
1994	11.90	10.97	11.07	11.10
1995	11.53	11.25	11.27	11.30
1996	11.40	10.58	10.75	10.77
1997	11.23	11.23	11.10	11.12
Across all years	11.57 (0.20) *b*	11.14 (0.26) *a*	11.12 (0.19) *a*	11.14 (0.17) *a*

Table C1 cont.

GDD to leaf on				
1989	189	198	232	–
1990	–	227	270	–
1991	–	–	–	–
1992	305	195	178	191
1993	–	180	227	229
1994	267	224	201	190
1995	205	182	213	222
1996	214	189	257	235
1997	214	152	209	225
Across all years	234 (43.34)	193 (24.14)	221 (3.59)	215 (31.98)
GDD to leaf off				
1989	1614	1782	1845	–
1990	1605	1832	1923	2110
1991	1737	1983	–	2200
1992	1395	1594	1722	1761
1993	1480	1642	1855	1929
1994	1564	1797	1840	2012
1995	1703	1933	1985	2139
1996	1578	1778	1821	2012
1997	1676	1786	1873	1985
Across all years	1595 (107.93) *a*	1792 (122.57) *b*	1858 (76.51) *bc*	2019 (136.93) *d*
Leaf duration (days)				
1989	133	140	144	147
1990	–	147	154	154
1991	–	–	–	–
1992	119	147	153	153
1993	–	147	150	154
1994	116	144	148	154
1995	126	140	143	146
1996	124	147	144	151
1997	127	133	136	138
Across all years	124 (6.76) *a*	143 (5.11) *b*	147 (5.95) *b*	150 (5.68) *b*

Table C2: Annual total litter (kg/ha), foliar litter (kg/ha), reproductive litter (kg/ha), leaf area index (LAI, m^2/m^2), and specific leaf area (SLA, g/cm^2) recorded from 1989-1997 at four northern hardwood sites located along a 500 km latitudinal gradient. Across-year means and standard deviations (in parentheses) from three plots are supplied for each site. The percentage of defoliation observed at each of the sites from 1989-1996 is also presented. Row means with different letters differ ($p < 0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude	46°52'N	45°33'N	44°23'N	43°40'N
Longitude	88°53'W	84°51'W	85°50'W	86°09'W
Total litter (g/m^2)				
1989	465.4 (8.2)	510.0 (15.1)	488.6 (35.1)	510.6 (53.5)
1990	358.1 (7.6)	376.1 (5.8)	535.9 (14.6)	547.7 (100.1)
1991	390.9 (14.0)	429.7 (27.8)	443.8 (19.7)	458.3 (31.6)
1992	418.8 (37.5)	432.8 (19.8)	448.6 (59.7)	522.1 (33.9)
1993	410.3 (14.3)	388.6 (19.3)	471.9 (21.2)	506.5 (56.9)
1994	380.8 (16.6)	433.0 (23.7)	516.2 (42.7)	505.5 (38.7)
1995	420.8 (28.1)	393.2 (20.5)	457.7 (20.8)	457.5 (12.4)
1996	391.1 (25.8)	516.8 (19.5)	494.5 (20.7)	484.9 (51.8)
1997	370.3 (15.0)	332.4 (15.7)	424.9 (14.6)	437.3 (24.2)
Across all years	399.6 (29.9) *a*	423.6 (60.3) *a*	475.8 (36.1) *b*	492.3 (35.6) *b*
Foliar litter (g/m^2)				
1989	262.3 (5.7)	341.3 (20.3)	398.2 (29.5)	402.6 (39.2
1990	299.0 (11.3)	299.8 (34.0)	416.3 (41.4)	391.9 (20.1)
1991	325.4 (15.4)	386.6 (19.2)	398.6 (11.2)	398.1 (42.7)
1992	364.8 (32.0)	348.8 (17.4)	275.7 (45.6)	406.3 (8.7)
1993	357.6 (29.9)	356.0 (23.0)	401.6 (17.7)	443.8 (52.5)
1994	326.4 (24.8)	413.4 (22.9)	428.6 (18.4)	436.6 (37.9)
1995	378.2 (45.9)	366.2 (26.8)	365.3 (2.4)	372.2 (42.1
1996	298.4 (9.6)	468.4 (16.1)	433.3 (17.0)	435.0 (37.5)
1997	331.9 (25.1)	318.9 (14.7)	379.9 (19.6)	375.8 (44.7)
Across all years	327.1 (36.7) *a*	366.6 (50.9) *ab*	388.6 (47.6) *b*	406.9 (26.3) *b*
Reproductive litter (g/m^2)				
1989	154.0 (13.0)	110.6 (2.8)	57.3 (15.0)	59.1 (10.9)
1990	28.0 (5.8)	21.2 (2.2)	40.2 (24.3)	28.4 (5.3)
1991	10.1 (3.3)	15.4 (0.9)	15.9 (3.8)	30.0 (20.3)
1992	28.0 (7.8)	38.3 (9.2)	60.9 (4.2)	50.7 (11.9)
1993	34.3 (33.7)	15.7 (1.7)	15.0 (1.3)	20.3 (7.2)
1994	30.4 (9.7)	13.8 (0.7)	22.7 (3.1)	31.1 (4.7)
1995	12.6 (2.0)	12.0 (3.6)	21.6 (1.5)	38.4 (8.9)
1996	68.0 (27.4)	42.0 (2.0)	34.6 (13.3)	27.5 (18.9)
1997	15.2 (7.4)	7.8 (1.8)	16.1 (9.1)	30.5 (15.4)
Across all years	42.3 (45.3)	30.8 (32.2)	31.6 (17.8)	35.0 (12.3)

Table C2 cont.

LAI (m^2/m^2)				
1989	4.7 (0.3)	6.6 (0.5)	6.7 (0.9)	7.5 (0.3)
1990	6.4 (0.2)	5.1 (0.7)	7.4 (0.5)	7.3 (0.4)
1991	7.0 (0.7)	8.5 (0.3)	8.6 (0.1)	8.4 (1.2)
1992	7.5 (1.0)	7.2 (0.5)	4.9 (1.4)	8.6 (0.6)
1993	6.7 (0.8)	6.5 (0.8)	7.3 (0.3)	8.1 (0.9)
1994	6.5 (0.3)	8.9 (0.7)	8.5 (0.5)	9.0 (1.1)
1995	7.0 (1.1)	7.1 (0.8)	7.2 (0.2)	7.0 (0.9)
1996	5.7 (0.6)	9.1 (0.1)	8.6 (0.7)	8.7 (0.4)
1997	6.7 (0.5)	5.5 (0.2)	7.2 (0.5)	7.6 (1.1)
Across all years	6.5 (0.8) *a*	7.2 (1.4) *ab*	7.4 (1.2) *ab*	8.0 (0.7) *b*
SLA ($cm^2\ g^{-1}$)				
1989	179.6 (14.9)	194.5 (2.0)	168.8 (9.7)	186.9 (10.6)
1990	214.1 (9.0)	168.6 (7.6)	179.0 (6.5)	186.7 (1.3)
1991	215.9 (12.1)	220.9 (3.2)	216.2 (6.9)	209.6 (8.1)
1992	204.5 (9.8)	207.4 (3.6)	176.7 (21.5)	211.6 (9.8)
1993	186.2 (6.5)	181.5 (12.3)	182.9 (9.6)	183.2 (1.7)
1994	199.5 (9.9)	214.6 (13.7)	199.0 (8.9)	206.0 (13.5)
1995	185.4 (14.5)	192.4 (11.8)	197.6 (5.6)	187.8 (5.1)
1996	189.4 (12.8)	194.9 (5.4)	198.8 (10.1)	201.2 (9.2)
1997	200.6 (5.9)	171.9 (1.3)	190.4 (7.1)	200.7 (5.2)
Across all years	197.3 (12.9)	194.1 (18.1)	189.9 (14.6)	197.1 (11.0)
% Defoliation				
1989		0	10	
1990		22	0	
1991		0	0	
1992	No defoliation observed at this site.	5	35	No defoliation observed at this site.
1993		0	11	
1994		0	5	
1995		0	0	
1996		0	0	
1997		–	–	

Table C3: Aboveground woody data recorded from 1989-1997 at four northern hardwood sites located along a 500 km latitudinal gradient. Mean net biomass (metric tons/ha), basal area (m^2/ha), and increments with standard deviations in parentheses are included. Also, mean survivor biomass, basal area, and increments are presented with standard deviations in parentheses. Mortality (number of stems/ha) for individual years and sites is included. Across-year means and standard deviations for each variable are supplied for all the sites. Row means with different letters differ ($p < 0.05$).

	Site A	**Site B**	**Site C**	**Site D**
Latitude	46°52'N	45°33'N	44°23'N	43°40'N
Longitude	88°53'W	84°51'W	85°50'W	86°09'W
Net biomass (metric tons ha^{-1})				
1989	289.7 (13.6)	267.8 (23.8)	283.8 (29.6)	245.2 (29.0)
1990	272.6 (12.9)	271.5 (22.7)	290.3 (29.6)	253.8 (30.6)
1991	276.8 (13.6)	274.0 (23.5)	293.6 (28.1)	258.9 (30.1)
1992	282.3 (14.3)	278.4 (24.9)	299.4 (27.6)	268.0 (31.5)
1993	287.3 (12.1)	281.8 (25.1)	304.0 (28.4)	274.3 (31.0)
1994	292.2 (12.8)	284.1 (28.5)	310.0 (27.7)	280.4 (30.6)
1995	296.0 (12.0)	288.3 (29.6)	314.7 (27.2)	285.0 (31.4)
1996	300.9 (11.4)	295.1 (29.7)	317.6 (27.2)	289.6 (31.4)
1997	307.1 (10.4)	295.7 (25.0)	319.0 (25.0)	291.4 (29.0)
Across all years	287.1 (13.1) *a*	281.8 (9.9) *a*	303.6 (12.7) *b*	271.9 (16.5) *a*
Net basal area (m^2 ha^{-1})				
1989	32.2 (0.4)	29.9 (1.3)	30.4 (2.7)	30.2 (2.0)
1990	32.4 (0.5)	30.2 (1.1)	30.9 (2.7)	30.9 (2.2)
1991	32.7 (0.6)	30.3 (1.2)	31.0 (2.5)	31.7 (2.0)
1992	33.1 (0.6)	30.6 (1.4)	31.5 (2.5)	32.0 (2.2)
1993	33.5 (0.4)	30.7 (1.4)	31.8 (2.5)	32.4 (2.1)
1994	33.7 (0.5)	30.7 (1.9)	32.2 (2.5)	32.9 (2.0)
1995	33.9 (0.4)	31.0 (1.9)	32.5 (2.4)	33.2 (2.1)
1996	34.2 (0.4)	31.5 (1.9)	32.5 (2.4)	33.5 (2.1)
1997	34.7 (0.4)	31.3 (1.3)	32.4 (2.3)	33.4 (1.8)
Across all years	33.4 (0.8) *c*	30.7 (0.5) *a*	31.7 (0.8) *b*	32.2 (1.2) *b*
Net biomass increment (metric tons ha^{-1})				
1989	4.4 (0.8)	3.5 (0.8)	2.6 (0.9)	3.6 (1.3)
1990	3.7 (1.2)	3.7 (1.3)	6.5 (0.7)	8.6 (2.4)
1991	4.2 (0.9)	2.4 (0.7)	3.0 (2.4)	5.0 (3.3)
1992	5.5 (0.7)	4.4 (1.9)	5.8 (0.6)	9.2 (3.6)
1993	5.0 (2.4)	3.4 (1.5)	4.6 (0.9)	6.2 (1.0)
1994	5.0 (0.8)	2.3 (3.8)	6.0 (1.1)	6.2 (1.8)
1995	3.8 (1.4)	4.2 (1.3)	4.7 (1.0)	4.6 (1.6)
1996	4.9 (0.7)	6.8 (0.3)	2.9 (0.8)	4.6 (1.0)
1997	6.2 (1.1)	0.7 (5.1)	1.4 (5.9)	1.8 (4.9)
Across all years	4.7 (0.8)	3.5 (1.7)	4.2 (1.7)	5.5 (2.3)

Table C3 cont.

Net basal area increment (m^2 ha^{-1})				
1989	0.33 (0.08)	0.28 (0.04)	0.13 (0.08)	0.15 (0.11)
1990	0.18 (0.19)	0.30 (0.15)	0.52 (0.05)	0.73 (0.20)
1991	0.28 (0.10)	0.08 (0.10)	0.14 (0.30)	0.24 (0.41)
1992	0.45 (0.08)	0.33 (0.19)	0.41 (0.05)	0.82 (0.39)
1993	0.35 (0.28)	0.11 (0.26)	0.33 (0.13)	0.40 (0.12)
1994	0.26 (0.17)	-0.01 (0.58)	0.46 (0.06)	0.55 (0.17)
1995	0.17 (0.15)	0.29 (0.05)	0.24 (0.19)	0.28 (0.17)
1996	0.33 (0.04)	0.50 (0.03)	0.06 (0.05)	0.29 (0.09)
1997	0.44 (0.07)	-0.21 (0.59)	-0.16 (0.54)	-0.16 (0.64)
Across all years	0.31 (0.10)	0.19 (0.22)	0.24 (0.22)	0.37 (0.30)
Survivor biomass (metric tons ha^{-1})				
1989	269.1 (13.5)	267.8 (23.8)	283.8 (29.6)	245.2 (29.0)
1990	273.7 (13.3)	272.0 (23.4)	290.8 (30.1)	254.0 (30.7)
1991	276.8 (13.7)	275.6 (22.9)	295.3 (29.4)	260.0 (31.2)
1992	282.3 (14.2)	279.3 (23.6)	299.9 (27.5)	268.3 (31.8)
1993	288.7 (14.1)	284.5 (25.3)	304.7 (28.1)	275.6 (31.5)
1994	292.4 (12.8)	286.2 (25.2)	310.0 (27.7)	280.7 (30.6)
1995	296.8 (12.3)	289.4 (29.1)	315.8 (27.7)	286.6 (30.6)
1996	301.0 (11.4)	295.9 (29.6)	319.5 (27.9)	290.5 (31.6)
1997	308.0 (10.7)	300.3 (29.2)	324.4 (26.1)	295.9 (31.7)
Across all years	287.6 (13.2) *b*	283.4 (10.8) *b*	304.9 (13.7) *b*	273.0 (17.3) *a*
Survivor basal area (m^2 ha^{-1})				
1989	32.3 (0.4)	29.9 (1.3)	30.4 (2.7)	30.2 (2.1)
1990	32.6 (0.4)	30.3 (1.2)	31.0 (2.7)	30.9 (2.2)
1991	32.7 (0.6)	30.5 (1.1)	31.3 (2.7)	31.4 (2.2)
1992	33.1 (0.6)	30.8 (1.2)	31.6 (2.4)	32.0 (2.2)
1993	33.7 (0.6)	31.1 (1.4)	31.8 (2.5)	32.7 (2.2)
1994	33.8 (0.5)	31.1 (1.3)	32.2 (2.5)	32.9 (2.0)
1995	34.0 (0.5)	31.1 (1.9)	32.7 (2.5)	33.5 (2.0)
1996	34.2 (0.3)	31.7 (1.9)	32.8 (2.5)	33.6 (2.2)
1997	34.8 (0.4)	31.9 (1.8)	33.1 (2.3)	34.0 (2.2)
Across all years	33.5 (0.9) *a*	30.9 (0.6) *b*	31.9 (0.9) *b*	32.4 (1.3) *b*

Table C3 cont.

Survivor biomass increment (metric tons ha^{-1})				
1989	5.5 (0.6)	6.4 (1.4)	4.8 (0.4)	5.2 (1.4)
1990	6.3 (2.4)	7.0 (2.0)	9.7 (2.2)	10.4 (3.4)
1991	6.1 (2.5)	6.5 (2.3)	9.3 (5.1)	7.5 (2.2)
1992	8.2 (4.6)	6.2 (1.1)	10.1 (5.0)	9.8 (4.6)
1993	6.4 (0.3)	6.1 (0.5)	10.2 (5.0)	7.6 (1.3)
1994	5.1 (0.8)	4.5 (0.1)	6.0 (1.1)	6.4 (2.0)
1995	4.6 (0.6)	5.3 (0.9)	5.8 (0.5)	6.2 (1.2)
1996	5.0 (0.7)	7.6 (0.6)	4.8 (1.1)	5.4 (0.2)
1997	7.0 (0.8)	5.0 (0.5)	6.8 (1.2)	6.3 (1.3)
Across all years	6.0 (1.1)	6.1 (1.0)	7.5 (2.3)	7.2 (1.8)
Survivor basal area increment (m^2 ha^{-1})				
1989	0.36 (0.11)	0.28 (0.04)	0.13 (0.08)	0.14 (0.11)
1990	0.39 (0.08)	0.37 (0.06)	0.60 (0.10)	0.77 (0.22)
1991	0.29 (0.13)	0.33 (0.09)	0.38 (0.07)	0.43 (0.16)
1992	0.45 (0.08)	0.45 (0.02)	0.51 (0.09)	0.88 (0.48)
1993	0.53 (0.05)	0.52 (0.00)	0.39 (0.07)	0.70 (0.10)
1994	0.35 (0.14)	0.34 (0.04)	0.46 (0.06)	0.56 (0.17)
1995	0.30 (0.03)	0.41 (0.06)	0.43 (0.04)	0.52 (0.08)
1996	0.34 (0.04)	0.66 (0.03)	0.34 (0.08)	0.43 (0.06)
1997	0.59 (0.04)	0.40 (0.08)	0.52 (0.12)	0.52 (0.08)
Across all years	0.40 (0.10)	0.42 (0.12)	0.42 (0.13)	0.55 (0.22)
Mortality (basal area; m^2 ha^{-1})				
1989	0.04 (0.04)	0	0	0
1990	0.21 (0.22)	0.06 (0.11)	0.07 (0.12)	0.03 (0.03)
1991	0.01 (0.02)	0.25 (0.11)	0.23 (0.26)	0.18 (0.28)
1992	0	0.12 (0.17)	0.07 (0.06)	0.06 (0.10)
1993	0.18 (0.31)	0.41 (0.26)	0.06 (0.06)	0.27 (0.21)
1994	0.10 (0.03)	0.35 (0.61)	0	0.01 (0.01)
1995	0.13 (0.12)	0.12 (0.02)	0.19 (0.14)	0.24 (0.13)
1996	0.02 (0.02)	0.15 (0.05)	0.28 (0.11)	0.13 (0.15)
1997	0.14 (0.04)	0.61 (0.51)	0.68 (0.57)	0.68 (0.60)
Across all years	0.09 (0.08)	0.23 (0.19)	0.18 (0.21)	0.18 (0.21)