

FOREST EDGES AND TREE GROWTH RATES IN THE NORTH CAROLINA PIEDMONT

ROBERT I. McDONALD¹ AND DEAN L. URBAN

Nicholas School of the Environment, Duke University, Durham, North Carolina 27708 USA

Abstract. Forest fragmentation is a common process in forests worldwide, with implications for tree species composition and abundance. In particular, the effects of forest–non-forest edges on microclimate are often profound, usually resulting in increased light available to plants along the forest–non-forest edge. Using dendrochronological techniques, we assessed the effect of edges on the growth rates of four overstory species common in the North Carolina Piedmont: *Acer rubrum*, *Liriodendron tulipifera*, *Liquidambar styraciflua*, and *Pinus taeda*. Transects from the edge into the forest interior were established on 62 edges of varying aspect and ages in the Duke Forest (Durham, North Carolina, USA). Within a transect, all stems >10 cm in diameter were cored, and their spatial positions relative to the edge were recorded. Along each transect, a set of environmental and edaphic variables was measured including soil texture, soil concentrations of plant nutrients, and percentage of canopy closure. All transects were geo-referenced, and land cover data classified from a time-series of Thematic Mapper images were used to assess the age of each edge. Two species, *P. taeda* and *L. tulipifera*, had significant increases in growth rates within 5 m of an edge relative to the forest interior. However, edges explain a substantially smaller portion of the variance in growth rate than soil texture, soil nutrients, and topographically derived variables. Possible interactions between soil texture and effects of edges on tree growth rate for *P. taeda* were found, although the interaction was opposite from our hypothesis that increased water availability would increase the positive effect of edges on growth rates. Although the edge effect on tree growth rate is small, as forest fragmentation becomes more prevalent worldwide, even small responses to edge effects by individual trees could have profound effects on regional patterns in carbon fixation and species composition over time.

Key words: *Acer rubrum*; dendrochronology; edge effects; fragmentation; growth rates; land cover; land use; *Liquidambar styraciflua*; *Liriodendron tulipifera*; North Carolina; *Pinus taeda*.

INTRODUCTION

Forest fragmentation, in which a continuous forested matrix is subdivided successively into discrete patches, is a widespread phenomenon occurring worldwide (Harrison and Bruna 1999). Effects of fragmentation on plant community dynamics can be quite profound in some cases (e.g., Saunders et al. 1991, Bowers and Dooley 1999), and so there is a clear need to further understand the ecological effects of this phenomenon. Edge effects, in which conditions near the forest–non-forest edge differ from the forest interior, have the potential to be important because a high proportion of forest habitat is near an edge. For example, in the conterminous United States, 44% of trees are estimated to be <90 m from an edge (Riitters et al. 2002). While some research has been performed on abiotic effects of forest edges (e.g., Chen et al. 1999), little work has been done on the effects of forest edges on vital demographic processes of trees, such as tree growth rates (cf. B. S. Pedersen and J. L. Howard, *unpublished man-*

uscript). An understanding of such vital demographic rates is crucial for predicting the response over time of forest communities to edges. This paper presents dendrochronological data that quantifies effects of edges on growth rates for four common tree species in the North Carolina Piedmont.

A growing body of literature has begun to explore the effects of forest fragmentation. These effects are generally divided conceptually into three categories (Sharpe et al. 1981, Saunders et al. 1991, Caley et al. 2001): the reduction in total forest area, the increase in distance between forest patches, and the alteration of physical characteristics of remnant patches due to changes in abiotic and biotic processes. This alteration of characteristics is usually more severe near edges than in the interior (Chen et al. 1999), and is often referred to as an “edge effect.” We chose to focus on only the edge effect component of forest fragmentation in this study, as it seemed likely to have the greatest effect on tree growth rates.

Numerous abiotic changes occur near edges. Solar radiation increases near an edge as the reduction in canopy closure allows more light into the forest compared to the interior (Mourelle et al. 2001, Dignan and Bren 2003). The horizontal distance from an edge at

Manuscript received 12 May 2003; revised 4 December 2003; accepted 17 December 2003. Corresponding Editor: D. P. C. Peters.

¹ E-mail: robert.mcdonald@duke.edu

which solar radiation remains elevated depends on its latitude and aspect (Ranney et al. 1981). Daytime temperature usually increases near an edge compared to the interior due to increased solar radiation (Chen et al. 1999), but nighttime temperatures can be lower near an edge because the reduced forest canopy cover absorbs less outgoing thermal radiation (Running et al. 1987, Chen et al. 1993, Bonan 2002, Klaassen et al. 2002, Redding et al. 2003). As both daytime temperature and solar radiation are increased near edges, potential evapotranspiration also significantly increases (Chen et al. 1999, Cienciala et al. 2002). This suggests that soil moisture levels should also vary at edges, modified by factors affecting soil water-holding capacity (e.g., soil texture).

Changes in the biotic system near edges can also be varied and significant. Established trees tend to increase in diameter and leaf area after a forest edge is created, sealing off the interior of the forest from elevated light levels after a number of years have passed since the creation of an edge (Laurence et al. 2001). In general, shade-intolerant species with a fast maximum photosynthetic rate seem more capable of taking advantage of increased light levels near edges (Chen et al. 1999). The effect of this asymmetry leads to the hypothesis that, all else being equal, distance to an edge is an analogue for successional time: Near a forest edge, early-successional species will dominate, while in the forest interior later successional species will dominate (Ranney et al. 1981).

The potential response of forest communities to edge effects, and forest fragmentation generally, is not well understood because it involves the complex integration of many of the abiotic and biotic factors discussed. As one step toward understanding dynamic changes that occur around edges over time, this paper examines growth rates of canopy trees near edges in the North Carolina Piedmont. The specific objectives of this study were to: (1) estimate edge effects on growth rates for several dominant species of varying levels of shade tolerance, and (2) determine how environmental conditions affect the magnitude of the edge effect on growth rate. We measured average annual ring increment as a proxy for growth rate for a large number of trees on 62 edges. In closed-canopy forests, average growth increment is negatively related to stand density and stand basal area (e.g., Peet and Christensen 1980). After controlling for these two trends, we hypothesized that shade-intolerant species would have a larger response to increased light availability near edges than shade-tolerant species (Ranney et al. 1981). Finally, we also hypothesized that sites with more soil moisture, either because of edaphic or topographic conditions, would have a larger response to the increased light available near edges than sites with less soil moisture.

METHODS

Study area

The forest edges studied are located in the Duke Forest, North Carolina, USA (36.0° N, 79.0° W, 100–

170 m elevation), which has been extensively examined for over 70 years (Billings 1938, Oosting 1942, Keever 1950, Peet and Christensen 1980, McDonald et al. 2002). Average temperatures range from a mean daily maximum of 31.5°C in July to a mean daily minimum of –1.2°C in January, with a mean annual precipitation of 1052 mm (North Carolina Climate Office 2003). Soils vary from sandy Triassic Basin sediments to plastic soils containing montmorillonite formed from diabase intrusions (Bain 1966), and topography is typically gentle, with rolling hills. *Pinus taeda* is a shade-intolerant, early-successional species that is dominant in abandoned agricultural fields (Bormann 1953). Sites that were not clear-cut are dominated by a wide variety of hardwood species depending on edaphic conditions and site history (Christensen and Peet 1984, McDonald et al. 2002). We focused on three species common in the North Carolina Piedmont: *Acer rubrum*, a slow-growing, shade-tolerant tree that has dramatically increased in abundance in recent years; *Liriodendron tulipifera*, a fast-growing, moderately shade-intolerant tree that prefers mesic soils; and *Liquidambar styraciflua*, a moderately fast-growing, shade-intolerant tree that often establishes in recently disturbed areas (Burns and Honkala 1990).

Data collection

In the summers of 2001 and 2002, 62 edges of varying edge orientation (the direction in which an edge faces), edge age, and forest composition (pine vs. hardwood dominance) were selected using aerial photos and satellite imagery. Selected edges had not had recent logging (within 10 years) or other management activity within the remaining forest, and bordered forest stands that ranged in age from 20 years (i.e., young pine stands) to >200 years (i.e., relict hardwood stands). Each edge was defined as the farthest horizontal extension of canopy trees over the non-forest area (i.e., the canopy dripline). We selected a random point along each edge and placed one 30-m transect perpendicular to the edge into the forest interior. All trees >1 cm diameter at breast height (dbh) and within 5 m of the transect were tallied by species, and their distance to the edge was recorded. Cores were taken on all trees larger than 10 cm dbh. Trends in species composition relative to distance to edge are discussed in a companion paper (R. I. McDonald and D. L. Urban, *unpublished manuscript*).

Canopy closure was measured using a hemispherical densiometer at each edge and every 5 m along each transect. At each measurement point, four readings were taken in the four cardinal directions, and the average canopy closure was calculated. In each transect, we measured edge orientation using a compass. As prior research has shown that forest composition and productivity respond to soil texture and chemistry (Coile 1933, Billings 1938, Applequist 1941), we wished to include information on soils as likely correlates with

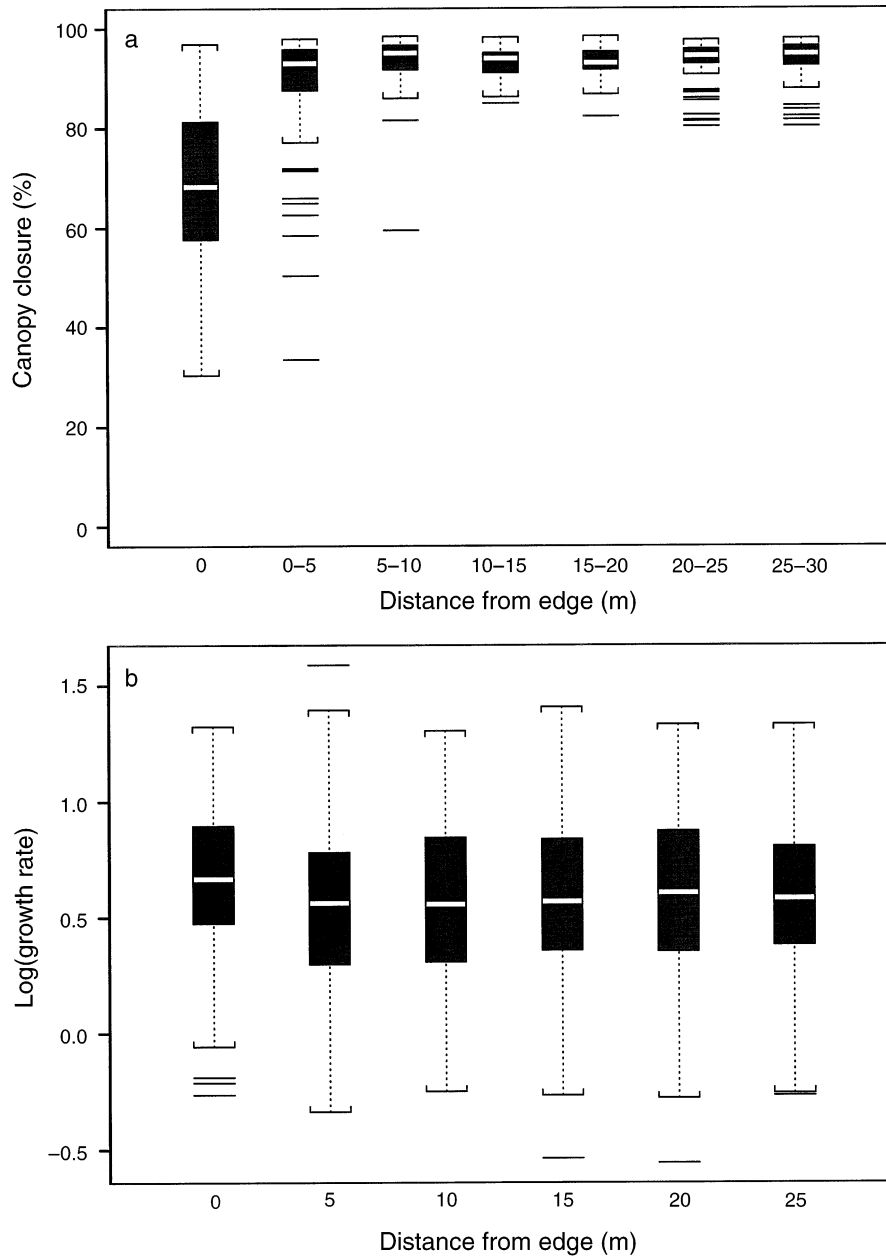


FIG. 1. (a) Percentage of canopy closure as a function of distance from edge at seven different distances from the edge. Within a box plot, the white line is the median value of canopy closure within that distance class. The middle 50% of values are within the shaded box, and the middle 95% of values are within the error bars. Individual lines represent outliers. (b) The log of the average tree growth increment (originally measured in mm) as a function of distance to edge (m). The white line in the box plots is the median value of log(growth rate) within that distance class. The middle 50% of values are within the shaded box, and the middle 95% of values are within the error bars. Individual lines represent outliers. Note the small difference between the mean growth rate in the first distance class and the second.

tree growth rate. Accordingly, we took a composite soil sample for each transect by combining the soil collected at five randomly located points along each transect. Soil samples were analyzed for plant nutrients using a Mehlich III extractant, and summarized here as extractable N, soluble S, available P, B, Fe, Mn, Cu, Zn (each measured as ppm), and base saturation (per-

centage). Soil texture was measured using standard flotation techniques, and is expressed as clay and silt fractions (percentage). Using digital elevation models from the Shuttle Radar Topography Mission database (USGS, *public communication*), a topographic convergence index (TCI, Beven and Kirkby 1979, Wolock and McCabe 1995) was calculated for each site as a

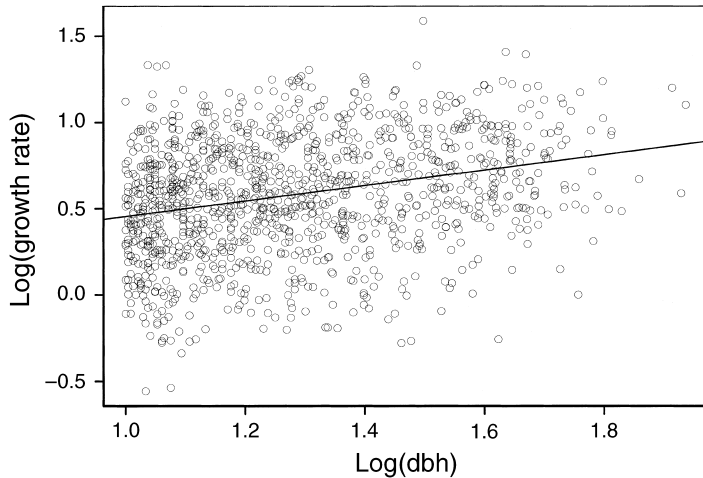


FIG. 2. The relationship between the log of the average tree growth increment (originally measured in mm) and the dbh (originally measured in cm) of the tree. The line is an OLS regression line to display the general trend ($R^2 = 0.08$, $P < 0.001$).

proxy for soil moisture. Moore et al. (1990) review the use of terrain-based proxies in hydrological and ecological applications. TCI ranges in value from -0.2 (extremely dry, steep ridges) to 20 (flat flood plains) for our study area. Slope aspect was transformed (Beers et al. 1966) to reflect differences in solar radiation and evapotranspiration on different slope facets. This transformation aligns the index in a NE–SW axis, reflecting maximum radiation loading on SW-facing slopes (Lookingbill and Urban 2003). Edge orientation was similarly transformed.

Anthropogenic disturbance along an edge can have significant effects on forest composition and structure (Ranney et al. 1981). Accordingly, the type of management at the edge was summarized by describing the edge state as: (1) “expanding,” if there was evidence apparent to an observer that the forest was expanding into the non-forested area (e.g., a lot of young stems recently established near the edge); (2) “stationary,” if the edge appeared to be spatially stationary over time; or (3) “contracting” if there was evidence apparent to an observer that the non-forested area was

expanding into the forested area over time (cf. Ranney et al. 1981). Stand age was determined from Duke Forest management records and from the cores of dominant canopy trees. The age of each edge was determined (within 5–10 years) using Duke Forest management records, aerial photographs, and satellite images. Finally, total basal area (square meters per hectare) of all tree species was calculated for each site, as a measure of competition to be accounted for before examining edge effects on growth rates.

Tree ring widths were recorded (within 0.001 mm), and average growth rate from 1996 to 2000 was calculated. A 5-year interval was chosen, as it was long enough to give meaningful averages yet short enough for the explanatory variables to be relatively constant. In a few cases with an unreadable year in this interval due to a break in the core, the average of the remaining four years of growth was used instead.

Statistical analysis

We log-transformed the average growth rate, which improved the normality of the data as well as the lin-

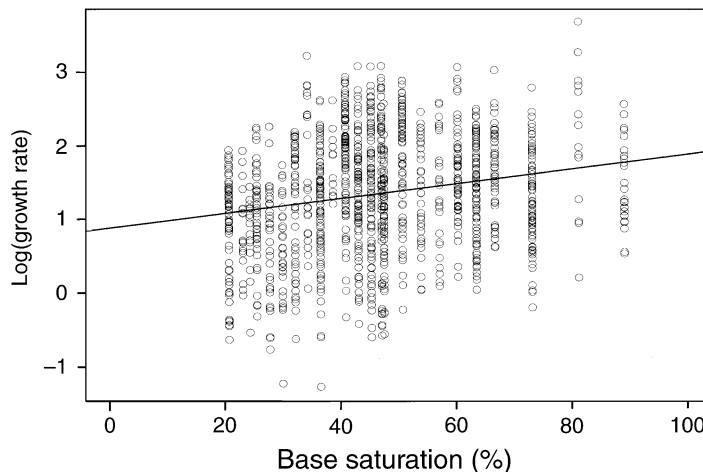


FIG. 3. The relationship between the log of the average tree growth increment (originally measured in mm) and the percentage of base saturation of the soil. The line is an OLS regression line to display the general trend ($R^2 = 0.04$, $P < 0.001$).

TABLE 1. ANOVA results from the dummy-variable ANOVA.

Species and variable	df	SS	MS	F	P
<i>Pinus taeda</i> ($R^2 = 0.71$)					
Log(dbh)	1	19.3830	19.3830	95.45	<0.001
Edge	1	3.4444	3.4444	16.96	<0.001
Transect	52	176.1823	3.38812	16.68	<0.001
Residual	423	85.8952	0.20306		
<i>Liriodendron tulipifera</i> ($R^2 = 0.59$)					
Log(dbh)	1	2.82209	2.822094	5.993738	0.018
Edge	1	2.9145	2.914537	6.190073	0.016
Transect	31	31.81992	1.026449	2.180036	0.007
Residual	51	24.01286	0.470840		
<i>Liquidambar styraciflua</i> ($R^2 = 0.60$)					
Log(dbh)	1	2.64546	2.645461	10.51106	0.002
Edge	1	0.04044	0.040443	0.16069	0.689
Transect	40	43.13691	1.078423	4.28484	<0.001
Residual	121	30.45370	0.251683		
<i>Acer rubrum</i> ($R^2 = 0.58$)					
Log(dbh)	1	0.27833	0.278330	0.820640	0.368
Edge	1	0.11585	0.115848	0.341570	0.561
Transect	33	36.42089	1.103663	3.254084	<0.001
Residual	79	27.13300	0.339163		

earity of the relationship between this variable and several explanatory variables. Box-plots of effects of distance-to-edge on growth rate suggested that the growth effect occurred within 5 m of the edge, and thus the data were reclassified into two categorical groups: within 5 m of an edge, and beyond 5 m from an edge. A log-transformation of dbh and stand age was used to make the relationship between these two variables and log(growth rate) linear.

For each species, two ANOVAs were performed (Sokal and Rohlf 1981). The first had log(growth rate) as the response variable, distance-to-edge and a dummy transect variable as fixed effects, and dbh and transect-level basal area as covariates. This set of "dummy-variable" ANOVAs was designed to clearly show the effect of distance-to-edge on growth rate. The second set of "environmental" ANOVAs replaced the transect dummy-variable with the other soil and site variables in an attempt to explain some of the transect-level variation in a more ecologically meaningful way. An interaction term between the distance-to-edge effect and TCI was included to test the hypothesis that the increase in growth rate near edges is less on dry sites than on wet sites. Since there were many potential explanatory variables, backward stepwise regression was used to eliminate unnecessary variables from the model. The assumption of normality of residuals was checked by graphically comparing the expected distribution of residuals with the actual. Residuals from all ANOVAs were examined for evidence of heteroscedasticity and spatial autocorrelation, and to confirm that the assumptions of ANOVA were met.

RESULTS

Average percentage of canopy closure was monotonically related to distance from the edge (Fig. 1a).

When canopy closure was measured at the edge, closure averaged 70%. Between 0–5 m from an edge, average canopy closure was slightly (5%) lower than the average in the forest interior. The graph of average growth increment as a function of distance to edge is similar (Fig. 1b). Within 5 m of the edge, mean growth rate averaged over all species appears elevated, but is relatively constant thereafter.

The relationship of dbh to growth rate appears linear in log–log space (Fig. 2), although there is considerable scatter, which implies a power-law relationship of the form $\text{growth} = e^{\alpha} \text{dbh}^{\beta}$, where α and β are the intercept and slope from a log-linear model. The ordinary least-squares (OLS) linear regression line implies that, averaging across all species and locations, for every 10% increase in dbh, the mean growth rate increases by 2.7%. We did not observe a decrease with increasing dbh as would be expected due to geometric constraints on growth in larger trees, possibly because most trees sampled were small relative to their maximum size. Soil macro- and micronutrients were generally positively correlated with average growth rate; one highly significant relationship was between percentage of base saturation and log(growth rate) (Fig. 3). The OLS line implies that, on average, with a 10% increase in percentage of base saturation, there is a 1.2 mm increase in average growth increment, although there is considerable scatter around the trend line.

Dummy-variable ANOVA

Distance-to-edge was significant for two of the four species tested, *P. taeda* and *L. tulipifera* (Table 1), and in both cases, individuals on the edge grew significantly faster than in the forest interior (Fig. 4). Individuals of larger dbh had more of an edge response in absolute

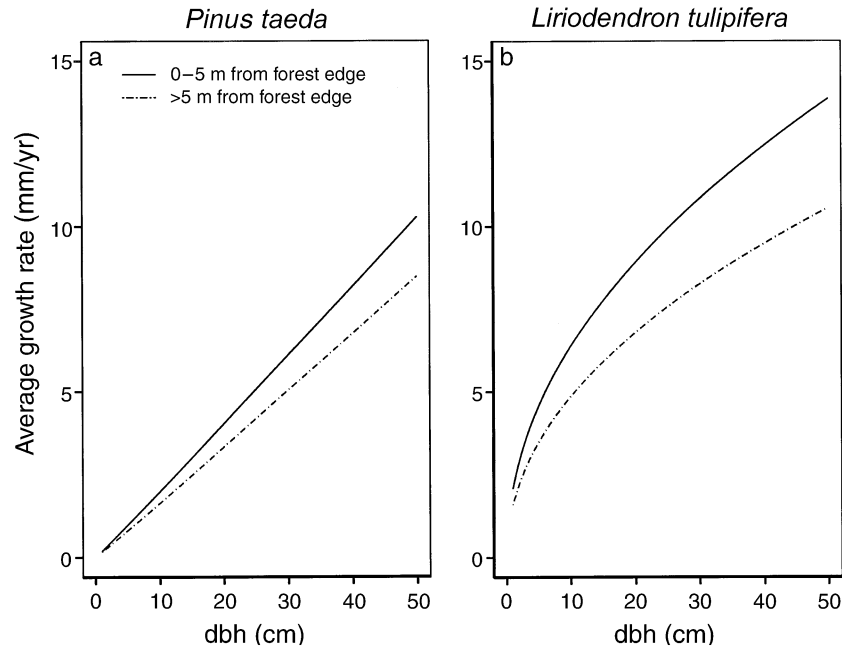


FIG. 4. Predicted growth rates (mm) near an edge and in the forest interior for two species: (a) *P. taeda* and (b) *L. tulipifera*.

terms, and *L. tulipifera* had a greater response than *P. taeda*. *L. tulipifera* has a faster average growth rate than *P. taeda*, but an examination of the data indicates it occurs on fewer, generally more mesic sites. There was a significant dbh term for all species except *A. rubrum*, although the small sample size may limit the power to detect such a relationship. In all three species with a significant coefficient for $\log(\text{dbh})$, the coefficient was >1 , implying that average growth rate increases slower than linearly with increase in dbh.

Environmental ANOVA

When soils and other site variables were included to ecologically account for the transect effect above, the major results did not change (Table 2). Distance to edge was significant only for *P. taeda* and *L. tulipifera*, and dbh was significant for every species except *A. rubrum*. Most soil ions, except Fe and S, were positively related to growth rates. For example, percentage of base saturation was positively related to average growth rate for *P. taeda* and *L. tulipifera*, although it was negatively related to *A. rubrum* growth rates. Soil texture variables were also important for three species, with *P. taeda* and *L. tulipifera* growing faster on sites with a greater percentage of silt, and *A. rubrum* growing faster on sites with a greater percentage of clay. Edge type was significant for every species except *L. styraciflua*, and in all cases, the trees in “contracting” edges grew faster than trees in “stationary” or “expanding” edges.

Several of the geospatial variables were significant as well. In particular, for all species except *L. tulipifera*, there was a significant positive relationship between

TCI and growth rates (i.e., wetter sites have faster growth rates). The interaction term between TCI and distance to edge was significant only for *P. taeda*, although the term is of the opposite sign of what we hypothesized: On wet edges, there was less of an increase in growth rates than on dry edges. Finally, for all species except *L. styraciflua*, older stands had lower growth rates. Overall, the environmental variables explained 67% of the variance accounted for by the transect factor in the dummy-variable ANOVA, suggesting some residual effect at the transect scale that is unaccounted for by the measured variables.

DISCUSSION

Enhancement of growth rates near forest edges was found for two of four species examined. However, the edge effect explains less of the variation in growth rates than topographic and edaphic factors. The magnitude of edge effects for any given species may be viewed as its realized response in growth rates after its maximum potential response has been reduced by other resource limitations. Other studies in different regions with a larger proportional increase in solar radiation near edges, such as sites at higher latitudes (Ranney et al. 1981), are expected to have a larger potential response in growth rates near edges. Similarly, regions with less severe edaphic conditions than the North Carolina Piedmont may have the maximum potential edge effect on growth rate reduced less by other resource limitations, and the edge effect may explain a larger portion of the variance in growth rates than in our study area.

TABLE 2. ANOVA results from the environmental ANOVA.

Species and variable	df	SS	MS	F	P(F)
<i>Pinus taeda</i> ($R^2 = 0.54$)					
Log(dbh)	1	12.465	12.465	43.945	0.000
Distance-to-edge	1	3.141	3.141	11.073	0.001
S	1	10.691	10.691	37.693	0.000
B	1	34.463	34.463	121.503	0.000
Cu	1	0.794	0.794	2.800	0.095
Base saturation (%)	1	0.247	0.247	0.872	0.351
Silt	1	11.956	11.956	42.152	0.000
Edge type	2	2.337	1.169	4.120	0.017
Log(stand age)	1	66.752	66.752	235.338	0.000
Transformed slope aspect	1	5.961	5.961	21.016	0.000
Topographic convergence index (TCI)	1	2.675	2.675	9.429	0.002
TCI: edge interaction	1	1.814	1.814	6.394	0.012
Residuals	464	131.609	0.284		
<i>Liriodendron tulipifera</i> ($R^2 = 0.40$)					
Log(dbh)	1	2.285	2.285	4.505	0.037
Distance-to-edge	1	2.729	2.729	5.379	0.023
N	1	0.010	0.010	0.019	0.890
Cu	1	5.531	5.531	10.902	0.001
Zn	1	1.248	1.248	2.461	0.121
Base saturation (%)	1	2.377	2.377	4.685	0.034
Silt	1	4.753	4.753	9.369	0.003
Edge type	2	2.893	1.446	2.851	0.064
Log(stand age)	1	0.988	0.988	1.947	0.167
Slope	1	1.721	1.721	3.393	0.070
Residuals	73	37.035	0.507		
<i>Liquidambar styraciflua</i> ($R^2 = 0.3$)					
Log(dbh)	1	2.412	2.412	7.069	0.009
B	1	2.095	2.095	6.139	0.014
Cu	1	1.077	1.077	3.157	0.078
Edge age	1	2.886	2.886	8.456	0.004
Slope	1	0.242	0.242	0.708	0.401
Transformed slope aspect	1	7.388	7.388	21.651	0.000
TCI	1	6.943	6.943	20.345	0.000
Residuals	156	53.234	0.341		
<i>Acer rubrum</i> ($R^2 = 0.45$)					
Log(dbh)	1	0.278	0.278	0.807	0.371
N	1	4.125	4.125	11.955	0.001
Fe	1	0.528	0.528	1.530	0.219
Cu	1	1.180	1.180	3.419	0.067
Base saturation (%)	1	3.468	3.468	10.051	0.002
Clay	1	3.720	3.720	10.782	0.001
Edge type	2	1.900	0.950	2.753	0.068
Log(stand age)	1	3.442	3.442	9.975	0.002
Slope	1	4.664	4.664	13.517	0.000
Transformed slope aspect	1	0.163	0.163	0.473	0.493
TCI	1	1.707	1.707	4.947	0.028
Transformed edge aspect	1	3.581	3.581	10.379	0.002
Residuals	102	35.193	0.345		

Our results provide some support for our hypothesis that early-successional species with high maximum photosynthetic rates would take advantage of increased light levels near edges (Ranney et al. 1981). The two most shade-intolerant species showed an increase in growth rates near edges, while two species that are more shade-tolerant showed no edge effect. *P. taeda* is often the pioneer species in old fields in the North Carolina Piedmont (e.g., Oosting 1942) and displays both a high maximum photosynthetic rate as well as greater drought tolerance than most other species in the region (Burns and Honkala 1990); either of these traits could prove advantageous along edges. *L. tulipifera* is

also a relatively fast-growing, shade-intolerant species that is less drought tolerant than *P. taeda* (Burns and Honkala 1990). It is possible that, since *L. tulipifera* is limited in occurrence to mesic sites, the increased evapotranspiration near edges (Bonan 2002) is not limiting. In contrast, *L. styraciflua* did not show an increase in growth rate near edges, which is surprising since it is a relatively fast-growing, shade-intolerant species (Burns and Honkala 1990). One possibility is that on the xeric sites where *L. styraciflua* occurs, it is very sensitive to increased evapotranspiration near edges, just as it is sensitive to drought stress in old fields (Bormann 1953). Finally, *A. rubrum* shows no

increase in growth rates near edges, likely as a result of its shade tolerance, although this finding is interesting in comparison with the general trend of increase in red maple populations in forests of the Eastern United States (Lorimer 1984, Abrams 1998, McDonald et al. 2002, 2003). The fact that our data show that tree growth rates are faster near edges for some species supports the assertion that light is a limiting resource even for some canopy and sub-canopy trees, although other factors that differ near an edge could also be important.

We hypothesized that there would be a positive interaction between soil moisture and tree growth rates near edges, with wetter edges more conducive to increased growth rates. Our results do not support this hypothesis; most species lack any significant interaction term between TCI and edge effect. Only *P. taeda* had an interaction term, and the interaction is opposite from what we hypothesized. This result could be a statistical artifact as the interaction term has a small effect size. Alternatively, at high TCI, *P. taeda* may already be growing near its optimum rate, and so an increase in light may not result in an increase in growth rates as much as on a drier site. Overall, given the lack of interactions in Table 2, light and water appear to act independently as resources. However, factors related to water availability explain a greater proportion of the total R^2 in growth rates than the distance-to-edge effect, suggesting that many of the trees sampled are more limited by water availability than light availability.

The interpretation of our results is limited by the scale mismatch between our measured environmental variables (plot level) and our measured response variable (tree level). This discordance in scales is common in many forest ecology studies because of the financial and logistical difficulties in measuring at each tree a large suite of potentially relevant variables. In addition, it is often difficult to know the appropriate spatial scale for a measurement. One of the main effects of the scale mismatch between our environmental variables and our response variable is that any variation in the environment at scales smaller than the plot level is missing from our analysis. This missing variability reduces our overall explanatory power, potentially explaining why many of the effects we found, while highly statistically significant, accounted for only a small proportion of the total variance in growth rates. Future studies of edge effects should aim to measure environmental conditions at spatial scales relevant to trees, whenever possible.

Nevertheless, we find that knowledge of growth rates near edges is important for understanding the dynamics of these forest communities. For a 30-cm *P. taeda* tree over one year, a tree near an edge would grow 0.18 cm more than a tree in the forest interior, while for a 30-cm *L. tulipifera* tree, the difference is 0.32 cm. The trend becomes more pronounced over time. For example, over 20 years, the same *P. taeda* tree would

grow 5.2 cm more than a tree in the forest interior, while the difference for *L. tulipifera* is 8.0 cm. Overall, the increase in growth rates at edges is of the same order of magnitude as increases in growth rates due to CO₂ fertilization (e.g., Oren et al. 2001). Classified Thematic Mapper imagery of this region (R. I. McDonald, unpublished data) shows that slightly >50% of forested pixels are within 30 m of an edge, the minimum resolution of the images. This implies a non-trivial portion of the landscape may have (on average) elevated growth rates due to edge effects. Clearly, edge effects can have significant effects on growth rates for some species and thus forest community dynamics.

ACKNOWLEDGMENTS

We wish to thank Patrick Halpin and Robert Peet for helpful discussions about this project. Two anonymous reviewers as well as Debra Peters made comments that substantially improved the manuscript. The work was funded by NSF grants DEB-9707664 and SBR-9817755.

LITERATURE CITED

- Abrams, M. D. 1998. The red maple paradox. *Bioscience* **48**: 355–364.
- Applequist, M. B. 1941. Stand composition of upland hardwood forests as related to soil type in the Duke Forest. Duke University, Durham, North Carolina, USA.
- Bain, G. L. 1966. Geology and ground-water in the Durham area, North Carolina. United State Geological Survey, Raleigh, North Carolina, USA.
- Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. *Journal of Forestry* **64**:691–692.
- Beven, K. J., and M. J. Kirkby. 1979. A physically based, variable contributing area model of basin hydrology. *Hydrologic Science Bulletin* **24**:43–69.
- Billings, W. D. 1938. The structure and development of old field shortleaf pine stands and certain associated physical properties of the soil. *Ecological Monographs* **8**:436–499.
- Bonan, G. 2002. *Ecological climatology: concepts and applications*. Cambridge University Press, Cambridge, UK.
- Bormann, F. H. 1953. Factors determining the role of loblolly pine and sweet gum in early old-field succession in the Piedmont of North Carolina. *Ecological Monographs* **23**: 339–358.
- Bowers, M. A., and J. L. Dooley. 1999. A controlled, hierarchical study of habitat fragmentation: responses at the individual, patch, and landscape scale. *Landscape Ecology* **14**:381–389.
- Burns, R. M., and B. H. Honkala. 1990. *Silvics of North America*. U.S. Department of Agriculture, Washington, D.C., USA.
- Caley, M. J., K. A. Buckley, and G. P. Jones. 2001. Separating ecological effects of habitat fragmentation, degradation, and loss on coral commensals. *Ecology* **82**:3435–3448.
- Chen, J. C., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology. *Bioscience* **49**:288–297.
- Chen, J. Q., J. F. Franklin, and T. A. Spies. 1993. An empirical-model for predicting diurnal air-temperature gradients from edge into old-growth Douglas-fir forest. *Ecological Modelling* **67**:179–198.
- Christensen, N. L., and R. K. Peet. 1984. Convergence during secondary forest succession. *Journal of Ecology* **72**:25–36.
- Cienciala, E., P. E. Mellander, J. Kucera, M. Oplustilova, M. Ottosson-Lofvenius, and K. Bishop. 2002. The effect of a north-facing forest edge on tree water use in a boreal Scots

- pine stand. *Canadian Journal of Forest Research—Revue Canadienne de Recherche Forestiere* **32**:693–702.
- Coile, T. S. 1933. Soil reaction and forest types in the Duke Forest. *Ecology* **14**:323–333.
- Dignan, P., and L. Bren. 2003. Modeling light penetration edge effects for stream buffer design in mountain ash forest in southeastern Australia. *Forest Ecology and Management* **179**:95–106.
- Harrison, S., and E. Bruna. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* **22**:225–232.
- Keever, C. 1950. Causes of succession on old fields of the piedmont, North Carolina. *Ecological Monographs* **20**: 229–250.
- Klaassen, W., P. B. van Breugel, E. J. Moors, and J. P. Nieveen. 2002. Increased heat fluxes near a forest edge. *Theoretical and Applied Climatology* **72**:231–243.
- Laurence, W. F., D. Perez-Salicrup, P. Delamonica, P. M. Fearnside, S. D'Angelo, A. Jerozolinski, L. Pohl, and T. E. Lovejoy. 2001. Rain forest fragmentation and the structure of Amazonian liana communities. *Ecology* **82**:105–116.
- Lookingbill, T. R., and D. Urban. 2003. Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology* **114**:141–151.
- Lorimer, C. G. 1984. Development of the red maple understory in northeastern oak forests. *Forest Science* **30**:3–22.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2002. Environmental correlates of oak decline and red maple increase in the North Carolina Piedmont. *Castanea* **67**:84–95.
- McDonald, R. I., R. K. Peet, and D. L. Urban. 2003. Spatial pattern of oak regeneration limitation in a complex forest environment. *Journal of Vegetation Science* **14**:441–450.
- Moore, I. D., R. B. Grayson, and A. R. Ladson. 1990. Digital terrain modeling: a review of hydrological, geomorphological and biological applications. *Hydrological Processes* **5**:3–30.
- Mourelle, C., M. Kellman, and L. Kwon. 2001. Light occlusion at forest edges: an analysis of tree architectural characteristics. *Forest Ecology and Management* **154**:179–192.
- North Carolina Climate Office. 2003. RDU climate normals. North Carolina State University, Durham, North Carolina, USA.
- Oosting, H. J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist* **28**:1–126.
- Oren, R., D. S. Ellsworth, K. H. Johnsen, N. Phillips, B. E. Ewers, C. Maler, K. V. R. Schäfer, H. McCarthy, G. Hendrey, S. G. McNulty, and G. G. Katul. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO₂-enriched atmosphere. *Nature* **411**:469–472.
- Peet, R. K., and N. L. Christensen. 1980. Succession: a population process. *Vegetatio* **43**:131–140.
- Ranney, J. W., M. C. Bruner, and J. B. Levenson. 1981. The importance of edge in the structure and dynamics of forest islands. Pages 67–92 in R. L. Burgess and D. M. Sharpe, editors. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Redding, T. E., G. D. Hope, M. J. Fortin, M. G. Schmidt, and W. G. Bailey. 2003. Spatial patterns of soil temperature and moisture across subalpine forest-clearcut edges in the southern interior of British Columbia. *Canadian Journal of Soil Science* **83**:121–130.
- Riitters, K. H., J. D. Wickham, R. V. O'Neill, K. B. Jones, E. R. Smith, J. W. Coulston, T. G. Wade, and J. H. Smith. 2002. Fragmentation of continental United States forests. *Ecosystems* **5**:815–822.
- Running, S. W., R. R. Nemani, and R. D. Hungerford. 1987. Extrapolation of synoptic meteorological data in mountainous terrain and its use for simulating forest evapotranspiration and photosynthesis. *Canadian Journal of Forest Resources* **17**:472–483.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* **5**:18–32.
- Sharpe, D. M., F. W. Stearns, R. L. Burgess, and W. C. Johnson. 1981. Spatio-temporal patterns of forest ecosystems in man-dominated landscapes. Pages 109–116 in S. P. Tjallingii and A. A. de Veer, editors. *Perspectives in landscape ecology*. Pudoc, Wageningen, The Netherlands.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. W. H. Freeman and Company, New York, New York, USA.
- Wolock, D. M., and J. McCabe. 1995. Comparison of single and multiple flow direction algorithms for computing topographic parameters for TOPMODEL. *Water Resources Research* **31**:1315–1324.