



Stand dynamics of an Appalachian old-growth forest during a severe drought episode

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Abstract

We analyzed data from 19 0.1 ha permanent plots of an old-growth cove forest in Walker Cove Research Natural Area (North Carolina), in order to understand the process affecting old-growth forest dynamics. During the study period (1979–1994) every stem with DBH larger than 5 cm was identified to species level and DBH was measured every 5 years. Between 1984 and 1989 censuses, a severe drought occurred in the forest. In the studied period, basal area proportions among dominant tree species changed: *Acer saccharum* and *Aesculus flava* showed significant increases, whereas *Tilia americana* and *Fagus grandifolia* decreased. Recruitment increased significantly during the study period. Mortality had a maximum during drought, having an U-shaped pattern as a function of diameter for *T. americana* and *F. grandifolia* and an L-shaped pattern for *A. saccharum* and *A. flava*. Diameter growth was negatively related to mortality, and was a stronger predictor of mortality than DBH. Surprisingly, diameter growth was highest during the drought. This pattern was constant among the dominant species, but varied considerably across the different size classes, with growth increases in the smaller size classes, but growth reduction for the largest size class. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: *Acer saccharum*; *Fagus grandifolia*; North Carolina; Old-growth forest; Permanent plot; Stand dynamics

1. Introduction

Models of disturbance in old-growth forests consist of a continuum between two extremes: the catastrophic cycle model (Peterson and Pickett, 1995) and the gap dynamics model (Brokaw and Busing, 2000). Both of these models assume that there is a competitive gradient from light-demanding, fast-growing, pioneer species to slower-growing, shade-tolerant, advanced successional species. In both cases, high recruitment and dominance of pioneer species

characterizes the initial stages of recruitment. As the forest matures and the canopy closes, the reduced light environment will favor shade-tolerant species, which will grow in the undercanopy, and eventually replace pioneer species.

In the catastrophic cycle model, the occurrence of major perturbations is so frequent that shade-tolerant species will not have time to exclude pioneer species before the next major perturbation (Abrams and Orwig, 1996). Thus the cycle will start again. If the frequency of disturbance is relatively high, advanced successional species can eventually become very scarce or absent. Different forms of catastrophic disturbance have been reported in the literature, including hurricanes (Peterson and Pickett, 1995; Batista et al.,

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1998; Brown et al., 1999), fire (Donnegan and Rebertus, 1999; Veblen et al., 1999), avalanches (Fischer, 1992; Walsh et al., 1994) and landslides (Allen et al., 2000). In this model, pioneer species will recruit in pulses, under the conditions created by perturbation, whereas shade-tolerant species will recruit more continuously.

In the gap dynamics model, the occurrence of major perturbations is infrequent, and does not affect whole stands. In this situation shade-tolerant species have the potential to dominate in an equilibrium state where recruitment is dependent on gaps created by dying trees (Runkle, 1981). Shade-tolerant species will colonize most of the newly created gaps, while the shade-intolerant species will be limited to larger, multi-tree gaps, as long as their propagules are available (Peterson and Carson, 1996). In this scenario recruitment will be continuous through time for both species groups. Despite the differences between both of these models, their mechanistic basis is similar, differing only in the rate, intensity and extension of perturbations.

As a disturbance type, drought does not fit comfortably within the catastrophic disturbance-gap dynamics continuum of models. Although much research has concentrated on the effect of catastrophic disturbance (e.g. Peterson and Pickett, 1995; Oliver and Larson, 1996; Batista et al., 1998) and gap dynamics (e.g. Runkle, 1981; Peterson and Carson, 1996), less is known about the effects of less intense but more extensive disturbances such as droughts. Droughts, despite lacking the intensity and massive mortality of some major perturbations, can affect vast areas of forests, modifying tree dynamics, and therefore are able to alter competitive relations among tree species. An increase in tree mortality during drought episodes is well documented (Fahey, 1998; Condit et al., 1999). The effect of drought is not limited to xeric habitats because it can also occur in mesic (Abrams et al., 1998) or even perhumid conditions (Condit et al., 1999; Nakagawa et al., 2000). Drought can reduce trees' vigor and may predispose them to disease or pathogens. Species (Abrams et al., 1998) and size class (Fahey, 1998; Condit et al., 1999) must be taken into account when explaining drought-induced mortality. Under the growing evidence of a climatic change (IPCC, 2001), droughts will probably increase in frequency and magnitude. Therefore, it is important to understand how drought affects forest dynamics.

With these considerations in mind, we analyze the data for 15 years (1979–1994) in an Appalachian old-growth cove forest. During this period, National Oceanic and Atmospheric Administration (NOAA, 2000) data reveal one of the longest regional drought episodes in the 20th century. Our aim is to answer several questions: How has the dominance in this forest changed during this period? How does drought affect the patterns of mortality and recruitment? Can stem mortality be predicted based on size or growth? How does drought affect trees' competitive hierarchies?

2. Methods

2.1. Study site

The Walker Cove Research Natural Area (WCRNA), which is located in the Pisgah National Forest, Buncombe County, North Carolina, is a 21.45 ha site consisting almost entirely of old-growth forest. Elevation ranges from 1195 to 1317 m, the average slope is 38% (5–65), and the average soil pH is moderately acid, 4.8 (4.5–5.7). The prevailing aspect is northwest (Dickison, 1980). No weather stations are available in the immediate vicinity of Walker Cove. However, Dickison (1980) reported estimates, derived from models in the literature, of 10.3 °C average temperature and an annual rainfall of 127–152 cm.

The dominant tree species are *Acer saccharum* Marsh., *Fagus grandifolia* (Ehrh.) little, *Tilia americana* Vent. and *Aesculus flava* Marsh. We found a total of 19 tree species in the study area. Previous research at WCRNA include Hepting (1944), Dickison (1980), Runkle (1979, 1981, 1982, 1998, 2000), Runkle and Yetter (1987) and Hardt and Swank (1997).

Regional hydric balance was quantified using the Palmer drought severity index (PDSI) and was provided by NOAA (2000). The PDSI is calculated based on precipitation and temperature data, as well as the local available water content of the soil. Despite its limitations (Alley, 1984), this index is a standard to describe moisture conditions. After the 1970s, one of the wettest decades in the 20th century, the 1984–1989 period comprised the driest 5 years in the century (Fig. 1).

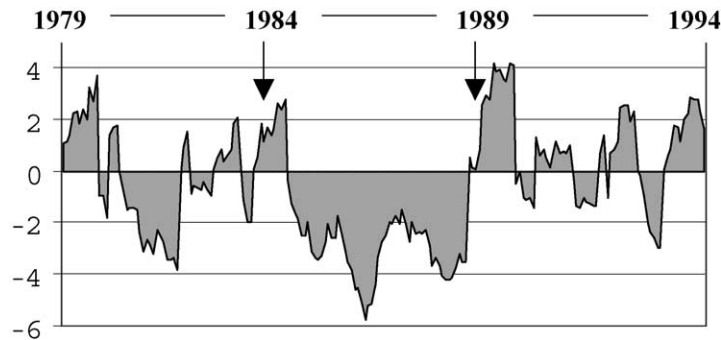


Fig. 1. Palmer drought severity index for the 1970–1994 period. Positive values indicate wet conditions, and negative values drought conditions. Data source: NOAA (2000).

2.2. Field methods

In 1979, 20 0.1 ha (20 m × 50 m) permanent plots along seven parallel transects were in WCRNA (Dickison, 1980). Transects were separated from each other by 100 m. Within each plot, each woody stem over 5 cm DBH was identified to species level, mapped and tagged. DBH was measured to the nearest millimeter. The plots were resurveyed in 1984, 1989 and 1994. For simplicity, 1979–1984 period is called the pre-drought period, 1984–1989 the drought period and 1989–1994 the post-drought period.

One of the 20 original plots, located at the periphery of WCRNA, is dominated by *Robinia pseudoacacia* L. and lacks large trees. This plot has probably been subjected to recent human disturbance (Dickison, 1980; H. McNab, personal communication) and therefore was omitted from subsequent analysis. Nomenclature of the taxa encountered follows Kartesz (1994).

2.3. Data analysis

Trees were grouped into four DBH classes (I: 5–10 cm, II: 10–20 cm, III: 20–40 cm, and IV: >40 cm). We assessed variables for normality using the Kolmogorov–Smirnov test and transformed when this assumption was not fulfilled. We used repeated measures analysis of variance, also called within-subjects design (Moser et al., 1989; Norušis, 1994; Ximénez and San Martín, 2000) to compare the effect of time on the variable of interest; this analysis accounts for temporal autocorrelation. We used Mauchly W to test

for sphericity; if the sphericity assumption was not fulfilled we used multivariate contrasts instead of univariate contrasts (Norušis, 1994). This test was performed for basal area, mortality (in percentage), recruitment and diameter growth (only for stems surviving the whole period). Trends between variables and time were tested using polynomial contrasts (Ximénez and San Martín, 2000).

We calculated mortality rate on a 5-year basis and then transformed it to an annual rate with the formula

$$\sigma(x) = 1 - (1 - m(x))^{1/n}$$

where $\sigma(x)$ is the annual mortality rate function, $m(x)$ the 5 years mortality function and n the number of years, five in this case. We performed all analyses with SPSS (v.10.0).

We built mortality models for the four dominant species for the drought and post-drought periods by means of a stepwise logistic regression (ter Braak and Looman, 1987; Legendre and Legendre, 1998). Diameter growth in the prior 5-year period, diameter at the beginning of the period, square diameter and an interaction term between diameter and growth were selected as independent variables. Variables were included in the model by the Wald forward stepwise selection, cut-off value for inclusion in the model was 0.05, and 0.1 to exclude a previously included variable; overall model significance was tested by the $-2LL$ procedure (Norušis, 1994). Since stepwise analyses compromise the strict use of inferential statistics (see, e.g., Hallgren et al., 1999), we treat our results as descriptive and exploratory.

3. Results

3.1. Stand density and basal area

The majority of trees in WCRNA belong to mesic and shade-tolerant species. These trees, consisting of *A. saccharum* (sugar maple), *T. americana* (white basswood), *F. grandifolia* (American beech) and *A. flava* (yellow buckeye), accounted in 1994 for more than 80% of the basal area and 75% of the stems (Table 1). Several light-demanding to intermediate species such as *Betula alleghaniensis* Britt. (yellow birch), *Fraxinus americana* L. (white ash), *Carya cordiformis* (Wangenh.) K. Koch (bitternut hickory) and *Magnolia acuminata* L. (cucumber magnolia), accounted for an appreciable proportion of total basal area (13.2%), but a relatively low proportion of stems (5.6%). In contrast, two medium-sized shade-tolerant understory tree species, *Ostrya virginiana* (Mill.) K. Koch (eastern hop hornbeam) and *Acer pensylvanicum* L. (striped maple), were well represented in terms of stem density (17.2%), although their contribution to basal area was small (2.4%). Total species richness declined in the study period from 19 to 18 as the only individual of *Quercus prinus* L. (chestnut oak), a 74.6 cm DBH tree died during the drought period.

There was no significant change in basal area of all species combined during the study period. However, some species exhibited significant changes. *A. saccharum* had a continuous increase in basal area through the whole period (13.12%, $p < 0.001$), as did *A. flava*, which increased during the pre-drought and drought periods and then remained stable (5.71%, $p < 0.001$). The two other dominant species showed opposite trends. *T. americana* decreased in the pre-drought census and then maintained its basal area (−6.56%, ns), whereas *F. grandifolia* showed a clear decrease (−17.56%, ns), despite census averages for this species had a linear decreasing trend, as detected by polynomial contrast ($p < 0.001$). Among the other species *F. americana* (24.56%, ns) and *B. alleghaniensis* (8.6%, ns) displayed the major variations in basal area.

3.2. Recruitment

As expected, more than half (55.2%) of the recruited stems belonged to the four dominant shade-tolerant species (*A. saccharum*, *F. grandifolia*, *T. americana*, *A. flava*). A high percentage (40.6%) consisted of the two understory trees (*A. pensylvanicum* and *O. virginiana*). The remaining species only

Table 1

Basal area and stem density in the four censuses (shade tolerance according to Iverson et al. (1999), except *Acer spicatum* (Hosier, 1974) and *Magnolia* spp. Trimble (1975))^a

Species	Shade	Basal area (m ² ha ⁻¹)				Density (stems ha ⁻¹)			
		1979	1984	1989	1994	1979	1984	1989	1994
<i>A. saccharum</i>	S	11.20	11.56	11.87	12.67	169	164	162	169
<i>A. flava</i>	S	3.85	4.00	4.10	4.07	81	78	76	73
<i>F. grandifolia</i>	S	5.75	5.21	4.88	4.74	146	136	119	121
<i>T. americana</i>	S	6.89	6.41	6.50	6.44	60	56	58	67
<i>A. pensylvanicum</i>	S	0.15	0.11	0.10	0.13	25	22	20	27
<i>O. virginiana</i>	S	0.69	0.57	0.64	0.68	47	47	55	72
<i>Acer rubrum</i> L.	S	0.81	0.73	0.79	0.85	8	8	7	7
<i>B. alleghaniensis</i>	I	1.51	1.56	1.59	1.64	14	13	12	13
<i>C. cordiformis</i>	I	0.60	0.63	0.29	0.31	2	2	2	2
<i>F. americana</i>	I	1.14	1.25	1.33	1.42	7	6	6	6
<i>M. acuminata</i>	I	0.25	0.29	0.33	0.23	4	4	4	4
Others ^b		0.63	0.66	0.47	0.52	13	12	11	13
Total		33.44	32.95	32.91	33.70	576	548	533	574

^a L: shade intolerant, I: intermediate, S: shade-tolerant.

^b Others include: *Q. prinus* (I), *B. lenta* (L), *Magnolia fraseri* (I), *Tsuga canadensis* (L) Corr. (S), *Carya glabra* (I), *L. tulipifera* (I), *P. serotina* (L) and *A. spicatum* (S).

Table 2
Recruitment rates during the study period

Species	Recruitment rates (stems ha ⁻¹ yr ⁻¹)		
	Pre-drought	Drought	Post-drought
<i>A. saccharum</i>	1.0	1.9	3.3
<i>A. flava</i>	0.2	0.4	0.4
<i>F. grandifolia</i>	0.5	0.8	2.6
<i>T. americana</i>	0.8	1.4	2.7
<i>A. pensylvanicum</i>	1.6	1.1	2.0
<i>O. virginiana</i>	1.7	2.2	3.9
<i>T. canadensis</i>	0.0	0.1	0.3
Others ^a	0.0	0.2	0.7

^a Others included *P. serotina*, *M. acuminata*, *A. spicatum*, *L. tulipifera*, *B. alleghaniensis*.

accounted for a small fraction (4.2%) of the recruits (Table 2). The rate of recruitment into the smallest size class increased during the studied period (5.37, 7.89–15.9 stems ha⁻¹ yr⁻¹, $p < 0.001$) following a linear trend ($p < 0.001$). This pattern was common to almost all the species recruiting. The number of species recruiting increased from 6 to 11.

3.3. Mortality

Roughly a fourth of the trees (26%) present in the initial 1979 census were dead in the final 1994 census. Mortality was negatively related to size (Fig. 2). Mortality varied during the study ($p = 0.044$): post-drought mortality was significantly lower ($p < 0.001$) than the two previous periods, but there were no significant differences between pre-drought and drought mortality.

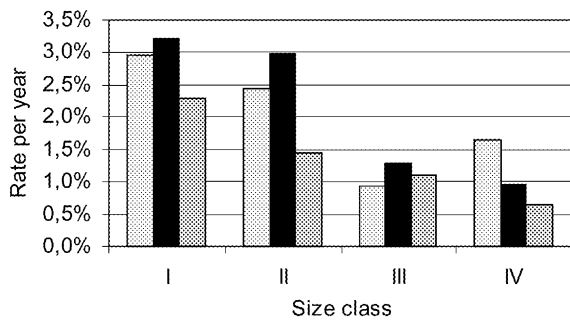


Fig. 2. Mortality rate per size class (I: 5–10 cm, II: 10–20 cm, III: 20–40 cm and IV: >40 cm). Dotted white pre-drought period (1979–1984), black drought period (1984–1989) and gray post-drought period (1989–1994).

Table 3
Mortality rates (%) for the four dominant species and DBH classes, in yr⁻¹

Species	DBH class			
	5–10 cm	10–20 cm	20–40 cm	>40 cm
<i>A. saccharum</i>	2.1	1.6	0.5	0.3
<i>A. flava</i>	1.4	1.3	0.7	0.3
<i>F. grandifolia</i>	3.2	2.1	1.8	3.8
<i>T. americana</i>	3.2	1.4	0.8	1.1

Mortality varied as a function of species and size (Table 3). Annual mortality rates for the smallest size class ranged from 1.6% for *A. flava* to 3.2% for *T. americana* and *F. grandifolia*. As diameter increased, mortality rates decreased for size classes II and III. The largest size class showed two contrasting patterns: *A. saccharum* and *A. flava* showed the lowest mortality rates, whereas *T. americana* and *F. grandifolia* had an increase for the largest size class. This change was especially noteworthy for *Fagus*. It had the highest mortality rate (3.8%) of the species in this size class, more than 50% of the stems (6 of 11) died in the pre-drought period.

Stepwise logistic models were always significant (Table 4). Diameter growth was the best predictor in all models, and mortality was negatively related to diameter growth. During post-drought census, the stepwise logistic regressions for *A. saccharum* and *T. americana* included diameter as a second parameter; mortality decreased as a function of size for both species.

3.4. Diameter growth

DBH growth rates for trees surviving for the whole period showed an unexpected pattern, since diameter growth rate had a maximum during the drought period (1.74–1.99–1.52 mm yr⁻¹). However this behavior depended on size class. The largest size class (DBH ≥ 40 cm) had minimal diameter growth rate during the drought period (Fig. 3, 3.4), a pattern that was common for the four dominant species. After drought, only *F. grandifolia* and *A. saccharum* recovered their former diameter growth rates. Size class III showed a different response (Fig. 3, 3.3). *T. americana*, *A. saccharum* and *A. flava* increased during the drought period, whereas *F. grandifolia* showed a

Table 4
Logistic models for mortality

Species	Mortality predicted for	Growth period considered	Number of stems in analysis	Model p	Parameters in model	Parameter p	R
<i>A. saccharum</i>	1989	1979–1984	303	0.0001	Diameter growth	0.0006	-0.2470
	1994	1984–1989	290	0.0013	Diameter growth Diameter	0.0433 0.0071	-0.1219 -0.1933
<i>A. flava</i>	1989	1979–1984	146	0.013	Diameter growth	0.025	-0.147
	1994	1984–1989	140	0.011	Diameter growth	0.020	-0.186
<i>F. grandifolia</i>	1989	1979–1984	253	0.002	Diameter growth	0.0071	-0.1552
	1994	1984–1989	218	0.0001	Diameter growth	0.0005	-0.2740
<i>T. americana</i>	1989	1979–1984	98	0.0052	Diameter growth	0.0241	-0.2474
	1994	1984–1989	98	0.0001	Diameter growth Diameter	0.0165 0.002	-0.2602 -0.3691

continuous decline. Size class II showed a clear increase during the drought period (Fig. 3, 3.2), which was significant for three of the dominant species, after drought diameter growth got close to pre-drought values. The smallest size class had a clear maximum

for all species during the drought period (Fig. 3, 3.1), significant for all considered species, but *A. flava* ($p = 0.056$). The average post-drought diameter growth was lower than pre-drought diameter growth for all of them.

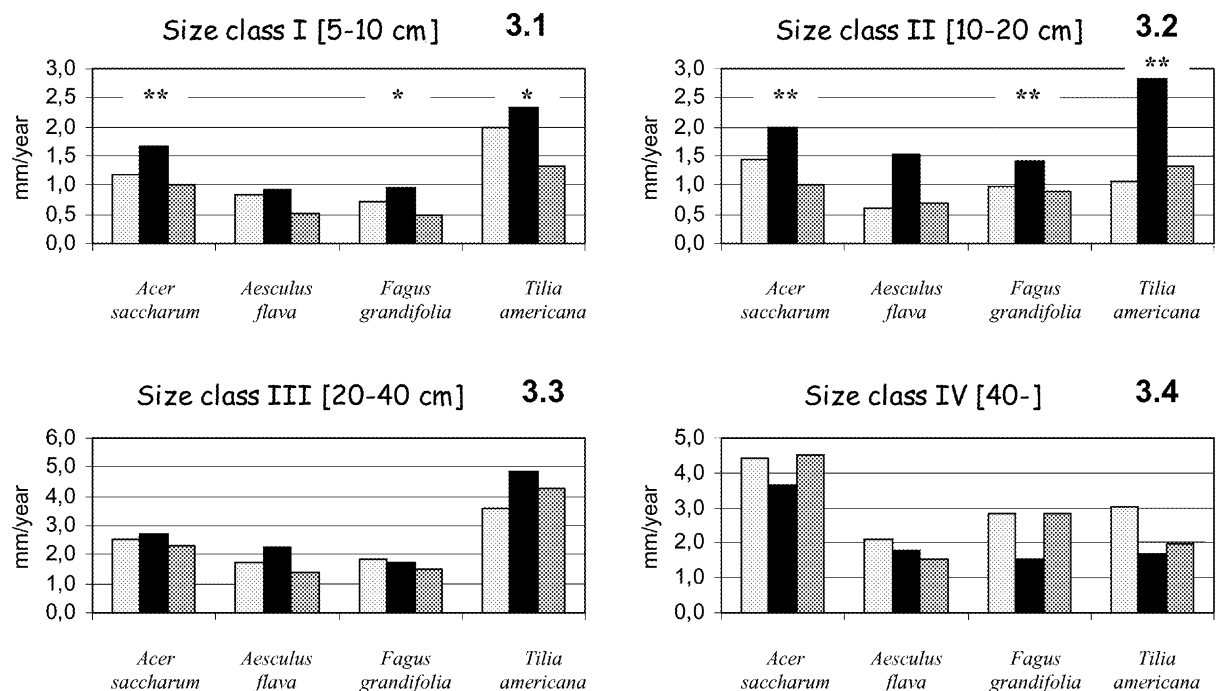


Fig. 3. Diameter growth rate per species. Dotted white pre-drought period (1979–1984), black drought period (1984–1989) and grey post-drought period (1989–1994). Significant differences among periods are indicated with asterisks: *: $p < 0.05$, **: $p < 0.01$.

4. Discussion

4.1. Stand dynamics

As can be expected in an old-growth forest, basal area showed no significant change during the study. The final basal area of 33.7 m²/ha was similar to that obtained in other old-growth forests with similar species composition (Abrell and Jackson, 1977; Muller, 1982; Parker et al., 1985; Martin and Bailey, 1999), but substantially lower than that from cove forests from the Great Smoky Mountains (Busing, 1998). The difference in basal area obtained in WCRNA by Runkle (2000), 47.3 m²/ha in 1990–1991, is probably an artifact due to a difference in the census techniques. Basal area diminished during the pre-drought period, mainly due to the high rates of mortality in the largest size class.

Species with high to moderate light requirements (*B. alleghaniensis*, *Betula lenta* L., *C. cordiformis* (Wangenh.) K. Koch, *C. glabra* (P. Mill.) Sweet., *F. americana*, *Liriodendron tulipifera* L., *M. acuminata*, *M. fraseri* Walt., *Prunus serotina* Ehrh., *Q. prinus*) exhibited no significant changes in their proportion of basal area in the forest (11.9–11.7%), remaining in secondary importance in WCRNA. Their size distribution became more skewed towards larger sizes than at the beginning of the research, due to an ageing of the trees, with low to non-existent recruitment in the entire study period. The sapling and seedling bank, dominated entirely by shade-tolerant species (Dickison, 1980; Hardt and Swank, 1997), confirms this pattern. The prevailing conditions in WCRNA do not seem favorable for pioneer species, despite the high mortality of canopy trees (1.19%) (cf. Barden, 1980, 1989; Runkle, 1982). Thus, the presence of pioneer species in WCRNA most likely reflects episodes of greater disturbance in the past. If such disturbances do not recur, they are likely to become even scarcer.

The fate of the dominant species, all considered shade-tolerant species (Sutherland et al., 2000) showed different patterns. While basal area had a significant increase for *A. flava* and *A. saccharum* (Table 1), it decreased for *T. americana* and *F. grandifolia*. This decrease was pronounced in *F. grandifolia* (17.56%), where mortality in medium and large trees was notably high (Table 3), and was also accompanied of a severe stem reduction. A similar pattern with

elevated mortality for larger diameters has been found for this species in south central New York (Fahey, 1998), but does not appear in other studies (Abrell and Jackson, 1977; Harcombe and Marks, 1983). *F. grandifolia* is supposed to be one of the most shade-tolerant species in this forest (even more than *A. saccharum*) (Beaudet and Messier, 1998); thus an increase rather than a decrease would be expected. Runkle (1981) estimated that for WCRNA the number of gaps created by *F. grandifolia* (39%) was higher than the presence of the species in the canopy (24%), and it is possible that this mortality may predate the establishment of these plots. Decrease of the importance of *F. grandifolia* in old-growth forests is not unusual in most of the forests studied (see Runkle, 2000 for a review). Various factors have been blamed for this decrease, including the expansion of beech-bark disease (Fahey, 1998; McGee, 2000). Even so, such a high mortality for *F. grandifolia* does not appear in other studies (Glitzstein et al., 1986; Batista et al., 1998), and under these conditions its future role in the forest is uncertain.

In contrast to *F. grandifolia*, *A. saccharum* basal area increased continuously through the study period. This increase in old-growth forests has been repeatedly reported (Abrell and Jackson, 1977; Parshall, 1995; Runkle, 2000, but see Woods, 2000). Several ideas are posed to explain this phenomenon. The most plausible seems the increase in drought periods, to which *A. saccharum* is more resistant and resilient (Parshall, 1995; but see Fahey, 1998). *T. americana* decreased in the pre-drought period census due to mortality in large trees, and it did not recover in the study period, although stem density did. The increase in basal area for *A. flava* was significant throughout the period, mainly because of the low mortality of larger trees, despite the decrease in stem density.

The forest dynamics in this study are consistent with the gap dynamic model. Pioneer species grew into larger size classes with little to none recruitment, and are expected to disappear, unless perturbations occur. However, contrasting patterns appear in shade-tolerant species, therefore predicting future dynamics is difficult, since shade tolerance, although being necessary is not enough to ensure dominance. Furthermore, the gap model is an intrinsically spatial model: growth is enhanced in gaps created by dying trees. In the current analyses, we have no assessment of the

importance of actual canopy gaps; it is possible that increased growth is linked to increased light caused by the decreased vigor of the canopy.

4.2. Patterns of mortality

Mortality was higher during drought, and had a significant decrease after it. Mortality was also dependent on species and size class. Decreasing dominants (*F. grandifolia* and *T. americana*) showed U-shaped size-mortality curves with higher mortality rates for small and big trees, whereas *A. saccharum* and *A. flava*, both increasing, showed L-shaped patterns with a monotonic decrease in mortality with size increase. However, diameter growth was better predictor for survivorship than diameter size. In this sense, Nakagawa et al. (2000) mentioned that mortality became less size dependent during drought. Slow growing trees may be suffering higher stress rates and therefore be more likely to be killed by an additional stress as drought (Fahey, 1998; Pedersen, 1998). Our data support this hypothesis since size was included in two of the stepwise models for the post-drought period, but in none during drought.

4.3. Effect of drought on growth

Surprisingly, diameter growth showed a maximum increase during the drought period. This result was unexpected since drought is expected to reduce tree vigor, as higher mortality for the drought period indeed reflects. High mortality in the pre-drought and drought periods could explain this observation. Reduced density enhances growth of survivors, as the resources available increase, due to a reduction in symmetric competition. According to this hypothesis, growth increase should be evenly distributed among all size classes. However, the decrease in diameter growth during drought appears in the largest size class, whereas there is a general increase in diameter growth among all species in the smaller size classes.

A reduction in asymmetric competition seems a more plausible explanation. Drought may produce an increase in light penetrating the canopy, most directly through mortality of canopy trees (thus creating gaps), but also in a more indirect way by decreasing diameter growth of survivors and reducing leaf area (Waring, 1987). Under these conditions an increase in diffuse

light and an increased frequency of sunflecks would ameliorate the conditions under the canopy. In the low light of the understory, light is expected to be even more limiting than water, so in most cases an increase in light is expected to increase diameter growth. Moreover, smaller size and canopy protection reduces water requirements and drought damage (van Hees, 1997; García-Plazaola and Becerril, 2000), giving understory trees some advantage in drought resistance. After the drought period, when dominant trees recover their initial diameter growth rates, shading increases again and a reduction of growth occurs for the smaller trees. As expected, this effect is more pronounced in the smallest size class, which is presumably under more severe light restrictions.

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References

- Abrams, M.D., Orwig, D.A., 1996. A 300-year history of disturbance and canopy recruitment for the co-occurring white pine and hemlock on the Allegheny Plateau. *USA J. Ecol.* 84, 353–363.
- Abrams, M.D., Ruffner, C.M., Morgan, T.A., 1998. Tree ring response to drought across species and contrasting sites in the ridge and valley of Central Pennsylvania. *For. Sci.* 44, 550–558.
- Abrell, D.B., Jackson, M.T., 1977. A decade of change in an old-growth beech-maple forest in Indiana. *Am. Midl. Nat.* 98, 22–32.
- Allen, R.B., Bellingham, P.J., Wisser, S.K., 2000. An earthquake's impact on the structure and dynamics of a New Zealand

- Nothofagus forest. In: Proceedings of the 41st IAVS Symposium, pp. 84–86.
- Alley, W.M., 1984. The Palmer drought severity index: limitations and assumptions. *J. Climate Appl. Meteorol.* 23, 1100–1109.
- Barden, L.S., 1980. Tree replacement in a cove hardwood forest of the southern Appalachians. *Oikos* 35, 16–19.
- Barden, L.S., 1989. Repeatability in forest gap research studies in the Great Smoky Mountains. *Ecology* 70, 558–559.
- Batista, W.B., Platt, W.J., Macchiavelli, R.E., 1998. Demography of a shade-tolerant tree (*Fagus grandifolia*) in a hurricane-disturbed forest. *Ecology* 79, 38–53.
- Beaudet, M., Messier, C., 1998. Growth and morphological responses of yellow birch, sugar maple and beech seedlings growing under a natural light gradient. *Can. J. For. Res.* 28, 1007–1015.
- Brokaw, N.V.L., Busing, R.T., 2000. Niche versus chance and tree diversity in forest gaps. *Tree* 15, 183–188.
- Brown, P.M., Kauffmann, M.R., Shepperd, W.D., 1999. Long-term, landscape patterns of past fire events in a montane ponderosa pine forest of central Colorado. *Landscape Ecol.* 14, 513–532.
- Busing, R.T., 1998. Structure and dynamics of cove forests in the Great Smoky Mountains. *Castanea* 63, 361–371.
- Condit, R., Ashton, P.S., Manokaran, N., LaFrankie, J.V., Hubbell, S.P., Foster, R.B., 1999. Dynamics of the forest communities at Pasoh and Barro Colorado: comparing two 50 ha plots. *Philos. Trans. Roy. Soc. Lond. Ser. B* 354, 1739–1748.
- Dickison, G.J., 1980. Composition and stand dynamics of an old-growth upper cove hardwood forest in Walker Cove Research Natural Area, Pisgah National Forest, North Carolina. Master of Science Thesis, Duke University, 96 pp.
- Donnegan, J.A., Rebertus, A.J., 1999. Rates and mechanisms of subalpine forest succession along an environmental gradient. *Ecology* 80, 1370–1384.
- Fahey, T.J., 1998. Recent changes in an upland forest in south-central New York. *J. Torrey Bot. Soc.* 125, 51–59.
- Fischer, A., 1992. Long term vegetation development in Bavarian Mountain Forest ecosystems following natural destruction. *Vegetatio* 103, 93–104.
- García-Plazaola, J.I., Becerril, J.M., 2000. Effects of drought on photoprotective mechanisms in European beech (*Fagus sylvatica* L.) seedlings from different provenances. *Tree* 14, 485–490.
- Glitzstein, J.S., Harcombe, P.A., Streng, D.R., 1986. Disturbance, succession and maintenance of species diversity. *Ecol. Monogr.* 56, 243–258.
- Hallgren, E., Palmer, M.W., Milberg, P., 1999. Data diving with cross validation: an investigation of broad-scale gradients in Swedish weed communities. *J. Ecol.* 87, 1037–1051.
- Harcombe, P.A., Marks, P.L., 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). *Oecologia* 57, 49–54.
- Hardt, R.A., Swank, W.T., 1997. A comparison of structural and compositional characteristics of southern Appalachian young second growth, maturing second-growth and old-growth stands. *Nat. Areas J.* 17, 42–52.
- Hepting, G.H., 1944. Sapstreak, a new killing disease of sugar maple. *Phytopathology* 34, 1069–1076.
- Hosier, P.E., 1974. Maples: mountain maple. In: Gill, J.D., Healy, W. (Eds.), *Shrubs and Vines for Northeastern Wildlife*. Gen. Tech. Rep. NE-9, Broomall, PA, US Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, pp. 93–95.
- IPCC, 2001. Climate change 2001: the scientific basis. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Xiaosu, D. (Eds.), *Summary for policymakers Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, UK, 944 pp.
- Iverson, L.R., Prasad, A.M., Hale, B.J., Sutherland, E.K., 1999. An atlas of current and potential future distributions of common trees of the eastern United States. USDA For. Serv. Gen. Tech. Rep. NE-265, 1–245.
- Kartesz, J.T., 1994. A Synonymized Checklist of the Vascular Flora of the United States, Canada, and Greenland, Vols. 1 and 2, 2nd Edition. Timber Press, Portland, Oregon.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*, 2nd English Edition. Elsevier, Amsterdam.
- Martin, C.W., Bailey, A.S., 1999. Twenty years of change in a northern hardwood forest. *For. Ecol. Manage.* 123, 253–260.
- McGee, G.G., 2000. The contribution of beech bark disease-induced mortality to coarse woody debris loads in northern hardwood stands of Adirondack Park, New York. USA *Can. J. For. Res.* 30, 1453–1462.
- Moser, E.B., Saxton, A.M., Pezeshki, S.R., 1989. Repeated measures analysis of variance, application to tree research. *Can. J. For. Res.* 20, 524–535.
- Muller, R.N., 1982. Vegetation patterns in the mixed mesophytic forest of eastern Kentucky. *Ecology* 63, 1901–1917.
- Nakagawa, M., Tanaka, K., Nakashizuka, T., Ohkubo, T., Kato, T., Maeda, T., Sato, K., Miguchi, H., Nagamasu, H., Ogino, K., Teo, S., Hamid, A.A., Seng, L.H., 2000. Impact of severe drought associated with the 1997–1998 El Niño in a tropical forest in Sarawak. *J. Trop. Ecol.* 16, 355–367.
- NOAA, 2000. Climate visualization website: URL (http://www.ncdc.noaa.gov/onlineprod/drought/temp/drought_15264.txt).
- Norušis, M., 1994. *SPSS Advanced Statistics 6.1*. SPSS Inc., Chicago, 606 pp.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*. Wiley, New York, 520 pp.
- Parker, G.R., Leopold, D.J., Eichenberger, J.K., 1985. Tree dynamics in an old-growth deciduous forest. *For. Ecol. Manage.* 11, 31–57.
- Parshall, T., 1995. Canopy mortality and stand-scale change in a northern hemlock-hardwood forest. *Can. J. For. Res.* 25, 1466–1478.
- Pedersen, B.S., 1998. The role of stress in the mortality of midwestern oaks as indicated by growth prior to death. *Ecology* 79, 79–93.
- Peterson, C.J., Carson, W.P., 1996. Generalizing forest regeneration models: the dependence of propagule availability on disturbance history and stand size. *Can. J. For. Res.* 26, 45–52.
- Peterson, C.J., Pickett, S.T.A., 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76, 763–774.

- Runkle, J.R., 1979. Gap phase dynamics in climax mesic forests. Ph.D. Thesis, Cornell University, New York.
- Runkle, J.R., 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62, 1041–1051.
- Runkle, J.R., 1982. Patterns of disturbance in some old-growth mesic forest of eastern North America. *Ecology* 63, 1533–1546.
- Runkle, J.R., 1998. Changes in south Appalachian canopy tree gaps sampled thrice. *Ecology* 79, 1768–1780.
- Runkle, J.R., 2000. Canopy tree turnover in old-growth mesic forests of eastern North America. *Ecology* 81, 554–567.
- Runkle, J.R., Yetter, T.C., 1987. Treefalls revisited: gap dynamics in the southern Appalachians. *Ecology* 68, 417–424.
- Sutherland, E.K., Hale, B.S., Hix, D.H., 2000. Defining species guilds in the central hardwood Forests. *USA Plant Ecol.* 147, 1–19.
- ter Braak, C.J.R., Looman, C.W.N., 1987. Regression. In: Jongmann, R.H., ter Braak, C.J.F., van Tongeren, O.F.R. (Eds.), *Data Analysis in Community Ecology*. Pudoc, Wagenigen, pp. 29–90.
- Trimble Jr., G.R., 1975. Summaries of some silvical characteristics of several Appalachian hardwood trees. USDA For. Serv. Gen. Techn. Rep. NE-16. Northeastern Forest Experiment Station, Broomall, PA, 5 pp.
- van Hees, A.F.M., 1997. Growth and morphology of pedunculate oak (*Quercus robur* L.) and beech (*Fagus sylvatica* L.) seedlings in relation to shading and drought. *Ann. Sci. For.* 54, 9–18.
- Veblen, T.T., Kitzberger, T., Villalba, R., Donnegan, J., 1999. Fire history in Northern Patagonia: the roles of humans and climatic variation. *Ecol. Monogr.* 69, 47–67.
- Walsh, S.J., Butler, D.R., Allen, T.R., Malanson, G.P., 1994. Influence of snow patterns and snow avalanches on the alpine tree ecotone. *J. Veg. Sci.* 5, 657–672.
- Waring, R.H., 1987. Characteristics of trees predisposed to die. *BioScience* 37, 569–573.
- Woods, K.D., 2000. Dynamics in late successional hemlock-hardwood forests over three decades. *Ecology* 81, 110–126.
- Ximénez, C., San Martín, R., 2000. *Análisis de Varianza con Medidas Repetidas*. Ed. La Muralla, Madrid.