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The effects of drought and disturbance on the growth and developmental instability of loblolly pine (*Pinus taeda* L.)

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ABSTRACT

Ecological indicators provide early warning of adverse environmental change, helping land managers adaptively manage their resources while minimizing costly remediation. In 1999 and 2000, we studied two such indicators, growth and developmental instability, of loblolly pine (*Pinus taeda* L.) influenced by mechanized infantry training at Fort Benning, Georgia. Disturbed areas were used for military training; tracked and wheeled vehicles damaged vegetation and soils. Highly disturbed sites had fewer trees, diminished ground cover, warmer soils in the summer, and more compacted soils with a shallower A-horizon. We hypothesized that disturbance would decrease the growth of needles, branches, and tree rings, increase the complexity of tree rings, and increase the developmental instability of needles. Contrary to our expectations, however, disturbance enhanced growth in the first year of the study, possibly by reducing competition. In the second year, a drought reduced growth of branches and needles, eliminating the stimulatory effect of disturbance. Growth-ring widths increased with growing-season precipitation, and decreased with growing-season temperature over the last 40 years. Disturbance had no effect on tree-ring complexity, as measured by the Hurst exponent. Within-fascicle variation of current-year needle length, a measure of developmental instability, differed among the study populations, but appeared unrelated to mechanical disturbance or drought.

1. Introduction

Modification of the physical environment changes the growth rate, density, age distribution, and genetic structure of populations, and these changes cascade up the biological hierarchy to ecological communities and ecosystems. Because many of these changes are undesirable, the ability to detect change is useful. But what populations, and which aspects of those populations, should one examine? Individual growth and homeostasis may be better indicators than population size and density (Graham et al., 1993). Moreover, plant species, especially woody plants, afford advantages over other taxonomic groups, such as animals and fungi (Freeman et al., 1993, 2003). Previously, we studied growth and developmental instability of herbs and shrubs in landscapes disturbed by military training at Fort Benning in the Fall-line Sandhills of west-central Georgia, USA (Duda et al., 2003; Freeman et al., 2004a,b, 2005). Here, we present the effects of military training and drought on growth and developmental instability of a tree, loblolly pine (*Pinus taeda* L.). We hypothesize that disturbance should decrease the growth of needles, branches, and tree rings, increase the complexity of tree-ring widths, and increase the developmental instability of needles. We found, however, that disturbance from military training actually enhances growth of loblolly pine, while drought lessens it. Moreover, neither disturbance nor drought change tree-ring complexity or increase developmental instability.

Trees are obvious and long-lived primary producers in forested landscapes. Because of their long generations, they should adapt slowly to disturbance (Smith and Donoghue, 2008, but see Rosenheim and Tabashnik, 1991), retaining a history of growing conditions in their growth rings. Consequently, trees may be better indicators of disturbance than herbs, particularly annuals, which have shorter generations and adapt quickly to alterations in their environment. Trees, on the other hand, are resilient, because of their size and multiple storage compartments (King et al.,

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1999). Compartmentalization allows trees to buffer environmental perturbations, generating time lags and consequent nonlinearity (Zutter et al., 1998; Tang et al., 1999a,b). Moreover, trees are more phenotypically plastic than herbs (Chambel et al., 2005).

By providing a cumulative, year-by-year history of growth, tree rings reveal environmental stress decades to centuries in the past. Moreover, one can correlate tree rings with past climate events (Fritts, 1976; Carrer and Urbinati, 2006). Pest outbreaks, masting, and competition may also influence growth-ring width, but the history of these events is normally unavailable. Thus, detecting the origins of stress amid the cacophony of noise is difficult. Nevertheless, few taxa provide such information decades into the past.

In contrast to tree rings, other indicators respond to stress on finer time scales. Physiological indicators, such as water potential and variable fluorescence, are useful for assessing environmental change and stress on scales of seconds to hours or weeks (Sword et al., 1998; Tang et al., 1999a,b). Measures of developmental instability, such as fluctuating asymmetry, integrate the response of trees over months to years, providing an intermediate time frame (Kozlov and Niemelä, 1999; Kozlov et al., 2002; see Freeman et al., 2003, for a review) for a review. Together, growth and developmental instability provide complementary indicators of stress.

Because plastic responses, such as growth, are under selection whenever stress appears, they should be sensitive to stress. Modification of leaf size, for example, alleviates the effects of drought and shade (Raz et al., 2011). Thus, plasticity should be adaptive. In addition, growth should be even more sensitive to stress; indeed one can restate the popular definitions of stress directly in terms of growth (Graham et al., 2010). For example, Grime (2001) defines stress as anything that limits productivity (i.e., growth). Conversely, Alekseeva et al. (1992) and Ozernyuk et al. (1992) define stress as anything that dissipates energy (i.e., away from growth). See Parsons (2005) for a recent review.

Developmental instability should be less sensitive to stress than either growth or plasticity (Graham et al., 2010). Nevertheless, developmental instability has advantages; it is non-adaptive, whereas plasticity is adaptive (even decreased growth can be adaptive if it increases fitness). Thus, developmental instability indicates when stress has adversely affected development.

Developmental instability is estimated from measures of fluctuating asymmetry, the random deviations from perfect symmetry (Graham et al., 2010). Most studies of fluctuating asymmetry deal with bilaterally symmetrical traits, but deviations from other kinds of symmetry can be used as well. Because plants are modular, they are excellent subjects for fluctuating asymmetry. The variation among parts, such as the variation among pine needles within a fascicle, is analogous to variation between right and left sides of a bilaterally symmetrical trait.

Loblolly pine (*Pinus taeda* L.) is a shade-intolerant, early successional species. It produces three leaves (14–25 cm) per fascicle and retains them for two to three years. Leaves are initiated in the fall, elongate in the spring, and require four to five months to mature (Tang et al., 1999a,b). We studied loblolly because it was the dominant native pine at our sites.

We might expect a complicated response of loblolly to disturbance—positive if disturbance removes competitors and negative if it damages the soil. Removal of understory herbs and shrubs increases subsequent growth of loblolly (Haywood et al., 1997; Cain and Shelton, 1998; Zutter et al., 1998; Tang et al., 1999a,b; Barnett et al., 2002; Marino et al., 2002). Soil compaction, however, reduces root growth, seedling survival, and shoot growth (Foil and Ralston, 1967) and overall performance is poor on shallow, eroded soils (Fowells, 1965).

2. Materials and methods

2.1. Study sites

Fort Benning is a 73,533 ha military installation in the Fall-line Sandhills near Columbus, Georgia (32°20′N, 84°41′W). Elevations range from 61 to 225 m above sea level. Mean summer temperature is 27 °C, and mean winter temperature is 9 °C; annual rainfall is 130 cm (Mason, 2003; Lozar, 2004). Upland forests at Fort Benning are disturbed by mechanized infantry training (Dale et al., 2002; Dilustro et al., 2002; Garten et al., 2003; Collins et al., 2006). The U.S. Army uses highly disturbed areas for training with tracked vehicles. Training here has removed much of the canopy, changed ground cover, compacted the soils, and exposed bare soil. The infantry uses other areas for training soldiers on foot, including navigation with map and compass, and bivouacking. Finally, parts of the installation are relatively pristine.

Fort Benning is managed for multiple uses, with large tracts of land also used for timber management, recreation, and management of threatened and endangered species. From a management perspective, the training throughout Fort Benning has created a mosaic of habitats of differing quality. Nearly pristine habitat is adjacent to heavily disturbed landscapes used for military training. This mosaic is suited for studies of landscape-level ecosystem change.

We initially assigned several potential sites into three disturbance classes: highly (H), moderately (M), and lightly (L) disturbed (Duda et al., 2003; Graham et al., 2004). Heavily disturbed areas had reduced plant cover, large patches of bare soil, thinner soil A-horizons, gullies, rock pedestals, and other signs of active erosion. There was also abundant evidence of mechanized infantry training (tank tracks, concertina wire, empty shell casings, etc.). Moderately disturbed areas had an intact canopy, established ground cover, and fewer signs of erosion. Nevertheless, gullies were present and there was evidence of soil loss. There was also less evidence of vehicle use. Lightly disturbed areas had minimal disturbance to soils, extensive ground cover, and the highest tree densities and canopy cover. There were also no signs of recent erosion. Moreover, there was little or no evidence of off-road vehicle and infantry use, except on well-established trails. Within each of the three disturbance classes, three sites were selected at random from upland mixed-pine hardwoods forest in two adjacent third-order watersheds. The sampling design was unbiased systematic-random, subject to the qualifications regarding disturbance class. Such a design insures adequate spatial coverage and representation, concurrent with sample independence and an accurate estimation of P values. All sites were in Troup–Cowarts–Nankin Loamy-Sand soils (NRCS, 2007). Two sets of sites were in the Bonham Creek watershed and one was in the Sally Branch watershed (both within HUC 031300030302).

Highly disturbed sites are used for mechanized infantry training with tracked and wheeled vehicles, foot solders, and bivouacs. Moderately disturbed sites had previously experienced such use, but at the time of the study had only foot traffic, with vehicles restricted to roads and trails. Lightly disturbed sites had not experienced recent military training and are being managed for their conservation value. All sites studied at Fort Benning experienced timber harvest, agriculture, and grazing before the 1940s, when these lands were added to the installation. The lightly disturbed sites function in lieu of true controls. There were no completely undisturbed sites of comparable character in the study area.

We selected research sites after a team of experienced field ecologists and resource managers had assessed damage to vegetation and soils. A discriminant-function analysis of six habitat variables effectively separated the three disturbance classes (Krzysik et al., 2005). Lightly, moderately, and highly disturbed sites differed from

each other in soil A-horizon depth and soil compaction. See Duda et al. (2003), Graham et al. (2004, 2008), and Krzysik et al. (2005) for descriptions of the nine sites, and photographs are available online (Graham and Graham, 2008).

Rainfall data were obtained from the U.S. Army Corp of Engineers Mobile District Water Management website (http://water.sam.usace.army.mil/enhw.htm). The Fort Benning Natural Resources Branch provided data on the history of prescribed burning and known wildfires. Temperature data were obtained from the Southeast Regional Climate Center (http://www.sercc.com/).

Based on available data from Fort Benning (1980–2002), the average time between wildfires was 15.07 ± 8.19 years (mean ± standard deviation), and the average time between prescribed burns was 3.84 ± 1.71 years (Graham et al., 2004). The installation's target for prescribed burns is a three year cycle. Ignoring the source of the fire, the average time between burns was 3.24 ± 1.66 years. There was no association between fire (none, wildfire, prescribed) and disturbance class ($\chi^2 = 7.162$, $df = 4$, $P = 0.128$).

2.2. Sampling

In July of 2001, we randomly sampled twenty loblolly at each of the nine sites. For each tree, we recorded the circumference breast height (CBH) and removed two branches 4–5 m above the ground (where possible). From each branch, we measured the annual growth (elongation) increment for 1999 and 2000 (±1 mm) and collected three fascicles of needles from each annual internode (1999 and 2000) per branch, selected at random from among all fascicles produced on the branch in a given year. The three needles of each fascicle were separated and scanned with an Epson Perfection 1200U Scanner at 125 dpi and Adobe Photoshop 5.0 software. Except for a small subsample, lengths were measured once using CI-400 Computer Image Analysis Software (CID Incorporated, Camas, Washington). Previous work with this system showed that measurement error to both scanner and the CI-400 software is a negligible (<1%) percent of the asymmetry variance (Freeman et al., 2004a).

2.3. Growth

We collected a 0.51 cm diameter core from each loblolly, trying to ensure that the core included pith. Cores were dried, mounted, sanded along one side to reveal ring structure, and then scanned (150 dpi) and measured using the same hardware and software as above. Because incremental growth-ring width typically decreases with plant age, we adjusted ring widths using a negative exponential of tree diameter (Fritts, 1976).

2.4. Developmental instability

Developmental instability was assessed as the within-fascicle mean absolute deviation (MAD) of needle length. This measure of variability is the expectation E of $|x_i - \mu|$, where the x_i are the needle lengths within a fascicle and μ is the average needle length for that fascicle. $E|x_i - \mu|$ is analogous to the most common index of fluctuating asymmetry: $E|l - r - \mu|$, where l is the value of a trait on the left and r the value of a trait on the right. $E|x_i - \mu|$ measures the variation in needle length within a fascicle.

Measurement error is a consideration in studies of fluctuating asymmetry (Graham et al., 2010). Because fluctuating asymmetry is a variance, or other measure of dispersion, measurement error augments the true variation among needles in a fascicle. The estimated measurement error (variance among replicates) was 0.002141, which was 32.3% of the asymmetry variance (variance among needles within a fascicle = 0.004486). The signal-to-noise ratio was moderate ($\sigma_{FA}{}^2/\sigma_{ME}{}^2 = 2.095$).

2.5. Statistical analysis

We used repeated-measures analysis of variance (ANOVA) to test the hypotheses that annual growth increment, needle length, and needle asymmetry differed among disturbance classes. Disturbance class was a fixed effect and year was a repeated effect. Sites were random effects nested within disturbance classes, and individual trees were nested within sites. For annual growth increment, branches were nested within individual trees. For needle length and asymmetry, fascicles were nested within branches within individual trees.

We used analysis of covariance (ANCOVA) to test the hypothesis that adjusted tree-ring width differed among disturbance classes. Average growing-season rainfall and temperature were covariates.

We used nested ANOVA to test the hypotheses that age and circumference (CBH) differed among disturbance classes. Disturbance class was a fixed effect, with sites nested within disturbance class and trees nested within sites.

The dependent variables required transformations to meet the assumptions of the ANOVA. Because age generally fits a Poisson distribution (i.e., counts of randomly occurring objects), we used the square root of age in all analyses. Because growth is a multiplicative process, we used $\log_{10}(\text{CBH} + 1)$ as the dependent variable for circumference. For needle length, we used a Box–Cox transformation ($[x^{\lambda} - 1]/\lambda$), where $\lambda = 0.7$. This was especially important for needle asymmetry to prevent either positive or negative size scaling (see Graham et al., 2010). The raw needle lengths exhibited positive size scaling (regression of $\text{var}(x_i)$ on $E(x_i)$, $F = 6.08$, $df = 1$, $P < 0.02$) while the coefficient of variation exhibited negative size scaling ($F = 141.40$, $df = 1$, $P < 0.001$). A Box–Cox transformation with a value of $\lambda = 0.7$ did not exhibit size scaling ($F = 0.010$, $df = 1$, $P > 0.90$).

Whenever there were more than two means, we used Tamhane's T2 post hoc test (Tamhane, 1979). Tamhane's T2 is a conservative test that does not assume equality of variances.

To further explore the effect of disturbance, we used growth-ring data from the four oldest trees (35 to over 50 years of age) at each site to examine the pattern of growth from 1948 to 2001 by computing the Hurst exponent (H) (Beran, 1994). The range of observations R in a time series depends upon the time period τ. The relationship fits the Hurst equation

$$\frac{R}{S} = (a\tau)^H,$$

where R is the range, S is the standard deviation of the range, a is a constant, τ is the time period, and H is the Hurst exponent. The rescaled range, R/S, is a dimensionless ratio. The Hurst exponent is a measure of the rate at which R/S increases with τ. The Hurst exponent is related to the fractal dimension of the time series: $D = 2 - H$.

The Hurst exponent differs depending upon the process producing the growth. Random processes have no memory and generate a random walk (e.g., Brownian motion). Random walks have a Hurst exponent of 0.5. Processes that demonstrate inertia, or persistence, tend to continue moving in the direction they are moving rather than shifting back. Such persistent processes have a Hurst exponent of greater than 0.5. In contrast, processes exhibiting a higher likelihood of changing direction have Hurst exponents less than 0.5. With respect to tree-ring growth, given no internal buffering (i.e., autocorrelation), the Hurst exponent should be 0.5 if favorable years occur at random. Prolonged periods of good (or bad) growing seasons should yield an exponent greater than 0.5, whereas if good years are followed by bad years, the Hurst exponent should be less than 0.5. To the extent that individuals buffer

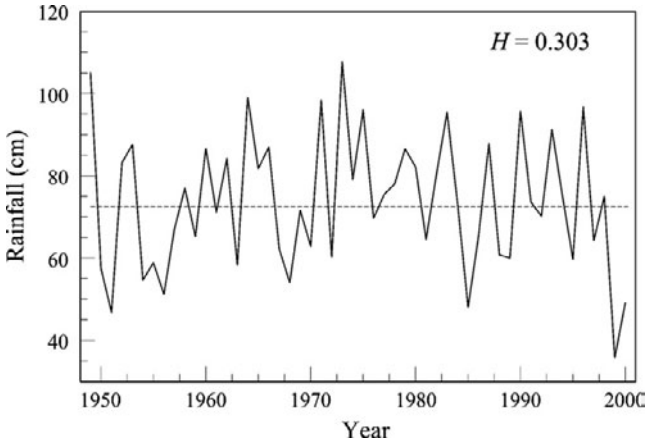

Fig. 1. Rainfall (in cm) for the water year (March–October) of the study period. The dashed line is the 55-year average.

themselves from environmental change, fluctuations in tree-ring width should be dampened relative to fluctuations in environmental conditions. This will manifest in a tree-ring Hurst exponent exceeding those of the climate conditions upon which growth depends (temperature and rainfall). A priori, we expected that plants at the lowest disturbance would display the highest Hurst exponents, since these plants should best buffer environmental fluctuations, whereas those at the heavily disturbed sites should display less persistent growth (Emlen et al., 1993; Beran, 1994).

3. Results

3.1. Rainfall

We used the record of rainfall at Fort Benning (Fig. 1) to evaluate conditions for growth and developmental instability of loblolly pine in the three years from 1998 to 2000. Over the 55-year period, average rainfall for the water year (October–April) was 72.9 cm. For the period 1948–2001, rainfall had a Hurst exponent (H) of 0.303 ± 0.0105 (mean $\pm$ 95% confidence interval, $r^2 = 0.850$, $P < 0.001$).

3.2. Temperature

Average annual temperatures, especially those during the growing season (March–October), also have the potential to influence growth and developmental instability of loblolly pine (Fig. 2). The

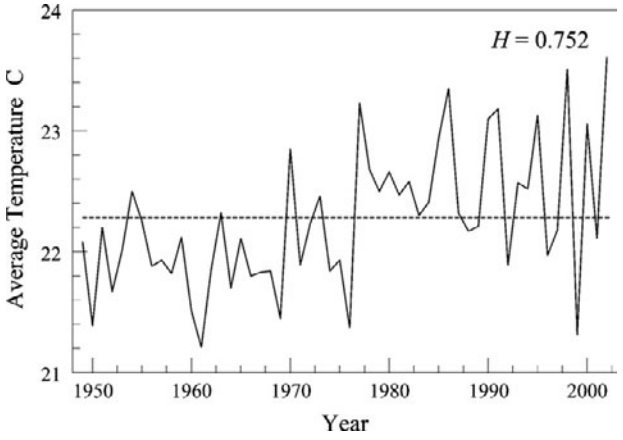

Fig. 2. Average growing season (March–October) temperature in °C. The dashed line is the 55-year average.

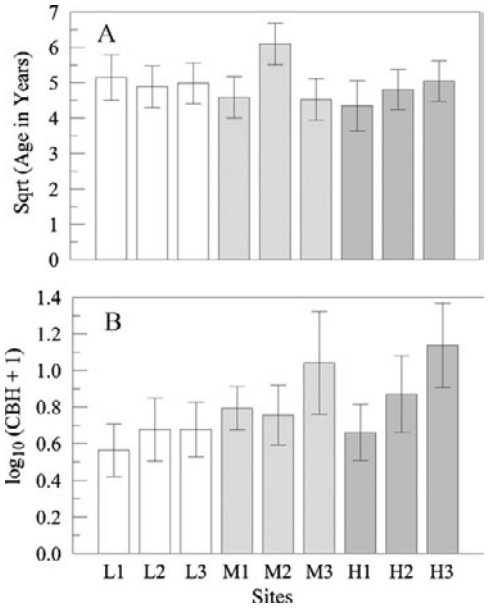

Fig. 3. Age and circumference breast height (CBH) by site within disturbance class. (A) Square root of age, and (B) $\log_{10}$(CBH + 1). Error bars are 95% confidence intervals. L1, L2, and L3 are light disturbance. M1, M2, and M3 are moderate disturbance. H1, H2, and H3 are heavy disturbance.

lowest average temperature during the growing season occurred in 1961 (21.2 °C), whereas the highest average temperature during the growing season occurred in 2002 (23.6 °C), the last year of record during the study. The average temperature, over all growing seasons, was 22.3 °C (standard deviation = 1.0).

The average annual temperature was correlated with the growing season annual temperature ($r = 0.624$, $df = 50$, $P < 0.0001$), and uncorrelated with precipitation during the growing season ($r = 0.035$, $df = 50$, $P > 0.75$). The average annual temperature had a Hurst exponent of 0.752 ± 0.005 (mean $\pm$ 95% confidence interval, $r^2 = 0.992$, $P < 0.001$). The average annual temperature during the growing season had a Hurst exponent of 0.75 ± 0.005 (mean $\pm$ 95% confidence interval, $r^2 = 0.992$, $P < 0.001$).

3.3. Loblolly pine age and size

Neither age (square root of age in years) nor circumference ($\log_{10}$[CBH + 1]) differed among the three disturbance classes (age: $F_{2,6} = 0.295$, $P > 0.75$; CBH: $F_{2,6} = 2.38$, $P > 0.17$). Much of the variation in age and CBH was among sites within disturbance classes (age: $F_{6,156} = 3.42$, $P < 0.005$; CBH: $F_{6,170} = 3.25$, $P < 0.01$). Ignoring disturbance class, there were differences in age ($F_{8,156} = 2.743$, $P < 0.01$) and CBH ($F_{8,170} = 4.335$, $P < 0.001$) among the nine sites (Fig. 3). Trees at M2 were older than those at M1, M3, and H1 (Tamhane T2, all $P < 0.05$). Trees at L1 had smaller CBH than those at either H3 (Tamhane T2, $P < 0.005$) or M3 (Tamhane T2, $P < 0.05$). Trees at H1 were marginally smaller than those at H3 (Tamhane T2, $P = 0.05$).

Circumference, standardized by age, is a measure of long-term growth. When age was used as a covariate in an analysis of covariance (ANCOVA), there was still no difference in CBH among disturbance classes ($F_{2,6} = 2.275$, $P > 0.180$).

3.4. Branch annual growth increment

The annual growth increment ($\log_{10}$[internode length + 1]) was greater in 1999 than in 2000 (repeated measures ANOVA, $F_{1,169} = 48.75$, $P < 0.001$) (Fig. 4). Moreover, there were differences in growth increment among disturbance classes (repeated measures

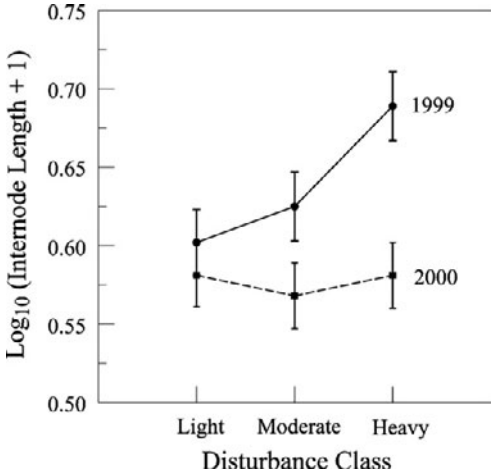

Fig. 4. Internode length by year and disturbance class. Error bars are 95% confidence intervals.

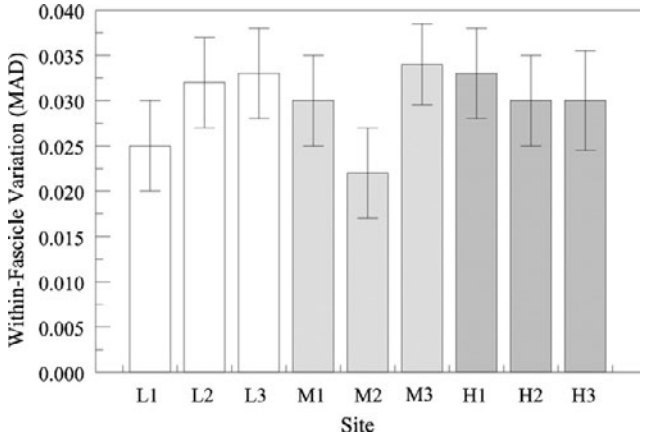

Fig. 6. Needle asymmetry [mean absolute deviation, with Box–Cox transformation ($\lambda = 0.7$) of needle lengths] by site and disturbance class. Error bars are 95% confidence intervals.

ANOVA, $F_{2,6} = 13.878$, $P < 0.001$). Trees at the highly disturbed sites had greater annual growth than trees at the lightly disturbed sites (Tamhane T2, $P < 0.025$) and they had marginally greater growth than trees at the moderately disturbed sites (Tamhane T2, $P < 0.06$). There was a disturbance-by-year interaction as well (repeated measures ANOVA, $F_{2,169} = 7.54$, $P < 0.001$). The differences in growth among disturbance classes were pronounced in 1999, but not in 2000 (Fig. 4).

Variation among sites within disturbance class was not nil (repeated measures ANOVA, $F_{6,165} = 28.58$, $P < 0.001$). Indeed, it accounts for much of the variation in yearly branch growth. Moreover, trees within sites within disturbance class differed as well (repeated measures ANOVA, $F_{165,169} = 2.42$, $P < 0.001$).

3.5. Average needle length

Average needle length (Box–Cox transformation, $\lambda = 0.7$) differed between years (repeated measures ANOVA, $F_{1,170} = 505.12$, $P < 0.001$). Needle length in 2000 was only 80.2% of what it was in 1999. It also increased with increasing disturbance (repeated measures ANOVA, $F_{2,6} = 4.021$, $P < 0.025$, Fig. 5), but the post hoc comparisons among disturbance classes were insignificant (Tamhane's T2, $P > 0.30$). There was also variation in needle length among sites within disturbance classes (repeated measures ANOVA, $F_{6,165} = 4.957$, $P < 0.001$) and among plants within sites (repeated measures ANOVA, $F_{165,170} = 3.428$, $P < 0.001$).

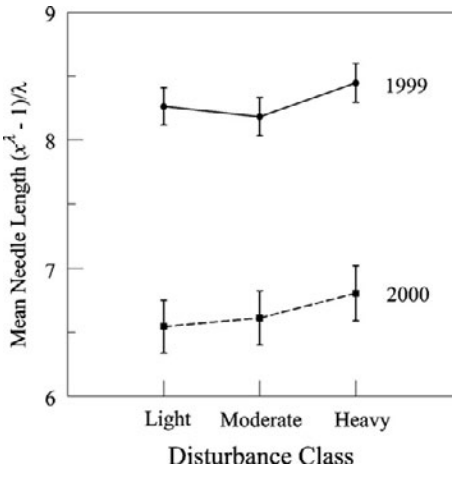

Fig. 5. Box–Cox transformation ($\lambda = 0.7$) of needle length by year and disturbance class. Error bars are 95% confidence intervals.

3.6. Developmental instability of needles

The within-fascicle mean absolute deviation (MAD) of needle length did not vary between years (repeated measures ANOVA, $F_{1,170} = 0.198$, $P > 0.65$) and disturbance classes (repeated measures ANOVA, $F_{2,170} = 0.463$, $P > 0.60$). Moreover, the interaction of years and disturbance was insignificant (repeated measures ANOVA, $F_{2,170} = 0.365$, $P > 0.33$). There was, however, variation among sites within disturbance classes (repeated measures ANOVA, $F_{6,165} = 3.261$, $P < 0.01$), but not among plants within sites (repeated measures ANOVA, $F_{165,170} = 1.214$, $P > 0.10$). In post hoc comparisons of the nine sites (repeated measures ANOVA, $F_{8,165} = 2.58$, $P < 0.015$), three comparisons were marginally significant (Tamhane T2, $P < 0.09$). Sites H1, M3, and L2 all showed greater variation in within-fascicle needle length than M2 (Fig. 6).

3.7. Growth ring width

The logarithm of the adjusted ring growth declined as the average growing-season temperature increased ($F_{1,4176} = 4.67$, $P < 0.05$) and as growing-season precipitation decreased ($F_{1,4176} = 3.92$, $P < 0.05$). After removing the effects of temperature and precipitation, ring width increased as disturbance increased ($F_{2,6.072} = 5.52$, $P < 0.05$, Fig. 7).

We examined the adjusted width of the growth rings over time to determine if disturbance influenced the persistence of growth patterns, as measured by the Hurst exponent (Emlen et al., 1993). As expected, the tree-ring Hurst exponent exceeded that for both rainfall and temperature. More importantly, it did not differ across the disturbance gradient (Fig. 7).

4. Discussion

We evaluated the effects of military training on growth and developmental instability of loblolly pine at Fort Benning, Georgia. Our data span several temporal scales. The annual increment of branch growth, needle length, and the developmental instability of needle length provide scales of less than two years. Tree growth rings and the Hurst exponent allow us to look at scales of fifteen to over fifty years. Overall, soil disturbance had little negative effect on loblolly performance. It enhanced growth, but had no effect on within-fascicle needle-length variation. Drought, on the other

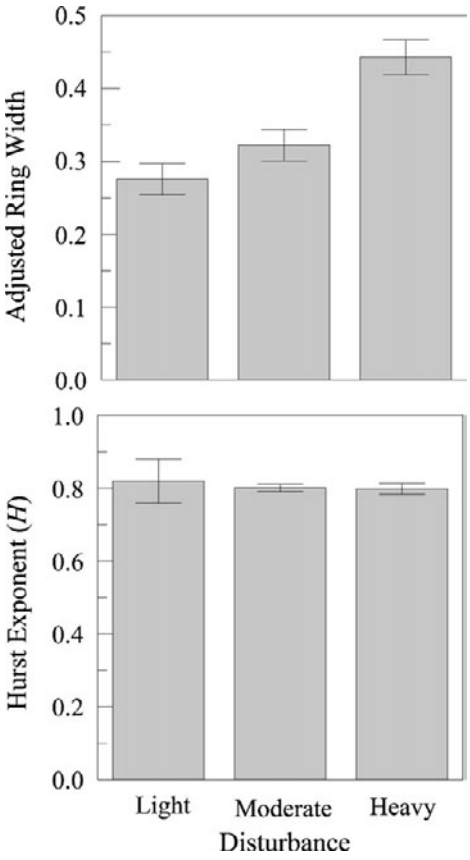

Fig. 7. Adjusted tree-ring widths and Hurst exponent by disturbance class. Error bars are 95% confidence intervals.

hand, had a negative effect on loblolly growth and tree-ring width, though it did not influence needle-length variation.

4.1. Rainfall and temperature

Hurst exponents for the time series of rainfall and temperature at Fort Benning indicate long-term climatic patterns. Rainfall was anti-persistent ($H < 0.5$), frequently swinging between moist and dry years. Especially relevant to our study, a drought began in 1999 and continued through 2000. Temperature was persistent ($H > 0.5$), moving in the same, warmer, direction rather than swinging between temperature extremes.

4.2. Growth

The annual increment of branch growth, needle length, and the adjusted width of growth rings all increased with military disturbance. Thus, disturbance positively influenced plant growth. Consequently, disturbance, per se, is not a stress for loblolly, though frequent disturbance does reduce the ability of the pines to grow during prolonged droughts (Zahner and Saucier, 1989; Chen et al., 1994; Oberhuber et al., 1998). The most likely explanation for this surprising outcome is that disturbance at Fort Benning removes understory competitors, thereby reducing stress.

There is evidence that understory plants can depress growth of loblolly through competition (Haywood et al., 1997; Marino et al., 2002; Martin and Jokela, 2004). Heavily disturbed sites at Fort Benning have more bare ground than the lightly and moderately disturbed sites (Duda et al., 2003; Krzysik et al., 2005). They also have less woody ground cover and less canopy cover.

Loblolly also does better on the edges of forest fragments. McDonald and Urban (2004) found that individuals growing on the edges grew faster than those in the interior. Nevertheless, the effect was small. Forest edges explained less of the variance in growth rate than did soil texture, soil nutrients, and topography.

Soil ammonia concentrations were highest at the undisturbed sites and lowest at the highly disturbed sites, while soil nitrate followed an opposite pattern (D.A. Kovacic, University of Illinois, unpublished data). Taken together, these suggest that competition from understory vegetation, along with soil organic matter, is mediating the nutrients available for loblolly growth. Because the soil carbon compartment is lacking at the highly disturbed sites (DeBusk et al., 2005; Maloney et al., 2008), its ability to influence nutrients is likely reduced, resulting in a simplified two-compartment system. Such simplification should lead to pronounced oscillations and reduced complexity in growth over time, though we were unable to detect such reductions in complexity. Pinyon pines having pronounced oscillations have increased mortality (Ogle et al., 2000).

The interaction of year and disturbance on annual increment of branch growth suggests that highly disturbed sites are less resilient to drought than lightly and moderately disturbed sites. In 1999, the trees had been exposed to one year of drought. By 2000, they had been exposed to two years of drought.

4.3. The effects on buffering of stress

The Hurst exponents for growth rings in loblolly ($H = 0.80–0.82$) exceeded those for temperature ($H = 0.75$) and precipitation ($H = 0.30$), indicating that loblolly's growth is more persistent than are the patterns of these climatic variables. Trees do indeed buffer themselves against the vicissitudes of nature.

4.4. The effect of year

We have data on needle length and branch length for two years: 1999 and 2000. A drought began in 1999 and intensified in 2000. Needle length in 2000 was 80.2% of what it was in 1999 at all disturbance levels; so there was a clear effect of year on needle growth. Similarly, branch growth was less in 2000 than in 1999. The interaction of year and branch growth suggests that drought blunts the positive effects of disturbance on growth. McDonald and Urban (2004) found a similar response in that the difference in growth between loblolly on a forest edge and those in the forest interior was greater on drier soils. Houle and Delwaide (1991) found that loblolly growing on rock outcrops were more sensitive to drought than those on nearby Piedmont.

4.5. Developmental instability

We used the within-fascicle mean absolute deviation (MAD) of needle lengths to assess developmental instability. Neither year nor disturbance class had an effect on developmental instability of needle length. There were differences in MAD among the nine sites, with H1, M3, and L2 having more variable needle lengths within a fascicle than those at M2. We are unsure what is responsible for these differences.

4.6. General comments

Our highly disturbed sites were obviously degraded. The bare ground and erosion suffice to convince. But the pattern of loblolly growth was unexpected: internode length, needle length, and tree-ring width all improved as disturbance increased. Clearly, growth does not provide a useful diagnostic indicator of stress for natural resource managers responsible for Fort Benning ecosystems.

Elsewhere, we reported the developmental instability of three other species sampled at the same sites, two herbs, finger rot (*Cnidoscolus stimulosus* [Michx.] Engelm. & Gray) and morning glory (*Ipomoea pandurata* [L.] G.F.W. Mey), and a shrub, sumac (*Rhus copallinum* L.) (Duda et al., 2003; Freeman et al., 2004a,b, 2005). This allows us to compare developmental instability across species. Finger rot had more asymmetric leaves at the highly disturbed sites. Morning glory, in contrast, had the lowest leaf asymmetry in the moderately disturbed sites.

We also examined net photosynthesis, transpiration, variable fluorescence, and water stress of sumac at these same sites (Duda et al., 2003; Freeman et al., 2004b). These are our short-term indicators of stress. Like growth, net photosynthesis of sumac and morning glory increased with increasing disturbance, especially after fire. There was no clear disturbance effect on water stress or variable fluorescence. The fluorescence did indicate that all sites were stressful; however, there was no pattern to the amount of stress (Duda et al., 2003; Freeman et al., 2004b).

Of necessity, we studied species found at all nine sites. Unfortunately, the landscape is a mosaic of disturbance, and individuals may occur only in favorable microhabitats surrounded by degraded habitat, precluding any real measure of stress (Duda et al., 2003).

Another explanation for the lack of increase in developmental instability with disturbance of loblolly could be that the ecosystem has adjusted to military activities, such that the disturbance no longer constitutes a stress. This simple conclusion is suggested by the increased growth in the disturbed areas, but is complicated by the higher developmental instability with high disturbance in both finger rot and sumac, and by the apparent loss of buffering capacity in loblolly with increased disturbance, as indicated by the reduction in growth in 2000 relative to 1999 at the most disturbed sites.

5. Conclusions

None of our indices of growth indicated that disturbance by military training was stressful to loblolly pine. Contrary to expectations, disturbance improved branch growth, needle length, and ring width, possibly by alleviating competition. Drought, on the other hand, depressed growth, thereby indicating these events to be stressful. These results are consistent with the idea that indicators of stress are useful only while stress-induced ecosystem changes are actually taking place. Once a change has occurred, the system adjusts to the new conditions, which cease being stressful. Unpredictable changes, however, such as drought, permit only a lagging response, and so continue to be stressful.

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