

HURRICANE DAMAGE INFLUENCES FOLIAR POLYPHENOLICS AND SUBSEQUENT HERBIVORY ON SURVIVING TREES

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Abstract. Hurricane damage results in tree mortality and variation in both light and nutrient availability for the individuals that remain. In turn, resource availability influences the interactions between plants and insect herbivores. We report effects of Hurricane Opal on the phenolic chemistry and levels of defoliation on surviving trees at the Coweeta Hydrologic Laboratory in North Carolina. We measured foliar astringency, hydrolysable tannins, and condensed tannins in the foliage of red maple and red oak saplings in hurricane-damaged and undamaged sites. We estimated inorganic nitrogen and phosphorus availability in the soil, and the accumulated leaf area removed by insect herbivores. The foliar astringency of both red maple and red oak was higher in sites damaged by the hurricane. Later in the growing season, condensed tannin levels were significantly higher in the foliage of red oak in damaged sites. There were no consistent differences in ammonium, nitrate, or phosphate availability between damaged and undamaged sites. Despite higher foliar astringency of trees in sites damaged by Hurricane Opal, levels of defoliation by insect herbivores were higher in damaged than in control sites on both tree species. Apparent increases in putative defensive compounds following hurricane damage did not protect trees from herbivory.

Key words: *Acer rubrum*; carbon : nutrient balance; disturbance; Hurricane Opal; plant defenses; *Quercus rubra*; tannins.

INTRODUCTION

Abiotic disturbance can have a profound effect on vegetation structure and the availability of resources for plants (Pickett and White 1985). Major disturbances to forested areas such as extensive windthrow are known to affect tree species composition and the trajectory of succession (Henry and Swan 1974, Oliver and Stevens 1977, Peterson and Pickett 1990, Walker 1991, Zimmerman et al. 1996), but may also have more subtle effects on the phenotype of surviving trees. For example, hurricane damage influences both the availability of light and nutrients for remaining (and regenerating) trees (Fetcher et al. 1983, Beatty 1984, Chazdon and Fetcher 1984, Peterson et al. 1990, Zimmerman et al. 1995). The relative availability of light and nutrients is central to current evolutionary (Coley et al. 1985) and ecological (Chapin 1980, Bryant et al. 1983, 1993) theory of allocation to defense, and plant–insect interactions.

One previous study has shown that insect community composition can change following hurricane damage (Schowalter 1994), although foliage quality was not measured explicitly. The generation of experimental forest gaps has been shown to influence both the foliage chemistry of resprouts in gaps and subsequent levels of insect herbivory (Shure and Phillips 1991, Shure and Wilson 1993, Dudd and Shure 1994). The studies

by Shure and colleagues clearly demonstrate the importance of gap formation and light availability for plant–insect interactions in temperate forests. However, experimental gaps may not mimic hurricane damage because they are usually generated in winter after leaf abscission, with selective removal of felled trees. In contrast, hurricane damage in temperate forests generally occurs when trees are foliated, and deposition of both green leaf material and woody debris is extensive.

Our study was designed to measure the effects of gaps formed by Hurricane Opal at the Coweeta Hydrologic Laboratory, North Carolina, on foliar astringency, tannin concentration, and herbivory on surviving red oak (*Quercus rubra*) and red maple (*Acer rubrum*) trees. We envisaged two alternative outcomes. First, if gaps formed by hurricanes are not qualitatively different from artificial gaps, we would expect to see increases in foliar astringency and tannins (Shure and Wilson 1993, Dudd and Shure 1994). Such increases are considered to be consistent with the carbon : nutrient balance hypothesis (Chapin 1980, Bryant et al. 1983, 1993), whereby increased carbon gain relative to nutrient availability favors allocation to carbon-based defenses. Alternatively, if hurricane damage results in a pulse of nutrient availability from deposition of green leaf material to the forest floor, we would expect declines in foliar astringency and tannin concentrations as carbon is allocated preferentially to growth over defense. In either case, we expected foliar astringency and tannin concentrations to be negatively

Manuscript received 13 May 1998; revised 30 November 1998; accepted 6 December 1998.

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associated with defoliation by insect herbivores (Shure and Wilson 1993, Dudt and Shure 1994).

SYSTEM OF STUDY AND METHODS

The 2185-ha Coweeta Hydrologic Laboratory is within the Nantahala Mountains of western North Carolina, within the Blue Ridge Physiographic province (35° N, 83°30' W). Elevations range from 686 to 1600 m and the climate of the region is characterized by cool summers, mild winters, and abundant rainfall evenly distributed in all seasons. Average annual precipitation ranges from 1700 mm at lower elevations to 2500 mm on the upper slopes. Mean monthly temperatures vary from 3.3°C in January to 21.6°C in July.

On Thursday, 5 October 1995, the Coweeta Long-Term Ecological Research Site was struck by Hurricane Opal (0400 to 1100). Sustained winds with gusts exceeding 130 km/h occurred, and rainfall totaled 23 cm. The hurricane event was characterized by heavy convection storms, creating microbursts in a patchwork across the landscape. Due to a combination of ground saturation and heavy winds, these microbursts produced extensive windthrow in relatively discrete patches of damage with adjacent undamaged areas. Damage was most severe on south- and east-facing slopes, particularly on ridges. The main tree casualties were the larger crowned trees, particularly oaks and some white pines. Several other species were also downed in the pathway of the larger crowned trees. Wind conditions also resulted in the loss of many live branches and twigs that still held green foliage, and the shredding of many leaves directly from the canopy. Observations suggested that most leaf deposition occurred from canopy trees, and that saplings lost relatively few leaves. However, we did not directly quantify leaf loss from understory saplings, and such losses have the potential to influence foliar chemistry in subsequent growing seasons. Overall, there was significant deposition of both greenfall (living green tissue) and woody debris on the forest floor. Independent estimates by state agencies suggest that increased inputs to the forest floor averaged 7 Mg/ha, with >135 Mg/ha of greenfall and woody debris in some patches. Historical records show that the last wind event of this magnitude occurred in 1835 and produced similar types of forest damage (U.S. Forest Service, *unpublished data*).

The pattern of forest damage caused by the microbursts of Hurricane Opal allowed us to compare discrete areas of windthrow with adjacent undamaged areas. We chose three sites for study within the drainage basin: Barker's Cove (elevation 954 m, aspect southeast, 0.25-ha damage), Dyke's Gap (elevation 994 m, aspect southeast, 0.2-ha damage), and Little Pinnacle (elevation 1151 m, aspect east-southeast, 0.4-ha damage). Each site was represented by an area of windthrow adjacent to an undamaged area, for a total of six study areas. Within each area, we measured the availability of mineral nitrogen and phosphorus, the concentration

of foliar tannins in surviving saplings of red oak and/or red maple, and the accumulation of insect herbivory. Due to difficulties of access, we were unable to begin our sampling until the 1997 growing season. One weakness of our study, therefore, is that we lack data for the 1996 growing season.

Red maple foliage was collected for chemical analysis at ~2-mo intervals (8 May, 8 July, and 10 September 1997). On each date, foliage was collected from 10 saplings, 1–2 m in height, in each study area. Saplings were chosen at random from all red maple saplings 1–2 m in height within 20-m radius circles centered within the damaged and undamaged areas of each site. Few red oak saplings survived the hurricane damage at Dyke's Gap, so oak collections were made only from Barker's Cove and Little Pinnacle. In addition, oak saplings were generally rarer than maple saplings at all sites and, to avoid repeated sampling of individual trees, we collected foliage from oak on only two dates (8 May and 10 September).

On each date, we collected 12 leaves distributed approximately evenly in the canopy of each tree. Samples were flash-frozen in liquid nitrogen and returned to the lab for analysis. Samples were lyophilized, ground to a fine powder, prewashed in diethyl ether, and extracted in 70% acetone. The acetone was removed by evaporation under reduced pressure, and proanthocyanidins, our estimate of condensed tannins, were assayed using methods described in Rossiter et al. (1988). The ability of extracts to bind protein was measured using the radial diffusion assay with bovine serum albumin as standard protein (Hagerman 1987). Gallotannins (hydrolysable tannins) were estimated using a potassium iodate technique developed by Bate-Smith (1977) and modified by Schultz and Baldwin (1982). Given recent concerns about the purity of tannic acid as a standard in tannin analysis (Hagerman and Butler 1991; J. C. Schultz, *unpublished data*), we used bulk-purified oak and maple tannin as standards for gallotannin and proanthocyanidin analyses. Standards were generated by multiple sequential washes of bulk samples in diethyl ether, followed by acetone extraction.

Nutrient availability was measured using cation and anion resin exchange bags (Amer et al. 1955, Binkley and Matson 1983). Ten anion and 10 cation bags, saturated either with OH⁻ or H⁺ (Binkley 1984), were buried at a depth of 8 cm in the soil at random coordinates within a 20-m radius circle at the center of each study area. Bags were introduced on 22 February 1997 and replaced on 18 April, and 19 June (~2-mo intervals) with a final collection on 26 August (i.e., three periods of measurement). Resins were extracted in KCl and assayed for anion (NO₃⁻, PO₄⁻) and cation (NH₄⁺) mineral nutrients using an Alpkem spectrophotometer (Alpkem, Clackamas, Oregon).

We measured the accumulation of insect defoliation in each study area on 10 September 1997. Twelve saplings of each tree species were chosen at random within

the 20-m circles centered at each study area. All the leaves on each sapling ($50 < N < 200$) were visually inspected for damage and scored as belonging to one of seven damage classes representing estimated percent leaf area removed (LAR) (Hunter 1987, Hunter and Schultz 1993, Hunter and Schultz 1995). These were then averaged to give a single value of LAR for each individual tree. Data were arcsine square-root transformed before analysis.

ANALYSES

After arcsine square-root transformation of the defoliation measures, no data deviated significantly from normal distributions (Proc Univariate Procedure, SAS 1985). Foliar astringency and tannin concentrations were compared separately for red oak and red maple. We used repeated-measures analysis of variance (SAS 1985) with Site and Hurricane Status as between-subject main effects and Date as the within-subject main effect. Degrees of freedom vary between the oak and maple analyses because the oaks were sampled at one less site, and on one less date, than the maples. In addition, two hydrolysable tannin and two condensed tannin samples were lost from red maple, reducing the sample size from 180 to 178 for both analyses ($10 \text{ trees} \times 6 \text{ study areas} \times 3 \text{ dates}$). Nitrate, ammonium, and phosphate availability were compared separately by repeated-measures analysis of variance as before, with Site and Hurricane Status as between-subject main effects and Date as the within-subject main effect. After transformation, defoliation levels were compared separately for each species using two-way analysis of variance, with Site and Hurricane Status as main effects. In all analyses, means were compared by Tukey's hsd test (SAS 1985).

RESULTS

The foliar astringency of red maple was higher in areas damaged by Hurricane Opal than in adjacent, undamaged areas ($F = 66.22$, $df = 1, 54$, $P < 0.0001$, Fig. 1A). The difference was consistent among sites and dates (no hurricane by site or date interactions). The elevated foliar astringency could not be explained by our estimates of either hydrolysable (Fig. 1B) or condensed (Fig. 1C) tannins. Astringency of red maple foliage may be related instead to concentrations of "acertannin" (Haslam 1989), which may not be adequately assayed by standard tannin procedures (A. E. Hagerman, *personal communication*). Hydrolysable tannins were marginally higher in two control areas undamaged by the hurricane, compared with their adjacent damaged areas (Site \times Hurricane interaction $F = 3.75$, $df = 2, 54$, $P = 0.030$, Fig. 1B). Condensed tannins varied among sites and dates (Site \times Date interaction $F = 18.47$, $df = 4, 106$, $P < 0.0001$, Fig. 1C), with no significant contribution of Hurricane Status. Rather, season and study site appear to dominate variation in foliar condensed tannin concentrations.

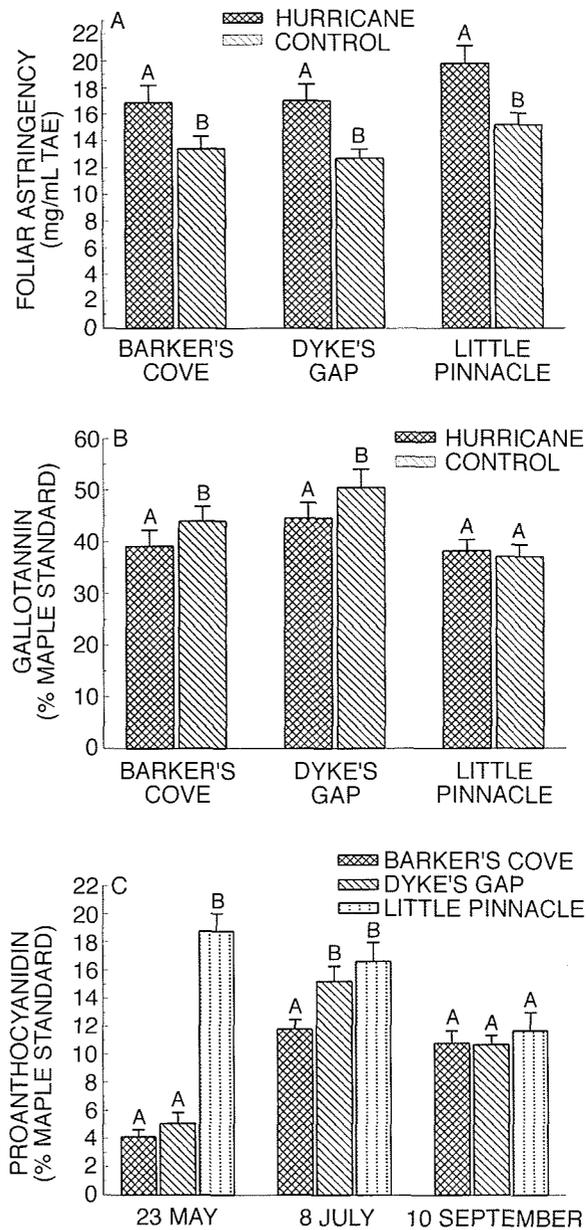


FIG. 1. Estimates of (A) foliar astringency, (B) hydrolysable tannin, and (C) condensed tannin from the foliage of *Acer rubrum* at the Coweeta Hydrologic Laboratory, North Carolina. Within groups, bars that share letters are not significantly different after Tukey's hsd test. Bars (+1 SE) represent (A) data pooled among dates with $N = 30$, (B) data pooled among dates with $N = 29$, and (C) data pooled among hurricane damage status with $N = 20$. TAE refers to tannic acid equivalents.

The foliar astringency of red oak was initially higher in areas damaged by the hurricane than in adjacent undamaged areas (Fig. 2A). The significant difference disappeared by the end of the growing season (Hurricane \times Date interaction $F = 6.94$, $df = 1, 36$, $P = 0.012$). Concentrations of hydrolysable tannin were

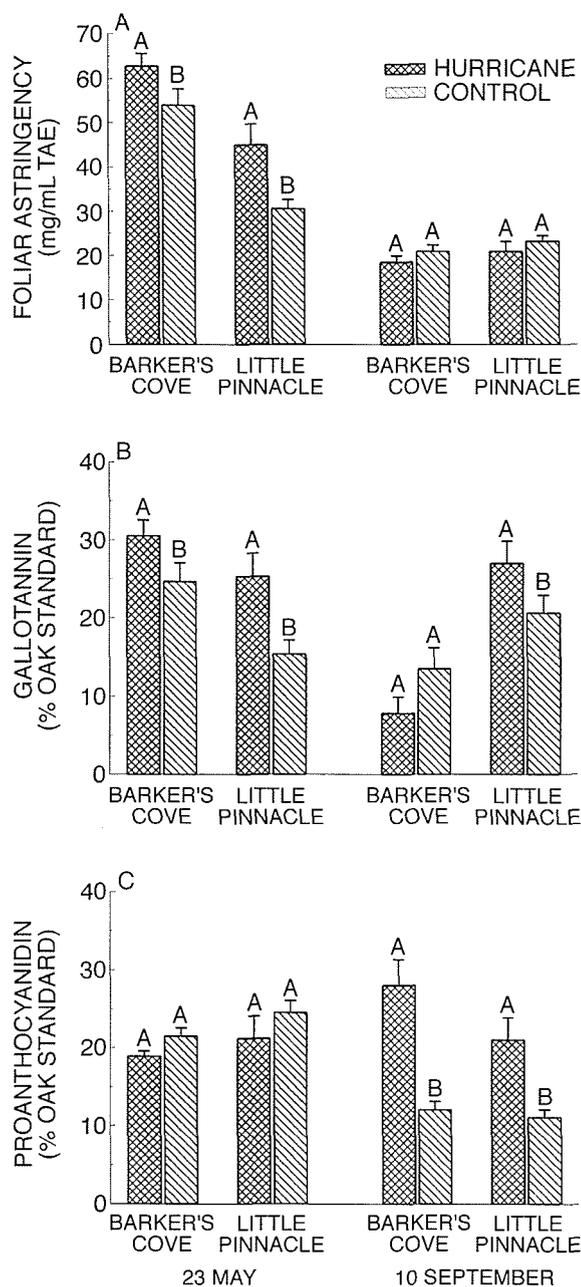


FIG. 2. Estimates of (A) foliar astringency, (B) hydrolysable tannin, and (C) condensed tannin from the foliage of *Quercus rubra* at the Coweeta Hydrologic Laboratory, North Carolina. Within groups, bars that share letters are not significantly different after Tukey's hsd test. Bars (with standard errors) represent the means of 10 samples (trees). TAE refers to tannic acid equivalents.

somewhat similar to patterns of astringency, with significantly higher levels in areas damaged by the hurricane at both sites in May, and at one site in September ($F = 7.10$, $df = 1, 36$, $P = 0.011$, Fig. 2B). When sites and dates were combined, hydrolysable tannins explained 59% of the variation in the foliar astringency

of red oak ($df = 79$, $P < 0.0001$, Fig. 3). Condensed tannin concentrations were significantly higher in areas damaged by the hurricane at the end of the growing season, although they were initially similar (Hurricane \times Date interaction $F = 29.37$, $df = 1, 36$, $P < 0.0001$, Fig. 2C).

Hurricane status had no significant effect on the availability of nitrate, ammonium, or phosphate in the soil. Nutrient availability appeared to vary idiosyncratically with site and date (Fig. 4). Defoliation by insect herbivores (Fig. 5) was higher in areas damaged by the hurricane ($F = 60.09$, $df = 1, 66$, $P < 0.0001$, and $F = 11.13$, $df = 1, 44$, $P = 0.002$ for red maple and red oak, respectively).

DISCUSSION

The most consistent effect of Hurricane Opal was to raise the foliar astringency of surviving saplings of red maple and red oak in comparison to saplings in undamaged control areas (Fig. 1A and 2A). It also elevated early-season concentrations of hydrolysable tannin and late-season concentrations of condensed tannin in red oak foliage (Fig. 2B and C). Surprisingly, defoliation by insect herbivores was also higher in areas damaged by the hurricane compared with adjacent undamaged areas (Fig. 5). There were no consistent effects of hurricane damage on mineral nutrient availability (Fig. 4).

Our results are in broad agreement with previous studies of foliar chemistry of trees in artificial gaps (Shure and Phillips 1991, Shure and Wilson 1993, Dudd and Shure 1994). For example, Shure and Wilson (1993) reported higher concentrations of total phenolics in the foliage of *Robinia pseudoacacia*, *Liriodendron tulipifera*, *Acer rubrum*, and *Cornus florida* regenerating in artificial gaps than in the foliage of trees growing in the understory. Similarly, *L. tulipifera* and *C. florida* saplings planted in microenvironments varying in light availability exhibited higher foliar phenolic concentrations in high-light than in low-light environments (Dudd and Shure 1994). The artificial gaps in the studies by Shure and colleagues were generated after leaf fall, and included selective removal of felled trees. Despite the considerable deposition of green leaf material and woody debris during Hurricane Opal, the results presented here are similar. Nutrient availability was highly variable among sites, and showed no consistent pattern with hurricane damage. However, the availability of nutrients may not reflect their uptake by plants. Similarly, increased light availability does not necessarily result in higher rates of photosynthesis, higher carbon : nutrient ratios, and allocation of carbon to phenolic defenses. Although our results can be interpreted within the framework of the carbon : nutrient balance hypothesis (Chapin 1980, Bryant et al. 1983, 1993), we measured neither nutrient uptake nor rates of photosynthesis in the present study. Although previous experimental work with oaks has shown that their

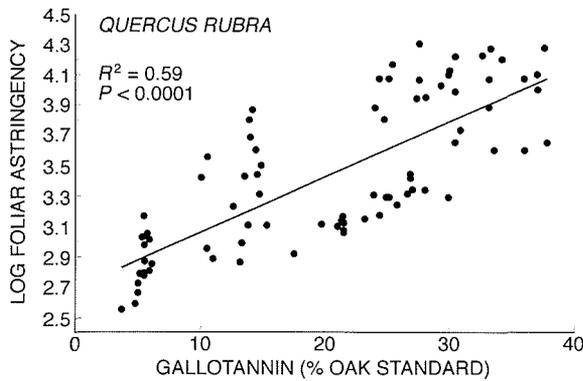


FIG. 3. The relationship between the gallotannin concentration of red oak foliage and foliar astringency. $N = 80$ points (10 trees \times 4 sites \times 2 dates). Although a simple correlation is also significant ($r^2 = 0.52$, $df = 79$, $P < 0.001$), the relationship is improved by using the natural log of foliar astringency (original units in mg/mL).

defenses vary according to the carbon : nutrient balance model (Hunter and Schultz 1995), it is premature to conclude that the increases in foliar phenolics observed in the current study were the result of high carbon : nutrient ratios resulting from increased light availability.

One notable difference between our study and previous work is the higher levels of defoliation by herbivores in hurricane-damaged sites (Fig. 5), despite their elevated foliar phenolics. In general, previous studies of artificial gaps have recorded lower levels of herbivory associated with large gaps and high foliar phenolic concentrations (Shure and Wilson 1993, Dudd and Shure 1994). Although our study was conducted in the same geographic region (the southern end of the Blue Ridge province of the Appalachians), there was only partial overlap in the tree species examined. Specifically, earlier studies focused upon black locust, dogwood, tulip poplar, and red maple (Shure and Wilson 1993), whereas we examined responses of red oak and red maple. Some of the differences may therefore simply reflect the responses of different suites of herbivores associated with particular tree species. This has been suggested previously by Schowalter (1994), who reported that herbivory varied more among tree species than disturbance category following damage by Hurricane Hugo at the Luquillo Experimental Forest, Puerto Rico. Nonetheless, Shure and Wilson (1993) reported lower levels of herbivory associated with high foliar phenolic concentrations in red maple, whereas we found higher levels of herbivory associated with high foliar phenolics. Like previous authors, we have made the assumption that foliar phenolics and tannins are the dominant antiherbivore compounds in the foliage of oak and maple. Certainly, there is considerable evidence that phenolic-based compounds dominate oak and maple defenses (Schultz et al. 1982, Rossiter et al. 1988, Kinney et al. 1997). However, other phytochem-

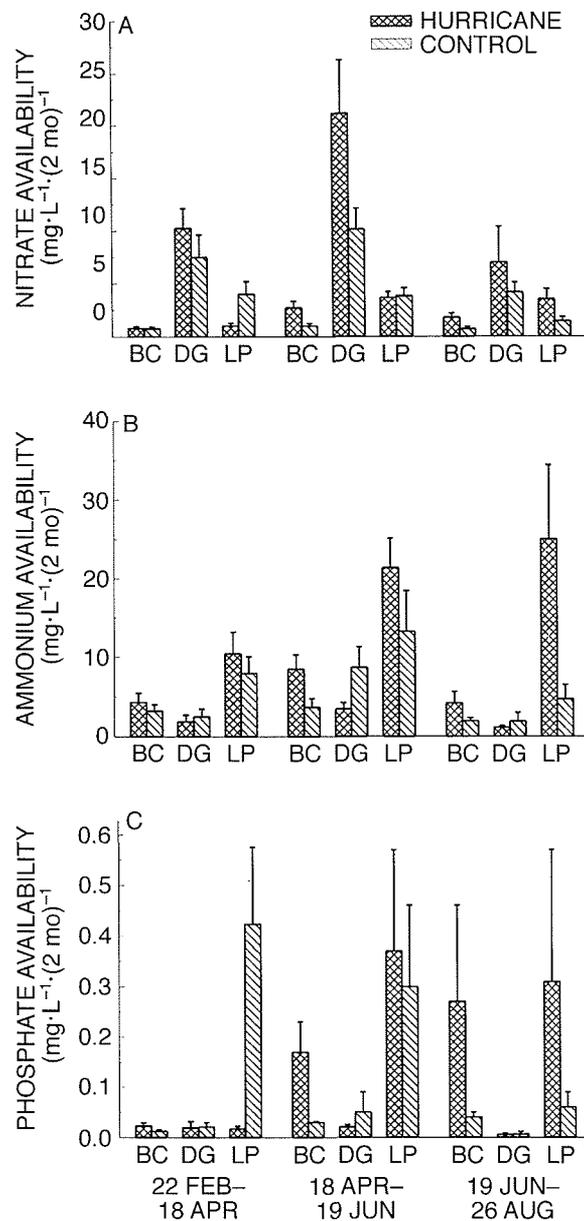


FIG. 4. The availability of (A) nitrate, (B) ammonium, and (C) phosphate in the soil at Coweeta Hydrologic Laboratory, North Carolina. Bars ($+1$ SE) represent the means of 10 samples (resin bags). BC = Barker's Cove, DG = Dyke's Gap, LP = Little Pinnacle. Dates represent the periods during which nutrient availability was measured.

icals such as esters and terpene hydrocarbons have been implicated in the resistance of maple species to insect herbivores (Loughrin et al. 1997), and we cannot eliminate the possibility that hurricane-induced changes in nonphenolic defenses were responsible for the patterns that we observed.

One alternative explanation for the differences between our results and those of previous studies could reflect the nature by which the gaps were formed. The

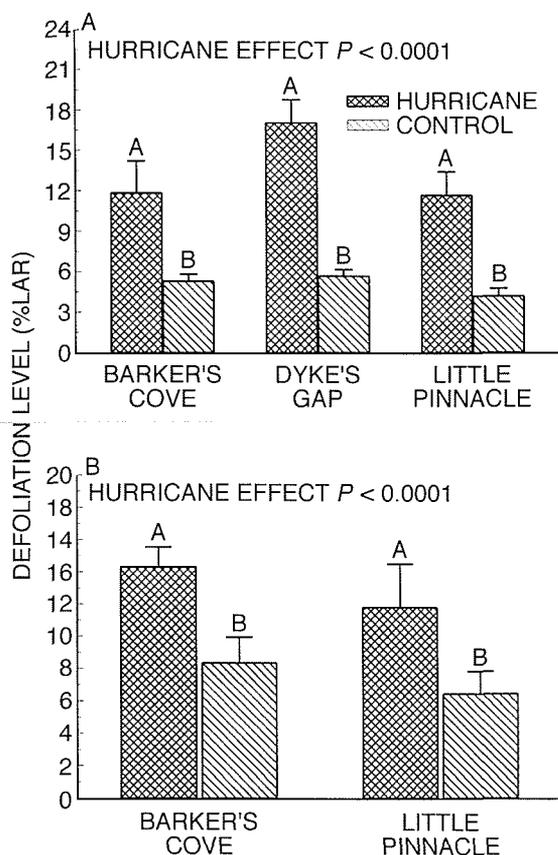


FIG. 5. Defoliation levels on (A) red maple and (B) red oak at three sites in the Coweeta Hydrologic Laboratory, North Carolina. Bars (+1 SE) represent the means of 12 samples (trees). Within groups, bars that share letters are not significantly different after Tukey's hsd test. Data were arcsine square-root transformed before analysis but have been back transformed for ease of interpretation. % LAR = percent leaf area removed by the end of the growing season.

clear-cutting of artificial gaps may result in abiotic conditions different from those in natural gaps (Phillips and Shure 1990) which may affect herbivore preference and performance. Additionally, the physiology of sprouts regenerating in clear-cuts is likely to be different from the physiology of surviving saplings in natural gaps (e.g., Donovan and Pappert 1998), which could influence the responses of insect herbivores. Further work would be required to reconcile these differences in results.

Given that both red maple (Schultz and Baldwin 1982) and red oak (Rossiter et al. 1988) respond to defoliation by insect herbivores with wound-induced increases in foliar phenolics, we cannot rule out the possibility that elevated phenolics in sites damaged by the hurricane were generated by higher levels of defoliation rather than carbon:nutrient balance. However, measurable induction of foliar astringency and hydrolysable tannins in red oaks takes ~6 wk to develop (Rossiter et al. 1988). We observed higher as-

tringency and higher hydrolysable tannins in red oak foliage sampled from hurricane sites in May (Fig. 2A,B), both before appreciable defoliation, and more rapidly than in previous reports of induction. Elevated condensed tannins in late-season oak foliage from hurricane sites (Fig. 2C) could have been the result of induction, but are consistent with artificial gap studies reporting higher late-season condensed tannins in foliage from light gaps with lower levels of herbivory (Shure and Wilson 1993). In either case, elevated condensed tannin concentrations in foliage at the end of the season have the potential to reduce rates of litter decomposition and rates of nutrient mineralization in areas damaged by the hurricane (DeMontigny et al. 1993, Clein and Schimel 1995, Schimel et al. 1996).

One further possibility is that the effects of Hurricane Opal on foliar phenolics that we observed in 1997 were responses to environmental conditions in 1996. We recognize the weakness of our lack of data for 1996, the year following the hurricane. For example, low nutrient availability in 1996 could have generated elevated phenolics in areas damaged by the hurricane on a 1-yr delay. At least one study has reported immobilization of inorganic nutrients following the deposition of woody debris during hurricane damage (Zimmerman et al. 1995), presumably as a result of microbial exploitation of nutrient-poor woody material. While recognizing this possibility, the site- and date-specific variation in nitrate, ammonium, and phosphate availability recorded during our study (Fig. 4), suggests to us that Hurricane Opal has not had a consistent effect on nutrient availability among sites at Coweeta. Rather, our results support the emerging view that light availability in gaps, whatever their origin, dominates the responses of the foliar phenolics of surviving trees (Shure and Wilson 1993, Dudt and Shure 1994). The variable responses of herbivore communities on different tree species merit further study (Shure and Phillips 1991, Schowalter 1994, Fig. 5).

ACKNOWLEDGMENTS

This research was supported by NSF grants DEB-9615661 and DEB-9527522 to M. D. Hunter and NSF Grant DEB-9632854 to the Coweeta LTER program. Invaluable field and laboratory assistance were provided by Kim Holton, Matt Wood, and Angela Barber. We thank Brian Kloepfel, Sharon Taylor, and Barry Clinton for help and advice at Coweeta, and Sharie Ketcho, Heidi Appel and Jack Schultz for advice on methods of foliar chemistry analyses. We thank two anonymous reviewers for helpful comments on an earlier draft of this manuscript.

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