Ecology, 79(2), 1998, pp. 604–617

RAINFALL EFFECTS ON PLANT–HERBIVORE PROCESSES IN AN UPLAND OAK FOREST

Donald J. Shure, Peter D. Mooreside, and Stephen M. Ogle[1]

Department of Biology, Emory University, Atlanta, Georgia 30322 USA

Abstract. We examined the patterns of foliar chemistry and insect herbivory in white oak (*Quercus alba*), chestnut oak (*Q. prinus*), and red maple (*Acer rubrum*) trees occupying an upland oak forest on the Walker Branch Watershed in Tennessee. Different size classes of each species were sampled to evaluate life cycle changes in foliar N and phenolic chemistry and their corresponding influence on insect herbivory. Oak trees had consistently higher foliar N and hydrolyzable tannin concentrations, and they experienced greater herbivore damage than did red maple trees; maple trees had higher condensed tannin levels. Foliar chemistry and herbivore damage were usually quite similar for all size classes. However, condensed tannins, and occasionally total phenolics, were higher in well-insolated mature trees than in shaded understory conspecifics, fitting the pattern expected through plant carbon/nutrient balance relationships.

Rainfall fluctuations during 1992–1994 significantly influenced plant–herbivore processes. Foliar N and phenolic concentrations were reduced in all species during the much drier summer of 1993, relative to 1992. The summer drought in 1993 was apparently severe enough to restrict carbon allocation to plant phenolics. In contrast, foliar N levels in oaks were somewhat elevated by the end of the wet 1994 growing season. Total phenol and hydrolyzable tannin levels remained quite low in 1994, when carbon may have been preferentially allocated to growth rather than differentiation, as N uptake increased during the wet summer following drought. Nevertheless, carbon allocation to condensed tannins was quite high for all species during the wet summer. Insect herbivore damage was directly correlated with rainfall totals over the 3-yr period. Herbivore damage on oaks was reduced during the 1993 drought, principally because of less impact by leaf skeletonizers. Insect feeding on oaks and maples was elevated during the wet 1994 summer, when strip feeding by lepidoptera larvae was at its highest. Our findings suggest that herbivore damage at Walker Branch appears to be largely dependent on the response of specific insect feeding guilds to moisture-related changes in foliar N and plant phenolics.

Key words: feeding guilds; foliar chemistry; forests; herbivory; insects; maples; nitrogen; oaks; phenolics; plant defenses; rainfall; tannins.

Introduction

Considerable evidence has accumulated linking herbivore damage with the levels of plant phenolics (i.e., tannins) in hardwood tree species (Feeny 1976, Schultz and Baldwin 1982, Coley et al. 1985, Coley 1986, Rossiter et al. 1988, Schultz 1988, Tuomi et al. 1988, Coley and Aide 1991, Herms and Mattson 1992, Tuomi 1992, Dudt and Shure 1994). One source of this evidence concerns the inverse correlations observed between levels of plant phenolics and herbivore damage along resource gradients of light or nutrients (Mole et al. 1988, Landsberg and Ohmart 1989, Shure and Wilson 1993, Dudt and Shure 1994). Changes in plant carbon/nutrient balance and growth/differentiation balance provide possible explanations for the phenotypic expression of plant phenolics across these resource gradients (Herms and Mattson 1992). Both hypotheses suggest that plants preferentially allocate carbon for growth when conditions are favorable, whereas carbon will often accumulate and be used for differentiation products, such as defenses, when high light or low nutrients promote photosynthesis in excess of growth (Bryant et al. 1983, Chapin et al. 1987, Muller et al. 1987, Mole et al. 1988, Fajer et al. 1992, Herms and Mattson 1992). The more inclusive growth/differentiation balance hypothesis predicts that any environmental factor that slows growth more than photosynthesis will increase the resource pool of carbohydrates available for allocation to secondary metabolites such as tannins (Herms and Mattson 1992, Tuomi 1992). However, the presence of counteradaptations among certain insect species has prompted debate concerning the efficacy of these phenolic compounds as putative defenses against herbivore populations (Bernays 1981, Faeth 1985, Bernays et al. 1989).

The lack of consistent correlations between plant defenses and insect herbivory has prompted a reconsid-

Manuscript received 15 May 1996; revised 4 December 1996; accepted 4 March 1997; final version received 11 April 1997.

[1] Present address: Botany Department, University of Wyoming, Laramie, Wyoming 82071 USA.

eration of factors other than plant defensive chemistry in possibly regulating herbivore populations (Landsberg and Ohmart 1989). Insect herbivores may be limited by other aspects of foliar chemistry, including leaf water content (Scriber 1984), toughness (Coley 1983), and especially nitrogen content (Mattson 1980, White 1984). Evidence supporting the importance of natural enemies in limiting insect herbivores is also accumulating (Faeth et al. 1981, Schowalter et al. 1986, Hunter and Schultz 1993, Marquis and Whelan 1994, Cornell and Hawkins 1995). In addition, climatic conditions such as drought may operate indirectly on herbivore populations through their effects on plant foliar chemistry. However, establishing predictions concerning the response of plant phenolics and insect herbivores to drought has proven difficult (Gershenzon 1984, Mattson and Haack 1987*b*, Larsson 1989, Ayres 1993). Earlier evidence suggested that drought and other stresses promoted outbreaks of herbivorous insects because of elevated plant nutrient levels (White 1984), lowered plant defenses (Rhoades 1985), or the development of a more suitable abiotic environment (Rhoades 1983, Mattson and Haack 1987*b*). More recent evidence (Mattson and Haack 1987*b*) implies a nonlinear response of insects to plant stresses such as drought, that are strongly specific to each insect feeding guild (Larsson 1989). These varied findings suggest a need for further evaluation of herbivore responses to these possible regulatory mechanisms.

The current study offered an opportunity to examine plant–herbivore processes throughout the life cycle of several important tree species occupying a mature upland oak forest in Tennessee. Our specific objectives involved (1) determining the levels of foliar N and plant phenolics in different size classes of tree species present within the forest; (2) evaluating the temporal changes in foliar chemistry over a 3-year period involving quite different rainfall regimes; (3) examining the type and extent of insect herbivore damage for different size classes of each tree species; and (4) assessing whether the responses of insect herbivores to rainfall-mediated changes in plant host chemistry are feeding-guild specific. We hoped, through our efforts, to provide much greater understanding of the spatiotemporal dynamics of plant–herbivore processes within a temperate deciduous forest. This type of information should prove important in assessing the mechanistic basis for future alterations in plant–consumer processes as a result of climate change effects on temperate forests.

METHODS

Study area

We conducted the study at the Walker Branch Watershed on the Oak Ridge National Laboratory site near Oak Ridge, Tennessee, USA. The project is part of a large-scale Throughfall Displacement Experiment (Hanson et al. 1995), which is examining the long-term impact of climate-induced rainfall modification on eastern deciduous forests. The overall study area consists of a 1.8-ha plot (80 m downslope × 240 m across slope) established on a south-facing slope at the top of the watershed. The plot has been subdivided into three contiguous 80 × 80 m subplots for the purposes of the experiment. The specific site was selected because of its uniform slope, consistent soil type, and relatively homogeneous vegetation distribution. A nearby meteorological station (~0.5 km away) provides continual rainfall data. Time domain reflectometers (TDR) are being used to follow changes in soil water content and soil matric potential at 310 locations within the 1.8-ha study area (Hanson et al. 1995). Paired TDR rods were inserted in the soil in April 1992 (0–35 cm and 0–70 cm depths at each location) and monitored at 2–4 wk intervals, thereafter.

The Walker Branch Watershed has been extensively studied over the past 25 years concerning its stand composition, hydrology, soils, and biogeochemistry (Johnson and Van Hook 1989). The climate is typical of the humid Southern Appalachians, with an annual precipitation of 140 cm and mean annual temperature of 13.3°C. Soils on the watershed are primarily typic Paleudults, quite acid (pH 4.2–4.6), cherty, infertile, and highly permeable (Garten and Taylor 1992, Garten 1993). The vegetation is characterized as an upland oak forest with a basal area of 20–25 m^2/ha, mean canopy height of 22 m, and a leaf area index (LAI) of 5.0 (Hutchison et al. 1986). Stand composition within the study area consists of white oak (*Quercus alba*), chestnut oak (*Q. prinus*), and red maple (*Acer rubrum*) as overstory dominants. Red oak (*Quercus rubra*), yellow poplar (*Liriodendron tulipifera*), black gum (*Nyssa sylvatica*), and sourwood (*Oxydendrum arboreum*) are important subdominant species. Dogwood (*Cornus florida*) occupies the forest understory.

The 1.8-ha experimental area was established prior to the initiation of our study in 1992. The actual Throughfall Displacement Experiment began in mid-July 1993, but had no real effect on the vegetation through 1994. This factor enabled us to combine trees from all three 80 × 80 m subplots to characterize plant–herbivore processes over a 3-yr (1992–1994) period.

Field sampling

We used white oak, chestnut oak, and red maple trees for sampling purposes. Nine individual trees of each of three diameter size classes ($<$2.5 cm dbh, $\geq$2.5 cm $<$10 cm dbh, $\geq$10 cm dbh) were permanently marked for each species from within each 80 × 80 m subplot. These size classes approximate seedling, sapling, and mature trees. However, the ''seedling'' size category was restricted to those trees containing sufficient foliage to enable sampling; most (71.6%) were $<$1.5 cm in diameter. We randomly selected three individuals of each size class from the bottom, mid, and top sections

TABLE 1. Models of three-way factorial designs used for ANOVA in our Walker Branch Watershed, Tennessee, study. We used Model A when comparing the three tree species on any date, and Model B to test individual species responses over the 3-yr study.

Source (Model A)	df	Source (Model B)	df
Species	2	Date	2
Size class	2	Size class	2
Species × Size class	4	Date × Size class	4
Elevation	2	Elevation	2
Species × Elevation	4	Date × Elevation	4
Size class × Elevation	4	Size class × Elevation	4
Species × Size × Elevation	8	Date × Size × Elevation	8
Error (trees)	216	Error (trees)	216

Note: Model A was used for ANOVA in Tables 3, 4, and 6, and in Figs. 2–5; Model B was used for ANOVA in Table 5 and Fig. 6. Species comparisons (Model A) in July (smallest size class not sampled) used 1 df for Size class, 2 df for Species × Size class and Size class × Elevation interactions, and 161 df for the Error term.

of each 0.64-ha subplot to monitor for topographic effects on plant–herbivore processes. In total, 243 trees (81 trees per species) were thus permanently tagged in June 1992 for use throughout the study. Tree sampling occurred in late August 1992, and in early July and late August of 1993 and 1994. The smallest size class was not sampled in July because of the limited number of leaves available each growing season.

Sampling consisted of obtaining 10 leaves from each tree on each sample date. Hand sampling of leaves was possible from smaller trees. We used extension pole cutters to remove two small branches (five leaves per branch) from larger trees. The cutters enabled us to sample up to a height of 14 m. All leaves were randomly selected to avoid visual biases in herbivory determinations. The 10 leaves were bagged, placed in styrofoam containers, and returned to the laboratory for processing. These sampling procedures, as well as the subsequent herbivory and plant chemical analyses, follow earlier studies (Shure and Wilson 1993, Dudt and Shure 1994).

Herbivory and plant chemistry

All leaves sampled in late August of each year were photocopied prior to chemical analysis. Each photocopy indicates the cumulative leaf area damaged or removed by fungal pathogens and different types of insect herbivores throughout the growing season (Hargrove et al. 1984). We used a magnetized digitizer (Micro-plan II, Laboratory Computer Systems, DCS Services, Natick, Massachusetts, USA) to determine total leaf area and percentage of leaf area damaged annually by fungi and different insect feeding guilds, including strip feeders, pit feeders, leaf skeletonizers, leaf miners, leaf rollers, and leaf galls (Coulson and Witter 1984). Interannual differences in insect damage reflect changes in herbivore abundance as well as consumption rates.

Plant chemical assays were performed to determine foliar N content, total phenols, and condensed and hydrolyzable tannin concentrations. The 10 leaves sampled from each tree were composited and oven-dried at 35°C for 48 h, ground to powder in a Wiley Mill (1.27 mm mesh size), and frozen at −15°C until analyzed. Low drying temperatures (<40°C) minimize the irrevocable fixing or denaturing of tannins that occurs at higher temperatures (Swain 1979). A pilot study comparing freeze-drying vs. oven-drying procedures yielded no consistent differences for the species being studied (D. J. Shure, *unpublished data*). Nevertheless, drying conditions can influence the extractability of certain phenolics (Lindroth and Pajutee 1987). Subsamples of the powdered material were analyzed for foliar N content using procedures (Leco Furnace, model-FP428) through the Plant and Soil Analysis Laboratory at the University of Georgia.

We used a 50% methanol extraction procedure as a precursor for plant phenolic analyses (Bate-Smith 1977, 1981). The Folin-Denis technique was used to assay for total phenolics (Swain and Hillis 1959). Hydrolyzable tannins (ellagitannins only) were measured under an N_2 environment using an acetic acid–sodium nitrate procedure (Bate-Smith 1972). Condensed tannins were estimated as proanthocyanidins using a butanol–HCl technique (Bate-Smith 1975, 1981). Total phenolic assays used tannic acid for standard curves, and are expressed as percentage (dry mass) of tannic acid equivalents (TAE). Hydrolyzable tannins are reported as milligrams (dry mass) of hexahydroxydiphenoylglucose equivalents (Bate-Smith 1981) and condensed tannins as percentage dry mass Quebracho tannin equivalents. The possible limitations in these and other procedures for phenolic analyses have been reviewed (Martin and Martin 1982, Mole and Waterman 1987, Wisdom et al. 1987, Hagerman 1988) and are considered elsewhere (Shure and Wilson 1993).

Data analysis

We used three-way (3 × 3 × 3) factorial designs for the ANOVA in our data sets (Table 1). Most ANOVAs included either species (white oak, chestnut oak, and red maple; Model A) or time (1992, 1993, 1994; Model B), along with tree diameter size classes and slope position (up, mid, and down-slope) as main effects.

TABLE 2. Monthly rainfall totals (cm) on the Walker Branch Watershed, Tennessee, during the 1992–1994 summers, in relation to average values ($\bar{X}$ ± 1 SE) recorded over a 13-yr period (1982–1994).

Year	June	July	August	Total
1992	10.2	13.0	8.6	31.8
1993	4.1	5.1	9.3	18.5
1994	19.4	12.8	9.0	41.2
1982–1994 average	10.1 ± 2.12	11.7 ± 1.13	9.8 ± 1.62	31.6 ± 3.15

These ANOVAs were performed for each chemical parameter and for total herbivory, as well as for damage by different insect feeding guilds. Exceptions to this basic design included analyses of the July N and phenolic chemistry data sets (smallest size class omitted), data analysis of fungal damage on leaves of each species (two-way ANOVA), and comparisons of N content across all five sample dates (unbalanced one-way ANOVA). All ANOVAs were nested to account for replicate samples (trees). Data from the three 80 × 80 m subplots were combined in all analyses (no subplot effect). Restricted least significant difference tests were used to locate pairwise differences when ANOVAs were significant (Carmer and Swanson 1973). Statements about main effects have been tempered when interaction terms proved significant.

RESULTS

Rainfall

Moisture relationships at Walker Branch varied over the 1992–1994 summers (Table 2). Precipitation in 1992 closely approximated the 13-yr average for the study area. Soil water content (0–35 cm) in 1992 averaged 12.9–21.9%, and the mean soil matric potential remained above −0.32 MPa from June through August (P. Hanson, *unpublished data*). A fairly severe midsummer drought developed in 1993. The total rainfall in June and July 1993 (9.2 cm) was lower than that of any other year since 1982. Soil water content averaged 7.3–14.0% (Hanson et al. 1995) and soil matric potential reached −1.41 MPa during the dry summer. In contrast, precipitation exceeded the long-term average over the early part of the 1994 summer. Soil water content averaged 18.0–23.2% from June through August, whereas soil matric potential never dropped below −0.11 MPa during the wet summer. This rainfall pattern thus offered an opportunity to compare plant–herbivore processes over a sequence of relatively average, dry, and wet summers.

Foliar chemistry

Leaf N concentrations varied significantly over time and among tree species (Fig. 1, Table 3). Nitrogen levels averaged ~2.0% dry mass in chestnut and white oak trees in late August 1992, and were significantly lower (~1.6%) in red maple. Similar concentrations were present in early July 1993. In contrast, foliar N concentrations dropped significantly (8–14%) in all three species as the drought progressed during 1993. Levels were again ~2.0% (oaks) and 1.6% (maple) in early July 1994. However, less seasonal decline occurred during the wet (1994) growing season. Interestingly, foliar N concentrations were usually quite similar when we compared tree size classes of each species on each date (Table 3). Elevational differences in foliar N levels were also generally lacking on each sample date. However, foliar N levels in chestnut oak trees often increased from upslope to downslope, with this trend being significant at the end of the drought in 1993 (Table 3). No trends were present for other species.

Leaf phenolic concentrations varied consistently among species and, to some extent, among different size classes (Table 4). Total phenolics in August 1992 were relatively similar in all three species (Fig. 2). However, larger white oak trees contained significantly

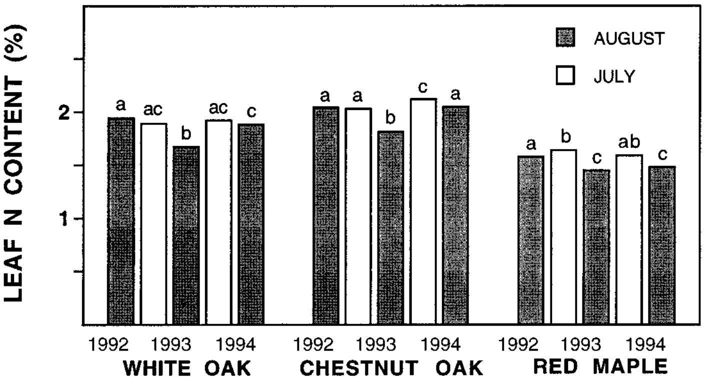

FIG. 1. Nitrogen content in leaves (percentage dry mass) of different tree species sampled on the Walker Branch Watershed, Tennessee, in August 1992 (average year), July and August of 1993 (dry), and 1994 (wet). Means represent all trees sampled for each species in the entire study area. Different letters above means for a particular species indicate significant differences, as determined from one-way ANOVA (white oak, F = 35.0, df = 4, 309; chestnut oak, F = 26.3, df = 4, 313; red maple, F = 18.2, df = 4, 346; all F values significant at $P < 0.0001$).

TABLE 3. Results of three-way factorial ANOVAs of foliar N content in tree species sampled on the Walker Branch Watershed, 1992–1994. The *F* values are presented for main effects and their interactions, with levels of significance indicated.

	Main effects			Interactions		
Date	Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
August 1992	236.0**	2.89	1.14	0.25	1.58	1.20
July 1993	63.4**	1.03	1.28	0.02	0.69	0.93
August 1993	92.3**	3.67*	7.41**	2.03	2.52*	0.65
July 1994	98.0**	0.40	1.71	1.19	0.70	0.02
August 1994	254.5**	1.98	1.44	1.62	0.55	1.00

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).

* $P < 0.05$; ** $P < 0.01$.

higher levels of total phenolics than did smaller size classes (Table 4). This pattern was absent for chestnut oak and red maple. Hydrolyzable tannins in 1992 were significantly higher in white oak leaves than in chestnut oak and especially in red maple leaves. Hydrolyzable tannin concentrations in all species were similar among size classes. In contrast, condensed tannins were generally higher in maple than in oak leaves, and higher in mature overstory than in understory conspecifics for all three species; many of these differences were significant (Table 4, Fig. 2). These patterns of leaf phenolics were present when reexamined in early July 1993 (Fig. 3). However, total phenolics were considerably higher in white oak leaves than in other species.

Species differences persisted at the end of the 1993 and 1994 growing seasons (Figs. 4 and 5). Total phenolics remained significantly higher in white oak trees than other species. Oak leaves again contained significantly higher hydrolyzable tannins whereas maple trees allocated more carbon to condensed tannin production (Table 4). This reciprocal response in allocation of hydrolyzable vs. condensed tannins was thus consistent on all sample dates (Table 4). However, the higher levels of total phenolics (white oak) and condensed tannins in overstory vs. understory conspecifics was less evident at the end of the drought in 1993 and during 1994 (Figs. 4 and 5, Table 4). Hydrolyzable tannins were significantly higher in mature than understory white oak trees during the wet 1994 summer.

The pronounced year-to-year differences in phenolic production appear to be weather related (Fig. 6). Eight of the nine measures of plant phenolics were reduced during the drier 1993, in comparison to the more normal 1992 summer, and most differences were significant. Results for the wet 1994 growing season were varied. Total phenolics and hydrolyzable tannins re-

TABLE 4. Results of three-way factorial ANOVAs of total phenolics and hydrolyzable (H) and condensed (C) tannins in tree species sampled at Walker Branch, 1992–1994. The *F* values are presented for main effects and interactions, with levels of significance indicated.

		Main effects			Interactions		
Date	Measure	Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
1992							
August	Phenolics	10.9**	8.16**	2.25	7.13**	0.36	0.70
	Tannins, H	101.4**	0.35	13.09**	1.15	3.91**	1.27
	Tannins, C	17.5**	13.29**	2.85	1.18	0.97	1.80
1993							
July	Phenolics	42.4**	1.39	4.39*	1.54	2.71*	0.80
	Tannins, H	212.4**	0.36	10.11**	1.83	4.75**	0.67
	Tannins, C	33.4**	12.95**	0.51	2.53	2.11	0.71
August	Phenolics	264.4**	0.22	3.43*	1.11	0.91	0.38
	Tannins, H	157.0**	3.98*	0.77	4.42**	3.02	1.52
	Tannins, C	44.6**	2.46	0.20	0.91	0.70	2.13
1994							
July	Phenolics	50.6**	3.04	4.34*	3.25*	2.85*	0.53
	Tannins, H	324.0**	6.52*	3.94*	4.49*	0.61	1.90
	Tannins, C	22.1**	0.27	3.62*	2.03	1.46	0.15
August	Phenolics	61.6**	5.04**	0.08	5.46**	0.77	0.77
	Tannins, H	550.2**	10.57**	2.31	5.17**	1.30	1.10
	Tannins, C	40.5**	13.02**	5.29**	2.12	1.41	1.11

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).

* $P < 0.05$; ** $P < 0.01$.

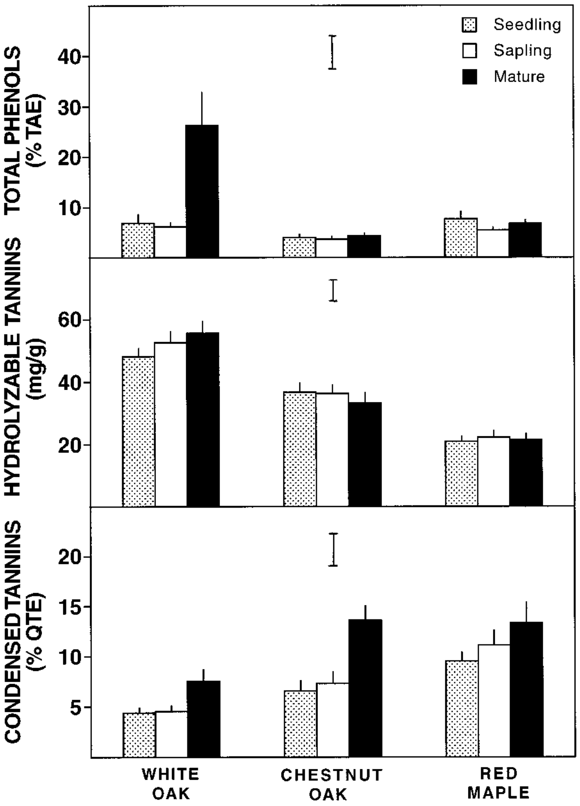

FIG. 2. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1992. Diameter size classes sampled are presented as seedling, sapling, and mature trees. Total phenols are expressed as percentage of tannic acid equivalents (TAE), hydrolyzable tannins as milligrams of hexahydroxydiphenoylglucose equivalents per gram of leaf tissue, and condensed tannins as percentage of Quebracho tannin equivalents (QTE). The interval at the top of each graph is the least significant difference ($P < 0.05$), which indicates where significant differences exist among all means presented.

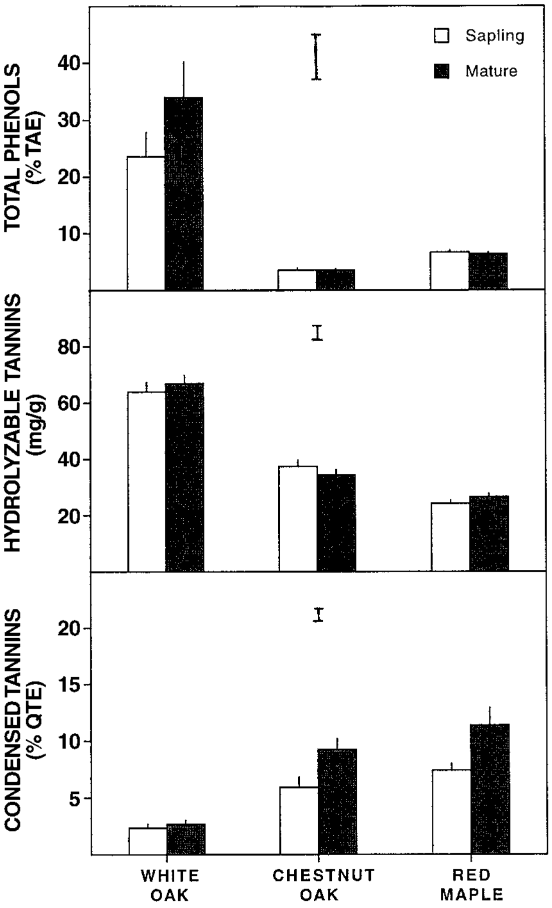

FIG. 3. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in July 1993. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The interval at the top of each graph is the least significant difference ($P < 0.05$), which indicates where significant differences exist among all means presented.

mained low in 1994, whereas condensed tannin production was significantly higher for all species during the particularly wet summer. Leaf phenolics exhibited no clear upslope-to-downslope patterns throughout the study, even when differences were significant (Table 4).

Insect herbivory

Insect herbivory varied significantly among species and over the 3-yr study (Tables 5 and 6). Total leaf area damaged was significantly higher on oak than on maple trees throughout the study; white oak leaves always had significantly more damage (Table 6). Herbivore damage was significantly reduced on white oak trees during the drier 1993 summer than that of 1992 (Table 6). A similar trend for chestnut oak was not significant. Damage on maple trees was identical in both years. In contrast, the extent of insect damage was significantly higher on all species during the wet summer of 1994. No significant differences emerged when we compared total damage on different size classes of trees of each species during any year (Table 6).

Tree species at Walker Branch differed somewhat in the relative importance of insect feeding guilds (Tables 5 and 6). Strip feeders (i.e., Lepidoptera larvae) caused the greatest damage on all three tree species throughout the study (Table 5). Leaf skeletonizers were also important herbivores on white oak and chestnut oak trees, but not on red maple (Table 5). Adhesive skeletonizers, which feed mainly within the cover afforded after adhesing two leaves together, caused much of the skeletonizing damage on both oak species. Leaf mining was significantly more important on oak than on maple trees, whereas pit feeding was greater on maple trees (Tables 5 and 6). Leaf galls and leaf rollers accounted for <0.1% of the leaf area damaged on any species throughout the study.

Insect feeding guilds varied in their response to

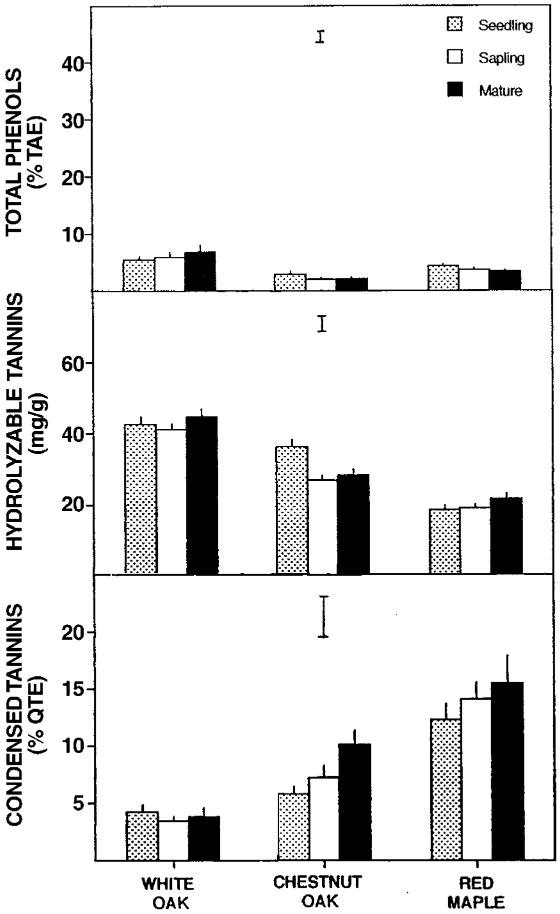

FIG. 4. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1993. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The interval at the top of each graph is the least significant difference ($P < 0.05$), indicating where significant differences exist among all means presented.

moisture changes during the study (Table 5). Strip feeding remained unchanged on all three tree species when comparing 1992 and 1993. In contrast, skeletonizing, pit feeding, and leaf mining were all reduced during the drought in 1993, and nearly all differences were significant. However, strip feeding was greater on all tree species during the wet 1994 growing season. Skeletonizing, pit feeding, and mining damage showed no clear increase during the wet year (Table 5). Only skeletonizing on chestnut oak trees was significantly elevated in 1994.

Fungal damage

The level of fungal damage differed between tree species and in response to rainfall variation (Table 7). Damage was considerably higher on maple than oak trees throughout the study. Very little fungal damage occurred on oak foliage each year. Nevertheless, all three tree species experienced less damage in 1993 than 1992 and the trend for red maple was significant (Table 7). Damage levels on red maple and chestnut oak leaves were highest during the wet 1994 summer.

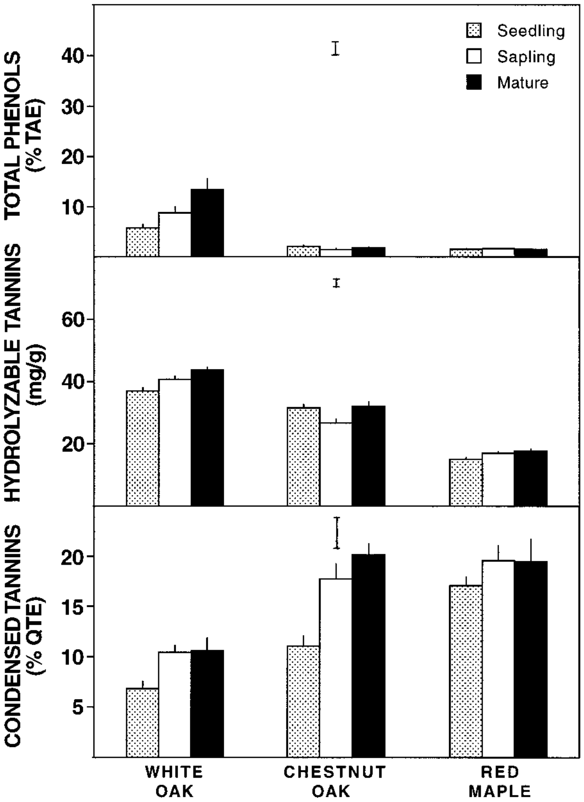

FIG. 5. Levels of phenolic chemistry (means + 1 SE) in leaves of tree species sampled at Walker Branch in August 1994. Total phenols, hydrolyzable tannins, and condensed tannins are expressed as in Fig. 2. The least significant difference ($P < 0.05$) interval is depicted as in Fig. 2.

DISCUSSION

Patterns of foliar chemistry

The tree species selected for study represent slow-growing canopy dominants occupying a rather nutrient-poor upland oak forest (Garten 1993). Thus these species should, in theory, employ relatively high levels of foliar phenolics in minimizing herbivore damage and subsequent tissue replacement costs (Coley et al. 1985). In fact, the three species actually exhibited quite different constitutive patterns of foliar N and plant phenolics. Oak trees maintained higher levels of foliar N and hydrolyzable tannins, whereas maple leaves were especially low in N content, but higher in condensed tannin production. Nevertheless, foliar N levels in all three species were relatively low for trees occupying temperate deciduous forests (Feeny 1970, Mattson 1980, Coley and Aide 1991). In contrast, species studied on the Walker Branch Watershed generally contained higher phenolic concentrations than did slow-growing hardwood species present in mature forests

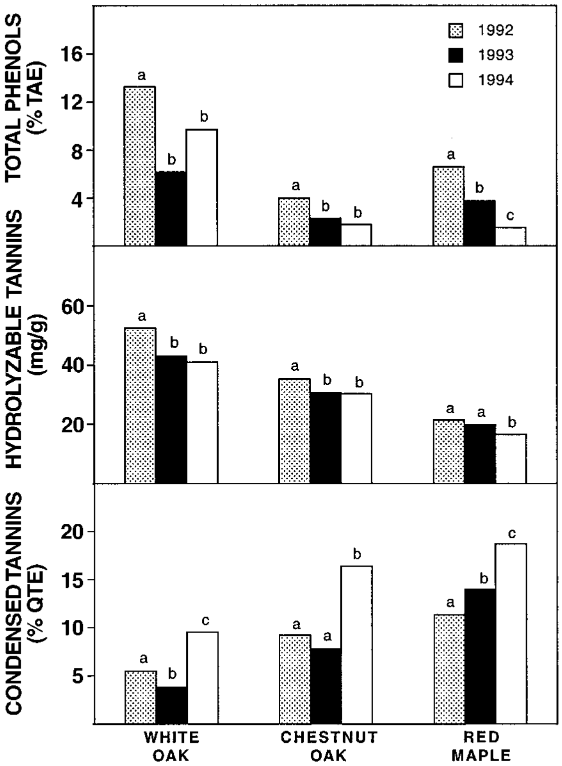

FIG. 6. Levels of phenolic chemistry in leaves of tree species sampled at Walker Branch in August of 1992 (average rainfall), 1993 (dry), and 1994 (wet). Means reflect all trees sampled for each species in the study area. Total phenols (TP), hydrolyzable tannins (HT), and condensed tannins (CT) are expressed as in Fig. 2. Means with different letters are significantly different. The *F* values derived from three-way ANOVA (Model B, Table 1, Date) for white oak were: TP, 4.8; HT, 21.4; CT, 33.8; for chestnut oak: TP, 20.8; HT, 5.7; CT, 39.3; and for red maple: TP, 57.2; HT, 10.5; CT, 16.5. All *F* values were significant at the $P < 0.01$ level.

within the Southern Appalachian Mountains in North Carolina (Shure and Wilson 1993). Tannin concentrations in maple trees at Walker Branch were actually comparable to those in conspecifics occupying highly insolated forest openings at the North Carolina site. Therefore, the species studied at Walker Branch were relatively low in foliar N and generally high in phenolic components.

Studies to date have rarely evaluated life cycle changes in foliar chemistry of forest tree species. Thus, very little information is available to test the relative fit of the carbon/nutrient balance or growth/differentiation balance hypotheses as plants shift from understory to canopy positions and potentially exploit nutrients available at different soil depths. Interestingly, our findings showed minimal variation in foliar N concentrations for different size classes of all three species studied. Year-to-year changes in N content followed similar trajectories and were of equal magnitude in all conspecifics within the population. This absence of size class differences may reflect existing constraints on plant N uptake in a nutrient-poor habitat (Garten 1993).

Leaf phenolic contents often exhibited size class differences that appeared to be directly correlated with available sunlight. Mature canopy-dwelling trees generally contained higher levels of condensed tannins and occasionally total phenolics (white oak) than did conspecifics occupying the shaded understory. These canopy trees receive greater rates of photosynthetically active radiation (Denslow et al. 1990), which can lead to the metabolic accumulation and storage of poorly translocatable phenolic compounds, such as the more structurally based condensed tannins (Mole et al. 1988). This response should prove especially true in N-limited habitats where growth is limited more than photosynthesis, and where buildups of secondary metabolites are expected (Mattson 1980, Bryant et al. 1983, Larsson et al. 1986, Chapin et al. 1987, Tuomi et al. 1988, Herms and Mattson 1992). In contrast, understory trees are light limited; thus, a similar accumulation of carbon-based differentiation products is prevented. The buildup of condensed tannins in canopy-dwelling conspecifics thus fits the carbon/nutrient balance hypothesis and further supports the trend of strong positive correlations between light availability and plant phenolic production (Langenheim et al. 1981, Waterman et al. 1984, Larsson et al. 1986, Bryant et al. 1987, Mole et al. 1988, Herms and Mattson 1992, Shure and Wilson 1993, Dudt and Shure 1994). In contrast, hydrolyzable tannins generally failed to show this canopy/understory relationship. The lack of size class differences in hydrolyzable tannin concentrations may reflect the ease of maintenance of similar constitutive levels of this more mobile category of tannins that are purported to be especially effective against insect herbivores (Zucker 1983).

Emerging patterns suggest a differential utilization of hydrolyzable vs. condensed tannins by forest tree species (Rossiter et al. 1988, Shure and Wilson 1993). Results from our upland oak forest indicate a clear difference between oaks and maples in their synthesis of hydrolyzable vs. condensed tannins. These observed differences in tannin production may represent adaptive trade-offs in phenolic utilization against insect herbivores or microbial pathogens (Zucker 1983). For example, condensed tannins were especially high in all species when fungal pathogens might have been particularly pronounced during the wet 1994 growing season. This was especially true for maple trees, which exhibited much greater susceptibility to fungal damage than did oaks throughout the study. Past reports of seasonal increases in condensed tannins and corresponding decreases in hydrolyzable tannins (Baldwin et al. 1987, Shure and Wilson 1993) could be related to changing pressures of herbivore vs. pathogen populations. Insect herbivore damage is often concentrated on young leaves early in the growing season (Feeny 1970, Reichle et al. 1973, Aide 1993), when the rapid

TABLE 5. Annual leaf area damaged (%) by feeding guilds of insect herbivores on tree species (size classes combined) sampled at Walker Branch Watershed during 1992–1994. The F values were determined through three-way ANOVA (see Table 1, Model B), with different letters indicating means that are significantly different. Totals ($\bar{X} \pm 1$ SE) include all six guilds.

Guild	1992	1993	1994	F
White oak				
Strip feeders	6.85^{b}	6.54^{b}	8.42^{a}	2.83†
Skeletonizers	4.52^{a}	3.11^{b}	4.07^{ab}	3.64*
Pit feeders	0.25^{a}	0.17^{b}	0.13^{b}	4.42*
Miners	0.56^{a}	0.12^{b}	0.10^{b}	25.36**
Total	12.4 ± 0.59^{a}	10.1 ± 0.57^{b}	13.0 ± 0.82^{a}	4.37*
Chestnut oak				
Strip feeders	4.47^{a}	4.99^{a}	5.56^{a}	1.57
Skeletonizers	3.66^{b}	2.44^{c}	4.94^{a}	8.44**
Pit feeders	0.15^{a}	0.09^{b}	0.09^{b}	3.47*
Miners	0.31^{a}	0.09^{b}	0.07^{b}	14.85**
Total	8.6 ± 0.53^{b}	7.7 ± 0.59^{b}	10.7 ± 0.78^{a}	6.25**
Red maple				
Strip feeders	4.93^{b}	5.38^{b}	7.47^{a}	5.42**
Skeletonizers	0.33^{a}	0.24^{a}	0.22^{a}	1.76
Pit feeders	0.56^{a}	0.26^{b}	0.31^{b}	36.92**
Miners	0.07^{a}	0.02^{b}	0.01^{b}	4.14*
Total	6.0 ± 0.52^{b}	6.0 ± 0.64^{b}	8.0 ± 0.61^{a}	3.87*

* $P < 0.05$; ** $P < 0.01$; † $P = 0.06$.

mobilization of hydrolyzable tannins might prove to be especially effective. The progressive increase in total incidences of herbivore damage over time facilitates the spread of microbial pathogens within leaves as foliar concentrations of condensed tannins are accumulating. Tree species may thus develop seasonal separation in the relative production of constitutive levels of different categories of tannins, and may possibly rely on induced accumulations when herbivores or pathogens are especially numerous (Rhoades 1979). Further research is needed to distinguish whether these tannin differences are adaptive or simply reflect passive accumulations under contrasting microenvironmental conditions.

Plant responses to moisture regimes

Plant populations exhibit a wide variety of responses in adjusting to alterations in moisture availability (Hsiao 1973, Gershenzon 1984, Horner 1990, Chapin 1991, Louda and Collinge 1992). The initial stages of drought may promote increases in foliar nutrients and soluble carbohydrate concentrations (Hsiao 1973,

TABLE 6. Results of three-way factorial ANOVAs of damage by different insect feeding guilds on tree species sampled on the Walker Branch Watershed during 1992–1994. The F values are presented for main effects and their interactions, with levels of significance indicated.

		Main effects			Interactions		
Year	Guild	Species (S)	Size (SC)	Elevation (E)	S × SC	S × E	SC × E
1992	Total	35.91**	0.66	0.25	1.06	1.58	1.09
	Strip	9.48**	1.62	0.74	0.77	1.95	0.62
	Skeletonizers	51.12**	0.12	0.29	1.88	1.87	1.68
	Pit	50.17**	2.94	3.50*	0.79	1.66	1.11
	Miners	20.96**	1.49	3.61*	1.50	1.99	0.59
1993	Total	13.25**	1.06	1.37	1.32	1.11	1.02
	Strip	2.47	0.90	0.18	0.78	0.43	0.95
	Skeletonizers	63.75**	0.31	5.97**	2.54*	2.76*	0.60
	Pit	14.69**	0.95	2.11	0.37	1.40	0.80
	Miners	4.23*	1.30	0.70	1.10	1.47	1.54
1994	Total	11.82**	0.98	0.48	6.19**	0.77	2.05
	Strip	3.84*	0.40	1.36	4.09**	0.94	1.60
	Skeletonizers	52.76**	3.29*	0.82	5.46**	0.43	1.42
	Pit	43.40**	1.40	0.73	2.53*	2.04	2.22
	Miners	13.66**	2.68	0.78	1.13	0.94	1.95

Note: Variance components and their degrees of freedom in all ANOVAs are as in Table 1 (Model A).

* $P < 0.05$; ** $P < 0.01$.

TABLE 7. Annual leaf area damaged (%) by fungal pathogens utilizing tree species sampled on the Walker Branch Watershed during 1992–1994. Data were obtained from all trees of each species ($N = 27$) present on the central 80 × 80 m subplot of the study area.

Type species	1992	1993	1994	F
White oak	0.22	0.10	0.11	0.94
Chestnut oak	0.17	0.09	0.21	0.98
Red maple	8.61^{a}	2.75^{b}	9.97^{a}	8.31**

Note: The F values were determined through two-way ANOVA (Date, df = 2; Size class, df = 2; Date × Size class, df = 4; Error, df = 72), with different letters indicating means that are significantly different.

** $P < 0.01$.

Hsiao et al. 1976, White 1984, Mattson and Haack 1987*a*, *b*, Louda and Collinge 1992) through plant osmotic adjustments in establishing drought tolerance (Kramer 1983). However, the potential for roots to absorb nutrients will gradually decline as water stress develops (Chapin 1991). Thus, moderate drought will reduce growth more than photosynthesis (Koslowski 1982, Kramer 1983, Wardlaw 1990), enabling carbohydrates to accumulate in plant foliage. Part of this excess pool of carbohydrates may be allocated preferentially to root development, thereby permitting root : shoot biomass ratios to increase adaptively until carbon fixation becomes limited as water stress progresses (Bradford and Hsiao 1982, Schulze et al. 1987, Chapin 1991). Any excess carbon remaining in leaves during moderate drought is available for storage or use in the production of secondary metabolites for possible defensive purposes (Gershenzon 1984, Herms and Mattson 1992). Ultimately, severe drought stress will reduce photosynthetic rates and the overall quality of leaf tissues (Ehleringer and Cook 1984, Chapin 1991). Leaf contents may also undergo resorption if leaf senescence occurs in response to drought (Killingbeck 1996).

These findings suggest a nonlinear response of plant phenolic production to increasing intensities of water deficits (Mattson and Haack 1987*a*, Horner 1990). Secondary metabolites, including phenolic compounds, should increase in leaves as N uptake rates and growth are curtailed during the transition from mild to moderate drought. However, the concentrations of these secondary metabolites should ultimately decrease, either because of a limitation in photosynthetic enzymes available for carbohydrate production, a reduction in the activity of enzymes involved in phenolic biosynthesis, or through resorption (Gershenzon 1984). Recent validation of this nonlinear response (Horner 1990) fits the major tenets of the carbon/nutrient and growth/differentiation balance hypotheses and offers a possible resolution of the long-standing enigma of inconsistent responses of plant phenolics to moisture stresses (Gershenzon 1984, Mattson and Haack 1987*a*, Ayres 1993). Past studies were apparently conducted at varying intensities of soil water stresses.

Tree species studied at Walker Branch exhibited similar responses to rainfall fluctuations over the study period. The changes in foliar chemistry during wet or dry summers were consistent for all size classes of trees of each species, and generally fit the patterns expected concerning shifts in resource allocation from growth to differentiation (Herms and Mattson 1992). Foliar N concentrations at Walker Branch normally decrease throughout the growing season, following peak levels in early spring (Garten 1993). Nevertheless, the decline in foliar N in oaks and maple trees during the midsummer drought in 1993 reached levels well below those present by late August in 1992 and 1994. The direct correlation observed between rainfall and foliar N levels should be expected, given the relatively low soil N levels present in the study area (Garten 1993). Any drought-induced shift to water uptake from deeper, more nutrient-impoverished soil strata would further reduce foliar N concentrations.

Nearly all measures of foliar phenolic chemistry were lower during the much drier growing season of 1993 than of 1992. The consistency of this response probably reflects the presence of severe soil water deficits in 1993. The reduction in foliar N levels during drought should have increased phenolic concentrations if photosynthetic rates had remained high and growth had ceased (Mattson and Haack 1987*b*, Horner 1990, Herms and Mattson 1992). Instead, the magnitude of the drought was apparently sufficient to limit either carbon production or phenolic biosynthesis (Gershenzon 1984). Either mechanism would promote declines in phenolic production as the possibility of carbon allocation to differentiation products, such as secondary metabolites, was limited. Early resorption and leaf senescence may not have occurred, because the timing of autumn litterfall was quite similar during wet and dry years at Walker Branch (Paul Hanson, *personal communication*).

The differential response of phenolic compounds during the wet 1994 summer is more difficult to reconcile. The failure of total phenol and hydrolyzable tannin levels to rebound following drought might reflect a preferential utilization of carbon for growth over differentiation as soil N uptake increased during high rainfall in 1994 (Bryant et al. 1983, Herms and Mattson 1992, Tuomi 1992). The fact that annual bole diameter growth of mature trees was 50.4% (white oak), 51.6% (chestnut oak), and 95.3% (red maples) higher in 1994 than in 1993 (Paul Hanson, *unpublished data*) supports this contention. In addition, any reduction in carbon production and subsequent storage during the 1993 drought would diminish the carbon pool available for phenolic production during the next growing season. Haukioja and Neuvonen (1985), Tuomi et al. (1988), and Marquis and Whelan (1994) have documented the role of herbivory and other plant stresses in causing delayed expressions of carbon and nutrient shortages through a second or subsequent year. The combination of shortages of stored carbon and high soil N availability in 1994 may have limited carbon allocation to differentiation products such as tannins, or may have promoted adaptive trade-offs in the relative production of different categories of phenolics. The occurrence of especially high levels of condensed tannins in all species in 1994 may represent such a trade-off, because fungal damage was greater on maple and, to some extent, chestnut oak trees during the wet than during the dry summers (Zucker 1983). Induced responses of this type would reflect optimal defense (Rhodes 1979, Zangerl and Rutledge 1996) if further fungal damage were restricted. However, the speculative nature of these explanations points out the need for further experimental validation of the mechanistic basis for plant phenolic responses under varying moisture regimes.

Insect herbivory

Insect herbivore damage on the Walker Branch Watershed varied among species and in response to rainfall fluctuations. Insect damage on oak trees exceeded average levels reported for broadleaf tree species occupying temperate deciduous forests (Schowalter et al. 1986, Coley and Aide 1991), but were comparable to or less than levels reported for oak seedlings and saplings in Missouri forests (Sork et al. 1993, Marquis and Whelan 1994). The high levels of leaf stripping and skeletonizing damage on oaks occurred despite relatively low levels of foliar N (Coley and Aide 1991, Garten 1993) and high concentrations of total phenolics and/or hydrolyzable tannins. In contrast, insect damage was quite low on red maple foliage, as a result of the absence of leaf skeletonizing. The especially low foliar N levels in maple trees at Walker Branch may prevent skeletonizers from utilizing maple tissue. Foliar N levels can significantly influence insect feeding (Fox and McCauley 1977, Mattson 1980, Scriber and Slansky 1981, White 1984, Mattson and Scriber 1987), particularly because of the metabolic constraints imposed by much lower N concentrations in leaf than in insect tissues (Mattson 1980, Ayres 1993). In fact, the incidence of insects feeding on leaves containing N concentrations $<2\%$ is generally quite limited (Fox and McCauley 1977).

Few, if any, studies have evaluated herbivore damage at different life cycle stages of forest tree species (Schowalter et al. 1986). Methodological constraints have often limited studies to smaller seedlings or saplings without including mature conspecifics. No patterns emerged when we compared insect damage on different size classes of oaks or maple species. Instead, the overall similarity in extent and type of herbivore damage throughout the life cycle of these species probably reflects the corresponding absence of major changes in foliar N, total phenol, or hydrolyzable tannin concentrations. The significantly higher condensed tannin levels in mature trees of each species apparently failed to reduce insect feeding, unless herbivore densities were greater on the more-insolated overstory conspecifics (Schupp and Feener 1991). Nevertheless, the overall absence of differences in herbivore pressure from early to late stages of forest tree development fails to support earlier predictions that acquired resistance should produce lower damage levels in mature trees (Karban 1987).

Considerable difficulty has existed in predicting the overall response of insect herbivores to moisture fluctuations (Gershenzon 1984, Mattson and Haack 1987*a*, Larsson 1989, Louda and Collinge 1992, Ayres 1993, Stowe et al. 1994). This difficulty seems to be largely a product of the varied responses of specific insect herbivores to changing ratios of foliar nutrients and plant phenolics as water stress increases (Bazzaz et al. 1987, Louda and Collinge 1992). Insect damage should increase during the initial stages of drought, if foliar nutrients and soluble carbohydrates accumulate through plant osmotic adjustments (Stowe et al. 1994). However, herbivores may become limited if secondary metabolites accumulate as moderate water stress retards growth more than photosynthesis (Horner 1990, Herms and Mattson 1992). The extent of this impact might depend on the relative ability of insect detoxification systems to handle the possible buildup of carbon-based defenses. Ultimately, severe water stress should limit photosynthesis as well as nutrient and water uptake, thereby rendering plant foliage largely unsuitable for insect herbivores (White 1984, Louda and Collinge 1992). Direct insect mortality should thus occur during severe droughts.

The level of insect damage on the Walker Branch Watershed was directly correlated with rainfall totals during the 3-yr study. Foliar N concentrations appeared to be quite important in regulating consumption by insects during these rainfall fluctuations. For example, the reduction in skeletonizing damage on oak trees during the 1993 drought occurred when foliar N levels declined below 2.0%. This drop in consumption during drought occurred despite a concomitant reduction in foliar phenolics in both oak species. The combination of low foliar N and possibly low leaf water content (Scriber 1984) in oaks may have caused sufficient insect mortality or reduced feeding to limit skeletonizing damage during the severe midsummer drought. The relative absence of skeletonizers from N-limited maple foliage provides support for this assertion. Thus, leaf skeletonizers at Walker Branch may be particularly sensitive to rainfall-related effects on foliar N concentrations.

Foliar chemistry appeared to be more favorable for insect herbivores during the wet 1994 growing season. The combination of higher leaf N (oaks) and continued reductions in total phenols and hydrolyzable tannins in 1994 may have promoted greater damage by strip feeders on oak and maple trees, and by skeletonizers on chestnut oaks. The allocation of considerable carbon to condensed tannin production in all species in 1994 may have proved more important in limiting fungal damage than insect herbivory. These results suggest that insect damage on our study area at Walker Branch involves the response of specific feeding guilds to weather-related effects on concentrations of foliar N, and probably to a lesser extent on plant phenolics. Louda and Collinge (1992) also reported guild-specific insect responses following soil water manipulations, and Larsson (1989) has clearly articulated why the actual response of insect herbivores to plant stress should be feeding-guild specific. Thus, a guild approach seems advisable in future attempts at isolating causal mechanisms for changes in consumption by insect herbivores during climatic fluctuations.

Acknowledgments

We thank Paul Hanson and Mike Huston of the Environmental Science Division of the Oak Ridge National Laboratory for enabling us to participate in the project at Walker Branch and for providing logistical support in conducting our studies. Allan Wilson, Kenny Peavy, Larry Wilson, Jason Legros, and Sue Carstensen were particularly helpful in field sampling and/or laboratory analyses. George Cotsonis provided statistical advice and assistance in analyzing the data, and Chris Mowry assisted with the graphical presentation of final results. Funding for the project was provided totally by the U.S. Department of Energy's (DOE) National Institute for Global Environmental Change and was administered through the NIGEC Southeast Regional Center at the University of Alabama, Tuscaloosa (DOE Cooperative Agreement No. DE-FC03-90ER61010). Financial support does not constitute an endorsement by DOE of the views expressed in this paper.

Literature Cited

Aide, T. M. 1993. Patterns of leaf development and herbivory in a tropical understory community. Ecology **74**:455–466.

Ayres, M. P. 1993. Plant defense, herbivory, and climate change. Pages 75–94 *in* P. M. Kareiva, J. G. Kingsolver, and R. B. Huey, editors. Biotic interactions and global change. Sinauer Associates, Sunderland, Massachusetts, USA.

Baldwin, I. T., J. C. Schultz, and D. Ward. 1987. Patterns and sources of leaf tannin variation in yellow birch (*Betula allegheniensis*) and sugar maple (*Acer saccharum*). Journal of Chemical Ecology **13**:1069–1078.

Bate-Smith, E. C. 1972. Detection and determination of ellagitannins. Phytochemistry **11**:1153–1156.

———. 1975. Phytochemistry of proanthocyanidins. Phytochemistry **14**:1107–1113.

———. 1977. Astringent tannins of *Acer* species. Phytochemistry **16**:1421–1426.

———. 1981. Astringent tannins of the leaves of *Geranium* species. Phytochemistry **20**:211–216.

Bazzaz, F. A., N. R. Chiarello, P. D. Coley, and L. F. Pitelka. 1987. Allocating resources to reproduction and defense. BioScience **37**:58–68.

Bernays, E. A. 1981. Plant tannins and insect herbivores: an appraisal. Ecological Entomology **6**:353–360.

Bernays, E. A., G. Cooper-Driver, and M. Billener. 1989. Herbivores and plant tannins. Advances in Ecological Research **19**:263–302.

Bradford, K. J., and T. C. Hsiao. 1982. Physiological responses to moderate water stress. Pages 264–324 *in* O. L. Lange, P. S. Nobel, C. B. Osmond, and H. Ziegler, editors. Encyclopedia of plant physiology. Volume 12B. Springer-Verlag, Berlin, Germany.

Bryant, J. P., F. S. Chapin, III, and D. R. Klein. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. Oikos **40**:357–368.

Bryant, J. P., F. S. Chapin, III, P. B. Reichart, and T. P. Clausen. 1987. Response of winter chemical defense in Alaska paper birch and green alder to manipulation of plant carbon/nutrient balance. Oecologia **72**:510–514.

Carmer, S. G., and M. R. Swanson. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. Journal of the American Statistical Association **68**:66–74.

Chapin, F. S., III. 1991. Integrated responses of plants to stress. BioScience **41**:29–36.

Chapin, F. S., III, A. J. Bloom, C. B. Field, and R. H. Waring. 1987. Plant responses to multiple environmental factors. BioScience **37**:49–57.

Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. Ecological Monographs **53**:209–233.

———. 1986. Costs and benefits of defense by tannins in a neotropical tree. Oecologia **70**:238–241.

Coley, P. D., and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. Pages 25–49 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes, and W. W. Benson, editors. Plant–animal interactions: evolutionary ecology in tropical and temperate regions. John Wiley, New York, New York, USA.

Coley, P. D., J. P. Bryant, and F. S. Chapin, III. 1985. Resource availability and plant anti-herbivore defense. Science **230**:895–899.

Cornell, H. V., and B. A. Hawkins. 1995. Survival patterns and mortality sources of herbivorous insects: some demographic trends. American Naturalist **145**:563–593.

Coulson, R. N., and J. A. Witter. 1984. Forest entomology: ecology and management. John Wiley, New York, New York, USA.

Denslow, J. S., J. C. Schultz, P. M. Vitousek, and B. R. Strain. 1990. Growth responses of tropical shrubs to treefall gap environments. Ecology **71**:165–179.

Dudt, J. F., and D. J. Shure, 1994. The influence of light and nutrients on foliar phenolics and insect herbivory. Ecology **75**:86–98.

Ehleringer, J. R., and C. S. Cook. 1984. Photosynthesis in *Encelia farinosa* Gray in response to decreasing water potential. Plant Physiology **75**:688–693.

Faeth, S. H. 1985. Quantitative defense theory and patterns of feeding by oak insects. Oecologia **68**:34–40.

Faeth, S. H., S. Mopper, and D. Simberloff. 1981. Abundances and diversity of leaf-mining insects on three oak host species: effects of host plant phenology and nitrogen content of leaves. Oikos **37**:238–251.

Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1992. The effect of nutrients and enriched CO_2 environments on production of carbon-based allelochemicals in *Plantago*: a test of the carbon/nutrient balance hypothesis. American Naturalist **140**:707–723.

Feeny, P. P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology **51**:565–581.

———. 1976. Plant apparency and chemical defense. Pages 1–40 *in* J. Wallace and R. L. Mansell, editors. Biochemical interactions between plants and insects. Recent Advances in Phytochemistry **10**.

Fox, L. R., and B. J. Macauley. 1977. Insect grazing on *Eucalyptus* in response to variation in leaf tannins and nitrogen. Oecologia **29**:145–162.

Garten, C. T., Jr. 1993. Variation in foliar ^{15}N abundance and the availability of soil nitrogen on Walker Branch Watershed. Ecology **74**:2098–2113.

Garten, C. T., Jr., and G. E. Taylor, Jr. 1992. Foliar δ^{13} C within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia **90**:1–7.

Gershenzon, J. 1984. Changes in the level of plant secondary metabolites under water and nutrient stress. Pages 273–320 *in* B. N. Timmermann, C. Steelink, and F. A. Loewus, editors. Phytochemical adaptation to stress. Recent Advances in Phytochemistry **18**.

Hagerman, A. E. 1988. Extraction of tannin from fresh and preserved leaves. Journal of Chemical Ecology **14**:453–461.

Hanson, P. J., D. E. Todd, N. T. Edwards, and M. A. Huston. 1995. Field performance of the Walker Branch Throughfall Displacement Experiment. Pages 307–313 *in* A. Jenkins, R. C. Ferrier, and C. Kirby, editors. Ecosystem manipulation experiments: scientific approaches, experimental design, and relevant results. Ecosystems Research Report Number 20. Commission of the European Communities.

Hargrove, W. W., D. A. Crossley, Jr., and T. R. Seastedt. 1984. Shifts in herbivory in the canopy of black locust, *Robinia pseudoacacia* L., following fertilization. Oikos **43**:322–328.

Haukioja, E., and S. Neuvonen. 1985. Induced long-term resistance of birch foliage against defoliators: defensive or incidental. Ecology **66**:1303–1308.

Herms, D. A., and W. J. Mattson. 1992. The dilemna of plants: to grow or defend. Quarterly Review of Biology **67**:283–335.

Horner, J. D. 1990. Nonlinear effects of water deficits on foliar tannin concentration. Biochemical Systematics and Ecology **18**:211–213.

Hsiao, T. C. 1973. Plant responses to water stress. Annual Review of Plant Physiology **24**:519–570.

Hsiao, T. C., E. Fereres, E. Acevedo, and D. W. Henderson. 1976. Water stress and dynamics of growth and yield of crop plants. Pages 281–305 *in* O. L. Lange, L. Kappen, and E. D. Schulze, editors. Water and plant life. Problems and modern approaches. Springer-Verlag, New York, New York, USA.

Hunter, M. D., and J. C. Schultz. 1993. Induced plant defenses breached? Phytochemical induction protects an herbivore from disease. Oecologia **94**:195–203.

Hutchison, B. A., D. R. Matt, R. T. McMillen, L. J. Gross, S. J. Tajchman, and J. M. Norman. 1986. The architecture of an East Tennessee deciduous forest canopy. Journal of Ecology **74**:635–676.

Johnson, D. W., and R. I. Van Hook. 1989. Analysis of biogeochemical cycling processes in Walker Branch watershed. Springer-Verlag, New York, New York, USA.

Karban, R. 1987. Herbivory dependent on plant age: a hypothesis based on acquired resistance. Oikos **48**:336–337.

Killingbeck, K. T. 1996. Nutrients in senesced leaves: keys to the search for potential resorption and resorption proficiency. Ecology **77**:1716–1727.

Koslowski, T. T. 1982. Water supply and tree growth: Part I. Water deficits. Forestry Abstracts **43**:57–95.

Kramer, P. J. 1983. Water relations of plants. Academic Press, New York, New York, USA.

Landsberg, J., and C. Ohmart. 1989. Levels of insect defoliation in forests: patterns and concepts. Trends in Ecology and Systematics **4**:96–100.

Langenheim, J. H., S. P. Arrhenius, and J. C. Nascimento. 1981. Relationship of light intensity to leaf resin composition and yield in the tropical leguminous genera *Hymenaea* and *Copaifera.* Biochemical Systematics and Ecology **9**:27–37.

Larsson, S. 1989. Stressful times for the plant stress-insect performance hypothesis. Oikos **56**:277–283.

Larsson, S., A. Wiren, L. Lundgren, and T. Ericsson. 1986. Effects of light and nutrient stress on leaf phenolic chemistry in *Salix dasyclados* and susceptibility to *Gallerucella lineola* (Coleoptera). Oikos **47**:205–210.

Lindroth, R. L., and M. S. Pajutee. 1987. Chemical analysis of phenolic glycosides: art, facts, and artifacts. Oecologia **74**:144–148.

Louda, S. M., and S. K. Collinge. 1992. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. Ecology **73**:153–169.

Marquis, R. J., and C. J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. Ecology **75**:2007–2014.

Martin, J. S., and M. M. Martin. 1982. Tannin assays in ecological studies: lack of correlation between phenolics, proanthocyanidins, and protein-precipitating constituents in mature foliage of six oak species. Oecologia **54**:205–211.

Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics **11**: 119–161.

Mattson, W. J., and R. A. Haack. 1987*a.* The role of drought stress in provoking outbreaks of phytophagous insects. Pages 365–407 *in* P. Barbosa and J. C. Schultz, editors. Insect outbreaks. Academic Press, New York, New York, USA.

Mattson, W. J., and R. A. Haack. 1987*b.* The role of drought in outbreaks of plant eating insects. BioScience **37**:110–118.

Mattson, W. J., and J. M. Scriber. 1987. Feeding ecology of insect folivores of woody plants: water, nitrogen, fiber, and mineral considerations. Pages 105–146 *in* F. Slansky, Jr., and J. G. Rodriquez, editors. The nutritional ecology of insects, mites, and spiders. John Wiley, New York, New York, USA.

Mole, S., J. A. M. Ross, and P. G. Waterman. 1988. Light-induced variation in phenolic levels in foliage of rain-forest plants. I. Chemical changes. Journal of Chemical Ecology. **14**:1–21.

Mole, S., and P. G. Waterman. 1987. A critical analysis of techniques for measuring tannins in ecological studies. I. Techniques for chemically defining tannins. Oecologia **72**: 137–147.

Muller, R. N., P. J. Kalisz, and T. W. Kimmerer. 1987. Intraspecific variation in production of astringent phenolics over a vegetation–resource availability gradient. Oecologia **72**:211–215.

Reichle, D. E., R. A. Goldstein, R. I. Van Hook, Jr., and G. J. Dodson. 1973. Analysis of insect consumption in a forest canopy. Ecology **54**:1076–1084.

Rhoades, D. F. 1979. Evolution of plant chemical defense against herbivores. Pages 3–54 *in* G. A. Rosenthal and D. H. Janzen, editors. Herbivores: their interactions with secondary plant metabolites. Academic Press, New York, New York, USA

———. 1983. Herbivore population dynamics and plant chemistry. Pages 155–200 *in* R. F. Denno and M. S. McClure, editors. Herbivore population dynamics and plant chemistry. Academic Press, Orlando, Florida, USA.

———. 1985. Offensive-defensive interactions between herbivores and plants: their relevance in herbivore population dynamics and ecological theory. American Naturalist **125**: 205–238.

Rossiter, M., J. C. Schultz, and I. T. Baldwin. 1988. Relationships among defoliation, red oak phenolics, and gypsy moth growth and reproduction. Ecology **69**:267–277.

Schowalter, T. D., W. W. Hargrove, and D. A. Crossley, Jr. 1986. Herbivory in forested ecosystems. Annual Review of Entomology **31**:177–196.

Schultz, J. C. 1988. Many factors influence the coevolution of herbivore diets, but plant chemistry is central. Ecology **69**:896–897.

Schultz, J. C., and I. T. Baldwin. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. Science **217**:149–151.

Schulze, E. D., R. H. Robichaux, J. Grace, P. W. Rundel, and J. R. Ehleringer. 1987. Plant water balance. BioScience **37**:30–37.

Schupp, E. W., and D. H. Feener, Jr. 1991. Phylogeny, life-form, and habitat dependence of ant-defended plants in a Panamanian forest. Pages 175–197 *in* C. R. Huxley and D. F. Cutler, editors. Ant–plant interactions. Oxford University Press, Oxford, UK.

Scriber, J. M. 1984. Host plant suitability. Pages 159–202 *in* W. J. Bell and R. T. Carde, editors. Chemical ecology of insects. Sinauer Associates, Sunderland, Massachusetts, USA.

Scriber, J. M., and F. Slansky, Jr. 1981. The nutritional ecology of immature insects. Annual Review of Entomology **26**:183–211.

Shure, D. J., and L. A. Wilson. 1993. Patch-size effects on plant phenolics in successional openings of the Southern Appalachians. Ecology **74**:55–67.

Sork, V. L., K. A. Stowe, and C. Hochwender. 1993. Evidence for local adaptation in closely adjacent subpopulations of northern red oak (*Quercus rubra* L.), expressed as resistance to herbivores. American Naturalist. **142**:928–936.

Stowe, K. A., V. L. Sork, and A. W. Farrell. 1994. Effect of water availability on the phenotypic expression of herbivore resistance in northern red oak seedlings (*Quercus rubra* L.). Oecologia **100**:309–315.

Swain, T. 1979. Tannins and lignins. Pages 657–682 *in* G. A. Rosenthal and D. H. Janzen, editors. Herbivores: their interaction with secondary plant metabolites. Academic Press, New York, New York, USA.

Swain, T., and W. E. Hillis. 1959. The phenolic constituents of *Prunus domestica.* I. The quantitative analysis of phenolic constituents. Journal of Agricultural and Food Science **10**:63–68.

Tuomi, J. 1992. Toward integration of plant defense theories. Trends in Ecology and Evolution **7**:365–367.

Tuomi, J., P. Niemela, M. Rousi, S. Siren, and T. Vuorisalo. 1988. Induced accumulation of foliage phenols in mountain birch: branch response to defoliation? American Naturalist **132**:602–608.

Wardlaw, I. F. 1990. Tansley Review Number 27: the control of carbon partitioning in plants. New Phytologist **116**:341–381.

Waterman, P. G., J. A. M. Ross, and D. B. McKey. 1984. Factors affecting levels of some phenolic compounds, digestibility, and nitrogen content of the mature leaves of *Barteria fistulosa* (Passifloraceae). Journal of Chemical Ecology **10**:387–401.

White, T. R. C. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia **63**:90–105.

Wisdom, C. S., A. Gonzalez-Coloma, and P. W. Rundel. 1987. Ecological tannin assays. Evaluation of proanthocyanidins, protein binding assays, and protein precipitating potential. Oecologia **72**:395–401.

Zangerl, A. R., and C. E. Rutledge. 1996. The probability of attack and patterns of constitutive and induced defense: a test of optimal defense theory. American Naturalist **147**: 599–608.

Zucker, W. V. 1983. Tannins: does structure determine function? An ecological perspective. American Naturalist **121**: 335–365.