PATCH-SIZE EFFECTS ON PLANT PHENOLICS IN SUCCESSIONAL OPENINGS OF THE SOUTHERN APPALACHIANS[1]

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Abstract. We examined the seasonal changes in plant chemical defenses of key tree species (*Robinia pseudoacacia, Liriodendron tulipifera, Acer rubrum,* and *Cornus florida*) regenerating during early succession in different patch sizes within Southern Appalachian forests. Trees of each species were sampled from five sizes of forest openings (0.016, 0.08, 0.4, 2.0, and 10 ha; two replicates each) and from the understory of surrounding forests. Leaves of rapidly growing, pioneer species (*Robinia* and *Liriodendron*) were slightly less tough and contained lower levels of hydrolyzable tannins and total phenolics, but higher condensed tannin concentrations than the slower growing, more shade-tolerant species (*Acer* and *Cornus*). These results generally support earlier findings indicating the evolutionary development of greater levels of constitutive phenolics in slow-growing than fast-growing species. The differential use of condensed and hydrolyzable tannins by slow- and fast-growing species may reflect adaptive trade-offs in the allocation of different types of phenolics.

Regenerating trees often had tougher leaves and contained higher levels of phenolics in large than small openings by midsummer. The differences in phenolics were more pronounced for condensed tannins and when comparing the smallest canopy openings with larger patch sizes. Plant phenolics were also generally lower in understory trees than in conspecific sprouts in openings. These findings may reflect phenotypic carbon/nutrient adjustments as light availability changes across the patch-size gradient. The greater sunlight in large than small openings apparently promotes excess carbon production and a metabolic buildup of phenolic compounds. Independent measures of phenolic compounds peaked at different times during the growing season. Hydrolyzable tannins reached peak levels quite early whereas condensed tannins increased later in the growing season. Total phenolics peaked in midsummer. Herbivore damage was consistently high (5–9%) on *Robinia* sprouts in all openings. Insect herbivory on the remaining three species (1–5%) was significantly lower in large than small patch sizes. Tree species regenerating in the high sunlight of larger openings in Southern Appalachian forests thus tend to have tougher leaves, contain greater phenolics, and experience less herbivore damage than conspecifics in small openings.

Key words: forests; gaps; herbivory; patch dynamics; phenolics; plant defenses; Southern Appalachian Mountains; succession; tannins.

INTRODUCTION

Considerable progress has occurred in elucidating the mechanistic basis for spatiotemporal patterns of plant antiherbivore defenses. The focus has shifted from earlier considerations of plant apparency as an organizing concept (Feeny 1976, Rhoades and Cates 1976) to more recent incorporations of resource availability, relative growth rates, and carbon/nutrient balance as determining factors. Current hypotheses suggest that plant species occurring in resource-limited habitats contain higher levels of carbon-based defenses than species found in resource-rich environments (McKey et al. 1978, Bryant et al. 1983, Coley et al. 1985, Chapin et al. 1987). Phenolic compounds including tannins are usually considered a major component of these carbon-based defenses (Coley 1986, Rossiter et al. 1988, Bryant et al. 1991, Coley and Aide 1991), although their actual effectiveness as antiherbivore agents has been questioned (Bernays 1981, Faeth 1985). Species exhibiting slow growth rates are also expected to contain greater levels of phenolic compounds than co-occurring species with more rapid growth rates (Coley 1983, 1988, Denslow et al. 1990). Evolutionary explanations for these interspecific trends often center on the heavy replacement costs associated with herbivore-induced tissue loss from slow-growing species, especially in resource-limited habitats (Coley et al. 1985).

Changes in the carbon/nutrient balance of plants are proving especially important in explaining intraspecific phenotypic variations in plant phenolics across environmental gradients (Bryant et al. 1983, 1987, 1991, Tuomi et al. 1984, 1988, Larsson et al. 1986, Bryant 1987, Chapin et al. 1987, Muller et al. 1987, Mole et al. 1988, Mihaliak and Lincoln 1989). For example,

plants will preferentially allocate carbon for growth if conditions are favorable, whereas carbon may accumulate and be converted to phenolic compounds if light is high and soil nutrients are limited (Larsson et al. 1986, Chapin et al. 1987). These short-term intraspecific changes in secondary metabolites reflect passive phenotypic adjustments to resource limitations, exclusive of antiherbivore functions. The extent to which herbivores respond to these intraspecific changes in plant phenolics remains largely undetermined (Mole and Waterman 1988).

Most experimental tests of these hypotheses have examined the effects of resource amendments (i.e., fertilization) or light limitations (sun vs. shade) in field or greenhouse environments (Larsson et al. 1986, Bryant et al. 1987, Denslow et al. 1990). Few studies have evaluated the relative plasticity of plant phenolics across subtle resource gradients within natural environments (Muller et al. 1987, Mole et al. 1988, Denslow et al. 1990). Further studies are thus needed to examine the phenotypic expression of constitutive phenolics in plant species occurring at different times during succession as well as those illustrating different distributional patterns across resource gradients. Attention should also be focused on the possible importance of the changes in plant phenolics in mediating herbivore impacts on plant replacement processes. Temperate zone studies are especially needed to complement ongoing work in tropical and boreal environments.

The basic objective of our study was to evaluate the changing patterns of plant–herbivore interactions during early succession in different patch sizes within the Southern Appalachian Mountains. We were specifically interested in (1) determining the interspecific levels of phenolic compounds in woody plant species representing different evolutionary "strategies" of occurrence during succession, (2) evaluating the intraspecific phenotypic plasticity of plant phenolics as resources change from small to large patch sizes, (3) contrasting the levels of phenolic compounds of woody successional sprouts with conspecific trees in the understory of surrounding forests, and (4) assessing the extent of herbivore damage as plant phenolics vary across a patch-size gradient. Satisfaction of these objectives should provide useful insight into the mechanisms underlying changes in plant secondary metabolites as resources vary in different disturbance patches within the landscape mosaic of the Southern Appalachians.

MATERIALS AND METHODS

Study area

We conducted the study within the Nantahala National Forest in the Southern Appalachian Mountains near Highlands, North Carolina. Five patch sizes were chosen (0.016, 0.08, 0.4, 2.0, and 10 ha) to represent the complete range of natural and human disturbances within the region (Phillips and Shure 1990). Each opening was 5 times larger than the next smaller one. The locations of all openings were controlled for elevation (975–1100 m), aspect (east to north), slope (30–40%), configuration (square), and stand type (predominantly *Quercus* spp., *Carya* spp., and *Liriodendron tulipifera*). We established two replicates of each size to prevent problems of pseudoreplication (Hurlbert 1984).

The study plots were located in two areas near Highlands. The 10-ha sites were ≈ 13 km west of Highlands. The remaining eight openings and two undisturbed control forest areas (≈ 1.0 ha each) were established along Wilson Gap Road ≈ 3–5 km southeast of Highlands. The extensive forest tracts in both areas are characteristic of the upland, mixed mesophytic stands of the Southern Appalachian section of the Blue Ridge Province (Braun 1950). Precipitation averages 175–200 cm/yr, and soils are primarily Hapludults and Dystrochrepts (Nelson and Zillgitt 1969). Detailed descriptions of the precut and early successional vegetation, logging procedures, and the litter-debris dynamics on these plots have been presented elsewhere (Buckner and Shure 1985, Shure and Phillips 1987, Phillips and Shure 1990).

All experimental plots were logged during winter and spring of 1981–1982. Revegetation was initiated simultaneously in all plots at the beginning of the 1982 growing season.

Species selection

We selected four tree species for analysis. Sprouts of each species were major components of the regenerating vegetation in each plot (Phillips and Shure 1990). Black locust (*Robinia pseudoacacia*) is the dominant pioneer species, which as a nitrogen fixer plays a critical role in nutrient retention and accretion until its demise by 20 yr postcutting (Boring et al. 1981, Boring and Swank 1984a). Yellow poplar (*Liriodendron tulipifera*) is another fast-growing pioneer species that often replaces black locust (Wallace and Dunn 1980, Clebsch and Busing 1989). *Liriodendron* trees persist in some mature stands such as cove forests (Leopold and Parker 1985, Clebsch and Busing 1989). Red maple (*Acer rubrum*) and dogwood (*Cornus florida*) represent more slow-growing, shade-tolerant species that remain as important late-successional canopy (*Acer*) and understory (*Cornus*) components (Phillips and Shure 1990). The canopy-dominant oaks and hickories exhibited only limited sprouting in our plots (Phillips and Shure 1990).

Field sampling

We randomly selected five individual trees of each species for sampling within each of the 10 openings. Five understory trees of the four species were also randomly selected in each control forest. A total of 240 trees were thus permanently marked for analysis. Basal diameter (forest openings) or diameter at breast height

(dbh) (control forests) were obtained from all trees in August 1985 and again in August 1987 for allometric estimates of tree size and growth rates (Boring and Swank 1984a, Phillips and Shure 1990).

Seven leaves were sampled from each tree at three intervals during 1985 (24–26 June, 22–24 July, 16–18 August) and on 17 August 1986. We used a system of randomly predetermined branch locations and leaf positions along the branch to ensure nonbiased leaf selection. A similar sampling procedure was used in August 1985 for five additional trees of each species in the two 2.0-ha openings. These trees represented the nearest conspecific neighbor of each regularly sampled tree and enabled an assessment of possible sampling-induced effects on plant phenolics and herbivory in these young sprouts. All leaves from each tree were bagged, placed in styrofoam containers, and returned to the laboratory within 2 h for processing. The large sample size and need for photocopying prevented freezing of samples in the field.

Herbivory and plant defenses

All leaves were photocopied before performing chemical analyses. The photocopy indicates leaf area damaged or removed by insect herbivores (Hargrove et al. 1984). A digitizer (Micro-plan II, Laboratory Computer Systems) was used to determine total leaf area and percent leaf area damaged by major feeding guilds, including strip feeders, pit feeders, leafminers, and leaf rollers.

Plant parameters measured included leaf moisture content, leaf toughness, total phenols, condensed and hydrolyzable tannins, and protein-binding capacity. Leaf moisture content was analyzed gravimetrically for three of the seven leaves obtained from each tree on each sample date in 1985. The leaves were weighed when fresh, oven-dried at 35°C for 48 h, and reweighed. Low drying temperatures (<40°C) minimize the irreversible fixing or denaturing of tannins that occurs at higher drying temperatures (Swain 1979) and has contributed to a more recent reliance on freeze-drying procedures. Different drying conditions can affect the extractability of certain phenolics (Lindroth and Pajutee 1987). A handmade penetrometer device (Feeny 1970) was used to measure leaf toughness from the remaining four leaves obtained from each tree in June and July 1985. Two measures were averaged for each leaf. These four leaves were also oven-dried at 35°C for 48 h. The composite seven leaves from each tree were ground to powder in a Wiley Mill and frozen until analyzed.

We used a 50% methanol extraction procedure as a precursor for plant chemical 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, 1977). Condensed tannins were estimated as proanthocyanidins using a bu-

tanol–HCL technique (Bate-Smith 1975, 1981). Protein-binding capacity was determined only in 1986 using hemoglobin as a substrate (Bate-Smith 1973, Schultz et al. 1981). Total phenolics and protein-binding capacity used tannic acid for standard curves and are expressed as percent (dry mass) tannic acid equivalents (TAE). Hydrolyzable tannins are reported as milligrams dry mass of hexahydroxydiphenoylglucose equivalents (Bate-Smith 1972, 1981) and condensed tannins as percent dry mass Quebracho tannin equivalents.

The Bate-Smith procedures have been widely used in assaying phenolic levels in plant tissues (Swain 1979, Shultz and Baldwin 1982, Marks et al. 1988, Rossiter et al. 1988). They yield nearly complete extractability of hydrolyzable tannins (Bate-Smith 1977), although differential extractability of certain proanthocyanidins can affect interspecific comparisons of condensed tannins (Bate-Smith 1977, Swain 1979, Wisdom et al. 1987). The use of tannic acid and Quebracho tannin as standards enabled relative but not absolute (percent dry mass) comparisons between plant samples (Coley and Aide 1991). Martin and Martin (1982), Wisdom et al. (1987), and Mole and Waterman (1987) have reviewed the possible limitations in these and other standard procedures of phenolic analyses.

Data analysis

We used a split-plot or repeated-measures design for the analysis of variance in analyzing our data sets (Freund and Littell 1985). Patch size, species, and time were the possible main effects in different analyses. In the split-plot design each of the experimental units (openings) received one of the treatments (opening size), and the second factor (species) was applied to subunits (sampled trees) within the experimental units. Similarly, the main effect (size) in the repeated-measures design was applied to openings and individual trees in openings were sampled repeatedly. All ANOVAs were balanced and nested to account for replicated samples (trees) present within each experimental unit. 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 in those few cases where interaction terms were significant.

RESULTS
Growth parameters

Robinia and *Liriodendron* sprouts grew more rapidly during early succession than the more shade-tolerant *Acer* and *Cornus* (Table 1). This greater growth rate of pioneer species occurred in all patch sizes. Three of the four species had progressively greater growth rates from small to large patch sizes. Growth rates for the fourth species (*Liriodendron*) were highest in 2.0-ha patches.

Leaf sizes showed little consistent change across the

TABLE 1. Growth rates of trees of the four species sampled in different-sized forest openings and in the mature forest (C). Data were calculated from biomass determinations of each tree in August 1985 and August 1987. Values are means ± 1 SE.

	Opening size (ha)					
Species	C	0.016	0.08	0.4	2.0	10
	Growth rate (kg/yr)					
Robinia	···*	334 ± 117	567 ± 140	1182 ± 464	1333 ± 308	1778 ± 478
Liriodendron	301 ± 84	1710 ± 469	1170 ± 450	6037 ± 1354	8328 ± 1515	4811 ± 1580
Acer	181 ± 42	78 ± 65	144 ± 64	584 ± 373	737 ± 324	1450 ± 490
Cornus	140 ± 72	143 ± 47	308 ± 76	856 ± 283	1298 ± 468	1441 ± 462

* Mortality of small Robinia trees in the mature forest between 1985 and 1987 prevented accurate growth rate calculations.

patch-size gradient (Table 2). *Liriodendron* leaves were smaller in large than small patches, but no clear trend existed for *Robinia, Cornus,* or *Acer.* Understory trees had smaller (*Liriodendron*) as well as larger leaves (*Acer*) than conspecific sprouts in openings.

Plant defenses

Leaf toughness exhibited greater change than leaf water content across the patch-size gradient (Fig. 1). *Robinia, Liriodendron,* and *Cornus* leaves all increased significantly in toughness from small to large patches (Fig. 1, Table 3). *Acer* leaves had less change in different patch sizes. The leaves of fast-growing, pioneer species were consistently less tough than the slower growing, shade-tolerant species. *Robinia* was the only species to drop significantly in leaf water content from small to large patches. No clear trends were present for the other species or when comparing slow- and fast-growing species. Understory trees generally had greater leaf water content and were less tough than conspecific sprouts in openings.

Plant phenolics varied between species and in different patch sizes in 1985 (Figs. 2–4, Table 4). The slow-growing *Acer* and *Cornus* sprouts almost always contained at least twice as much total phenolics as *Robinia* and *Liriodendron* in different patch sizes (Fig. 2). The slower growing species also exhibited greater patch size changes in total phenolic concentrations than pioneer species. Levels of total phenolics in *Robinia* and *Liriodendron* remained relatively similar in 0.016-ha through 0.4-ha patches, but were slightly higher in the largest opening sizes. In contrast, total phenolic concentrations in *Acer* and *Cornus* were up to several-

fold higher in large than small openings by midsummer; most of this increase occurred between 0.016-ha and 0.4-ha patch sizes. Forest understory trees generally contained similar total phenolic concentrations as conspecifics in the smallest openings (Fig. 2). Interestingly, the understory trees dropped significantly in total phenolic levels over the growing season whereas sprouts in openings usually peaked in mid-to-late summer.

Fast- and slow-growing species were markedly different in their allocation of hydrolyzable vs. condensed tannins (Figs. 3 and 4). *Acer* and *Cornus* sprouts contained relatively high levels of hydrolyzable tannins, but quite low concentrations of condensed tannins. This response was especially true for *Cornus* leaves that had the highest levels of hydrolyzable tannins and the lowest levels of condensed tannins among the four species sampled. In contrast, leaves of fast-growing pioneer species contained particularly high levels of condensed tannins and had lower concentrations of hydrolyzable tannins than slow-growing species. Condensed tannins were highest in *Robinia* leaves.

Patch size changes in tannin concentrations varied over the growing season (Figs. 3 and 4, Table 4). *Robinia, Acer,* and *Cornus* exhibited no consistent patch size trends in June. However, these species generally contained lower levels of tannins in the 0.016-ha vs. larger openings in July and August and the differences for *Robinia* and *Cornus* were often significant (Table 4). All three species showed no consistent change in tannin concentrations from 0.08-ha to 10-ha patches. In contrast, *Liriodendron* sprouts increased significantly in condensed and hydrolyzable tannin concentrations across the patch size gradient in all cases but condensed tannins in June. Forest understory trees al-

TABLE 2. Leaf sizes (cm²) of four tree species occurring in different-sized forest openings and in the understory of mature forest (C) in the Southern Appalachian Mountains in July 1985. Values represent means for 10 trees in each opening size ± 1 SE.

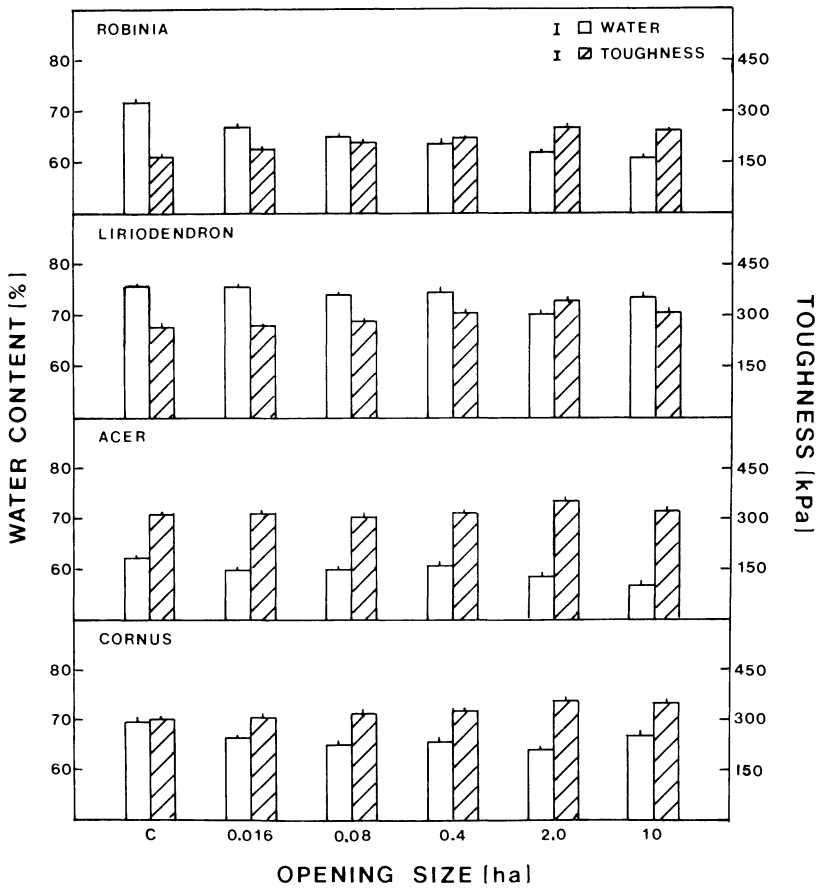|	Opening size (ha)					
	C	0.016	0.08	0.4	2.0	10
	Leaf area (cm²)					
Robinia	154.4 ± 8.8	191.1 ± 5.9	89.0 ± 7.0	132.6 ± 10.0	83.1 ± 6.2	89.5 ± 4.6
Liriodendron	113.5 ± 7.7	181.4 ± 11.7	155.8 ± 12.4	154.1 ± 10.4	148.9 ± 5.7	132.9 ± 7.3
Acer	84.0 ± 6.1	66.4 ± 4.0	60.9 ± 4.1	68.6 ± 5.0	66.2 ± 5.4	60.3 ± 3.0
Cornus	45.3 ± 2.8	52.9 ± 4.0	48.1 ± 2.6	48.6 ± 2.9	53.6 ± 3.7	51.0 ± 3.5

FIG. 1. Leaf water content and leaf toughness of four tree species occurring in different-sized forest openings and in the understory of mature forest (C) in the Southern Appalachians in 1985. Values represent composite means for 10 trees in each opening size, plus 1 SE. Intervals shown at the top of the figure are least significant differences, which apply for all means presented.

most always (20 of 24 cases) had the lowest levels of tannins among all conspecifics sampled.

Phenolic compounds exhibited different patterns of change over the growing season (Figs. 2–4, Table 5). Hydrolyzable tannin concentrations in leaves were relatively similar throughout the growing season with peaks occasionally occurring in June. In contrast, condensed tannins increased later in the growing season. Total phenolics usually peaked in midsummer.

Repeated sampling from the same trees each month had no apparent inducible effects on plant physical or chemical properties (Table 6). Sample trees and their nearest neighbor conspecifics had nearly identical levels of water content, toughness, and phenolic compounds in late August. Sample variances were also quite similar for sample trees and their neighbors. These results point out the close similarity in phenolic levels that can occur for conspecific trees on similar microsites.

The overall patterns of plant phenolics persisted during 1986 (Fig. 5). The slower growing, shade-tolerant species contained significantly more (Table 3) total

phenolics and hydrolyzable tannins and significantly less condensed tannins than pioneer species. The levels of phenolics in each of the four species were relatively similar in late summer of both years. Acer and Cornus leaves did contain somewhat less total phenolics in 1986 than 1985. The different measures of phenolics were sometimes higher in large than small patches in 1986, but these trends were only significant for condensed tannins (Table 3). Understory trees always contained lower levels of phenolics than sprouts in openings. Interestingly, the overall protein-binding capacity of the four species was relatively similar (5–13% TAE), although Cornus was always highest. Protein-binding capacity of all species was not significantly higher in large than small openings. No trends emerged when comparing understory trees vs. sprouts in openings or fast- vs. slow-growing species.

Herbivory

Leaf area damaged by insect herbivores varied between 1 and 11% in 1985 (Fig. 6). Herbivore damage in openings was significantly (Table 3) highest for Ro-

TABLE 3. Results of split-plot ANOVAs of leaf water content, leaf toughness, and percent leaf herbivory in 1985 and for total phenolics, hydrolyzable (H) tannins, condensed (C) tannins, and protein-binding capacity in 1986.‡

| | F values | | |
Measure	Opening size	Species	Size × species
1985			
Water	3.85†	265.7**	3.46**
Toughness	4.89*	129.3**	0.87
Herbivory	22.96**	26.8**	3.38**
1986			
Phenolics	0.82	10.3**	0.67
H tannins	1.02	103.5**	0.50
C tannins	5.20*	97.0**	3.28*
Binding	1.34	51.9**	0.35

* $P < .05$, ** $P < .01$, † $P < .10$.

‡ The F values are presented for main effects (opening size, species) and their interactions, with levels of significance indicated. The results for leaf water content and toughness were averaged over the summer for each tree (time not a factor), whereas the ANOVA for herbivory was only for the end of the growing season (August). Variance components and their degrees of freedom in all split-plot ANOVAs are: opening size 5 df; replicate cut (size) 6 df; species 3 df; size × species interaction 15 df; replicate cut × species (size) 18 df; error 192 df.

binia (5–9%) and relatively similar (1–5%) for the remaining species. Leaf area damaged on *Robinia* showed no consistent change along the patch size gradient. However, *Acer* and *Cornus* had significantly greater herbivore damage in small than large openings and a similar patch size response for *Liriodendron* was nearly significant ($P < .06$). Herbivore damage in *Acer* and *Liriodendron* was significantly greater on understory trees than sprouts in openings. Damage to *Acer* trees in the forest exceeded 11%.

DISCUSSION

The prominence of sprouting as a mode of revegetation in the Southern Appalachians promotes the co-occurrence of fast- and slow-growing woody species following disturbance (Boring et al. 1981, Phillips and Shure 1990). Tree species sprout and begin developing in a relatively nutrient-rich successional environment (Boring and Swank 1984a, Vitousek 1985, Montagnini et al. 1986). Nutrient mineralization from slash and fallen trees, high N fixation from *Robinia* (Boring and Swank 1984b), and sprout mobilization of nutrients stored in the roots of felled trees collectively enhance nutrient availability in all sizes of disturbance patches. The occurrence of these processes in a series of forest openings that were located to minimize site variations
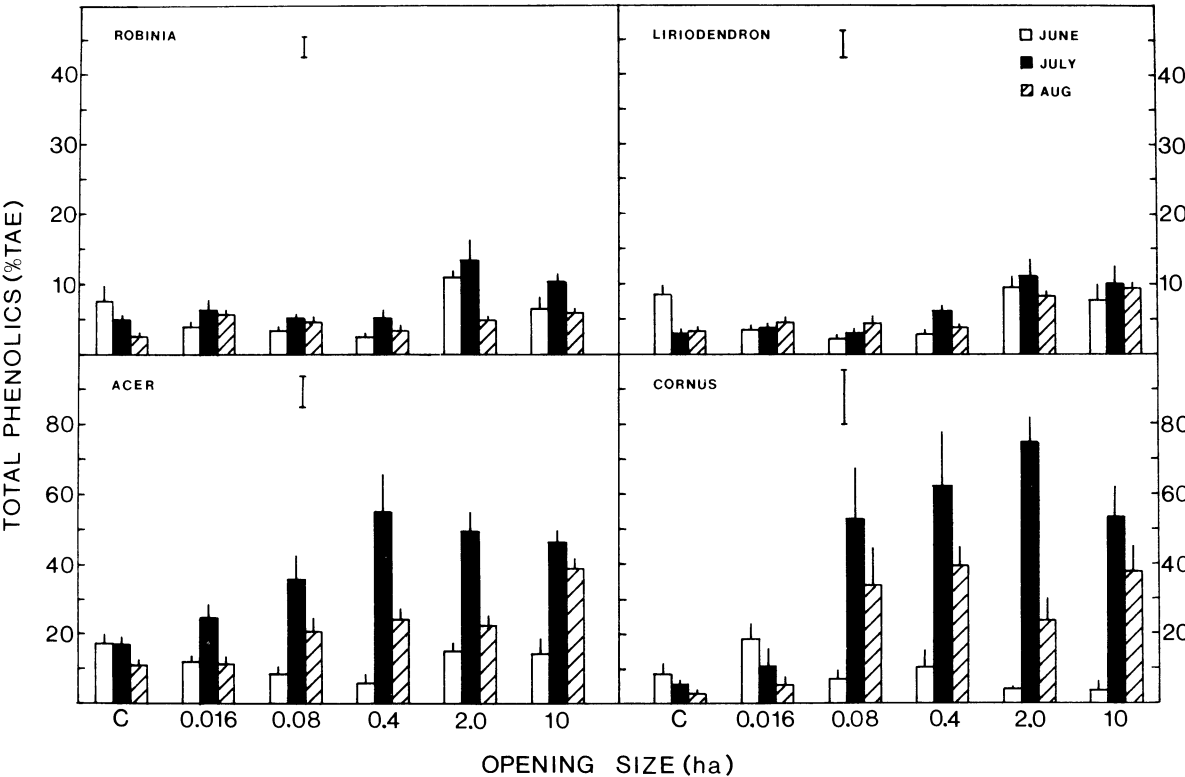

FIG. 2. Total phenolic concentrations (percent tannic acid equivalents [TAE]) in leaves of four tree species occurring in different-sized forest openings and in the understory of mature forest (C) in the Southern Appalachians in 1985. Means (plus 1 SE) are for the 10 trees sampled on each date. Interval shown at the top of individual figures is the least significant difference ($P < .05$), which indicates where significant differences exist among all means presented.
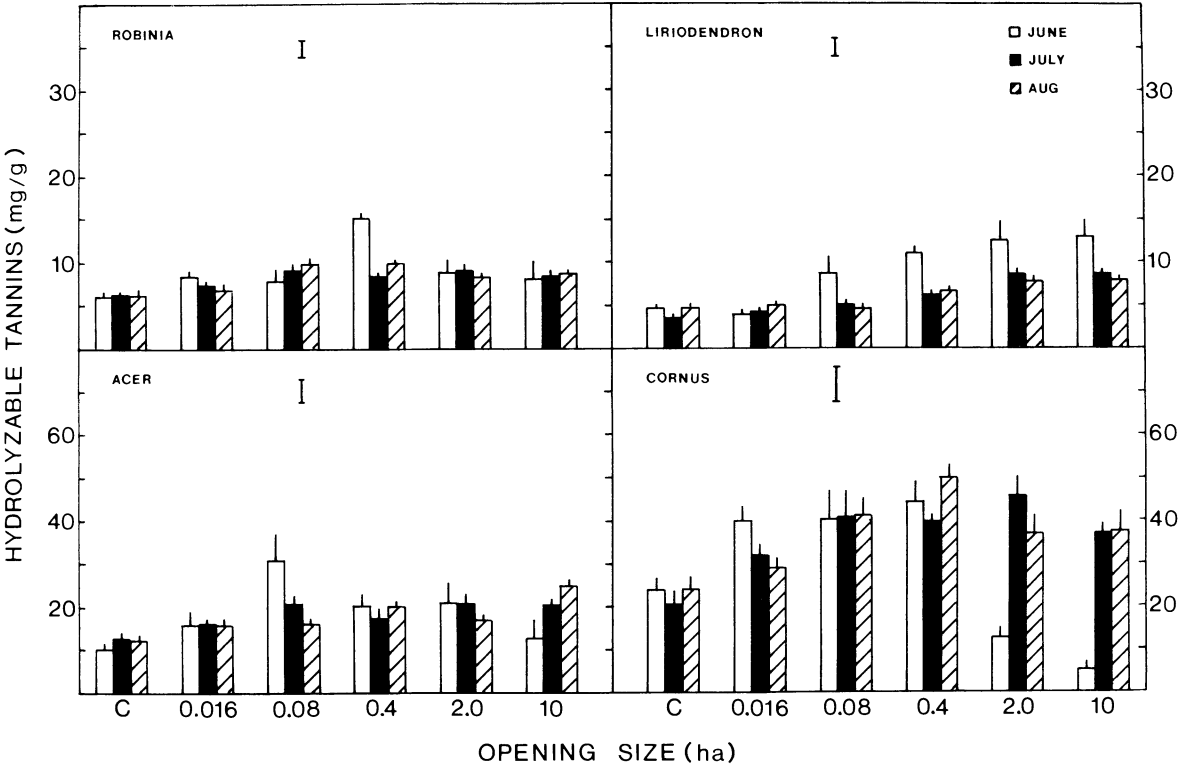
FIG. 3. Hydrolyzable tannin concentrations in leaves of four tree species occurring in different-sized forest openings and in the understory of mature forest (C) in the Southern Appalachians in 1985. Means (and 1 SE) are presented as milligrams of hexahydroxydiphenoylglucose per gram of leaf tissue for the 10 trees sampled on each date. Interval shown at the top of individual graphs is the least significant difference ($P < .05$), which indicates where significant differences exist among all means presented.

TABLE 4. Results of repeated-measures ANOVAs of total phenolics and hydrolyzable (H) and condensed (C) tannin data sets for each tree species in 1985.‡

	F values		
Species	Opening size	Date	Size × date
Phenolics			
Robinia	3.32†	2.68	1.10
Liriodendron	1.45	0.31	0.33
Acer	1.63	16.93**	1.53
Cornus	2.45†	12.46**	1.99
H tannins			
Robinia	1.88	1.95	2.63
Liriodendron	4.48*	5.72*	0.71
Acer	1.26	0.07	1.06
Cornus	3.25†	5.70*	4.36*
C tannins			
Robinia	3.29*	8.95**	2.29
Liriodendron	22.34**	24.75**	6.64**
Acer	2.43	9.82**	1.74
Cornus	3.75**	7.88**	0.95

* $P < .05$, ** $P < .01$, † $P < .10$.

‡ The F values are presented for main effects (opening size, date) and their interaction, with levels of significance indicated. Variance components and their degrees of freedom in all repeated-measures ANOVAs are: opening size 5 df, replicate cut (size) 6 df, date 2 df, size × date interaction 10 df, replicate cut × date (size) 12 df, error 144 df.

should limit soil nutrient differences between patch sizes. Light availability should thus prove more important than soil nutrients in influencing plant growth rate and phenolic allocation in different sizes of openings.

Species differences

Phenolic allocation varied in sprouts of fast-growing vs. slow-growing tree species. The leaves of fast-growing pioneer trees were slightly less tough and contained significantly lower levels of total phenols and hydrolyzable tannins, but higher concentrations of condensed tannins, than slower growing species. The results for all measures except condensed tannins thus support earlier studies indicating that fast-growing species should contain lower levels of carbon-based secondary metabolites than slow-growing species (Coley et al. 1985, Coley 1988). The fact that our four species co-occurred on similar substrates in all openings suggests that intrinsic growth rates rather than resource availability was the reason for species differences in phenolic allocation (Coley 1988). This is especially true since the patterns persisted over a wide range of light variation in different patch sizes.

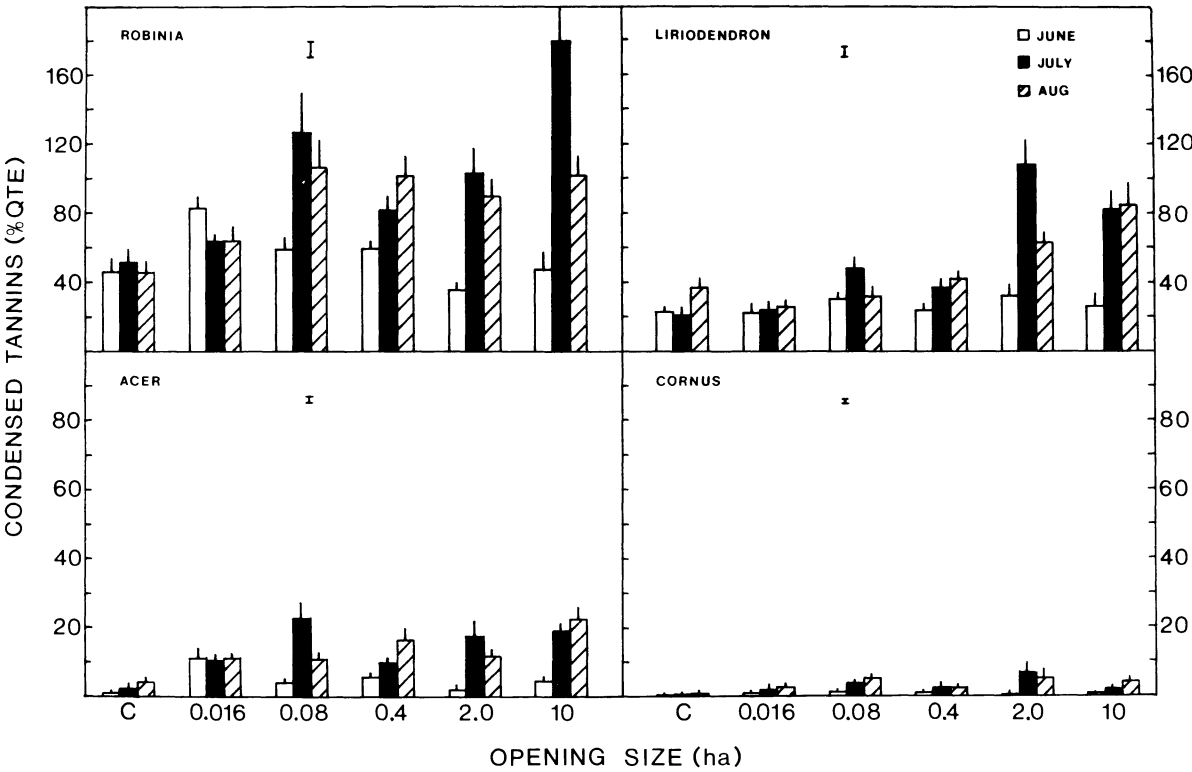Several factors offer possible explanations for the

Fig. 4. Condensed tannin concentrations (percent Quebracho tannin equivalents [QTE]) in leaves of four tree species occurring in different-sized forest openings and in the understory of mature forest (C) in the Southern Appalachians in 1985. Means (and 1 SE) are for the 10 trees sampled on each date. Interval shown at the top of individual graphs is the least significant difference ($P < .05$), which indicates where significant differences exist among all means presented.

evolutionary differences in phenolic allocation among fast-growing and slow-growing species. Nitrogen fixation by *Robinia* is particularly high early in succession, which favors rapid growth (Boring and Swank 1984b). *Liriodendron*'s conical architecture, horizontal leaf orientation, and high allocation of carbon to bole formation all promote high rates of production and growth in canopy openings (Wallace and Dunn 1980). These adaptations favoring rapid growth may prevent the buildup and allocation of excess carbohydrates for the production and storage of certain phenolics including hydrolyzable tannins (Tuomi et al. 1984). Instead, these pioneer tree species utilize a variety of qualitative toxins including alkaloids for possible defense (Barbosa and Krischik 1987, Barbosa et al. 1990) and accumulate large concentrations of condensed tannins as the growing season progresses. In contrast, the slower growing *Acer* and *Cornus* sprouts are less efficient photosynthetically at high light intensities in openings (Wallace and Dunn 1980), their leaves contain little (*Acer*) or no (*Cornus*) N-based defenses (Barbosa et al. 1990), and they accumulate hydrolyzable rather than condensed tannins as secondary metabolites. *Robinia* and *Cornus* exhibited the greatest difference in their production of hydrolyzable vs. condensed tannins, and these species are at the opposite ends of a shade tol-

erance/longevity gradient among the species tested (Wallace and Dunn 1980).

The failure of condensed tannins to also be higher in slow-growing than fast-growing species may reflect evolutionary trade-offs in the allocation of different types of phenolics. Inverse relationships exist between condensed and hydrolyzable tannin concentrations in other species (Bate-Smith 1977, Baldwin et al. 1987, Rossiter et al. 1988), which precludes the expression of similar trends for both categories of tannins. However, metabolic shifts in the relative production of the two tannin pathways could prove adaptive (Zucker 1983). Our results from early successional habitats in the Southern Appalachians suggest that slower growing tree species may rely mainly on constant levels of hydrolyzable tannins for putative defense against insect

TABLE 5. Time of peak concentrations of different measures of plant phenolics. Values for each sampling period reflect cases where clear differences were apparent for each species and patch size (Figs. 2-4). A total of 24 species × patch size comparisons were included.

	June	July	August
Total phenolics	4	14	2
Hydrolyzable tannins	8	1	3
Condensed tannins	1	8	9

TABLE 6. Physical and chemical properties of leaves in nearest neighbor conspecifics sampled once (S) vs. several times (R) in 2.0-ha openings during the 1985 growing season. Means ($N = 10$) $\pm$ 1 SE are presented. Numbers in parentheses are t values determined from paired t tests.

Species		Water (%)	Toughness (KPa)	Phenolics (%TAE)	Hydrolyzable tannins (mg/g)	Condensed tannins (%QTE)
Robinia	R	60.7 ± 0.45	261.8 ± 12.85	4.8 ± 0.49	8.31 ± 0.50	89.6 ± 9.16
	S	60.7 ± 0.61	255.0 ± 10.20	4.4 ± 0.82	9.20 ± 0.55	108.8 ± 12.39
		(0.06)	(0.60)	(0.50)	(1.29)	(1.63)
Liriodendron	R	68.2 ± 0.89	330.5 ± 9.71	8.3 ± 0.79	7.8 ± 0.44	63.3 ± 5.38
	S	70.5 ± 1.04	328.5 ± 9.51	6.6 ± 0.69	7.9 ± 0.33	64.9 ± 6.61
		(1.72)	(0.20)	(1.32)	(0.16)	(0.19)
Acer	R	58.1 ± 1.66	318.7 ± 11.67	22.8 ± 2.97	17.3 ± 1.01	11.9 ± 1.54
	S	57.7 ± 0.82	309.9 ± 9.02	20.9 ± 3.12	18.4 ± 0.83	13.9 ± 2.58
		(0.26)	(0.58)	(0.40)	(0.89)	(0.97)
Cornus	R	64.5 ± 0.86	343.2 ± 5.98	23.8 ± 6.38	37.5 ± 3.55	5.1 ± 2.63
	S	66.8 ± 0.97	339.3 ± 11.57	28.3 ± 5.37	42.2 ± 2.12	2.7 ± 1.27
		(2.45)*	(0.30)	(0.79)	(1.10)	(0.91)

* Significant at $P < .05$.

herbivores. Pioneer, rapidly growing species contain a wider array of possible chemical defenses against herbivores and accumulate high levels of condensed tannins either in limiting certain herbivores (Manuwoto et al. 1985) or in minimizing microbial damage before and after leaf fall (Zucker 1983). For example, White et al. (1988) reported that Robinia leaves serve as a long-term sink for organic matter and N storage in mountainous soils of the Southern Appalachians, principally because the complexing of leaf polyphenolics with proteins forms lignin-like substances that retard decomposition and promote soil humic buildup. The especially high levels of condensed tannins in Robinia leaves may thus play an important role in minimizing nutrient losses and facilitating long-term succession in these mountainous areas (White et al. 1988). The po-
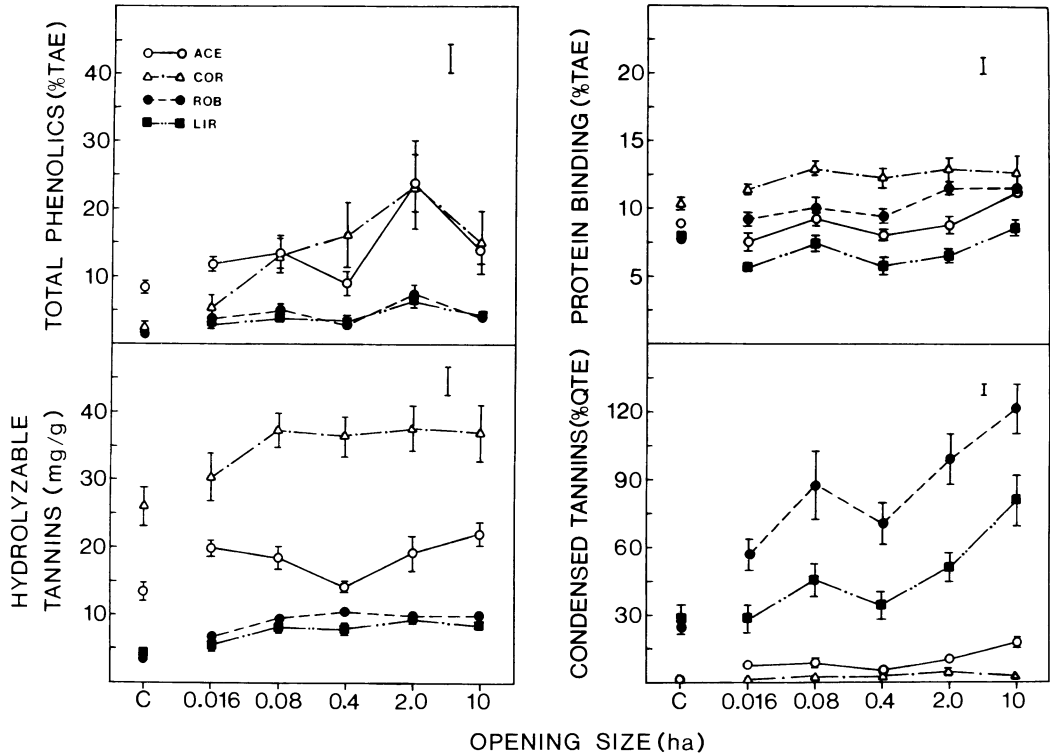

FIG. 5. Species changes in total phenolics, hydrolyzable tannins, condensed tannins, and protein-binding capacity in different size forest openings and in the understory of mature forest (C) in the Southern Appalachians in 1986. Values represent means of 10 trees sampled in each opening size, ±1 SE. Intervals shown are the least significant difference ($P < .05$), which indicate where significant differences exist among all means presented.

tential effects of similar evolutionarily based variations in types of phenolics in different plant species needs further assessment.

Patch size effects

Regenerating sprouts often contained higher levels of plant phenolics in large than small patch sizes. This phenotypic pattern developed by midsummer and was strongest for condensed tannins. When occurring, the patch size increases in phenolic allocation were either gradual or more pronounced between the relatively shaded smallest canopy openings (0.016 ha) and the more insolated larger patch sizes. Tannin levels were almost always lowest in understory conspecifics experiencing heavily shaded conditions. These positive correlations between light availability and plant phenolic production have been demonstrated in other studies comparing conspecifics in different light regimes (Waterman et al. 1984, Waring et al. 1985, Van Horne et al. 1988, Aide and Zimmerman 1990), where shading has been added experimentally (Langenheim et al. 1981, Larsson et al. 1986, Bryant 1987, Bryant et al. 1987), or in contrasting leaves from shaded vs. insolated portions of individual trees (Mole et al. 1988). Increases in phenolics have also been demonstrated as soil nutrients and soil moisture decline along subtle elevational gradients (Muller et al. 1987).

The current explanation for the correlation between light availability and phenolic production centers on plant carbon/nutrient balance (Bryant et al. 1983, 1987, Gershenzon 1984, Tuomi et al. 1984, 1988, Waterman et al. 1984, Larsson et al. 1986). Assuming soil nutrient levels are relatively similar in each of our patch sizes, then the increased light availability (Phillips and Shure 1990) and greater photosynthetically active radiation (Denslow et al. 1990) in larger openings often promoted greater phenolic production than in smaller openings or in the forest understory. Plant carbon surpluses occurring in the high light of larger openings could lead to the metabolic accumulation and storage of poorly translocatable phenolic compounds in an "overflowing" capacity (Mole et al. 1988). Excess carbon apparently occurred despite continued increases in plant production and growth in larger patch sizes. This response thus suggests a shift from carbon stress under low light conditions of understory or small patches to possible nutrient stress developing at the limits to growth in well-insolated larger openings (Bryant et al. 1983, Larsson et al. 1986, Tuomi et al. 1988). A complex set of factors including aspect, degree of canopy closure, microsite conditions, and proximity to the edge of openings may influence phenolic production in individual trees within each opening. Nevertheless, those cases where phenolic production increased across our patch size gradient add support concerning the effects of light on plant carbon/nutrient balance (Mole et al. 1988).

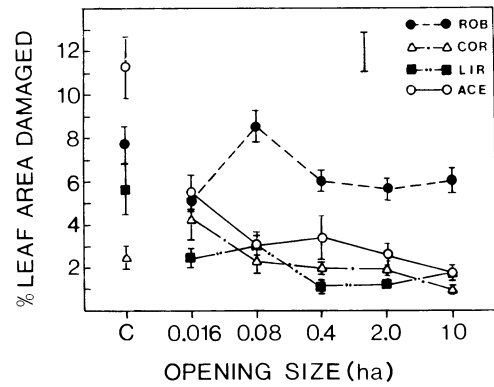Slow- and fast-growing species had no consistent dif-

FIG. 6. Percent leaf area damaged for four tree species occurring in different-sized forest openings and in the understory of mature forests (C) in the Southern Appalachians in 1985. Plant species include *Robinia* (ROB), *Cornus* (COR), *Liriodendron* (LIR), and *Acer* (ACE). Means (±1 SE) are presented for 10 trees sampled in each opening size. Interval shown at the top of the figure is the least significant difference ($P < .05$), which indicates where significant differences exist among all means presented.

ferences in their relative plasticity of phenolic production across our patch size gradient. The slow-growing, shade-tolerant species exhibited greater plasticity in total phenolics from small-to-large openings whereas shade-intolerant pioneer trees showed greater changes in condensed tannins along the gradient. The magnitude of patch size change in toughness, hydrolyzable tannins, and protein-binding capacity were fairly similar for slow- and fast-growing species. These results offer no clear support for recent findings (Bryant et al. 1987, 1991, Denslow et al. 1990) indicating greater plasticity in phenolic production for rapidly growing, shade-intolerant than slower growing, shade-tolerant species. Species differences in phenolic plasticity may actually involve a multitude of local conditions influencing carbon/nutrient balance. Additional testing for possible trends is needed, particularly in examining the adaptive significance of changes in plasticity of different types of plant phenolics. Bryant et al. (1987, 1991) have provided the conceptual framework for future efforts.

Seasonality

Independent measures of plant phenolics in our study peaked at different times over the growing season. Phenological changes in levels of phenolics in tree species are proving quite varied. The initial viewpoint was that high carbon demand for growth early in the growing season promoted an increased palatability of less well defended leaves (Feeny 1970, Rhoades and Cates 1976, Bryant et al. 1983). However, other studies have reported greater levels of phenolics in young than mature leaves (Coley 1983, Puttick 1986, Meyer and Montgomery 1987, Rossiter et al. 1988, Coley and Aide 1991). Coley's (1983) and Coley and Aide's (1991) findings suggest that the widespread prevalence of high-

er phenolics in young than mature leaves of tropical plants (but see Aide and Zimmerman 1990) warrants revision of the earlier viewpoints. Nevertheless, distinctions must be made between short-term seasonal changes in temperate areas vs. more long-term leaf age development in tropical systems.

Explanations for these temporal differences in leaf phenolic production may ultimately involve selective pressures for growth or defense at different stages of leaf development (Bryant et al. 1983). Harper (1989) has proposed that the timing of leaf defense may depend on the fate of leaf assimilates. Leaves of species with continual (free) growth should be defended early since their assimilates are crucial for subsequent leaf development. In contrast, species with a fixed flush of leaves early in the growing season rely more on carbon assimilates produced by older leaves at the end of the prior growing season; these older leaves may need to be well defended. Tropical plants may fit more of a continuous growth pattern requiring active defense of young leaves, whereas many temperate deciduous species have a fixed leaf flush and possess well-defended older leaves. Rapidly growing young sprouts in our study area produce a flush of new leaves in the spring, which subsequently export photosynthates for further leaf development throughout the growing season. These early successional sprouts may thus employ aspects of both strategies and utilize varying degrees of hydrolyzable (early buildup) and/or condensed tannins (later buildup) to ensure continued growth and possible protection throughout the growing season. Considerable work is obviously needed to provide definitive causal explanations for the varied patterns noted (Harper 1989).

Herbivory

Limited correlations existed between herbivore damage and plant quality. Herbivory was highest from pioneer *Robinia* sprouts that contained high levels of symbiotically fixed N, were low in toughness, and had relatively low levels of hydrolyzable tannins and total phenols. Herbivore damage was lower for slow-growing *Acer* and *Cornus* sprouts that were tougher and contained higher levels of hydrolyzable tannins and total phenols than *Robinia*. However, the relatively low herbivory from fast-growing *Liriodendron* sprouts failed to fit this trend and may reflect the diverse and highly effective defenses of this species (Manuwoto et al. 1985, Barbosa et al. 1990). These results thus offer only partial support for the idea that plant phenolics are generally lower and herbivory higher from fast-growing than slow-growing species (Coley 1983, 1988).

Herbivore damage from the slow-growing species tended to be inversely correlated with plant phenolics across the patch size gradient; no clear trend was apparent for either fast-growing species. Herbivore loads on vegetation were also significantly lower in large than small patches during the first year of succession in our

plots (Shure and Phillips 1991). Nevertheless, the lower herbivory from several species in our larger patches could reflect a harsher microenvironment, tougher leaves, reduced leaf N levels or a greater abundance of natural enemies in large than small patches. For example, key insectivorous predators were much more numerous in our large than small openings initially following disturbance (Shure and Phillips 1991). Controlled experiments are thus needed to test for possible causality in observed correlations between light, phenolics, and insect herbivory (Larsson et al. 1986, Bryant 1987, Bryant et al. 1987, Mole and Waterman 1988). This is especially true since additional factors such as plant nutrition or natural enemies may be sufficiently important to override the postulated relationships between insect herbivory and plant phenolic defenses (Faeth 1985, Puttick 1986).

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