

The influence of carbon - nutrient balance on herb and woody plant abundance in temperate forest understories

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Abstract

Question: We present a general structural carbon - nutrient balance hypothesis parallel to Bryant et al.'s defensive chemistry hypothesis. Our hypothesis suggests that because herb species require a lower investment of carbon per unit length of stem than do woody plants, herbs should be at a competitive advantage where the leaf area of plants in the ground layer is limited by light (or fixed carbon, C) rather than soil resources (R) such as nutrients or water. We test the derivative predictions that in temperate deciduous forests (1) herb cover and species richness increase as soil resources increase, and (2) woody ground-layer cover, density, and species richness increase as soil resources decrease.

Location: To maximize generality, the eight temperate deciduous forest sites were dispersed along an 800 km band from the Coastal Plain of eastern North Carolina to the Central Basin of middle Tennessee, USA.

Methods: Soil nutrients and moisture, herb cover and woody stem densities were observed in six plots at each site, randomly located in high, medium, and low herb cover areas. Multiple regression, correlation, and Redundancy Analysis ordination were used to test predictions.

Results: Plants with herbaceous (low C:R) stems are generally abundant where soil moisture and basic cations (Ca, Mg) are high (low C:R environments), and woody (high C:R) plant cover, basal area, stem density, and species richness are all greatest on dry or nutrient-poor soils (high C:R environments). Plots with intermediate soil resource availability and herb cover have the most species, and maximum herb species richness occurs at higher soil resource levels than maximum woody species richness.

Conclusions: Our observations are consistent with our structural carbon - nutrient balance hypothesis.

Keywords: Allocation; Carbon; Competition; Structural tissues; Stem; Carbon - nutrient balance hypothesis; Growth form; Resource ratio; Soil nutrient; Species diversity; Tree seedling; Soil water.

Nomenclature: Kartesz (1999).

Abbreviations: C = fixed carbon; R = soil resource (minerals and water)

Introduction

The carbon - nutrient balance hypothesis of Bryant et al. (1983) predicts carbon-based defenses to be more prevalent in plants growing where nutrient supply is low relative to light. This prediction derives from two assertions: losses to herbivory are more difficult to replace on low-nutrient sites, and carbon is abundant on such sites relative to other resources (Bryant et al. 1983; Coley et al. 1985). We extend the carbon - nutrient balance hypothesis to plant growth form. This extension, which we call the structural carbon - nutrient balance hypothesis, predicts that in forest floor environments, as the abundance of light relative to soil resources (R, including soil nutrients and water) increases (C:R ratio increases), the success of woody relative to herbaceous plant species should increase. In contrast, herbs should be favoured where the supply of fixed carbon (C) is low (owing to limited light) but soil resources are abundant (low C:R ratio).

Herbaceous plants require less carbon per unit height than woody stems, but require cumulatively more soil nutrients per unit biomass because they must annually replace losses of ephemeral tissues. On mesic, nutrient-rich sites, the low carbon investment per unit of stem and rapid extension of stem tissue allows herbs to grow tall quickly each spring, overtop woody plant seedlings, and pre-empt light resources. In contrast, on dry or infertile sites, the nutrient cost of annually discarding stems, or the demand for continuous water supply to support stems by turgor through the growing season, precludes abundant herb growth with the consequence that herb cover is sparse and light is more available to woody plants. So, forest floor plant communities dominated by herbaceous growth forms should be found in moist, nutrient-rich forests with closed canopies where deep shade severely limits fixed carbon available to ground-layer plants (Fig. 1). Further, greater densities of high-carbon woody growth forms should be found either in canopy gaps where light is relatively abundant (higher C), or where a soil resource (nutrient or moisture) is scarce (lower R).

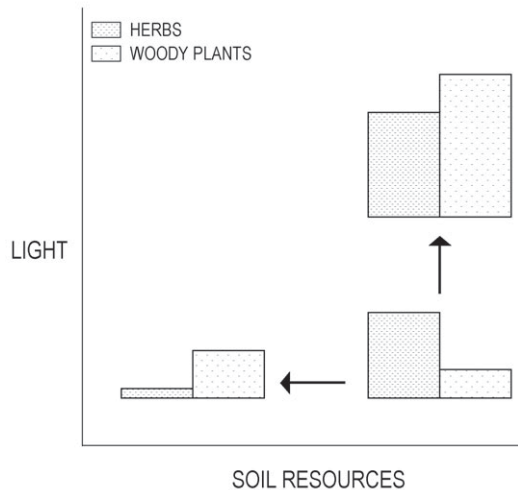


Fig. 1. Expected relative abundance of herbs and woody plants under combinations of low and high light and soil resources. Arrows indicate changes toward greater relative abundance of woody plants.

In this study we evaluate the structural carbon-nutrient balance hypothesis in forest ground-layer vegetation across soil resource gradients under closed forest canopies within a wide range of temperate deciduous forests distributed across an 800 km east-west band in the southeastern United States. We test two predictions: (1) herb cover and species richness increase as soil resources increase; and, (2) woody ground-layer cover, basal area, density, and species richness increase as soil resources decrease. We limited the range of light conditions to closed forest, but any increase in light should favour woody plants more than herbs by increasing the C:R supply ratio. Thus, we also predict that (3) if significant positive effects of gaps are detected, these effects are more significant for woody plants than for herbs.

Methods

We quantified the relationship between soil resource availability and abundance of woody and herbaceous plants at eight temperate deciduous forest sites where strong gradients in ground-layer cover occurred under a closed tree canopy (Apps. 1 and 2). Ground-layer cover ranged from less than 10% to near 100% within each site. Each site was less than 500 m in linear extent, greater than 50 m from canopy openings, and free of apparent within-site variation in land-use history and barriers to animal movement. To increase the generality of the results, study sites were selected to differ substantially in elevation, land forms, hydrology, parent material, and species composition, and were distributed geographically across an 800 km east-west band from the Coastal Plain of North Carolina to the Central Basin of Tennessee (Fig. 2; Apps. 1 and 2).

Six 10-m² plots (3.16 m × 3.16 m) were sampled at each of the eight sites, for a total of 48. At each site, two plots were randomly located in areas where summer ground-layer cover was high (> 75%, measured as the vertical projection of all vegetation < 1.4 m tall), two where cover was intermediate (25-75%), and two where cover was low (< 25%). The 10-m² plot is the principal observational unit, but species richness was observed at multiple scales using nested square quadrats (16 0.01 m², eight 0.1 m², four 1 m², the one 10-m² plot, and one quadrat of 25 m², obtained by extending the 10-m² plot 0.92 m on all sides).

Canopy openness (gap index) was measured in each plot with a spherical densiometer (Lemmon 1956). The gap index confirmed that canopy closure was consistently greater than 92%.

Several variables related to soil moisture availability were measured including soil field moisture (%),

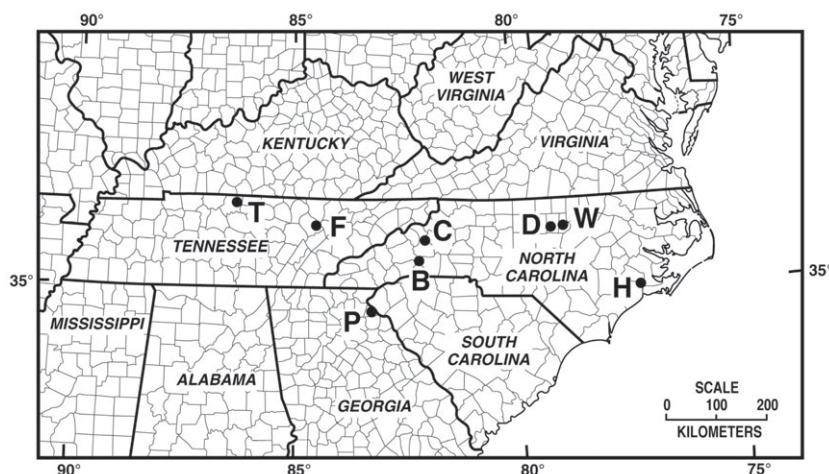


Fig. 2. Locations of study sites: Bat Cave (B); Catawba River (C); Duke Forest (D); Frozen Head (F); Haywood Landing (H); Panther Creek (P); Taylor Hollow (T); Willie Duke's Bluff (W).

the ratio of distance up slope over which water drains toward the plot to distance down slope to surface water (unitless moisture index), slope, aspect, elevation, bulk density, particle size distribution (% sand, silt, clay), surface rock (%), average soil depth to rock ($n = 10$), average litter depth ($n = 10$), and a root mat index (from 0 = very few roots, to 3 = root mats with tough or fibrous roots difficult to penetrate with a thin surveyor's pin).

Soil and vegetation sampling

Soil samples were collected at least four days after rain for each of the four 1-m² quadrats. Soil cores 2.5 cm diameter were taken from the top 10 cm of mineral soil in random locations in each of nine 33 × 33 cm square sectors within the square meter, and mixed to form one composite sample. The four samples for each plot were weighed field moist, air dried, and dried again at 40 °C to constant weight. Field moisture was calculated as field moist weight minus dry weight divided by dry weight. Soil samples were analysed by Brookside Laboratories, Inc., New Knoxville, Ohio, for bulk density, particle size distribution (% sand, silt, and clay), cation exchange capacity, percent base saturation, pH (1:1 distilled water), percent organic matter (loss on ignition), and Mehlich-3 extractable SO₄, PO₄, Ca, Mg, K, Na, B, Fe, Mn, Cu, Zn, and Al. Values used for data analysis are means of the four samples.

Vegetation was sampled in summer (June - August) following a phenological gradient from lower Piedmont and Coastal Plain sites to upper Piedmont, Central Basin of Tennessee, Cumberland Highlands, and finally the North Carolina Blue Ridge Mountains. In each 1-m² quadrat, we estimated total and species percent cover (percent of horizontal ground surface area covered by the vertical projection of above-ground vegetation) for all herb species, herbs > 0.4 m tall, and woody vegetation < 0.4 m tall. Woody plants taller than the herbs have survived competition with herbs to establish in the understorey. To obtain stem densities and basal areas of woody stems established above the herbs, stem diameters were measured just above ground level for all living woody stems > 0.4 m tall and < 2.5 cm DBH (diameter at breast height; 1.4 m) in 25-m² quadrats. Species richness of herbs and of woody species < 0.4 m tall were determined for 0.01-, 0.1-, 1-, 10- and 25-m² quadrats. Species richness of woody vegetation 0.4 - 6.4 m tall was determined for 1-, 10-, and 25-m² quadrats.

Data analysis

To test the predictions we used Spearman rank correlation to identify significant monotonic relationships between pairs of resource and vegetation variables, and used multiple linear regression to account for the simultaneous effects of soil moisture and nutrients (Anon. 1990).

Resource variables were log-transformed for use in regression models because plant abundance generally varies linearly with log-transformed values of resource variables (Palmer 1993). Moisture and available Ca (indices of soil resource supply), and gap index (an index of carbon supply) were included in all models. Moisture and Ca were selected because these two variables are not collinear and are both strongly correlated with herb cover. Calcium is a surrogate for several nearly collinear basic cations and soil pH. Additional environmental variables were added if significant to the model with $p < 0.10$. Interactions and unimodal responses (quadratic terms) are common in many biological settings (Austin et al. 1990), and were added when graphs of the data and/or theoretical considerations suggested these could be important. We diagnosed collinearity using the SAS regression procedure, removing one or more variables when any variance inflation factor exceeded 10, or when one of the principal components in the collinearity diagnosis had two or more variance proportions greater than 0.5 (Kleinbaum et al. 1988; Anon. 1990). When selecting among collinear variables, we chose the variable having highest Spearman rank correlations with other variables in the group.

We tested our prediction that herb cover can be explained by soil resources by comparing regression models with and without site (block) effects, predicting that site effects do not add significantly to a model that already contains soil effects.

To test the prediction that low supply of either moisture or basic cations will result in low herb cover, we tested whether both moisture and Ca have significant positive effects in a regression model of herb cover. Further, because plant response to Ca should be suppressed by low water availability, and *vice versa*, we predicted the moisture × Ca interaction to have a significant positive effect in the model.

Species richness has been suggested to be a unimodal function of resource supply and plant production in herbaceous communities (Al-Mufti et al. 1977; Grime 1979; Willems et al. 1993), but this pattern is not widely reported for deciduous forest ground layers (Peet & Christensen 1988; Newell et al. 1999; Dupré et al. 2002). We predicted that herb cover is positively correlated with herb species richness, but checked for a negative effect of (herb cover)² in species richness models as an indication of the unimodal 'intermediate stress' response.

We used Redundancy Analysis (RDA) to order the 48 plots based on similarity in the structure of their herbaceous and woody vegetation along axes that are linear combinations of environmental variables (CANOCO version 3.12, ter Braak 1988); 15 vegetation variables were treated as 'species':

Herb cover; Winter-deciduous herb cover; Herb cover < 0.4 m tall;
Herb cover 0.4 - 0.8 m tall; Number of herb species / 0.1 m²;
Number of herb species / 25 m²; Woody cover < 0.4 m tall;
Canopy tree species cover < 0.4 m tall;
Shrub-size woody basal area (> 0.4 m tall and < 2.5 cm DBH);
Shrub-size stem density; Shrub-size canopy tree species stem density;
Number of woody species / 0.1 m²; Number of canopy tree species / 25 m².

These broad quantitative measures of vegetation structure are better suited to the linear response model used by RDA than to the unimodal response model in canonical correspondence analysis. Axes were constrained by 14 non-collinear environment variables: soil Ca, P, K, Mn, S, clay, silt, bulk density, moisture, organic matter, litter depth, root mat index, and exposed rock; and gap index.

Results

Abundant herbs

Herb cover is high where soils are moist and nutrient rich (high cation availability; Table 1; Fig. 3), as predicted by the structural carbon - nutrient balance hypothesis. These are deep, fine-textured soils found on lower slopes and floodplains with circumneutral pH, high cation exchange capacity, high organic matter, low bulk density, no tough root mat, and usually thin litter layers. Moisture, measured as field moisture percent, is a strong contributor to models of vegetation and, along with Ca, is strongly associated with herb cover and with Redundancy Analysis (RDA) axis 1 (eigenvalue 0.45, Fig. 3). Ca represents several collinear basic cations in our models. Soils with high available Ca also have high pH, cation exchange capacity (CEC), Mg, B, Zn, Mn, Cu, and low Al (respectively, $r = 0.94, 0.94, 0.92, 0.92, 0.75, 0.72, 0.71, -0.78$).

Table 1. Spearman rank correlations between vegetation and environmental variables.

	Environmental variables																		
	M	MI	Ca	pH	P	K	Mn	Fe	OM	AH	CL	SA	RO	Al	BD	LD	RM	G	
maximum value	88	1.2	4950	7.6	84	154	510	410	18	4	23	48	95	1350	99	7	3	7	
minimum value	14	-1.3	130	4.1	10	30	0	50	2	1	4	3	0	290	65	1	0	1	
Vegetation variables																			
Herbs:																			
cover, all herb species	++	+++	++	+					+	+				-	-	-	-		
cover, non-evergreen herbs	++	++	++	+		+			+	+				-	-	-	-		
cover, evergreen herbs														+	++				
height maximum	+	++	++	+		+			+	+				-	-	-	-		+
species richness, $n/0.01$ m ²	++	++	++	+		+			+	+				-	-	-	-		+
species richness, $n/1$ m ²	++	++	++	+		+			+	++				-	-	-	-		
species richness, $n/25$ m ²	+	+	+	+		+			+	+				-	-	-	-		
evergreen species richness, $n/10$ m ²	+										+	-	+						+
Woody plants:																			
cover, 0 to 0.4 m tall	-		-		-	-											+		
cover, 0.4 to 3.2 m tall	-	-									+			+		+			
cover, 3.2 to 6.4 m tall	-																		
basal area of stems < 2.5 cm DBH	-	-																	+
density of stems < 2.5 cm DBH	-				-	+					+								
species richness, 0-0.4 m, $n/0.01$ m ²	-						-	-											+
species richness, 0-0.4 m, $n/1$ m ²	-	-	-				-	-						-		+			+
species richness, 0-0.4 m, $n/25$ m ²	-	-	-				-	-						-	+	+			+
species richness, 0.4-6.4 m, $n/1$ m ²	-	-					-	-			+			+					+
species richness, 0.4-6.4 m, $n/25$ m ²	-	-					-	-											

Note: Environment symbols, variables, and units of measurement are as follows: AH (soil A horizon depth, code 1 to 4), Al (ppm), BD (bulk density, g/cm³), Ca (ppm), CL (clay, %), Fe (ppm), G (gap index, %), K (ppm), LD (litter depth, cm), M (moisture, %), MI (moisture index, log(distance to ridge/distance to water)), Mn (ppm), OM (organic matter, %), P (ppm), pH (-log[H⁺]), RM (root mat index, code 1-3), RO (rock at ground surface, %), SA (sand, %). Soil B, cation exchange capacity, and Mg (not shown) are highly collinear with Ca, and are correlated with vegetation in a similar way. Sign and significance of correlation coefficients are indicated as follows: ++ = $r > 0.28$ ($p < 0.05$); +++ = $r > 0.48$ ($p < 0.0005$); ++++ = $r > 0.70$ ($p < 0.00005$); -- = $r < -0.28$ ($p < 0.05$); --- = $r < -0.48$ ($p < 0.0005$); ---- = $r < -0.70$ ($p < 0.00005$), where r is the Spearman rank correlation coefficient; n 48 plots.

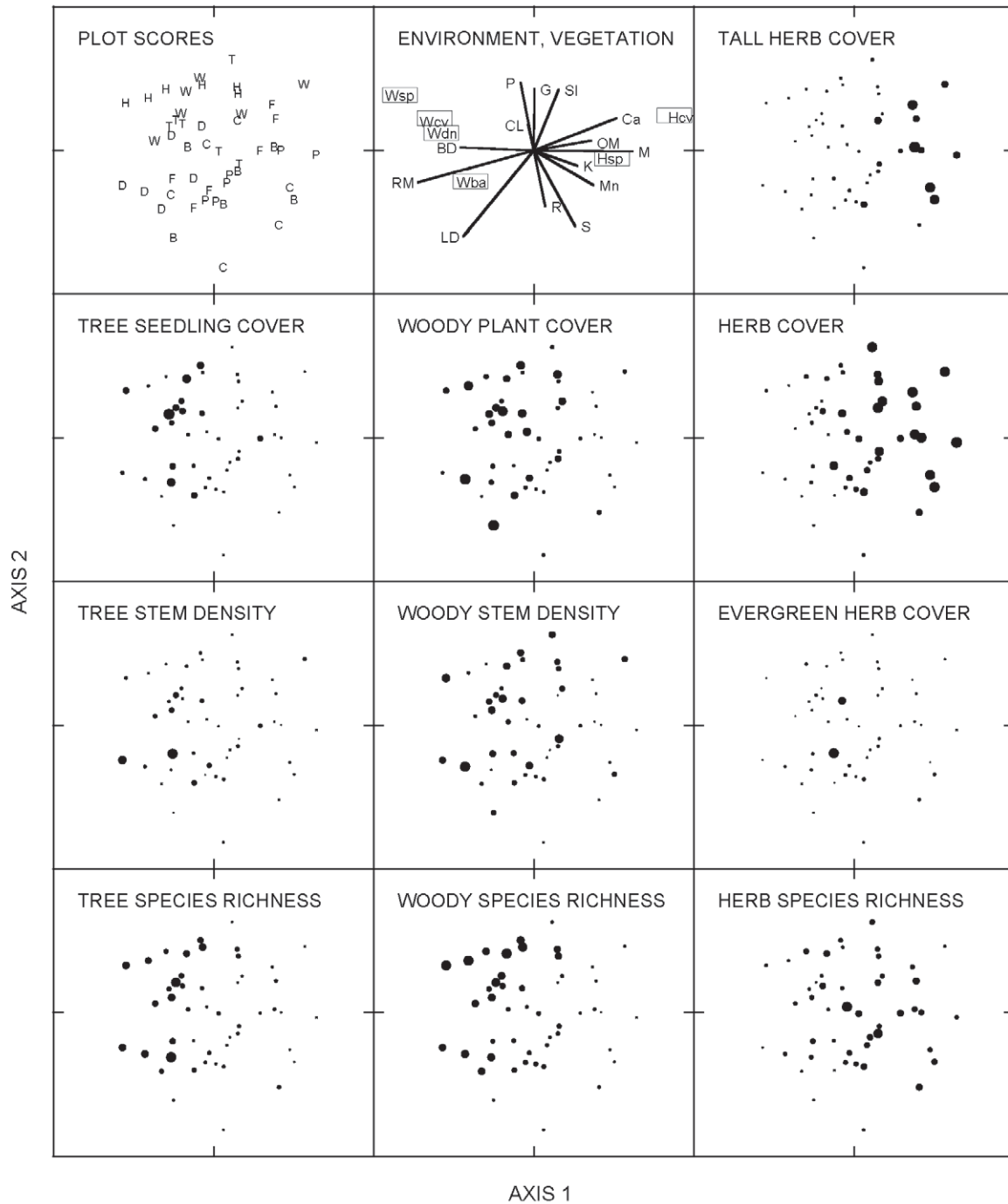


Fig 3. Redundancy Analysis ordination of temperate deciduous forest floor plots based on similarities in vegetation and constrained by environmental variables.

PLOT SCORES: locations of 48 plots with respect to AXIS 1 and AXIS 2 of the ordination. Study site locations of the plots are as in Fig. 2.

ENVIRONMENT, VEGETATION: vectors represent the strength of association between ordination axes and soil silt (SI), Ca, organic matter (OM), moisture (M), K, Mn, S, surface rock (R), litter depth (LD), root mat index (RM), soil bulk density (BD), clay (CL), and P, and the gap index (G). Outlined symbols mark scores of selected vegetation variables used as 'species' in the ordination: herb cover % (Hcv), number of herb species per 25 m² (Hsp), woody stem basal area (Wba), woody stem density (Wdn), woody plant cover < 0.4 m tall (Wcv), and number of woody species per 25 m² (Wsp). Each remaining graph is the same analysis:

TREE SEEDLING COVER < 0.4 m tall (0 to 7.9 %); TREE STEM DENSITY of individuals over 0.4 m tall and less than 2.5 cm DBH (0 to 18000 / ha); TREE SPECIES RICHNESS (0 to 13 species / 10 m²); WOODY PLANT COVER less than 0.4 m tall (0 to 19 %); WOODY STEM DENSITY of individuals > 0.4 m tall and < 2.5 cm DBH (0 to 29 000 / ha); WOODY SPECIES RICHNESS (0 to 25 species / 10 m²); TALL HERB COVER 0.4 to 0.8 m in height (0 to 68 %); HERB COVER TOTAL (0 to 96 %); EVERGREEN HERB COVER (0 to 68 %); HERB SPECIES RICHNESS (1 to 36 species / 10 m²).

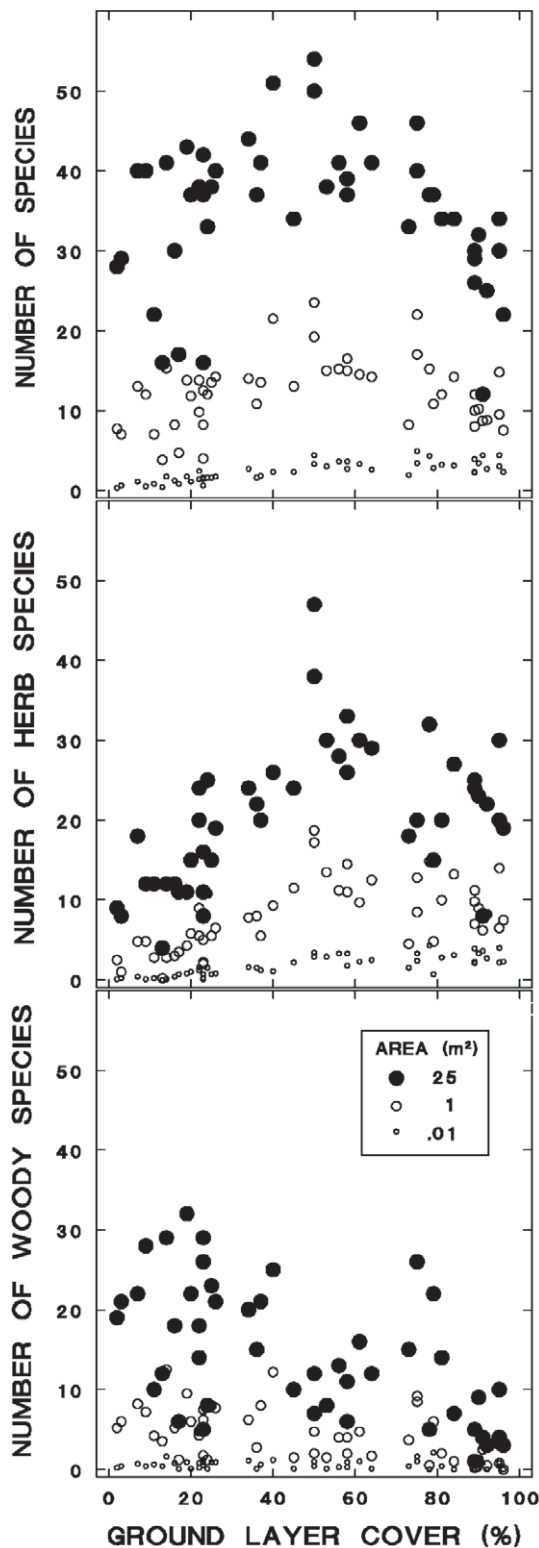


Fig. 4. Herb species richness in temperate deciduous forests at three scales in relation to ground layer cover. Study site locations are as in Fig. 2.

Geographically and floristically distant plots with similar resource and light levels have similar plant growth forms, and plots from the same site are widely separated in the ordination when resource levels are different (Fig. 3). As predicted, site effects do not add significantly to regression models of herb cover that already include soil resources ($p > 0.05$, App. 3).

Herb cover is near 100 % only where both Ca and moisture availability are high, whereas low herb cover occurs where soils are dry or low in Ca, and we see a significant Ca \times moisture interaction in the multiple regression analysis (App. 3). Tough root layers near the soil surface (with high root mat index), like those under ericaceous shrubs, are never associated with abundant herbs. Similarly, deep litter is strongly associated with low herb cover (Table 1, Fig. 3). However, three moist and high-nutrient plots have deep litter and abundant herbs, so litter depth alone cannot explain this response.

Herb species richness

On all eight sites, herb species richness (at scales $> 0.01 \text{ m}^2$) is greatest where resources and plant cover are intermediate (Fig. 3, 4). The unimodal relationship between species richness and cover is modelled in multiple regression as a strong positive effect of herb cover with a strong negative effect of (herb cover)² (App. 3).

Unlike herb cover models, herb species richness models are improved by site effects (r^2 improved from 0.78 to 0.92), as would be predicted owing to inherent differences in the available species pool (Pärtel et al. 1996; Peet et al. 2003; Zobel 1997). Sites differ in species richness, but also differ qualitatively in species composition and in the relative abundance of herb growth forms (Graves 1995). For example, ground layers with abundant herb cover are dominated variously by graminoid, evergreen, tall annual, and robust perennial species at the Haywood Landing, Duke Forest, Taylor Hollow, and Frozen Head sites, respectively (App. 2).

Woody plant response to soil resources

Woody ground-layer cover, understorey basal area, stem density, and species richness are low on moist, Ca-rich plots where herbs are most abundant, and high across a range of conditions where soils are dry, or wet and base-poor, and where the competing herb cover is lower (Table 1; Figs. 3 and 4). Woody plants grow in a variety of conditions, so regression models predicting woody plant cover have lower r^2 -values than herb cover models (App. 3). Measured predictors account

for woody species richness much better ($r^2 = 0.84$). As predicted, high woody species richness occurs on drier, more nutrient-poor plots than those with highest herb species richness, especially on soils low in K and Mn, where herbs and the evergreen shrub *Rhododendron maximum* are not abundant. Irrespective of Ca, woody species richness is high where soil is dry (Table 1, Fig. 3, App. 3).

Response to light

Within the narrow range of canopy openness observed (1 to 7 %), the gap response of herbs is weak and non-significant (Fig. 3, App. 3). In RDA, the second axis represents, in part, a light gradient (associated with the gap index, G), but the eigenvalue is low (0.05) and plots with high herb cover are widely scattered along this axis (Fig. 3). High herb cover can occur in deep shade. At Bat Cave, a plot has 89 % herb cover and a gap index of 1 %, the lowest encountered in the study.

Woody plants are more responsive than herbs to small variations in light. Woody cover < 0.4 m tall is positively associated with the gap index (App. 3), though owing to the narrow range of light observed, this effect is weak, and not evident in Spearman rank correlations (Table 1). Moreover, gap index does not help predict stem density, basal area, or diversity of larger understorey woody plants that established years ago in gaps that have long been filled.

Woody cover is negatively associated with herb cover (Fig. 3). Herb cover is, in part, a surrogate for soil resource effects, but it is also an index of the reduction by herbs of light available to small woody plants. Cover of taller herbs (> 0.4 m) is negatively correlated with cover and species richness of woody plants < 0.4 m tall (r ranges from -0.45 to -0.72 , $p < 0.001$).

Growth form diversity

Some herbaceous and some woody plants are not distributed as predicted by the structural carbon - nutrient balance hypothesis. For example, the evergreen pteridophytes *Polystichum acrostichoides* and *Lycopodium digitatum* account for moderately high herb cover (65 to 71%) on two plots in Duke Forest where soils are dry and low in Ca. Deciduous herb cover on these plots is under 15 %, consistent with other plots having similar resource availability. Evergreen herbs are nearly absent on high-resource plots (Table 1, Fig. 3).

Woody species also vary in habitat preference. Canopy tree species respond to soil resources as pre-

dicted by the structural carbon - nutrient balance hypothesis with highest stem densities, cover, and species richness occurring on dry or infertile plots where the ratio of light to soil resources is highest (Figs. 3, 4). However, certain woody species can occur in relatively high densities on resource-rich and/or very shady plots with abundant herbs (Fig. 3). The forest shrub *Hydrangea arborescens* with hollow stems is successful among robust herbs at those Taylor Hollow sites where soils are moderately high in moisture and basic cations.

Discussion

A trade-off between herbs and woody plants

We have shown that in forest understories on moist, nutrient-rich soils (low C:R environments), herbs typically form a continuous tall layer and woody plants tend to be scarce. In contrast, woody plants are generally abundant in the understorey on dry or nutrient-poor soils (high C:R environments). There are at least two mechanisms potentially responsible for this pattern, both of which derive from the structural carbon - nutrient balance hypothesis. First, where the C:R ratio is low, plants having stems with low C:R demand, such as herbaceous species, should have faster vertical growth rates than plants with high C:R demand rates, such as tree seedlings. In low C:R environments where absolute soil resources are high, temperate forest understorey herbs can quickly form a nearly continuous canopy each spring that overtops tree seedlings. On these rich sites, light competition from herbs should reduce survivorship of the slower-growing, woody-plant seedlings, thereby suppressing seedling density and shifting species composition of the seedling bank (Graves 1995; George & Bazzaz 1999a, b). Elsewhere we report experiments that tested the hypotheses that competition with herbs limits tree seedling success where C:R supply rate is low, and that an increase in light supply or a decrease in soil resource supply will increase tree seedling survivorship (Graves, Peet & White unpubl.; Graves 1995). As a consequence of this asymmetric competition for light, woody plant density in the seedling and sapling layers of temperate forests on moist, fertile sites should be relatively low compared to the denser understories on less fertile sites. The second, alternative mechanism is that where the C:R ratio of resource supply is low, levels of phenolic defenses in tree seedlings are low (Shure & Wilson 1993), and vulnerability to herbivory is high, as predicted by the original Bryant et al. (1983) hypothesis.

Species richness

Maximum woody species richness occurs at lower soil resource supply than maximum herb species richness, presumably because populations of many woody species cannot persist in competition with tall, dense herb layers. Experiments have shown that many tree species have lower survival rates under herb cover (e.g. Graves 1995; George & Bazzaz 1999b). At larger scales, woody species diversity could remain high, provided herb cover is discontinuous. For example, tree species that survive poorly within dense clones of ferns can be maintained in the seedling pool of the forest outside patches of ferns (George & Bazzaz 1999b).

Only rarely does the supply of soil resources sufficiently exceed the demand by canopy trees that herb cover can approach 100% in summer. As a consequence, species richness in deciduous forests is generally seen to increase along nearly the entire length of the resource gradient (Peet & Christensen 1988; Grubb 1987). The unimodal association between species richness and ground layer cover we observe at all eight study sites indicates that this uncommon pattern can be expected where soils are sufficiently moist and fertile to support summer herb cover above 50%. The pattern has been observed in a few other forests where resource gradients are long and include high resource sites (e.g. Newell et al. 1999; Dupré et al. 2002).

Extending the carbon - nutrient balance hypothesis

To have broad applicability, the structural carbon - nutrient balance hypothesis should account for responses to resource environments not examined in this study of closed temperate deciduous forests. For example, herb superiority over woody plant competitors in closed forests on rich sites presents the conundrum of how the canopy trees can successfully reproduce in these habitats. In canopy gaps on high-resource sites, the high light (carbon) availability shifts the C:R ratio, providing an environment where woody plants can compete effectively with herbs. After gap closure, the established woody stems allow the taller woody plants to retain their vertical advantage over herbs. Plant allocation of carbon to wood in canopy gaps (Canham 1985; Pickett & White 1985; Poulson & Platt 1989; Reader & Bricker 1992) parallels the increase in leaf phenolics seen in gaps (Dustin & Cooper-Driver 1992; Shure & Wilson 1993). Allocation of carbon to wood on resource-poor soils (Aerts 1995; Monk 1966; Bryant et al. 1983; Coley et al. 1985; Chapin et al. 1993) parallels the allocation of carbon to phenolic compounds (Bryant et al. 1983; Dustin & Cooper-Driver 1992; Chapin et al. 1993) or to roots that increase drought tolerance (Latham 1992).

Thus, woody-stemmed plants are adapted to a wide range of soil nutrient conditions (Chapin et al. 1996), but total as well as relative supply rates of carbon and soil resources influence woody plant response (Davis et al. 1998; Fajer et al. 1992).

Herbs dominate forest floors in low C:R environments, but some woody plants survive with the herbs, and some herbs survive with the woody plants in high C:R environments. Trade-offs in carbon and nutrient allocation to roots, stems, leaves, carbon-based allelochemicals, and cell respiration could account for within-site growth form differences between herbs and woody plants (Grubb 1998; Rusch et al. 2003; Lindroth et al. 1993). Shade-tolerant tree seedlings may survive in low C:R environments by growing woody stems slowly and waiting for a canopy opening to grow tall, growing roots slowly and forfeiting drought tolerance, and allocating much of the limited carbon to leaves (Latham 1992). In contrast, some evergreen herbs (this study), shrubs (Chapin et al. 1996), and trees (Catovsky & Bazzaz 2000) are associated with higher C:R environments (nutrient-poor soils) than deciduous forms. Trade-offs among plant compartments help explain the coexistence of herbs and small woody plants. Thus, because of possible trade-offs, a general carbon - nutrient balance hypothesis must focus on whole plants. Where patterns of allocation to stems appear to be inconsistent with the structural carbon - nutrient balance hypothesis, we predict that total carbon and nutrient budgets will reflect the C:R environment.

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