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Plant Competition and Nutrient Limitation during Early Succession in the Southern Appalachian Mountains

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ABSTRACT.—An experimental approach was used to examine the potential importance of nutrient limitation and competition on early successional development in Southern Appalachian forests. Treatments included tree removal, herb-shrub removal or NPK fertilization on 12 × 12 m plots established within a 20-ha clear-cut. A reciprocal increase in primary productivity following tree or herb-shrub removal suggests competition between these vegetation components. Black locust (*Robinia pseudo-acacia*) exhibited greater growth following herb-shrub removal. *Aster* and *Solidago* biomass increased significantly in the absence of trees. Herbaceous and tree productivity both increased following fertilization, indicating nutrient limitation during early succession. Tulip poplar (*Liriodendron tulipifera*) and red maple (*Acer rubrum*) had significantly greater productivity in fertilized areas than in control areas; other tree species were unaffected. In contrast, the occurrence of blackberry (*Rubus* spp.) in the 2nd yr of succession was restricted to fertilized plots. The vigorous growth of *Rubus* in fertilized areas apparently limited *Robinia* production. Herbs such as fireweed (*Erechtites hieracifolia*) and pokeweed (*Phytolacca americana*) were important in woody removal plus fertilization treatments. These findings suggest that competition and nutrient limitation interact in controlling species composition, relative productivity and time of species occurrence during early succession in the Southern Appalachians.

INTRODUCTION

Early successional vegetation is often important in retaining nutrients following disturbances such as fire and clear-cutting (Marks and Bormann, 1972; Vitousek and Reiners, 1975; Vitousek *et al.*, 1979; Gorham *et al.*, 1979; Shure and Phillips, 1987; Phillips and Shure, 1990). Nutrient cycling following disturbance in the southern Appalachian Mountains involves an initial rapid loss of nutrients and sediment (Johnson and Swank, 1973), followed by a slow return to predisturbance levels. Much of this temporal decline in nutrient losses is attributed to the rapid regrowth of vegetation. Aboveground vegetation net primary productivity (NPP) reaches ca. 20% of precutting levels in the 1st yr of succession. In contrast, aboveground nutrient pools in biomass reach ca. 30–40% of precut levels (Boring *et al.*, 1981). Factors which affect the rate of recovery to normal nutrient cycles include cutting method (Vitousek and Matson, 1984, 1985), rate of vegetation regrowth (Marks, 1974; Boring *et al.*, 1981) and the relative importance of nitrogen-fixing plants which replenish nutrients (Boring *et al.*, 1981; Boring and Swank, 1984a; Montagnini *et al.*, 1986).

Stump sprouts and herb-shrub growth dominate early succession in Southern Appalachian forests (Boring *et al.*, 1981; Phillips and Shure, 1990). Herbaceous vegetation grows rapidly and sequesters nutrients which would otherwise be lost from the system. Sprouts remobilize underground nutrient reserves and quickly re-establish the aboveground vegetation structure (Boring *et al.*, 1981). Early successional trees such as *Prunus pensylvanica* (Marks and Bormann, 1972; Marks, 1974) in the Northeast and *Robinia pseudo-acacia* sprouts in the Southern Appalachians (Boring and Swank, 1984a), retain nutrients through rapid growth or add nitrogen to the system via nitrifying bacteria. Changes in soil nutrient levels in the first years after disturbance may influence the order of occurrence and amount of plant biomass in particular systems (Rice *et al.*, 1960; Parrish and Bazzaz, 1982; Tilman, 1986).

The co-occurrence of early (herb-shrub) and late (tree) successional species in pioneer stages of recovery in the Southern Appalachians affords an opportunity to evaluate possible competitive interactions between these contrasting vegetation types. The present study was initiated to determine the interactions between herb-shrub and tree species during early succession and to examine the effects of nutrient levels on these interactions.

METHODS

We conducted the study in a 20-ha forest opening in the southern Appalachian Mountains near Highlands, N.C. The site is at an elevation of 930–1100 m with a 30–40% slope and a NW-facing aspect. The study site was logged from autumn 1983 through spring, 1984. Precut vegetation consisted mainly of mixed oaks (*Quercus*) and tulip poplar (*Liriodendron tulipifera*). Rainfall in the vicinity averages 181 cm/yr. There is a mean annual temperature of 13 C (Day and Monk, 1974).

The experimental design included fertilization and vegetation (woody or herb) removal treatments. Twelve 12 × 12 m plots were established randomly within the clear-cut in June 1984. All plot sites had equivalent amounts of logging slash present. Four plots each had either woody vegetation (trees) or herb-shrub (hereafter called herb) vegetation removed monthly throughout the 1984 and 1985 growing seasons; four plots were left as controls (reference plots). Two of the four plots in each set, including reference plots, were fertilized. Fertilizer (13:13:13 NPK, slow N release) was applied by hand at an amount equivalent to 500 kg/ha during July 1984 and in early June and mid-August 1985.

Tree biomass estimates were made by identifying, tagging and measuring the basal diameters of all stems on the eight plots with trees. Measurements were obtained after the completion of the 1984 (1st yr of succession) and 1985 (2nd yr) growing seasons. The sprout measurements were converted into biomass (leaf, wood and total) using regression equations derived from a similar clear-cut in the nearby Coweeta Hydrologic Laboratory, N.C. (Boring and Swank, 1984a). Net primary productivity for all tree species was determined as the total (leaf + wood) biomass at the end of the second growing season minus the wood biomass present from the previous year. Five major sprouting species, red oak (*Quercus rubra*), red maple (*Acer rubrum*), black locust (*Robinia pseudo-acacia*), dogwood (*Cornus florida*) and tulip poplar (*Liriodendron tulipifera*), were chosen for detailed examination.

Herbaceous biomass samples were harvested from the central 10 × 10 m area of the eight herb plots to minimize edge effects. Six randomly selected 0.5 m^2 samples were collected from each plot on 23–24 September 1984, and on 7–9 July, 12–15 August and 12–16 September 1985. Samples were sorted to genus or species, oven-dried at 80 C until reaching constant weight (24 h) and weighed. Community net primary productivity was calculated by summing woody species NPP and the peak biomass of each herb taxon.

Statistical analysis used one-way, nested ANOVA ($n = 48$) in testing for treatment effects (Kirchner, 1977). For the tree analysis, each plot was subdivided into six equal subplots.

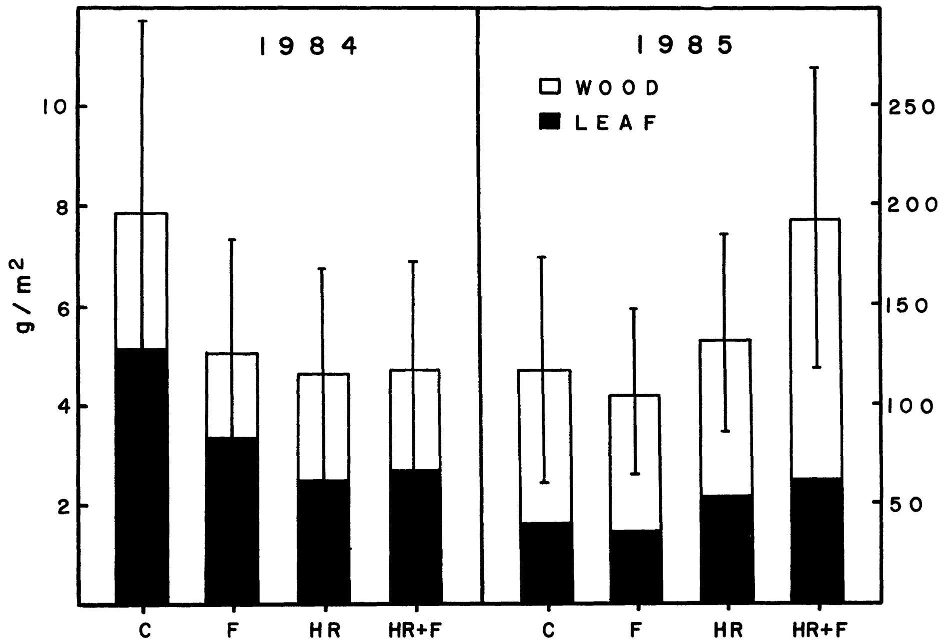

FIG. 1.—Total aboveground woody biomass ($\bar{x} \pm$ SE, n = 12) in the treatment plots by the end of the 1st and 2nd growing seasons after clear-cutting. Treatments include reference (C), fertilization (F), herb removal (HR), and herb removal + fertilization (HR + F). Note different ordinate scales for the 2 yr

Quercus was analyzed using the whole plot as replicates because of nonhomogeneous variances. Herb analysis used the six harvest samples per plot. Analysis of variance was performed on total biomass and leaf biomass for the tree species, and on total herb biomass, blackberry, *Aster, Solidago* and the remaining biomass (after blackberry, *Aster* and *Solidago* had been removed).

RESULTS

Aboveground biomass growth was minimal (approximately 5 g m^{-2}) during the 1st yr following disturbance (Fig. 1). Tree biomass increased 15–40 fold (115–190 g m^{-2}) by the end of the 2nd growing season. Less than 1% of the stems were advance regeneration seedlings or saplings that survived the cut. Leaf biomass was similar in all treatments ($F = 1.12$, $P = 0.35$, 1984; $F = 1.77$, $P = 0.17$, 1985) and averaged 61% of total tree biomass during 1984, and 36% in 1985 (Fig. 1). However, tree biomass was somewhat higher in the herb-removal, fertilized plots (HR + F) by the end of the 2nd yr.

Treatment effects were present for several tree species in 1985 (Fig. 2). *Robinia,* the most important sprouter, had significantly greater aboveground biomass ($F = 3.15$, $P < 0.05$) in herb removal (HR and HR + F) than reference plots. Nutrient enrichment without herb removal (F) had a negative effect on *Robinia* biomass. In contrast, *Liriodendron* growth was significantly increased ($F = 3.94$, $P < 0.05$, 1984; $F = 3.44$, $P < 0.05$, 1985) in fertilized areas both years, whereas *Acer* had somewhat greater growth (total—$F = 1.14$, $P > 0.2$; leaves—$F = 2.80$, $0.05 < P < 0.1$) in plots receiving fertilizer plus herb-removal

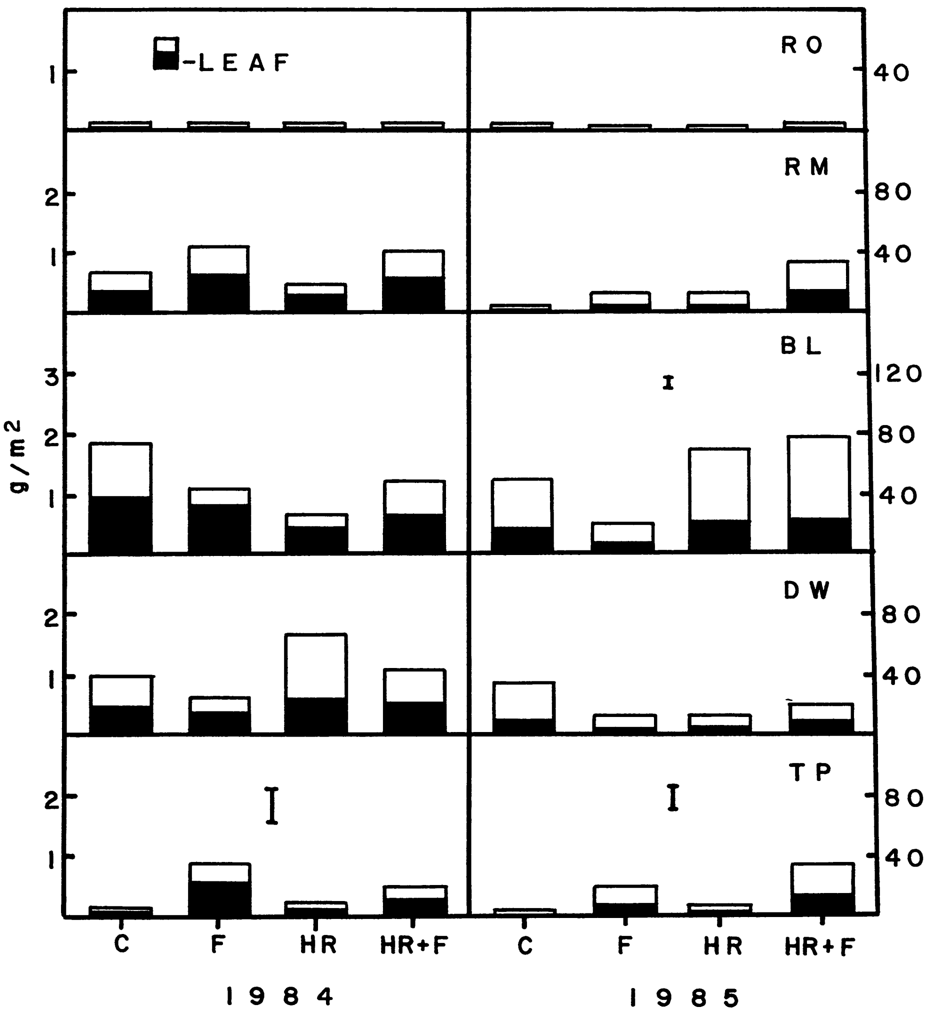

FIG. 2.—Aboveground biomass (x̄, n = 12) of five woody species at the end of the 1st and 2nd growing seasons after clear-cutting. Proportions of leaf biomass and wood biomass are indicated by key. Treatments include reference (C), fertilization (F), herb removal (HR) and herb removal + fertilization (HR + F). Species are red oak (RO), red maple (RM), black locust (BL), dogwood (DW) and tulip poplar (TP). Least significant differences are included where ANOVA results were significant. Note different ordinate scales

treatments. *Cornus* growth was slightly depressed in all treatment plots. *Quercus* biomass was similar on treatment and reference plots.

Tree sprout densities were relatively stable by the end of the 1st growing season (Table 1). Total stem densities increased slightly from 1984 to 1985 on all but the fertilized (F) areas. Stem densities of four of the five major species actually decreased during the 2nd yr in fertilized plots. *Robinia* and *Cornus* exhibited opposite responses in treated vs. reference plots; *Robinia* generally had greater biomass per stem, whereas *Cornus* had higher densities

TABLE 1.—Number of woody stems per hectare for 1st and 2nd yr following clear-cutting for all woody species (total), red oak (RO), red maple (RM), black locust (BL), dogwood (DW) and tulip poplar (TP). Treatments include reference (C), fertilization (F), herb removal (HR), and herb removal + fertilization (HR + F)

	1st yr				2nd yr			
	C	F	HR	HR + F	C	F	HR	HR + F
RO	1145	971	1219	1559	1104	907	1219	1698
RM	1246	1496	1873	1014	1461	1311	1765	1268
BL	3200	1247	2368	1972	3099	944	2256	2615
DW	1903	2533	3340	2198	2227	2365	3784	3005
TP	2396	1042	2778	1736	2673	1285	2743	1910
Other	6950	5836	6095	10,305	7248	5444	6427	9017
Total	16,840	13,125	17,637	18,784	17,812	12,256	18,194	19,513

of smaller sprouts on treated than control areas (Table 1, Fig. 2). No other treatment effects were evident.

The herbaceous community was well-established during the 1st growing season (Fig. 3). *Aster* and *Solidago* were both important species though no major treatment effects were evident. Total herbaceous biomass was significantly higher (July: F = 4.94, P = 0.005;

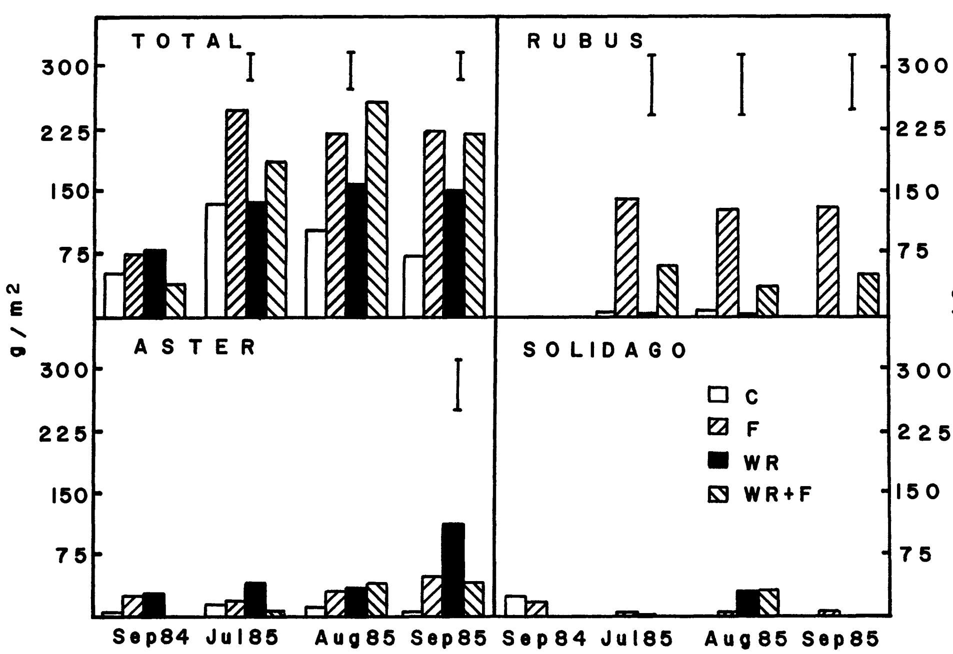

FIG. 3.—Aboveground herb biomass ($\bar{x}$, n = 12) for total, *Rubus, Aster* and *Solidago* in the treatment plots. Treatments include reference (C), fertilization (F), woody removal (WR), and woody removal + fertilization (WR + F). Least significant differences are included where ANOVA results were significant

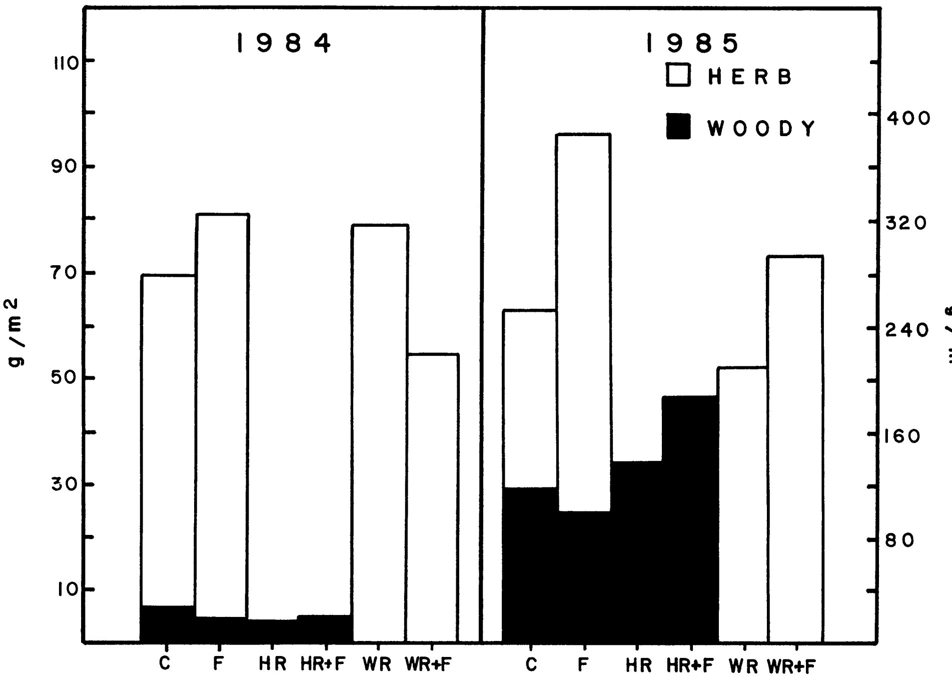

FIG. 4.—Total aboveground productivity for the 1st (1984) and 2nd (1985) yr following clear-cutting. Values represent averages of two replicate plots. Herb production represents the sum total of peak biomass values for all individual species. Wood production during the 2nd yr was estimated by subtracting wood biomass totals at the end of the 1st yr from wood biomass totals at the end of the 2nd yr. Treatments include reference (C), fertilization (F), herb removal (HR), herb removal + fertilization (HR + F), woody removal (WR), and woody removal + fertilization (WR + F)

August: $F = 6.03$, $P = 0.002$; September: $F = 4.46$, $P = 0.008$) in fertilized than reference plots throughout the 2nd yr. Blackberry (*Rubus* spp.) was responsible for most of this enrichment effect. *Rubus* comprised 40–55% of the herbaceous biomass in fertilized plots, but was nearly absent in reference and woody removal (WR) plots. Herbaceous biomass was also somewhat elevated in woody removal plots by the end of the 2nd growing season. *Aster* accounted for much of this increase, particularly in September ($F = 2.63$, $P = 0.06$). *Solidago* biomass was occasionally higher in woody removal areas. The remaining herbs had significantly higher biomass in the woody removal + fertilization (WR + F) than reference plots in August ($F = 6.93$, $P = 0.0006$) and September ($F = 3.66$, $P = 0.02$) 1985.

The experimental treatments promoted distinct changes in community net primary productivity by the end of the 2nd growing season (Fig. 4). NPP of fertilized plots (F) increased 49.5% over that of reference plots as a result of greater herb production. Woody vegetation production increased slightly above reference plots in the absence of herbaceous vegetation, particularly following fertilization. Herbaceous vegetation showed a similar compensatory response in the absence of woody vegetation. Fertilization increased herbaceous production even further, although the fertilizer effect was similar in the presence or absence of woody vegetation (F vs. WR + F).

DISCUSSION

Forest openings in the southern Appalachian Mountains usually have high levels of available nutrients due to rapid decomposition of the debris remaining after logging (Boring *et al.,* 1981; Seastedt and Crossley, 1981). The extent of this nutrient release may have a significant impact on revegetation processes. In the present study, *Liriodendron* and *Acer* showed a positive response to the addition of fertilizer; the biomass of several other tree species was unaffected. Thus, there is evidence for differential nutrient limitation among tree species present in the 1st 2 yr following disturbance. Tilman (1985, 1986, 1988) has demonstrated how differential nutrient usage by plants can lead either to dominance by a single species or to many coexisting species in the community. Three of our species, *Quercus, Robinia* and *Cornus,* showed equal or less growth in fertilized (F) than reference (C) areas. *Liriodendron* or *Acer* may outcompete these species in highly enriched areas.

Stump sprouts comprise most of the aboveground biomass in the early years of succession in the southern Appalachian Mountains (Boring *et al.,* 1981; Phillips and Shure, 1990). Tree biomass exceeded herb biomass by the end of the 2nd yr after disturbance. Most of the 15–40 fold increase in tree biomass was from existing sprouts and not new recruitment, since stem density did not change appreciably over this 2-yr period. Stem densities in our areas (12,256 to 19,513 ha^{-1}) were much higher than in a 7-yr-old clear-cut (9654 ha^{-1}) and uncut forest (3042 ha^{-1}) in nearby areas in North Carolina (Johnson and Swank, 1973). Pronounced competition apparently occurs among the tree species during the successional process.

Competition also exists to some degree between the co-occurring herb and tree vegetation. Total tree biomass was only slightly elevated in the absence of herbs. *Robinia,* a nitrogen-fixing legume (Boring and Swank, 1984a, b), was the only tree species which increased in biomass following herb removal. In contrast, herb biomass and productivity increased in the 2nd growing season following woody sprout removal. *Aster* and *Solidago* were the principal beneficiaries. The remaining herb species did not change much in species composition or biomass. However, fireweed (*Erechtites hieracifolium*) and pokeweed (*Phytolacca americana*) biomass increased threefold in the woody removal + fertilization (WR + F) treatment during the 2nd growing season.

Rubus begins to develop in the 2nd yr of succession in the Southern Appalachians and comprises most of the herb biomass present by the 4th yr (Boring and Swank, 1984a). *Rubus* showed the most vigorous response to fertilization, and was the dominant herb in the fertilized plots during the 2nd yr. Tamm (1974) reported a similar increase of *Rubus* following fertilization in spruce plantations in Sweden. Interestingly, *Rubus* production was much higher in the fertilized (F) than tree removal + fertilized (WR + F) treatment. The rapid growth of *Erechtites* and *Phytolacca* probably accounted for the reduction in *Rubus* growth in WR + F areas. *Erechtites* and *Phytolacca* together amounted to almost 30% of the herb biomass in WR + F plots vs. 9% in the F treatment. *Rubus* was not apparently inhibited by tree species in the early stages of succession.

The enhanced growth of *Robinia* in the absence of herbs is believed due to release from *Rubus* competition. *Robinia* biomass was inversely related to *Rubus* biomass in plots where both species co-occurred. This suppression of *Robinia* during early succession probably ceases as *Rubus* dies back with the initial development of a tree canopy. Nonetheless, *Rubus* plays an important functional role during early succession in the Southern Appalachians by sequestering released nutrients and inhibiting the initial growth of *Robinia.* The timing and extent of *Rubus* development can have a marked influence on *Robinia* growth and thus N-fixation and nutrient accretion in these forests following disturbance (Boring and Swank, 1984a, b).

Aster spp. and *Solidago* spp. are present in mature forests of the Southern Appalachians; cutting increases their relative importance (Boring *et al.,* 1981). In this study, *Aster* and *Solidago* were important in the herb layer during the 1st yr when *Rubus* was largely absent. *Aster* grew especially well in the absence of woody vegetation, but also increased somewhat despite the dominance of *Rubus* following fertilization. Thus, in the first few years after disturbance *Aster* and *Solidago* tend to dominate the herbs in areas of low to moderate nutrients, particularly when tree vegetation is reduced or absent. *Rubus* dominates areas of high nutrient availability, although it can be inhibited by *Erechtites* or *Phytolacca.* This dominance by *Rubus* tends to persist until canopy closure when most herbs are reduced or eliminated (Marks, 1974).

Nutrient enrichment supposedly decreases species diversity and increases vegetation biomass (Odum, 1969; Kirchner, 1977). In this study, species richness did not change although certain species were favored (*i.e.,* had higher biomass) in particular treatments. Our findings support other studies. Harcombe (1977) reported that fertilization enhanced the competitive ability of a forb species in Central American clear-cuts. Carson and Barrett (1988) found that nutrient enrichment of old fields increased biomass of certain species, but produced little change in species richness. These findings support resource-based theories of plant community structure (Tilman, 1985, 1986, 1988; Inouye and Tilman, 1988; but *see* Shipley and Peters, 1990), which suggest that plant competition is based on differential resource usage by particular species. Parrish and Bazzaz (1982) have illustrated this fact in demonstrating differential patterns of resource use between annual and perennial species. Early plant succession following disturbance in the southern Appalachian Mountains thus involves a dynamic competitive response for resources such as light or soil nutrients. Low nutrient levels favor *Aster,* whereas high nutrient levels favor *Liriodendron, Acer, Rubus, Phytolacca* and *Erechtites. Robinia* sprouts dominate early succession in these forests, although the extent of *Rubus* development can significantly influence the importance of *Robinia.*

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