INTERFERENCE WITH SHOOT GROWTH AND FLOWERING OF DITTANY (*CUNILA ORIGANOIDES* (L.) BRITTON) BY HARDWOOD LEACHATES

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Abstract: This study examined the potential role of hardwood leachates in the reduction of understory forbs in oak-hickory stands following invasion by sugar maple and dense-canopy shrubs. We conducted a shaded greenhouse experiment during two summers using stonemint dittany (*Cunila origanoides* (L.) Britton) as an indicator species. We used a modified stair-step bioassay with donor pots producing two levels of recycled leachates from hardwood seedlings root exudates, foliage washes, and decaying leaves. At the lower density, each donor pot had three hardwood seedlings and three applications 300 cm^2 of mature leaves of the same species to the litter layer (LAI = 1.5). At the higher density, we doubled the number of seedlings and surface area of mature leaves in the litter layer (LAI=3.0). Donor species tested for 1 or 2 years included sand-only, sugar maple, white oak, flowering dogwood, pawpaw, and black walnut. Dittany stem height ranged from 38 cm when exposed to leachates from white oak seedlings to 49 cm when exposed to leachates from sand-only donor pots. Dittany stem dry weights showed no differences in either year in response to leachates produced by different hardwood seedlings or at the two donor densities. Most dittany stems produced nearly 2,000 flowers during a 10 week period which began with completion of axillary shoot elongation. No differences in date of flower initiation or cumulative flower production were found in response to any of the hardwood leachates. We conclude that allelopathic interference of dittany by hardwoods, if it occurs at all, may require more stressful conditions than were created in this study and that the absence of dittany in oak-hickory stands after the invasion by sugar maple or pawpaw results primarily from competition for light and other resources.

INTRODUCTION

The oak-hickory forests in the central hardwoods region were heavily disturbed by fire before being cut during post-European settlement (Fralish 1991). Without periodic fire, the regenerated oak forests are now being replaced by sugar maple and dense-canopy shrubs such as pawpaw on the more mesic sites and by flowering dogwood on the drier sites (Parker and others 1985, Schlesinger 1989). As the mid-canopy layer increases in density, this succession typically is accompanied with a loss of forest forbs such as stonemint dittany (*Cunila origanoides* (L.)Britton).

Although little information has been published on dittany, personal observations confirm dittany is a common aromatic forb found in most mature oak-hickory forests of the central hardwoods region. In the spring, multiple stems emerge from underground perennial storage roots. During the summer, the semi-decumbent woody stems reach lengths of 30 to 60 cm before initiating rapid axillary shoot elongation. Insect-pollinated flowers are formed in clusters along the primary and axillary shoots in early to late fall. We found no information on the mechanisms through which hardwood overstories might affect dittany growth and reproduction as overstory densities increase.

Plant-plant interference can result either from competition for resources or allelopathy (Horsley 1991, Rice 1987). Competition involves removal of essential resources by adjacent plants while allelopathy involves the production and release of chemicals that alter the competitive ability of other plants. The donor plant may affect the germination or growth of the receiver plant through release of allelochemicals from the foliage or roots, through microbial formation of allelochemicals within the rhizosphere, or by affecting bacteria and mycorrhizae populations important for cycling soil nutrients, especially nitrogen and phosphorus (Horsley 1993).

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Well-documented cases exist describing how grasses or forbs interfere with the regeneration of hardwoods (Fisher 1980); however, few studies document that the production of allelochemicals by hardwoods gaves them a competitive advantage over the competing understory. Rietveld (1983) showed that juglone, an allelochemical produced by black walnut, could inhibit germination and growth of many grasses, forbs, shrubs, and trees. Similarly, Gant and Clebsch (1975) suggested that sassafras produces allelochemicals that effectively eliminated 10 of the 37 forest forbs surveyed.

Separating the effects of allelopathy from those of competition, herbivory, disease, and other stresses under natural conditions is extremely difficult (Putnam and Tang 1986, Horsley 1991). The most common method for showing putative allelopathy is with seed germination and seedling growth bioassays, although novel approaches using in vitro bioassays have been tried (Preece and others 1991). Unfortunately, these bioassays frequently use concentrated plant extracts or leachates that may not occur in natural systems. In addition, most germination and growth bioassays used to date eliminate the associated microorganisms found in natural ecosystems.

The "stairstep bioassay" was designed to incorporate more of the components found in natural systems while still separating the effects of allelochemicals from competition for light, water, and nutrients (Lovett and Jokinen 1984, Quasem and Hill 1989). With the stairstep bioassy, allelochemical concentrations are allowed to increase slowly over time as the leachates are continuously recycled between the receiver plants and donor system including test plants, decaying plant parts, and developing litter layers. Various modifications such as addition of soil cores allow for normal destruction or conversion of suspected allelochemicals (Horsley 1991). Other modifications have been made to evaluate the possible interactions between allelochemicals and moisture stress (Rink and Van Sambeek 1985, 1987), nutrient stress (Stowe 1979), or various microorganisms (Qasem and Hill 1989).

Our objective was to learn whether growth and reproduction of dittany were affected by allelochemicals produced by exudates and decomposing leaves of white oak (*Quercus alba* L.), of dense canopy species like sugar maple (*Acer saccharum* Marsh.), pawpaw (*Asimina triloba* (L.) Dunal), flowering dogwood (*Cornus florida* L.), or of black walnut (*Juglans nigra* L.) which is known to produce the toxic allelochemical juglone. Experiments were designed to test two levels of leachate formation under conditions that included microorganisms associated with dittany grown under field conditions.

METHODS

Our greenhouse study was designed as two dose-response experiments in which dittany plants were grown in sand culture and watered by leachates from four test hardwoods and a sand-only control. For this study, three coats of calcium carbonate were applied to the greenhouse ceiling each spring to reduce light intensity by 92% to 140 $umol \cdot m^{-2} \cdot s^{-1}$ on clear summer days. Four greenhouse benches were separated to create south-facing stairsteps 60 and 120 cm above the concrete and gravel floor as shown in Figure 1. Each bench served as one complete block with 10 experimental units in a 5 (donor species) x 2 (donor density) factorial arrangement of donor treatments.

Dittany plants with stems approximately 10 cm long were collected in mid-April 1991 from a local oak-hickory stand. Each plant was dug keeping 0.2- to 1.5-kg of water-saturated soil around the root system. Two plants were planted in each of forty 20 L plastic pots (30 cm diameter by 40 cm deep). Before planting, the soil from plants with a large soil and small soil mass were pressed together and placed on a layer of washed river sand in the bottom of each pot. Holes were punched in the top of the soil to direct movement of leachates through the soil before the pot was filled with sand. Each pot was placed on a 30 x 45 cm fiberglass tray. A total of 10 pots were placed along the lower level of each bench. In 1991, each pot of dittany was thinned to a single stem from each root ball. After the dittany shoots were harvested in 1991, the pots containing the dittany plants were labelled and moved to a large cooler at 4°C until April 1992. The pots were returned to their original position in April 1992. After shoot emergence, each pot was thinned to three stems (one in the center and one each on opposite sides of the pot) for the 1992 experiment.

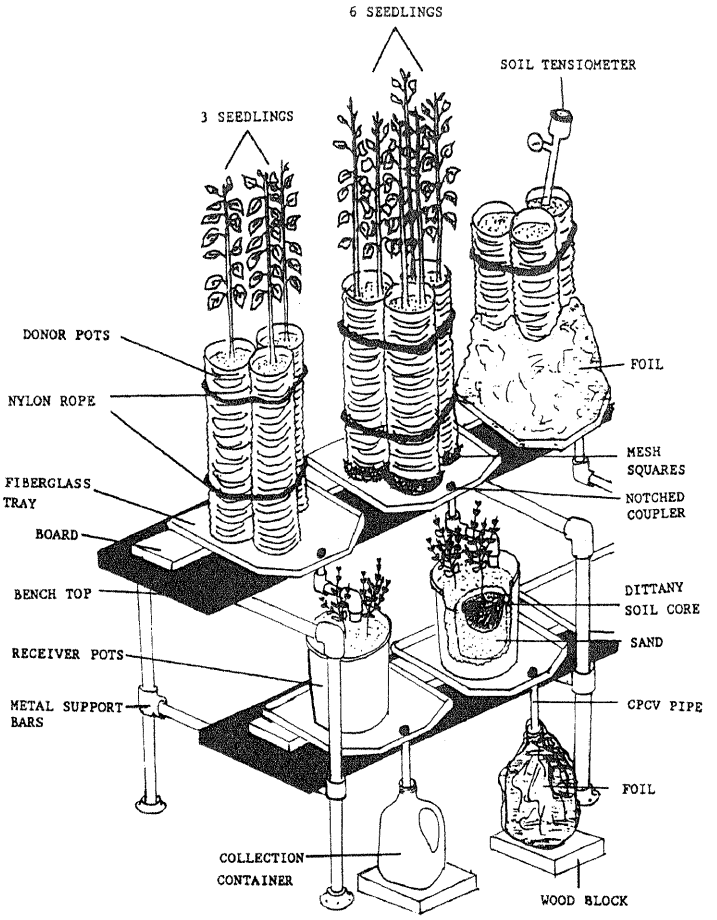

Figure 1. Diagram showing how experimental units were assembled.

Hardwood seedlings (1-0 stock) of sugar maple, white oak, flowering dogwood, and pawpaw were obtained from the Illinois state tree nursery or a commercial tree nursery. In mid April 1991, one or two hardwood seedlings were planted in washed river sand into 50-cm-long sections of 15-cm-diameter corrugated plastic pipe. Three pipe sections containing either one or two seedlings of the same species were tied together and placed on 30 x 45 cm fiberglass trays. Ten trays were set on the upper level of each bench to include two donor densities of four different hardwoods plus two sand-only controls. During the summer, greenhouse temperatures were allowed to fluctuate daily between 18 and 35°C with an average daily maximum of 32°C. Minimum temperatures were reduced to 12°C from November 1991 to April 1992 to harden-off the hardwood seedlings before repeating the experiment. Dead seedlings in the donor units were replaced in April 1992. Because of the high mortality and lack of any treatment responses, pawpaw seedlings were replaced by black walnut seedlings for the 1992 experiment.

Holes were drilled near the front edge of 40 fiberglass tray before cementing in PVC couplers with elbows. A 20- to 30-cm-long segment of 1.3-cm-diameter PVC pipe was added to each elbow in order to drain leachates into the center of a receiver pot or the collection jug. Four-liter, semi-transparent plastic jugs were used to collect excess leachates. These jugs were filled with unbuffered tapwater before recycling leachate on a semi-weekly schedule from April 18 (Julian date 108) to October 7 (Julian date 280) in 1991 and from April 15 (Julian date 106) to September 30 (Julian date 101) in 1992. When recycling, approximately one liter of leachate was poured directly over the dittany foliage and one liter of leachate was added to each donor tube. Once a month, the foliage of the

donor seedlings was rinsed with tapwater and throughfall added to the donor pots. Because leachates were continually recycled and not periodically discarded during each experiment, we monitored the leachates for toxicity by testing acidification (pH) and for salt accumulation (conductivity).

One month after starting the 1991 experiment and during the entire 1992 experiment, 200 ml of 0.25x-strength Hoagland's solution (Machlis and Torrey 1956) were added weekly to each pot of dittany to provide an excess of essential nutrients within each experimental unit. In 1991, this corrected the visible symptoms of a nitrogen deficiency. No other visible symptoms of nutrient deficiencies were observed in either the dittany or donor seedlings. To reduce algal growth, the pots and trays of each experimental unit and the collection jugs were covered with aluminum foil.

Leaves of each donor species were collected from a local stand and added monthly to the top of each donor pot during the first 3 months of each experiment. Approximately 300 cm^2 of mature leaves (measured with a leaf area meter) of the same species as the donor seedlings were added to the low density donor pots each month. Double this amout was added to the high density donor treatment pots each month. This amount of leaves for each addition is equivalent to the leaf surface over the surface of each pot of dittany from hardwood canopies with an LAI of 1.5 and 3.0, respectively.

Approximately 2, 4, and 6 months after the start of each experiment, the number of leaves on each donor seedling was estimated. Several representative leaves of each species were removed to find the average leaf area. Stem volumes were estimated as the sum of basal diameter squared times height of each stem. Approximately bi-monthly after the start of each experiment, leachate samples from each experimental unit were collected to measure pH and conductivity.

Plant height of each dittany stem was measured bi-weekly until elongation ceased. In addition, a pair of leaflets near the apex of each stem was marked and shoot elongation of the two axillary shoots from this node was measured bi-weekly until flower initiation in early July. Each stem was monitored semi-weekly to determine the Julian date for the first open flowers. An attempt was made to count total number of flowers per stem each week; however, number of flowers were estimated when stems had over 500 open flowers. At the end of each growing season, stem height and number of axillary shoots were measured before plants were cut off to determine above ground stem dry weight (60°C).

The experiment was set up as a 5 x 2 randomized complete block design with 4 blocks of 10 experimental units. In 1991, each block consisted of a factorial arrangement of five donor species (sand-only control, sugar maple, white oak, flowering dogwood, or pawpaw) at two densities. The two sand-only controls were randomly assigned to low and high density within each block. In 1992, the pawpaw treatment was replaced with a black walnut treatment. Means were determined for each experimental unit for stem height, axillary shoot number and length per stem, stem dry weight, date of first flower, number of open flowers, and estimated total flower production. Means were subjected to analysis of variance as a randomized complete block design with four blocks of a 5 x 2 factorial arrangement of treatments for donor species and donor density (SAS Institute Inc. 1988). To determine were significant differences existed among donor species, donor density, or their interaction, the 5% t-test value was calculated from the Type III mean sums of squares (population variance) for doing multiple comparisons.

RESULTS AND DISCUSSION

Donor seedling survival ranged from a low of 28% for the pawpaw seedlings to 100% for the sugar maple seedlings (Table 1). Because of the low seedling survival, pawpaw effects are probably in response to decomposition of the leaves added to the donor pots and not to any chemicals produced by the 1+0 seedlings. Responses to sugar maple, white oak, flowering dogwood, and black walnut could result from chemicals released from the decomposing leaves and/or from chemicals produced by the planted seedlings. With the frequent recycling of leachates and addition of Hoagland's solution, most of the planted hardwood seedlings showed rapid shoot and leaf growth, except for pawpaw. Many white oak seedlings showed multiple flushes with gradually expanding leaf areas until the experiment was ended each year.

Table 1. Survival, estimated foliage area, and final stem volume of donor seedlings during the two experiments

Hardwood donor spp.	Number planted	Survival	Estimated foliage area/seedling Week 8	Week 16	Week 22	Stem volume
		- % -	------ cm^2 -----			- cm^3 -
1991 EXPERIMENT:						
White oak	36	72	513	1,144	1409	13
Sugar maple	36	100	1,363	2,659	2,073	64
Dogwood	36	81	476	1,959	1,690	85
Pawpaw	36	28	40	119	57	3
1992 EXPERIMENT:						
White oak	36	89	351	568	—	—
Sugar maple	36	100	1,008	2,366	—	—
Dogwood	36	75	555	1,690	—	—
Black walnut	36	100	20	390	—	—

Leachate conductivity was higher in experimental units containing hardwood seedlings than in the sand-only controls suggesting that organic compounds were being released from the seedlings and decomposing leaves (Table 2). During the first and second year, leachate conductivity was highest for sugar maple which also had the greatest shoot growth of the tested hardwood species. During the 1991 experiment, leachate conductivity was similar for the white oak and flowering dogwood which were higher than that for the pawpaw and the sand-only control (Kobe 1992). During the 1992 experiment, recycled leachate conductivities were consistently lower than during the 1991 experiment. One possible explanation is that recycled leachates, which were discarded at the end of the 1991 experiment, resulted in a loss of exchangeable nutrients from the donor and receiver pots that were not replaced in the 1992 experiment.

Leachate conductivity in the 1991 experiment was negatively correlated with the estimated weight of the soil core surrounding the dittany plants ($r = -0.31$, 39 df). This reinforces the conclusion that increased conductivity resulted from chemicals released from the decomposing leaves and the hardwood seedlings. The negative correlation also suggests that released compounds were being bound to the soil particles or that microorganisms within the soil core were decomposing the compounds responsible for increasing leachate conductivity.

Minor differences in leachate pH were found among the donor treatments during each growing season (Table 2). Lack of differences suggests that nutrient toxicities did not develop from the addition of nutrient solutions or continued recycling of the leachates. We have no explanation why the recycled leachate pHs were more alkaline in the 1992 experiment than the 1991 experiment. We assume that nutrients lost after discarding the recycled leachates from the 1991 experiment or washed from the donor pots when they were watered during the winter may have contributed to the increased pH of leachates in the 1992 experiment.

No differences in dittany stem height were found in the 1991 experiment in response to the donor species, density of the donor seedlings, or their interaction (Table 3). Most of the height growth occurred during the first 8 weeks and may have occurred before allelochemicals started to accumulate in the recycled leachates (Figure 2). Mean height of dittany the first year ranged from 38 cm when treated with white oak leachates to 49 cm when exposed to leachates from sand-only (Kobe and others 1992). Similar responses were observed the second year when mean height ranged from 47 cm when exposed to white oak or black walnut leachates to 52 cm when exposed to sand-only leachates. In both years, mean dittany stem height when exposed to sugar maple leachates was statistically the same as when exposed to any other leachate.

Table 2. Mean pH and conductivity of recycled leachates during the 1991 and 1992 experiments

Donor species	Donor density[1]	pH		Conductivity	
		1991	1992	1991	1992
				—uSiemens—	
Sand-only	High	7.76[2]	8.38	728	692
	Low	7.76	8.45	740	680
White oak	High	7.83	8.37	848	787
	Low	7.77	8.61	834	717
Sugar maple	High	7.77	8.42	1115	955
	Low	7.83	8.55	933	876
Dogwood	High	7.85	8.54	815	896
	Low	7.78	8.58	896	815
Pawpaw	High	7.72	—	765	—
	Low	7.62	—	712	—
Black walnut	High	—	8.40	—	764
	Low	—	8.37	—	680
5% t-test values		0.35	0.94	171	141

[1]The low densities consisted of three donor seedlings and three additions of 300 cm^2 of mature leaves of the same species to the litter layer. The high donor densities had double this amount for each donor species.
[2]Mean value of 12 samples in 1991 and 1992.

Table 3. Mean stem length, number of axillary shoots, stem dry weight, Julian date for flower initiation, and number of open flowers during week 17 for dittany plants exposed to leachates produced by six hardwoods at two plant densities

Donor species	Donor density[1]	Height		Number of lateral shoots		Stem dry weight		Flower init.	Week 17 flowers
		1991	1992	1991	1992	1991	1992	1991	1991
		— cm —		— # —		— g —		day	#
Sand-only	High	46.0[2]	50.9	4.0	12.3	7.1	13.1	183	421
	Low	48.9	52.8	6.0	12.6	8.5	13.2	198	546
White oak	High	41.7	48.5	4.4	12.6	5.9	11.9	198	418
	Low	47.5	41.0	4.6	10.1	4.3	10.2	186	206
Sugar maple	High	42.0	52.7	4.6	10.4	5.3	11.2	198	425
	Low	44.4	49.2	5.8	12.6	6.4	10.8	200	413
Dogwood	High	42.3	44.3	5.4	13.4	7.2	13.7	191	651
	Low	45.0	52.7	5.0	11.5	6.7	9.9	193	594
Pawpaw	High	45.4	—	5.0	—	8.4	—	193	757
	Low	45.3	—	5.4	—	8.0	—	194	596
Black walnut	High	—	46.2	—	4.6	—	13.5	—	—
	Low	—	48.1	—	13.7	—	11.2	—	—
5% t-test values		8.6	7.6	2.1	3.0	2.8	4.9	15	376

[1]The low densities consisted of three donor seedlings and three additions of 300 cm^2 of mature leaves of the same species to the litter layer. High donor densities had double this amount for each donor species.
[2]Mean value of 4 replications with 2 stems each in 1991 and 3 stems each in 1992.

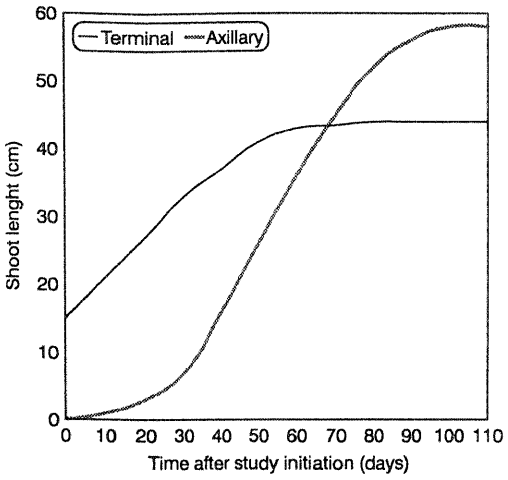

Figure 2. Average terminal and axillary shoot elongation during the first 16 weeks after initiating 1991 study.

Most of the axillary shoot growth occurred 4 to 12 weeks after initiating the study (Figure 2). We found no differences for axillary shoot growth among the donor species, their density, or possible interaction (Kobe 1992). Because axillary growth occurs later than the growth of the main stem, we had expected axillary shoot growth to be a more sensitive indicator of the increasing amounts of recycled compounds in the leachates. One problem with using axillary shoot growth from only one node near the apex to detect allelochemicals was the wide plant-to-plant variation. Future studies should measure total axillary shoot lenght at the end of the experiment or increase the number of replications to reduce the population variance.

Similar responses for height growth and axillary shoot growth were found in the 1992 experiment when pawpaw seedlings were replaced with black walnut seedlings (Table 3). Interesting, when dittany plants were exposed to leachates containing juglone, a known allelochemical of black walnut, they produced more axillary shoots per stem than dittany plants exposed to leachates from sugar maple and white oak. Again, no differences were found in dittany growth in response to leachates produced by any of the hardwood seedlings. These results further reinforce the conclusion that allelochemicals did not accumulate rapidly in the recycled leachates or that shoot growth is not a good variable for measuring dittany reponse to allelochemicals.

Exposure to leachates from both sugar maple and white oak seedlings reduced stem dry weight by the end of the first season compared with leachates from the sand-only control and the pawpaw treatment (Table 3). Responses to flowering dogwood leachates were intermediate and not different from any of the other leachates. We found that the stem dry weight of the dittany plants was positively correlated with the estimated soil core volume ($r = 0.44$, 39 df). Dittany plants with the smaller soil cores began to show nutrient deficiencies one month into the 1991 experiment. The addition of Hoagland's solution visually corrected the problem; however, the positive correlation suggests nutrient deficiencies were not fully corrected with plants still obtaining one or more essential elements from the soil core. A similar response was found after the second growing season where exposure to hardwood seedling leachates also did not result in any statistically significant differences in dittany stem dry weight.

Because shoot growth occurred relatively early in both experiments when the amount of dissolved organic compounds was still low, we chose to also examine effects of the leachates on dittany reproduction. In another study, we found that flowering on dittany normally started in the apical region of the upper shoots and rapidly moved basipetally to the lower nodes and that individiual dittany flowers remained open for approximately 12 days before wilting and abscission of the petals. We concluded that we could count flowers bi-weekly and get a reasonable estimate of total flower production.

In the 1991 experiment, minor differences were found as to the Julian date when the first flowers appeared on each plant (Table 3). Flower initiation began shortly after terminal shoot elongation stopped and before axillary shoot

elongation ceased or approximately 12 weeks after the study was initiated. Most plants had more than 500 open flowers 4 to 8 weeks after flower initiation. Analysis of the number of open flowers 17 weeks after initiating the study showed dittany plants exposed to white oak leachates had fewer flowers than dittany plants exposed to dogwood or pawpaw leachates (Table 3). The number of flowers on plants exposed to sugar maple leachates did not differ from that of any of the other hardwood leachates or sand-only control.

We estimate that many plants produced nearly 2,000 flowers over a 10-week period (Figure 3). The large number of flowers per plant in our study compared to the number of flowers found on plants under forest conditions, suggests our plants in the greenhouse were under little or no stress. No seeds were produced, so we could not determine if hardwood leachates affected seed production. It is unknown whether the high number of flowers occurred because of the excellent growing conditions or because early flowers did not set seed.

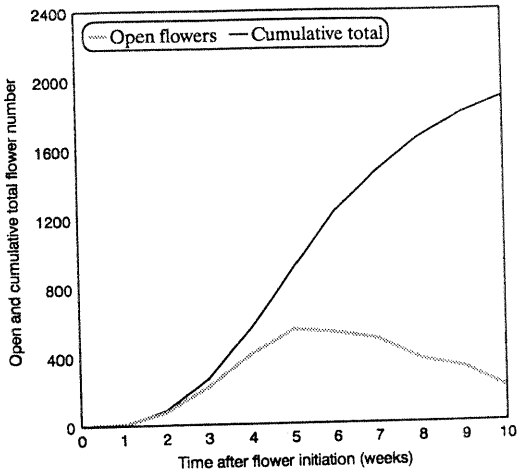

Figure 3. Number of open flowers and cumulative totals during the 10 weeks following initiation.

Exposure to leachates from several hardwoods reduced stem dry weight and altered flower production; however, doubling the number of donor seedlings did not alter these responses. There was an indication that white oak leachates were more toxic than sugar maple leachates. If, however, one or more of the hardwood species were producing allelochemicals in significant quantities, we should have observed a donor species x donor density interaction. This interaction was not detected in the 1991 or the 1992 experiment. The results of this study strongly suggest that the loss of dittany in oak-hickory forests following the invasion by sugar maple is not due to allelopathy but probably results from competition for light or the heavy accumulation of leaf litter in the stands.

In conclusion, we could not totally rule out the occurrance of allelopathic interference of hardwoods on understory forbs such as dittany. In other studies moisture and nutrient stresses have been shown to significantly affect plant responses to allelochemicals (Stowe 1979, Rink and Van Sambeek 1985, Van Sambeek and others 1996). Additional studies designed to vary light intensity or moisture availability are needed to better separate interference into its components of competition and allelopathy.

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