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Abstract

We report the influence of fertilization on the susceptibility of sweetgum (*Liquidambar styraciflua* L.) seedlings to naturally occurring insect herbivores. Thirteen-week-old potted sweetgum were placed in a pasture near the margin of a hardwood forest containing scattered sweetgum trees. Groups of 14 seedlings were treated weekly with either no (0), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentrations of 20-20-20 soluble fertilizer. Seedling performance was assessed by measuring height and leaf number and rating seedling condition throughout the 11-week experiment. Types and numbers of insect herbivores were recorded at 2- to 3-week intervals for each seedling throughout the experiment and cumulative damage was estimated for each seedling at the end of the experiment. Herbivore damage was generally light, except for weeks 2 through 5, when seven seedlings were defoliated and killed. Six of these seedlings were in the medium and high fertilizer treatments. Defoliations were due to late instar larvae of the yellowstriped armyworm (*Spodoptera ornithogalli* Gn.). Other insect herbivore species were detected, but their impacts were minor. Eleven seedlings received no detectable herbivore damage during the experiment; 10 of these received zero and low fertilizer treatments. Results suggest that the susceptibility of potted sweetgum seedlings to insect herbivore damage was associated with fertilizer concentration. This effect was not related to differences in seedling size because major defoliation events occurred before significant differences in seedling size among fertilizer treatments were detected. Yellowstriped armyworm has potential as a pest of sweetgum seedlings in intensively managed plantings.

Keywords: Herbivore-plant interactions, *Liquidambar styraciflua*, nutrient levels, short-rotation plantings, yellowstriped armyworm.

Introduction

The anticipation of an increased demand for renewable woody biomass is leading forestry into a new era of more intensive silviculture; hardwoods seem to fit this need very well (Farnum and others 1983). Large productivity gains are already being realized in forest plantations through the use of a combination of intensive management practices, including selection of superior genotypes, intensive site preparation, competition and pest control, irrigation, and fertilization (Ranney and others 1987). One of the hardwoods widely used by forest industry in intensive culture plantings is sweetgum (*Liquidambar styraciflua* L.). Although sweetgum grows more slowly than such intensively managed species as American sycamore (*Platanus occidentalis* L.) and cottonwood (*Populus* L. spp.), it appears to have relatively few insect pest problems, in spite of being host to a variety of insect herbivores such as fall webworm (*Hyphantrea cunea* Drury), luna moth (*Actias luna* L.), white-marked tussock moth (*Orgyia leucostigma* J.E. Smith), forest tent caterpillar (*Malacosoma disstria*

Hubner), gypsy moth (*Lymantria dispar* L.), a variety of tortricid and pyralid leaf-tiers/folders (*Choristoneura* spp., *Platynota* spp., *Nephoterix* spp., *Pococera* spp.), and gracillariid leafminers (*Phyllocnistis* spp.).¹

There is relatively little information on potential insect problems in intensively cultured short-rotation sweetgum plantings. It is reasonable to expect populations of certain insect herbivores to reach damaging levels as acreage planted to sweetgum increases. In addition, intensive cultural practices, including irrigation and fertilization, may affect the nutritional quality of host tissue, which could lead to or intensify insect herbivore infestations.

Materials and Methods

Study Area and Experimental Setup

Sweetgum seedlings were obtained by germinating seeds in plastic tubs of commercial potting medium (Pro-Mix™ BX) in April 1998. Seedlings were transferred after 6 weeks, each to an 11.4-L black plastic pot containing the same potting medium. After 6 weeks of acclimation, 14 potted seedlings were randomly assigned to each of 4 treatments. Treatments were application of water only (0) or the application of 20-20-20 soluble fertilizer (Peter's™; N, P, and K derived from ammonium phosphate, potassium nitrate, urea, and potassium sulfate) at 1.5 g/L (21.4 mM N; low), 3.0 g/L (42.8 mM N; medium) or 6.0 g/L (85.6 mM N; high). Initial applications were made on June 28, 1998, in the greenhouse. Solutions were applied so that the potting medium was saturated to the point of runoff. Potted seedlings were transferred on July 2 to the Winfred Thomas Agricultural Research Station (WTARS), Alabama A&M University, located approximately 8 miles north of Huntsville, AL. Subsequent applications of treatment solutions were made weekly throughout the experiment, which was terminated after 11 weeks. It was necessary during parts of August and September to water the seedlings between scheduled applications due to drought.

At WTARS, potted seedlings were placed in a pasture near the margin of a small bottomland mixed hardwood forest

¹ Ward, K. and Ward, R. 1997. Unpublished data. On file with: Alabama A&M University, P.O. Box 1208, Normal, AL 35762.

that contained scattered mature sweetgum trees. The location and time of year were considered optimum for colonization by the most common sweetgum herbivores in the area, primarily pyralid and tortricid leaf-tiers/folders, graciariid leafminers, white-marked tussock moth, and fall webworm (see footnote 1). Treatments were replicated by randomly assigning 1 seedling from each treatment group to each of 14 blocks. Blocks of four potted seedlings each were randomly aligned in a single row along the margin of the woodland. Seedlings within blocks were spaced approximately 1 m apart; blocks were spaced approximately 3 m apart. This arrangement placed all seedlings in a similar light environment and at similar distances from sources of herbivore colonization. Vegetation adjacent to pots was clipped regularly and removed to avoid excess shading. Plastic saucers were placed under pots to prevent root escape into underlying soil.

Seedling and Herbivore Damage Measurements

Seedling condition was quantitatively estimated by measuring height and counting the number of leaves at 2- to 3-week intervals. In addition, seedling condition was assessed qualitatively at 2- to 3-week intervals by evaluating relative leaf

chlorosis on a scale of 1 to 4: (1) poor (highly chlorotic), (2) fair, (3) good, and (4) excellent (no visible chlorosis).

Every 2 to 3 weeks throughout the experiment, numbers and types of insect herbivores found on seedlings were recorded, and each seedling was assigned a damage rating of 1 to 4: (1) no damage, (2) light damage (< 5 leaves damaged), (3) moderate damage (between 6 and 20 leaves damaged), and (4) heavy damage (> 20 leaves damaged). Cumulative estimates of damage were made for each seedling at the end of the experiment.

Statistical Analysis

Seedling height, number of leaves, and seedling condition as a function of fertilizer treatment were evaluated by a repeated measures analysis of variance. Cumulative herbivore damage by the end of the experiment, as related to fertilizer treatment, was assessed using a randomized complete block analysis of variance with 14 blocks. Main and interaction effects were considered significant at probability $P \leq 0.05$. The Tukey test at $P \leq 0.05$ was used to detect significant differences between means.

Table 1—Repeated measures analysis of variance for sweetgum seedling height, leaf number, and condition as related to fertilizer treatment and time since treatment initiation

Source	df	SS	MS	F-value	$P > F$ -value
Seedling height					
Fertilizer (A)	3	2,031.0	677.0	12.86	< 0.001
Time (B)	4	23,299.9	5,825.0	110.63	< 0.001
A x B	12	2,447.9	204.0	3.87	< 0.001
Residual	235	12,373.4	52.7		
Leaf number					
Fertilizer (A)	3	4,657.9	1,552.6	11.4	< 0.001
Time (B)	3	55,933.3	18,644.4	136.7	< 0.001
A x B	9	11,056.6	1,228.5	9.0	< 0.001
Residual	191	26,047.2	136.4		
Seedling condition					
Fertilizer (A)	3	73.8	24.6	58.8	< 0.001
Time (B)	4	29.4	7.4	17.6	< 0.001
A x B	12	52.9	4.4	10.5	< 0.001
Residual	234	97.9	0.4		

df = degrees of freedom; SS = sum of squares; MS = mean square; $P > F$ -value = probability of a greater F-value.

Results

Seedling Growth

Fertilizer treatment, as expected, had significant effects on seedling height and leaf number by the end of the experiment (table 1); however, significant effects did not appear

before week 8, as seedlings receiving fertilizer treatments attained significantly greater height and leaf numbers than seedlings receiving no fertilizer treatment (figs. 1 and 2). Interestingly, although not statistically significant, the medium (3.0 g/L) fertilizer treatment elicited greater height growth and added more leaves than the high (6.0 g/L) fertilizer treatment, which was similar to the low (1.5 g/L)

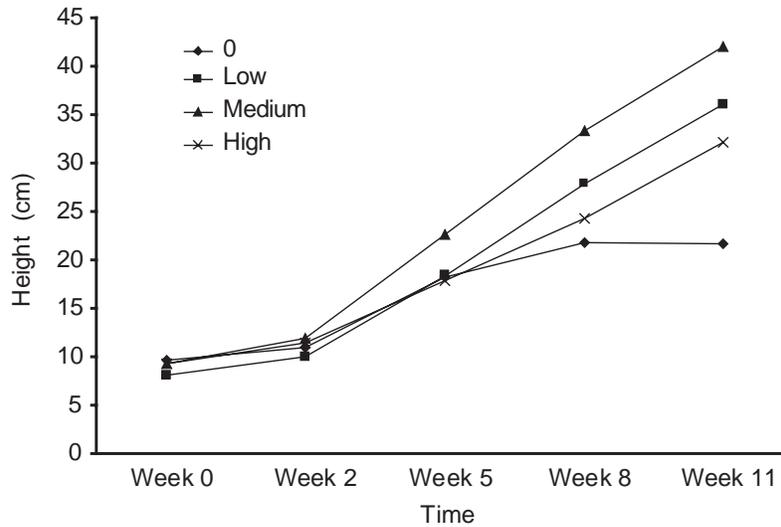


Figure 1—Sweetgum seedling height (cm) in response to fertilizer treatment over time since treatment initiation. Fertilizer treatments are application of 0 (no fertilizer), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentration of Peter's™ 20-20-20 soluble fertilizer.

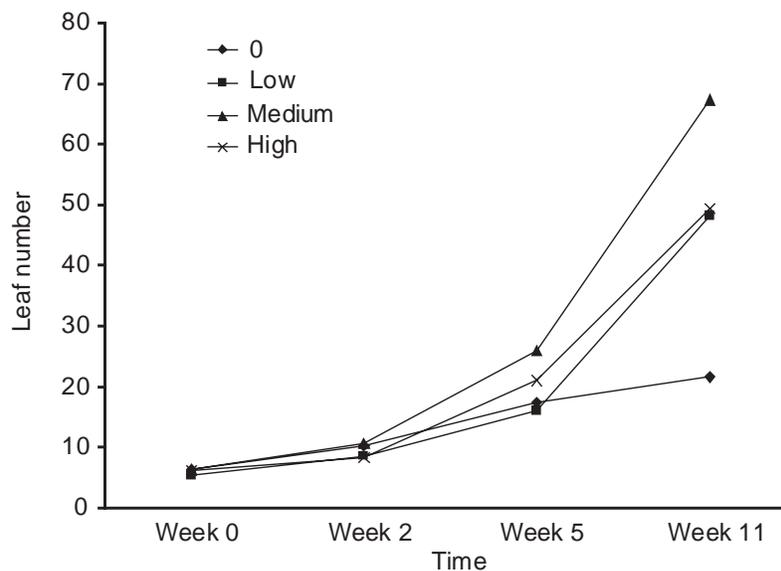


Figure 2—Sweetgum seedling leaf number in response to fertilizer treatment over time since treatment initiation. Fertilizer treatments are application of 0 (no fertilizer), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentration of Peter's™ 20-20-20 soluble fertilizer. Data are missing for week 8.

fertilizer treatment. This suggests the high fertilizer treatment may have actually been supraoptimal (Mengel and Kirkby 1982). The zero fertilizer treatment produced seedlings with dramatically fewer leaves and less height growth than any other treatment.

Seedling Condition

In general, seedling condition was also affected significantly by fertilizer treatment over the course of the experiment (table 1). Initially, seedlings in the low fertilizer treatment group had a significantly lower condition rating, but recovered to a similar level with other groups by week 2 (fig. 3). At week 5, seedling condition was significantly lower for the seedlings receiving no fertilizer, while other groups remained similar. By the end of the 11-week experiment, seedling condition was similar for the medium and high treatments and the condition of these seedlings was numerically, though not statistically, higher than the condition of seedlings receiving the low fertilizer treatment. The condition of seedlings receiving the zero fertilizer treatment was significantly lower than for any other treatment at week 11.

Herbivore Damage

Although herbivore pressure was generally light during most of the 11-week experiment, two distinctive patterns were evident. First, there was a burst of herbivore activity

during weeks 2 through 5, when seven seedlings were completely defoliated and killed (fig 4.). Of these seedlings, 33 and 57 percent received medium and high fertilizer treatments, respectively (table 2). Furthermore, defoliations occurred before significant effects of fertilizer treatment on seedling height, leaf number, and seedling condition were detected (figs. 1 through 4). In all cases, defoliation was caused by late instar larvae of the yellowstriped armyworm (*Spodoptera ornithogalli* Gn.), which were usually found on the potting medium surface of the defoliated seedlings. We were unable to find a record of sweetgum as a host for yellowstriped armyworm. However, several larvae of this species were successfully reared to adults on sweetgum foliage in the laboratory (see footnote 1). Secondly 11 seedlings received no detectable defoliation during the experiment. Of these seedlings, 64 and 27 percent were from the zero and low fertilizer treatments, respectively.

By the end of the experiment, seedlings receiving no fertilizer sustained significantly less cumulative herbivore damage than those receiving low, medium, or high fertilizer treatments (tables 2 and 3) (fig. 4). Although not significant, a trend of increased cumulative herbivore damage with higher rates of fertilization was also apparent.

In addition to yellowstriped armyworm, other insect herbivores encountered during the experiment included several unidentified noctuid and geometrid species, several species of pyralid or tortricid leaf-tiers/folders, white-marked

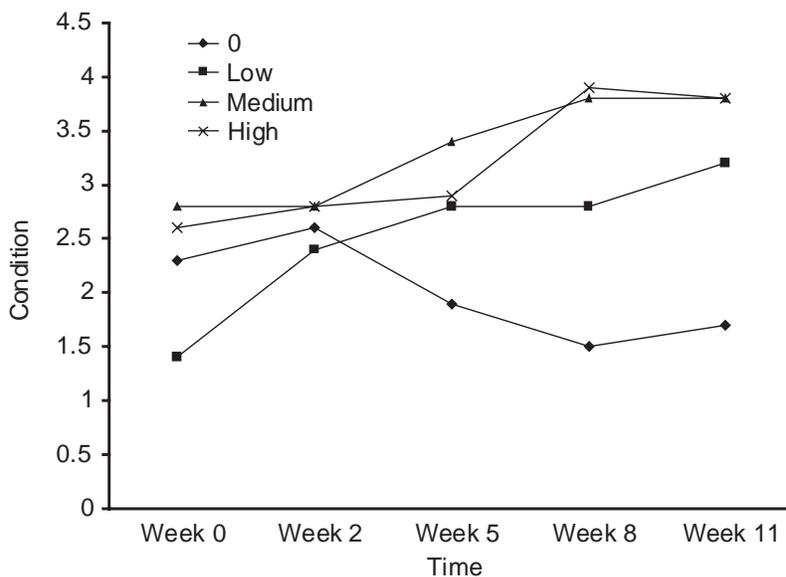


Figure 3—Sweetgum seedling condition in response to fertilizer treatment over time since treatment initiation. Fertilizer treatments are application of 0 (no fertilizer), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentration of Peter's™ 20-20-20 soluble fertilizer.

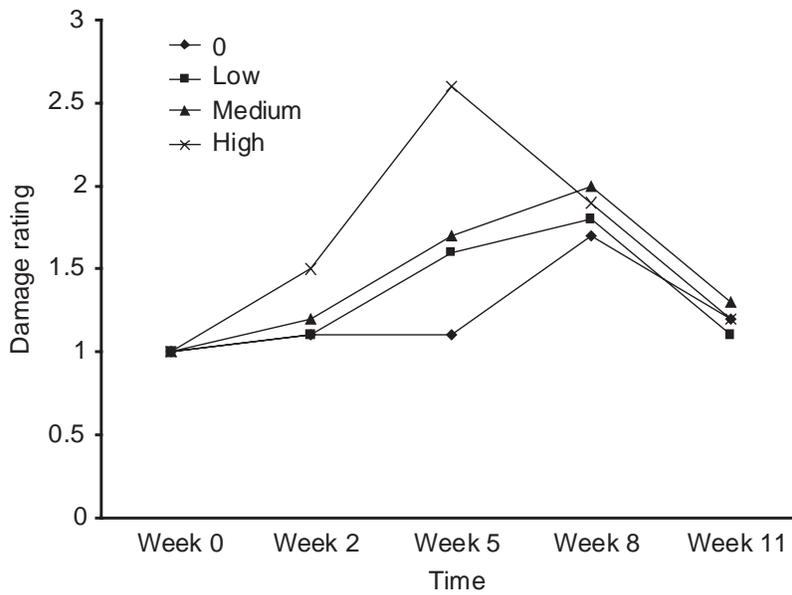


Figure 4—Sweetgum seedling herbivore damage rating in response to fertilizer treatment over time since treatment initiation. Fertilizer treatments are application of 0 (no fertilizer), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentration of Peter's™ 20-20-20 soluble fertilizer.

Table 2—Randomized complete block analysis of variance for sweetgum seedling cumulative herbivore damage as related to fertilizer treatment

Source	df	SS	MS	F-value	<i>P</i> > F-value
Block (A)	13	11.4	0.88	1.38	0.213
Fertilizer (B)	3	13.1	4.38	6.87	< 0.001
Residual	39	24.9	0.64		

df = degrees of freedom; SS = sum of squares; MS = mean square; *P* > F-value = probability of a greater F-value.

Table 3—Mean cumulative insect herbivore damage rating (standard errors in parentheses), number of potted sweetgum seedlings killed by defoliation, and number of seedlings with no defoliation at week 11, as related to fertilizer treatment^a

Fertilizer treatment ^b	Damage rating ^c	Seedlings killed by defoliation	Seedlings with no defoliation
0	1.5 (0.17)a	0	7
Low	2.1 (0.22)b	1	3
Medium	2.5 (0.20)b	2	0
High	2.7 (0.28)b	4	1

^a Cumulative insect herbivore damage ratings were 1 to 4 (1 = no foliar damage; 2 = light damage (< 5 leaves damaged); 3 = moderate damage (6 to 20 leaves damaged); 4 = heavy damage (> 20 leaves damaged).

^b Fertilizer treatments are application of 0 (no fertilizer), low (1.5 g/L), medium (3.0 g/L), or high (6.0 g/L) concentration of Peter's™ 20-20-20 soluble fertilizer.

^c Damage ratings followed by different letters are significantly different at *P* ≤ 0.05 by the Tukey test.

tussock moth, and several species of cicadellid leafhoppers. The majority (75 percent) of observed insect herbivores occurred on seedlings that received the medium and high fertilizer treatments.

Discussion

The concentration of essential nutrients in plant tissue influences interactions between insect herbivores and their host plants. As with plants, nitrogen is most often the limiting nutrient for insect herbivores (Mattson 1980). However, insects typically have a much higher nitrogen concentration in their tissues than plants (Southwood 1973). Scarcity of nitrogen-rich plant tissue may directly limit resource utilization by insect herbivores or their population density or both (Mattson 1980, White 1974). In addition, plant nitrogen may indirectly influence insect herbivore performance or population levels through effects on production of plant secondary metabolites such as terpenoids and tannins (Mattson 1980, Price 1997). Many secondary metabolites protect plants by reducing the palatability or nutritional quality of plant tissues, thus causing a decrease in insect growth and survival (Mattson 1980, Price 1997).

How insect herbivores respond to the nutrient concentration of their host depends on a variety of factors, including degree of feeding specialization, host plant species, and feeding mode, i.e., tissue chewer vs. phloem feeder. Based on fertilizer studies, a few patterns have emerged regarding the response of tree-feeding insect herbivores to host nutrient concentration. Fertilization apparently improves the quality of deciduous host trees as food for insect herbivores by increasing nutritional quality and water content which, in turn, results in enhanced larval growth and survival (Kyto and others 1996). In addition, increases in mineral nutrient availability have sometimes been associated with decreases in the foliar concentration of carbon-based defensive compounds, resulting in further increases in insect performance (Kyto and others 1996). In conifers the effect of fertilization is often more complicated; in some cases simultaneously increasing tree host nutrient content and defensive compound levels resulting in counteracting effects (Kyto and others 1996). Finally, a positive impact of fertilization on growth and survival at the level of individual insects does not necessarily translate into enhanced population growth for insect herbivores. This is attributed to impacts of fertilization on higher trophic levels such as natural enemies, which, in turn, impact insect herbivore populations (Kyto and others 1996).

Conclusions

Pressure from naturally occurring insect herbivores on potted sweetgum seedlings observed in this study appeared to be related to level of fertilization. Most observed insect herbivores occurred on seedlings receiving the highest fertilizer treatments. Major defoliation events occurred primarily on seedlings receiving the highest fertilizer treatments and cumulative herbivore damage showed a positive trend with increasing level of fertilizer. Surprisingly, the major herbivore encountered was the yellowstriped armyworm, well known as a pest of various field crops and herbaceous species, but not as a tree-feeding herbivore. This insect may have potential as a pest of seedling stage sweetgum in short-rotation plantings.

Summary

1. Herbivore pressure on potted sweetgum seedlings receiving four fertilizer treatments was observed as complete defoliation at weeks 2 through 5 and cumulative herbivore damage at week 11 which was the end of the experiment.
2. Complete defoliation of seedlings by insect herbivores at weeks 2 through 5 was not associated with seedling size and was positively related to the application and rate of fertilizer applied.
3. Insect herbivore pressure on potted sweetgum seedlings, measured as cumulative damage to foliage at week 11, was positively related to the application and rate of fertilizer applied.
4. Late instar armyworm larvae represent a potential insect pest in fertilized sweetgum plantations.

Acknowledgments

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Keywords: Herbivore-plant interactions, *Liquidambar styraciflua*, nutrient levels, short-rotation plantings, yellowstriped armyworm.



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