Agricultural and Forest Entomology

Agricultural and Forest Entomology (2010), **12**, 89–97 DOI: 10.1111/j.1461-9563.2009.00456.x

DE- AI09-00SR22188 Journal Article 2010 10-03-P

Erythroneura lawsoni abundance and feeding injury levels are influenced by foliar nutrient status in intensively managed American sycamore

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Abstract

1 Abundance and feeding injury of the leafhopper *Erythroneura lawsoni* Robinson was measured in an intensively-managed American sycamore *Platanus occidentalis* L. plantation. Trees were planted in spring 2000 in a randomized complete block design, and received one of three annual treatments: (i) fertilization (120 kg N/ha/year); (ii) irrigation (3.0 cm/week); (iii) fertilization + irrigation; or (iv) control (no treatment).

2 Foliar nutrient concentrations were significantly influenced by the treatments because only sulphur and manganese levels were not statistically greater in trees receiving fertilization.

3 Over 116 000 *E. lawsoni* were captured on sticky traps during the study. Leafhopper abundance was highest on nonfertilized trees for the majority of the season, and was positively correlated with foliar nutrient concentrations. Significant temporal variation in *E. lawsoni* abundance occurred, suggesting five discrete generations in South Carolina.

4 Significant temporal variation occurred in *E. lawsoni* foliar injury levels, with the highest injury ratings occurring in late June and August. Foliar injury was negatively correlated with foliar nutrient content, and higher levels of injury occurred more frequently on nonfertilized trees.

5 The results obtained in the present study indicated that increased *E. lawsoni* abundance occurred on trees that did not receive fertilization. Nonfertilized trees experienced greater foliar injury, suggesting that lower foliar nutrient status may have led to increased levels of compensatory feeding.

Keywords Cicadellidae, Homoptera, leaf quality, micronutrients, nitrogen, *Platanus occidentalis*, sticky trap, temporal variation.

Introduction

The existing paradigm that increased soil resource availability enhances tree resistance to insects has recently come under scrutiny. Herms (2002) suggested that fertilization actually decreases woody plant resistance to insect pests by encouraging plants to grow rather than invest resources into defensive compounds (Herms & Mattson, 1992). Fertilization increases soil nitrogen availability, which in turn promotes leaf growth and mediates host quality and availability for herbivores (Mattson, 1980; Prestidge, 1982; Altieri & Nicholls, 2003). Sucking insects generally benefit from fertilization (Kytö *et al*., 1996; Rowe *et al*., 2006). For example, the leafhopper *Carneocephala floridana* exhibited increased feeding rates and body weight on fertilized salt-marsh cord grass *Spartina alterniflora* (Rossi & Strong, 1991; Rossi *et al*., 1996), and potato leafhopper *Empoasca fabae* (Harris) oviposition and nymphal survival were positively correlated with foliar nitrogen amendments (Bentz & Townsend, 2001, 2003). Greater abundances of whiteflies (Bentz *et al*., 1995), thrips (Chau *et al*., 2005),

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aphids (Cisneros & Godfrey, 2001) and psyllids (Pfeiffer & Burts, 1983; Daugherty *et al*., 2007) have been found on fertilized plants.

Plant water stress has been suggested to influence insect performance because it increases the concentration of nutritive compounds in plant tissues (White, 1969, 1974; Mattson & Haack, 1987; Thomas & Hodkinson, 1991). However, Huberty and Denno (2004) suggested that plant water stress could be detrimental to most herbivore guilds, especially sap-feeders. Their meta-analysis of the available literature indicated that sap-feeders experienced decreased survivourship, fecundity and reduced population densities on water-stressed plants. Several studies have demonstrated the negative effects of plant water stress on the leafhoppers *E. fabae* (Hoffman & Hogg, 1991, 1992; Hoffman *et al*., 1990, 1991), *Erythroneura variabilis* (Trichilo *et al*., 1990; Daane & Williams, 2003; Costello, 2008) and *Erythroneura elegantula* (Trichilo *et al*., 1990; Costello, 2008).

Increasing tree productivity and reducing production cost is necessary for forest products to remain competitive in the current market. One way that producers aim to attain these goals is by planting intensively managed forests. Productivity gains of almost 5.7- and 2.5-fold have been realized in intensively managed pine and hardwoods, respectively (Samuelson *et al*., 2001). However, the monocultural environment can contribute to lower pest resistance compared with more diverse stands, which may lead to decreased productivity (Altieri & Nicholls, 2003; Coyle *et al*., 2005). In spring 2000, a large intensively managed forest plantation was established on the Upper Piedmont of South Carolina to measure the effects of fertilization and irrigation on tree production (Coleman *et al*., 2004). After three growing seasons, American sycamore *Platanus occidentalis* L. trees in this plantation responded positively to increased resource availability via increased biomass accumulation (Coyle & Coleman, 2005) and foliar nitrogen concentration (Allen *et al*., 2005b). *Erythroneura lawsoni* Robinson, a leafhopper specific to sycamore (McClure, 1974, 1975; McClure & Price, 1975, 1976), was very abundant in this plantation (DRC, personal observation). Sap-feeding insects have a strong preference for vigorously-growing trees (Kytö *et al*., 1996; Cornelissen *et al*., 2008). This insect–host system offered an opportunity to test the hypothesis that more vigorously growing trees (i.e. those receiving fertilization and irrigation): (i) would support higher *E. lawsoni* abundance and (ii) have higher feeding injury levels; and (iii) that foliar nutrient concentrations would be positively correlated with abundance and feeding injury.

Materials and Methods

The study location and experimental design have been reported previously (Coleman *et al*., 2004; Allen *et al*., 2005b; Coyle & Coleman, 2005) and only a brief overview is provided here.

Study location and site description

The study took place at the U.S. Department of Energy Savannah River Site, a National Environmental Research Park, located near Aiken, South Carolina, U.S.A. (33°23′N, 81°40′E). The sandy soil previously supported a pine *Pinus* spp. plantation, with an oak *Quercus* spp. understory. Between 1 April and 30 October 2003, the site received 7.5 cm of rain and temperatures were in the range 0.3–33.4°C (mean = 21.1°C).

Experimental design and silvicultural treatments

Four treatment plots were located in each of three blocks in a randomized complete block design. Bare-root, 1-0 *P. occidentalis* seedlings (open pollinated mixed orchard seed source obtained from Westvaco Corp., Summerville, South Carolina) were hand planted during the first week of February 2000. Trees were planted at 2.5 × 3 m spacing in 0.22-ha plots. Each treatment plot had 294 trees (14 rows of 21 trees) and contained a central 0.04-ha measurement plot with 54 trees (nine rows of six trees). At least four rows of trees served as a buffer between the measurement plot and adjacent treatment plots. Weed control was accomplished with a spring application of oxyfluorfen, a pre-emergence herbicide (Goal® 2XL; Dow AgroSciences LLC, Indianapolis, Indiana) and additional applications of glyphosate (Foresters'®, Riverdale Chemical Co., Burr Ridge, Illinois) as required throughout the growing season.

Beginning in 2000, treatment plots received one of the treatments: (i) fertilization (F) at 120 kg N/ha/year; (ii) irrigation (I) at 3.0 cm/week; (iii) fertilization + irrigation at the aforementioned rates (FI); or (iv) untreated control (C). Irrigated plots (I and FI) received 5 mm of water 6 days/week via an automated drip irrigation system. Fertilized plots (F and FI) received liquid fertilizer (8:8:8, N : P : K with micronutrients; Liberty Acres, Darlington, South Carolina) delivered in the 5-mm/week irrigation amendment, which was the minimum amount of water required to apply fertilizer and flush trickle tube lines. Treatments were applied equally over a 26-week period between 1 April and 30 September from 2000 to 2003. Control plots received 5 mm/week of water to maintain experimental consistency with fertilized plots.

Foliar nutrients

Foliage was collected on 6 and 30 May, 10 July and 7 August 2003 to determine concentrations of N, P, K, Ca, Mg, S, B, Fe, Mn, Cu, Zn and Al. Three leaves were collected from each of two randomly chosen trees (total of 18 leaves per plot) directly adjacent to each tree sampled for *E. lawsoni* with sticky traps (see below). Sample trees were located in the north-west, centre and south-east portions of the measurement plots, and were surrounded by at least three buffer trees in each direction. From each tree, one leaf from the lower 2 m of the tree canopy was randomly chosen from each of three cardinal directions; the cardinal directions were randomly chosen for each tree on each sample date. All leaves chosen were within the five youngest leaves on the branch. Collected leaves were pooled within plots (therefore, $n = 3$ per treatment), oven-dried at 60°C to constant weight, ground and homogenized in a Wiley mill (Arthur H. Thomas Co., Philadelphia, Pennsylvania) and submitted to a commercial laboratory for analysis (Brookside Laboratories, Inc., New Knoxville, Ohio).

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Leafhopper abundance

Yellow sticky traps were used to measure leafhopper flight activity as an indirect measure of leafhopper abundance, a method and trap colour statistically shown to be effective for leafhopper sampling (DeGooyer *et al*., 1998a). One trap (194 cm^2 of adhesive area; Seabright Laboratories, Emeryville, California) was hung 2 m above the ground on the south side of each sample tree (three per plot). This height was chosen because the majority of *E. lawsoni* feeding typically takes place on the lower 2 m of the tree canopy (McClure & Price, 1975). Sample trees were located in the north-west, centre and south-east portions of the measurement plots. On the basis on *E. fabae* sampling conducted in alfalfa, this number of traps is more than adequate for this sampling area (DeGooyer *et al*., 1998b). Traps were changed weekly, starting 2 April to 16 July, bi-weekly until 27 August, and once in September and October during the 2003 growing season. Traps were placed on the same trees throughout the study. Preliminary identification of *E. lawsoni* was performed by G. Balme (North Carolina State University, Raleigh, North Carolina). *Erythroneura lawsoni* from sticky traps were identified and counted by J. Bentz and A. Barbosa (USDA-ARS, Beltsville, Maryland).

Feeding injury

Feeding injury by *E. lawsoni*, as measured by the degree of stippling, was assessed nondestructively. Three lower canopy leaves of each sample tree were randomly selected (one leaf on each of three cardinal directions, with each leaf being one of the five youngest leaves on the branch; similar to those collected for foliar nutrient concentration) on each sticky trap collection date from 2 April to 27 August 2003, with the exception of 11 and 18 June, 23 July and 6 August. These leaves were arbitrarily rated using a visual assessment: $0 =$ no feeding injury (i.e. no stippling); $1 \leq 25\%$ feeding injury; $2 = 25–50\%$ feeding injury; $3 = 50 - 75\%$ feeding injury; $4 \leq 75\%$ feeding injury (McClure, 1974). Ratings from all three leaves per tree per plot ($n = 9$ leaves per plot) were averaged for analysis. Throughout the entire study, all feeding injury ratings were performed by the same individual to maintain experimental consistency.

Statistical analysis

Analyses were performed using the SAS software, version 9.1.3 (SAS Institute, Cary, North Carolina). For continuous variables, the Shapiro–Wilks' test for normality and boxplots (PROC UNIVARIATE) were used to test whether the distribution of residuals was statistically different from normal at $\alpha < 0.05$. Homogeneity of variances was examined using the boxplot procedure (PROC BOXPLOT).

Foliar nutrient concentrations were arcsine square root-transformed to normalize variance (Zar, 1996). The experimental design was a multi-factorial, repeated measures analysis of variance for a randomized complete block design with unequally-spaced sampling intervals. Block-by-treatment combinations were treated as the random, among-subject factor, whereas week was treated as the fixed, repeated factor. Fertilization and irrigation were treated as fixed treatment factors. Denominator degrees of freedom were computed according to the Kenward–Roger method (Kenward & Roger, 1997). Foliar nutrient concentration data were analysed individually using a repeated measures technique as described above for transformed count data rather than multivariate analysis of variance techniques because the repeated measures procedure allows for modelling the correlation within an experimental unit over time.

Leafhopper trap counts were $\log_{10}(x + 1)$-transformed before analysis to normalize variance and account for zero count data. Transformed trap capture data were then analysed using the mixed models procedure (PROC MIXED) with a design similar to that used for foliar nutrient concentrations. We analysed transformed count data using covariance structures that were appropriate for the experimental design and sampling frequency (i.e. unequally-spaced sampling periods across subjects) and selected the structure based on corrected Akaike Information Criterion (Burnham & Anderson, 1998). To investigate interactions, we performed tests of simple main effects using the SLICE option in the LSMEANS statement (Schabenberger *et al*., 2000; Littell *et al*., 1996) and compared treatment means using Fisher's least significant difference test.

Feeding injury (i.e. ordinal response with five levels) was analysed using logistic regression techniques (PROC LOGISTIC) with date, fertilization and irrigation included in the model. We began with a saturated model containing all possible interactions but a backward (reverse stepwise) selection process suggested that only the sampling date-by-fertilization interaction and main effects adequately explained the greatest amount of variability in the dependent variable data. Data were further examined using the frequency procedure (PROC FREQ) to test whether frequencies within feeding injury levels differed significantly among treatments.

Spearman correlation (PROC CORR) and canonical correlations (PROC CANCORR) were performed to assess the overall relationship between *E. lawsoni* abundance, feeding injury level and foliar nutrient concentration. Foliage sampled on 6 May, 30 May, 10 July and 7 August was paired with *E. lawsoni* abundance and injury data on 7 May, 28 May, 9 July and 6 August, respectively. We ran multiple correlations to determine whether relationships with insect activity were stronger using all nutrients individually, paired combinations of N, P and K, or if the entire group of foliar nutrients together improved the relationship.

Results

Foliar nutrients

All foliar element amounts except Fe changed significantly over the course of the growing season (Table 1). Concentrations of N, P, K and Cu decreased over the growing season but Mg increased. Foliar concentrations of Ca, S, B, Mn and Al peaked on 30 May, whereas Zn levels dropped to their lowest level in July before increasing again. Fertilization and irrigation significantly influenced many foliar nutrient concentrations (Table 1). Foliar N, K, B, Fe, Mn, Zn and Al levels were greater on trees receiving fertilization, whereas nonfertilized trees exhibited greater levels of foliar Mg and S. Trees receiving irrigation had greater levels of foliar K, Mg and Cu. The only

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Table 1 Mean ± SE foliar nutrient content of *Platanus occidentalis* study trees averaged over all treatments during the 2003 growing season at the Savannah River Site in South Carolina

	Foliar element					
Sample date	N (%)	P (%)	K (%)	Ca (%)	Mg (%)	S (%)
May 6	2.26 ± 0.09[a]	0.15 ± 0.01[a]	0.92 ± 0.07[a]	0.79 ± 0.03[c]	0.33 ± 0.01[b]	0.30 ± 0.01[bc]
30 May	1.80 ± 0.08[b]	0.13 ± 0.01[b]	0.70 ± 0.05[b]	1.30 ± 0.03[a]	0.51 ± 0.02[a]	0.41 ± 0.03[a]
10 July	1.38 ± 0.06[c]	0.10 ± 0.00[c]	0.54 ± 0.04[c]	1.21 ± 0.03[ab]	0.48 ± 0.02[a]	0.34 ± 0.02[b]
7 August	1.46 ± 0.05[c]	0.11 ± 0.00[c]	0.51 ± 0.03[c]	1.16 ± 0.05[b]	0.50 ± 0.02[a]	0.29 ± 0.01[c]
Effect						
Time (T)	<0.0001	<0.0001	0.0002	<0.0001	<0.0001	0.0012
Fertilization (F)	0.0005	0.2163	0.0002	0.0929	0.0030	0.0039
T × F	0.7078	0.2634	0.8812	0.4355	0.3118	0.2886
Irrigation (I)	0.0703	0.2027	0.0091	0.1814	0.0154	0.1666
T × I	0.4380	0.7731	0.3421	0.8642	0.3750	0.5877
F × I	0.4556	0.3042	0.6665	0.6212	0.0072	0.7203
T × F × I	0.3860	0.4424	0.1096	0.9757	0.9434	0.1673
Sample date	B (p.p.m.)	Fe (p.p.m.)	Mn (p.p.m.)	Cu (p.p.m.)	Zn (p.p.m.)	Al (p.p.m.)
6 May	23.1 ± 1.1[c]	63.0 ± 3.7	241.2 ± 19.6[b]	9.3 ± 1.4[a]	17.5 ± 0.8[a]	73.4 ± 5.2[c]
30 May	34.3 ± 2.8[a]	69.4 ± 3.4	363.4 ± 32.0[a]	6.8 ± 0.4[b]	16.0 ± 0.9[ab]	124.7 ± 9.4[a]
10 July	30.5 ± 2.3[ab]	70.5 ± 5.6	327.6 ± 24.4[a]	5.3 ± 0.4[b]	14.5 ± 0.8[b]	91.6 ± 5.5[b]
August 7	28.8 ± 1.7[b]	64.6 ± 4.6	259.0 ± 30.9[b]	5.2 ± 0.2[b]	16.3 ± 0.7[a]	96.1 ± 6.4[b]
Effect						
Time (T)	0.0044	0.2279	< 0.0001	0.0005	0.0027	0.0011
Fertilization (F)	0.0034	0.0057	0.0009	0.3951	0.0484	0.0497
T × F	0.3003	0.9994	0.1136	0.7195	0.3173	0.9449
Irrigation (I)	0.1600	0.1964	0.2014	0.0006	0.1071	0.7396
T × I	0.3474	0.0777	0.8178	0.0313	0.4993	0.7136
F × I	0.3836	0.6340	0.4108	0.9487	0.6678	0.0992
T × F × I	0.4782	0.2720	0.4043	0.1983	0.0295	0.3488

For each element, means sharing the same superscript letter are not significantly different ($P < 0.05$). The P-values for the main effects and their interactions are presented below each element.

nutrient concentrations not influenced by any silvicultural treatment were P and Ca (Table 1).

Leafhopper abundance

A total of 116 468 *E. lawsoni* were captured during the study. Fertilization but not irrigation ($F_{1,27.2} = 0.02$, $P = 0.8947$) significantly influenced *E. lawsoni* abundance, although the fertilization effect was dependent upon week (week × fertilization interaction; $F_{17,17.9} = 3.31$, $P = 0.0079$) (Fig. 1). When a fertilization effect occurred, nonfertilized trees had higher *E. lawsoni* abundance on sticky cards except during the first sample period and one period late in the growing season, when the pattern was reversed (Fig. 1). Abundance varied significantly among weeks ($F_{17,17.9} = 56.13$, $P < 0.0001$) regardless of fertilization and irrigation (Fig. 1).

Erythroneura lawsoni abundance was significantly but weakly positively correlated with feeding injury (Spearman correlation = 0.4305, $P = 0.0023$). There was no significant relationship between *E. lawsoni* abundance and foliar NPK levels (canonical correlation = −0.1537, $P = 0.0953$). When all foliar elements were considered, however, a strong negative relationship was detected (canonical correlation = −0.7347, $P = 0.0022$). As the overall foliar element concentrations declined, *E. lawsoni* abundance increased. Relationships between *E. lawsoni* abundance and individual foliar elements were variable, although, when significant, foliar elements were often negatively correlated with abundance (Table 2). Sulphur was the only element to have a positive correlation with *E. lawsoni* abundance (Table 2). The only foliar elements that did not have a significant relationship with *E. lawsoni* abundance at any point during the study were Mg, Fe, Cu and Zn.

Feeding injury

Overall rates of feeding injury were generally low, primarily falling in categories 1 and 2 (Table 3). Fertilization and irrigation ($\chi^2 = 5.80$, d.f. = 1, $P = 0.0161$) significantly influenced feeding injury but the fertilization effect was dependent upon week (fertilization × week interaction; $\chi^2 = 9.21$, d.f. = 1, $P = 0.0024$). There were few significant differences among feeding injury level frequencies, which showed no discernable pattern (Table 3). Feeding injury increased during the growing season but decreased at the end of the season in nonfertilized trees (Fig. 2). However, the overall effect of feeding injury for a given date was often a combination of different feeding injury levels based on fertilization treatment. No fertilization-related differences occurred on 47% of the observations.

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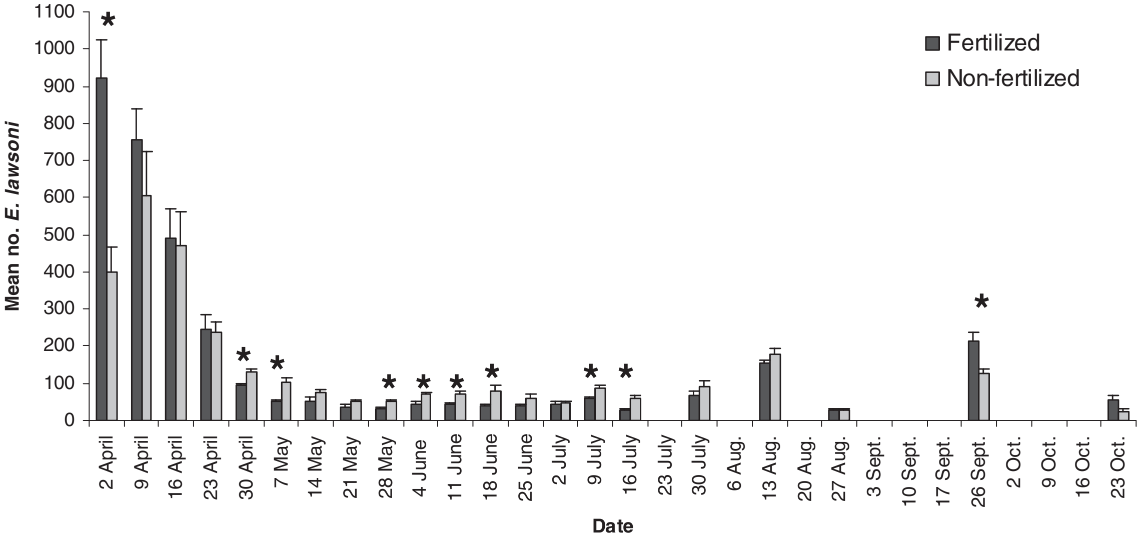

Figure 1 *Erythroneura lawsoni* abundance (mean ± SE) on *Platanus occidentalis* trees during the 2003 growing season in South Carolina. *Significant difference ($P < 0.05$) between fertilized and nonfertilized trees within a sampling period.

Table 2 Relationships among foliar elements and *Erythroneura lawsoni* abundance on four dates during the 2003 growing season

	Sample date							
	7 May		30 May		10 July		7 August	
Foliar element	Spearman correlation	*P*	Spearman correlation	*P*	Spearman correlation	*P*	Spearman correlation	*P*
N	−0.154	0.6331	−0.473	0.1206	−0.796	0.0019	−0.329	0.2960
P	−0.333	0.2897	−0.548	0.0649	−0.676	0.0158	−0.608	0.0358
K	−0.049	0.8779	−0.319	0.3117	−0.832	0.0008	−0.133	0.6806
Ca	0.042	0.8970	−0.241	0.4509	−0.209	0.5149	−0.816	0.0012
Mg	0.284	0.3715	−0.054	0.8665	0.356	0.2559	−0.018	0.9569
S	0.259	0.4168	0.365	0.2435	0.662	0.0190	0.042	0.8970
B	−0.158	0.6247	−0.380	0.2236	−0.648	0.0227	−0.459	0.1335
Fe	0.056	0.8629	−0.354	0.2584	−0.463	0.1294	−0.515	0.0867
Mn	−0.385	0.2170	−0.733	0.0066	−0.795	0.0022	−0.601	0.0386
Cu	0.277	0.3831	0.053	0.8705	−0.211	0.5111	0.028	0.9309
Zn	−0.172	0.5931	−0.175	0.5855	−0.357	0.2542	0.228	0.4759
Al	−0.606	0.0368	−0.130	0.6876	−0.483	0.1114	−0.434	0.1591

Nonfertilized trees experienced greater levels of injury on 40% of the observations, whereas fertilized trees experienced greater levels of injury on only the final two observations (i.e. 13% of observations). Nonfertilized trees had a significantly greater number of foliar injury level 2 ratings on 4 June ($\chi^2 = 7.00$, d.f. = 1, $P = 0.0082$). When feeding injury from both treatments was considered together, there was a positive linear relationship between time and injury level (Fig. 2).

Feeding injury by *E. lawsoni* was negatively correlated with foliar NPK levels (canonical correlation = −0.5238, $P = 0.0026$), although this relationship was greatly improved by including all foliar nutrients in the analysis concomitantly (canonical correlation = −0.7585, $P = 0.0007$). Only B, Mn and Zn had any significant relationship with *E. lawsoni* feeding injury during the study, and the occurrence of this relationship was intermittent at best (Table 4). In general, feeding injury increased as foliar concentrations of B, Mn and Zn increased.

Discussion

The data obtained in the present study only partially supported our hypothesis that the highest *E. lawsoni* abundance would be on trees receiving fertilization and irrigation amendments. Fertilization appeared to be the primary driver of *E. lawsoni* abundance, yet abundance was not consistently higher on fertilized trees throughout the entire growing season: other than the beginning and end of the growing season, nonfertilized trees almost always had higher *E. lawsoni* abundance. Irrigation did not affect *E. lawsoni* abundance in the present study. Prior to late August, nonfertilized trees consistently had higher levels of *E. lawsoni*. Early spring and fall *E. lawsoni* abundance was highest on fertilized trees, possibly because those trees were the first to leaf out and last to senesce. *Erythroneura lawsoni* abundance was low during the summer compared with spring and fall but was highest on nonfertilized trees. We found a

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Table 3 Distribution of *Erythroneura lawsoni* feeding injury levels on *Platanus occidentalis* leaves during the 2003 growing season in South Carolina

	Stippling level				
Silvicultural treatment	0	1	2	3	4
No fertilization	42	420	235	106	61
Fertilization	41	483	204	85	51
χ^2	0.0120	4.3954	2.1891	2.3089	0.8929
P	0.9126	0.0360	0.1390	0.1286	0.3447
No irrigation	50	468	194	98	54
Irrigation	33	435	245	93	58
χ^2	3.4819	1.2060	5.9248	0.1309	0.1429
P	0.0620	0.2721	0.0149	0.7175	0.7055

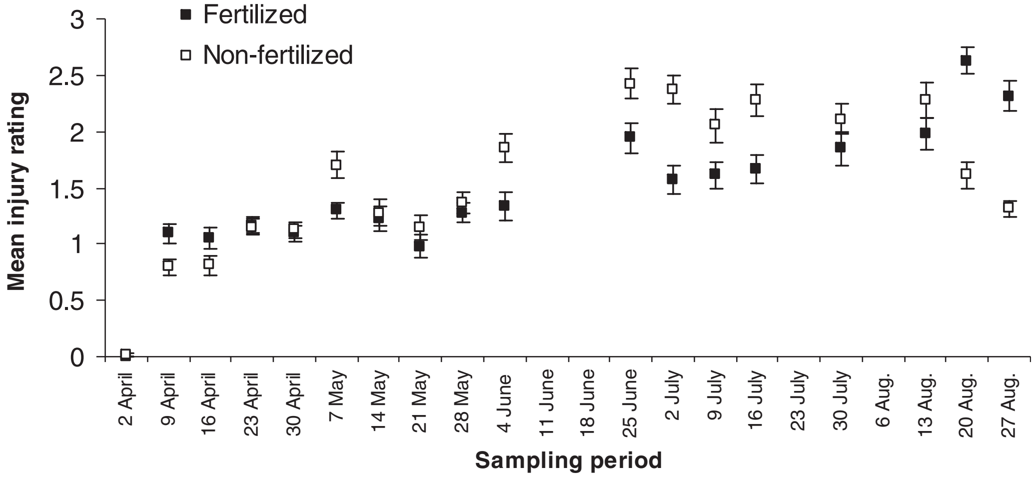

Figure 2 Mean *Erythroneura lawsoni* injury ratings (on a 0–4 scale) on lower canopy *Platanus occidentalis* foliage during the 2003 growing season in South Carolina.

positive relationship between total foliar nutrient concentrations and *E. lawsoni* abundance. This relationship has been shown for many sap-feeding insects, including leafhoppers (Prestidge, 1982; Rossi *et al*., 1996), planthoppers (Prestidge, 1982; Stiling *et al*., 1991; Stiling & Moon, 2005), whiteflies (Bentz *et al*., 1995; Bi *et al*., 2003), aphids (Cisneros & Godfrey, 2001; Davies *et al*., 2004), psyllids (Pfeiffer & Burts, 1983) and thrips (Brodbeck *et al*., 2001; Stavisky *et al*., 2002). Nitrogen is a limiting factor for insect development (Mattson, 1980) and is often elevated in plants receiving fertilization (Allen *et al*.,

Table 4 Relationships among foliar elements and *Erythroneura lawsoni* foliar injury on four dates during the 2003 growing season

	Sample date							
	7 May		30 May		10 July		7 August	
Foliar element	Spearman correlation	*P*	Spearman correlation	*P*	Spearman correlation	*P*	Spearman correlation	*P*
N	−0.575	0.0507	−0.007	0.9826	−0.523	0.0810	−0.207	0.5192
P	−0.324	0.3044	−0.325	0.3025	−0.095	0.7684	0.229	0.4735
K	−0.553	0.0621	0.011	0.9740	−0.438	0.1542	−0.229	0.4735
Ca	−0.227	0.4781	−0.452	0.1399	−0.081	0.8017	0.025	0.9392
Mg	0.398	0.2002	−0.041	0.9002	0.509	0.0911	0.203	0.5265
S	0.241	0.4502	−0.272	0.3931	0.427	0.1664	0.363	0.2457
B	−0.782	0.0027	0.306	0.3340	−0.187	0.5607	−0.159	0.6216
Fe	−0.078	0.8095	0.123	0.7023	−0.378	0.2256	−0.322	0.3081
Mn	−0.582	0.0473	−0.138	0.6698	−0.656	0.0205	−0.289	0.3618
Cu	−0.061	0.8518	0.039	0.9044	0.061	0.8516	0.392	0.2078
Zn	−0.676	0.0158	0.021	0.9479	−0.236	0.4596	−0.179	0.5783
Al	−0.306	0.3342	0.109	0.7351	−0.021	0.9479	0.102	0.7517

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2005a). However, trace nutrients can be essential for leafhopper development, as demonstrated by *Macrosteles fascifrons* (Hou & Brooks, 1978). The study by Hou & Brooks (1978) highlights the importance of including micronutrients because N, P and K are most commonly highlighted in studies regarding insect–host relationships as well as insect pest management in cropping systems.

One week after each peak in *E. lawsoni* trap captures, we observed an increase in stippling injury, specifically on 7 May, 25 June, 16 July and 20 August. This may have been the result of a delayed appearance of the stippling injury, leading to a lag in visual detection compared with *E. lawsoni* abundance. We could not find any mention of this phenomenon in the avaiable literature.

We expected *E. lawsoni* foliar injury levels to be positively correlated with foliar nutrient levels. There are many examples of fertilization leading to increased foliar injury as caused by a wide variety of insect pests (Kytö *et al*., 1996; Herms, 2002). We found a negative relationship between foliar nutrient concentration, and certain elements in particular (Tables 2 and 4), with *E. lawsoni* abundance and feeding injury. One hypothesis is that *E. lawsoni* could have been forced into compensatory feeding on lower quality leaves, thus causing a greater amount of feeding injury to these leaves. This was demonstrated in a study using the pear psylla *Cacopsylla pyricola* (Pfeiffer & Burts, 1984) because increased feeding rates and honeydew production occurred on nonfertilized plants. Psyllids had to consume greater amounts of fluid to obtain the necessary nutrition. This appears to agree with our findings in that we found a greater frequency of highly injured leaves on nonfertilized trees. Another possible explanation is that N, and foliar nutrients as a whole, are beneficial to an insect up to a certain level only. Beyond this point, phloem with high solute concentrations may become too saturated for leafhoppers to effectively break down, resulting in poor feeding efficiency and mild toxicity to the insect. Studies with artificial diets of other insects indicate that diets consisting of balanced amino acid profiles are more efficiently metabolized (Dadd, 1985). High proportions of a single amino acid in the diet of insects may be unusable or even toxic (Brodbeck & Strong, 1987). For example, the pea aphid *Acyrthosiphon pisum* (Harris) showed decreased survival and fecundity above optimal levels of sugar solute concentrations (Douglas *et al*., 2006). We did not test any of these parameters in our study, however, and are unable to substantiate this hypothesis.

In conclusion, the available literature on *E. lawsoni*, especially in sycamore, is scarce. Basic information regarding the economic injury level of *E. lawsoni* on intensively-managed sycamore, whether or not sycamore employs resistance or tolerance mechanisms to *E. lawsoni* feeding, and how tree development relates to susceptibility to *E. lawsoni*, is still lacking. This study is the first that we are aware of to examine the relationships among *E. lawsoni* abundance, injury and the amount of macro- and micronutrients present in sycamore leaves. Other leafhoppers exhibited a positive relationship between abundance and injury (Allen *et al*., 1940; Murray *et al*., 2001); this result was not unexpected.

The question of how much *E. lawsoni* injury is detrimental to sycamore production remains unanswered and, in general, the effect of sap-feeding arthropod injury on hardwoods is sparse. Population densities of ten sycamore aphids *Drepanosiphum platanoides* (Schr.) per leaf resulted in a 62% reduction in *Acer pseudoplatanus* woody biomass accumulation in seedlings, as well as significantly reduced leaf area and weight (Dixon, 1971b). Lime aphid *Eucallipterus tiliae* L. infestations in lime *Tilia* × *vulgaris* saplings can result in earlier leaf senescence and reduce woody biomass production by 92% (Dixon, 1971a). Presumably, the large trees in this study could tolerate moderate amounts of injury, although even small amounts of injury can result in economic damage in some crops (Martinson *et al*., 1997) and on some individuals because many hardwood trees exhibit genotypic differences in their susceptibility to sucking insects (Bentz & Townsend, 1999; Coyle *et al*., 2005).

Intensive management practices, such as fertilization and irrigation, which are meant to increase productivity, may also contribute to a reduction in natural tree defense to herbivores. In the present study, fertilization increased foliar nutrient levels but did not contribute to higher *E. lawsoni* populations. Productivity benefits gained from fertilization may very well offset the negative impacts of feeding by *E. lawsoni*. The results obtained in the present study could be used in management programmes for intensively managed hardwood crops. By altering foliar chemistry via fertilization, it may be possible to decrease palatability to insects without sacrificing productivity.

Acknowledgements

Partial funding was provided by the U.S. Department of Energy-Savannah River Operations office through the USDA-Forest Service Savannah River and the Forest Service Southern Research Station under Interagency Agreement DE-IA09-76SR00056. We thank M. Coleman and J. Blake (USDA Forest Service) for project support, as well as A. Slack and M. Hall (USDA Forest Service) and A. Barbosa (USDA, ARS, USNA, FNPRU) for technical assistance. This project was conducted as part of the Short Rotation Woody Crops Cooperative Research Program (USDA Forest Service, Southern Research Station). This manuscript was improved by the comments of R. Groves (University of Wisconsin), R. Zalesny (USDA Forest Service, North Central Research Station), C. Sadof (Purdue University), D. Herms (The Ohio State University) and P. Weston (Cornell University). This article reports the results of research only. Mention of a commercial or proprietary product does not constitute an endorsement or a recommendation by the USDA for its use.

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Accepted 30 June 2009
First published online 22 October 2009

