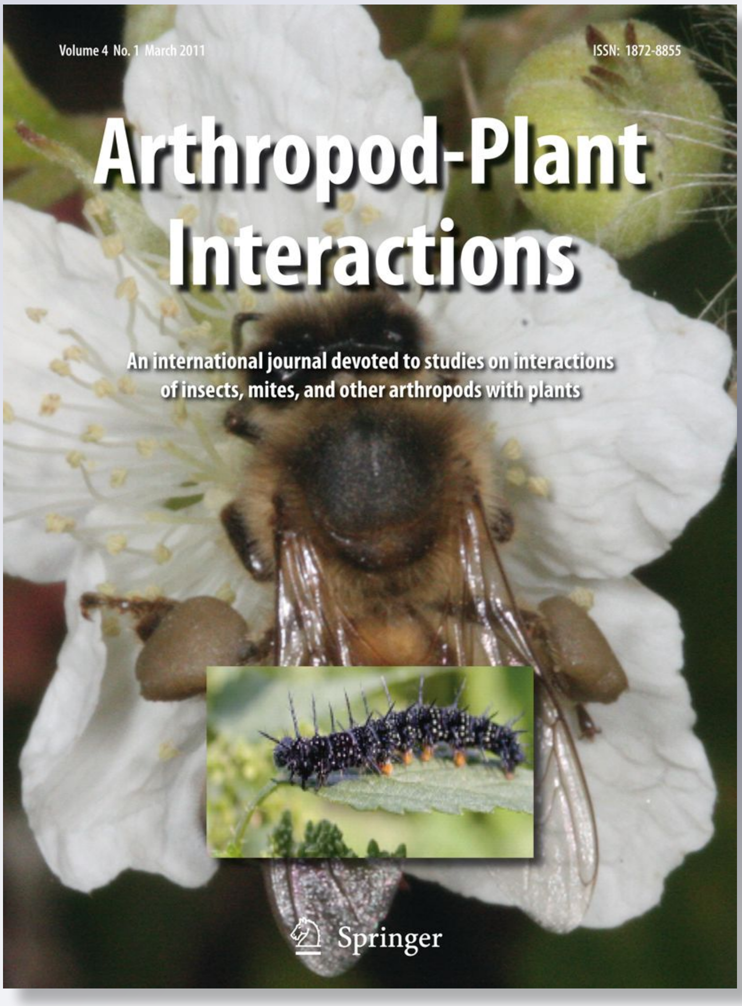
Interactive effects of light environment and herbivory on growth and productivity of an invasive annual vine, Persicaria perfoliata

Judith Hough-Goldstein & Shane J. LaCoss

Arthropod-Plant Interactions
An international journal devoted to studies on interactions of insects, mites, and other arthropods with plants

ISSN 1872-8855
Volume 6
Number 1

Arthropod-Plant Interactions (2012) 6:103-112
DOI 10.1007/s11829-011-9158-z



Arthropod-Plant Interactions (2012) 6:103–112
DOI 10.1007/s11829-011-9158-z

ORIGINAL PAPER

Interactive effects of light environment and herbivory on growth and productivity of an invasive annual vine, *Persicaria perfoliata*

Judith Hough-Goldstein · Shane J. LaCoss

Received: 28 March 2011 / Accepted: 15 September 2011 / Published online: 15 October 2011

Abstract Plant populations often exist in spatially heterogeneous environments with varying light levels, which can affect plant growth directly through resource availability or indirectly by altering behavior or success of herbivores. The plant vigor hypothesis predicts that herbivores are more likely to attack vigorously growing plants than those that are suppressed, for example in more shaded conditions. Plant tolerance of herbivory can also vary under contrasting resource availability. Observations suggest that damage by *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), introduced into the United States in 2004 as a biological control agent for mile-a-minute weed (*Persicaria perfoliata* [L.] H. Gross), is greater in the sun than in shade. We compared weevil densities and plant growth in paired plots in full sun or under shade cloth; a second experiment included insecticide-treated plots in sun and shade, to assess the ability of the plant to compensate for herbivore damage. Greater density of weevils and more node damage (indicating internal larval feeding) were found on *P. perfoliata* plants growing in sun than on those in shade. Nodes were 14% thicker in the sun, which may have provided better larval habitat. Biomass produced by plants without weevils in the sun was about twice that produced in any other treatment. Herbivory had a greater effect on plant growth in the high-light environment than in the shade, apparently because of movement into the sun and increased feeding there by the monophagous herbivore, *R. latipes*. Results support the plant vigor hypothesis and suggest that high weevil densities in the sunny habitats favored by *P. perfoliata* can suppress plant growth, negating the resource advantage to plants growing in the sun.

Keywords *Persicaria perfoliata* · *Polygonum perfoliatum* · *Rhinoncomimus latipes* · Weed biological control · Light

Introduction

Plant populations often exist in spatially heterogeneous environments with varying amounts of shade. Light level can affect plant growth directly through effects on light energy resource availability (Pierson et al. 1990; Lechowicz and Bell 1991; Lentz and Cipollini 1998) or indirectly by altering behavior or success of biotic agents, such as herbivores or their natural enemies (Bach 1984; Lincoln and Mooney 1984; Rodriguez et al. 1994). Among many hypotheses that attempt to explain the patterns of attack by herbivorous insects, the plant vigor hypothesis (Price 1991) has gained strong support (Cornelissen et al. 2008). This hypothesis predicts that insect herbivores will preferentially choose larger, more vigorously growing plants and that offspring will be more successful on these more vigorous plants. Price (1991) further predicted that herbivore species closely involved in the process of plant growth, such as plant-galling and shoot-boring insects, would conform closely to the plant vigor hypothesis. Females of such species should evolve oviposition behaviors that

Handling Editor: Gimme Walter.

J. Hough-Goldstein (✉)
Department of Entomology and Wildlife Ecology,
University of Delaware, Newark, DE 19716-2160, USA
e-mail: jhough@udel.edu

Present Address:
S. J. LaCoss
DuPont Experimental Station, Building E357 Room 1024H,
Route 141, Henry Clay Rd., Wilmington, DE 19880, USA

maximize larval performance; this preference–performance hypothesis has also gained strong empirical support (Gripenberg et al. 2010). The plant vigor hypothesis is often contrasted with the plant stress hypothesis, which posits that stressed plants are more beneficial to herbivores than vigorous plants (White 1974, 1984; Larsson 1989; Koricheva et al. 1998). The appropriate hypothesis may differ depending on the life cycle of the insect in question, with flush feeders, insects that feed on new growth, doing better on vigorously growing plants, and insects that feed on fully mature and senescing foliage responding positively to plant stress (White 2009).

The impact of herbivory on individual plants and on plant populations can vary dramatically among microhabitats and along the gradients of environmental conditions (Harper 1969; Louda and Rodman 1996; Miller et al. 2009), with variation observed in palatability of plants grown in different environments (Guerra et al. 2010), with abundance of herbivores in different habitats (Salgado-Luarte and Gianoli 2010) and also in tolerance of plants to a given amount of herbivore damage. The compensatory continuum hypothesis (Maschinski and Whitham 1989), as modified by Wise and Abrahamson (2005, 2007), suggests that when a focal resource limits plant performance and is affected by herbivory, then the plants will tolerate herbivory better under conditions where that resource is present at higher levels.

If variation in herbivore abundance, damage levels, or plant tolerance consistently reduces the success of a plant in one part of its range or under one set of environmental conditions but not another, this can contribute to observed plant distributions. For example, Huffaker and Kennett (1959) stated that *Hypericum perforatum* L. (St. Johnswort) was suppressed in sunny open areas but not in the shade because the beetles introduced for its control, *Chrysolina quadrigemina* (Suffrian), "do not achieve full success under shade," and "shun heavy shade for sunnier locations" when laying their eggs. Experiments and observations subsequently provided evidence of beetle preference for laying eggs in open sunny areas rather than in shade (Clark 1953; Huffaker 1967). This interaction has been cited as a classic example of the influence of herbivory on plant distribution, which might otherwise be attributed to plant preference for shade (e.g., Maron and Vilà 2007).

More recently, Miller et al. (2009) showed that the tree cholla cactus, *Opuntia imbricata* (Haw.) D.C., is restricted to high elevations because of reduced herbivory there compared with that found at lower elevations. Insect herbivory was also shown to be an important factor in determining the distribution of bittercress (*Cardamine cordifolia* A. Gray), a native crucifer found mostly in the shade (Louda and Rodman 1996). Artificially exposing this plant species to sun increased herbivory, leading to lower plant density, while insecticide treatment led to equivalent growth in sun and shade. Salgado-Luarte and Gianoli (2010) reported more herbivores and greater damage to seedlings of a temperate rainforest tree, *Embothrium coccineum* J.R. Forst, growing in the sun than in shade, but also greater tolerance to herbivory in the sun, apparently contributing to higher populations of seedlings in the sun. High rates of herbivory in the sun were also found by Norghauer et al. (2008) for seedlings of a neotropical tree, *Swietenia macrophylla* (King).

The annual vine *Persicaria perfoliata* (L.) H. Gross (Polygonales: Polygonaceae), or mile-a-minute weed, is a non-native invasive plant in the eastern United States, often found in light-intense areas. *Persicaria perfoliata* was accidentally introduced in southeastern PA, USA, in the 1930s (Moul 1948) and has been expanding its range since then. It is currently found in 12 states in North America (Lake et al. 2011), most recently North Carolina (Poindexter 2010). Throughout its North American range, mile-a-minute weed can form dense monocultures, inhibiting both commercial reforestation and natural forest regeneration, interfering with recreational use of natural areas, reducing quality wildlife habitat and potentially reducing populations of native flora (Mountain 1989; McCormick and Hartwig 1995; Wu et al. 2002; Hough-Goldstein et al. 2008a). It is primarily riparian in its native range of Asia (Hyatt and Araki 2006). In North America, *P. perfoliata* grows in full sun or partial shade, with typical habitats including roadsides, edges of woods, reforestation clear-cuts and stream banks (Cusick and Ortt 1987; Mountain 1989; Wu et al. 2002). Its vining habit suggests that it is adapted to high-light environments, and single isolated plants in field cages produced 5.5 times as much biomass and 4.4 times as many seeds in full sun compared to partial sun or shade (Hough-Goldstein 2008).

The host-specific weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), was introduced into North America in 2004 as part of a biological control program targeting *P. perfoliata* (Colpetzer et al. 2004a; Ding et al. 2004; Hough-Goldstein et al. 2008a, 2009; Frye et al. 2010). This insect feeds on *P. perfoliata* leaves as an adult, chewing characteristic small round holes, and its larvae develop internally in *P. perfoliata* plant stems. Observations and limited data suggest that both adult and larval damage by *R. latipes* may be greater on *P. perfoliata* plants growing in sun than on plants growing in shade. For example, an open meadow near West Chester, PA, was observed to have considerable mile-a-minute, heavily eaten by *R. latipes*, in 2007, while there was little or no weevil feeding on mile-a-minute in a nearby woodland edge that year (personal communication, R. Lighty, former director, Mt. Cuba Center for the Study of Piedmont Flora, Greenville, DE). In July 2010, however, only a few heavily damaged *P. perfoliata* plants remained in full sun at this site, and weevils were present and feeding on the more abundant plants in the shade (personal observation, JHG). At another site, plant terminals collected in full sun in White Clay Creek State Park, DE, in July 2010 had much higher weevil damage and almost five times as many damaged nodes, indicating larval feeding, compared with nearby plants in full shade (unpublished data, JHG).

In addition to allowing the assessment of interactive effects of biotic and abiotic factors, a better understanding of insect populations and impacts on mile-a-minute weed under different environmental conditions is important for predicting the potential for success of the biological control program in different areas. The impacts of the weevils on *P. perfoliata* have been studied in field cages (Hough-Goldstein et al. 2008b), where they delayed seed production, stunted plants by causing loss of apical dominance, and contributed to plant mortality in the presence of competing vegetation. Monitored weevil release sites have shown substantial reductions in spring seedling densities of the weed within one to 3 years in some areas (Hough-Goldstein et al. 2009). As the plant invades additional areas, it will be important to be able to predict habitats where biological control with *R. latipes* will be effective and those where additional control methods may be needed.

Here, both plants and weevils were studied in the field under shade (artificially applied) and full sun conditions, to test the hypothesis that *R. latipes* is more abundant and damaging on vigorously growing plants in full sun. In a second field experiment, sun and shade conditions were applied to *P. perfoliata* with abundant *R. latipes* present and also to plots with weevils eliminated using insecticide. Our prediction for both experiments was that weevils would feed and oviposit more on plants in the sun. The fully factorial design of the second experiment allowed us to determine whether increased weevil damage to plants growing in the sun would be compensated for by the direct benefits to plant growth and possible higher tolerance to herbivory in the higher-light environment.

Materials and methods

Study organisms

Persicaria perfoliata seeds germinate in early spring, and vines grow rapidly during the summer, with small spines on leaves and stems helping the plant to grow up and over other vegetation. Leaves are alternate and triangular, and a diagnostic feature is the presence of saucer-shaped ocreae or fused stipules that surround the stem at each leaf node (Hough-Goldstein et al. 2008a). Seed production may occur as early as June, but most seeds are produced in the fall (Hough-Goldstein et al. 2008a, b). Plants die with the first sustained frost in the fall.

The small (approximately 2 mm long) adult *R. latipes* weevils emerge in early spring, soon after mile-a-minute seedlings appear. They lay their eggs on *P. perfoliata* stems, terminals, and leaves, with oviposition beginning about 6 days after adult emergence and continuing at a rate of about three eggs per female per day for at least 2 months under laboratory conditions (Colpetzer et al. 2004b). Larvae bore into the stem at nodes soon after hatching, complete their development internally, and then exit the stem and drop to the soil for pupation (Price et al. 2003; Hough-Goldstein et al. 2008a). Nodes are permanently scarred by larvae entering or exiting the stem, leaving a season-long record of their presence. The weevils go through at least three or four overlapping generations during the growing season in the Mid-Atlantic region, USA, with each generation taking about 1 month to develop (Lake et al. 2011). Adults stop producing eggs between late August and late September, and adult weevils overwinter in the leaf litter or soil. Although herbivores other than *R. latipes* are found on *P. perfoliata* in the United States, all are external feeders, mostly polyphagous insects, and the resulting herbivory is described as "casual" (Wheeler and Mengel 1984).

Study site

The experiments were conducted in White Clay Creek State Park, DE, at a site where 200 weevils had been released in 2004. Weevils were relatively abundant by 2006 and 2007 (site DE-2 in Hough-Goldstein et al. 2009). The site (39°43′36″ N, 75°46′15″ W) was a long narrow clearing, approximately 80 m by 20 m, surrounded by forest on three sides and a hay field on the fourth. Aside from scattered shrubs and small trees, the vegetation consisted mostly of mile-a-minute weed, three-leaf blackberry (*Rubus triphyllus* Thunb.), and Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus), all of which are non-native to the region.

Test of weevil abundance and plant damage in sun and shade

On May 22, 2008, ten plots were established in areas with full noonday sun and abundant mile-a-minute seedlings. Plots were paired, approximately 0.5 m apart, and one of the each pair was assigned randomly to either a sun or shade treatment using PROC PLAN of the SAS system (SAS Institute 2008). The five paired replicates were placed at different intervals along the clearing, choosing areas with maximum possible *P. perfoliata* populations (minimum of about 20% cover). Each plot was delineated by a 2 m × 2 m × 1.3 m PVC frame. For the shade treatment, the frames were covered with shade cloth that blocked 40% of sunlight (Griffin Greenhouse Supply Inc., Morgantown, PA). A 1 m × 1 m area was marked for data collection in the center of each plot, using strings that were attached to the frame and could be lowered to the level of the foliage. The extra 0.5 m of shade cloth on all sides of the center square shaded the center when the sun was not directly overhead. Although additional shade was present in both sun and shade plots in the mornings and evenings along the edges of the clearing, the blocked design randomized these effects by treatment. Adult weevils and feeding damage were present in the plots on emerging mile-a-minute seedlings before the shade cloth was installed, but at low levels.

Data were collected weekly for 12 weeks, beginning on 3 June, 1.5 weeks after the frames were installed. Weevils were counted each week within the central 1 m^2 by carefully approaching the plot, lowering the strings, and looking for weevils on the terminals, leaves, and ocreae. Counts generally occurred mid-morning to mid-afternoon; each block was counted at one time, and all counts were carried out by the same person. Weevils are typically present on plants at all times, usually near the terminals (Colpetzer et al. 2004b), which facilitated relatively complete counts.

On the first sample date, the total number of mile-a-minute weed seedlings in the central 1 m^2 was also recorded. Each week thereafter the percentage of weevil feeding damage on *P. perfoliata* was estimated to the nearest 5% by comparing leaves to a diagram showing different levels of defoliation of soybean leaflets (Kogan and Kuhlman 1982), with all estimates made by the same person.

The total percentage cover of *P. perfoliata* in each plot was estimated by looking directly down at the 1-m^2 central plots. Percentage cover provided a good comparative estimate of the amount of mile-a-minute weed present in the plots between early June and late July, but by August, this metric was less useful due to the growth of the vines out of the center and accumulation of large amounts of overlapping biomass, and therefore, this measure was discontinued in early August.

Each week a plant, located outside the central 1 m^2 but within the 2 m × 2 m plot, was selected haphazardly and collected by carefully untangling it from the surrounding plants and clipping at soil level. Later as plants became larger and more tangled, it was impossible to recover the entire plant, but the terminal and most of the plant stem was always collected. Each plant specimen was placed in a self-sealing plastic bag and returned to the laboratory, where stem length, total number of nodes, and number of damaged nodes (indicating *R. latipes* larval feeding) were recorded. Percentage of nodes damaged and number of damaged nodes per m of stem was calculated. The five terminal internodal distances were measured for each plant. Calipers were used to determine the thickness (diameter) of an undamaged node near the terminal: the second node from the top, or if damaged then the nearest undamaged node, was measured for each plant.

Test of plant response to herbivory in sun and shade

On May 22, 2010, plots were established at the same site as in 2008, with four treatments consisting of sun plots with and without weevils and shade plots with and without weevils, arranged in a randomized complete block design with five replicates. Each plot was delineated by a 2 m × 2 m × 1.3 m PVC frame, and plots within the blocks were approximately 0.5 m apart. For the shade treatments, the frames were covered with shade cloth that blocked 60% of sunlight (Griffin Greenhouse Supply Inc., Morgantown, PA). The no-weevil treatments were treated with the systemic neonicotinoid insecticide, dinotefuron (Safari 20 SG, Valent U.S.A. Corporation, Walnut Creek, CA) with 51 g in 28.4 l water (1.8 oz per 7.5 gal of water) applied as a drench to each 2 m × 2 m plot on 2 June and again on 29 July. A 1 m^2 area was marked for data collection in the center of each plot, and weevils were counted and percent cover of mile-a-minute weed was estimated each week from 1 June through 20 July. Adult weevil feeding damage was assessed each week on a scale from 0 to 5 [0, none (no damage); 1, low (holes in a few scattered leaves); 2, medium–low (holes in about half the leaves); 3, medium (holes in many leaves); 4, medium–high (holes in most leaves); 5, high (extensive damage on most leaves)]. On August 10, 2010, all *P. perfoliata* above-ground biomass was harvested from each 2 m × 2 m plot. Mile-a-minute weed vines were gently pulled out of each plot (cut at the base of the plants if necessary), separated from all other vegetation and collected into large plastic bags. The *P. perfoliata* plant material was subsequently transferred to paper bags, placed in a drying oven at 95–100°C for 11 days, and then weighed.

Statistical analyses

For all experiments, data were tested for normality using the Shapiro–Wilk test and for homogeneity of variance residuals using Levene's test. Where necessary, data were either log or square root transformed to improve homogeneity or normality. The arcsine-square root transformation was applied to percentages where at least some were more than 70% or less than 30% (Snedecor and Cochran 1980). Non-transformed data are shown in figures. For the first experiment, numbers of *P. perfoliata* seedlings counted in sun and shade plots at the beginning of the experiment were compared using a two-way analysis of variance (ANOVA).

Because adult weevils were present only on mile-a-minute weed, and percent cover of mile-a-minute weed varied from plot to plot, all weevil numbers were adjusted by percent cover of the host plant, with the number of weevils per plot divided by the proportion of mile-a-minute cover present in the plot. Thus, a plot with 50% mile-a-minute cover and 50 weevils was given the same weight as a plot with 100% mile-a-minute cover and 100 weevils, and these numbers are expressed as “weevils per m^2 of mile-a-minute” or as “density” of weevils. Mile-a-minute percent cover and damage estimates were compared by repeated measures ANOVA, beginning several weeks after treatments were applied to allow time for the applied shade treatment to impact the plants and herbivores before its effects were assessed. The REPEATED statement in PROC GLM of the SAS system (Littell et al. 2002; SAS Institute 2008) was applied to data collected between July 7 and August 4, 2008 for analyses requiring percent cover data, and for the period July 7 through August 18, 2008 for percent defoliation, percent and number of nodes damaged, and plant internode lengths and node thickness.

For the 2010 experiment, repeated measures analyses were conducted on weevil density and feeding damage data collected from June 22 through July 20, 2010 in sun and shade treatments where weevils were present. Mile-a-minute weed percent cover each week from 22 June through 20 July, and final dry biomass data were analyzed using an ANOVA for a two-way factorial experiment, where factors were shade versus no shade and weevils versus no weevils (Littell et al. 2002). Where a significant interaction was found between the shade treatment and the insecticide treatment, the effects of each factor were determined using the SLICE option in the LSMEANS statement of SAS to obtain *F* tests for simple effects (Littell et al. 2002). Where no interaction was found, main effects of shade treatment and insecticide treatment were compared using the MEANS statement and Tukey’s test (SAS Institute 2008).

Results

Test of weevil abundance and plant damage in sun and shade

The number of *P. perfoliata* seedlings counted in 1 m^2 plots on June 3, 2008 did not differ between sun (69.8 ± 12.1 mean ± SEM) and shade (65.4 ± 10.7; $F_{1,4} = 0.06$, $P = 0.82$). Percent *P. perfoliata* cover in sun and shade treatments for the period July 7 through August 4, 2008 did not significantly differ ($F_{1,8} = 1.80$, $P = 0.22$; Fig. 1a). Density of adult weevils increased over the course of the summer, and weevils were significantly more abundant on mile-a-minute weed in the sun plots than in the shade plots for the period 7 July through 4 Aug ($F_{1,8} = 6.78$; $P = 0.031$; Fig. 1b).

Defoliation by adult weevils was low in both sun and shade, with a maximum average defoliation of just over 10% in mid-July and no significant difference between the treatments ($F_{1,8} = 0.05$, $P = 0.83$; Fig. 2a). Larval damage assessed on collected plants did differ by treatment, with both the percentage of nodes damaged ($F_{1,8} = 6.28$, $P = 0.037$, Fig. 2b) and the number of damaged nodes per m^2 of stem ($F_{1,8} = 8.63$, $P = 0.019$, Fig. 2c) higher in the sun than in the shaded plots. After the first sample, about 20–30% of all nodes were damaged on plants in full sun, with 6–9 damaged nodes per m of plant stem, while shaded plants averaged about 15–20% of all nodes damaged per plant, with 3–6 damaged nodes per m of stem (Fig. 2b, c).

The five terminal internode distances were on average 8% shorter ($F_{1,8} = 6.12$, $P = 0.038$, Fig. 3a), and the undamaged nodes near the terminal were 14% thicker in the sun than in the shade ($F_{1,8} = 11.50$, $P = 0.0095$, Fig. 3b).

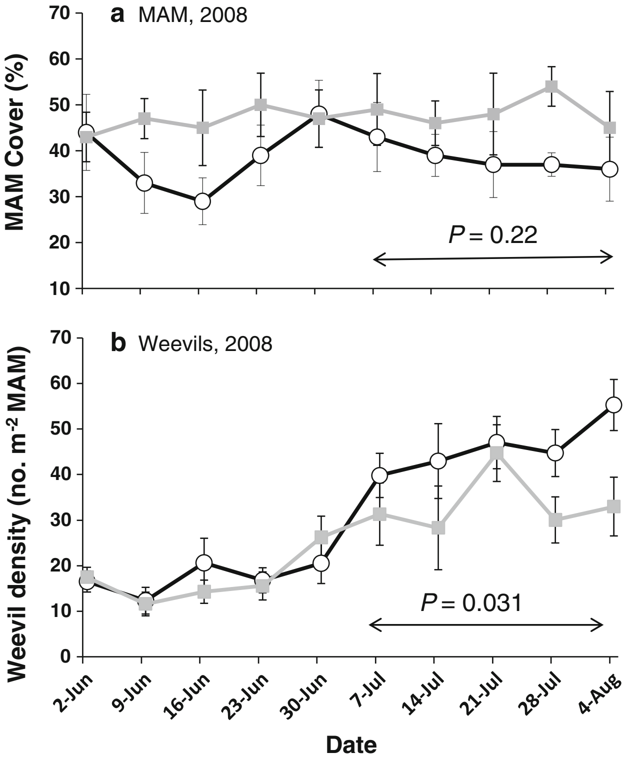


Fig. 1 2008 experiment, **a** percentage of mile-a-minute weed (MAM) cover and **b** number of weevils m^{-2} MAM in paired plots in full sun (*open circles*) and under 40% shade cloth (*filled squares*; *N* = 5 sun and 5 shade; means ± SEM). *P* values shown for repeated measures ANOVA for 7 July–4 August

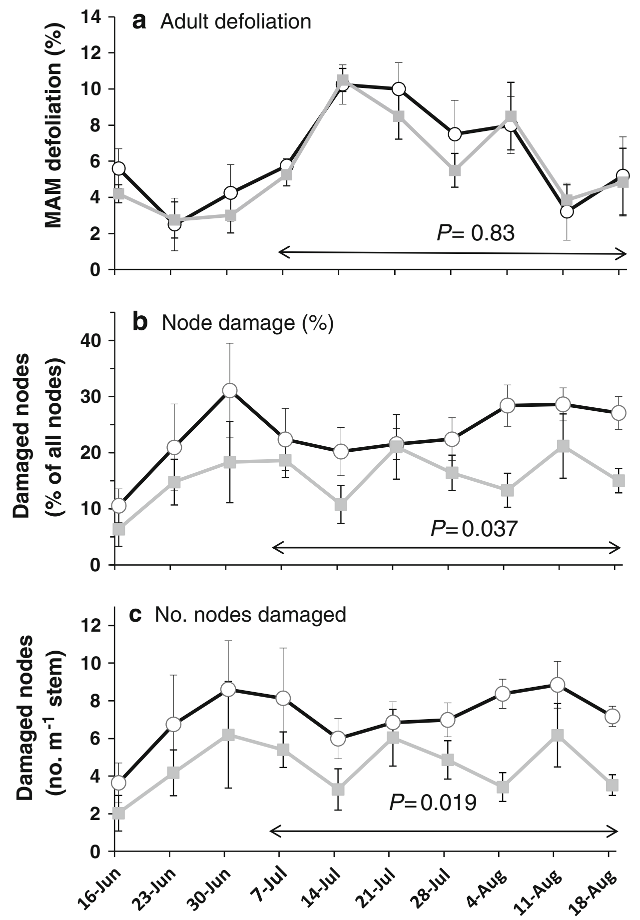


Fig. 2 2008 experiment, **a** percentage of MAM defoliated, **b** percentage of nodes with larval damage, and **c** number of damaged nodes per m plant stem, for plants from paired plots in full sun (*open circles*) and under 40% shade cloth (*filled squares*; $N = 5$ sun and 5 shade; means ± SEM). *P* values shown for repeated measures ANOVA for 7 July–18 August

Test of plant response to herbivory in sun and shade

No *R. latipes* were found in any of the plots treated with dinotefuron for 5 weeks following the June 2, 2010 application, and fewer than 10 in total were found each subsequent week in treated plots before the second insecticide application on 29 July, which again reduced the numbers to zero. The density of weevils increased to about 130 per m^2 of mile-a-minute weed in late June 2010 in the sun plots, more than twice as high as the peak densities recorded in the 2008 experiment. There was a trend toward higher density of weevils in the sun than in the shade ($F_{1,8} = 4.73$, $P = 0.061$; Fig. 4a). Adult feeding damage (on a scale of 0–5) was almost always 0 in the insecticide-treated plots after the first 2 weeks following treatment. In the plots with weevils present, feeding damage ratings were significantly higher in the sun plots than in the shade plots ($F_{1,8} = 5.42$, $P = 0.048$; Fig. 4b).

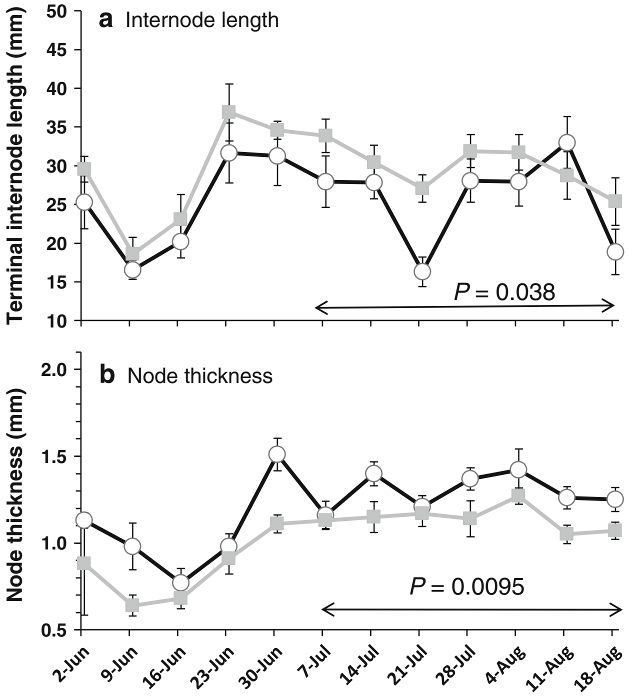


Fig. 3 2008 experiment, **a** average of five terminal internode lengths and **b** average thickness of undamaged nodes near terminals, for plants harvested from paired plots in full sun (*open circles*) and under 40% shade cloth (*filled squares*; $N = 5$ sun and 5 shade; means ± SEM). *P* values shown for repeated measures ANOVA for 7 July–18 August

Factorial analysis of percent cover of mile-a-minute weed indicated no significant interactions between shade treatment and weevil treatment in any of weeks 4 through 8 of the experiment ($F_{1,16}$ ranged from 0.12 to 0.74, *P* from 0.7344 to 0.4033), and therefore, the main effects were examined. There was a significant effect of the shade treatment on week 4 ($F_{1,16} = 6.67$, $P = 0.0200$) and week 5 ($F_{1,16} = 5.70$, $P = 0.0296$), with shaded plots showing significantly higher percent cover than non-shaded plots. The shade treatment had marginally higher cover in week 6 ($F_{1,16} = 4.09$, $P = 0.0602$), and there was no significant difference by shade treatment in week 7 ($F_{1,16} = 1.92$, $P = 0.1848$) or 8 ($F_{1,16} = 2.08$, $P = 0.1687$). The weevil-free (insecticide-treated) plots had significantly higher *P. perfoliata* cover in weeks 5 ($F_{1,16} = 4.40$, $P = 0.0521$), 6 ($F_{1,16} = 7.73$, $P = 0.0134$) and 7 ($F_{1,16} = 5.72$, $P = 0.0295$). Cover did not differ significantly by insecticide treatment in week 4 ($F_{1,16} = 1.77$, $P = 0.2026$) or week 8 ($F_{1,16} = 1.47$, $P = 0.2437$).

The dry biomass of *P. perfoliata* harvested from the plots was about twice as high from the insecticide-treated sun plots than from any other treatment ($F_{3,12} = 9.88$, $P = 0.0015$, Fig. 5). Both the shade treatment ($F_{1,16} = 9.26$, $P = 0.0077$) and the dinotefuron treatment ($F_{1,16} = 14.31$, $P = 0.0016$) significantly affected mile-a-minute

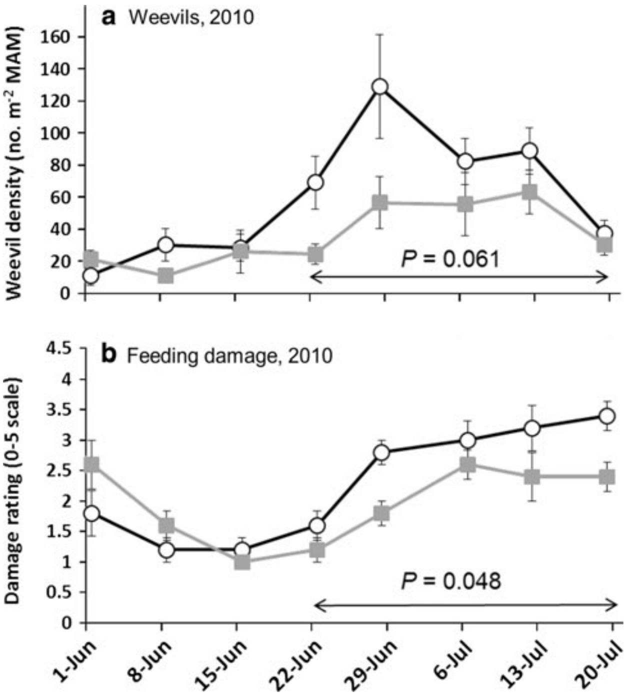


Fig. 4 2010 experiment, non-insecticide plots only, **a** number of weevils m^{-2} MAM, and **b** feeding damage ratings in plots in full sun (*open circles*) and under 60% shade cloth (*filled squares*; $N = 5$ plots per treatment; means ± SEM). *P* values shown for repeated measures ANOVA for 22 June–20 July

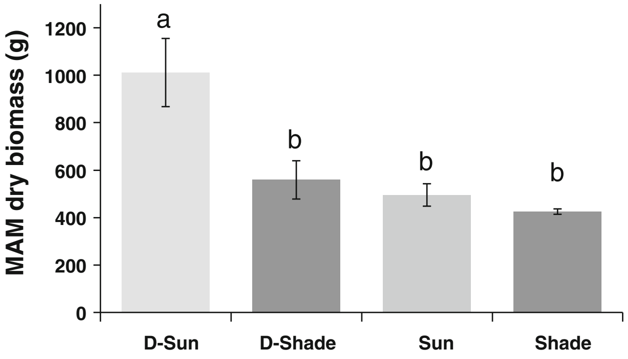


Fig. 5 2010 experiment, dry biomass of mile-a-minute weed (MAM) from plots in full sun and under 60% shade cloth, with and without dinotefuron insecticide treatment (indicated with D; $N = 5$ plots per treatment; means ± SEM). Bars with same letter are not significantly different (two-way ANOVA, $F_{3,12} = 9.88$, $P = 0.0015$; Tukey's test for mean separation)

biomass. The interaction between the shade and dinotefuron treatments was also significant ($F_{1,16} = 4.95$, $P = 0.041$), and therefore, simple effects, i.e., how levels of one factor affected the response variable for a given level of the other factor, were tested (Littell et al. 2002). With the sun or shade treatment held constant, the presence or absence of weevils had a significant effect on biomass in the sun ($F_{1,16} = 18.05$, $P = 0.0006$) but the insecticide effect was not significant in the shade ($F_{1,16} = 1.21$, $P = 0.29$). With the weevil or no-weevil treatment held constant, the shade treatment significantly affected biomass in the dinotefuron (no-weevil) treatment ($F_{1,16} = 13.88$, $P = 0.0018$) but not with weevils present ($F_{1,16} = 0.33$, $P = 0.57$).

Discussion

Results support the prediction of greater concentration of *R. latipes* in sun than in shade, with greater density of weevils and more node damage (indicating internal larval feeding and, indirectly, oviposition) found on *P. perfoliata* plants growing in full sun than on those in shade. This is consistent with the plant vigor hypothesis of Price (1991), because *P. perfoliata* is known to grow more vigorously in sun than in shade (Hough-Goldstein 2008). *Rhinoncomimus latipes* feeds and oviposits primarily on new growth near plant terminals (Colpetzer et al. 2004b) and thus may be expected to select more vigorous, actively growing plants (White 2009). Plant host selection in this species is strictly by ovipositing females, since larvae feed internally and complete their development on a single plant. Weevils are somewhat sedentary, but are known to disperse among host plants through walking and flight (Lake et al. 2011).

Plants growing vigorously in full sun may provide higher quality food for developing *R. latipes* larvae. Because shade plants have less photosynthetic carbon available due to the lack of light and may use more of their resources to grow rapidly outward through stem elongation, there may be a relative deficit of necessary resources for larval survival within the stems and nodes in the shade (Lincoln and Mooney 1984). Terminal *P. perfoliata* internode lengths were longer (Fig. 3a) and undamaged nodes were thinner (Fig. 3b) in the shade than in the sun, possibly indicating a less favorable habitat for weevil larvae. Other species of stem-boring insects have shown decreased larval survivorship with smaller stem size (Jeanneret and Schroeder 1992; Tscharntke 1993; Eber et al. 1999; Losey et al. 2002). Agrawal and Van Zandt (2003) found that when neighboring grasses were clipped to reduce light competition, focal milkweed plants had 20% shorter internode lengths and 90% thicker stems, and these plants also received significantly more damage and oviposition by a specialist stem-attacking weevil.

Higher *R. latipes* populations in the sun could also reflect a preference by the weevils for a sunny habitat due to direct effects of higher light levels and generally higher temperatures in sunny areas. Because *R. latipes* populations are able to complete at least three or four overlapping generations during a growing season (Lake et al. 2011), they may be selecting sunny areas where generally warmer temperatures would allow for more rapid growth and development, giving weevils in the sun a selective advantage with respect to increased reproductive output over the course of the season compared to those in cooler shaded areas.

Similar positive response to sunny areas or to plants growing in full sun has been observed for other insects, including the St. Johnswort beetle, *C. quadrigemina* (Clark 1953; Huffaker and Kennett 1959; Huffaker 1967), *Euphydryas chalcedona* Doubleday butterflies (Williams 1983; Lincoln and Mooney 1984), *Acalymma innubum* (Fab.) leaf beetles (Bach 1984), and various herbivores of bittercress, *C. cordifolia* (Louda and Rodman 1996). However, other insect species preferentially feed or oviposit in shaded habitats (MacGarvin et al. 1986; Sousa et al. 2003; Niesenbaum and Kluger 2006; Muth et al. 2008; Guerra et al. 2010). Differences in plant physiology, plant quality, and plant chemistry are typically found when plants are grown in sun versus shade, some of which undoubtedly influence oviposition behavior, larval survival, or both, either positively or negatively depending on the plant and its herbivore species. Numerous secondary compounds have been isolated from *P. perfoliata* (Park 1987; Sun and Sneden 1999; Sun et al. 2000; Chang et al. 2008; Jin et al. 2009), which undoubtedly play a role in the host specificity of *R. latipes*, but little is known concerning the role of these compounds in biotic or abiotic interactions.

Typically the distance between nodes becomes elongated in the shade, as the plant attempts to grow toward the light (Corre 1983), and this was observed in our study (Fig. 3a). However, the shorter internode lengths observed in the sun plants were probably also affected by the greater *R. latipes* larval weevil feeding damage observed in the sun, since shortened "stacked" nodes and loss of apical dominance are frequently observed in *P. perfoliata* plants with heavy weevil damage (Hough-Goldstein et al. 2008a). If the damage to the nodes from weevil feeding reduced the internode lengths even more than what would normally occur in the sun versus shade, this would make the sun plants less competitive. Hough-Goldstein et al. (2008b) showed that when surrounding plants were removed from around a single mile-a-minute weed plant, the plant was able to compensate for weevil damage with very robust growth. However, when some vegetation was left, the combination of weevil feeding and plant competition resulted in the death of many of the mile-a-minute plants. Thus, *P. perfoliata* is susceptible to competition by other plants in combination with host-specific herbivory, and reduced competitive advantage may contribute to a greater negative plant response to herbivory in the sun than in the shade.

In the second experiment, the total biomass of mile-a-minute weed produced by sun plants without weevils (treated with dinotefuron insecticide) was about twice as high as for any other treatment (Fig. 5). The magnitude of the difference between insecticide-treated and insecticide-untreated plants in full sun was notable and likely due to the difference in weevil populations rather than to possible physiological or fertilization effects of the insecticide on the plants, as there was no significant effect of the dinotefuron treatment on mile-a-minute biomass in the shade. Any effects of the insecticide on plant growth apart from elimination of weevils would be expected to show up in the shade as well as in the sun. In addition, two separate greenhouse trials of dinotefuron on potted *P. perfoliata* plants showed that it effectively killed weevils, but in the absence of weevils had no positive or negative effects on plant growth (Cutting 2011).

Percentage cover of mile-a-minute weed in the center of the plots did not completely reflect final biomass, with shade treatments having higher cover than sun plots in weeks 4 and 5. Shade leaves are often larger but thinner than sun leaves (Pierson et al. 1990; Guerra et al. 2010), and this may have translated into greater percent cover early in this experiment. By week 7, however, the shade effect on cover was no longer significant but the weevils were exerting a significant effect, with plots where weevils were eliminated showing significantly higher cover of mile-a-minute weed than those with weevils.

Biomass of mile-a-minute weed is a better indicator of plant success than cover and impacts on biomass indicate that while shade itself had a large negative effect on plant growth, adding weevils (in relatively low numbers) had little additional impact. With no weevils present, sun had a large positive impact on plant growth compared to shade, but this advantage was negated in the presence of weevils (in relatively high numbers). While other studies have shown that shaded plants are often less able to compensate for herbivory (Pierson et al. 1990; Lentz and Cipollini 1998; Wise and Abrahamson 2007), in those studies simulated herbivory was applied equally to plants growing in sun and shade, while in our study natural rates of herbivory were higher in the sun.

In our experiments, increased weevil damage to plants growing in the sun was not compensated for by the direct benefits to plant growth or possible increased tolerance to herbivory in the higher light environment. While high levels of weevil damage in the sun may result in *P. perfoliata* population distributions shifting into more shaded areas with fewer growth-suppressing weevils, shade provides a poor refuge because it also suppresses plant growth. As the plant invades new areas, we can expect higher *P. perfoliata* populations initially in sunny areas, but weevil populations should increase in these areas over time. Extent of control in different habitats may then depend more on the presence of other competing vegetation (Cutting 2011; Lake 2011) rather than the extent to which the invaded habitats are in sun or shade.

Acknowledgments Thanks to Jeffrey Smith, Joseph Thomas, Ellen Lake, Kayla Iuliano, Kiri Cutting, Matt Frye, Kelsey Paras and Rachel Schnaitman for assistance with field work and data collection, to William Bartz for applying dinotefuron and to White Clay Creek State Park for allowing use of their land. Funding was provided by the Forest Health Technology Enterprise Team, USDA Forest Service, Morgantown, WV.

References

Agrawal AA, Van Zandt PA (2003) Ecological play in the coevolutionary theatre: genetic and environmental determinants of attack by a specialist weevil on milkweed. J Ecol 91:1049–1059

Bach CE (1984) Plant spatial pattern and herbivore population dynamics: plant factors affecting the movement patterns of a tropical cucurbit specialist (*Acalymma innubum*). Ecology 65:175–190

Chang C, Tsai F, Chou C (2008) Natural products from *Polygonum perfoliatum* and their diverse biological activities. Nat Prod Commun 3:1385–1386

Clark LR (1953) The ecology of *Chrysomela gemellata* Rossi and *C. hyperici* Forst, and their effect on St. John's wort in the Bright District, Victoria. Aust J Zool 1:1–69

Colpetzer K, Fu W, Ding J, Hough-Goldstein J (2004a) Host specificity of the Asian weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), a potential biological control agent of mile-a-minute weed, *Polygonum perfoliatum* L. (Polygonales: Polygonaceae). Biol Control 30:511–522

Colpetzer K, Hough-Goldstein J, Harkins KR (2004b) Feeding and oviposition behavior of *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae) and its predicted effectiveness as a biological control agent for *Polygonum perfoliatum* L. (Polygonales: Polygonaceae). Environ Entomol 33:990–996

Cornelissen T, Fernandes GW, Vasconcellos-Neto J (2008) Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. Oikos 117:1121–1130. doi:10.1111/j.2008.0030-1299.16588.x

Corre WJ (1983) Growth and morphogenesis of sun and shade plants. II. The influence of light quality. Acta Bot Neerl 32:185–202

Cusick AW, Ortt M (1987) *Polygonum perfoliatum* L. (Polygonaceae): a significant new weed in the Mississippi drainage. Sida 12:246–249

Cutting KJ (2011) An integrated approach to the restoration of areas invaded by mile-a-minute weed (P*ersicaria perfoliata)* using herbaceous native seeding. MS Thesis, University of Delaware, Newark

Ding JQ, Fu WD, Reardon R, Wu Y, Zhang GL (2004) Exploratory survey in China for potential insect biocontrol agents of mile-a-minute weed, *Polygonum perfoliatum* L., in Eastern USA. Biol Control 30:487–495. doi:10.1016/j.biocontrol.2004.02.009

Eber S, Brandl R, Knoll S (1999) Endophagous insects and structural niches on plants: ecology and evolutionary consequences. Ecol Entomol 24:292–299

Frye MJ, Lake EC, Hough-Goldstein J (2010) Field host-specificity of the mile-a-minute weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae). Biol Control 55:234–240

Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. Ecol Lett 13:383–393. doi:10.1111/j.1461-0248.2009.01433.x

Guerra PC, Becerra J, Gianoli E (2010) Explaining differential herbivory in sun and shade: the case of *Aristotelia chilensis* saplings. Arthropod-Plant Inte 4:229–235. doi:10.1007/s11829-010-9099-y

Harper JL (1969) The role of predation in vegetational diversity. Brookhaven Sym Biol 22:48–62

Hough-Goldstein JA (2008) Assessing herbivore impact on a highly plastic annual vine. In: Julian MH, Sforza R, Bon MC, Evans HC, Hatcher PE, Hinz HL, Rector BG (eds). In: Proceedings of XII International Symposium Biological Control Weeds, La Grande Motte, France, 22–27 April 2007. CAB International, Wallingford, UK, pp 283–286

Hough-Goldstein J, Lake E, Reardon R, Wu Y (2008a) Biology and biological control of mile-a-minute weed. USDA Forest Service FHTET-2008-10

Hough-Goldstein J, Butterworth B, Lake E, Schiff M (2008b) Impact of the biological control agent *Rhinoncomimus latipes* (Coleoptera: Curculionidae) on mile-a-minute weed, *Persicaria perfoliata*, in field cages. Biol Control 46:417–423. doi: http://dx.doi.org/10.1016/j.biocontrol.2008.04.001

Hough-Goldstein J, Morrison P, Reardon R, Robbins G, Mayer MA, Hudson W (2009) Monitored releases of *Rhinoncomimus latipes* (Coleoptera: Curculionidae), a biological control agent of mile-a-minute weed (*Persicaria perfoliata*), 2004–2008. Biol Control 51:450–457. doi: http://dx.doi.org/10.1016/j.biocontrol.2009.08.005

Huffaker C (1967) A comparison of the status of biological control of St. Johnswort in California and Australia. Mushi 39:51–73

Huffaker C, Kennett C (1959) A ten-year study of vegetational changes associated with biological control of klamath weed. J Range Manage 12:69–82

Hyatt LA, Araki S (2006) Comparative population dynamics of an invading species in its native and novel ranges. Biol Invasions 8:261–275. doi:10.1007/s10530-004-5572-9

Jeanneret P, Schroeder D (1992) Biology and host specificity of *Mecinus janthinus* Germar (Col.: Curculionidae), a candidate for the biological control of yellow and dalmatian toadflax, *Linaria vulgaris* (L.) Mill. and *Linaria dalmatica* (L.) Mill. (Scrophulariaceae) in North America. Biocontrol Sci Technol 2:25–34

Jin S, Guo X, Zhang Y, Li P, He P, Wang Q, Fang Y (2009) Determination of bioactive components in *Polygonum perfoliatum* L. by capillary electrophoresis with electrochemical detection. Chin J Chem 27:773–776

Kogan M, Kuhlman DE (1982) Soybean insects: identification and management in Illinois Agricultural Experiment Station Bulletin 773. Agricultural Experiment Station, College of Agriculture, University of Illinois at Urbana-Champaign, Urbana

Koricheva J, Larsson S, Haukioja E (1998) Insect performance on experimentally stressed woody plants: a meta-analysis. Annu Rev Entomol 43:195–216

Lake EC (2011) Biological control of mile-a-minute weed, *Persicaria perfoliata,* and integrating weed management techniques to restore invaded sites. PhD Dissertation, University of Delaware, Newark

Lake EC, Hough-Goldstein J, Shropshire KJ, D'Amico V (2011) Establishment and dispersal of the biological control weevil *Rhinoncomimus latipes* on mile-a-minute weed, *Persicaria perfoliata* (Polygonaceae). Biol Control 58:294–301. doi:10.1016/j.biocontrol.2011.05.005

Larsson S (1989) Stressful times for the plant stress-insect performance hypothesis. Oikos 56:277–283

Lechowicz MJ, Bell G (1991) The ecology and genetics of fitness in forest plants. 2. Microspatial heterogeneity of the edaphic environment. J Ecol 79:687–696

Lentz KA, Cipollini DF Jr (1998) Effect of light and simulated herbivory on growth of endangered northeastern bulrush, *Scirpus ancistrochaetus* Schuyler. Plant Ecol 139:125–131

Lincoln DE, Mooney HA (1984) Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. Oecologia 64:173–176

Littell RC, Stroup WW, Freund RJ (2002) SAS® for linear models, 4th edn. SAS Institute, Inc., Cary, USA

Losey JE, Silverman SA, Carter ME (2002) The effect of stem diameter on European corn borer behavior and survival: potential consequences for IRM in *Bt*-corn. Entomol Exp Appl 105:89–96. doi: http://www.kluweronline.com/issn/0013-8703/contents

Louda SM, Rodman JE (1996) Insect herbivory as a major factor in the shade distribution of a native crucifer (*Cardamine cordifolia* A. Gray, bittercress). J Ecol 84:229–237

MacGarvin M, Lawton JH, Heads PA (1986) The herbivorous insect communities of open and woodland bracken: observations, experiments and habitat manipulations. Oikos 47:135–148

Maron J, Vilà M (2007) Exotic plants in an altered enemy landscape: effects on enemy resistance. In: Tilmon KJ (ed) Specialization, speciation and radiation—the evolutionary biology of herbivorous insects. University of California Press, Berkeley, pp 280–295

Maschinski J, Whitham TG (1989) The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. Am Nat 134:1–19

McCormick LH, Hartwig NL (1995) Control of the noxious weed mile-a-minute (*Polygonum perfoliatum*) in reforestation. Northern J Appl For 12:127–132

Miller TEX, Eckberg JO, Rose KA, Louda SM (2009) Impacts of insect herbivory on cactus population dynamics: experimental demography across an environmental gradient. Ecol Monogr 79:155–172

Moul ET (1948) A dangerous weedy *Polygonum* in Pennsylvania. Rhodora 50:64–66

Mountain WL (1989) Mile-a-minute (*Polygonum perfoliatum* L.) update—distribution, biology, and control suggestions. Regulatory Hort 15:21–24

Muth NZ, Kluger EC, Levy JH, Edwards MJ, Niesenbaum RA (2008) Increased per capita herbivory in the shade: necessity, feedback, or luxury consumption? Ecoscience 15:182–188. doi:10.2980/15-2-3095

Niesenbaum RA, Kluger EC (2006) When studying the effects of light on herbivory, should one consider temperature? The case of *Epimecis hortaria* F. (Lepidoptera: Geometridae) feeding on *Lindera benzoin* L. (Lauraceae). Environ Entomol 35:600–606. doi: http://www.entsoc.org/pubs/periodicals/ee/index.htm

Norghauer JM, Malcolm JR, Zimmerman BL (2008) Canopy cover mediates interactions between a specialist caterpillar and seedlings of a neotropical tree. J Ecol 96:103–113. doi:10.1111/j.1365-2745.2007.01325.x

Park CW (1987) Flavonoid chemistry of *Polygonum* sect Echinocaulon—a systematic survey. Syst Bot 12:167–179

Pierson EA, Mack RN, Black RA (1990) The effect of shading on photosynthesis, growth, and regrowth following defoliation for *Bromus tectorum*. Oecologia 84:534–543

Poindexter DB (2010) *Persicaria perfoliata* (Polygonaceae) reaches North Carolina. Phytoneuron 30:1–9

Price PW (1991) The plant vigor hypothesis and herbivore attack. Oikos 62:244–251

Price DL, Smith MT, Hough-Goldstein J (2003) Biology, rearing, and preliminary evaluation of host range of two potential biological control agents for mile-a-minute weed, *Polygonum perfoliatum* L. Environ Entomol 32:229–236. doi: http://www.entsoc.org/pubs/periodicals/ee/index.htm

Rodriguez J, Jordano D, Haeger JF (1994) Spatial heterogeneity in a butterfly—host-plant interaction. J Anim Ecol 63:31–38

Salgado-Luarte C, Gianoli E (2010) Herbivory on temperate rainforest seedlings in sun and shade: resistance, tolerance and habitat distribution. PLoS ONE 5(7): e11460 doi:10.1371/journal.pone.0011460

SAS Institute (2008) The SAS system for windows. Version 9.2. SAS Institute Inc., Cary

Snedecor GW, Cochran WG (1980) Statistical methods, 7th edn. Iowa State University Press, Ames

Sousa WP, Quek SP, Mitchell BJ (2003) Regeneration of *Rhizophora mangle* in a Caribbean mangrove forest: interacting effects of canopy disturbance and a stem-boring beetle. Oecologia 137:436–445. doi:10.1007/s00442-003-1350-0

Sun XZ, Sneden AT (1999) Neoflavonoids from *Polygonum perfoliatum*. Planta Med 65:671–673

Sun XZ, Zimmermann ML, Campagne JM, Sneden AT (2000) New sucrose phenylpropanoid esters from *Polygonum perfoliatum*. J Nat Prod 63:1094–1097. doi:10.1021/np000055e

Tscharntke T (1993) Connections of insect population dynamics with community structure in *Phragmites* habitats. In: den Boer PJ, Mols PJM, Szyszko J (eds) Dynamics of populations. Agricultural University, Warsaw, pp 37–44

Wheeler AG, Mengel SA (1984) Phytophagous insect fauna of *Polygonum perfoliatum*, an Asiatic weed recently introduced to Pennsylvania. Ann Entomol Soc Am 77:197–202

White TCR (1974) Hypothesis to explain outbreaks of looper caterpillars, with special reference to populations of *Selidosema suavis* in a plantation of *Pinus radiata* in New Zealand. Oecologia 16:279–301

White TCR (1984) The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. Oecologia 63:90–105

White TCR (2009) Plant vigour versus plant stress: a false dichotomy. Oikos 118:807–808. doi:10.1111/j.1600-0706.2009.17495.x

Williams KS (1983) The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants. III. Oviposition behavior and host plant quality. Oecologia 56:336–340

Wise MJ, Abrahamson WG (2005) Beyond the compensatory continuum: environmental resource levels and plant tolerance of herbivory. Oikos 109:417–428

Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. Am Nat 169:443–454

Wu Y, Reardon RC, Ding J (2002) Mile-a-minute weed. In: Van Driesche R., Lyon S, Blossey B, Hoddle M, Reardon R (eds) Biological control of invasive plants in the Eastern United States. USDA Forest Service, FHTET-2002-04