NRC Research Press

ARTICLE

Effects of an invasive herbivore at the single plant scale do not extend to population-scale seedling dynamics

David R. Coyle, William J. Mattson, Jr., Alexander L. Friend, and Kenneth F. Raffa

Abstract: A complex of nine invasive weevils has established in the northern hardwood forests of the Great Lakes Region. These weevils have become the numerically dominant arthropod fauna in the lower vegetation strata of this ecosystem. Effects of these folivorous adults and rhizophagous larvae on seedling survival and density are unknown. We measured the impact of adult weevil defoliation on individual sugar maple (*Acer saccharum* Marshall) seedlings, the numerically dominant flora in these stands. Over 14 500 seedlings were measured to examine the effects of larval abundance, adult abundance, and adult defoliation on seedling dynamics during 2005–2009. Heavy defoliation led to individual sugar maple seedling mortality. However, at the stand level there was no measureable net effect of invasive weevils against the high natural background rates of seedling mortality. Seedling growth and biomass were reduced by high adult or larval populations, which were associated with heavy leaf and root herbivory, but not by moderate adult or larval populations. We conclude that high levels of redundancy and compensatory processes in this environment allow sugar maple seedling populations to tolerate high levels of weevil damage, although additional stresses could reduce this resilience.

Résumé : Un complexe de neuf charançons invasifs s'est établi dans les forêts de feuillus nordiques de la région des Grands lacs. D'un point de vue numérique, ces charançons sont devenus la faune dominante d'arthropodes dans les strates inférieures de végétation de cet écosystème. Les effets de ces adultes folivores et de ces larves rhizophages sur la survie et la densité des semis sont inconnus. Nous avons mesuré l'impact de la défoliation causée par les charançons adultes sur des semis individuels d'érable à sucre (*Acer saccharum* Marshall), la flore numériquement dominante dans ces peuplements. Plus de 14 500 semis ont été mesurés pour étudier les effets de l'abondance des larves, de l'abondance des adultes et de la défoliation causée par les adultes sur la dynamique des semis durant la période 2005–2009. Une défoliation sévère a entraîné la mort de certains semis d'érable à sucre. Cependant, à l'échelle du peuplement il n'y avait pas d'effet net mesurable des charançons invasifs considérant le taux naturellement élevé de mortalité des semis. La croissance et la biomasse des semis étaient réduites par de fortes populations d'adultes ou de larves associées au broutage sévère des feuilles et des racines, mais ce n'était pas le cas lorsque les populations d'adultes ou de larves étaient modérées. Nous concluons que la présence de nombreux processus redondants et compensatoires dans cet environnement permet aux populations de semis d'érable à sucre de tolérer des dommages importants causés par les charançons mais des stress additionnels pourraient réduire cette résilience. [Traduit par la Rédaction]

Introduction

Exotic insect herbivores can cause substantial environmental and economic harm to native ecosystems (Bohlen et al. 2004), but our ability to assess and mitigate impacts is limited, especially with root-feeding species. These difficulties arise largely from our poor understanding of belowground herbivory in general, the high spatiotemporal complexity of belowground population distributions, the large number of abiotic and biotic factors contributing to their highly variable reproductive success, and the logistical and experimental difficulties of conducting controlled experiments in this environment (Detling et al. 1980; Ingham and Detling 1990; Hunter 2001, 2008; Murray et al. 2002; Sackett et al. 2013). Further, it is well established from work in other systems that the scale at which research is conducted can strongly influence our interpretations and management recommendations (Hobbs 2003; Leblond et al. 2011; Coyle et al. 2012). However, we have little understanding of this dimension with root herbivores.

Forest ecosystems are particularly susceptible to exotic pest invasions because of the vast areas and diverse biomes they encompass (Liebhold et al. 1995; Niemelä and Mattson 1996). Over 400 invasive insect species inhabit US forests (Mattson et al. 1994, 2007), and at least 10% have caused significant injury and mortality to indigenous woody plants (Liebhold et al. 1995; McClure and Cheah 1999; Peterson et al. 2004). Invasive species have altered tree species composition through direct mortality, reduced ecosystem productivity, reduced nutrient and water uptake, affected biogeochemical cycles, and reconfigured spatial arrays and connectivity of ecosystem elements within landscapes (Tkacz et al. 2008; Kenis et al. 2009; Adkins and Rieske 2013). These impacts are increasingly important because of the growing need to maximize carbon and nutrient sequestration to mitigate rising levels of CO_2.

A complex of nine invasive weevils (Coleoptera: Curculionidae) has become established in northern hardwood forests in the Great Lakes Region of North America (Coyle et al. 2008). This complex is dominated by four species, *Phyllobius oblongus* (L.), *Polydrusus sericeus* (Schaller), *Sciaphilus asperatus* Bonsdorff, and *Barypeithes pellucidus* Boheman (Witter and Fields 1977; Pinski et al. 2005*a*; Coyle et al. 2008), which account for over 99% of all weevils captured in

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Received 29 July 2013. Accepted 24 October 2013.

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Can. J. For. Res. **44**: 8–16 (2014) dx.doi.org/10.1139/cjfr-2013-0307

this area (Coyle et al. 2012). Adults emerge in early summer and feed on the foliage of several woody plant species (Witter and Fields 1977; Pinski et al. 2005*a*, 2005*b*; Coyle et al. 2010*a*, 2010*b*, 2012), whereas larvae feed and overwinter beneath the soil (Witter and Fields 1977; Coyle et al. 2011). Adult feeding is known to injure sugar maple seedlings (Simmons and Knight 1973; Witter and Fields 1977), but no studies have examined the broader effects of feeding by this complex of invasive weevils on sugar maple seedling health.

We evaluated the effects of folivory by adults, rhizophagy by larvae, and the combined effects of above- and below-ground herbivory on sugar maple seedling growth and dynamics. Aboveground herbivory by lepidopteran larvae can have serious negative effects on sugar maple seedling growth and survival (Gardescu 2003), but the effects of these invasive weevils on seedling survival are unknown (Simmons and Knight 1973; Witter and Fields 1977). Fine roots (i.e., larval food source) show high turnover rates in sugar maple stands (Fahey et al. 2012), and belowground herbivory is suspected to contribute to these high turnover rates (Stevens and Jones 2006). Our first objective was to determine how feeding by adult weevils affects individual sugar maple seedlings. Our second objective was to determine whether sugar maple seedling dynamics are affected by the combined effects of above- and below-ground herbivory by this invasive weevil complex. This higher scale dimension incorporates the high mortality of sugar maple seedlings that occurs from other causes (Hett 1971; Hett and Loucks 1971; Gardescu 2003; Hane 2003). We hypothesized that herbivory by invasive weevils would negatively affect tree seedling survival and growth and reduce stand-level plant biomass and productivity.

Materials and methods

Site description

The study was conducted in a mature northern hardwood ecosystem near Taylor Lake in the Ottawa National Forest, Gogebic Co., Michigan (N46°14.4′, W89°2.9′). Sugar maple (*Acer saccharum* Marshall) is the dominant tree species, with ironwood (hophornbeam; *Ostrya virginiana* (Mill.) K. Koch.), American basswood (*Tilia americana* L.), and yellow birch (*Betula alleghaniensis* Britton) also present (Goodburn 1996; Pinski et al. 2005*a*). Raspberry (*Rubus* spp.), gooseberry (*Ribes* spp.), and leatherwood (*Dirca palustris* L.) are common understory shrubs. Soils are Gogebic series sandy loam (61% sand, 32% silt, and 7% clay) (Alfic Oxyaquic Fragiorthods), have low fertility (Supplementary data Table S1),[1] and becomes more clayey and rocky at depths >30 cm. Air temperatures, soil temperatures, and precipitation over the study period are provided in Supplementary data Table S2.[1]

Impact of herbivory on individual seedlings

In June 2008, we identified 26 pairs of sugar maple seedlings between 15 and 45 cm tall that consisted of one seedling with heavy (i.e., >75%) defoliation and one with no or light (i.e., <25%) defoliation. Seedlings within a pair were no more than 30 cm apart, and each pair was at least 3 m away from other pairs. Defoliation was rated visually on a scale of 0 = none, 1 = <10%, 2 = 10%–20%, 3 = 20%–30%, 4 = 30%–40%, 5 = 40%–50%, 6 = 50%–60%, 7 = 60%–70%, 8 = 70%–80%, 9 = 80%–90%, and 10 = >90%. Based on feeding patterns observed in the laboratory and field (Simmons and Knight 1973; Coyle et al. 2010*a*, 2010*b*), and the overwhelming dominance of this weevil complex in the stand (Pinski et al. 2005*a*; Coyle et al. 2012), all defoliation was almost certainly caused by adult weevils. In June 2009 and 2010, we revisited these same trees and recorded survival and defoliation. We identified 40 additional pairs of sugar maple seedlings in June 2009 and monitored them identically, with final survival and defoliation ratings taken in June 2010.

Impact of herbivory on seedling dynamics

Ten 7 m × 7 m blocks, each containing four 2 m × 2 m treatment plots with a 1 m buffer on all sides, were established in September 2004. Blocks were arranged in a randomized complete block design. Each block had at least a 2 m buffer between other blocks or dominant trees (defined as having a DBH > 50 cm).

We applied four treatments (including a control) to achieve different above- and below-ground weevil densities (Table 1). Treatment 1 was an unmanipulated control exposed to natural weevil populations. Treatment 2 was exposed to natural levels of folivory and oviposition by adults, but received a soil drench insecticide application (452 g AI imidacloprid·ha^{-2} (0.18 g AI·plot^{-1}), Merit 75 WP, Bayer Corp., Montvale, New Jersey) in late August each year to kill larvae. Treatments 3 and 4 were enclosed in a screen (charcoal fiberglass mesh, Phifer Inc., Tuscaloosa, Alabama) cages (2 m × 2 m × 1.7 m) cage with a PVC frame from early June until late July each year. These caged treatments were intended to administer additional adult weevils beyond ambient levels. To determine how many adult weevils to add to treatments 3 and 4, we conducted sweep net sampling each year near the study site to estimate an average abundance of adult weevils in a known area. The weevils were counted and transferred to 50 mL vials to calibrate volume estimates for a known number of adults. We then added the corresponding volume of between 250 and 400 weevils to each cage to double the natural population. Treatment 3 received an imidacloprid soil drench as previously described. Treatments not receiving the insecticide soil drench (i.e., 1 and 4) received an equivalent volume of water.

Treatment efficacy was measured by sampling larval abundance, emerging adult abundance, and defoliation. Larval abundance was measured with soil cores (5.1 cm in diameter and 30 cm deep) collected each fall after leaf senescence from 2005 to 2008. Cores were taken at three random locations per treatment plot in the area outside the central 1 m². Holes were refilled with sterile sand to provide a medium for new roots. Samples were transported to the laboratory in a cooler and stored at 4 °C until processed. All arthropods and earthworms were sieved from samples and placed into 70% ethanol until identification.

Adult abundance was measured using emergence traps (n = 20 per plot) placed on the ground in 2007–2009 (Coyle et al. 2012). Traps consisted of a 2 L clear plastic bottle (Ball Corp., Watertown, Wisconsin) with the top third removed. The inside of the top portion was painted with textured black paint (Rust-Oleum Corp., Vernon Hills, Illinois). The remainder of the bottle was inverted onto the top portion and secured to the ground by a stake wire flag (Forestry Suppliers, Inc., Jackson, Mississippi) attached to the side of the bottle with duct tape. Emerging adult weevils crawled up the inside of the painted portion, through the opening, and fell into the trap. Traps were checked approximately weekly from 13 June to 11 July 2007, from 13 May to 29 July 2008, and from 30 April to 20 July 2009. Adults were placed into vials and transported to the laboratory for identification and preservation. Voucher specimens are housed in the Department of Entomology Insect Research Collection at the University of Wisconsin-Madison (Coyle et al. 2010*b*).

Defoliation was visually estimated once each summer from 2005 to 2009 at the conclusion of peak weevil foliar feeding. To prevent possible edge effects, only seedlings within the measurement plot (the central 1 m² of each plot, hereafter referred to as a plot) were measured. Each plot was visually divided into four 0.5 m × 0.5 m quadrants, and the average defoliation level of each quadrant was estimated to the nearest 5%. Defoliation estimations from each quadrant were then averaged to obtain a single defoliation percentage for each plot. All defoliation estimations over

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[1] Supplementary data are available with the article through the journal Web site at http://www.nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0307.

Table 1. Treatments implemented in a northern hardwood ecosystem dominated by sugar maple (*Acer saccharum*) in the Ottawa National Forest, Gogebic Co., Michigan, USA.

	Weevil population		
Treatment No.	Adult	Larvae	Treatment
1	Natural	Natural	Control — no manipulation
2	Natural	Killed	Natural adult herbivory, insecticide to decrease larval herbivory
3	Enhanced	Killed	Introduce weevils to increase adult herbivory, insecticide to decrease larval herbivory
4	Enhanced	Enhanced	Introduce weevils to increase adult herbivory, and allow oviposition to increase larval herbivory

Note: During the 2005–2008 summers, cages were installed from early May through early July, and insecticide was applied in late August.

Table 2. Parameters for sugar maple (*Acer saccharum*) biomass regression equations from trees harvested in 2005 ($n = 54$), 2006 ($n = 71$), 2008 ($n = 56$), and 2009 ($n = 34$) in the Ottawa National Forest, Gogebic Co., Michigan, USA.

	Parameter		
Biomass component	*a*	*b*	R^2
Leaf	0.0179	2.3252	0.8123
Branch	0.0003	4.0399	0.7081
Stem	0.0205	2.8248	0.9521
Shoot*	0.0388	2.6852	0.9406
Stump	0.0099	3.0097	0.9090
Coarse root	0.0001	4.2859	0.6866
Fine root (1 < 5 mm diam.)	0.0015	3.2431	0.8062
Fine root (<1 mm diam.)	0.0173	2.3113	0.9015
Root†	0.0256	2.8057	0.9353
Total biomass‡	0.0657	2.7295	0.9466

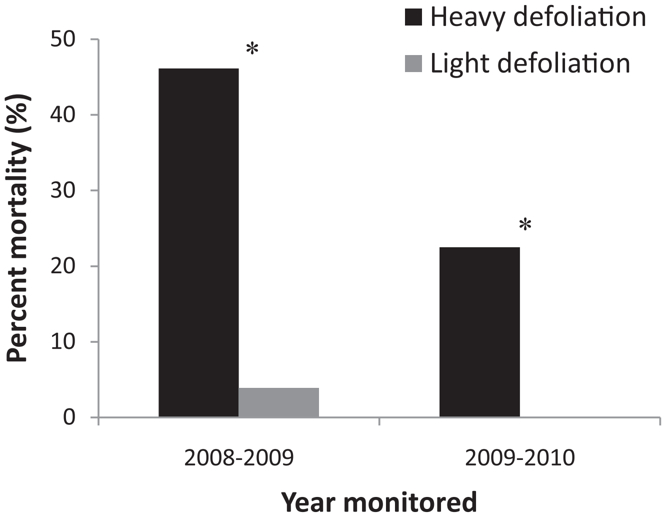
Note: Regression equations were of the form $y = ax^b$, where y is the individual tree biomass (g·tree^{-1}), a and b are the estimated model parameters, and x is the basal diameter (mm).

*Shoot = leaf + branch + stem.

†Root = stump + coarse root + fine roots.

‡Total biomass = shoot + root.

Fig. 1. Percent mortality of heavy and lightly defoliated sugar maple (*Acer saccharum*) seedlings during 2 years in the Ottawa National Forest in Gogebic Co., Michigan, USA. Levels of heavy and light defoliation on seedlings were significantly different in 2008 (77% vs. 11% defoliation; $F = 318.18$; df = 1, 51; $P > 0.001$) and 2009 (74% vs. 33% defoliation; $F = 924.32$; df = 1, 79; $P > 0.001$). An asterisk indicates a significant difference in mortality from one year to the next between defoliation groups (McNemar's test, $\alpha = 0.05$).



the course of the study were taken by the first author to maintain experimental consistency.

Seedling growth was recorded each year from 2005 through 2009. In early June 2005, we recorded basal diameter (to the nearest mm) of a subset of 15 permanently marked sugar maple seedlings in each plot. In August 2005, we recorded the species and basal diameter of every woody plant, including marked seedlings, in each plot. We recorded basal diameter of all woody plants in each measurement plot in May 2006 through 2009. Basal diameter was taken in two cardinal directions, and these values were averaged to obtain the final diameter.

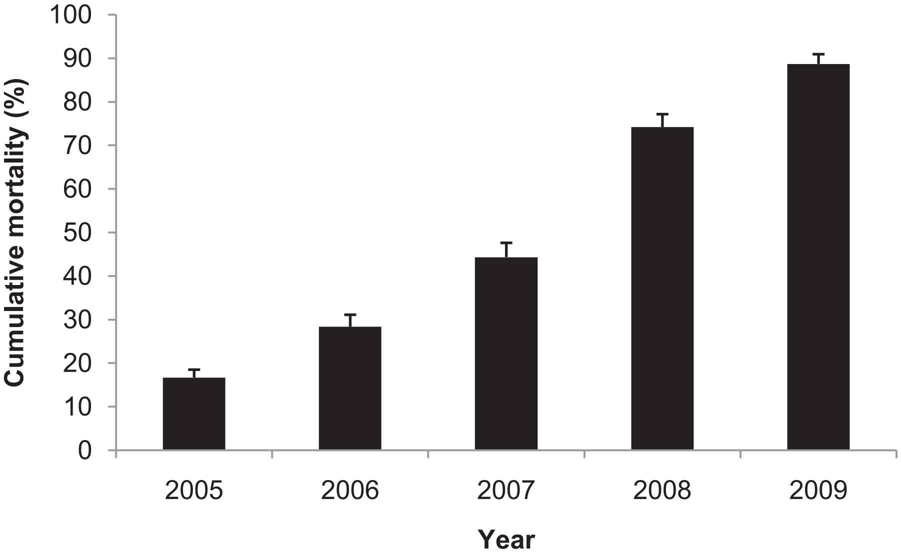
During midsummer of 2005, 2006, 2008, and 2009, sugar maple seedlings (n = 34 to 71) that encompassed the range of diameters found within the plots were systematically selected, excavated, and destructively harvested. Seedlings with minimal defoliation were chosen from areas in close proximity to, but not within, the study area. Basal diameter was measured prior to excavation, and seedlings were carefully excavated by hand so as not to damage or break any roots. Seedlings were transported to the laboratory in a cooler and divided into fine root (<1 mm and 1 ≤ 5 mm in diameter), coarse root, stump, stem, branch, and leaf components. Plant tissues were dried at 60 °C for 7 days and weighed to the nearest 0.1 mg. Allometric regression equations, based on stem diameter, were calculated for each biomass component in each year (Supplementary data Table S3),[1] allowing nondestructive plot-level biomass estimates to be made for living trees.

We tested whether shading by cages might confound our results, as prior studies have yielded mixed results on how shade affects sugar maple seedlings (Clark and Schlarbaum 2003; Hane 2003). Separate plots ($n = 9$) were established and received cages at the same time as the main study. Differences in seedling growth between caged and uncaged plots were <3%. We also tested for a potential fertilization effect from imidacloprid. Ten sugar maple seedlings were carefully excavated during dormancy following the 2006 growing season. Seedlings were transplanted in field soil into pots and brought to the greenhouse at the University of Wisconsin-Madison. During the summers of 2007 and 2008, we treated five trees with the same dose of imidacloprid as in the field. The remaining five trees received water only. Trees were destructively harvested after two growing seasons. Tree growth differed by only 8% between trees receiving imidacloprid and untreated controls, indicating that imidacloprid did not affect tree growth.

Statistical analyses

All statistical analyses were conducted in SAS (SAS Institute, Cary, North Carolina). We examined herbivory levels within each group of paired seedlings (2008, $n = 26$; 2009, $n = 40$) using a one-way analysis of variance (ANOVA) (ANOVA; Proc Glm). We used McNemar's test (Proc Freq) to determine if herbivory affected the survival of individual seedlings. Groups of seedling pairs were

Fig. 2. Cumulative sugar maple (*Acer saccharum*) seedling mortality in the Ottawa National Forest, Gogebic Co., Michigan, USA. Seedlings were randomly selected (n = 15 seedlings in each of 40 plots) in May 2005, and mortality was recorded in August 2005 and yearly in May thereafter.



analyzed separately, with each analysis weighted by the number of pairs each year. To determine if defoliation levels on individual seedlings were correlated across growing seasons, we performed linear regressions (Proc Reg) between 2008 and 2009, and 2008 and 2010 for the seedling pairs identified in 2008, and between 2009 and 2010 for the seedling pairs identified in 2009.

We tested treatment efficacy yearly by evaluating larval abundance (Supplementary data Table S4),[1] adult abundance, and defoliation. Larval and adult abundance (weevils·m^{-2}) were $\log_{x+1}$ transformed prior to analyses. Larval distributions were clustered within plots (Proc Candisc) in 2005 (F = 2.39; df = 9, 30; P = 0.035), 2006 (F = 2.92; df = 9, 30; P = 0.013), and 2007 (F = 2.74; df = 9, 30; P = 0.018), but not in 2008 (P > 0.06). Adult distributions were not clustered (all P > 0.69). The effects of treatments on larval and adult abundance and defoliation were tested using a one-way ANOVA (Proc Mixed), with mean separations performed using the Tukey's test. We tested the relationship between larval abundance in year$_t$ and adult emergence in year$_{t+1}$ from 2006 to 2009 (Proc Reg). Larval abundance in 2006 was correlated with adult emergence in 2007 (F = 4.17; df = 1, 38; P = 0.048; R^2 = 0.10), but this relationship did not occur in any other year (all P > 0.09).

The dependent variables in this study were seedling mortality and growth. As difficulties in successfully manipulating belowground herbivore populations are well documented (Dawson and Byers 2008), we began with two a priori contingencies: (1) analyze using ANOVA, should the administered treatments yield discrete categories or (2) analyze using regression, should the treatments result in a range of adult and larval abundance or defoliation. Since the treatments did not generate consistent distinct categories of larval abundance (all P > 0.33), adult abundance (all P > 0.21), or defoliation (2006 P = 0.036, all other P > 0.18), we analyzed our data as continuous variables by regression, with insect abundance or defoliation in each plot (n = 40) in each year as independent variables. Overall plot-level defoliation levels were <15% during this study.

Seedling mortality was examined using the 15 tagged seedlings in each plot. In 2005, mortality was calculated as the difference in the number of surviving seedlings between June and August. For each subsequent year, mortality was the difference between year$_t$ and year$_{t-1}$. The proportion of new mortality in each year was analyzed by regression (Proc Reg) against the independent variables of larval abundance during the prior autumn, adult abundance from emergence traps in the same year, and percent defoliation in that year. We also tested for relationships of seedling mortality with cumulative adult weevil abundance, larval abundance, and defoliation.

Power functions, using sugar maple seedling basal diameter as the independent variable, were used to calculate individual seedling fine root (<1 mm and 1 ≤ 5 mm), coarse root, stump, stem, branch, and leaf components. Root biomass was the sum of all fine root, coarse root, and stump biomass; shoot biomass was the sum of stem, branch, and leaf biomass; total biomass was the sum of root and shoot biomass; root mass fraction (RMF) was root biomass divided by total biomass. Biomass relationships with basal diameter were strong (most R^2 > 0.80) for most components (Supplementary data Table S3).[1] We combined harvest trees from all years to generate a single equation for each biomass component (Table 2). Biomass was estimated each year using all sugar maple seedlings in each plot.

Because sugar maple seedlings comprised >98% of all woody plants measured, we only used these in diameter and biomass calculations. However, we calculated the basal area of non-sugar maple species by measuring the diameters of all other woody plants. Plot means were used to analyze sugar maple growth and biomass components, weighted based on the number of seedlings. Since we only recorded the initial diameters of 15 sugar maple seedlings, we could not calculate the proportion of seedling diameter change and, therefore, plot biomass, in 2005. For all other years, the average proportion of diameter and plot biomass change was the difference between year$_t$ and year$_{t-1}$. We tested the relationship between growth and biomass parameters and the independent variables of larval abundance, adult emergence, defoliation, and the number of seedlings in each plot; these variables were also used as covariates in the model to account for initial biomass or seedling density in the plots (Proc Reg, "selection" option).

Results

Severe defoliation caused seedling mortality

Seedlings with heavy defoliation in 2008 (S = 9.31, df = 1, P = 0.002) and 2009 (S = 9.00, df = 1, P = 0.003) had over 200% greater mortality than lightly defoliated seedlings after 1 year (Fig. 1). Seedlings with initially low defoliation levels tended to have low defoliation levels the following year. Furthermore, defoliation levels on surviving seedlings (which tended to be seedlings with low initial defoliation levels) had similar defoliation levels the first year following initial readings. Defoliation levels on surviving seedlings in 2008 were positively correlated in 2009 (F = 5.39; df = 1, 30; P = 0.028; R^2 = 0.16), and defoliation levels on surviving seedlings in 2009 were positively correlated in 2010 (F = 8.74; df = 1, 66; P = 0.004; R^2 = 0.12). However, seedling defoliation levels in 2008 were not correlated with those in 2010 (F = 0.80; df = 1, 30; P > 0.38; R^2 = 0.02).

Sugar maple seedling populations experienced high mortality, but this cannot be attributed to invasive weevils

As expected, the mortality of sugar maple seedlings was high, with only 10% surviving until the end of this 5 year study (Fig. 2). Against this high background rate, seedling mortality was rarely related to larval or adult abundance of weevils, or root or leaf defoliation. Larval abundance was not correlated with seedling mortality in any year (all P > 0.12). Only defoliation, which was highest in 2005 (F = 460.07; df = 4, 156; P > 0.001), when average defoliation was 46.9% ± 1.1% compared with a range of 11.1% ± 0.5% to 12.3% ± 0.7% between 2006 and 2009, and adult abundance was positively correlated with sugar maple seedling mortality. Seedling mortality in spring 2006 was positively correlated with high defoliation in 2005 (F = 10.65; df = 1, 38; P = 0.002; R^2 = 0.22), and adult abundance in summer 2007 was positively correlated with seedling mortality in fall 2007 (Fig. 3).

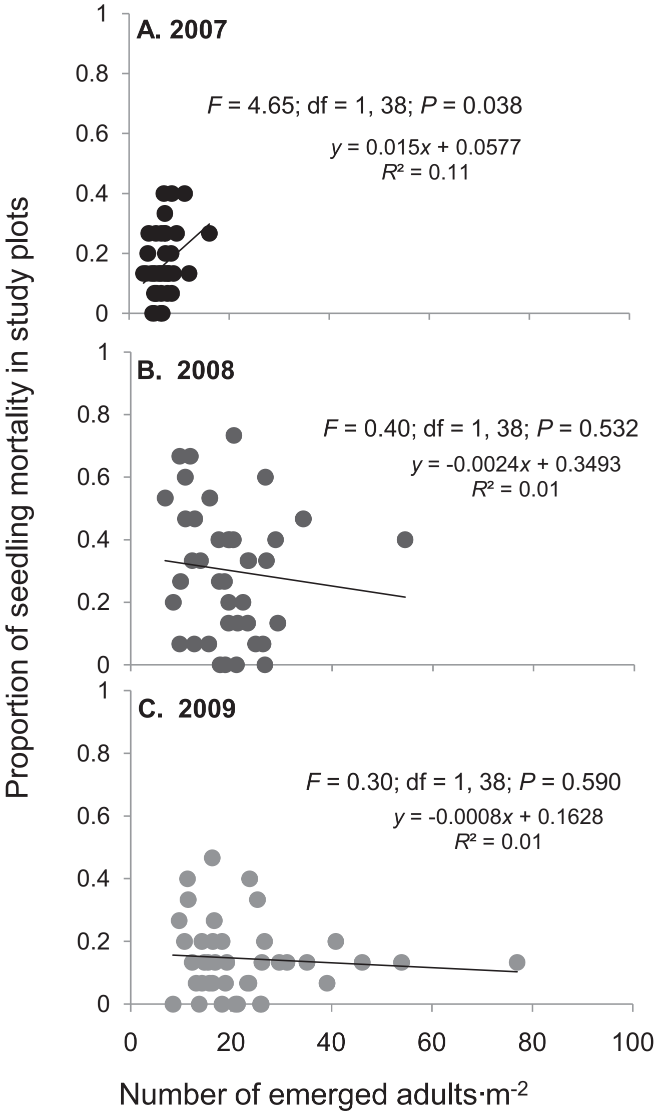
Seedling communities were rarely affected by invasive weevils

Sugar maple seedling density was negatively affected by larval abundance in 2006 (F = 4.10; df = 1, 38; P = 0.049; R^2 = 0.10), but not in 2007, 2008, or 2009 (all P > 0.54; all R^2 < 0.01). Adult abundance had no measurable effect on sugar maple seedling density in any year (all P > 0.06; all R^2 < 0.09). High defoliation in 2005 affected the proportion of mortality that occurred during that growing season, but low defoliation levels did not affect seedling mortality (Fig. 4). Defoliation was associated with decreased sugar maple seedling density in 2005 (F = 7.08; df = 1, 38; P = 0.014; R^2 = 0.16), but not in 2006, 2007, 2008, or 2009 (all P > 0.10; all R^2 < 0.07). Basal area was not affected by larval abundance (all P > 0.06; all R^2 < 0.09), adult abundance (all P > 0.17; all R^2 < 0.05), or defoliation levels (all P > 0.09; all R^2 < 0.07) in any year. Both sugar maple seedling density and the average diameter of individual sugar maple seedlings changed yearly, resulting in a highly dynamic population (Fig. 5).

The total biomass of this sugar maple seedling population decreased by over 50% from 2005 to 2009 (Fig. 6). Larval weevil abundance (all P > 0.15; all R^2 < 0.06), adult abundance (all P > 0.09; all R^2 < 0.07), or adult defoliation (all P > 0.09; all R^2 < 0.07) did not affect individual or population-level sugar maple seedling biomass or root mass fraction in any year. Larval abundance, adult emergence, defoliation, and initial seedling density did not consistently explain variations in sugar maple seedling survival or biomass (Supplementary data Tables S5 and S6).[1] However, certain variables, such as sugar maple seedling density in 2007 and adult abundance in 2009, tended to have strong effects on growth and biomass, whereas other measures of weevil density seemed not to affect sugar maple seedling metrics.

The total shrub and seedling community, which included American basswood, American black elderberry (*Sambucus nigra* L. ssp. *canadensis* [L.] R. Bolli), American elm (*Ulmus americana* L.), gooseberry, hophornbeam, leatherwood, raspberry, and slippery elm (*Ulmus rubra* Muhl.), was not affected by invasive weevils and remained stable throughout the study. In our study plots, the mean proportion of sugar maple seedlings was 0.97 ± 0.01 in 2005 and 2006 and 0.98 ± 0.01 in 2007, 2008, and 2009. The mean proportion of basal area accounted for by sugar maple was 0.94 ± 0.02 in 2007, 0.95 ± 0.01 in 2005, 0.95 ± 0.02 in 2009, and 0.96 ± 0.01 in 2006 and 2008. The proportion of sugar maple seedlings in plots was not affected by larval abundance (all P > 0.22), adult emergence (all P > 0.56), or defoliation (all P > 0.23). Likewise, larval abundance (all P > 0.19), adult emergence (all P > 0.72), or defoliation (all P > 0.17) did not affect the proportion of basal area accounted for by sugar maple seedlings in our plots.

Fig. 3. Relationship between adult emergence from the soil and sugar maple (*Acer saccharum*) seedling mortality in 2007 (A), 2008 (B), and 2009 (C).



Discussion

We hypothesized that herbivory by invasive weevils would negatively affect seedling survival and growth. We found that high levels of defoliation decreased individual seedling survival, but low levels had negligible effects. This is consistent with previous reports of sugar maple seedling growth (Ellsworth et al. 1994; Kruger et al. 1998) and survival (Gardescu 2003). However, we did not find evidence that mortality associated with high defoliation scales up to population-level impacts on total sugar maple seedling biomass or growth. In fact, our data suggest a high level of forest resilience in the face of this exotic species invasion. This ecosystem has been inhabited by this complex of exotic insects for at least six decades (W.J. Mattson, personal communication (2006)), yet we detected negligible effects on the seedling and woody shrub community. Vigorous forests with an abundance of

Fig. 4. Effect of defoliation on sugar maple (*Acer saccharum*) seedling mortality in 2005 (A), 2006 (B), 2007 (C), 2008 (D), and 2009 (E). High levels of defoliation in 2005 were correlated with increased mortality, but not in any other year. Within a year, each data point represents one plot ($n = 40$ per year).

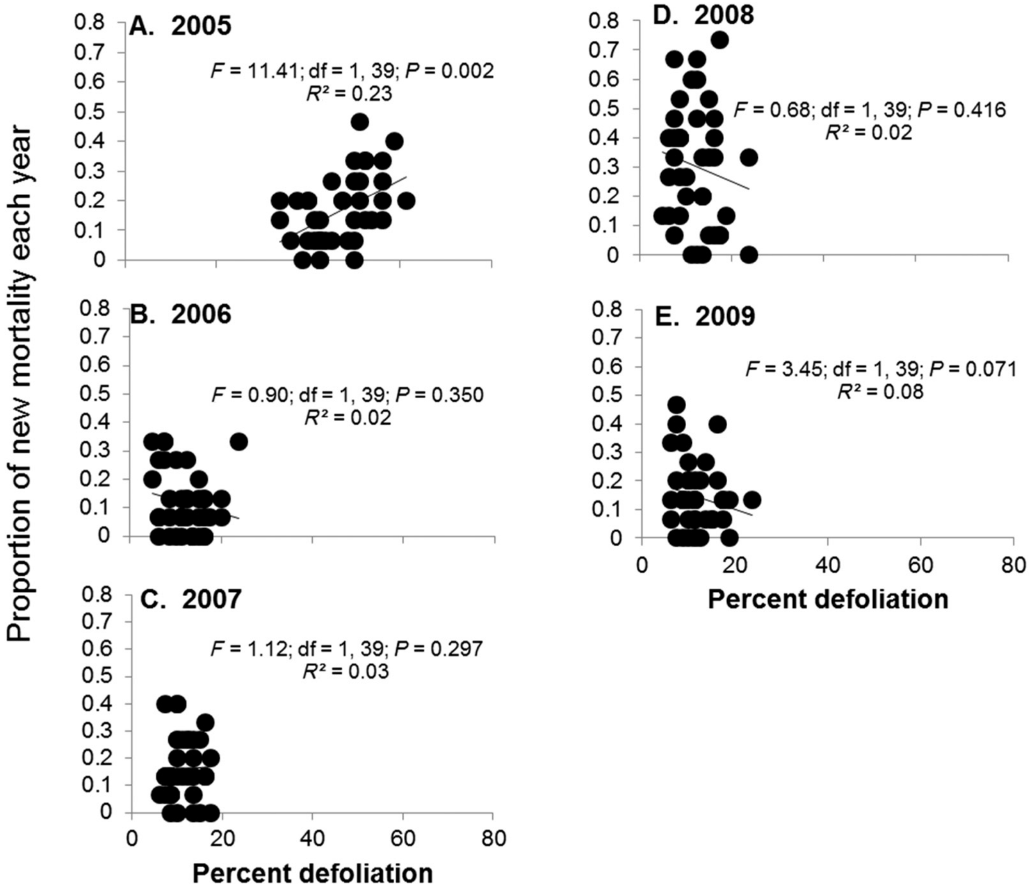


Fig. 5. Relationship between sugar maple (*Acer saccharum*) seedling basal area (using diameter at ground level) and seedling density over a 5 year period in the Ottawa National Forest, Gogebic Co., Michigan, USA. Within a year, each data point represents the mean of 40 plots. Arrows show seedling-community dynamics over time. In 2005, there were a moderate number of seedlings with a high basal area, indicating that seedlings were relatively large. After mortality of a moderate amount of presumably larger seedlings (2006), the pattern in 2007 suggests a high number of new smaller seedlings. Many of these new smaller seedlings appeared to die in 2008, but the remaining seedlings grew in size and basal area was not affected. In 2009, moderate seedling mortality occurred, but the remaining seedlings nearly doubled in size.

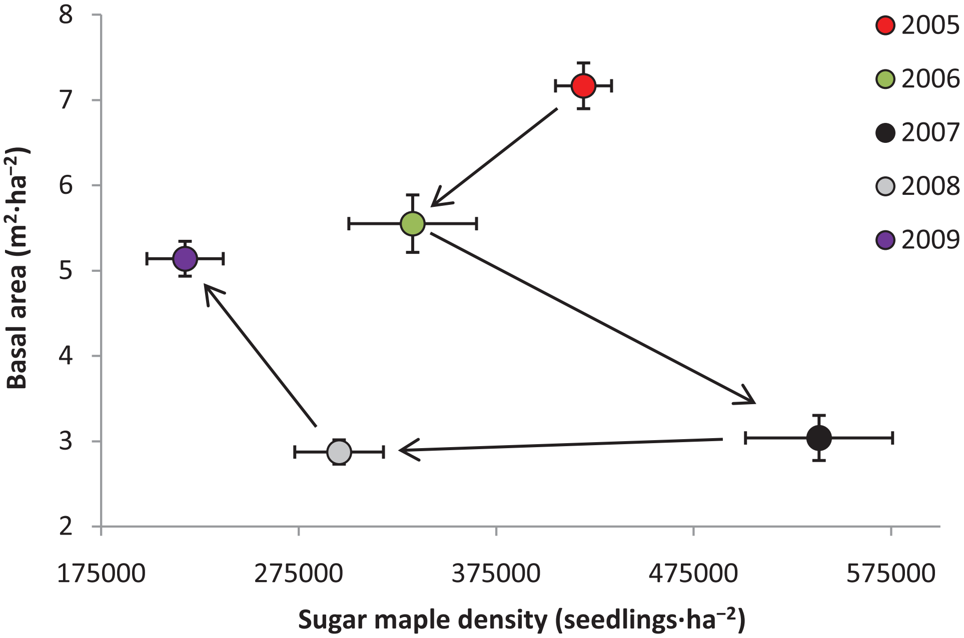
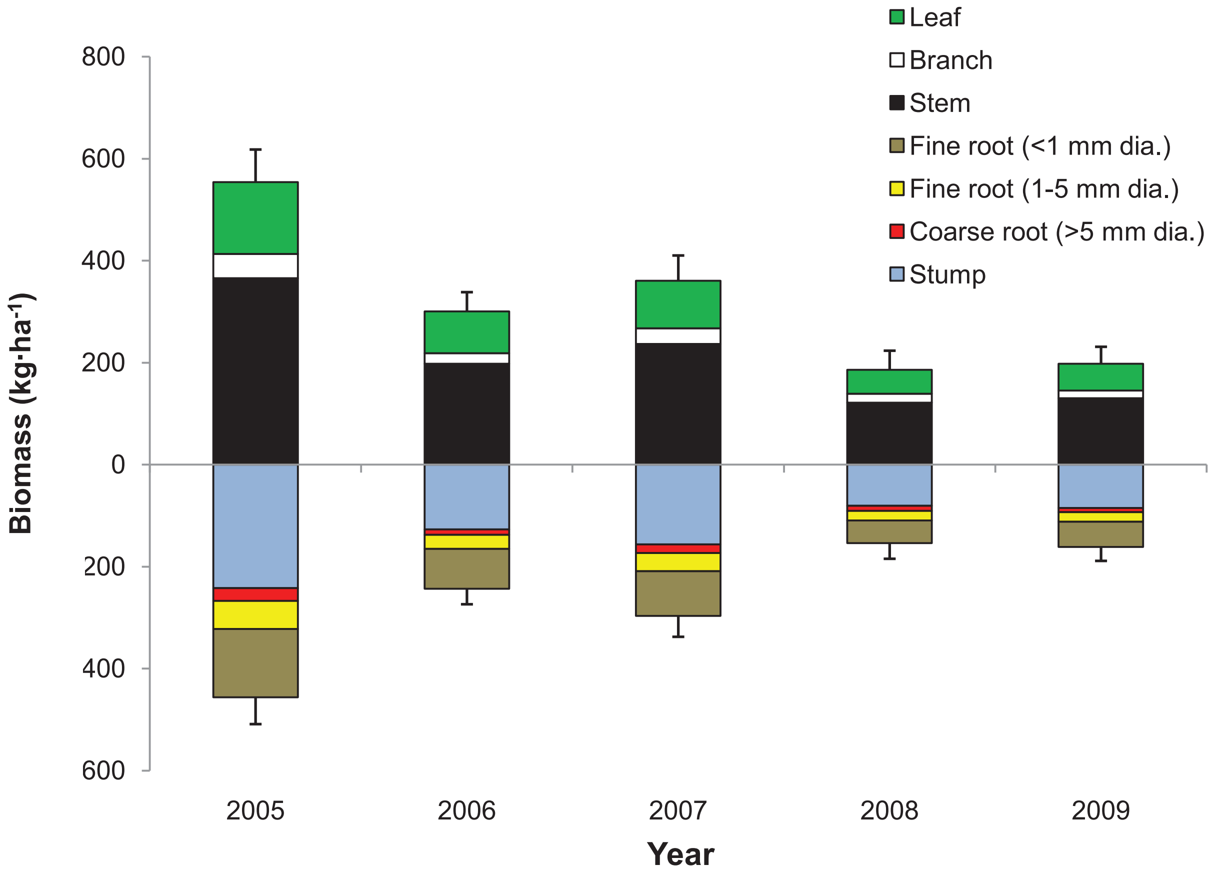


Fig. 6. Total sugar maple (*Acer saccharum*) seedling biomass over five growing seasons (n = 40 per year) in a northern hardwood forest in the Ottawa National Forest, Gogebic Co., Michigan, USA. Zero on the *Y* axis represents the groundline. Aboveground components (stem, branch, and leaf) are plotted above 0 (groundline) and belowground components (stump and roots) are plotted below 0. Standard error bars refer to shoot (above 0) and root (below 0).



resources have the capacity to recover from or withstand fire (Turner et al. 2004; Johnstone et al. 2010; Larson et al. 2013), natural disturbances (Alongi 2008), and some aspects of climate change (Huntingford et al. 2013). Ecosystems that display resilience to disturbance are often assumed to be diverse, but, in this system, a forest community heavily dominated by a single native species showed a high level of resilience.

The simplest explanation for why these seedling-killing insects did not exert stand-level impacts is that the impact of herbivory was masked by stronger environmental stressors. That is, sugar maple seedling communities experience high levels of natural mortality, consistent with this species' life history as an *r* strategist (Hett 1971; Hett and Loucks 1971; Bartlett et al. 1991; Sipe and Bazzaz 1995; Marks and Gardescu 1998; Hane 2003). Poor soils, such as in our study area, or drought, such as the one that occurred during this study, can further reduce seedling survival. Many of the seedlings killed by weevils would have died from other causes, particularly intraspecific competition, based on comparisons between plots with low and high weevil abundance. At a population scale, the impact of herbivory was apparently buffered.

Several factors, however, may pose limits to the resilience of maple seedling communities to these exotic weevils. First, overall herbivory by these weevils during the study period was <15%, so the higher levels observed during outbreak years (e.g., population levels in 1998 were nearly 30% greater than during our study; Coyle et al. 2008) could have stand-level impacts (Moser and Schütz 2006; Long et al. 2007; Belden and Pallardy 2009). Second, white-tailed deer (*Odocoileus virginianus* Zimmermann) herbivory was rarely apparent, and exotic earthworm populations were very low in our study plots, but these disturbance agents can be abundant elsewhere in this region (Larson et al. 2010; Matonis et al. 2011; Salk et al. 2011). Where anthropogenically induced high deer populations and (or) invasive earthworms co-occur with invasive weevils, their compounded or interacting effects may exceed system resilience. Third, increased drought effects associated with climate change (Williams et al. 2012) could reduce seedling tolerance to defoliation, as is commonly observed (Canham et al. 1999; Lopez-Toledo et al. 2012). Fourth, these weevils show strong preference for and high reproductive increases when feeding on raspberry (Coyle et al. 2010*b*), which is a common invader along roadsides and other clearings. Therefore, increases in certain types of human activities could foster further population buildups. Fifth, the high mortality currently occurring at the individual seedling level may be altering the genetic composition of sugar maple populations, if certain genotypes are more susceptible than others. This is consistent with our observation that certain seedlings were repeatedly more or less attacked and could have unknown interactions with each of these processes.

Larval abundance was highly clustered and likely contributed to the lack of plot-level treatment effects. Belowground herbivory is typically more chronic than acute (Andersen 1987; Yang and Karban 2009), and belowground herbivores are highly spatially heterogeneous in many cover types (Raffa and Hunt 1989; Yang and Karban 2009). There was a trend for high larval herbivory to reduce growth in plots with high larval abundance, but these relationships were not statistically significant. Increasing sampling intensity might better account for larval variability.

In addition to direct effects on seedlings, these invasive weevils may pose additional environmental consequences. First, it is likely they displaced native weevils, which seems the most plausible explanation for the consistently extremely low numbers of native beetle species in these stands (Pinski et al. 2005*a*; Coyle et al. 2012). Second, they could favor subsequent establishment rates of other invasive belowground invertebrates such as earthworms. This study system provides an opportunity to test such interactions, as only 20% of soil core samples in Pinski (2004) and 11% of our soil cores had earthworms present, indicating this region is not yet heavily infested (Holdsworth et al. 2007).

Future studies should address potential interactions among various disturbance agents affecting maple seedling communities, particularly those identified previously as potentially exceeding the limits of resilience (Folke et al. 2004). Additionally, we recommend that studies of anthropogenic inputs be conducted at both the individual plant and plant community scales under controlled manipulated conditions to facilitate rigorous comparisons, inform interpretations, and guide appropriate mitigation and management responses.

Acknowledgements

We thank Aaron Adams, Kyle Buechel, Allison Czechowitz, Morgan Jones, Michelle Jordan, Alex Kendrick, Mike Komp, Carly Lapin, Matt Moore, and Joe Schmidt (University of Wisconsin-Madison), and Bruce Birr, JoAnn Lund, and Anita Voss (USDA Forest Service, Rhinelander, Wisconsin) for field and laboratory assistance. Rick Nordheim, Peter Crump, and Nick Keuler (University of Wisconsin-Madison) provided statistical consultation and assistance. We thank the Ball Corp. (Watertown, Wisconsin) for graciously donating materials for emergence traps. We thank the Editor and two anonymous reviewers for their thoughtful comments that greatly improved this paper. This research has been funded wholly or in part by McIntire-Stennis Project No. WIS04969, the University of Wisconsin College of Agricultural and Life Sciences, Applied Ecological Services, Inc. (Brodhead, Wisconsin), and the United States Environmental Protection Agency (EPA) under the Science to Achieve Results Graduate Fellowship Program. The EPA has not officially endorsed this publication and the views expressed herein may not reflect those of the EPA.

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