



# Mile-a-minute weed (*Persicaria perfoliata*) and weevil (*Rhynoncomimus latipes*) response to varying moisture and temperature conditions



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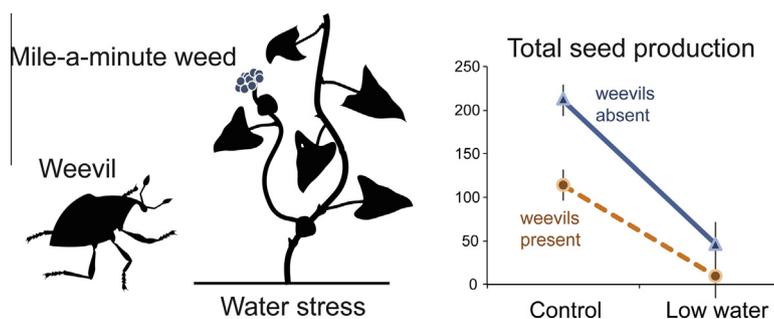
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## HIGHLIGHTS

- Effectiveness of a biocontrol agent can vary with different abiotic conditions.
- Herbivory and moisture effects on mile-a-minute weed were tested in a greenhouse.
- Both water limitation and herbivory reduced mile-a-minute reproduction and growth.
- Results are consistent with observed resurging plant populations with high rainfall.

## GRAPHICAL ABSTRACT



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## ABSTRACT

The combined effects of herbivory and water stress on growth and reproduction of mile-a-minute weed (*Persicaria perfoliata* (L.) H. Gross) were investigated in greenhouse trials over two years, with well-watered or water-limited plants either exposed or not exposed to herbivory by the mile-a-minute weevil (*Rhynoncomimus latipes* Korotyaev). Moisture limitation and weevil herbivory significantly reduced the number of seeds produced by *P. perfoliata*, with the fewest seeds produced when both factors were present. Seed weight was reduced by moisture limitation and weevil herbivory the second year, and seed viability was reduced by herbivory both years. Plant biomass was lower both years under conditions of water limitation, with an additional effect of herbivory the second year. Well-watered plants the second year also produced substantially more weevils than water-limited plants by the end of the season. Results are consistent with field observations suggesting that years of high rainfall allow resurgence of *P. perfoliata* plant populations that were previously suppressed by *R. latipes*. An additional environmental chamber trial assessed the interaction between the weed and weevil at two different temperatures. Here, plant mortality occurred only at the higher temperature with weevil herbivory, suggesting that herbivory has a greater negative effect on *P. perfoliata* under warm conditions. Additional studies on temperature effects are needed for a more complete understanding of interactions between *P. perfoliata* and *R. latipes* under different abiotic conditions.

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## 1. Introduction

Biological control of weeds by arthropods relies on damage inflicted by herbivores to limit plant growth and reproduction. Variation in abiotic factors affects plants directly, and also

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influences the feeding and reproduction of their herbivores, both directly and indirectly through effects on host-plant quality (Koricheva et al., 1998; Larsson, 1989). Physiological and chemical changes due to differences in moisture availability can alter plant nutritional quality and palatability to herbivores (Gutbrodt et al., 2011; Huberty and Denno, 2004). In addition, temperature affects plants and herbivores differently, which modifies the impact that herbivores have on their host plants (Bale et al., 2002). Abiotic variability in the environment thus can influence the effectiveness and outcome of a biological control program.

The dual impact of limited moisture and herbivory on invasive weeds has been explored in several biological control systems. Moisture limitation combined with herbivory by the cinnabar moth, *Tyria jacobaeae* (L.), reduced growth and reproduction of tansy ragwort, *Senecio jacobaea* L., under both natural and experimental conditions (Cox and McEvoy, 1983). Similar reductions in target weeds under limited moisture conditions have been observed in other biological control programs (Dhileepan, 2003; Dhileepan et al., 2000; Willis et al., 1993). However, some plants exhibit higher tolerance to herbivory under low-moisture conditions. For example, Sun et al. (2010) reported greater tolerance to simulated herbivory under low water conditions than with adequate moisture levels for the invasive weed *Alternanthera philoxeroides* (Martius) Grisebach (alligatorweed), a species that colonizes both aquatic and terrestrial habitats. Spotted knapweed, *Centaurea stoebe* L., subsp. *micranthos*, was not affected by summer drought, but feeding by the root weevil *Cyphocleonus achates* (Fahraeus) reduced knapweed growth regardless of drought conditions (Corn et al., 2007).

*Persicaria perfoliata* (L.) H. Gross (Polygonaceae), also known as mile-a-minute weed or Devil's tearthumb, is an aggressive annual vine native to Asia that was accidentally introduced into the mid-Atlantic region of the USA in the 1930s (Moul, 1948). The Asian weevil *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae) was first released in the USA in 2004 as a biological control agent of *P. perfoliata*, following extensive testing to verify its host-specificity (Colpetzer et al., 2004a; Frye et al., 2010; Hough-Goldstein et al., 2009; Lake et al., 2011). The weevils overwinter as adults, emerging in the spring when *P. perfoliata* plants are first available (Lake et al., 2011). They lay eggs on *P. perfoliata* leaves, stems, and capitula (Colpetzer et al., 2004b). Larvae bore into the stems at plant nodes, feed internally until fully developed, and pupate in the soil. The weevils go through at least three to four overlapping generations during the summer in the mid-Atlantic region (Lake et al., 2011).

Feeding damage by *R. latipes* has been shown to reduce *P. perfoliata* percent cover and biomass, and delay and reduce seed production (Cutting and Hough-Goldstein, 2013; Hough-Goldstein and LaCoss, 2012; Hough-Goldstein et al., 2008, 2009; Lake et al., 2011). However, the impact of *R. latipes* on mile-a-minute populations has varied from year to year. For example, monitored release quadrats had low percent cover of *P. perfoliata* and high weevil densities in 2008 and 2010, but relatively high percent cover and low weevil densities in 2009, possibly due to higher moisture and cooler temperatures that year (Lake, 2011). In other field plots, *P. perfoliata* biomass was reduced by weevil feeding in 2010, but not in 2011 (Cutting and Hough-Goldstein, 2013). Again, higher temperatures and lower precipitation in 2010 may have caused greater weevil impact on drought-stressed plants, while in 2011 good moisture conditions and moderate temperatures may have fostered extensive weed growth (Cutting and Hough-Goldstein, 2013). However, the interacting effects of moisture and temperature on the impact of *R. latipes* on *P. perfoliata* have not been verified experimentally.

The objective of this study was to examine the interaction between *R. latipes* and *P. perfoliata* under controlled moisture

conditions. An additional trial assessed the interactions between the weed and weevil at two different temperatures. Our goal was to determine how different abiotic conditions affect the ability of this insect to control mile-a-minute weed.

## 2. Materials and methods

Mile-a-minute plants for all experiments were grown from cuttings dipped in powdered rooting hormone (Hormodin<sup>®</sup> 1, OHP Inc., Mainland, PA, USA) and placed in vermiculite cells for two weeks. Rooted cuttings were transplanted into 13-cm pots (in 2012) or larger flats (in 2013) filled with Pro-Mix BX (Premier Tech Horticulture, Rivière-du-Loup, Québec, Canada). Plants were approximately 4–5 weeks old (from cutting) when used in experiments. Weevils for all experiments were shipped overnight by the New Jersey Department of Agriculture Philip Alampi Beneficial Insects Laboratory, Trenton, NJ.

### 2.1. Water limitation experiment, 2012

Four treatments were compared in a greenhouse trial in 2012, using potted plants placed individually in 36 × 36 × 61 cm fabric cages (BioQuip Products, Rancho Dominguez, CA, USA). A 30-cm diameter dish with 5 cm of vermiculite was placed under each plant to provide additional substrate for pupating weevils. Treatments consisted of all combinations of two factors, water limitation and weevil herbivory. Water-limited plants were checked three times per week, and watered only when at least half of the plants had wilting leaves on at least one-third of the plant. During the 11-week experiment, these plants were watered 12 times, approximately every 6.4 days. Control plants were watered three times per week. Both treatments were given 500 ml of water in pots plus 250 ml in vermiculite each time they were watered. Herbivory treatments had five male and five female weevils. Cages were arranged in a completely randomized block design with five blocks, and rotated within their blocks once per week to limit bench effects.

This experiment began on 8 August. Temperature in the greenhouse ranged from 21.1 to 25.6 °C during the day and 18.3 to 22.8 °C at night, and no supplemental lights were used. Plants were fertilized with all-purpose 21-5-20 fertilizer (Peters Excel Base Formulation, Everris NA, Inc., Dublin, OH, USA) once per month. Seeds that had fallen from plants were collected and counted three times per week. On 24 October, plants were clipped at soil level and placed in a drying oven at 95–100 °C for one week. All remaining seeds and all weevils were collected and counted. A mile-a-minute terminal in water was placed in each cage for an additional week to collect missed and newly emerged weevils. Root growth in both treatments was constrained by the size of the containers, essentially filling all available soil, and therefore roots were not weighed for analysis.

Fifty mature blue seeds (or all seeds if there were fewer than 50) were randomly selected from each plant to calculate average seed weight. The outer perianth of these seeds was removed before weighing. Seed viability was assessed with a triphenyl tetrazolium chloride (TZ) assay (Peters, 2000; Smith et al., 2014), on 25 randomly selected seeds (or all that were available) from each plant. A small incision was made in each seed coat. Seeds were soaked in distilled water for 24 h, and then in a 1% solution of 2,3,5-triphenyl-2H-tetrazolium chloride (Sigma-Aldrich Chemical Supply Company, St. Louis, MO, USA) for 24 h. In viable seeds, dehydrogenase enzymes present in living tissue reduce the TZ and stain the embryo red (Roberts, 1972). Treated seeds were examined visually for red staining and scored as viable or non-viable.

## 2.2. Water limitation experiment, 2013

The 2013 experiment followed a similar protocol to the 2012 experiment, but was conducted over the entire growing season rather than just August through October, and provided more substrate for weevil pupation than in the 2012 trial. Single plants in 2013 were grown in  $36 \times 51 \times 15$  cm deep greenhouse flats, filled with approximately 10 cm of Pro-Mix BX, enclosed in  $60 \times 60 \times 60$  cm domed fabric cages (BugDorm, Taichung, Taiwan). The experiment started on 22 May, with 10 replicates of each treatment, two in each of five blocks. During the first part of the experiment, supplemental greenhouse lighting was provided whenever ambient light was below 12 klx between the hours of 06.00 and 22.00. Supplemental lights were turned off on 5 August so plants and weevils would be exposed to natural photoperiods as fall approached.

Herbivory treatments again received five male and five female weevils. Water-limited plants in 2013 were all watered to saturation once per week, but individual plants that showed signs of moisture stress were watered immediately to prevent plant death. Control plants were watered to saturation three times per week. Plants were monitored and rotated within their blocks once per week. On 7 October, all plants were clipped at their base, placed in a drying oven at 95–100 °C for 3 weeks, and weighed. Weevils present in cages were counted and removed; missed and newly emerged weevils were collected for two more weeks, with mile-a-minute terminals in water placed in each cage. Plant roots again filled all available space in all containers, and were not weighed.

All seeds were removed at the end of the experiment and counted. Twenty-five mature seeds were chosen at random from each plant, cleaned to remove their perianths, and weighed as a group to obtain the average seed weight. To test seed viability, 20 seeds from each plant were tested using the same TZ assay method as in 2012.

## 2.3. Temperature experiment

For this experiment, all combinations of two factors were tested: temperature (23 or 30 °C) and weevil herbivory (five male plus five female weevils or no weevils). The lower temperature is close to the mean temperature in Newark, DE, in June–August, while the higher temperature is close to the average high temperature during June–August (<http://countrystudies.us/united-states/weather/delaware/newark.htm>). Two incubators with eight plants each (four with and four without herbivory) were used to test the two temperatures simultaneously; after six weeks a second trial was run with the temperatures assigned to each incubator switched, to control for any incubator effects. The first trial began on 5 June, and the second on 24 July, 2013. Plants were grown individually in  $54 \times 28 \times 6$  cm soil flats filled with Pro-Mix BX, and enclosed in  $36 \times 61 \times 36$  cm fabric cages. For each trial, plants were fertilized once, and rotated weekly. At the end of each trial, weevils were counted, and additional weevils were collected from the cages for two more weeks. Plants were cut at soil level, placed in a drying oven at 80 °C for two weeks, and weighed.

## 2.4. Statistical analysis

Data from both water limitation experiments were analyzed using a linear mixed model in R statistical software (lmerTest package; R Core Team, 2013). Moisture level and herbivory were assigned as fixed factors and block as a random factor. The model was generated with the lmer() command, and degrees of freedom were estimated using the Kenward–Rogers method. The model to test seed viability results from the TZ assay was generated with

blocks using the glm() command with a binomial distribution and tested with an ANOVA with a chi-square distribution.

In the temperature experiment, near 100% plant death in the high temperature treatment with weevils prevented the use of complete factorial comparisons. A test of equal proportions with continuity correction was used to compare plant mortality for plants with weevils at high versus low temperatures. Excluding the treatment at high temperature and with weevils, plant dry biomass was compared using a mixed model with Tukey's HSD (mult-comp package; R Core Team, 2013). The two trials were considered blocks in this analysis, to account for any incubator effects.

## 3. Results

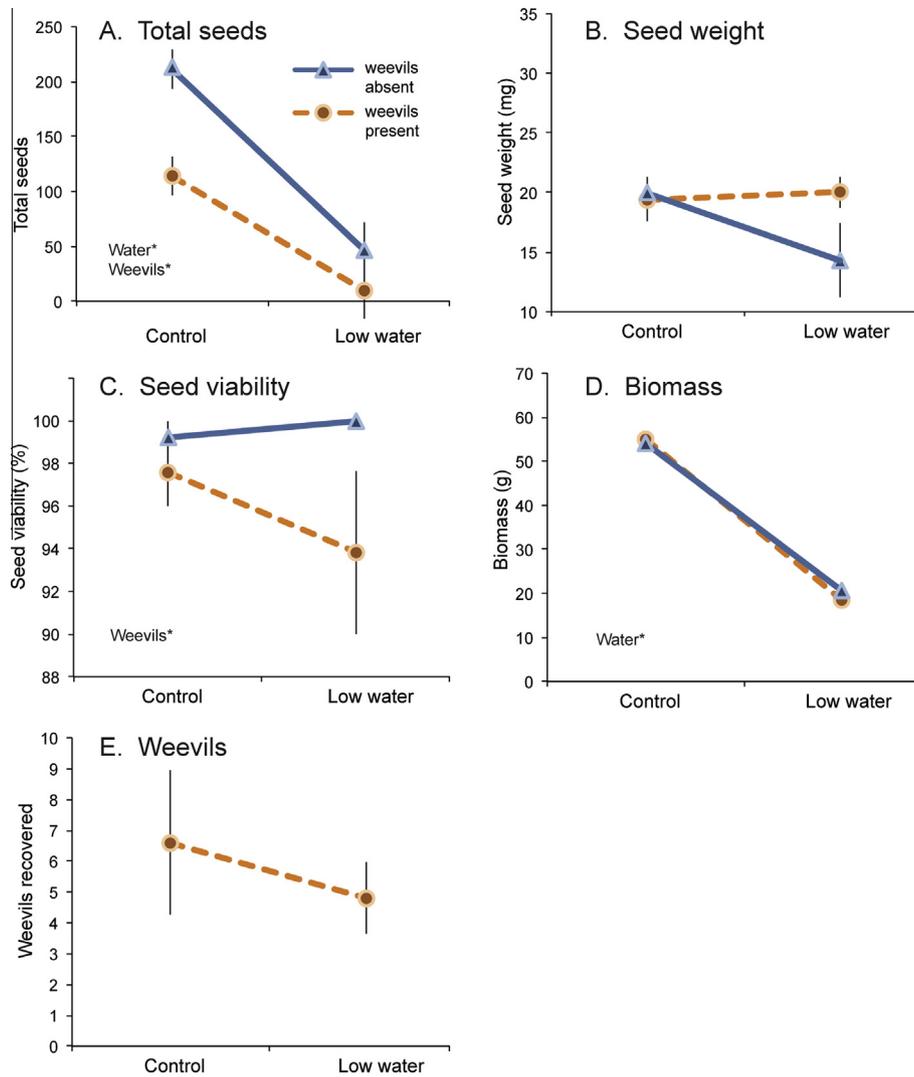
### 3.1. Water limitation experiment, 2012

The date of first seed collection was not influenced by water limitation ( $F_{1,10.5} = 0.06$ ,  $P = 0.806$ ) or herbivory ( $F_{1,10.9} = 0.17$ ,  $P = 0.684$ ) with no significant interaction ( $F_{1,10.9} = 0.17$ ,  $P = 0.684$ ). Both water limitation and herbivory significantly reduced the total number of seeds produced by plants (water:  $F_{1,12} = 26.36$ ,  $P < 0.001$ ; herbivory:  $F_{1,12} = 6.52$ ,  $P = 0.025$ ), with no significant interaction ( $F_{1,12} = 2.72$ ,  $P = 0.125$ ). Under well-watered conditions, plants without weevils produced almost twice as many seeds as those with weevils; very few seeds were produced under low water conditions with weevils present (Fig. 1A). Seed weight was not affected by water conditions ( $F_{1,12} = 1.81$ ,  $P = 0.203$ ) or herbivory ( $F_{1,12} = 1.86$ ,  $P = 0.197$ ) and there was no significant interaction ( $F_{1,12} = 2.85$ ,  $P = 0.1174$ ; Fig. 1B). Based on the TZ test, seed viability averaged more than 90% for all treatments. Viability was significantly reduced by herbivory ( $X^2_1 = 5.38$ ,  $P = 0.020$ ), but not by low water ( $X^2_1 = 0.28$ ,  $P = 0.593$ ), with no significant interaction ( $X^2_1 = 1.96$ ,  $P = 0.161$ ; Fig. 1C).

Plant biomass was reduced by more than half in the low-water treatment ( $F_{1,12} = 1520.49$ ,  $P < 0.001$ ), but was not affected by herbivory ( $F_{1,12} = 0.32$ ,  $P = 0.581$ ) and there was no significant interaction between the factors ( $F_{1,12} = 2.72$ ,  $P = 0.125$ ; Fig. 1D). Low water conditions did not significantly impact overall weevil survival or reproduction in 2012 in the weevil-present treatments ( $F_{1,4} = 0.48$ ,  $P = 0.528$ ; Fig. 1E). However, an increase in weevil numbers from the original ten introduced was only seen in a single (control) cage.

### 3.2. Water limitation experiment, 2013

As in 2012, the number of days to first mature seed in 2013 did not differ by water conditions ( $F_{1,32} < 0.001$ ,  $P = 0.948$ ) or herbivory ( $F_{1,32} = 1.94$ ,  $P = 0.173$ ), with no significant interaction ( $F_{1,32} = 1.94$ ,  $P = 0.173$ ). Total seed production was significantly reduced by low water conditions ( $F_{1,32} = 49.69$ ,  $P < 0.001$ ) and herbivory ( $F_{1,32} = 46.81$ ,  $P < 0.001$ ), and there was a significant interaction between water and herbivory treatments ( $F_{1,32} = 13.44$ ,  $P = 0.001$ ; Fig. 2A). Plants without weevils produced 2.7 and 2.1 times more seeds than those with weevils, under control and low water conditions, respectively. The average seed weight was also significantly reduced by both low water ( $F_{1,32} = 7.85$ ,  $P < 0.001$ ) and herbivory ( $F_{1,32} = 36.21$ ,  $P < 0.001$ ) in 2013, with a significant interaction between factors ( $F_{1,32} = 6.88$ ,  $P = 0.013$ ; Fig. 2B). There was a 9.9% weight reduction due to weevil presence under normal watering, and <0.5% difference under low water conditions. Seed viability in 2013 averaged about 90% with weevils and >98% without weevils. As in 2012, viability was significantly reduced by the presence of weevils ( $X^2_1 = 29.41$ ,  $P < 0.001$ ), but not by water conditions ( $X^2_1 = 1.07$ ,  $P = 0.301$ ), with no significant interaction ( $X^2_1 = 0.001$ ,  $P = 0.971$ ; Fig. 2C).



**Fig. 1.** Mean ( $\pm$ SEM) (A) total seeds, (B) seed weight, (C) seed viability, (D) aboveground biomass, and (E) recovered weevils from the 2012 water limitation experiment (8 August–24 October). \* Indicates main effects differed significantly ( $P \leq 0.05$ , linear mixed model).

Plant biomass in 2013 was significantly reduced by low water ( $F_{1,32} = 54.13$ ,  $P < 0.001$ ) and herbivory ( $F_{1,32} = 4.81$ ,  $P = 0.035$ ), with no significant interaction between the two factors ( $F_{1,32} = 0.01$ ,  $P = 0.908$ ; Fig. 2D). At the end of this experiment, most cages contained more than the original ten weevils, indicating successful reproduction. The number of weevils was significantly reduced by low water conditions ( $F_{1,14} = 55.98$ ,  $P < 0.001$ ), with more than eight times as many weevils recovered from plants in the control than in the low-water treatment (Fig. 2E).

### 3.3. Temperature experiment

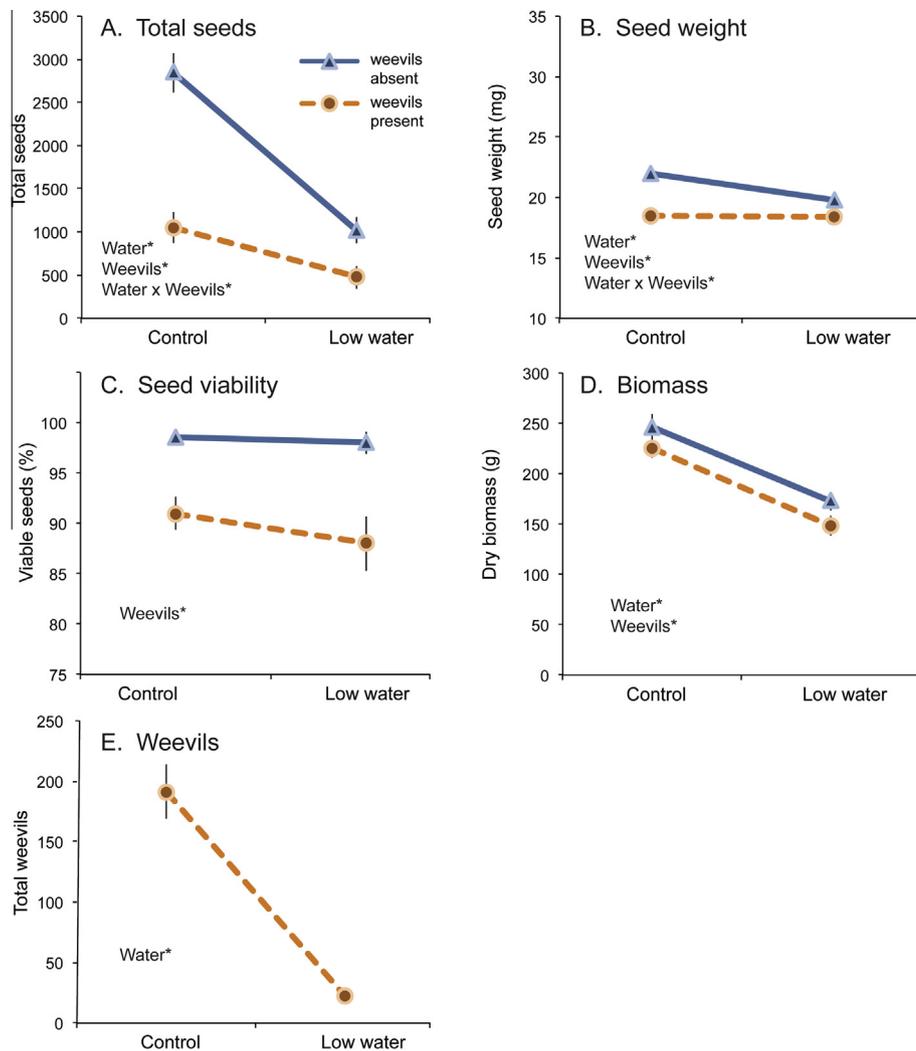
Seven of the eight plants kept at 30 °C with weevils did not survive the six-week experiment, while no plants died in the other treatments (Table 1). Significantly more plants died at 30 °C than at 23 °C ( $X^2_1 = 9.14$ ,  $P = 0.002$ ). Plants with weevils at 23 °C had significantly lower biomass than plants without weevils at either temperature (Table 1).

## 4. Discussion

Moisture limitation and weevil herbivory had significant effects on the numbers of seeds produced by *P. perfoliata* both years of this

experiment, with the fewest seeds produced when both factors were present. A similar reduction in total numbers of seeds with herbivory was found by Smith and Hough-Goldstein (2014). However, a delay in seed production, observed in previous studies (Hough-Goldstein et al., 2008; Smith and Hough-Goldstein, 2014) did not occur here. In the mid-Atlantic region, *P. perfoliata* seed production often begins in late June, but the majority of seeds are produced later in the season, from August to October (Mountain, 1989; Hough-Goldstein et al., 2008; Cutting and Hough-Goldstein, 2013; Smith et al., 2014). The timing of seed production varies by location, and is probably influenced by various microclimatic conditions (Sultan and Bazzaz, 1993; Sultan, 2001) in addition to photoperiod, but specific factors affecting phenology of seed production in *P. perfoliata* are not known.

Seed weight was reduced by moisture limitation and weevil herbivory the second year, when the experiment was conducted over a longer time period and with greater weevil reproduction than in the first year. Seed viability and viability are also affected when weevils feed directly on developing seed clusters (Colpetzer et al., 2004b; Smith and Hough-Goldstein, 2014). In general the production of larger (heavier) seeds is advantageous to plants, assuming no reduction in seed number, because larger seeds



**Fig. 2.** Mean ( $\pm$ SEM) (A) total seeds, (B) seed weight, (C) seed viability, (D) aboveground biomass, and (E) recovered weevils from the 2013 water limitation experiment (22 May–7 October). \* Indicates main effects differed significantly ( $P \leq 0.05$ , linear mixed model).

**Table 1**

Plant mortality and plant dry biomass (mean  $\pm$  SEM) at low or high temperatures, with and without weevil herbivory.

Treatment	Plant mortality (out of eight)	Biomass (g)
23 °C, no weevils	0	2.14 $\pm$ 0.39 a
30 °C, no weevils	0	1.88 $\pm$ 0.28 a
23 °C, with weevils	0	1.44 $\pm$ 0.33 b
30 °C, with weevils	7	0.58

Means followed by the same letter are not significantly different (mixed model, Tukey's HSD;  $F_2 = 9.24$ ,  $P = 0.001$ ). The 30 °C treatment with weevils was excluded from analysis.

usually have higher germination and emergence rates and produce larger seedlings than smaller seeds (Hendrix et al., 1991; Winn, 1988). Thus the presence of weevils under limited water conditions can have a substantial impact on both seed quantity and quality, which may translate into large cumulative effects on plant populations over time (Maron and Crone, 2006).

Plant biomass was also much lower both years under conditions of water limitation, with an additional effect of weevil herbivory the second year. In other studies, the biomass of *P. perfoliata* was reduced by *R. latipes* herbivory (Cutting and Hough-Goldstein, 2013; Hough-Goldstein and LaCoss, 2012), and also by light

limitation (Hough-Goldstein and LaCoss, 2012; Smith and Hough-Goldstein, 2013). A meta-analysis of plant responses to herbivory under low or high resource conditions (light, water, or nutrients) found that typically the main effects of the treatments were most important, with fewer seeds and lower biomass produced under herbivory and low resources compared to no herbivory and high resources (Hawkes and Sullivan, 2001). Our observations followed this pattern, with water limitation causing significant reduction in *P. perfoliata* reproductive output and biomass, and only additive effects of herbivory in most cases.

Weevils in the control conditions reproduced in much higher numbers compared to the water-limited treatments in the second year experiment. The well-watered control plants were larger, providing more substrate for egg-laying and stem material for larval development. In previous studies, when given a choice, weevils preferred larger, more vigorous sun-grown plants over smaller, etiolated, shade-grown plants (Hough-Goldstein and LaCoss, 2012; Smith and Hough-Goldstein, 2013). In addition, Hough-Goldstein et al. (2014) found much higher production of F1 weevils in sun than in shade. It is likely that the more vigorous well-watered plants in this experiment produced more weevils due to higher plant quality and quantity. Similar results have been found in other studies, with more insects recovered from high-resource plants (Center et al., 2014; Crush et al., 2008).

However, lower reproduction by weevils on the water-limited plants in this experiment may have been in part an artifact of experimental conditions. Weevils here were limited to a 10-cm deep layer of soil for pupation, which may have become too dry in the water-limited treatment, causing death of pupating weevils. In the field, weevils may have the option of either moving deeper into the soil or finding more suitable microhabitats to pupate in times of drought.

The temperature experiment reported here was probably not very realistic, because it only lasted six weeks, and was conducted in environmental chambers with lower than optimal light levels. However, under the conditions tested, plant mortality occurred only at the higher temperature with weevil herbivory, suggesting that herbivory has a greater negative effect on *P. perfoliata* under warm conditions.

Temperature is the dominant abiotic factor directly affecting the development rate of herbivorous insects (Bale et al., 2002). For a multivoltine insect like *R. latipes*, the expectation is that more generations per year will be produced under warmer temperatures, which could increase its impact on the weed. Larsson (1989) notes that warm, dry periods in temperate areas may directly enhance growth, survival and reproduction of insects, while stressing their host plants at the same time. Similarly, Mattson and Haack (1987) describe a variety of ways in which drought conditions can provide a more favorable environment for phytophagous insects. They suggest that insect responses to drought effects are nonlinear, with suitability of conditions for insect growth and reproduction first increasing to an optimum, and then decreasing under conditions of severe and prolonged drought.

With *P. perfoliata*, we currently do not have any indications of favorable effects of “slight” drought on the weevil, although higher temperatures are likely favorable up to a point (J.H.-G., unpublished data). In the experiments reported here, relatively severe (but not lethal) water limitation substantially reduced weevil reproduction compared to that on the well-watered plants. *P. perfoliata* is shallowly rooted (Mountain, 1989), making it susceptible to drought. In field releases of the weevil, at least one monitored release site was subject to dry conditions that caused the plants to die back substantially at both release and control sites, and weevil numbers were also much reduced (Hough-Goldstein et al., 2009). Because our experiments here used only two levels of both watering and weevils, we are limited in conclusions that can be drawn concerning interactions in the field. The temperature trial was further limited due to plant mortality in the high temperature plus herbivory treatments.

Recent studies have emphasized the context-specific nature of biological control, with both biotic and abiotic environmental conditions potentially affecting success or failure (Center et al., 2014; Ortega et al., 2012; Shea et al., 2005). For example, van Wyk and van Wilgen (2002) found resurgence of invasive water hyacinth in South Africa following above-average rainfall, which increased nutrient input. In this system, a low resident population of biological control weevils (caused by poor host plant quality) allowed the resurging plant population to temporarily ‘escape’ control. With improved nutrient conditions and plant growth, the insects multiplied and again reduced the weed population over the next two years (van Wyk and van Wilgen, 2002). A similar scenario may occur with *P. perfoliata*, with years of high rainfall allowing resurgence of plant populations that were previously suppressed by *R. latipes*, followed by increased weevil populations that are again able to suppress the weed. Ongoing studies on temperature effects should allow for a more complete understanding of interactions between *P. perfoliata* and the *R. latipes* under different abiotic conditions.

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