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Relationship of Black Vine Weevil Egg Density and Damage to Two Cranberry Cultivars

Betsey Miller[1]
Department of Horticulture, Oregon State University, 4017 Ag and Life Sciences Building, Corvallis, OR 97331

Denny J. Bruck
USDA-ARS, Horticultural Crops Research Laboratory, 3420 NW Orchard Avenue, Corvallis, OR 97331

Vaughn Walton
Department of Horticulture, Oregon State University, 4017 Ag and Life Sciences Building, Corvallis, OR 97331

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Abstract. **Black vine weevil (BVW), *Otiorhynchus sulcatus* (Coleoptera: Curculionidae, Fabricius), is a serious pest of cranberry, *Vaccinium macrocarpon* Ait. Larvae feed undetected within the soil and cause damage to roots and underground vines. We correlated damage caused by feeding larvae from known BVW egg densities. Two cultivars of potted cranberry vines, 'Stevens' and 'McFarlin', were inoculated with 0, 5, 10, 20, 40, and 80 eggs per pot. Root damage and canopy health were assessed. 'Stevens' exceeded 'McFarlin' in dry shoot weight, total shoot length, total leaf area, and dry root weight before egg treatments. Damage to underground vines increased with increasing egg density and more damage was found in 'Stevens' than 'McFarlin' at the highest egg densities. In August, plant water use and total shoot length in 'McFarlin' were significantly greater in plants treated with 0–5 eggs per pot compared with plants treated with 40–80 eggs per pot. The effect on total shoot length was more pronounced in October. 'Stevens' showed no response to increasing BVW density for up to 24 weeks. Destructive measurements showed decreased root weight in 'McFarlin' but not 'Stevens'. Both cultivars showed a similar decrease in dry shoot weight, total shoot length, and percent green leaf area with increasing BVW egg density. Root damage increased as BVW egg density increased and this damage resulted in reduced plant water use for 'McFarlin'. Reduced shoot growth and leaf area was recorded for both cultivars, although these effects were more apparent in 'McFarlin' and at an earlier stage than in 'Stevens'.**

American cranberry *Vaccinium macrocarpon* Ait. is one of North America's most important indigenous commercially produced crops (Pollack and Perez, 2001). The U.S. cranberry industry is valued at ≈$444 million annually with 15,459 ha in production; in the Pacific Northwest (PNW) region, ≈1618 ha are dedicated to cranberries (National Agricultural Statistics Service, 2009; Thomson et al., 1999). A large proportion of production in the PNW is planted with two cultivars. 'Stevens' comprises 75% of cranberry production in Oregon and 38% in Washington. 'McFarlin' comprises 54% of production in Washington (Cranberry Marketing Committee, 2008).

There are several insect pests threatening cranberry production in the PNW including BVW *Otiorhynchus sulcatus* (Fabricius) (Coleoptera: Curculionidae) (Patten and Daniels, 2010). This prolific species is part of a complex of polyphagous root weevils that attack crops worldwide; cranberry is one of more than 80 plant species that serve as host for BVW (Smith, 1932). Adults feed on foliage, causing notching along the margins of leaves; however, this damage is rarely of economic importance. Larvae feed on belowground plant tissues and this causes major root damage (Smith, 1927). Larvae consume fine roots and girdle subsurface stems of cranberry vines, which lead to plant desiccation (Crowley, 1923; Schread, 1972). This desiccation is most likely a result of the negative impact of root damage on water absorption and transpiration as is the case in kiwi vines (Black et al., 2011). Impacts of BVW root feeding are not clearly described in cranberry beds (Ingraham, 1991). A better description of this impact will in the future help to quantify longer-term effects of BVW feeding in this cropping system.

Black vine weevils exhibit cryptic behavior. Subterranean larvae feed throughout the growing season, and damage can go undetected in the field through most of the year. During warmer and drier periods of summer, however, plants experience increased water stress and previously undetected damage becomes visibly evident as vines wilt, become dry and brittle, or die (K.D. Patten, personal communication). Light soils such as peat and sand are typical of West Coast cranberry beds. BVW larvae prefer these soils over heavier soils (Wilcox et al., 1934) and these fields are often prone to BVW attack. It is estimated that in Washington cranberry beds, infestations exceeding 12 BVW larvae per square meter create patches of dead or dying vines within two seasons (Booth et al., 2002). Field observations indicate that damaged areas left untreated may quadruple in size within one year (Ingraham, 1991).

Timing and targeting of control of BVW are difficult as a result of their cryptic behavior and lack of suitable control options. Monitoring for larvae is destructive and prohibitively time-consuming because it involves digging up whole cranberry vines and carefully inspecting soil and roots. For these reasons, it is recommended that growers monitor BVW populations by sweep-netting for nocturnal adults (Patten and Daniels, 2010). Numerous researchers have quantified the fecundity of BVW (Cram and Pearson, 1965; Fisher, 2006; Garth and Shanks, 1978; Nielson and Dunlap, 1981; Smith, 1927, 1932; Son & Lewis, 2005). Of these studies, only one has examined the potential fecundity of BVW in cranberry. In British Columbia, when Cram and Pearson (1965) fed cranberry foliage ('McFarlin') to BVW, their average fecundity was 163 eggs with a viability of 74%. It is therefore possible to make a crude estimation of potential egg quantities by quantifying adult populations. Research in other insect–plant systems has demonstrated that the number of eggs applied to plants is equivalent to herbivore density (Björkman et al., 2008). The focus of our study was to examine the relationship between BVW egg density and damage to cranberry roots and its association with plant desiccation and vine growth.

Materials and Methods

Planting and maintenance. Plants were grown in pots under simulated field conditions. Cultivars were selected based on the large proportion of production they represent

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[1]To whom reprint requests should be addressed; e-mail betsey.miller@hort.oregonstate.edu.

in the PNW. In Feb. and Mar. 2009, cranberry plants were collected from Grayland, Pacific County, WA ('McFarlin') and Langlois, Curry County, OR ('Stevens'). All plant material was collected as sod mats ≈60 × 90 cm with a root and soil depth of 10 to 15 cm. Square plugs, sized ≈10 × 10 cm, were cut from mats and planted into pots (10 × 10 × 12 cm). The potting media (pH 4.9–5.2; electrical conductivity 0.5 $dS \cdot m^{-1}$) was a 2:1 mixture of sand (dredged from the Willamette River, Corvallis, OR) to peat (Sungro Horticulture, Vancouver, British Columbia, Canada) and was formulated to reflect the texture and water-holding capacity of the field soils in Langlois, OR, which have a significant amount of coarse sand and minimally decomposed organic matter (Bullards Ferrelo-Hebo complex) (Natural Resources Conservation Service, 2011). We planted vines to allow ≈6 cm of headspace from the soil surface to the top edge of the pot for top-dressing with soil media after the first application of fertilizer (a technique used to discourage growth of algae and moss). Aboveground lateral stems were pruned to 2.5 cm above the rim of the pot. The two cultivars, McFarlin and Stevens, were planted on 15 Feb. and 20 Mar. 2009, respectively.

We maintained vigorous growth with weekly applications of liquid fertilizer (Scotts MiracleGro, Marysville, OH; 18N–7.9P–17.4K) at a rate of 1.92 $mL \cdot L^{-1}$ for the first 4 weeks of the experiment. Initially, plants were maintained in a greenhouse at a mean daytime temperature of 17 ± 2 °C. All plants were moved to a screen house for a 1-month acclimation period and then transferred and maintained outdoors.

We constructed outdoor raised beds (30 cm deep) inside of a mesh exclusion cage (1.68 × 1.68 × 1.68 m) and filled them completely with the described sand:peat media in two locations in Corvallis, OR. We placed each potted plant within an empty pot that was permanently installed in the raised bed to facilitate easy removal of plants for data collection. Plants were spaced ≈5 cm apart and 5 cm from the edge of the bed. Each trial consisted of four blocks of each cultivar (18 plants per block). Plants were assigned to blocks based on size and vigor; within each block, treatments were randomly assigned to three plants (12 plants per treatment). Plants were irrigated as needed throughout the study.

Black vine weevil egg inoculation. We obtained viable BVW eggs (brown to dark brown) from a colony maintained at the USDA-ARS Horticultural Crops Research Laboratory in Corvallis, OR (Fisher and Bruck, 2004). Treatment groups included 0, 5, 10, 20, 40, and 80 eggs per pot. These egg densities represent a proportion of larvae feeding on root tissues (Cram and Pearson, 1965; Son and Lewis, 2005). Eggs were placed onto petri dishes fit with moist filter paper (Whatman No. 1) and stored at 4 °C for no more than 2 weeks until the time of inoculation (Fisher and Bruck, 2004). We performed egg inoculations twice over a 14-d interval with half of the total egg density applied at each inoculation. For the five-egg treatment, all eggs were applied in a single application.

All plants were irrigated before inoculation. To inoculate, we made a 15-mm diameter, 1-cm depth depression in the soil next to cranberry stems and washed eggs from each dish into the depression with deionized water from a laboratory squirt bottle. Because of egg availability and to promote uniformity of growth at the time of inoculation, 'McFarlin' plants were inoculated 2 weeks earlier (29 May and 12 June) than 'Stevens' (12 and 25 June). We collected all subsequent plant health measurements first on 'McFarlin' plants and 2 weeks later on 'Stevens' plants. In this study we did not directly determine BVW larval survival as a result of the difficulty in recovering individuals (Fisher and Bruck, 2008; Garth and Shanks, 1978). We assumed that egg viability would be between 75% and 89% (Cram and Pearson, 1965; Son and Lewis, 2005) based on the mean ambient temperatures at which cranberry plants were grown during the experimental period (Fig. 1). Therefore, we expected larval damage to be proportional to the initial levels of egg inoculations.

Time-zero reference sampling. To get a reference base for cranberry plant health, we measured a subsample of 24 plants from each trial (three plants from each block of each cultivar) for total length of upright shoots, shoot weight, leaf area, and root weight using destructive techniques. We measured shoot length from the lateral stem (or the soil level, if the shoot came from an underground lateral) to the tip of the most terminal leaf to the nearest millimeter. Leaf surface area (cm^2) was measured with a leaf area meter fitted with a conveyor belt (LI-3000/LI-3050A; LI-COR, Lincoln, NE). Root material was rinsed and all plant material was dried in an oven at 73 ± 3 °C (shoots for 48 h; roots for 96 h) and weighed (Stieber and Peterson, 1987).

Repeated sampling. We measured the water use and shoot length of each plant on 1 June, 11 Aug., and 7 Oct. for 'McFarlin' and on 16 June, 28 Aug., and 19 Oct. for 'Stevens'. We measured water use gravimetrically as the weight of water lost in transpiration over 24 h (Ramirez et al., 2006). All pots were watered and weighed at container capacity at dawn and reweighed after 24 h to determine daily water use in each treatment. Plant water use was measured during periods with no precipitation.

Destructive sampling. Surviving plants were destructively sampled during Feb. 2010. Tissues were sampled in the same manner as described previously. In this case, we measured leaf area by separating green from purple or dead leaf areas, excluding leaves that had fallen from the plant. These measurements were converted into percentage of total leaf area for analysis.

Rinsed root material was air-dried at room temperature for a minimum of 48 h before we determined the number of underground vines with feeding damage. All vines longer than 2 cm were separated from the root mass and feeding damage was recorded to determine a percentage of vines with damage. A vine was considered damaged when evidence of stem injury by BVW larvae was observed.

Statistical analysis. For time-zero reference data, we compared mean total shoot length, dry shoot weight, total leaf surface area, and dry root weight between cultivars using General Linear Model (GLM) analysis of variance (ANOVA). In addition, we performed a linear regression analysis to test for correlation between total shoot length and total leaf area. The initial model included a parameter to test for similarity between regression coefficients of each cultivar (Kleinbaum et al., 2008).

Preliminary tests indicated that egg density levels of 0–5, 10–20, and 40–80 eggs resulted in similar plant responses; t tests for similarities in means did not differ significantly between 0- and 5-egg, 10- and 20-egg, and 40- and 80-egg treatments for repeated sampling data ($t < 1.0$, df = 286, $P > 0.04$) or for shoot length, shoot weight, and root weight from destructive sampling ($t < 1.7$, df = 94, $P > 0.10$). Hence, for subsequent tests, treatments were grouped into three egg density categories: low (0–5 eggs), medium (10–20 eggs), and high (40–80 eggs). In all experiments, blocks were assigned to standardize treatment means for plant vigor, so differences between blocks were expected and not of interest. Therefore, in all analyses, block was included as a nuisance variable to account for variation between blocks, but interactions involving this factor were not considered (Lomax, 2001).

Data from repeated sampling were analyzed using factorial repeated measures ANOVA with trial location, BVW egg density, and cultivar as between-subjects factors and sampling date as the within-subjects factor. Univariate repeated-measures analyses require that data have sphericity, meaning that the difference scores of paired levels of the repeated measures factor have equal population variance (Hedeker and Gibbons, 2006). Mauchly's test for sphericity assesses the probability of obtaining a value for the test statistic (W) as extreme as that observed given the null hypothesis (sphericity). To correct for this violation, df must be adjusted with one of several correction factors. However, this correction is not necessary if a multivariate approach is used (that is, an approach that assumes that the response variable is influenced by multiple factors). Our data produced highly significant values for Mauchly's test, suggesting a violation of the sphericity assumption for both shoot length data ($W = 0.95$, df = 2, $P < 0.001$) and plant water use data ($W = 0.80$, df = 2, $P < 0.001$). Thus, we used multivariate tests for these analyses.

Mean shoot weight, shoot length, root weight, percent vine damage, and percent green leaf area from destructive sampling were compared between trial locations, egg density groups, and cultivars using GLM ANOVA. Percentage data were ArcSin$\sqrt{x}$ transformed to fit a normal distribution.

Significant differences between means from both repeated and destructive sampling data were determined with Tukey's honestly significant difference (HSD) test. For repeated-measures analyses, df were large enough to allow for the use of a pooled error term to account for effects of treatment within and across sampling dates (Winer et al., 1991). All analyses were performed using STATISTICA 7.1 (2010).

Results

Time-zero reference sampling. Before BVW egg inoculation, 'Stevens' displayed higher mean shoot weight, total shoot length, leaf surface area, and root weight than 'McFarlin' ($F > 5.67$, df = 1, 40, $P < 0.002$; Table 1). We found, however, that cultivar had no effect on the linear relationship between shoot length and leaf surface area ($F = 0.69$, df = 1, 44, $P = 0.412$) and therefore data from both cultivars were combined to describe this relationship. Our analysis showed that leaf area (y) increased with shoot length (x) ($R^2 = 0.9487$, $F = 435.67$, df = 2, 45, $P < 0.001$). The function describing this correlation was:

$$y = 0.117 + 0.0784x$$

As a result of this strong association and the destructive nature of measuring leaf area, shoot length was regarded as an indicator of leaf area for repeated measurements.

Repeated sampling. There was a significant interaction between the effects of cultivar, sampling date, and trial location on plant water use ($F = 4.12$, df = 6, 480, $P = 0.017$) and total shoot length ($F = 8.42$, df = 6, 480, $P < 0.001$); therefore, each cultivar is presented separately. For 'Stevens', data from both sites were pooled, because the effect of location was not significant for this cultivar ($F < 0.062$, df = 1, 120, $P > 0.802$). Increasing BVW egg density had no effect on 'Stevens' plant water use ($F = 1.89$, df = 1, 120, $P = 0.156$) or total shoot length ($F = 0.993$, df = 1, 120, $P = 0.373$) on any of the sampling dates.

For 'McFarlin', however, we detected statistically different responses in each location

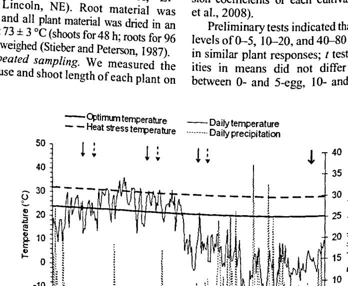

Fig. 1. Maximum daily temperature (°C) and daily precipitation (mm) in Corvallis, OR, from May 2009 to Mar. 2010. Bold lines indicate the optimal temperature for cranberry growth (24 °C) and the temperature at which cranberry plants experience significant heat stress (32 °C) (Xu et al., 2011). Solid and dashed arrows indicate dates of repeated sampling for 'McFarlin' and 'Stevens', respectively. The bold arrow indicates the date of destructive sampling.

Table 1. Time-zero mean dry shoot weight, total shoot length, total leaf area, and dry root weight by cultivar.

Cultivar	Dry shoot wt (g/pot)	Total shoot length (cm/pot)	Total leaf area (cm^2/pot)	Dry root wt (g/pot)
Stevens	0.63 ± 0.09 a[z]	121 ± 14 a	95.3 ± 11.8 a	13.8 ± 0.5 a
McFarlin	0.35 ± 0.05 b	81 ± 9 b	63.9 ± 7.0 b	6.5 ± 0.6 b

[z]Means ± SE within a column followed by the same letter do not differ significantly (General Linear Model analysis of variance, $P > 0.05$).

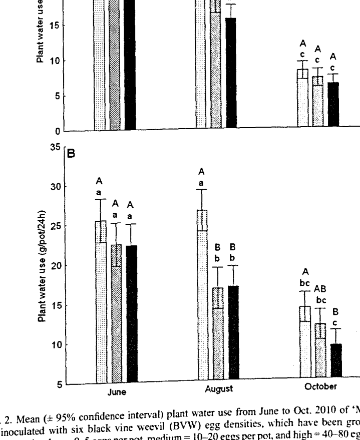

Fig. 2. Mean (± 95% confidence interval) plant water use from June to Oct. 2010 of 'McFarlin' plants inoculated with six black vine weevil (BVW) egg densities, which have been grouped into three categories; low = 0–5 eggs per pot, medium = 10–20 eggs per pot, and high = 40–80 eggs per pot. Trial Sites 1 (A) and 2 (B) are displayed. Bars within one location accompanied by the same lower case letter are not significantly different between treatment groups across all sampling dates; bars within one location accompanied by the same capital letter are not significantly different between treatment groups on that sample date ($P > 0.05$, Tukey's honestly significant difference).

to increasing BVW density ($F > 3.19$, df = 2, 120, $P < 0.045$). Results are therefore presented separately for each location (Sites 1 and 2).

Data from each site showed a significant sampling date by egg density interaction ($F > 3.92$, df = 4, 120, $P < 0.004$). The first measurements in June showed statistically similar plant water use at all egg densities at both sites ($F < 1.79$, df = 2, 60, $P > 0.176$; Fig. 2A–B). By August, however, 8 weeks after initial egg inoculation, plant water use in the low-egg density group was significantly greater compared with the high-egg density group at site 1 ($F = 8.20$, df = 2, 60, $P < 0.001$; Fig. 2A) and significantly greater compared with the medium- and high-egg density groups at Site 2 ($F = 18.7$, df = 2, 60, $P < 0.001$; Fig. 2B). In October, 16 weeks after inoculation, plant water use was uniform between egg density groups at Site 1 ($F = 2.31$, df = 2, 60, $P = 0.108$; Fig. 2A). At Site 2, plant water use was greater in the low-egg density group compared with the high-egg density group ($F = 6.38$, df = 2, 60, $P = 0.003$; Fig. 2B).

Total shoot length in 'McFarlin' was similarly uniform between egg density groups at both locations in June ($F < 3.07$, df = 2, 60, $P > 0.054$; Fig. 3A–B). At Site 1 in August, total shoot length was greater in the low- and medium-egg density groups compared with the high-egg density group ($F = 4.01$, df = 2, 60, $P = 0.021$; Fig. 3A). This pattern continued into October with more pronounced differences ($F = 5.50$, df = 2, 60, $P = 0.006$; Fig. 3A). At Site 2 in August, total shoot length was greater in the low-egg density group compared with the medium-egg density group and greater in the medium-egg density group compared with the high-egg density group ($F = 20.4$, df = 2, 60, $P < 0.001$; Fig. 3B). By October, there was no difference between the medium- and high-egg densities and the low-egg density group had greater total shoot length than the other two groups ($F = 23.4$, df = 2, 60, $P < 0.001$; Fig. 3B).

Destructive sampling. The effect of location was not significant for any of the destructively measured parameters ($F < 3.63$, df = 1, 240, $P > 0.05$) and therefore data from both locations were combined. Cultivar did not significantly impact dry shoot weight ($F = 1.36$, df = 2, 264, $P = 0.245$) or total shoot length ($F = 0.062$, df = 2, 264, $P = 0.804$); therefore, these data were pooled by cultivar data for ANOVA. Dry shoot weight ($F = 35.9$, df = 2, 276, $P < 0.001$) and total shoot length ($F = 20.319$, df = 2, 276, $P < 0.001$) both significantly decreased with increasing BVW egg density (Table 2). The effect of BVW density on dry root weight varied by cultivar ($F = 240$, df = 1, 264, $P < 0.001$). Mean dry root weight was significantly greater in 'Stevens' than in 'McFarlin' by 82.2% ± 3.8% (df = 264, $P < 0.05$, Tukey's HSD; Table 3). 'Stevens' dry root weight did not change significantly as egg density increased ($F = 0.448$, df = 2, 132, $P = 0.640$; Table 3). In 'McFarlin', however, dry root weight was significantly greater in the low-egg density group compared with the higher egg density categories ($F = 7.83$, df = 2, 132, $P < 0.001$; Table 3).

When looking at percent vine damage (injury to underground vines) and percent green leaf area, the effects of egg density were statistically different between cultivars ($F > 7.62$, df = 2, 264, $P < 0.001$); therefore, each cultivar is presented separately. In 'Stevens', increasing BVW egg density resulted in a significant increase in percent vine damage ($F = 57.5$, df = 2, 132, $P < 0.001$; Fig. 4A) and a significant decrease in percent green leaf area ($F = 58.03$, df = 2, 132, $P < 0.001$; Fig. 4B). 'McFarlin' showed a similar response with an increase in percent vine damage ($F = 29.0$, df = 2, 132, $P < 0.001$) and a decrease in percent green leaf area ($F = 19.8$, df = 2, 132, $P < 0.001$) as BVW egg densities increased. The differences in means between egg density treatments were less pronounced for 'McFarlin' (Fig. 4A–B). 'Stevens' displayed a higher percent vine damage than 'McFarlin' at high BVW egg densities and higher percent green leaf area at the low-egg density level (df = 264, $P < 0.05$, Tukey's HSD; Fig. 4A–B).

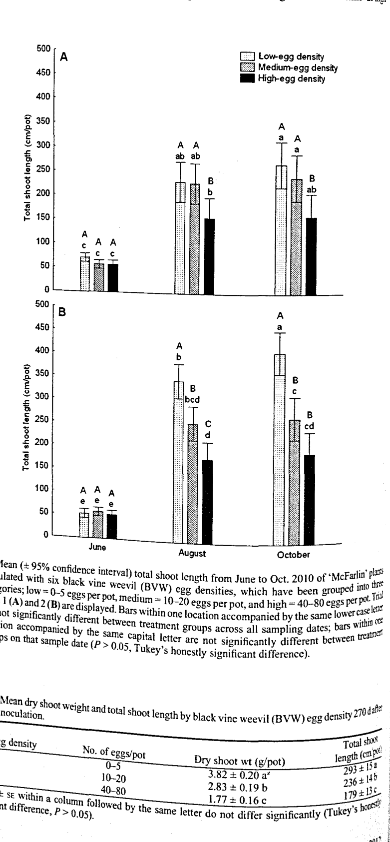

Fig. 3. Mean (± 95% confidence interval) total shoot length from June to Oct. 2010 of 'McFarlin' plants inoculated with six black vine weevil (BVW) egg densities, which have been grouped into three categories; low = 0–5 eggs per pot, medium = 10–20 eggs per pot, and high = 40–80 eggs per pot. Trial Sites 1 (A) and 2 (B) are displayed. Bars within one location accompanied by the same lower case letter are not significantly different between treatment groups across all sampling dates; bars within one location accompanied by the same capital letter are not significantly different between treatment groups on that sample date ($P > 0.05$, Tukey's honestly significant difference).

Table 2. Mean dry shoot weight and total shoot length by black vine weevil (BVW) egg density 270 d after egg inoculation.

BVW egg density	No. of eggs/pot	Dry shoot wt (g/pot)	Total shoot length (cm/pot)
Low	0–5	3.82 ± 0.20 a[z]	293 ± 15 a
Medium	10–20	2.83 ± 0.19 b	236 ± 14 b
High	40–80	1.77 ± 0.16 c	179 ± 13 c

[z]Means ± SE within a column followed by the same letter do not differ significantly (Tukey's honestly significant difference, $P > 0.05$).

Table 3. Mean dry root weight by cultivar and black vine weevil (BVW) egg density 270 d after egg inoculation.

BVW egg density	No. of eggs/pot	Dry root wt (g/pot)	
		Stevens	McFarlin
Low	0–5	9.41 ± 0.41 a[z]	5.80 ± 0.30 a
Medium	10–20	8.91 ± 0.32 a	4.60 ± 0.25 b
High	40–80	9.03 ± 0.44 a	4.61 ± 0.27 b

[z]Means ± SE within a column followed by the same letter do not differ significantly (Tukey's honestly significant difference, $P > 0.05$).

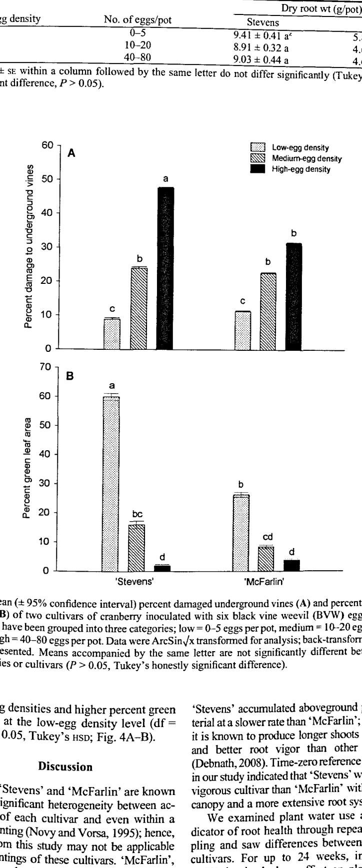

Fig. 4. Mean (± 95% confidence interval) percent damaged underground vines (**A**) and percent green leaf area (**B**) of two cultivars of cranberry inoculated with six black vine weevil (BVW) egg densities, which have been grouped into three categories; low = 0–5 eggs per pot, medium = 10–20 eggs per pot, and high = 40–80 eggs per pot. Data were ArcSin√x transformed for analysis; back-transformed means are presented. Means accompanied by the same letter are not significantly different between egg densities or cultivars ($P > 0.05$, Tukey's honestly significant difference).

Discussion

Both 'Stevens' and 'McFarlin' are known to have significant heterogeneity between accessions of each cultivar and even within a single planting (Novy and Vorsa, 1995); hence, results from this study may not be applicable to all plantings of these cultivars. 'McFarlin', a highly productive cultivar, is best known for having high fruit quality and resistance to frost and diseases (Strik et al., 2002). 'Stevens' is a cross between 'McFarlin' and 'Potter' and is known for its vigor. Our data indicated that 'Stevens' accumulated aboveground plant material at a slower rate than 'McFarlin'; however, it is known to produce longer shoots and roots and better root vigor than other cultivars (Debnath, 2008). Time-zero reference sampling in our study indicated that 'Stevens' was a more vigorous cultivar than 'McFarlin' with a larger canopy and a more extensive root system.

We examined plant water use as an indicator of root health through repeated sampling and saw differences between the two cultivars. For up to 24 weeks, increasing BVW density had no effect on plant water use in 'Stevens'. 'McFarlin' plants, however, displayed compromised transpiration during August as evidenced by significantly lower plant water use in the low-egg density compared with the high-egg density inoculation. These results are consistent with those of Ma et al. (2009), who found that mechanical root pruning resulted in a significant decrease in water consumption of potted wheat plants. In our study, this decrease in water consumption was most pronounced during high temperature conditions, which occurred in August, indicating that high BVW density has an effect on the plant's ability to overcome heat stress. Incidentally, in the PNW, the highest temperatures coincide with a period of increased larval feeding intensity (Smith, 1932).

Cranberry physiology renders the plant particularly susceptible to heat stress. The guard cells, which regulate the opening and closing of stomata, do not respond readily to changes in environmental conditions. Thus, compared with other crop plants, cranberry has a high transpiration rate and relatively low water use efficiency (Strik and Davenport, 2002). In our study, the damaged root system and subsequent desiccation of the canopy most likely increased plant stress at high BVW egg densities. 'Stevens', which showed no change in plant water use with increasing BVW egg density, also showed no difference in total shoot length between egg density treatments during the growing season. These results suggest that the more vigorous root system of 'Stevens' was better able to tolerate feeding damage by BVW larvae and deliver needed moisture to the canopy. Our data are consistent with Baumann et al. (2005), who demonstrated that 'Stevens' has a deeper rooting system and a higher root-to-shoot ratio compared with other cultivars, making it less susceptible to drought stress. Conversely, in 'McFarlin', plants subjected to higher egg density treatments displayed lower total shoot length, and this effect became more pronounced over time, even after average temperatures and differences in water consumption decreased. This response, consistent with the findings of Ma et al. (2009), was most likely a result of a compromised root system.

Photosynthesis was not measured directly in this study as a result of the small size of cranberry foliage, which necessitates the use of specialized equipment or destructive techniques (Jeranyama and DeMoranville, 2009; Wei et al., 2010). In young plants, photosynthesis is proportional to leaf area (Koyama and Kikuzawa, 2009). Our data showed that, for both cultivars of cranberry, shoot length was an accurate indicator of leaf surface area. This correlation allowed for an indirect, nondestructive estimation of photosynthetic capacity during the growing season. Taking into account the impact of plant architecture on light transmittance to individual leaves, we conclude that increased BVW damage to roots resulted in reduced shoot length and most likely reduced the total photosynthetic capacity of the plant. This conclusion is supported by other studies showing that plants can exhibit reduced rates of growth and photosynthesis in response to root herbivory (Gange and Brown, 1989; Hou et al., 1997).

Destructive sampling revealed effects of BVW egg density in both cultivars. 'Stevens' maintained root vigor throughout the study, showing no root response to increasing BVW egg density. Compared with 'McFarlin', 'Stevens' plants had larger root systems despite having a greater percentage of damaged vines at high egg densities. Both cultivars, however, exhibited decreased shoot weight and shoot length as BVW egg density increased with no significant differences between cultivars.

'Stevens' plants treated with low egg density had greater percent green leaf area than 'McFarlin'. However, as BVW egg density increased, there was no difference in green leaf area between the cultivars. Increasing egg density resulted in more damage to underground vines in 'Stevens' and had a greater effect on 'Stevens' green leaf area than it did on 'McFarlin'.

In both cultivars, we found reduced green leaf area in plants inoculated with only a moderate density of BVW eggs. This reduced total photosynthetic surface area will most likely be coupled with lower yield and fruit quality as found in perennial crops such as apples (Zhang and Dai, 2011), wine grapes (Keller et al., 1998), and coffee (Bote and Struik, 2011), but these impacts were not determined in this study. In regard to yield, the delayed effect of BVW pressure observed in 'Stevens' may be an important factor to consider. 'Stevens' is a midseason cultivar and ripens earlier in the season than 'McFarlin', which is a late-season cultivar; the 'Stevens' crop may therefore be potentially less affected because of the delayed onset of BVW impacts.

Our results indicate that increased BVW egg density has a negative effect on cranberry plant health and that the nature of this effect depends on cultivar and seasonal conditions. In our study, 'Stevens' appeared to be more tolerant to BVW damage than 'McFarlin', although, over time, it may also be affected by increasing BVW densities. With existing knowledge of the fecundity of BVW adults (Cram and Pearson, 1965), crude estimation of egg density is possible by quantifying adult populations. Such estimates can be used as an alternative to destructive methods for predicting the timing and severity of effects of BVW damage to 'Stevens' and 'McFarlin' cranberry beds. The impact of root damage on actual yield or translocation of water and nutrients from the roots to the plant canopy is yet to be determined. Cranberry producers in the PNW should consider BVW tolerance when selecting cultivars for new plantings and more cranberry cultivars should be screened to assess sensitivity to BVW damage. The results of this study provide useful information on the relative risk of BVW damage to two prominent cranberry cultivars grown in the PNW. We also believe that the methods discussed in this report provide initial screening methods to indicate BVW tolerance in future cultivars.

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