Ground Covers Influence the Abundance and Behavior of Japanese Beetles

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ABSTRACT Ground covers were tested for 3 consecutive yr for their effect on Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), abundance and behavior in a blueberry planting. Alsike clover (*Trifolium hybridum* L.), buckwheat (*Fagopyrum esculentum* Moench), perennial ryegrass (*Lolium perenne* L.), and bare ground were compared within row-middles for their effect on abundance of adult female beetles, female beetle behavior after landing, density of larvae in the soil, and survival of larvae. Adult beetles were consistently most abundant on buckwheat, followed by clover and ryegrass, while they were generally absent from bare ground plots. Larval density was three times greater in ryegrass and clover than in buckwheat, with the fewest found in bare ground. There was high variability in larval survival within treatments, but overall survival was highest in plots with ryegrass. Observations of adult beetles revealed that the proportion of time spent feeding and the frequency of feeding were higher on buckwheat and clover than on ryegrass, and the average duration of digging bouts lasted longer on ryegrass than on the other two plant treatments. These results reveal that adult *P. japonica* behavior is affected by cover crops and that this behavior translates into variation in larval density of this pest.

KEY WORDS *Popillia japonica*, generalist, pest, cultural control, insect–plant interaction

Cultural control of insect populations in agricultural fields can be achieved by planting cover crops that affect pest dispersal, colonization, or reproduction (Bugg and Waddington 1994). A cover crop is any living ground cover that is planted in the main crop (Hartwig and Ammon 2002) for its positive horticultural effects, such as weed control, reduction of soil erosion, improvement of the biological, physical and chemical properties of the soil, or pest control (USDA 1992). Increasing the diversity of plants in agricultural production can reduce pest abundance (Root 1973), but the mechanisms and degree of pest reduction are dependent on the biology and behavior of the insect species. In many agricultural systems, insect behavior is disrupted by cover crops planted with a main crop, such that the pest is repelled or reduced in abundance (Risch 1981, Tonhasca and Stinner 1991, Bugg 1992, Bugg and Waddington 1994, Prokopy 1994, Hartwig and Ammon 2002).

Popillia japonica Newman is currently the most important insect pest for producers of highbush blueberry, *Vaccinium corymbosum* L., in the Midwestern United States (Pest Management Strategic Plan 2001, Isaacs et al. 2004). It is a univoltine insect, with greatest adult abundance from mid-July to August (Fleming 1972), when beetles feed on leaf tissue and ripe blueberry fruits. If beetles are not controlled, fruit can be contaminated when harvesting machines knock beetles off the bushes. More than 70% of Michigan's 7,285 ha of blueberry crop is harvested mechanically (Kleweno and Matthews 2004), and because the market demands fruit completely free of insect contamination, strategies are needed to minimize the risk of adult beetles being present during harvest. Foliar insecticide applications continue to be the foundation of *P. japonica* management in blueberries and many other fruit crops, as growers strive to meet exacting quality standards. Strategies are needed to reduce populations of *P. japonica* within infested blueberry production regions and minimize the risk of beetles spreading into uninfested areas, while minimizing the need for insecticide inputs.

Shortly after the introduction of *P. japonica* into the United States, Langford et al. (1940, 1941) and Hawley (1944) conducted extensive larval population surveys in crop fields, revealing the relative suitability of different systems for this pest. More recent work found that reduced-till soybean plots had higher adult *P. japonica* densities than tilled fields (Hammond and Stinner 1987, Smith et al. 1988) and intercropping and strip-cropping in soybean and corn fields have been recommended as part of an integrated pest management (IPM) program to reduce movement of adult *P. japonica* (Bohlen and Barrett 1990, Tonhasca and Stinner 1991, Holmes and Barrett 1997). In a comparison of larval abundance in nursery fields, *P. japonica*

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were 10-fold more abundant in weedy fields compared with cultivated fields (Smitley 1996). Cultivation of row-middles of highbush blueberry fields reduces the number of *P. japonica* larvae in the soil by 72% compared with field with permanent sod (Szendrei et al. 2005). Despite documenting the effect of soil cover on larval abundance, it is not clear whether the observed patterns were caused by female preference for egg-laying habitats or differential larval survival in fields with varying plant composition. Soil parameters such as moisture, texture, and organic matter content (Régnière et al. 1981, Allsopp et al. 1992), short plant cover (Hawley 1944), and light intensity (Dalthorp et al. 1999) can influence the number of eggs laid by *P. japonica.* These findings suggest that using different plant species and tillage practices in the larval habitat of *P. japonica* can manipulate oviposition and/or larval development as a component of IPM programs. Although cultivation between the rows of blueberry plants can reduce larval abundance of *P. japonica* (Szendrei et al. 2005), the negative horticultural implications of this management method require development of alternative strategies to reduce egg laying and/or larval survival. One potential alternative is to plant ground covers in blueberry row middles that reduce *P. japonica* oviposition and larval development.

The larvae of *P. japonica* are facultative monophages because of their limited mobility, so the mother's oviposition site selection decisions are crucial for survival of the offspring and for determining subsequent population distributions (Dalthorp et al. 1999). This selectivity for oviposition sites (Jaenike 1978) may provide an opportunity for behavioral manipulation of this destructive pest. Development of such an approach will require an understanding of the specific cues used by beetles during egglaying, the method by which this can be successfully manipulated, and the implementation of this method for the protection of a commercial crop (Foster and Harris 1997).

As part of an integrated response to the invasion by this pest into blueberry production regions, there is a need for testing cover crop species that do not attract *P. japonica* and that reduce their oviposition or larval survival. These plants must withstand the acidic and wet conditions typical of highbush blueberry fields and satisfy grower's horticultural needs. In this study, three acid-tolerant ground covers were evaluated in blueberry fields for their suitability for *P. japonica.* Alsike clover (*Trifolium hybridum* L.), buckwheat (*Fagopyrum esculentum* Moench), and perennial ryegrass (*Lolium perenne* L.) were chosen because their morphological and biological characteristics are different from each other, and these plants are recommended cover crops in other perennial fruit systems (USDA 1992). These plants were compared with bare ground within a blueberry planting to determine their ability to manipulate (1) abundance of adult female beetles, (2) female beetle behavior after landing on the ground cover, (3) abundance of *P. japonica* larvae in the soil, and (4) survival of *P. japonica* larvae.

Materials and Methods

Experiments were conducted in a replicated field experiment at the Trevor Nichols Research Complex, Fennville, MI. The 4,050-m^2 highbush blueberry planting (*Vaccinium corymbosum* variety Bluecrop) was established using 2-yr-old bushes in 2001 on a 3.7 by 1.4-m plant spacing with 12 bushes in each row. Four row-middle treatments were established with either perennial ryegrass, alsike clover, buckwheat, or bare ground between the rows of bushes. Each plot consisted of a set of two row-middles with the same treatment on either side of a row of blueberry bushes, and treatments were randomized with five replicates. Cover crops were seeded in the row-middles (53 m^2) in May and June 2002. Buckwheat was reseeded in the third week of June in 2003 and 2004. The seeding rates were 27 kg/ha for perennial ryegrass, 22 kg/ha for clover, and 67 kg/ha for buckwheat (Michigan State Seed Solutions, Grand Ledge, MI). The bare ground plots received herbicide (Roundup Ultra 4WSL, glyphosate; Monsanto, St. Louis, MO at 31.3 ml/liter), spot-applied with a 3.8-liter hand-held sprayer when needed, to keep the soil free of vegetation during the growing seasons. Overhead irrigation of all the row-middles was started from the time of seeding and continued weekly or as needed throughout the growing season in each year of this study to create conditions typical of a commercial blueberry field. Ryegrass plots were mowed throughout the growing season as needed.

Effect of Cover Crops on Adult *P. japonica*. One of the row-middles from adjacent pairs containing the same treatment was selected at random, and the number of *P. japonica* adults (both males and females) that naturally occurred in these plots was counted weekly in July and August 2002, 2003, and 2004. Observations were made from 1200 to 1400 hours on sunny days with low wind speed. Each visual survey of a row-middle lasted 2 min, measured with a timer. The observer walked down one side of the row-middle and back on the other side, focusing on the area in the row-middle and counting the number of beetles. The observer walked on the periphery of the plot, wore neutrally colored clothes, and moved evenly and slowly so as to minimize disturbance of the beetles. At the end of the 2 min, the total number of beetles per row-middle was recorded.

Larval Density Under Different Cover Crops. The naturally established population of *P. japonica* was surveyed by taking soil samples on 17 May 2002 before the cover crop seeds were sown in the plots. Subsequently, larval density was sampled in the same plots on 9 October 2002, 22 September 2003, and 8 October 2004. Larvae were sampled by taking five 15-cm-deep soil cores from the two row-middles in each plot (total of 10 samples per plot) using a cylindrical golf cup cutter (area = 95 cm^2; Parmenter & Andre, Grand Rapids, MI), with samples distributed randomly across the plots. Soil cores were examined in the field, and all beetle larvae were placed in plastic bags with a small amount of soil. The bags were labeled with date, treatment, and number of larvae. Bags were transported to the laboratory in a cooler containing an icepack. Larvae were identified to species using the diagnostic rastral patterns and morphological features of the labrum (Vittum et al. 1999).

Survival of *P. japonica* Larvae Under Cover Crops. Plots for this experiment were established in a different part of the same blueberry field as above to create row-middles with bare ground, clover, buckwheat, or ryegrass in a completely randomized design with five replicates (same seeding rates as above). To obtain first-instar *P. japonica,* adult beetles were collected from a grassy field (East Lansing, MI) with Japanese beetle Expando Traps baited with floral and sex lures (Great Lakes IPM, Vestaburg, MI), deployed on 1 July 2002, 2003, and 2004. Adults were transported to the laboratory daily, and ≈500 beetles (≈50:50 sex ratio) were put into each of ten 36 by 24 by 12-cm plastic containers. The lid of each container had a 10 by 15-cm opening for ventilation, which was covered with nylon mesh to stop beetles from escaping. A 5-cm-deep layer of moist sand (Dixie Cut Stone & Marble, Bridgeport, MI) was provided as an oviposition medium in each container. Slices of apple were placed on top of the sand to provide moisture and food ad libitum. Containers were kept at constant environmental conditions (16 L:8 D, 30% RH, 24–26°C), and fresh slices of apples were added as needed. First instars were collected by placing a handful of sand in a no. 18 mesh sieve and washing the sand with running tap water. Larvae were transferred using a paintbrush (no. 12; Loew-Cornell, Grand Haven, MI) to moist filter paper (90 mm diameter; Whatman International, Maidstone, UK) in 10-cm-diameter petri dishes (Becton Dickinson and Co., Franklin Lakes, NJ) and kept at room temperature in the laboratory until further use in the field, but not longer than 12 h.

First instars were transported from the laboratory to the field plots in a cooler. Five PVC pipes (15 cm deep by 8 cm diameter) were pounded into the soil in each row-middle, for a total of 25 pipes per treatment. A 10-cm-deep hole was made in the soil in the middle of the PVC pipe with the end of a paintbrush, and five larvae were carefully placed in the hole with the brush. The hole was covered with soil and irrigated with 500 ml water to wash soil particles close to the larvae and to provide moisture. After placement of larvae in the soil, the PVC pipes were covered with mesh to prevent oviposition by naturally occurring *P. japonica.* First instars were placed in the field in the last week of July, and PVC pipes were removed in the first week of September in 2002, 2003, and 2004. Soil was shaken from the pipes onto a tray and examined for *P. japonica* larvae. The number of *P. japonica* larvae per PVC pipe was recorded.

Effect of Cover Crops on *P. japonica* Behavior. The behavior of individual adult female *P. japonica* was observed in row-middles planted with clover, buckwheat, or ryegrass. Beetles were not observed on bare ground plots, because they were not present in these row-middles. Sex was distinguished by observing the shape of the front tibia (Fleming 1972) without disrupting the insect's natural behavior. Observations were conducted in July and August 2002 and 2003 weekly from 1000 to 1600 hours on sunny days with low wind speed. A total of 35 observations were made in buckwheat and ryegrass and 39 in clover during the 2 yr of this study. Observations were recorded by the same observer throughout, and the order of observations on the three cover crop treatments was randomized. An observation began as soon as a beetle was located by the observer on one of the cover crops and lasted for a maximum of 1 h or until the beetle left the plot or disappeared under the surface of the soil. The observer wore neutrally colored clothes and moved evenly and slowly so as to minimize the disturbance of the beetles. Continuous focal sampling, in which all of the behaviors of the subject are recorded, was conducted using The Observer 3.0 (2002) and 4.0 (2003) software (Noldus Information Technologies, Wageninger, The Netherlands) loaded onto a laptop computer that was carried by the observer. Behaviors that were observed and recorded are defined in Table 1, including digging behavior that is associated with oviposition (Szendrei and Isaacs 2005).

Table 1. Description of behavioral elements of *P. japonica* observed on four row-middle treatments in a highbush blueberry planting.

Characteristic	Description
Behavior	
Stationary	Standing motionless
Walk	Moving on a surface by means of leg motions
Groom	Using legs or mouthparts to clean abdomen or antennae
Feed	Moving mouthparts for the purpose of ingesting food
Dig	Moving first pair of legs to loosen the soil surface
Position	
Crop	At least two thirds of insect's body is in contact with plant
Soil	At least two thirds of insect's body is in contact with soil surface

Data Analysis. Adult density, natural larval density, and larval survival data did not meet the assumptions of parametric analysis of variance (ANOVA). For analysis of adult density data, Friedman's test was used to determine overall effect of treatment on the mean ranks, followed by Fisher least significant difference (LSD) test for means separation (SAS Institute 2001). Comparisons of grand means for these three experiments were also performed with a Friedman's test, followed by Fisher LSD test (SAS Institute 2001). Subsamples taken for the natural larval infestation and larval survival experiments were averaged for each plot. Larval density and larval survival data were analyzed using Kruskall-Wallis tests (SAS Institute 2001), and means separations were done using a Mann–Whitney *U* test.

Average rate of behavior (frequency/min), average duration (min) of each behavior, and duration as a percent of the total observed time (% observation) of each behavioral element were compared among the

Table 2. Comparison of *P. japonica* adult density in four different row-middle treatments in highbush blueberry

Treatment	Mean ± SE *P. japonica* adults/row-middle/2 min			
	2002	2003	2004	Grand mean
Bare ground	0.00 ± 0.00c	0.20 ± 0.12d	0.00 ± 0.00c	0.07 ± 0.12c
Buckwheat	2.07 ± 0.39a	11.45 ± 1.78a	0.67 ± 0.27a	3.91 ± 0.67a
Clover	0.87 ± 0.47b	2.50 ± 0.53b	0.37 ± 0.18ab	1.14 ± 0.18b
Ryegrass	0.60 ± 0.34b	1.55 ± 0.38c	0.03 ± 0.03bc	0.59 ± 0.14b

Values within a column followed by the same letter are not significantly different ($\alpha = 0.05$).

three cover crops using a multivariate ANOVA (SAS Institute 2001), providing a comparison of the overall behavior among cover crops. Pairwise contrasts between mean values of the different measures of behavior were made to determine significant differences between cover crops. The proportions of time spent on plant or soil surfaces were compared using a two-way ANOVA (SAS Institute 2001), with type of surface (plant or soil) and cover crop treatments as factors.

Results

Effect of Cover Crops on Adult *P. japonica*. The proportion of adult *P. japonica* observed was significantly different among the row-middle treatments throughout this study (2002: $\chi^2 = 2.87$; df = 3; 2003: $\chi^2 = 6.34$; df = 3; 2004: $\chi^2 = 6.95$; df = 3; $P < 0.01$ for all dates). There was a general trend in *P. japonica* abundance on the four treatments; it was greatest on buckwheat, with decreasing abundance on clover, ryegrass, and bare ground (Table 2). Significantly more adults were found on buckwheat than on the other treatments over the 3 yr ($F = 16.57$; df = 3,12; $P < 0.01$). Bare ground had consistently fewer beetles (0.07 beetles/sample) than the plants (1.88 beetles/sample) when comparing the grand means. In 2002 and 2003, there were significantly fewer beetles on clover and ryegrass than on buckwheat. In 2002 and 2004, no adult beetles were observed on bare ground. The proportions of adults were not significantly different between ryegrass and clover in 2002 and 2004 (Table 2).

Larval Density Under Different Cover Crops. *Popillia japonica* larvae were not found in any of the soil samples from the blueberry field at the beginning of this study. After the row-middle treatments were established, *P. japonica* larval density varied significantly among the four treatments throughout the 3 yr of this study ($F = 3.68$; df = 3,12; $P < 0.01$). Row-middles with bare ground had significantly fewer larvae than clover and ryegrass treatments when comparing the grand means from the 3 yr (Table 3). Larval density was highest on ryegrass and clover in the 3 yr, and the average larval densities were not significantly different between these two treatments in any of the years. Across the 3 yr, larvae were three times more abundant in ryegrass and clover than in buckwheat. In 2003, bare ground had significantly fewer larvae than the other treatments ($\chi^2 = 16.12$; df = 3; $P < 0.01$), whereas in 2004 ($\chi^2 = 11.95$; df = 3; $P < 0.01$), the larval density in bare ground and buckwheat was significantly lower than in the two other row-middle treatments.

Survival of *P. japonica* Larvae Under Cover Crops. *Popillia japonica* larval survival was significantly different among the four row-middle treatments in 2002 ($\chi^2 = 8.91$; df = 3; $P = 0.03$), but not in the other 2 yr (2003: $\chi^2 = 5.26$; df = 3; $P = 0.15$ and 2004: $\chi^2 = 5.81$; df = 3; $P = 0.12$; Table 4). Compared with ryegrass, all of the row-middle treatments significantly reduced larval survival across the 3 yr (Table 4). In 2002, the proportion of larvae found in buckwheat and bare ground was significantly lower than in ryegrass. This result was not consistent throughout the study; in 2003 and 2004, there was no significant response to row-middle treatments (Table 4). Variation across years was the lowest for larvae in plots of ryegrass.

Effect of Cover Crops on *P. japonica* Behavior. Beetle behavior was affected by the different cover crops tested in the row middles of blueberries. Beetles were stationary approximately twice as frequently on buckwheat than on the other two treatments ($F = 10.47$; df = 2,106; $P < 0.01$; Fig. 1A). Beetles walked

Table 3. Comparison of *P. japonica* larval density in four different row-middle treatments in a highbush blueberry planting

Treatment	Mean ± SE *P. japonica* larvae/sample			
	2002	2003	2004	Grand mean
Bare ground	0.00 ± 0.00b	0.10 ± 0.04c	0.06 ± 0.03b	0.05 ± 0.01c
Buckwheat	0.30 ± 0.08ab	0.64 ± 0.14b	0.00 ± 0.00b	0.31 ± 0.06bc
Clover	0.88 ± 0.31a	2.06 ± 0.19a	0.22 ± 0.07a	1.05 ± 0.12ab
Ryegrass	0.88 ± 0.19a	2.58 ± 0.24a	0.30 ± 0.08a	1.25 ± 0.12a

Values within a column followed by the same letter are not significantly different ($\alpha = 0.05$). Samples were 95-cm^2 surface area by 15-cm-deep soil cores.

Table 4. *Popillia japonica* larval survival in four row-middle treatments in a highbush blueberry planting

Treatment	Mean ± SE *P. japonica* larvae/PVC pipe			
	2002	2003	2004	Grand mean
Bare ground	0.41 ± 0.24c	1.21 ± 0.27a	0.40 ± 0.17a	0.63 ± 0.11a
Buckwheat	0.40 ± 0.09bc	1.11 ± 0.19a	0.13 ± 0.06a	0.53 ± 0.10a
Clover	1.04 ± 0.19ab	0.46 ± 0.13a	0.20 ± 0.09a	0.54 ± 0.01a
Ryegrass	1.33 ± 0.36a	1.21 ± 0.59a	0.57 ± 0.15a	0.98 ± 0.15a

Values shown are the no. of larvae surviving out of five first instars in the summer of 2002, 2003, and 2004. Values within a column followed by the same letter are not significantly different ($\alpha = 0.05$).

almost 50% less frequently on clover than on ryegrass or buckwheat ($F = 3.89$; df = 2,106; $P = 0.02$; Fig. 1A) and fed significantly more frequently on buckwheat and clover than on ryegrass ($F = 12.49$; df = 2,106; $P < 0.01$). The frequency of digging was higher in ryegrass than in buckwheat ($F = 3.95$, df = 2,106; $P = 0.02$). Average digging frequency was similar on ryegrass and clover ($F = 2.56$ df = 1,106; $P > 0.05$; Fig. 1A).

The average durations of stationary, walking, and grooming behaviors were not significantly different among the ground covers ($F = 0.07$; df = 2,106; $F = 0.71$; df = 2,106; and $F = 0.01$; df = 2,106; respectively; $P > 0.05$ for all tests; Fig. 1B). In contrast, the durations of feeding and digging behaviors were highly affected by ground covers, but in opposite ways. Feeding bouts (time from when the behavior starts to when it ends) lasted 1.65 ± 0.73 and 1.87 ± 0.45 min on buckwheat and clover, respectively, but *P. japonica* spent significantly less time feeding on ryegrass (0.006 ± 0.006 min; $F = 11.60$; df = 2,106; $P < 0.01$). Throughout all observations, only 12 instances of feeding behavior were seen on ryegrass, compared with 63 for buckwheat and 112 for clover. Digging bouts lasted an average of 1.32 ± 0.44 min in ryegrass, significantly longer than in clover (0.52 ± 0.24 min) or in buckwheat (0.05 ± 0.05 min; $F = 6.18$; df = 2,106; $P < 0.01$; Fig. 1B).

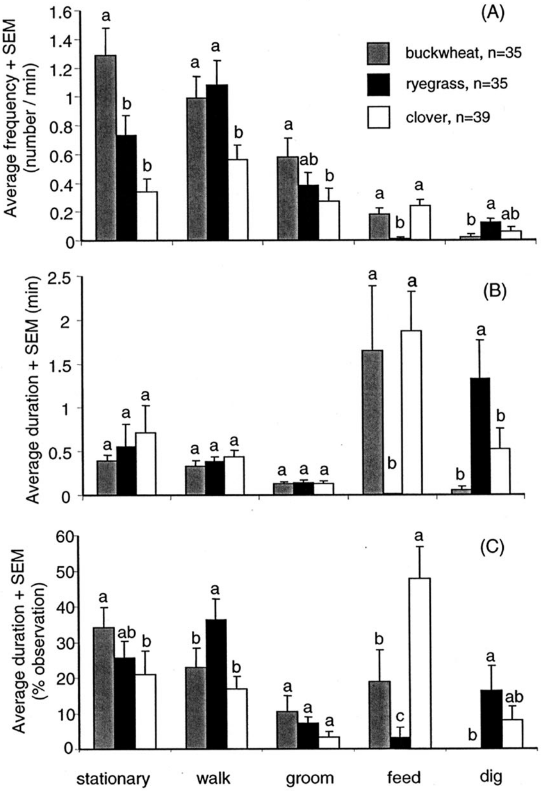

Fig. 1. Behavior of adult female *P. japonica* on different cover crops (n = number of observations within a treatment) in a planting of highbush blueberry in 2002 and 2003. Within each behavioral element, bars with the same letter are not significantly different ($\alpha = 0.05$). (A) Frequency of behaviors, (b) Duration of behavior bouts, (c) Proportion of observation in different behaviors.

The proportion of time allocated by *P. japonica* females to particular behaviors was also affected by ground cover ($F = 4.11$; df = 2,106; $P = 0.02$; Fig. 1C). A significantly higher proportion of time was spent stationary on buckwheat (34 ± 6%) than on clover (21 ± 7%). Beetles spent more of their time walking on ryegrass (36 ± 6%) than on either buckwheat or clover ($F = 3.97$; df = 2,106; $P = 0.02$), but time spent grooming was not affected by cover crop. The proportion of time spent feeding was significantly different among the three cover crops ($F = 20.19$; df = 2,106; $P < 0.01$), with the greatest proportion of time spent feeding on clover (48 ± 9%). This was 2.5 times higher than the proportion of time spent feeding on buckwheat and 15 times higher compared with ryegrass. The proportion of time spent digging was significantly different among cover crops ($F = 4.26$; df = 2,106; $P = 0.02$); beetles spent most of their time digging in ryegrass (16 ± 7%), and ≈8% was spent digging in clover, but this was not significantly different from the other two treatments. Only one beetle was observed digging (<1% of time spent) in buckwheat.

Adult *P. japonica* spent significantly more time on each of the plants than on the soil ($F = 51.58$; df = 2,2; $P < 0.01$). The time beetles spent on plants versus on soil varied depending on the cover crop they were observed on. In buckwheat, female beetles were on the plants for 99 ± 1% of the observation on average, which was not significantly different from those on clover plants (83 ± 7%, $P = 0.21$). Female beetles spent a significantly lower proportion of their time on the plants in the ryegrass row middles (74 ± 8%) than on the other two plants ($P < 0.05$).

Discussion

Cover crops can reduce pest damage in agricultural fields by serving as a sink for pests, through the disruption of sensory inputs, or by making microclimates less suitable for insect pests (Bugg 1992). In this study, cover crop treatments influenced the adult and larval densities of *P. japonica* and the behavior of adult beetles in row-middles of highbush blueberry fields. Ryegrass was the most preferred host for oviposition and larval development, whereas the other plants tested were relatively less suitable for larval development or oviposition. Bare soil was consistently not selected by adult beetles, leading to the lowest larval densities throughout.

Within the plant treatments, *P. japonica* larvae were most common in ryegrass and clover, whereas adult population density was lowest on ryegrass and highest on buckwheat across three growing seasons. Thus, plant susceptibility for adult beetle colonization did not correspond to a plant's susceptibility for oviposition. In a choice test conducted on potted plants in the greenhouse, *P. japonica* larvae preferred to feed on roots of perennial ryegrass compared with five other turfgrass species (Crutchfield and Potter 1994). Larval survival also varies with plant species: third-instar *P. japonica* survived better on large crabgrass than on dandelion, white clover, or Kentucky bluegrass (Crutchfield and Potter 1995). While these controlled studies can help elucidate plant suitability for larval development, evaluation under field conditions will be essential to determine the influence of ground covers on beetle colonization and oviposition.

Bare ground row-middles harbored the fewest larvae in our study, indicating that *P. japonica* density is decreased in the absence of plants in the row-middles. Crutchfield and Potter (1995) found in a greenhouse study that survival of third-instar *P. japonica* larvae was higher in the presence of plants than in no-plant treatments. Although naturally occurring larvae were rarely found in our bare ground plots, first instars survived and developed in PVC pipes in bare ground treatments (Table 4). There may have been sufficient organic matter in the soil of the experimental field to provide developing larvae with food, and the PVC pipes may have altered the microclimate or prevented natural enemy access to the larvae. These findings also suggest that the lack of larvae in bare ground is caused by female beetle oviposition site selection behavior. Fewer adult beetles were found in bare ground plots than in plots with cover crops, suggesting that beetles avoid landing on brown (nongreen) surfaces (Kostal and Finch 1994); alternatively, their tenure time on bare ground may be very brief. It is also possible that the herbicide that was applied to these row middles repelled the beetles, although it was applied infrequently. Beetle avoidance of bare ground explains the lower abundance of larvae in these plots and suggests a potential mechanism underlying the reduction in *P. japonica* larval density in clean cultivated blueberry fields (Szendrei et al. 2005).

Among the three cover crops, the highest numbers of adult beetles were found on buckwheat throughout this study, indicating that this plant attracts beetles, making it an unsuitable ground cover for reducing adult beetle populations in blueberry fields. Observations of female beetle behavior under field conditions suggest that plant suitability for feeding and oviposition explain the beetle abundance and larval density observed in the three tested ground covers. Beetles spent more time and more frequently fed on buckwheat and clover than on ryegrass, but they dug more frequently and for longer durations on ryegrass than on buckwheat. Because *P. japonica* adults fed only minimally on ryegrass, but laid eggs in this treatment, it seems that host plant evaluation for oviposition involves a different mechanism from food plant evaluation. Duration and frequency data revealed the dominant behaviors on the different plants: stationary on buckwheat, feeding on clover, walking and digging on ryegrass (Fig. 1).

A link between digging behavior and oviposition by *P. japonica* was found by Szendrei and Isaacs (2005) in laboratory studies, and this finding is further supported by this field study. The high larval density on ryegrass was associated with a high proportion of digging behavior on this plant, and the low larval density in buckwheat occurred when there was very little digging behavior. Interestingly, the frequency and duration of digging behavior on clover was not statistically different from either of the other two treatments (Fig. 1), but larval densities were similar to those in ryegrass (Table 3). Clover is different from the other two plants in that it is a suitable host for feeding, oviposition, and for larval survival by *P. japonica,* and this combination of qualities will likely make this plant unsuitable as a cover crop for reduction of *P. japonica* populations in agricultural systems. Buckwheat is not a host for oviposition and is not ideal for larval survival, but adults were common on the flowering stems, using them for basking and feeding (Z.S., unpublished data). Adult beetles did not consume ryegrass, but as expected, this was an ideal host for oviposition and larval survival. Further evaluation of acid-tolerant cover crops will be necessary to identify plants that have a potential to suppress *P. japonica* populations.

The behavior of *P. japonica* on the tested plants with different architecture may point toward future lines of investigation of factors driving oviposition by *P. japonica.* Buckwheat is 50- to 60-cm tall during the beetle flight period, whereas the other two plants are 10- to 30-cm tall. Taller plants could serve as a barrier separating the beetles from the soil surface and thus reduce oviposition. Perennial ryegrass is a monocotyledonous plant with a thin leaf blade, wheras the other two plants have broad leaves; this feature could be significant in influencing *P. japonica* behavior if the leaf shape is used as an orientation cue. In a study with artificial grass blades, gravid females responded differently to stem density and diameter, suggesting that *P. japonica* uses visual cues to evaluate potential oviposition sites (Szendrei and Isaacs 2005). Visual cues have been shown to be important factors in host orientation, location, and choice for many species of Diptera, Lepidoptera, Hemiptera, and Coleoptera (Prokopy and Owens 1983). In *P. japonica,* vision has already been proven important during the development of an effective monitoring trap (Fleming 1969). Olfactory and/or tactile cues may also be involved in oviposition, but the chemical basis of oviposition decisions requires further investigation.

Our experiments revealed the extent to which adult and larval *P. japonica* densities can be altered by the row-middle treatments through differential plant use in the two life stages. Further study is needed to determine whether successful control of one life stage reduces the other and also whether behavioral management practice translates into effective pest control on the main crop. Depending on the type of main crop and on growers' pest control goals, certain cover crop species are more suited to control adults while others reduce larval abundance. Our findings may be useful in agricultural systems where cover crops are being considered for reduction of the larval stage of pests that lay eggs in soil, because they suggest that oviposition behavior can be manipulated to reduce local abundance of some pest species. Studies on commercial farms at larger scales are required to determine whether integrating cover crops into fields can provide effective reduction of pest populations.

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