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ORIGINAL PAPER

Feeding damage by *Bagrada hilaris* (Hemiptera: Pentatomidae) and impact on growth and chlorophyll content of Brassicaceous plant species

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Abstract *Bagrada hilaris* Burmeister is an invasive species native to the old world and is currently threatening commercial vegetable production in the southwestern USA. A series of no-choice experiments were conducted to investigate multiple plant responses in six *Brassica* crops to feeding by *B. hilaris*. Varying numbers of adults were caged onto cotyledon, 2-true leaf, and 4-true leaf-stage plants of broccoli, green cabbage, red cabbage, cauliflower, kale, and radish for a 48-h infestation period. Feeding damage on leaf surfaces, total leaf area, and relative chlorophyll content on plants of each crop were measured before and after the 48-h infestation period. In addition, dry weights and total leaf area for the 4-leaf-stage plants were measured at 21 days post-infestation to estimate the residual impacts on older plants. In all crops tested, feeding damage increased with greater numbers of *B. hilaris* adults caged on cotyledon and 2-leaf-stage plants. Significantly more feeding damage occurred on the upper (younger) two leaves than on the lower (older) two leaves of the 4-true leaf plants for all host plants suggesting that *B. hilaris* feeds preferentially on newer leaf tissue. Significant reductions in leaf area, relative chlorophyll content, and dry weight in all crops indicated negative impacts on plant growth by *B. hilaris*. Moreover, cotyledon and 2-leaf plants were more severely impacted by *B. hilaris*-induced injury than the 4-leaf plants, and kale appeared to be less sensitive to *B. hilaris* feeding than the other five Brassicaceous hosts.

Keywords Feeding damage · Bagrada bug · Chlorophyll loss · Plant growth · Dry weight · *Brassica*

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Introduction

Bagrada hilaris Burmeister (Hemiptera: Pentatomidae), commonly referred to as the Bagrada bug or Painted bug, is an invasive stink bug species that has been infesting Brassicaceous crops in the desert southwest of the USA for the past few years (http://cisr.ucr.edu/bagrada_bug.html). Populations of *B. hilaris* have expanded their range into the coastal cole crop production regions of California and central Arizona, and more recently have been reported in Nevada, New Mexico, and Utah (Bundy et al. 2012). It is considered a serious economic pest of a variety of Brassicaceous vegetable crops grown during the fall and winter months in the desert agricultural valleys of Arizona and southern California (Palumbo and Natwick 2010). Seedling stages of Brassicaceous crops appear to be highly susceptible to direct feeding damage on cotyledons, newly emerged leaves, and apical meristems. Excessive feeding damage to apical meristems may result in destruction of the terminal growing points, leading to either adventitious bud break (e.g., cabbage plants with multiple, and unmarketable heads) or plants with no marketable heads being formed (e.g., broccoli with no crowns) (Palumbo and Natwick 2010). In the three years since the initial outbreaks in 2009 of *B. hilaris* on desert vegetable crops, it has become evident that the invasive stinkbug has become an established pest of commercial Brassicaceous crops.

Recent surveys of broccoli growers from Yuma, AZ, and the Imperial Valley, CA estimated that about 90 % of the broccoli acreage planted since 2010 have been infested with *B. hilaris* at some point in the growing season, which on average has resulted in considerable stand losses and plant injury, often exceeding 10 % yield losses. (https://extension.arizona.edu/sites/extension.arizona.edu/files/resourcefile/resource/marcop/052913%20Bagrada%20Bug%20Survey_2013_Report.pdf). Furthermore, the potential economic impact of *B. hilaris* on the western vegetable industry could be significant considering that the production of broccoli, cauliflower, cabbage, and other Brassicaceous crops in Arizona and California was collectively valued at over $1 billion in 2011 (CDFA 2012; USDA-NASS 2011, 2012).

Limited information is available on the impact of feeding by *B. hilaris* on Brassicaceous vegetables. Recently, field and laboratory observations demonstrated the damage potential of *B. hilaris* infesting broccoli in Arizona (Palumbo and Natwick 2010; Huang et al. 2013). Plant responses of broccoli to herbivory have been quantified for a related stink bug species, the harlequin bug, *Murgantia histrionica* Hahn (Ludwig and Kok 2001), but scientific information is lacking on the direct effects of feeding damage by *B. hilaris* on *Brassica* host plants and associated growth responses. In other studies, reductions in plant height, dry root, and leaf weights on seedling corn were reported by the feeding of three pentatomids, the brown stink bug, *Euschistus servus* Say, one-spotted stink bug, *E. variolarus* Palisot de Beauvois, and the green stink bug, *Chinavia hilaris* Say (Townsend and Sedlacek 1986). Negative plant growth responses as influenced by feeding of other hemipterans has been studied in the grass bug, *Irbisia pacifica* Uhler (Hansen and Nowak 1988), silverleaf whitefly, *Bemisia argentifolii* Bellows & Perring (Palumbo et al. 2000), a phloem-sap feeding aphid, *Uroleucon caligatum* Richard, and a xylem-sap feeding meadow froghopper, *Philaenus spumarius* (L.) (Meyer and Whitlow 1992).

Feeding and oviposition by two phytophagous pentatomids, the southern green stink bug, *Nezara viridula* (L.), and *M. histrionica* were shown to negatively affect photosynthesis of French bean, *Phaseolus vulgaris,* and savoy cabbage, *Brassica oleracea* (Velikova et al. 2010). Losses of chlorophyll content in leaves in response to feeding by other hemipterans have been reported on the sweetpotato whitefly, *Bemisia tabaci* Gennadius (Buntin et al. 1993; Palumbo et al. 1996), azalea lace bug, *Stephanitis pyrioides* Scott (Buntin et al. 1996), Russian wheat aphid, *Diuraphis noxia* Mordvilko (Ni et al. 2002; Heng-Moss et al. 2003), black pecan aphid, *Melanocallis caryaefoliae* Davis (Cottrell et al. 2009), and pea aphid, *Acyrthosiphon pisum* Harris (Goławska et al. 2010). Similar reductions in leaf area and relative chlorophyll content resulting from *B. hilaris* feeding have not been previously documented.

A clear understanding of plant health and growth responses associated with the feeding injury on host crops caused by *B. hilaris* will be important for the development of pest management approaches for this new pest. This is particularly important considering that recent field observations showed that *B. hilaris* adults are often attracted in large numbers to seedling stages of broccoli during crop establishment (Huang et al. 2013). The main objectives of this study were to quantify feeding damage of *B. hilaris* on cotyledon, 2-leaf, and 4-leaf stages of six commercial *Brassicas* and to evaluate host plant responses to *B. hilaris* feeding intensity by measuring leaf growth, relative chlorophyll content, and dry weight in a series of laboratory trials.

Materials and methods

Insects and plants

Commercial Brassicaceous vegetable crops including broccoli (*B. oleracea* var. *italica* Plenck 'Emerald Crown,' Sakata Seed, Morgan Hills, CA), green cabbage (*B. oleracea* var. *capitata* L. 'Gazelle F1,' Bejo Seeds, Oceano, CA), red cabbage (*B. oleracea* var. *capitata* L. 'Ruby Perfection Hybrid,' American Takii, Inc., Salinas, CA), cauliflower (*B. oleracea* var *botrytis* L. 'Ponderet RZ Hybrid,' Rijk Zwaan USA Inc, Salinas, CA), kale (*B. oleracea* var. *acephala* DC.'Winterbor Hybrid,' Terriorial Seeds, Cottage Grove, OR), and radish (*Raphanus sativus* var. sativus L. 'Rover Hybrid') were selected as test crops based on previous choice experiments that showed these host plants to be preferentially attractive to *B. hilaris* (Huang et al. 2014). All plants were direct-seeded into 5 × 5 cm^2 pots for germination with potting soil (Miracle-Gro®, Marysville, OH) and irrigated daily in the greenhouse. Once plants reached the 2-leaf stage, they were fertilized weekly with an all-purpose water-soluble fertilizer (20-20-20) (Miracle-Gro®). No fertilizer was applied to plants at the cotyledon stage. Plants of uniform size at the cotyledon stage (6–8 day-old), 2-leaf stage (20–22 day-old), and 4-leaf stage (~35 day-old) were selected for the no-choice experiment.

All adult insects used for the experiment were obtained from a *B. hilaris* colony maintained at the Yuma Agricultural Center, Yuma, AZ, where all life stages were supplemented with organic broccoli heads (Earthbound Farm, Salinas, CA) and sweet alyssum plants. Single adult *B. hilaris* (females), one mating pair (sexually mature), and two mating pairs were chosen and starved for 24 h before being caged on plants used in the studies.

Table 1 Analysis of the interaction between plant growth stage and number of *B. hilaris* infested in percentage of feeding damage using a two-way ANOVA with slice option for each host plant

Host plant	Sliced by plant stage			Sliced by # adults infested		
	Stage	*F*	*P*	# Adult infested	*F*	*P*
Broccoli	Cotyledon	101.14	<.0001	Non-infested	0.00	1.0000
	2-Leaf	28.41	<.0001	1 female	22.89	<.0001
	4-Leaf (upper)	8.74	<.0001	1 mating pair	58.58	<.0001
	4-Leaf (lower)	1.65	0.1846	2 mating pairs	90.63	<.0001
Green cabbage	Cotyledon	54.58	<.0001	Non-infested	0.00	1.0000
	2-Leaf	36.59	<.0001	1 female	12.01	<.0001
	4-Leaf (upper)	3.08	0.0324	1 mating pair	45.67	<.0001
	4-Leaf (lower)	0.09	0.9656	2 mating pairs	53.70	<.0001
Red cabbage	Cotyledon	35.64	<.0001	Non-infested	0.00	1.0000
	2-Leaf	17.05	<.0001	1 female	5.67	0.0015
	4-Leaf (upper)	2.37	0.0771	1 mating pair	17.40	<.0001
	4-Leaf (lower)	0.94	0.4762	2 mating pairs	30.58	<.0001
Cauliflower	Cotyledon	145.20	<.0001	Non-infested	0.00	1.0000
	2-Leaf	11.79	<.0001	1 female	20.72	<.0001
	4-Leaf (upper)	7.80	0.0001	1 mating pair	108.19	<.0001
	4-Leaf (lower)	0.10	0.9569	2 mating pairs	118.25	<.0001
Kale	Cotyledon	77.78	<.0001	Non-infested	0.00	1.0000
	2-Leaf	8.26	<.0001	1 female	4.18	0.0086
	4-Leaf (upper)	12.34	<.0001	1 mating pair	22.15	<.0001
	4-Leaf (lower)	0.22	0.8847	2 mating pairs	63.47	<.0001
Radish	Cotyledon	67.02	<.0001	Non-infested	0.00	1.0000
	2-Leaf	58.96	<.0001	1 female	36.95	<.0001
	4-Leaf (upper)	21.87	<.0001	1 mating pair	32.16	<.0001
	4-Leaf (lower)	0.93	0.4298	2 mating pairs	57.72	<.0001

$df = 3, 75$ for both sliced by plant stage and sliced by # *B. hilaris* infested

No-choice tests

A 4 × 3 factorial design experiment was conducted in an upright growth chamber (model I-36 LLVL, Percival Scientific, Perry, IA) by caging *B. hilaris* adults (zero, a single female, one mating pair, and two mating pairs) on individual host plants (cotyledon, 2-true leaf, and 4-true leaf stages). Environmental condition was maintained a photoperiod of 12:12 (L:D) h and temperature at 30 °C during the day and 20 °C at night; these conditions were confirmed and monitored using a data logger (HOBO Pendant, Onset Computer Corp., Cape Cod, MA). Individual potted host plants were transferred into small cages constructed from an 8.5-cm-diameter plastic cup and placed into the growth chamber 24 h before the experiment. The top of the plastic cup was covered by a 9-cm-diameter Petri-dish cap drilled with 15–20, 0.2-cm-diameter round holes for ventilation. *B. hilaris* adults (a single female, one mating pair, and two mating pairs) were caged onto separate plants, and no adults were caged on the control group plants. Each combination (e.g., two mating pairs on 2-true leaf-stage plant) was replicated six times. *B. hilaris* were allowed to feed on the plant for 48 h, after which time all adults were removed from the plants. Leaf area measurements for each plant were recorded immediately before the experiment (24 h in the chamber) and again following the 48-h infestation period. Nondestructive estimates of total leaf area were conducted using a USB digital microscope (Dino-Lite®) and measured using Dino Capture 2.0 graphic software. Leaf growth/loss was determined based on positive or negative changes in leaf area after the 48-h feeding period. Feeding damage on leaf tissue, as described by Palumbo and Natwick (2010), was measured after the 48-h period similar to methods used in a previous study (Huang et al. 2013). Relative chlorophyll content in leaf tissue was determined immediately before and after the 48-h infestation period using a nondestructive chlorophyll meter (SPAD-502 Plus, Minolta Corp., Spectrum Technologies, Inc.). Two measurement points were randomly selected on both sides of each cotyledon, four points were selected on both sides of each leaf for the 2-leaf groups, and six sample points were measured on both sides of all

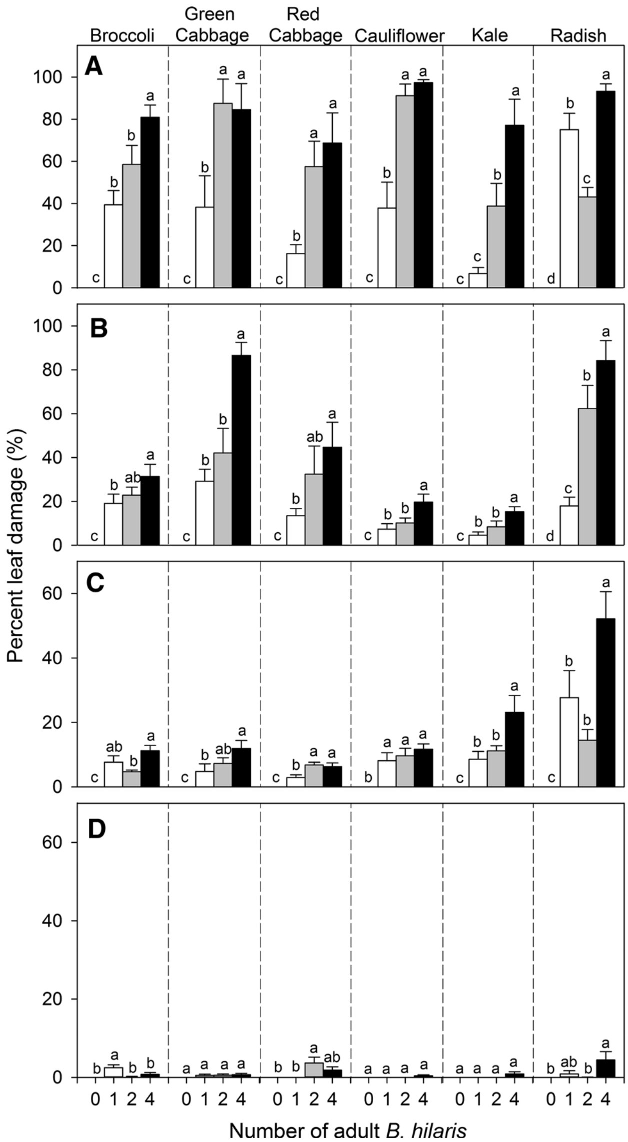

Fig. 1 Mean ± SEM percentage leaf damage of six *Brassica* crops exposed to various numbers of *B. hilaris* adults for 48 h on seedling plants at **a** cotyledon stage, **b** 2-leaf stage, **c** 4-leaf stage, younger two leaves, and **d** 4-leaf stage, older two leaves. Leaf damage was based on the direct measurement of the chlorotic leaf tissue induced by feeding of *B. hilaris*. Percentage of leaf damage was based on the chlorotic leaf area/total leaf area. Means followed by the *same letter* are not significantly different ($P < 0.05$; LSMEANS test)

leaves for the 4-leaf-stage plants. SPAD (Soil and Plant Analyzer Development) values obtained from each plant were averaged for further analyses. Chlorophyll change was based on positive or negative changes in SPAD values after the 48-h period of *B. hilaris* infestation.

All 4-leaf-stage plants were transferred into the greenhouse following the 48-h infestation period and allowed to continue to grow for 21 days to measure residual impacts of feeding on plant growth. After the 21-day period, plants were abscised 1 cm above soil surface and total leaf area was calculated by measuring the leaf area of all leaves on each plant with a LI-3100 leaf-area meter (LI-COR, Inc., Lincoln, NE). Dry weights for each plant were measured by drying all leaves, petioles, and stems in a forced air oven held at 150 °C for 24 h. Dried bulb weight (underground portion) was also recorded in radish plants using the same method as dry plant weight.

Statistical analyses

This study was designed to measure the effects of plant stage and numbers of *B. hilaris* per plant for each *Brassica* host rather than comparisons among hosts. Thus, data obtained from each *Brassicas* host were analyzed separately using a two-way ANOVA (PROC GLIMMIX; SAS Institute 2009). Plant stage and number of *B. hilaris* infested were modeled as fixed effects, and replicates were modeled as a random effect. The response variables, such as percentage of feeding damage (damaged area/total leaf area), were subjected to arcsine square root transformation before analysis (Zar 1999). Actual untransformed data are presented in the tables and figures. Treatment means were separated using the LSMEANS test ($P < 0.05$) and the slice option (SAS Institute 2009) if there was a significant interaction. A *t* test (PROC TTEST, SAS Institute 2009) was used to determine whether there were differences in feeding damages between upper two leaves and lower two leaves of 4-leaf-stage plants. Analyses of dry weight and total leaf area (4-leaf stage only) were performed using a one-way ANOVA (PROC GLIMMIX; SAS Institute 2009) to compare the difference between number of *B. hilaris* infested. Relationship between number of *B. hilaris* infested and response variables was quantified using regression analysis (PROC REG) and Spearman's rank correlation coefficient. A paired *t* test was conducted to compare the changes (before and after *B. hilaris* infestation) in chlorophyll content in each host.

Results

Feeding damage

When examining the percentage of feeding damage caused by *B. hilaris*, there was a significant interaction between plant stage and number of *B. hilaris* infested in each Brassicaceous host: broccoli (two-way ANOVA, $F_{9,75} = 17.27$, $P < 0.0001$), green cabbage (two-way ANOVA, $F_{9,75} = 12.53$, $P < 0.0001$), red cabbage (two-way ANOVA, $F_{9,75} = 5.94$, $P < 0.0001$), cauliflower (two-way ANOVA, $F_{9,75} = 27.26$, $P < 0.0001$), kale (two-way ANOVA, $F_{9,75} = 13.27$, $P < 0.0001$), and radish (two-way ANOVA, $F_{9,75} = 15.20$, $P < 0.0001$). Further

Table 2 Relationship between feeding damage and number of *B. hilaris* infested at different growth stages of *Brassica* plants

Host plant	Feeding damage	Cotyledon	2-True leaf	4-True leaf (upper)	4-True leaf (lower)
Broccoli	Direct[a]	$r^2 = 0.89$; $F = 55.44$	$r^2 = 0.72$; $F = 16.79$	$r^2 = 0.74$; $F = 31.38$	$r^2 = 0.02$; $F = 0.27$
		$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.7670$
	Percentage[b]	$r^2 = 0.81$; $F = 29.17$	$r^2 = 0.64$; $F = 11.72$	$r^2 = 0.49$; $F = 21.00$	$r^2 = 0.03$; $F = 0.43$
		$P < .0001$	$P < .0001$	$P = 0.0001$	$P = 0.6590$
Cabbage	Direct[a]	$r^2 = 0.63$; $F = 17.82$	$r^2 = 0.74$; $F = 61.53$	$r^2 = 0.36$; $F = 5.99$	$r^2 = 0.09$; $F = 2.21$
		$P < .0001$	$P < .0001$	$P = 0.0087$	$P = 0.1513$
	Percentage[b]	$r^2 = 0.67$; $F = 19.52$	$r^2 = 0.79$; $F = 84.25$	$r^2 = 0.48$; $F = 20.42$	$r^2 = 0.11$; $F = 2.79$
		$P < .0001$	$P < .0001$	$P = 0.0002$	$P = 0.1088$
Red cabbage	Direct[a]	$r^2 = 0.72$; $F = 26.90$	$r^2 = 0.51$; $F = 11.00$	$r^2 = 0.60$; $F = 15.98$	$r^2 = 0.16$; $F = 4.07$
		$P < .0001$	$P = 0.0001$	$P < .0001$	$P = 0.0560$
	Percentage[b]	$r^2 = 0.63$; $F = 11.66$	$r^2 = 0.44$; $F = 7.94$	$r^2 = 0.50$; $F = 21.94$	$r^2 = 0.12$; $F = 3.07$
		$P = 0.0001$	$P = 0.0027$	$P = 0.0001$	$P = 0.0939$
Cauliflower	Direct[a]	$r^2 = 0.83$; $F = 51.64$	$r^2 = 0.73$; $F = 59.12$	$r^2 = 0.60$; $F = 10.07$	$r^2 = 0.27$; $F = 2.46$
		$P < .0001$	$P < .0001$	$P = 0.0003$	$P = 0.0921$
	Percentage[b]	$r^2 = 0.84$; $F = 58.69$	$r^2 = 0.61$; $F = 16.49$	$r^2 = 0.52$; $F = 7.43$	$r^2 = 0.21$; $F = 5.75$
		$P < .0001$	$P < .0001$	$P = 0.0016$	$P = 0.0254$
Kale	Direct[a]	$r^2 = 0.78$; $F = 77.86$	$r^2 = 0.62$; $F = 36.15$	$r^2 = 0.65$; $F = 40.57$	$r^2 = 0.26$; $F = 2.45$
		$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.0932$
	Percentage[b]	$r^2 = 0.71$; $F = 53.33$	$r^2 = 0.64$; $F = 38.43$	$r^2 = 0.59$; $F = 31.17$	$r^2 = 0.21$; $F = 5.70$
		$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.0260$
Radish	Direct[a]	$r^2 = 0.61$; $F = 34.42$	$r^2 = 0.88$; $F = 54.90$	$r^2 = 0.57$; $F = 29.58$	$r^2 = 0.26$; $F = 7.91$
		$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.0102$
	Percentage[b]	$r^2 = 0.56$; $F = 28.37$	$r^2 = 0.81$; $F = 28.80$	$r^2 = 0.51$; $F = 23.12$	$r^2 = 0.25$; $F = 7.56$
		$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.0117$

[a] Direct leaf damage was based on the direct measurement of the chlorotic leaf tissue induced by feeding of *B. hilaris*

[b] Percentage of leaf damage was based on the chlorotic leaf area/total leaf area

analyses of the interaction, sliced by plant stage and by number of *B. hilaris* infested, are shown in Table 1. When caged with one female, one mating pair, or two mating pairs of *B. hilaris*, the percentage of feeding damage varied significantly among different growth stages in all hosts (Table 1). In addition, the percentage of feeding damage varied significantly among different numbers of *B. hilaris* infested in cotyledon, 2-leaf stage, and 4-leaf (upper two leaves) stages of all hosts (Table 1). In general, the percentage of feeding damage increased as the numbers of *B. hilaris* increased; this was true in most of the cotyledon and 2-leaf-stage plants from all hosts (Fig. 1). Percentage feeding damage was generally lower in the 4-leaf-stage plants compared to the cotyledon and 2-leaf-stage plant stages, but in most cases, damage was significantly greater on infested plants compared to the non-infested control (Fig. 1). However, regardless of number of *B. hilaris* infested, estimates of feeding damage on the upper (younger) two leaves were significantly greater than those measured on the lower (older) two leaves of the 4-leaf-stage plants in broccoli (t test, $t = 6.28$, $P < 0.0001$), green cabbage (t test, $t = 5.67$, $P < 0.0001$), red cabbage (t test, $t = 6.31$, $P < 0.0001$), cauliflower (t test, $t = 7.84$, $P < 0.0001$), kale (t test, $t = 6.01$, $P < 0.0001$), and radish (t test, $t = 6.37$, $P < 0.0001$). Regression analyses showed a positive relationship between feeding damage and number of *B. hilaris* infested in cotyledon, 2-leaf, and 4-leaf (upper two leaves) stages, but not in the 4-leaf (lower two leaves) stage (Table 2).

Leaf area growth/loss

When examining the growth/reduction in total leaf area as a response to *B. hilaris* feeding, there was a significant interaction between plant stage and number of *B. hilaris* infested in broccoli (two-way ANOVA, $F_{9,75} = 21.53$, $P < 0.0001$), green cabbage (two-way ANOVA, $F_{9,75} = 7.45$, $P < 0.0001$), red cabbage (two-way ANOVA, $F_{9,75} = 5.76$, $P < 0.0001$), cauliflower (two-way ANOVA, $F_{9,75} = 4.62$, $P < 0.0001$), kale (two-way ANOVA, $F_{9,75} = 2.13$, $P = 0.0370$), and radish (two-way ANOVA, $F_{9,75} = 8.63$, $P < 0.0001$). Further analyses of these interactions, sliced by plant stage and by number of *B. hilaris* infested, are shown in Table 3. When caged with zero adult, one female,

Table 3 Analysis of the interaction between plant growth stage and number of *B. hilaris* infested in leaf growth/loss using a two-way ANOVA with slice option for each host plant

Host plant	Sliced by plant stage			Sliced by # adults infested		
	Stage	*F*	*P*	# Adult infested	*F*	*P*
Broccoli	Cotyledon	3.49	0.0197	Non-infested	7.29	0.0002
	2-Leaf	90.77	<.0001	1 female	34.36	<.0001
	4-Leaf (upper)	4.72	0.0045	1 mating pair	24.51	<.0001
	4-Leaf (lower)	4.12	0.0092	2 mating pairs	53.23	<.0001
Green cabbage	Cotyledon	2.15	0.1015	Non-infested	12.49	<.0001
	2-Leaf	41.70	<.0001	1 female	12.76	<.0001
	4-Leaf (upper)	3.97	0.0111	1 mating pair	14.10	<.0001
	4-Leaf (lower)	4.15	0.0089	2 mating pairs	22.09	<.0001
Red cabbage	Cotyledon	1.53	0.2125	Non-infested	10.94	<.0001
	2-Leaf	23.11	<.0001	1 female	34.61	<.0001
	4-Leaf (upper)	10.96	<.0001	1 mating pair	10.46	<.0001
	4-Leaf (lower)	0.53	0.6635	2 mating pairs	27.72	<.0001
Cauliflower	Cotyledon	5.30	0.0023	Non-infested	15.47	<.0001
	2-Leaf	23.25	<.0001	1 female	26.60	<.0001
	4-Leaf (upper)	16.31	<.0001	1 mating pair	14.03	<.0001
	4-Leaf (lower)	0.56	0.6451	2 mating pairs	15.35	<.0001
Kale	Cotyledon	8.40	<.0001	Non-infested	38.36	<.0001
	2-Leaf	5.48	0.0019	1 female	42.05	<.0001
	4-Leaf (upper)	4.77	0.0043	1 mating pair	54.51	<.0001
	4-Leaf (lower)	0.16	0.9206	2 mating pairs	41.05	<.0001
Radish	Cotyledon	4.00	0.0106	Non-infested	6.38	0.0007
	2-Leaf	47.33	<.0001	1 female	6.34	0.0007
	4-Leaf (upper)	22.96	<.0001	1 mating pair	7.79	0.0001
	4-Leaf (lower)	3.29	0.0251	2 mating pairs	6.78	0.0004

$df = 3, 75$ for both sliced by plant stage and sliced by # *B. hilaris* infested

one mating pair, or two mating pairs of *B. hilaris*, changes in total leaf area varied significantly among the different growth stages in all hosts (Table 3). In addition, leaf growth/loss varied significantly among different numbers of *B. hilaris* infested, except for cotyledon stage of green cabbage, red cabbage, and 4-leaf stage (lower two leaves) of red cabbage, cauliflower, and kale (Table 3). In the control groups, leaf area increased in all stages within a 48-h period. In general, the leaf growth decreased as the numbers of *B. hilaris* increased, especially in cotyledon and 2-leaf stages (Fig. 2). Regression analyses showed a negative relationship between leaf growth and number of *B. hilaris* infested; this was especially obvious in cotyledon and 2-leaf-stage plants from all hosts (Fig. 2; Table 4).

Change in relative chlorophyll content

When examining the relative chlorophyll content in plant leaves in response to *B. hilaris* feeding, there was a significant interaction between plant stage and number of *B. hilaris* infested in broccoli (two-way ANOVA, $F_{9,75} = 2.72$, $P = 0.0085$), green cabbage, (two-way ANOVA, $F_{9,75} = 3.33$, $P = 0.0018$), red cabbage (two-way ANOVA, $F_{9,75} = 2.49$, $P = 0.0152$), cauliflower (two-way ANOVA, $F_{9,75} = 6.02$, $P < 0.0001$), kale (two-way ANOVA, $F_{9,75} = 3.12$, $P = 0.0031$), and radish (two-way ANOVA, $F_{9,75} = 4.48$, $P = 0.0001$). Further analyses of the interactions, sliced by plant stage and by number of *B. hilaris* adults infested, are shown in Table 5. When caged with one female, one mating pair, or two mating pairs of *B. hilaris*, the relative chlorophyll change varied significantly among different growth stages in all hosts, but not in the controls (Table 5). The relative chlorophyll content varied significantly among different numbers of *B. hilaris* infested in cotyledon, 2-leaf, and 4-leaf (upper two leaves) plants, but not in the 4-leaf (lower two leaves) plants (Table 5). Regression analyses showed a negative relationship between relative chlorophyll change and number of *B. hilaris* infested (Table 6). In general, the SPAD value decreased with the increase in *B. hilaris* infested in cotyledon, 2-leaf, and 4-leaf (upper two leaves) from all hosts (Fig. 3). However, the SPAD values

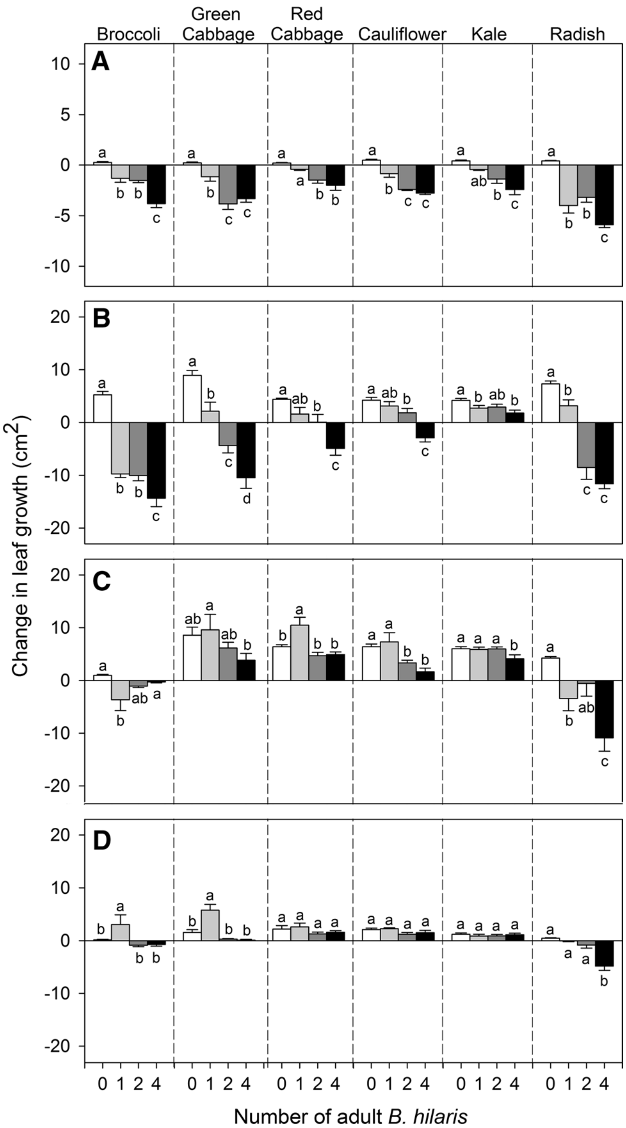

Fig. 2 Mean ± SEM change in leaf growth (cm^2) of six *Brassica* crops exposed to various numbers of *B. hilaris* adults for 48 h on seedling plants at **a** cotyledon stage, **b** 2-leaf stage, **c** 4-leaf stage, younger two leaves, and **d** 4-leaf stage, older two leaves. Leaf growth was based on positive or negative changes in leaf area after a 48 h of *B. hilaris* infestation. Means followed by the *same letter* are not significantly different ($P < 0.05$; LSMEANS test)

measured at 4-leaf (lower two leaves) was not influenced by the increase in *B. hilaris* infested. There was a negative correlation between relative chlorophyll change and amount of feeding damage in all hosts (Spearman's coefficient: broccoli = − 0.6937; green cabbage = −0.7298; red cabbage = −0.7043; cauliflower = −0.7671; kale = −0.7561; and radish = −0.7895).

Dry weight and total leaf area in 4-true leaf-stage plants

There were significant differences in both total leaf area and dry plant weight between the different numbers of *B. hilaris* infested in broccoli, green cabbage, red cabbage, cauliflower, and radish, but not in kale (Table 7). Dry plant weight and total leaf area were greatest in the control groups, and lowest in plants infested with the groups of 2-mating pairs of *B. hilaris*. In radish, the dry bulb weight varied significantly among the different *B. hilaris* infestation levels (one-way ANOVA, $F_{3,20} = 6.98$, $P = 0.0021$), where control groups had the greatest bulb weight and groups of 2-mating pairs had the lowest bulb weight. Spearman's correlation coefficient analyses showed a negative correlation between leaf area/dry plant weight and number of *B. hilaris* infested. These variables decreased as the number of *B. hilaris* increased, with kale as the only exception (Table 7).

Discussion

Our results clearly demonstrate that feeding by adult *B. hilaris* can cause negative impacts on the leaf growth, chlorophyll content, and dry weights of several important Brassicaceous host plants. Feeding damage measured on individual host plants varied significantly, depending on adult density and stage of plant growth. Feeding was particularly destructive to the younger developmental plant stages such as cotyledon and 2-true leaf-stage plants. In general, 4-true leaf-stage plants were less vulnerable to *B. hilaris* feeding in all the host plants evaluated. Differences in feeding damage measured between the upper (younger) two leaves and lower (older) two leaves of the 4-leaf-stage plants further showed that *B. hilaris* fed preferentially on younger growing tissue. Furthermore, feeding damage on the upper two leaves (younger) caused significant residual growth effects on the 4-leaf-stage plants. Although the study was not designed to compare differences among the six Brassicaceous host plants, it was quite evident that older kale plants at the 4-true leaf stage were less susceptible to *B. hilaris* feeding compared to other 4-leaf host plants based on the minimal differences in total leaf area and dry weight 21 days after the 48 h of *B. hilaris* infestation period.

In addition to plant stage, negative impacts on leaf area reduction and relative chlorophyll loss were significantly related to the number of *B. hilaris* infested. Relative chlorophyll loss was also related to the amount of feeding damage caused by *B. hilaris*. These data are consistent with anecdotal observations and empirical studies (J. C. Palumbo, unpublished) that have shown that heavy infestations of *B. hilaris* occurring in seedling broccoli and cauliflower fields can cause significant plant injury and yield reductions. Individual females were used for the 1-adult group rather than males in our study because previous research revealed that female *B. hilaris* fed for significantly longer durations and caused almost fivefold more

Table 4 Relationship between leaf growth and number of *B. hilaris* infested at different growth stages of *Brassica* plants

Host plant	Cotyledon	2-true leaf	4-true leaf (upper)	4-true leaf (lower)
Broccoli	$r^2 = 0.83$; $F = 31.86$	$r^2 = 0.91$; $F = 66.12$	$r^2 = 0.16$; $F = 3.54$	$r^2 = 0.09$; $F = 3.67$
	$P < .0001$	$P < .0001$	$P = 0.0331$	$P = 0.0295$
Cabbage	$r^2 = 0.77$; $F = 22.11$	$r^2 = 0.81$; $F = 28.93$	$r^2 = 0.22$; $F = 1.93$	$r^2 = 0.18$; $F = 4.94$
	$P < .0001$	$P < .0001$	$P = 0.1571$	$P = 0.0369$
Red cabbage	$r^2 = 0.63$; $F = 11.37$	$r^2 = 0.62$; $F = 10.76$	$r^2 = 0.14$; $F = 9.13$	$r^2 = 0.15$; $F = 1.18$
	$P = 0.0001$	$P = 0.0002$	$P = 0.0005$	$P = 0.3415$
Cauliflower	$r^2 = 0.89$; $F = 52.29$	$r^2 = 0.73$; $F = 17.86$	$r^2 = 0.40$; $F = 6.67$	$r^2 = 0.15$; $F = 2.41$
	$P < .0001$	$P < .0001$	$P = 0.0027$	$P = 0.0917$
Kale	$r^2 = 0.67$; $F = 13.16$	$r^2 = 0.38$; $F = 4.04$	$r^2 = 0.32$; $F = 3.18$	$r^2 = 0.05$; $F = 0.35$
	$P < .0001$	$P = 0.0214$	$P = 0.0463$	$P = 0.7862$
Radish	$r^2 = 0.83$; $F = 32.28$	$r^2 = 0.87$; $F = 43.07$	$r^2 = 0.58$; $F = 9.04$	$r^2 = 0.77$; $F = 22.87$
	$P < .0001$	$P < .0001$	$P = 0.0005$	$P < .0001$

Table 5 Analysis of the interaction between plant growth stage and number of *B. hilaris* infested in chlorophyll content (SPAD value) using a two-way ANOVA with slice option for each host plant

Host plant	Sliced by plant stage			Sliced by # adults infested		
	Stage	*F*	*P*	# Adult infested	*F*	*P*
Broccoli	Cotyledon	17.08	<.0001	Non-infested	0.97	0.4107
	2-Leaf	5.85	0.0012	1 female	5.21	0.0025
	4-leaf (upper)	8.42	<.0001	1 mating pair	13.17	<.0001
	4-Leaf (lower)	0.56	0.6411	2 mating pairs	15.80	<.0001
Green cabbage	Cotyledon	8.94	<.0001	Non-infested	1.07	0.3652
	2-Leaf	9.48	<.0001	1 female	5.94	0.0011
	4-Leaf (upper)	13.16	<.0001	1 mating pair	6.66	0.0005
	4-Leaf (lower)	0.18	0.9089	2 mating pairs	14.59	<.0001
Red cabbage	Cotyledon	14.73	<.0001	Non-infested	0.25	0.8593
	2-Leaf	2.16	0.1000	1 female	7.69	0.0002
	4-Leaf (upper)	9.26	<.0001	1 mating pair	7.67	0.0002
	4-Leaf (lower)	1.04	0.3811	2 mating pairs	8.75	<.0001
Cauliflower	Cotyledon	26.65	<.0001	Non-infested	1.53	0.2137
	2-Leaf	17.43	<.0001	1 female	13.40	<.0001
	4-Leaf (upper)	10.85	<.0001	1 mating pair	14.22	<.0001
	4-Leaf (lower)	0.12	0.9480	2 mating pairs	27.93	<.0001
Kale	Cotyledon	16.07	<.0001	Non-infested	0.31	0.8146
	2-Leaf	10.04	<.0001	1 female	3.06	0.0332
	4-Leaf (upper)	6.65	0.0005	1 mating pair	12.16	<.0001
	4-Leaf (lower)	0.15	0.9266	2 mating pairs	15.98	<.0001
Radish	Cotyledon	12.12	<.0001	Non-infested	0.22	0.8790
	2-Leaf	10.45	<.0001	1 female	6.81	0.0004
	4-Leaf (upper)	15.84	<.0001	1 mating pair	11.18	<.0001
	4-Leaf (lower)	0.08	0.9711	2 mating pairs	20.33	<.0001

$df = 3, 75$ for both sliced by plant stage and sliced by # *B. hilaris* infested

feeding damage than males (Huang et al. 2013). Another related species, *M. histrionica*, was reported to cause plant mortality in broccoli plants more quickly as insect density increased (Ludwig and Kok 2001).

Brown et al. (2003) showed that glucosinolates, the secondary plant-defensive compound in the family of Brassicaceae, were detected at higher concentration in younger leaves than older leaves. Preferential feeding of *B. hilaris* on

Table 6 Relationship between change in relative chlorophyll content and number of *B. hilaris* infested at different growth stages of each *Brassica* host plant

Host plant	Cotyledon	2-True leaf	4-True leaf (upper)	4-True leaf (lower)
Broccoli	$r^2 = 0.74; F = 19.32$	$r^2 = 0.55; F = 8.20$	$r^2 = 0.59; F = 9.79$	$r^2 = 0.05; F = 0.40$
	$P < .0001$	$P = 0.0009$	$P = 0.0003$	$P = 0.7566$
Cabbage	$r^2 = 0.59; F = 6.51$	$r^2 = 0.63; F = 11.40$	$r^2 = 0.63; F = 11.42$	$r^2 = 0.04; F = 0.29$
	$P = 0.0030$	$P = 0.0001$	$P = 0.0001$	$P = 0.8327$
Red cabbage	$r^2 = 0.52; F = 7.12$	$r^2 = 0.48; F = 5.97$	$r^2 = 0.75; F = 20.52$	$r^2 = 0.11; F = 0.90$
	$P = 0.0019$	$P = 0.0044$	$P < .0001$	$P = 0.4562$
Cauliflower	$r^2 = 0.68; F = 13.88$	$r^2 = 0.70; F = 15.88$	$r^2 = 0.70; F = 15.53$	$r^2 = 0.09; F = 0.63$
	$P < .0001$	$P < .0001$	$P < .0001$	$P = 0.6062$
Kale	$r^2 = 0.65; F = 12.17$	$r^2 = 0.62; F = 11.07$	$r^2 = 0.42; F = 4.85$	$r^2 = 0.06; F = 0.46$
	$P < .0001$	$P = 0.0002$	$P = 0.0108$	$P = 0.7135$
Radish	$r^2 = 0.68; F = 13.92$	$r^2 = 0.44; F = 5.18$	$r^2 = 0.68; F = 13.87$	$r^2 = 0.05; F = 0.38$
	$P < .0001$	$P = 0.0082$	$P < .0001$	$P = 0.7671$

younger leaf tissue in 4-leaf-stage plants suggests that putatively higher concentrations of glucosinolates caused no significant reduction in *B. hilaris* feeding. Gols and Harvey (2009) reported that insect herbivore specialists on Brassicaceous plant species have evolved adaptations to excrete or detoxify glucosinolates. The flea beetle, *Phyllotreta cruciferae* Goeze, did not discriminate between cotyledons having sinigrin [major glucosinolate of *Brassica juncea* (L.) Czern.] and glucobrassicin (major glucosinolate of *B. napus* L.), and both glucosinolate types, and concentrations had little effect protecting seedlings of these two *Brassica* from *P. cruciferae* feeding damage (Bodnaryk and Palaniswamy 1990). These relationships need to be explored further for *B. hilaris* and susceptible Brassicaceous hosts.

The impact of insect feeding often varies by species. For instance, insects such as aphids can feed without affecting plant growth or fitness, while feeding by other insects such as spittlebugs and beetles can reduce vegetative growth and seed production (Meyer and Whitlow 1992; Meyer 2000). In this study, we observed that leaf growth was negatively affected by the feeding of *B. hilaris*. Significant reductions in total leaf area at the cotyledon and 2-leaf stages for all tested host crops indicated that early developmental plant stages are very sensitive to *B. hilaris* feeding. Other hemipterans have been shown to reduce leaf area following feeding bouts. The grass bug, *I. pacifica*, was reported to cause a similar reduction in both green and total leaf area on Great Basin wildrye and intermediate wheatgrass (Hansen and Nowak 1988). Feeding by *Bemisia* whiteflies was demonstrated to cause negative impacts on alfalfa growth, forage yield, and quality (Palumbo et al. 2000). Rice bug, *Leptocorisa oratorius* (F.), was reported to reduce grain quality, seed germination rates, and yield loss in the Philippines (Jahn et al. 2004).

The chlorophyll meter used in this study provided a nondestructive, quick, and reliable method for measuring chlorophyll changes associated with insect feeding damage. In our study, chlorophyll content in host plant leaf tissue was negatively affected even when plants were only exposed to a single female. As anticipated, no significant decrease in chlorophyll content was detected in control groups because of the lack of feeding damage. Relative SPAD values did, however, fluctuate among host plants as would be expected. Although different parameters were measured, Velikova et al. (2010) reported a significant reduction in chlorophyll fluorescence parameters on herbaceous plants resulting from the feeding and oviposition of two pentatomids, *M. histrionica* and *N. viridula*. They confirmed that the permanent impairment of photosynthetic phytochemistry was restricted to the damaged areas on the leaf (Velikova et al. 2010).

Losses of chlorophyll content due to insect herbivory have been quantified in other hemipterans using similar chlorophyll analyses. Feeding by *B. tabaci* was reported to reduce relative leaf chlorophyll levels (SPAD values) in lettuce leaves (Palumbo et al. 1996). Feeding by *A. pisum* caused significant loss of chlorophyll *a* and *b* in the Fabaceae plants (Goławska et al. 2010). Infestation of *D. noxia* was reported to be associated with the loss of chlorophyll content in cereal crops using a chlorophyll meter (Heng-Moss et al. 2003). Measurements with a Spectronic 401(Milton Roy, Rochester, NY) showed that feeding injury by *S. pyrioides* reduced chlorophyll content and adversely affected net leaf photosynthesis and transpiration in azalea (Buntin et al. 1996). *B. tabaci* was reported to reduce leaf photosynthesis in tomato leaves by reducing content and photosynthetic capacity of chlorophyll (Buntin et al. 1993).

Residual dry weights and total leaf areas for the host plants 21 days following the infestation period were not available for the cotyledon and 2-leaf stages in our experiment. Because each leaf was detached from the plant at the end of the 48-h period for measurements of leaf area

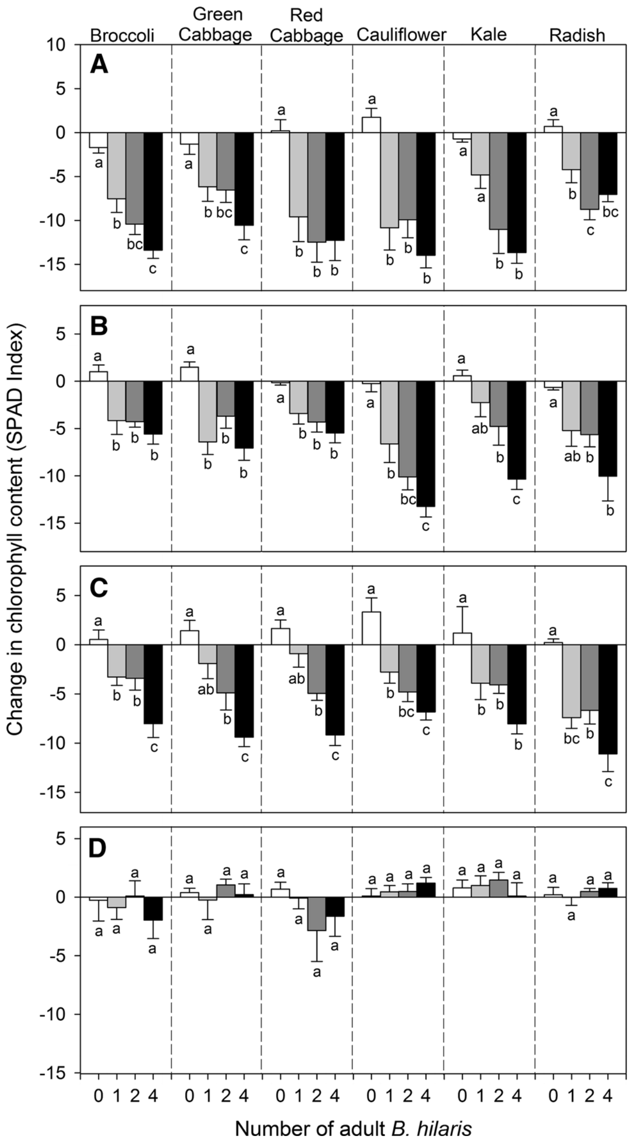

Fig. 3 Mean ± SEM change in leaf chlorophyll content (SPAD values) of six *Brassica* crops exposed to various numbers of *B. hilaris* adults for 48 h on seedling plants at **a** cotyledon stage, **b** 2-leaf stage, **c** 4-leaf stage, younger two leaves, and **d** 4-leaf stage, older two leaves. Chlorophyll change was based on positive or negative changes in SPAD value after a 48-h period of *B. hilaris* infestation. Means followed by the *same letter* are not significantly different ($P < 0.05$; LSMEANS test)

and feeding damage under the digital microscope, these plants could not be used. However, 4-leaf plants were large enough that a nondestructive method was used to measure leaf area and damage without removing the leaves from the plant (Huang et al. 2013). Although yields of host plants were not examined in this study, increases in total leaf area by greater than tenfold following the 21-day growth period in the greenhouse suggested that 4-leaf-stage plants may be able to compensate for short bouts of feeding by *B. hilaris*. However, the significant reductions in dry plant weight (above ground) and dry bulb weight (underground) in the damaged radish plants indicated that feeding of *B. hilaris* can likely reduce yields and market value of radish crops under field conditions. Reductions in yield and quality by

Table 7 Correlation between number of *B. hilaris* infested and mean ± SEM total leaf area and dry weight from 4-leaf-stage plants 21 days following the infestation period for each host plant

Host plant	# Adults infested	Total leaf area (cm^2)[a]	Dry weight (g)[a]
Broccoli	Non-infested	766.7 ± 56.8a	2.6 ± 0.2a
	1 female	669.5 ± 80.3ab	1.9 ± 0.3b
	1-Mating pair	600.3 ± 50.3b	1.8 ± 0.1b
	2-Mating pairs	522.3 ± 21.6b	1.5 ± 0.1b
	F	3.40	4.99
	P > *F*	0.0377	0.0096
	Spearman's coefficient	−0.5976	−0.6424
Green cabbage	Non-infested	1,125.3 ± 61.8a	2.4 ± 0.3a
	1 female	956.0 ± 81.2ab	1.7 ± 0.2b
	1-Mating pair	816.8 ± 24.3b	1.1 ± 0.2c
	2-Mating pairs	529.3 ± 96.1c	0.9 ± 0.1c
	F	12.54	14.83
	P > *F*	<.0001	<.0001
	Spearman's coefficient	−0.8453	−0.7847
Red cabbage	Non-infested	1,083.3 ± 27.9a	2.4 ± 0.2a
	1 female	933.5 ± 50.3b	1.9 ± 0.2ab
	1-Mating pair	725.8 ± 28.5c	1.5 ± 0.1bc
	2-Mating pairs	657.2 ± 39.8c	1.2 ± 0.2c
	F	26.65	9.78
	P > *F*	<.0001	0.0004
	Spearman's coefficient	−0.8937	−0.7609
Cauliflower	Non-infested	1,073.2 ± 52.6a	2.2 ± 0.2a
	1 female	950.0 ± 42.3ab	1.9 ± 0.1b
	1-Mating pair	779.5 ± 78.6bc	1.6 ± 0.1bc
	2-Mating pairs	741.7 ± 56.5c	1.5 ± 0.1c
	F	6.81	6.67
	P > *F*	0.0024	0.0027
	Spearman's coefficient	−0.6945	−0.6807
Kale	Non-infested	550.3 ± 30.8	1.2 ± 0.1
	1 female	455.7 ± 61.1	1.1 ± 0.1
	1-Mating pair	597.0 ± 45.9	1.2 ± 0.1
	2-Mating pairs	448.7 ± 13.2	0.9 ± 0.1
	F	3.04	1.4
	P > *F*	0.0528	0.2710
	Spearman's coefficient	−0.2747	−0.2486
Radish	Non-infested	440.7 ± 30.9a	0.8 ± 0.0a
	1 female	339.3 ± 58.5a	0.6 ± 0.1a
	1-Mating pair	367.8 ± 83.2a	0.3 ± 0.1b
	2-Mating pairs	70.5 ± 34.1b	0.2 ± 0.1b
	F	8.40	12.3
	P > *F*	0.0008	<.0001
	Spearman coefficient	−0.5976	−0.8169

[a] Means followed by the same letter are not significantly different ($P < 0.05$; LSMEANS test)

feeding of pentatomids were reported in cotton (Barbour et al. 1990; Greene et al. 1999) and vegetables (Ludwig and Kok 2001; Kuhar et al. 2012). Townsend and Sedlacek (1986) reported that feeding by *C. hilaris* and *Euschistus* species produced significant detrimental effects to seedling and early development stages of corn, including reductions in plant height, dry root, and leaf weights.

Our data provide essential information on the impact of *B. hilaris* feeding on plant growth and chlorophyll for several commercial Brassicaceous vegetables. Losses in total leaf area, chlorophyll content, and dry weight in response to short bouts of *B. hilaris* feeding suggest a feeding-induced stress response in early developmental stages of Brassicaceous species. Because of the economic significance and large number of acres of Brassicaceous crops grown in the desert southwest, control of this pest during crop establishment is critical. To date, insecticides have been the primary method for *B. hilaris* management. Action thresholds have not yet been established for *B. hilaris* on these crops largely due to the lack of data describing density/damage relationships between this pest and commercial cole crops. Data generated in this study have provided a better understanding of the impacts of *B. hilaris* feeding damage on seedling Brassicaceous plants and should be useful in developing pest management strategies during crop establishment. Field studies are presently underway to examine which phenological growth stages of seedling broccoli and cauliflower plants (i.e., cotyledon through 6-leaf-stage plants) can tolerate or compensate *B. hilaris* feeding damage without suffering economic reductions in yield, quality, and harvest maturity.

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