Buttercup Squash Provides a Marketable Alternative to Blue Hubbard as a Trap Crop for Control of Striped Cucumber Beetles (Coleoptera: Chrysomelidae)

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ABSTRACT Winter squash is a vital agricultural commodity worldwide. In the Northeastern United States, the primary insect pest is the striped cucumber beetle, *Acalymma vittatum* F. Using a Blue Hubbard squash (*Cucurbita maxima* Duchesne) perimeter trap crop system can reduce insecticide use by >90% in butternut squash (*C. moschata* Poir), the primary winter squash grown in this region. Despite the savings in insecticide costs, growers may be reluctant to give up field space for a perimeter crop of Blue Hubbard squash, which comprises only 5% of the winter squash market in New England as compared with 19% for buttercup squash. Finding a more marketable trap crop would lower the barrier for adoption of this system. We tested eight varieties of three species of cucurbits for attractiveness to beetles relative to Blue Hubbard and butternut squash, and chose buttercup squash as the most promising replacement. We compared the effect of a buttercup border, Blue Hubbard border, or control (no border) on beetle numbers, herbivory, insecticide use, pollination, and pollen limitation in the main crop. We found that buttercup squash performed equally well as Blue Hubbard as a trap crop, with 97% reduction in total insecticide use compared with control fields. Honey bees (*Apis mellifera* L.) and squash bees (*Peponapis pruinosa* Say) were the predominant pollinators, and border treatments did not affect visitation. Hand pollination did not increase reproduction or yield, indicating that natural pollination was sufficient for full yield. This study confirms the effectiveness of perimeter trap crop systems and offers growers a more marketable trap crop for managing cucumber beetle damage.

KEY WORDS *Acalymma vittatum*, butternut squash, *Cucurbita maxima*, integrated pest management (IPM), pollination

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Cucurbits are an important agricultural crop across the globe (Paris 1989). Cucumber beetles (*Diabrotica* spp. and *Acalymma vittatum* F.; Coleoptera: Chrysomelidae) constitute some of the most serious pests of cucurbit crops in the world (Metcalf and Metcalf 1992) and in the United States, and are the primary target of insecticide applications on these crops in the Northeastern U.S. (Hoffmann et al. 1996, Hollingsworth et al. 1998, Stivers 1999). Trap cropping using Blue Hubbard squash (*Cucurbita maxima* Duchesne) reduced the need for insecticides to control cucumber beetles by as much as 90% in butternut and other squash (*C. moschata* Poir) (Pair 1997, Boucher and Durgy 2004, Cavanagh et al. 2009). However, the need to dedicate a portion of the field to a trap crop with limited market demand may deter growers from using the system. Although trap cropping with Blue Hubbard dramatically reduced pesticide use, finding a more marketable alternative to Blue Hubbard is necessary for this method to be widely adopted for controlling *A. vittatum.*

Winter squash is an economically important cucurbit crop in the Northeastern U.S., and yield can be strongly affected by interactions with both pests and pollinators. Winter squash production has an estimated value greater than $5 million for the state of Massachusetts, where this study was conducted (Hollingsworth et al. 1998), and butternut squash constitutes 54% of all winter squash harvested in New England (Clifton and Duphily 2006). Striped cucumber beetle and the bacterial wilt disease it vectors are two of the most important factors affecting butternut yield (Northeastern IPM Center Vegetable Working group 2009). However, recent, dramatic losses of honey bees (*Apis mellifera* L.) because of Colony Collapse Disorder (Cox-Foster et al. 2007) have led to concerns about potential yield declines in pollinator-reliant crops such as butternut squash. Although supplemental pollination increased yield in many cucurbits (Stanghellini et al. 1997, 1998, Kremen et al. 2002, Strauss and Murch 2004), recent work in watermelon suggests that crops in the Northeastern U.S. may receive adequate pollination from the existing bee com-

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munity (Winfree et al. 2007). More studies are needed to provide creative pest management options and to assess the importance of pollinators for butternut yield on farms.

Perimeter trap cropping (PTC hereafter) with Blue Hubbard has been shown to significantly reduce the need for insecticide applications in butternut crops. Perimeter trap cropping systems are designed to take advantage of pest colonization behavior and host preference. Border defenses are established by planting a more attractive trap crop to completely encircle the main crop, resulting in reduced infestation and need for insecticides in the main crop (Aluja et al. 1997; Mitchell et al. 2000; Boucher and Durgy 2003, 2004). Blue Hubbard is highly preferred by striped cucumber beetles relative to butternut squash (McGrath 2000), summer squash (*C. pepo* L.), and cucumber (*Cucumis sativus* L.) (Boucher and Durgy 2004). When early season beetles encounter a perimeter of Blue Hubbard, they tend to remain there rather than move to the main crop. Insecticides can be used to kill pest populations in the perimeter, while the need for pesticides is eliminated or dramatically reduced in the main crop. Small plot experimental trials suggest that trap crop borders do not affect pollinator visitation in the main crop (Adler and Hazzard 2009). However, pollinator behavior can vary with spatial scale (Cariveau and Norton 2009), and the effect of border crops on main crop pollination has not been assessed at the scale of farm fields.

While PTC with Blue Hubbard has been effective in controlling pest populations and reducing pesticide applications in butternut crops, this system relies on devoting a portion of the main crop area to the trap crop, which can result in an overall reduction in yield per hectare if the trap crop is not marketable. Blue Hubbard represents only 5% of the total winter squash market in New England (Clifton and Duphily 2006). Buttercup squash (*C. maxima*) and acorn squash (*C. pepo*) have much greater market value than Blue Hubbard (19 and 11% of the market respectively, Clifton and Duphily 2006). Perimeter trap crop systems would be more likely to be accepted by growers if Blue Hubbard could be replaced with a more marketable alternative, such as buttercup or acorn squash. However, these crops have not been compared with Blue Hubbard as potential PTC alternatives.

We performed variety trials to evaluate the attractiveness of eight types of winter squash from three species of cucurbits in comparison to Blue Hubbard and butternut squash. The most promising of these, in terms of both attractiveness to beetles and market potential, was then used in commercial field trials. We compared beetle numbers, herbivory, insecticide use, and pollinator visits in a PTC treatment with a Blue Hubbard border, a PTC treatment with a border of the selected variety, and a conventional treatment with no border. To determine if reproduction and yield were pollen-limited because of the local pollinator community, we also conducted hand-pollination treatments within each field.

Materials and Methods

Preference Trial. *Experimental Design.* In 2004 we tested the relative attractiveness of winter squash cultivars as potential trap crops for butternut squash. We included eight cultivars from three species of cucurbits: 'Burgess' buttercup (*C. maxima*), 'Red Kuri' hubbard squash (*C. maxima*), 'Blue Hubbard' hubbard squash (*C. maxima*), 'Waltham' butternut (*C. moschata*), 'La Estrella' calabasa (*C. moschata*), 'Bush Delicata' delicata squash (*C. pepo*), a standard mix of gourds (*C. pepo*), and 'Table Ace' acorn squash (*C. pepo*). We chose cultivars that were of commercial interest to growers. The buttercup, 'Red Kuri', butternut, delicata, standard gourd mix, and Blue Hubbard squash seed were provided by Johnny's Selected Seeds (Winslow, ME), and the acorn and calabasa squash seed were provided by Rupp Seeds (Wauseon, OH). Five blocks were planted by hand on 3 June at the University of Massachusetts Crop Research and Education Center, South Deerfield, MA. Each block contained one plot of each cultivar, for a total of 40 plots. Cultivars were randomly assigned to plots within the block. Plots contained three rows of seven plants with 35.6 cm between each plant and 1.52 m between each row. Plots within each block were separated by 3.05 m, and blocks were separated by 4.57 m. Plots were fertilized on 28 May with 19–19-19 (Crop Production Services, South Deerfield, MA) at a rate of 560.43 kg per hectare (500 lbs per acre) based on soil test recommendations (Howell 2008). Weed control was achieved with a commercial mixture of ethalfluralin and clomazone (Strategy herbicide, Loveland Products, Greeley, CO) applied at the rate of 4.68 liters per hectare on 4 June, followed by mechanical cultivation as needed thereafter.

Measuring Beetle Numbers and Herbivory. Plants were monitored at weekly intervals from 18 June to 1 July. Five plants from the middle row of each plot were scouted for number of live beetles, cotyledon damage, and overall defoliation of the plant. We rated cotyledon and overall defoliation on a 1–5 scale in 20% increments, with 0 for no damage.

Statistical Analysis. Our responses were beetle numbers and defoliation. Presence of cotyledon damage was not included in analysis because nearly all plants had cotyledon damage. Responses were averaged over censuses to produce one value per response per plot. All data here and below were analyzed using PROC GLM in SAS V.9.1 (SAS Institute 2004). To evaluate the effect of different cucurbit cultivars and species on attractiveness to beetles, we used analysis of variance (ANOVA) to compare beetle numbers and defoliation using species (*C. maxima, moschata,* or *pepo*) and cultivar nested within species as the independent factors. We also performed separate ANOVAs on cultivar with a priori contrasts of each cultivar with butternut squash and Blue Hubbard. Cultivars that attracted significantly more beetles than butternut squash were considered potential trap crops, and those that attracted as many or more beetles than Blue Hubbard were considered the best trap crop possibilities.

Commercial Fields. *Experimental Design.* The preference trial indicated that the buttercup and 'Red Kuri' squashes were significantly more attractive to beetles than butternut squash. The buttercup squash cultivar was as attractive as Blue Hubbard, and 'Red Kuri' was more attractive than Blue Hubbard (see Results). However, buttercup squash are much more marketable than 'Red Kuri' (Clifton and Duphily 2006). Because our goal was to find a more marketable PTC alternative than Blue Hubbard with equivalent beetle attraction, buttercup was chosen for tests in commercial field trials. To assess the effectiveness of buttercup squash as a replacement for a Blue Hubbard trap crop in butternut squash, we haphazardly assigned 21 commercial butternut squash fields to one of three treatments (n = seven per treatment): a PTC system with a Blue Hubbard border, a PTC system with a buttercup squash border, and a conventional treatment with no treated border. We used two border rows on field edges next to woods or scrub, which can be potential overwintering sites for striped cucumber beetles, and one row if the field edge was not adjacent to woods or scrub. The border of one Blue Hubbard PTC field was destroyed during early cultivation and that field was eliminated from the study. At planting, both the Blue Hubbard and the buttercup PTC borders were treated with the systemic insecticide imidacloprid (Admire 2 F, Bayer CropScience, Research Triangle Park, NC), and received no further treatment. The butternut did not receive insecticide at planting in any treatment. Fields ranged in size from 0.81 to 4.05 hectares. All growers planted their fields as they normally would, except for the inclusion of the treated border in the PTC fields. Cultivation and nutrient management were performed by the grower, as per the needs of the field and standard management practices.

Measuring Herbivory and Beetle Numbers. Each field was monitored at least once a week from seedling emergence until the first sign of beetles, and then censused weekly for 4 wk. During each census, 25 plants were randomly selected and scouted in the field borders to determine total beetle numbers, defoliation, and cotyledon damage using the same methods as the variety trial. Another 25 were randomly selected and scouted from a row half way between the border and the center of the field to determine beetle numbers, cotyledon damage, and defoliation in the main crop.

Pesticide Use. In all treatments, no pesticides were used on the butternut main crop until beetles reached an economic threshold (one beetle per plant on average from emergence up to three true leaves, then two beetles per plant on average until flowering), and sprayed with a foliar insecticide if the threshold was exceeded. Thresholds were adapted from previously published work on cucurbit crops (Burkness and Hutchison 1998, Brust and Foster 1999). When thresholds were exceeded, pesticides were applied to the entire field for all treatments. We recorded pesticide use as the proportion of each field that required treatment, based on growers' spray records. Pesticide use was analyzed as total proportion of field sprayed, summing over multiple sprays. For example, if a control field was sprayed twice over the season, this would be a proportion of two because the entire area was sprayed twice. For PTC treatments, the initial border treatment with imidacloprid was counted in the measurement of pesticide use. Using the proportion of the field that was treated as our response variable allows us to account for the use of the systemic insecticide in the borders of the PTC fields, which contains different active ingredients and is applied at different rates than the foliar materials. As fields were of uneven size and shape, proportion of field requiring pesticides was a more universal measurement than area treated, amount of insecticide used, or other absolute measures of insecticide use. Because fields were roughly rectangular but unevenly shaped, the border area was estimated as if the fields were rectangular with length to width proportions of 1:2. For example, a two hectare field of irregular proportions would be standardized as a rectangular two hectare field with a width of 100 m and a length of 200 m. Assuming that the PTC borders were 1.8 m wide (the width of standard between-row spacing for butternut fields), this would give an estimated border area of 1,092 m^2, or a proportion of 0.05. Standardizing the fields in this way allowed us to quantify and compare pesticide use between fields of different size and shape (as in Cavanagh et al. 2009). Exact measurement of the sometimes curved or jagged field edges was not practical; given how dramatically and similarly both PTC treatments reduced pesticide use compared with the conventional treatment (see Results), using the precise dimensions should not change our results.

Pollinator Observations. We observed insect visits to flowers in the border and main crop of 19 fields on 18 separate dates between 12 July and 14 August. Seven fields were observed twice, 12 fields were observed once, and one field was not observed because of delayed phenology. We conducted 5-min observations on up to five individual male and female flowers per date in both the main crop and border of each field, for a total of 20.4 h in the main crop and 13.4 h in the border crops. All observations took place between 0530 and 1130, when flowers are open and pollinators are active. We recorded the number of visits and insect taxa for all visits, and we counted beetles in each observed flower. Because squash plants are vines that readily intertwine, we did not distinguish between individual plants.

Assessing Pollen Limitation. To determine if pollen receipt limited fruit or seed set, we hand-pollinated female flowers once (nine fields) or twice (11 fields) over the season; treatment dates and frequency were determined by field phenology. On each date, we walked two randomly selected transects through the main crop and identified up to 30 open female flowers. We randomly assigned flowers in groups of five to receive hand-pollination or control treatments. We considered flower the unit of replication and did not identify individual plants. Pollen was collected from at least five male donor flowers per field, mixed in a petri dish, and applied with a camelhair paintbrush to coat stigmas. Control flowers were marked but not pollinated, and all flowers were open to natural pollination. After 2 wk we noted whether each flower aborted or set fruit, and at harvest we weighed each mature fruit. A subsample of up to five fruits per treatment per field per date was randomly chosen and assessed for number of developed seeds, proportion of developed seeds, and weight per developed seed (total seed weight/number of developed seeds).

Statistical Analysis. To compare the effectiveness of border treatments for managing herbivory and reducing pesticide use, our responses were beetle numbers, cotyledon damage, and leaf herbivory in the border and main crop, and proportion of field treated with pesticide. We compared beetle numbers and damage in the main crops using one-way ANOVA with border treatment (Blue Hubbard, buttercup, or conventional) as the independent factors. All responses were per weekly census and averaged over censuses to compare herbivory across the early growing season. We also compared beetle counts and damage in the borders of each field, with border treatment as the independent variable. Cotyledon damage in the borders was $\log(x + 1)$ transformed to normalize the data; all other data were normal without transformation. The total proportion of fields sprayed in each system was compared using one-way ANOVA with border treatment as the independent variable. We used $\log(x + 1)$ transformation instead of the arcsine(sqrt(x)) transformation typically used for proportional data because multiple sprays of the entire field resulted in proportions greater than one.

For the pollinator observations, we used ANOVAs to ask how border treatment affected the mean number of squash bee visits, honey bee visits, and total visits per flower over 5-min periods, and the number of cucumber beetles per flower. Bumblebee visits were not analyzed separately because of low frequencies (see Results) but were included in total visits. Separate analyses were conducted for male and female flowers, and for borders and main crops. Responses were $\log(x + 1)$ transformed to improve normality.

The goal of our hand-pollination manipulation was to determine if pollination limited yield and seed set within field. Assessing effects of border treatments, or interactions between border treatment and hand-pollination, on yield was not a goal of our study because grower's fields vary in butternut cultivar and numerous other factors that could not be controlled and have major effects on yield. We analyzed whether pollination treatment, field, date, and the pollination × field interaction affected flower fate (fruit or aborted) using binary logistic regression, fruit weight using ANOVA, and number of developed seeds, proportion developed seeds, and developed seed weight using MANOVA followed by ANOVA when MANOVA results were significant (Scheiner 1993). Fruit weight was considered separately from seed responses because seeds were only assessed for a subset of mature fruit. Fruits that were damaged, moldy or lost were eliminated from analyses. Fruit weight was $\log(x + 1)$ transformed and proportion of developed seeds was arcsine(square root (x)) transformed to improve fit to normality; other responses were normal without transformation.

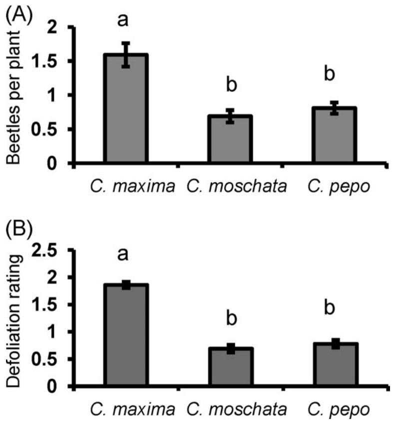

Fig. 1. (A) Beetle numbers and (B) defoliation by species in the preference trial. Means with the same letter are not significantly different. Error bars represent standard error.

Results

Preference Trial. There were significantly more beetles on *C. maxima* compared with *C. moschata* or *C. pepo* ($F_{2,28} = 20.27$; $P < 0.0001$), and correspondingly higher defoliation ($F_{2,28} = 139.88$, $P < 0.0001$; Fig. 1). Cultivars within species also differed in beetle numbers ($F_{5,28} = 3.01$; $P = 0.01$) and defoliation ($F_{5,28} = 3.37$; $P = 0.02$). A separate ANOVA using a priori contrasts between cultivars revealed that buttercup squash ($F_{1,32} = 10.08$; $P = 0.003$), Blue Hubbard ($F_{1,32} = 8.23$; $P = 0.007$), and 'Red Kuri' squash ($F_{1,32} = 41.64$; $P < 0.0001$) were all more attractive to beetles than butternut squash (Fig. 2A). Buttercup was as attractive to beetles as Blue Hubbard ($F_{1,32} = 0.09$; $P = 0.76$), and 'Red Kuri' squash was more attractive than Blue Hubbard ($F_{1,32} = 12.85$, $P = 0.001$; Fig. 2A). Defoliation followed a similar pattern, with higher defoliation in Blue Hubbard ($F_{1,32} = 64.88$; $P < 0.0001$), 'Red Kuri' ($F_{1,32} = 124.91$; $P < 0.0001$) and buttercup squash ($F_{1,32} = 91.98$; $P < 0.0001$) compared with butternut, and higher defoliation in 'Red Kuri' than Blue Hubbard ($F_{1,32} = 9.74$; $P = 0.004$). All of the other cultivars had significantly lower defoliation than Blue Hubbard and were not different from butternut, with the exception of the standard gourds, which had more defoliation than butternut ($F_{1,32} = 6.58$; $P < 0.013$) but less than Blue Hubbard ($F_{1,32} = 29.56$, $P < 0.0001$; Fig. 2B).

Commercial Fields. *Herbivory and Pesticide Use.* There was a notable increase in beetles in the PTC borders compared with the conventional borders ($F_{2,17} = 5.25$, $P = 0.02$; Fig. 3); there were no significant

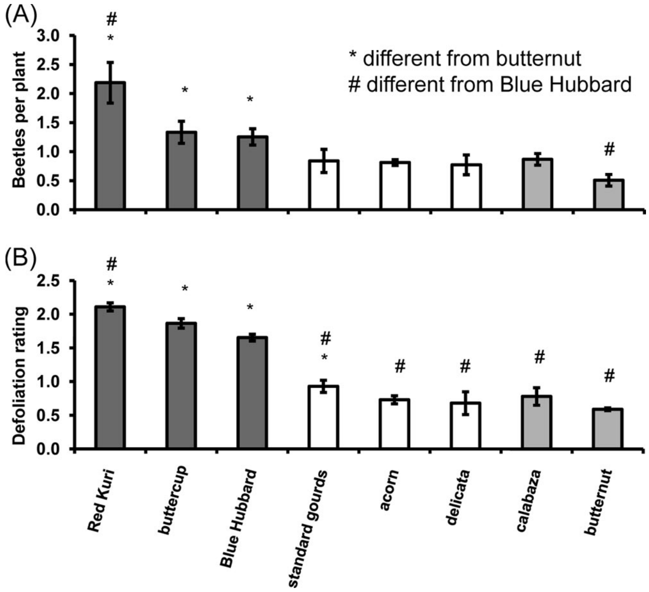

Fig. 2. (A) Beetle numbers and (B) defoliation by variety in preference trial. Species are grouped by color. Error bars represent standard error.

differences in cotyledon damage (means ± SE: Conventional: 1.55 ± 0.18, Hubbard: 1.51 ± 0.47, Buttercup: 1.08 ± 0.18; $F_{2,17} = 0.94$, $P = 0.41$) or defoliation (means ± SE: Conventional: 0.64 ± 0.12, Hubbard: 0.76 ± 0.14, Buttercup: 0.51 ± 0.10; $F_{2,17} = 1.10$, $P = 0.36$). In the main crop, cotyledon damage, beetle numbers, and defoliation were highest in the conventional compared with PTC treatments both overall and at most weekly censuses (means ± SE, summary across weeks, *cotyledon damage:* Conventional: 1.85 ± 0.38, Hubbard: 1.52 ± 0.29, Buttercup: 0.99 ± 0.27; *beetles:* Conventional: 0.68 ± 0.16, Hubbard: 0.34 ± 0.05, Buttercup: 0.51 ± 0.11; *defoliation:* Conventional: 0.68 ± 0.13, Hubbard: 0.47 ± 0.03, Buttercup: 0.49 ± 0.06), but there was no statistically significant effect of border treatments on any response in the main crop either when summarized across weeks ($F < 1.92$; $P > 0.17$ for all) or at any weekly census ($F < 2.3$; $P > 0.16$ for all). Despite the lack of statistical significance, beetle numbers exceeded thresholds in five of the seven conventional fields, which were sprayed from 1 to 5 times over the season as a control measure. Beetle numbers did not exceed thresholds in any of the 13 PTC fields, and so none of these fields were sprayed. Using a PTC system with either a Blue Hubbard or buttercup border reduced the proportion of the field that was sprayed by 97 and 97.4%, respectively (treatment effect: $F_{2,15} = 180.63$, $P < 0.0001$; Fig. 4), because most conventional fields required spraying one or more times while the only pesticide use in the PTC fields was the systemic applied to borders at planting.

Pollinator Observations. Honey bees (*Apis mellifera* L.) comprised 64.5% of main crop flower visits, followed by squash bees (*Peponapis pruinosa* Say; 32%) and bumble bees (*Bombus* spp.; 3.5%). The proportion of visits by honey bees was twice as high to Blue Hubbard and buttercup border flowers com-

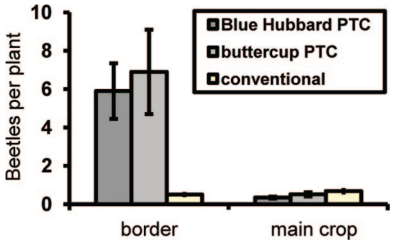

Fig. 3. Beetle numbers in the borders and main crops of PTC and conventional fields. Means with the same letter are not significantly different. Error bars represent standard error.

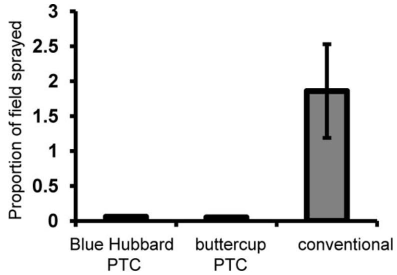

Fig. 4. Total proportion of experimental fields requiring treatment for beetle control. Means with the same letter are not significantly different. Error bars represent standard error. There are no error bars on the PTC treatments because there was no variation in pesticide requirement; all PTC fields had borders treated initially and required no further pesticide application. Multiple insecticide applications to individual fields resulted in proportions greater than one.

pared with butternut border flowers (75 and 66%, respectively, vs. 34%), but this difference was not significant ($F < 0.9$; $P > 0.4$ for all). Border crops had almost no visitation by bumble bees (1%). There was no effect of border treatment on the number of beetles, squash bee visits, honey bee visits, or total pollinator visits to male or female flowers in the main crop or border ($F < 2.4$; $P > 0.12$ for all except honey bees visiting male border flowers: $F_{2,\ 16} = 3.23$; $P = 0.066$).

Pollen Limitation. Of 677 flowers included in analysis, 71.6% set fruit. The probability of setting fruit varied with date (df = 1; Wald $\chi^2 = 7.9$; $P < 0.005$) and field (df = 18; Wald $\chi^2 = 55.2$; $P < 0.0001$), but not pollination treatment or the field by pollination interaction ($P < 0.8$ for both). The main effect of pollination was also not significant for any fruit or seed responses. Fruit weight did vary significantly with field ($F_{18,\ 417} = 38.3$; $P < 0.0001$) and the field by pollination interaction ($F_{18,\ 417} = 2.05$, $P < 0.007$), as did seed parameters (MANOVA: *Field:* Wilks' Lambda = 0.14, $F_{54,\ 456.7} = 7.81$, $P < 0.0001$; *Field by pollination:* Wilks' Lambda = 0.58, $F_{54,\ 456.7} = 1.71$, $P < 0.002$; ANOVA: *Field:* $F > 7.0$, $P < 0.0001$ for all; *Field by pollination:* $F > 1.6$, $P < 0.055$ for all). The significant interaction between field and pollination treatment without a significant main effect of pollination indicates that the effect of hand-pollination varied with field and did not consistently improve fruit weight or seed set.

Discussion

The preference trial showed that *C. maxima* species were more attractive to the striped cucumber beetle than either *C. pepo* or *C. moschata,* based on both beetle numbers and defoliation. Direct comparisons showed that 'Red Kuri' and the buttercup squash cultivar were as or more attractive than Blue Hubbard, and both were more attractive than the butternut cultivar. It is interesting to note that the *C. pepo* cultivars were not more attractive to beetles than *C. moschata,* with the exception of the standard gourds. This indicates that it may be possible to control striped cucumber beetles in some *C. pepo* cultivars using a PTC system, as suggested by previous work (Boucher and Durgy 2004). There is a great deal of variation in attractiveness within *C. pepo* cultivars (McGrath 2000), and additional field trials would be necessary to determine the range of cultivars that would benefit from a PTC treatment.

Variation in beetle attractiveness between cucurbit species has been well established in the literature (Andersen and Metcalf 1987, Brust and Rane 1995, Pair 1997, McGrath 2000, Smyth et al. 2002, Boucher and Durgy 2004), and is generally held to be associated with different concentrations and ratios of the bitter cucurbitacin compounds within the plant (Chambliss and Jones 1966, Metcalf et al. 1980). The preference patterns we found are consistent with the hypothesis that cucurbitacin drives preference; Blue Hubbard and buttercup squash are relatively high in cucurbitacin B, which is highly attractive to beetles (Chambliss and Jones 1966), while butternut squash is relatively low in cucurbitacins (Andersen and Metcalf 1987). It should be noted, however, that in one study field-collected beetles consumed more tissue from cucumbers lacking cucurbitacins than from an isogenic line with high cucurbitacin levels in no-choice tests (Smyth et al. 2002), despite a general preference of colony-reared beetles for the high cucurbitacin line in choice trials. This suggests that low cucurbitacin levels may confer some resistance to beetle feeding only when crops are grown in proximity to a high cucurbitacin crop, as is the case with PTC systems.

The results of the commercial field experiment confirm that buttercup squash is an effective replacement for Blue Hubbard as a perimeter trap crop in butternut squash. Using either a Blue Hubbard or buttercup PTC system reduced insecticide use by 97% compared with conventionally managed fields (Fig. 4). Beetle numbers exceeded threshold levels in most of the conventional fields but none of the PTC fields, although there was no statistically significant difference in beetle numbers or herbivory between the main crops in any treatment (Fig. 3). Indeed, the lack of statistically significant differences between conventional and PTC treatments may be because of spraying in the conventional field to reduce beetle numbers; such spraying was unnecessary in PTC fields because beetle numbers did not exceed thresholds. Thus, both PTC treatments controlled damage to the main crop as effectively as the conventional treatment, but with substantially less pesticide use. This research provides growers with a more marketable alternative to Blue Hubbard that can be used to dramatically reduce the need for pesticides in their butternut squash fields.

Employing a PTC system offers many benefits to growers beyond simply reducing the amount of insecticide needed to produce a viable crop. Perimeter trap crop systems also allow a large portion of the field to be used as an unsprayed refuge. This refuge can help to protect beneficial insects (Cilgi and Jepson 1992, Stary and Pike 1998) as well as potentially delaying the development of insecticide resistance in the target pest (Liu and Tabashnik 1997, Ives and Andow 2002). Insecticide resistance is not widespread in *A. vittatum,* but has been reported in the closely related *Diabrotica virgifera* LeConte (Zhu et al. 2001). In addition, leaving the majority of the field untreated with insecticides can potentially increase yield by protecting pollinators (Brust and Foster 1995) and reduce the likelihood of secondary pest outbreaks (Foster and Brust 1995). Pest management strategies that offer multiple benefits of delaying insecticide resistance, reducing environmental impacts, and preserving pollinators and natural enemies are essential goals of any IPM program.

Despite the benefits of implementing a system that offers these advantages, there are still many barriers before growers adopt a new system. Growers may be unlikely to adopt a new system if it is time intensive, involves new or unfamiliar equipment, or reduces the acreage available for marketable crops. Perimeter trap cropping in butternut squash is a good candidate for adoption because it integrates well with growers' existing crop systems and equipment, and does not require additional time. Using Blue Hubbard squash as a trap crop effectively reduces pesticide use while controlling pest insects (Pair 1997, Boucher and Durgy 2004, Cavanagh et al. 2009), but can also reduce total marketable yield. Our research demonstrates that buttercup squash is as effective as Blue Hubbard in reducing the need for pesticides, providing a more marketable border crop alternative for growers who wish to try a PTC system.

Pollination is critical for yield in over 90 major United States crops including many cucurbits (Delaplane and Mayer 2000, Kemp and Bosch 2001), and recent declines in both managed and native bees have prompted concerns about agricultural losses because of lack of pollination services (Allen-Wardell et al. 1998, Kearns et al. 1998, Cox-Foster et al. 2007, Winfree et al. 2007). We found that butternut squash yield was not limited by pollination across 19 farm fields in western Massachusetts. The effect of hand-pollination on fruit set varied across fields, suggesting no overall pollen limitation for yield. Furthermore, border treatment did not affect pollinator visitation to main crop flowers. Thus, both Blue Hubbard and buttercup squash can be used as effective PTC borders without competing with main crops for pollinator services. Honey bees were the most common visitors to these fields, in contrast with on-farm studies with *Cucurbita* and *Cucumis* in mid-Atlantic states, in which native bees provided more visits than honey bees (Shuler et al. 2005, Winfree et al. 2007). Given the high proportion of honey bee visits at our fields and concerns about honey bee decline, future research should continue to monitor pollen limitation for cucurbits in the Northeastern U.S.

We conclude that these results support previous work indicating that using a Blue Hubbard PTC system can reduce the need for insecticides (Cavanagh et al. 2009), and demonstrate that buttercup squash would be a suitable replacement for growers desiring a more marketable trap crop than Blue Hubbard. Having the option of using a more marketable variety of squash should provide additional incentive for growers to use PTC for beetle control in their butternut squash crops. In addition, the preference trial suggests the potential for buttercup squash as a trap crop to reduce insecticide use in some *C. pepo* squash, though further studies are needed to test this hypothesis. Finally, the results of our hand pollination treatment suggest that butternut squash are receiving adequate pollination from the existing bee community, consistent with other studies on cucurbits in the Northeastern U.S.

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References Cited

Adler, L. S., and R. V. Hazzard. 2009. Comparison of perimeter trap crop varieties: effects on herbivory, pollination, and yield in butternut squash. Environ. Entomol. 38: 207–215.

Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, S. Buchmann, J. Cane, P. A. Cox, V. Dalton, P. Feinsinger, M. Ingram, D. Inouye, C. E. Jones, K. Kennedy, P. Kevan, H. Koopowitz, R. Medellin, S. Medellin-Morales, G. P. Nabhan, B. Pavlik, V. Tepedino, P. Torchio, and S. Walker. 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. Conserv. Biol. 12: 8–17.

Aluja, M., A. Jimenez, M. Camino, J. Pinero, L. Aldana, V. Castrejon, and M. E. Valdes. 1997. Habitat manipulation to reduce papaya fruit fly (Diptera: Tephritidae) damage: orchard design, use of trap crops and border trapping. J. Econ. Entomol. 90: 1567–1576.

Andersen, J. F., and R. L. Metcalf. 1987. Factors Influencing distribution of *Diabrotica* spp (Coleoptera, Chyrsomelidae) in blossoms of cultivated *Cucurbita* spp. J. Chem. Ecol. 13: 681–699.

Boucher, T. J., and R. Durgy. 2003. Perimeter trap cropping for summer squash and cucumbers, pp. 217–19. Proceedings: New England vegetable and berry conference and trade show, Manchester, NH.

Boucher, T. J., and R. Durgy. 2004. Demonstrating a perimeter trap crop approach to pest management on summer squash in New England. J. Extension 42: 1–8.

Brust, G. E., and R. E. Foster. 1995. Semiochemical based toxic baits for control of striped cucumber beetle (Coleoptera: Chrysomelidae) in cantaloupe. J. Econ. Entomol. 88: 112–116.

Brust, G. E., and K. K. Rane. 1995. Differential occurrence of bacterial wilt in muskmelon due to preferential striped cucumber beetle feeding. Hort. Sci. 30: 1043–1045.

Brust, G. E., and R. E. Foster. 1999. New economic threshold for striped cucumber beetle (Coleoptera: Chrysomelidae) in cantaloupe in the midwest. J. Econ. Entomol. 92: 936–940.

Burkness, E. C., and W. D. Hutchison. 1998. Action thresholds for striped cucumber beetle (Coleoptera: Chrysomelidae) on 'Carolina' cucumber. Crop Prot. 17: 331–336.

Cariveau, D. P., and A. P. Norton. 2009. Spatially contingent interactions between an exotic and native plant mediated through flower visitors. Oikos 118: 107–114.

Cavanagh, A., R. Hazzard, L. S. Adler, and J. Boucher. 2009. Using trap crops for control of *Acalymma vittatum* (Coleoptera: Chrysomelidae) reduces insecticide use in butternut squash. J. Econ. Entomol. 102: 1101–1107.

Chambliss, O. L., and C. M. Jones. 1966. Cucurbitacins: specific insect attractants in Cucurbitaceae. Science 153: 1392-&.

Cilgi, T., and P. C. Jepson. 1992. The use of tracers to estimate the exposure of beneficial insects to direct pesticide spraying in cereals. Ann. Appl. Biol. 121: 239–247.

Clifton, N. P., and A. Duphily. 2006. New England winter squash profile, pp. 44. University of Massachusetts, Amherst, Massachusetts. (http://www.pronewengland.org/

INFO/PROpubs/Profile/WinterSquashProfile2006-04-14.pdf).

Cox-Foster, D. L., S. Conlan, E. C. Holmes, G. Palacios, J. D. Evans, N. A. Moran, P. L. Quan, T. Briese, M. Hornig, D. M. Geiser, V. Martinson, D. vanEngelsdorp, A. L. Kalkstein, A. Drysdale, J. Hui, J. H. Zhai, L. W. Cui, S. K. Hutchison, J. F. Simons, M. Egholm, J. S. Pettis, and W. I. Lipkin. 2007. A metagenomic survey of microbes in honey bee colony collapse disorder. Science 318: 283–287.

Delaplane, K. S., and D. F. Mayer. 2000. Crop pollination by bees. CABI Publishing, Cambridge, MA.

Foster, R. E., and G. E. Brust. 1995. Effects of insecticides applied to control cucumber beetles (Coleoptera: Chrysomelidae) on watermelon yields. Crop Prot. 14: 619–624.

Hoffmann, M. P., J. J. Kirkwyland, R. F. Smith, and R. F. Long. 1996. Field tests with kairomone-baited traps for cucumber beetles and corn rootworms in cucurbits. Environ. Entomol. 25: 1173–1181.

Hollingsworth, C., C. A. Mordhurst, R. Hazzard, and J. Howell. 1998. Pumpkin and winter squash project: 1998 grower survey and ICM project goals. UMass Extension Vegetable Notes.

Howell, J., [ed.]. 2008. New England Vegetable Management Guide. New England Extension Systems, University of Massachusetts, Amherst, MA.

Ives, A. R., and D. A. Andow. 2002. Evolution of resistance to Bt crops: directional selection in structured environments. Ecol. Lett. 5: 792–801.

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. Annu. Rev. Ecol. Syst. 29: 83–112.

Kemp, W. P., and J. Bosch. 2001. Bees in your backyard. Am. Bee J. 141: 183–185.

Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. Proc. Nat. Acad. Sci. USA 99: 16812–16816.

Liu, Y. B., and B. E. Tabashnik. 1997. Experimental evidence that refuges delay insect adaptation to *Bacillus thuringiensis.* Proc. R. Soc. London Series B. 264: 605–610.

McGrath, M. T. 2000. Comparison of Cucurbit crop types and cultivars for their attractiveness to cucumber beetles and susceptibility to bacterial wilt. Biological and Cultural Tests for Control of Plant Diseases (online). The American Phytopathogical Society, St. Paul, Minnesota.

Metcalf, R. L., and E. R. Metcalf. 1992. Plant kairomones in insect ecology and control. Chapman & Hall, New York.

Metcalf, R. L., R. A. Metcalf, and A. M. Rhodes. 1980. Cucurbitacins as kairomones for diabroticite beetles. Proc. Nat Acad. Sci. 77: 3769–3772.

Mitchell, E. R., G. G. Ho, and D. Johanowicz. 2000. Management of diamondback moth (Lepidoptera: Plutellidae) in cabbage using collard as a trap crop. Hort. Sci. 35: 875–879.

Northeastern IPM Center Vegetable Working Group. 2009. IPM needs and priorities for vegetable crops and strawberries in the Northeast region.

Pair, S. D. 1997. Evaluation of systemically treated squash trap plants and attracticidal baits for early-season control of striped and spotted cucumber beetles (Coleoptera: Chrysomelidae) and squash bug (Hemiptera: Coreidae) in cucurbit crops. J. Econ. Entomol. 90: 1307–1314.

Paris, H. S. 1989. Historical records, origins, and development of the edible cultivar groups of *Cucurbita pepo* (Cucurbitaceae). Econ. Bot. 43: 423–443.

SAS Institute. 2004. Base SAS 9.1 Procedures Guide, vol. 1–4. SAS Publishing, Cary, NC.

Scheiner, S. M. 1993. MANOVA: Multiple response variables and multispecies interactions, pp. 94–112. *In* S. M. Scheiner and J. Gurevitch (eds.), Design and Analysis of Ecological Experiments. Chapman & Hall, New York.

Shuler, R. E., T. H. Roulston, and G. E. Farris. 2005. Farming practices influence wild pollinator populations on squash and pumpkin. J. Econ. Entomol. 98: 790–795.

Smyth, R. R., D. W. Tallamy, J.A.A. Renwick, and M. P. Hoffmann. 2002. Effects of age, sex, and dietary history on response to cucurbitacin in *Acalymma vittatum.* Entomol. Exp. Appl. 104: 69–78.

Stanghellini, M. S., J. T. Ambrose, and J. R. Schultheis. 1997. The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. Am. Bee J. 137: 386–391.

Stanghellini, M. S., J. T. Ambrose, and J. R. Schultheis. 1998. Using commercial bumble bee colonies as backup pollinators for honey bees to produce cucumbers and watermelons. Hort. Technol. 8: 590–94.

Stary, P., and K. S. Pike. 1998. Uses of beneficial insect diversity in agroecosystem management, pp. 49–68. *In* W. W. Collins and C. O. Qualset (eds.), Biodiversity in Agroecosystems. CRC, Boca Raton, FL.

Stivers, L., (ed.). 1999. Crop profile for squash in New York. Cornell Cooperative Extension, Cornell University, Ithaca, NY.

Strauss, S. Y., and P. Murch. 2004. Towards an understanding of the mechanisms of tolerance: compensating for herbivore damage by enhancing a mutualism. Ecol. Entomol. 29: 234–239.

Winfree, R., N. M. Williams, J. Dushoff, and C. Kremen. 2007. Native bees provide insurance against ongoing honey bee losses. Ecol. Lett. 10: 1105–1113.

Zhu, K. Y., G. E. Wilde, R. A. Higgins, P. E. Sloderbeck, L. L. Buschman, R. A. Shufran, R. J. Whitworth, S. R. Starkey, and F. He. 2001. Evidence of evolving carbaryl resistance in western corn rootworm (Coleoptera: Chrysomelidae) in areawide-managed cornfields in north central Kansas. J. Econ. Entomol. 94: 929–934.

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