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Associational resistance, gall-fly preferences, and a stem dimorphism in *Solidago altissima*

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ABSTRACT

In most populations of *Solidago altissima*, a small proportion of plants have a growth pattern in which the stem bends early in the season so that the apex is pointing downward (i.e., a "candy-cane" stem) then straightens up again later in the season. The majority of plants, however, do not show this pattern. Instead their stems remain erect from emergence through flowering and senescence. It has recently been shown that the candy-cane stems are a result of a ducking strategy that reduces the risk of attack by apex-attacking herbivores. With such a resistance advantage, it is unclear why the candy-cane morphology is always in the minority, and why the erect morphology persists at all in *S. altissima* populations. In this study, we tested the hypothesis that the advantage of ducking is inversely frequency dependent and thus will not be an effective resistance strategy when ducking plants are in the majority. In a series of trials, we introduced gall flies (*Eurosta solidaginis*) into enclosures with relatively low (15%) and relatively high (85%) frequencies of candy-cane versus erect stems. Candy-cane stems were more resistant than erect stems regardless of relative frequency; thus, the hypothesis was rejected. Overall, attack rates were lower for both stem types in the high candy-cane frequency groups than in the low candy-cane frequency groups. This frequency-dependent attack rate suggests that erect-stemmed plants gain "associational resistance" by having a majority of candy-cane neighbors, while candy-cane plants suffer from "associational susceptibility" when surrounded by erect-stemmed neighbors.

1. Introduction

It is well known that the amount of herbivory a plant suffers may depend not only on the characteristics of the plant itself but also on the composition and characteristics of the neighboring plant community (Tahvanainen and Root, 1972; Atsatt and O'Dowd, 1976; Hjältén et al., 1993; Milchunas and Noy-Meir, 2002; Agrawal et al., 2006; Rautio et al., 2008). For instance, a plant may gain associational resistance if neighboring plants are more resistant and physically or chemically mask the first plant from searching herbivores, or repel herbivores from the vicinity of that plant (Tahvanainen and Root, 1972; Andow, 1991; Hambäck et al., 2000; Karban, 2007). A plant may also gain associational resistance from relatively more palatable neighbors if these neighbors lure herbivores away from the plant (i.e., attractant-decoy effect) (Atsatt and O'Dowd, 1976; Miller et al., 2007). Conversely, a plant may incur associational susceptibility if herbivores key in on neighboring plants that are more apparent or palatable and then switch from the neighbors to the first plant (Parker and Root, 1981; White and Whitham, 2000; Pusenius et al., 2003; Alm Bergvall et al., 2006; Moravie et al., 2006).

The concept of associational resistance is generally applied to between-species interactions (Andow, 1991; Hambäck et al., 2000; Miller et al., 2007). For instance, agronomists have advocated the use intercropping, or planting another species with the susceptible crop species to either serve as a trap crop (attractant-decoy effect), to repel herbivores, or to make the crop plants harder to find (Vandermeer, 1989; Hokkanen, 1991; Agrawal et al., 2006). However, the principles involved in associational resistance and susceptibility should be just as applicable to within-species interactions. Specifically, a relatively palatable plant genotype may be protected by growing in the midst of more resistant genotypes, or resistant plant genotypes may be more vulnerable if growing near more susceptible neighbors (Cantelo and Sanford, 1984). Such interactions could lead to frequency-dependent herbivory that protects less resistant genotypes, and thus the interactions could help to maintain genetic variation in resistance in plant populations.

In this paper, we address whether frequency-dependent preferences on the part of herbivores may help explain the

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maintenance of genetic variation for a resistance trait in tall goldenrod, *Solidago altissima* L. (Asteraceae). Specifically, *S. altissima* populations display a genetically controlled stem dimorphism (Fig. 1) that affects resistance to galling flies (Wise and Abrahamson, 2008). In populations we have surveyed, the majority of genets (usually 80–95%) produce erect stems, with the apices pointing upward from shoot emergence through flowering. For a minority of the genets, the stems emerge erect, but then begin to nod at the apex about 3–4 weeks after emergence. The apices of these "candy-cane" stems point downward for several weeks until flower buds are formed, whereupon the stems straighten out and are erect by anthesis.

We have previously shown (Wise and Abrahamson, 2008) that the stem nodding of candy-cane plants coincides with the oviposition period of at least two common apex-attacking herbivores (*Eurosta solidaginis* and *Rhopalomyia solidaginis*) that have been shown to diminish goldenrod fitness (Hartnett and Abrahamson, 1979; Stinner and Abrahamson, 1979; Abrahamson and McCrea, 1986; Abrahamson and Weis, 1997). In a field study and common-garden experiment, candy-cane plants experienced significantly lower levels of attack than erect-stemmed plants by both of these herbivores (Wise and Abrahamson, 2008). Because a candy-cane plant lowers its apical bud during the time when these herbivores are ovipositing, then raises it again when the herbivores are gone, we termed this tactic "resistance by ducking."

Given the resistance advantage of ducking, an interesting question is why the candy-cane morphology is consistently in the minority in *S. altissima*. One possibility is that the advantage of candy-cane stems is inversely frequency dependent. Specifically, when there are relatively fewer erect-stemmed plants to either hide the candy-cane plants or to lure the flies away, then the flies may focus their attack on the candy-cane plants. In other words, candy-cane plants may receive associational resistance from erect plants via an attractant-decoy effect, and this resistance diminishes as the relative frequency of erect plants is lower. Thus, the strategy of ducking may work best for a plant when the majority of its neighbors are not also ducking.

To test the hypothesis of frequency-dependent advantage, we performed oviposition trials with *E. solidaginis* introduced to goldenrod plants at different stem-morph frequencies. With a two-way factorial experiment, we addressed three main questions: (1) Do the gall flies prefer stems of one morphology over the other regardless of the relative frequency of stem morphs? (i.e., stem-morph main effect); (2) Does the overall attack rate on a population of plants depend on which stem morph is in the majority? (i.e., relative-frequency main effect); and (3) Does the strength of the preference for a particular stem morph depend on whether that stem morph is in the majority? (i.e., stem morph-by-relative frequency interaction). More specifically, with this interaction term, we ask whether the putative resistance advantage that candy-cane plants have exhibited when they are less abundant than erect plants is lost when the candy-cane stems become the more abundant morphology.

Fig. 1. The two stem morphs of *Solidago altissima*: erect stem on the left and nodding, or "candy-cane," stem on the right.

2. Materials and methods

2.1. Study species

S. altissima is a rhizomatous perennial herb abundant in old agricultural fields, roadsides, and disturbed areas throughout its native range of eastern North America and in its introduced ranges in Europe, Asia, and elsewhere (Weber, 2000, 2001; Barkley et al., 2006). Throughout its native range, *S. altissima* is commonly attacked by the ball-gall-inducing fly, *E. solidaginis* (Fitch) (Diptera: Tephritidae) (Abrahamson and Weis, 1997). Adult flies emerge from galls in late spring and mate on young *S. altissima* plants. Adults do not feed, and they generally live for only a couple of days, though individuals have been reported to live an average of about 10 days in an insectary (Uhler, 1951). A female oviposits into apical-leaf buds of goldenrod stems, often after walking up and down a bud and puncturing it several times with her ovipositor (Uhler, 1951; Walton et al., 1990). Females appear undeterred by previous ovipositions in a bud (Craig et al., 2000); thus, a single bud may receive numerous ovipositions. An egg hatches within about a week, and the young larva induces the formation of a roughly spherical, single-chambered gall near the top of the stem. The larva feeds inside the gall until plant senescence and it diapauses inside the gall over winter.

The *S. altissima* plants used in this study came from rhizomes excavated from a field population in Union County, PA (N40° 57.9′ W76° 57.3′) in April of 2003, soon after shoots began to emerge. Rhizomes were collected from 26 genets (genetic individuals), separated by at least 30 m, without respect to stem morphology. We later determined that 21 genets produced erect-stemmed ramets (stems), and five genets produced candy-cane ramets. These 26 genets have been propagated from new rhizome growth each spring since 2003 in 28-cm diameter plastic standard pots in commercial growing medium (ProMix BX, Premier Horticulture Ltd., Dorval, Quebec, Canada). In mid-April of 2007, rhizomes of all 26 genets were cut into numerous 2-ml segments, which were measured by water displacement in a 100-ml graduated cylinder. The rhizomes were planted in flats, and in mid-May the healthy ramets that emerged were transplanted into 16.5-cm diameter plastic azalea pots for use in oviposition trials with adults of *E. solidaginis*.

The *E. solidaginis* flies used in this study came from galls collected from *S. altissima* populations in Union County and neighboring counties in January of 2007. The galls were stored in a freezer at −10 °C until April, when they were moved to a refrigerated room at 4 °C. In mid-to-late May, the galls were moved to emergence cages composed of mesh bags over PVC-pipe frames. The cages were placed into incubators at 20 °C with a daily photoperiod of 14:10 h of light:dark. Cages were checked daily, and newly emerged flies were placed in groups of six in 300-ml clear plastic cups, which were then refrigerated until the day before they were used in the experiments. On that day, flies were placed en masse in a mating cage in the greenhouse. This cage was similar to

the emergence cages, but it contained fresh cuttings of *S. altissima*, which encourages mating of the flies.

2.2. Experimental design

The experiment consisted of five trials in which flies were released into a pair of cages on greenhouse benches: one cage with a low frequency (15%) of candy-cane stems and one with a high frequency (85%) of candy-cane stems. The cages were constructed of PVC-pipe frames, 1.5 m on each side, enclosed by screen cloth. For each trial, we chose 20 erect (E) and 20 candy-cane (CC) ramets of comparable main-stem length from a mixture of the 26 *S. altissima* genets described above. We measured the height of each ramet from the ground to the highest point on the plant, which for a candy-cane ramet was typically lower because of the nodding apex (Fig. 2). We assigned ramets randomly into frequency groups (3CC:17E or 17CC:3E) and placed them into randomly assigned positions in the designated cages.

At the beginning of the first trial – on the morning of 14 June – we released 20 male and 20 female flies into each cage. After a trial began, we checked the ramets hourly during daylight. At each check, we counted the number of male and female flies on each ramet, and we noted the presence of ovipuncture scars. The trial was terminated when more than half the ramets in at least one cage were ovipunctured. At the end of a trial, all ramets were removed from both cages, and apical-leaf buds were excised from ramets with ovipunctures. We counted the number of ovipunctures under a dissecting scope and dissected the leaf buds to count the number of eggs.

We immediately began the next trial by placing the next set of ramets into their randomly designated positions in the two cages. Because of high fly mortality, we added flies to each cage at the beginning of each trial. The same procedures were followed through the fifth trial, which ended on the morning of 19 June. The same cage served as the low-CC cage (and the other served as the high-CC cage) for each of the first four trials. By then it was clear that flies were ovipuncturing less in the high-CC cage. For the fifth trial, we changed the identity of the low-CC and high-CC cages in case it was the position of the cage, rather than the frequency treatment, that was driving the overall ovipuncture rate.

2.3. Data analysis

We analyzed several fly preference (or plant resistance) variables: the total number of male (and female) fly sightings per ramet, the proportion of ramets with ovipunctures and with eggs, and the total number of ovipunctures and eggs per ramet. Each cage in the five trials gave an independent estimate of each of these measurements for candy-cane stems and for erect stems. Our analyses consisted of a two-way factorial multivariate analysis of variance (MANOVA) for all six response variables combined, and separate univariate analyses of variance (ANOVAs) for each preference/resistance variable, with the cage as the unit of analysis ($n = 10$). The two explanatory factors were the stem morphology (CC or E) and stem frequency (high-CC or low-CC), and a significant interaction of the two factors would indicate that the resistance of a stem type differed depending on its relative frequency.

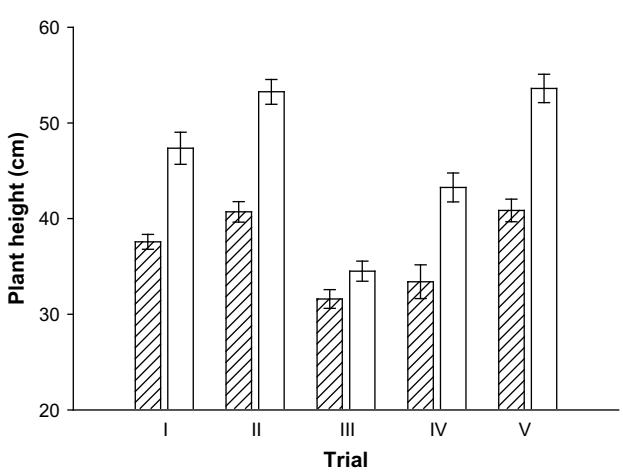

Fig. 2. Stem height (mean ± 1 SEM) of candy-cane ramets (hatched bars) and erect ramets (open bars) in the five trials. The heights were measured from the ground to the highest point, which was the tip of the leaf-bud apex for erect ramets only.

3. Results

Candy-cane ramets were more resistant than erect-stemmed ramets in all five trials (Tables 1 and 2, Fig. 3). Regardless of the relative frequency of stem types, erect stems were several times more likely to be ovipunctured or to receive eggs than candy-cane stems. The difference in resistance to ovipunctures and ovipositions could not be attributed to differences in number of visits from flies, as both male and females were found with equal frequency on candy-cane and erect-stemmed ramets (Table 2, Fig. 3). The majority of flies on any count, however, were found on the mesh walls of the cages rather than on a plant.

The overall attack rate (of both stem morphs) for all measures of ovipuncture and oviposition were greater when candy-canes ramets were in the minority (Tables 1 and 2, Fig. 3). This pattern occurred in all five trials, including the fifth, in which the frequency treatments were switched between cages. Oddly, fly presence on plants did not match this pattern of greater ovipositions in low-CC cages. In fact, there was a trend for male flies to be found more times on ramets in high-CC cages than in low-CC cages ($P = 0.08$, Table 2). Thus, flies seemed equally likely to land on ramets regardless of relative frequency, but egg-laying activity was lower in cages when candy-cane stems were in the majority. In fact, when candy-cane stems were in the majority, no stems (erect or candy-cane) received more than one egg. In contrast, when erect stems were in the majority, individual candy-cane stems received up to three eggs and erect stems received up to six eggs.

In summary, candy-cane stems were more resistant than erect stems in general, and the numbers of punctures and eggs on both stem types were lower in cages in which candy-cane stems were in the majority. There was no evidence, however, that the magnitude of the difference in resistance between candy-cane and erect stems depended on the relative frequency of stem morphs: There were no significant interactions between stem type and relative frequency in the ANOVAs for any resistance measure (Table 2), or in the MANOVA for all resistance measures combined ($P = 0.34$, Table 1). Specifically, the magnitude of the candy-cane stem advantage did not diminish when the candy-cane stems were in the majority. Thus, the effectiveness of the ducking resistance strategy was not inversely frequency dependent.

Table 1
Summary of *F*-tests from MANOVA of resistance on stem morphology and the relative frequency of stem morphs. The Wilks' lambda for the whole model was 0.110 (approximate $F_{15,33.528} = 2.7426$, $P = 0.0075$).

Model parameter	$F_{5,12}$	P
Intercept	10.7084	0.0004
Stem morphology	3.9041	0.025
Relative frequency	8.1500	0.0015
Morphology × frequency	1.2663	0.34

Table 2
Summary of ANOVA results of six resistance measures on stem morphology and the relative frequency of stem morphs.

	df	MS	*F*	*P*
# of male observations				
Stem morphology	1	0.17349	1.5405	0.23
Relative frequency	1	0.39310	3.4905	0.08
Morphology × frequency	1	0.02924	0.2596	0.62
Error	16	0.11262		
# of female observations				
Stem morphology	1	0.00017	0.0002	0.99
Relative frequency	1	0.00017	0.0002	0.99
Morphology × frequency	1	0.22009	0.2913	0.60
Error	16	0.75561		
% ramets with punctures				
Stem morphology	1	1.25983	22.6455	0.0002
Relative frequency	1	0.14217	2.5556	0.13
Morphology × frequency	1	0.00769	0.1382	0.71
Error	16	0.05563		
# of punctures per ramet				
Stem morphology	1	33.24154	15.9343	0.0011
Relative frequency	1	29.89252	14.3289	0.0016
Morphology × frequency	1	6.13658	2.9416	0.11
Error	16	2.08620		
% of ramets with eggs				
Stem morphology	1	0.99056	13.0139	0.0024
Relative frequency	1	0.15919	2.0914	0.17
Morphology × frequency	1	0.00325	0.0427	0.84
Error	16	0.07612		
# of eggs per ramet				
Stem morphology	1	2.54702	15.1355	0.0013
Relative frequency	1	1.68427	10.0087	0.0060
Morphology × frequency	1	0.43253	2.5703	0.13
Error	16	0.16828		

4. Discussion

Whether judged by the likelihood of being ovipunctured, oviposited on, the number of punctures received, or the number of eggs laid, candy-cane ramets were less susceptible to *E. solidaginis* than erect-stemmed ramets. The results of these greenhouse trials are the third line of evidence that the candy-cane morphology may serve as a resistance mechanism against gall flies in *S. altissima*. In a previous field survey of more than 10,000 ramets across 110 erect and 11 candy-cane genets, candy-cane ramets were only 55% as likely to be ovipunctured by *E. solidaginis* as erect ramets (Wise and Abrahamson, 2008). In a common-garden experiment of ~75 ramets from each of 21 erect and 5 candy-cane genets, candy-cane ramets were 82% as likely to be ovipunctured by *E. solidaginis* as erect ramets, and they were only 48% as likely to form rosette galls induced by the gall midge *R. solidaginis* (Wise and Abrahamson, 2008). While the selective forces that act on stem morphology remain unidentified, results of the current experiment add to the evidence that candy-cane stems serve an important role in resistance to herbivory.

Several physical consequences of the nodding stems of candy-cane ramets may contribute to their greater resistance. Most simply, nodding makes the maximum height of the candy-cane stem shorter than for an erect stem of equal total-stem length. Many herbivorous insects, including *E. solidaginis*, have been shown to prefer taller plants (Bach, 1981; Karban and Courtney, 1987; Walton et al., 1990; Marquis, 1992). Greater height may be an indication of greater vigor and host quality, or taller plants may just be more visually or chemically apparent to searching herbivores (Lawton, 1983). Apical-leaf buds of candy-cane ramets are also likely to be less apparent because they are often partially hidden among stem leaves. In addition, the "abnormal," upside-down orientation of the apical-leaf bud in candy-cane stems may confuse the ritualized mating or oviposition behavior of the flies (Milne, 1940; Uhler, 1951; Walton et al., 1990).

The lack of a statistically significant difference in the occurrence of flies on candy-cane versus erect stems argues in favor of the fly-confusion explanation. Males tended to occur more often on erect stems than candy-cane stems, though the difference was not statistically significant. This trend would be expected because males ought to pick taller plants on which to display for females. There was no tendency whatsoever for females to be found on erect stems in favor of candy-cane stems. However, the females were much more likely to ovipuncture and to lay more eggs in erect stems. It is possible that there is something about the upside-down orientation of the candy-cane apex that inhibits oviposition behavior of females, especially considering their stereotypic behavior of walking up and down the apex several times before ovipositing (Uhler, 1951; Walton et al., 1990). It is also possible that flies might cue on potential differences between candy-cane and erect stems (such as potential differences in turgor pressure or chemical scents) other than the obvious morphological difference. More detailed studies of individual fly behavior and chemical differences between candy-cane and erect stems will be needed to reach a more definitive mechanistic conclusion, however.

Given the evidence that the candy-cane morphology confers increased resistance against common herbivores that have a substantial negative effect on host fitness (Hartnett and Abrahamson, 1979; Stinner and Abrahamson, 1979; Abrahamson and McCrea, 1986; Abrahamson and Weis, 1997), the question remains as to why candy-cane stems are generally in the minority in *S. altissima* populations. The hypothesis we tested in this experiment is that the resistance advantage of ducking would disappear when candy-cane ramets were in the majority. The rationale for this hypothesis of inverse-frequency dependence is that ducking would only be effective when most of the neighboring plants are not also ducking.

The results of our experiment provide no evidence in support of this frequency-dependence hypothesis. Specifically, there were no stem morphology-by-frequency interactions for any of the resistance measures. In fact, candy-cane ramets were more resistant to ovipunctures and ovipositions than erect ramets in all trials, regardless of whether candy-cane ramets were in the minority or the majority. Moreover, there was no sign that the frequency of stem types had any effect on the relative magnitude of the advantage. Therefore, these results suggest that any selective advantage candy-cane genets enjoy from reduced gall-fly attack would not diminish if the candy-cane trait spread and became the majority morph in *S. altissima* populations.

Even though relative differences in resistance between stem morphs did not change as the frequencies of morphs changed, the overall attack rate on both stem morphs combined did depend on relative frequency. Specifically, when the frequency of candy-cane ramets was higher, ovipuncturing and egg-laying rates were lower for both candy-cane and erect ramets. This result suggests that erect stems gain a degree of associational resistance from candy-cane neighbors. In a field population of goldenrod, gall flies might be less attracted to a patch dominated by candy-cane stems, or the mating and oviposition behavior of flies in such a patch might be slowed. Thus, an erect-stemmed genet growing in a patch dominated by candy-cane stems may be expected to enjoy reduced gall-fly attack due simply to having a majority of more resistant neighbors. On the flip side, candy-cane genets are likely to suffer associational susceptibility when they are in a patch dominated by erect-stemmed neighbors.

The issue of associational resistance and susceptibility emphasizes the importance of spatial scale in assessing fly preferences for

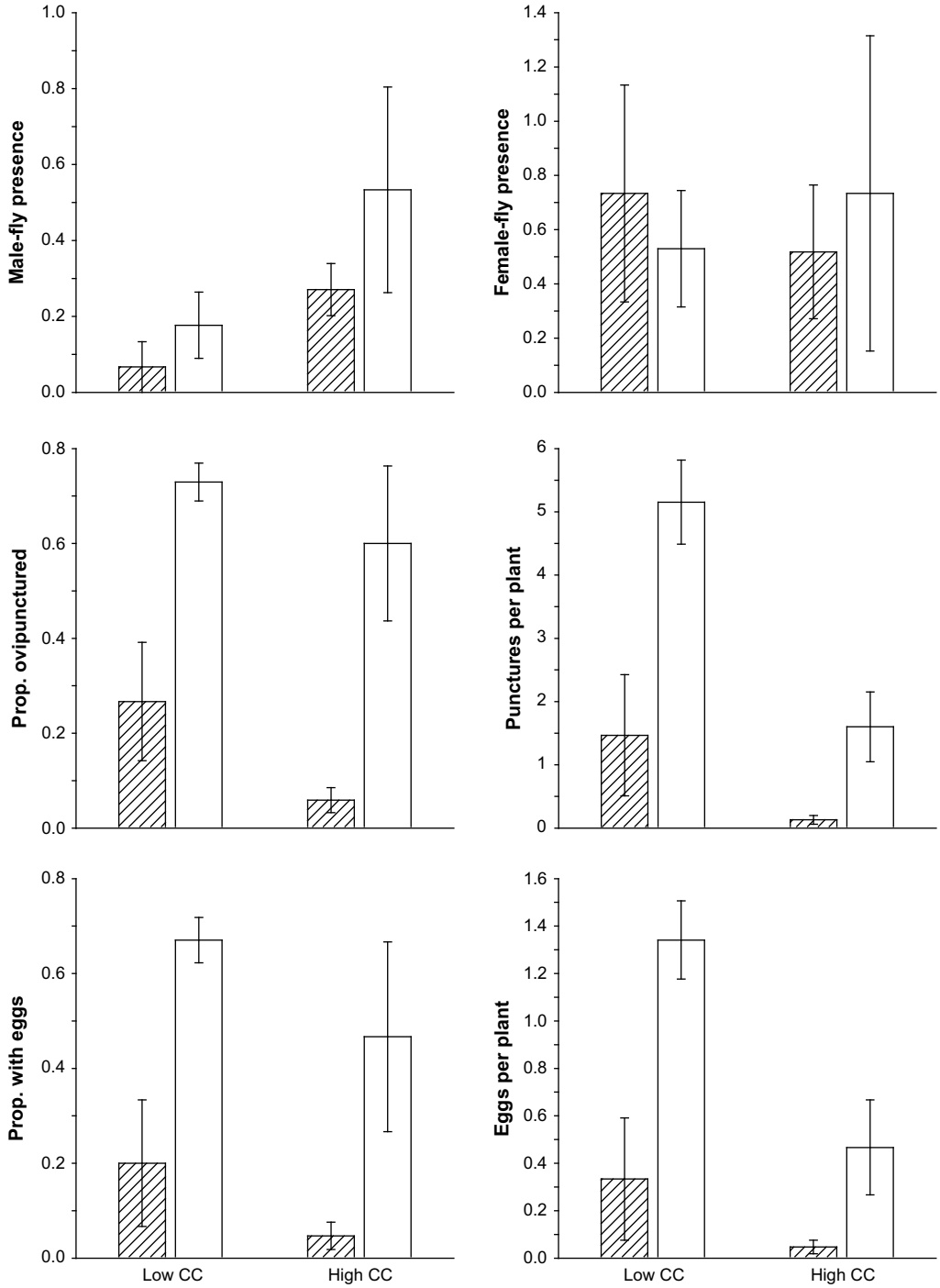

Fig. 3. Means (±1 SEM) of plant-resistance measurements (i.e., fly-preference measurements) for candy-cane ramets (hatched bars) and erect ramets (open bars) in the five low candy-cane-frequency (3CC:17E) cages and five high candy-cane-frequency (17CC:3E) cages.

the two stem morphs (Tahvanainen and Root, 1972; Bell, 1990; Milchunas and Noy-Meir, 2002; Agrawal et al., 2006; Alm Bergvall et al., 2006; Miller et al., 2007; Viswanathan et al., 2008). While our study examined fly behavior at a patch size of 20 ramets, *E. solidaginis* in nature may be making oviposition decisions on much larger spatial scales – at least up to 51 m for most females in a large plant population (Cronin et al., 2001). Thus, it is worth investigating whether the lower rates of oviposition in high candy-cane frequency patches holds up if the patches are larger than the 1.5-m width of our experimental cages.

5. Conclusion

S. altissima is an early successional, clonal weed that invades disturbed sites as seeds. As time passes, single-ramet seedlings become clumps of genetically identical ramets. Some genets will expand and others will decline (Abrahamson and Weis, 1997). As a candy-cane genet expands into several then perhaps hundreds of ramets, every ducking, candy-cane ramet will be surrounded by more and more similarly ducking neighbors. Contrary to our expectations of an inverse-frequency dependence in the

effectiveness of ducking, our results suggest that the resistance benefit of ducking will not attenuate as a candy-cane genet expands. Instead, flies are likely to migrate to patches dominated by erect-stemmed genets – as long as such patches are available. Where erect-stemmed ramets are intermingled with a majority of candy-cane ramets, erect ramets will probably have a resistance advantage over pure clumps of erect ramets, but they will still be at a disadvantage compared to candy-cane ramets. Therefore, there must be some constraint on the evolution of candy-cane stems other than a negative correlation between frequency and resistance. Future studies are planned to examine other potential constraints.

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