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Plant traits in fig as indicators of resistance to shoot borer, *Dyscerus? fletcheri* Marshall (Coleoptera: Curculionidae)

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ABSTRACT

A comparative study was conducted on fig (*Ficus carica* L.) cultivars Deanna and Poona to test whether antixenosis due to plant traits was at least partially responsible for a differential susceptibility to the shoot boring curculionid weevil, *Dyscerus? fletcheri*. Field evaluation revealed significant difference in borer incidence in cvs. Poona (6.25%) and Deanna (75%). Further, traits of plant architecture such as number of primary/ secondary/ terminal shoots, plant vigour and density of terminal shoots were significantly higher in cv. Deanna, which was highly susceptible to shoot borer. However, latex-flow index was significantly higher in cv. Poona that was resistant to the borer. A step-wise multiple regression analysis revealed that the tested plant traits explained 60% of the total variation in stem borer infestation ($y=-0.96-0.02x_1+0.23x_2-0.03x_3+0.24x_4+1.28x_5-1.31x_6$, $R^2=0.60$) in the susceptible cultivar, Deanna. Role of these traits in preference/non-preference of *D. fletcheri* for a cultivar is discussed.

Key words: Fig, *Ficus carica* L., resistance, cultivars, stem borer, *Dyscerus? fletcheri*

INTRODUCTION

Cultivation of the common fig (*Ficus carica*) is picking up in India amid growing acceptance of the fruit with high curative and lacerative nutritional values. Commercial cultivation of the common (edible) fig is confined mostly to the western parts of Maharashtra, Gujarat, Uttar Pradesh (Lucknow & Saharanpur), Karnataka (Bellary, Chitradurga & Srirangapatna) and Tamil Nadu (Coimbatore). Of the 470 varieties listed, cvs.'Poona' and *'Deanna'* are popularly grown for fresh fruit. In India, fig trees are prone to attack by as many as 50 species of insect pests (Butani, 1979). Of these, the stem boring beetles (that include *Batocera rufomaculata*, *B. rubus*, *Aclees cribratus*, *Apriona cinerea*, *A. rugicollis*, *Olenecamptus bilobus* and *Rhytidodera* species) (Verghese *et al*, 2001, 2003) cause severe damage to plants. However, a new curculionid weevil, *Dyscerus? fletcheri* Marshall (Coleoptera: Curculionidae) has been found damaging fig plants heavily during the post-rainy season, by directly damaging the terminal fruit bearing shoots (Kamala Jayanthi *et al*, 2015, in press). Our preliminary studies showed differential susceptibility of fig cultivars to this stem borer, suggesting a need to identify marker traits involved in host-plant selection by the pest. However, no literature is available on the effect of plant architecture traits on incidence of shoot borer, *D. fletcheri*, in fig. Therefore, this study was carried out to determine whether these traits contributing to antixenosis in fig cultivars by *D. fletcheri*.

MATERIAL AND METHODS

In the present study, a differential susceptibility of two common fig varieties, Deanna and Poona, to the curculionid weevil *D. fletcheri*, was assessed through field evaluation at Indian Institute of Horticultural Research (IIHR), Bangalore (12°58'N; 77°35'E), India. Observations were recorded during September – December, 2010 to assess the incidence of *D. fletcheri* on two year old plants growing adjacent to each other. Each of the cultivars was planted in five rows, each row consisting of 16 plants. Plant architecture traits were recorded in both the varieties (n=80) before flowering (September – December). Traits like number of primary shoots, secondary shoots, terminal shoots, plant vigour, density of terminal shoots and latex-flow were measured to relate these traits to varietal preference and non-preference of the curculionid borer, *D. fletcheri* for a variety. Of these traits, the number of primary shoots, secondary shoots, terminal shoots and density of terminal

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shoots were grouped under canopy traits as these can be altered through canopy management, whereas, plant vigour and latex-flow index were grouped as inherent plant traits. Plant vigour was visually scored on a 1-5 scale where, 1= least vigorous and 5= most vigorous. Density of terminal shoots in each tree was also visually scored on a 1-5 scale where, 1= less dense with less compactness, and 5= highly dense with more compactness. Latex flow was measured on a 1-3 scale where, 1= low and 3= profuse. Latex-flow index was measured by uniformly piercing the base of the tender terminal shoot with a pin, and the amount of latex that oozed out was expressed in relative terms (as described above). Sampling for borer infestation was carried out on terminal, fruit-bearing shoots on each tree, based on fresh feeding-damage (external deposition of a fine powder at the base of the shoot), wilting and withering of tender shoots.

Data collected on plant traits, viz., number of primary shoots, secondary shoots, terminal shoots, plant vigour, density of terminal shoots and latex-flow index were analyzed using one way ANOVA to determine differences in the above-mentioned parameters as significant or non-significant, between the two cultivars as per Little and Hills (1978). Correlation, step-wise multiple regression and path-coefficient analyses between the plant parameters studied and stem-borer incidence were carried out. To get a further insight, a step-wise regression procedure (Ryan, 1997) was employed to select the most crucial plant traits influencing variability in borer incidence. This technique consists of essentially identifying, stage by stage, trait(s) significantly related to borer incidence (y). Further, as a measure of goodness-of-fit of the models developed, values pertaining to Co-efficient of Determination (R^2) (Agostid'no and Stephens, 1986) were calculated. Variance Inflation Factor (VIF) value was computed to test the multi-colinearity of variables.

RESULTS AND DISCUSSION

Severe borer infestation was noticed (75%) in cv. Deanna (n=80) and significantly ($P = 0.05$) lower infestation (6.5%) was observed in cv. Poona (n=80), during August-December. Within a tree too, significantly higher infestation was noticed on tender terminal-shoots (7.82%) in cv. Deanna (n=4286), and 0.32% in cv. Poona (n=1863) (t=8.17, df=79, P<0.01).

Among canopy traits, the number of primary shoots, secondary shoots, terminal tender-shoots, and density of terminal shoots ranged from 1-5, 0-28, 6-89 and 1-5 respectively in cv. Deanna and 2-4, 5-19, 4-48 and 1-4, respectively, in cv. Poona. Inherent plant traits, viz., plant vigour and latex-flow index ranged from 1-5 & 1-2, and 1-5 & 2-3, respectively, in cvs. Deanna and Poona, respectively (Table 1).

Data revealed significant variation in canopy and plant traits between cultivars Deanna and Poona. Mean number of primary shoots (3.80), secondary shoots (16.15), terminal tender-shoots (53.58), plant vigour (3.38) and density of terminal shoots (2.90) was significantly higher in cv. Deanna compared to cv. Poona (Table 1). Mean latex-flow index was significantly higher in cv. Poona (2.94) compared to cv. Deanna (1.06) (Table 1).

Influence of various plant traits on differential susceptibility of the two common fig varieties revealed that the number of primary shoots (r=0.28; P=0.01); number of secondary shoots (r=0.64; P=0.001), number of terminal tender-shoots (r=0.58; P=0.001), plant vigour (r=0.54; P=0.001), density of terminal shoots (r=0.67; P=0.001) had a significant, positive correlation with incidence of the shoot borer, *D. fletcheri*. However, latex-flow index had a significant, negative correlation with the incidence of *D. fletcheri* (r=-0.53; P=0.001) (Table 2).

Table 1. Plant traits in two fig cultivars

Variety	Canopy traits			Inherent traits of the plant				
	No. of primary shoots (+SE)	No. of secondary shoots (+SE)	No. of terminal tender shoots (+SE)	Density of shoots (+SE)	Plant vigour (+SE)	Latex-flow index (+SE)	Per cent infested trees(n=80)	Per cent infested shoots/ tree
Deanna	3.80 + 0.08 (1.0 - 5.0)	16.15 + 0.66 (0.0 - 28.0)	53.58 + 1.94 (6.0 - 89.0)	2.90 + 0.15 (1.0 - 5.0)	3.38 + 0.14 (1.0 - 5.0)	1.06 + 0.03 (1.0 - 2.0)	75.00	7.82†
Poona	3.41 + 0.08 (2.0 - 4.0)	10.83 + 0.37 (5.0 - 19.0)	23.29 + 1.06 (4.0 - 48.0)	2.04 + 0.10 (1.0 - 4.0)	2.46 + 0.11 (1.0 - 5.0)	2.94 + 0.03 (2.0 - 3.0)	6.25	0.32††
CD (*P=0.05*)	0.22	1.48	4.33	0.34	0.34	0.08		

Figures in parentheses show the range of values; †n = 4286; ††n = 1863

Multiple regression analysis indicated that plant traits could explain 60% of the total variation in stem-borer infestation. Considering the traits viz., number of secondary shoots, density of terminal shoots, and latex-flow index, being significant based on *r*/SE (a stringent criterion for identifying significant variables for regression analysis), variability in stem borer infestation on the two cultivars can be explained to an extent of 59% ($y=-1.56+0.18x_2+1.35x_5-1.04x_6$, $R^2=0.59$) (Table 3). Further, traits like number of primary shoots, secondary shoots, terminal tender-shoots, plant vigour, density of terminal shoots and latex-flow index as lone, independent factors explained 8, 41, 33, 29, 49, 28% of the total variation in stem borer incidence, respectively, in linear equations. Maximum variation in stem borer infestation was explained by canopy traits and density of terminal shoots (49%), followed by the number of secondary shoots (41%) (Table 4). However, step-wise multiple regression analysis showed that various combinations of host-plant traits could not explain variability in stem borer infestation beyond 60% (Tables 5-6). Nevertheless, canopy traits, viz., number of secondary shoots and density of terminal shoots, alone, could explain variability in stem borer infestation to an extent of 53% ($y=-4.83+0.25x_2+1.43x_5$, $P=0.01$; $R^2=0.53$), with lesser VIF value (2.13) indicating a low level of collinearity among variables (Table 5). Further, a combination of canopy traits, viz., number of terminal shoots and density of terminal shoots, could explain variability in stem borer infestation to an extent of 51% ($y=-3.97+0.05x_3+1.63x_5$, $R^2=0.51$). A combination of canopy traits (density of terminal shoots) and inherent plant traits (latex-flow index) could explain variability in stem borer

Table 2. Direct and indirect effects of plant traits in fig cultivars

Pathways of association	Direct effects	Indirect effects	'r'
1. Primary branches (No.)			0.28*
a. Direct effect	-0.05		
b. Indirect effect via			
Tertiary branches (No.)		-	
Secondary branches (No.)		-	
Plant vigour		-	
Density of branches		-	
Latex flow		-	
2. Secondary branches (No.)			0.64**
a. Direct effect	0.33		
b. Indirect effect via			
Primary branches (No.)		0.13	
Tertiary branches (No.)		0.24	
Plant vigour		0.16	
Density of branches		0.20	
Latex flow		-0.15	
3. Tertiary branches			0.58**
a. Direct effect	-0.16		
b. Indirect effect via			
Primary branches (No.)		-0.06	
Secondary branches (No.)		-0.12	
Plant vigour		-0.08	
Density of branches		-0.09	
Latex flow		0.12	
4. Plant vigour			0.54**
a. Direct effect	0.08		
b. Indirect effect via			
Primary branches (No.)		0.01	
Secondary branches (No.)		0.04	
Tertiary branches (No.)		0.05	
Density of branches		0.04	
Latex flow		-0.03	
5. Density of branches			0.67**
a. Direct effect	0.40		
b. Indirect effect via			
Primary branches (No.)		0.12	
Secondary branches (No.)		0.24	
Tertiray branches (No.)		0.22	
Plant vigour		0.26	
Latex flow		-0.13	
6. Latex flow			-0.53**
a. Direct effect	-0.33		
b. Indirect effect via			
Primary branches (No.)		0.08	
Secondary branches (No.)		0.15	
Tertiray branches (No.)		0.24	
Plant vigour		0.12	
Density of branches		-0.33	

*Significant at 1% level; **Significant at 0.1% level

Table 3. Linear regression models explaining the variability in shoot borer, *D. fletcheri*, infestation in fig using plant traits

Variables considered	Model	R^2	VIF
i) Significant variables based on *r** (x_1=no. of primary shoots; x_2=no. of secondary shoots; x_3= no. of terminal shoots.; x_4=plant vigour; x_5=density of terminal shoots; x_6=latex-flow index)	$y=-0.96-0.02x_1+0.23x_2-0.03x_3+0.24x_4+1.28x_5-1.31x_6$	0.60	2.47
ii) Only significant variables based on (*r*/SE)** (x_2=no. of secondary shoots; x_5=density of terminal shoots; x_6=latex-flow index)	$y=-1.56+0.18x_2+1.35x_5-1.04x_6$	0.59	2.42

r=correlation coefficient; **SE=Standard error

Table 4. Linear models to estimate variability in shoot borer, *D. fletcheri,* infestation in fig using various plant traits

Variables considered	Model	R^2	VIF
i) No. of primary shoots (x_1)	$y=-3.15+1.46x_1$	0.08	1.09
ii) No. of secondary shoots (x_2)	$y=-3.86+0.44x_2$	0.41	1.69
iii) No. of terminal shoots (x_3)	$y=-1.95+0.110x_3$	0.33	1.50
iv) Plant vigour (x_4)	$y=-2.87+1.71x_4$	0.29	1.40
v) Density of terminal shoots (x_5)	$y=-3.19+2.16x_5$	0.49	1.81
vi) Latex-flow index (x_6)	$y=6.25-2.06x_6$	0.28	1.38

Table 5. Various linear equations for estimating variability in shoot borer (*D. fletcheri*) infestation

Variables considered	Model	R^2	VIF
With the no. of primary shoots kept at a constant			
i) No. of primary shoots (x_1)+ no. of secondary shoots (x_2)	$y=-4.51+0.22x_1+0.43x_2$	0.41	1.70
ii) No. of primary shoots (x_1)+ no. of terminal shoots (x_3)	$y=-3.37+0.45x_1+0.10x_3$	0.34	1.52
iii) No. of primary shoots (x_1)+ plant vigour (x_4)	$y=-6.19+1.01x_1+1.61x_4$	0.32	1.47
iv) No. of primary shoots (x_1)+ density of terminal shoots (x_5)	$y=-4.58+0.44x_1+2.07x_5$	0.46	1.85
v) No. of primary shoots (x_1)+ latex-flow index (x_6)	$y=2.95+0.83x_1-1.91x_6$	0.30	1.43
With the no. of secondary shoots kept at a constant			
i) No. of secondary shoots (x_2)+ no. of terminal shoots (x_3)	$y=-3.89+0.33x_2+0.04x_3$	0.43	1.76
ii) No. of secondary shoots (x_2)+ plant vigour (x_4)	$y=-5.27+0.35x_2+0.94x_4$	0.47	1.89
iii) No. of secondary shoots (x_2)+ density of terminal shoots (x_5)	$y=-4.83+0.25x_2+1.43x_5$	0.53	2.13
iv) No. of secondary shoots (x_2)+ latex-flow index (x_6)	$y=-0.27+0.35x_2-1.16x_6$	0.48	1.92
With the no. of terminal shoots kept at a constant			
i) No. of terminal shoots (x_3)+ plant vigour (x_4)	$y=-3.88+0.08x_3+1.06x_4$	0.41	1.70
ii) No. of terminal shoots (x_3)+ density of terminal shoots (x_5)	$y=-3.97+0.05x_3+1.63x_5$	0.51	2.04
iii) No. of terminal shoots (x_3)+ latex-flow index (x_6)	$y=1.05+0.08x_3-0.91x_6$	0.36	1.56
With the plant vigour kept at a constant			
i) Plant vigour (x_4)+ density of terminal shoots (x_5)	$y=-3.85+0.52x_4+1.81x_5$	0.46	1.85
ii) Plant vigour (x_4)+ latex flow index (x_6)	$y=1.42+1.28x_4-1.51x_6$	0.42	1.72
With the density of terminal shoots kept at a constant			
i) Density of terminal shoots(x_5)+ latex-flow index (x_6)	$y=0.37+1.79x_5-1.32x_6$	0.55	2.22

Table 6. Step-wise linear models to estimate variability in shoot borer (*D. fletcheri*) infestation in fig

Variables considered	Model	R^2	VIF
i. No. of primary shoots (x_1) + no. of secondary shoots (x_2) + no. of terminal shoots (x_3)	$y=-4.25+0.12x_1+0.32x_2+0.04x_3$	0.43	1.75
ii. No. of primaries (x_1) + no. of secondary shoots (x_2) + no. of terminal shoots (x_3) + plant vigour (x_4)	$y=-5.69+0.18x_1+0.27x_2+0.026x_3+0.86x_4$	0.48	1.92
iii. No. of primary shoots (x_1) + no. of secondary shoots (x_2) + no. of terminal shoots (x_3) + plant vigour (x_4) + density of terminal shoots (x_5)	$y=-5.21+0.02x_1+0.19x_2+0.02x_3+0.31x_4+1.19x_5$	0.54	2.17
iv. No. of secondary shoots (x_2) + no. of terminal shoots (x_3) + plant vigour (x_4)	$y=-5.16+0.28x_2+0.03x_3+0.86x_4$	0.48	0.92
v. No. of secondary shoots (x_2) + no. of terminal shoots (x_3) + plant vigour (x_4) + density of terminal shoots (x_5)	$y=-5.14+0.19x_2+0.02x_3+0.03x_4+1.19x_5$	0.54	2.17
vi. No. of secondary shoots (x_2) + no. of terminal shoots (x_3) + plant vigour (x_4) + density of terminal shoots (x_5) + latex-flow index (x_6)	$y=-1.03+0.23x_2-0.03x_3+0.24x_4+1.28x_5-1.30x_6$	0.60	2.50
vii. No. of terminal shoots (x_3) + plant vigour (x_4) + density of terminal shoots (x_5)	$y=-4.33+0.05x_3+0.31x_4+1.45x_5$	0.51	2.04
viii. No. of terminal shoots (x_3) + plant vigour (x_4) + density of terminal shoots (x_5) + latex-flow index (x_6)	$y=-0.58+0.01x_3+0.26x_4+1.56x_5-1.15x_6$	0.55	2.22

infestation to an extent 55% ($y=0.37+1.79x_5-1.32x_6$; $R^2=0.55$) (Table 6).

Pathways through which the six plant traits studied operate, to produce their association with shoot borer infestation reveal direct and indirect contribution (Table 2). Path-coefficient analysis showed that direct effect of number of primary shoots on stem borer infestation was negative and was not too pronounced. Indirect effects through other traits also exhibited a similar trend. Direct effect of the number of secondary shoots on stem-borer infestation was positive and high in magnitude (0.33). The total correlation between number of secondary shoots and stem-borer infestation was highly positive and significant (0.64). Indirect effect of the number of secondary shoots via other plant traits, viz., number of primary shoots (0.13), number of terminal shoots (0.24), plant vigour (0.16) and density of terminal shoots (0.20) was positive and of a reasonable magnitude, contributing to the total correlation coefficient. However, indirect effect through latex-flow index was found to be negative (-0.15).

Number of terminal shoots exhibited moderate, negative, direct effect (-0.16) as well as indirect effects via the number of primary shoots (-0.06), number of secondary shoots (-0.12), plant vigour (-0.08) and density of terminal shoots (-0.09). However, it exhibited a positive, indirect effect through latex-flow index (0.12). Similarly, plant vigour also showed moderate, positive, direct effect (0.08) besides indirect effects via the number of primary shoots (0.01), number of secondary shoots (0.04), number of terminal shoots (0.04) and density of terminal shoots (0.05). However, it exhibited a negative, indirect effect through latex-flow index (-0.03).

Density of terminal shoots exhibited a very high magnitude of positive, direct effect with reference to stem borer infestation (0.40). Indirect effects via the number of primary shoots (0.12), number of secondary shoots (0.24), number of terminal shoots (0.22) and plant vigour (0.26) were positive and high in magnitude. Total correlation coefficient (0.71) was also found to be highly significant. However, with latex-flow index, it exhibited a negative, indirect effect (-0.13) for stem borer incidence. Therefore, by managing canopy traits such as the number of secondary shoots, terminal shoots and density of terminal shoots, stem borer infestation can be reduced.

Latex-flow index showed a negative, direct effect of high magnitude (-0.33), but showed positive, indirect effects through the number of primary shoots (0.08), number of secondary shoots (0.15), number of terminal shoots (0.24), density of terminal shoots (0.11) and plant vigour (0.12). Therefore, inherent plant characters, viz., plant vigour and latex-flow index, can be used as marker traits to induce resistance against stem borer in the common fig cultivars.

Plant genotypes possess trait-variations that can alter insect preference/non-preference (also referred to as antixenosis), i.e., insects are attracted to, or repelled by, a plant due to a variety of plant characteristics (Karban *et al*, 1997; Ernest, 1989) such as plant shape, size, surface texture, presence of trichomes and toughness of the tissue, tough vascular bundles, etc. Antixenosis refers to potential plant-traits, either morphological or allelochemical, impairing or altering insect behaviour towards the host (preference) in a way as to reduce chances of infestation by insects, for oviposition, food or shelter.

Preliminary comparative study conducted during 2010-11 showed significant differences in susceptibility of fig genotypes, viz., Deanna and Poona, to shoot borer, *D. fletcheri* (Table 1). These variations can be attributed to several canopy traits and inherent plant-trait variations, as explained in this study (Tables 1-6). The present study clearly revealed highly significant differences in per cent stem-borer infestation among two common fig cultivars, Deanna and Poona. Further, canopy traits, viz., number of secondary shoots, number of tertiary shoots, plant vigour and density of terminal shoots had a significant, positive relationship with stem borer infestation, and, latex-flow index had a significant, negative relationship with stem-borer incidence. High concentration of fresh latex in *Ficus* spp. (Moraceae) was reported to range between 15-30% (Mooibroek and Cornish, 2000). It is generally accepted that the primary function of latex is to provide stickiness to entrap whole insects (Dussourd 1993, 1995) or mire their mouthparts (Dussourd & Eisner 1987); the latex is mobilized and transported to the site of damage immediately upon onset of damage. However, the mechanism of these effects (even for stickiness) is not well-documented. In the present study, the high latex-flow index in cv. *Poona* can be seen as primarily effective on early-instar grubs of *D. fletcheri*, as reported by Zalucki *et al* (2001 a and b) in the case of milkweed caterpillars. They reported that mortality in specialist caterpillars armed with tiny mandibles feeding on milkweeds is the highest in earlier instars, and, especially high at the first bite after hatching (as, latex is mobilized and transported to the site of damage immediately upon the damage, and can travel over 70cm to the point of damaged, as reported in *Cryptostegia grandiflora*) (Buttery and Boatman, 1976). However, larger herbivores that feed on whole-plants can be expected to be much less affected, because, accumulation of latex at the site of damage in this case will be ineffective. Therefore, in the present study, the high latex-flow index observed in cv. Poona may have hampered establishment of early-instar grubs of *D. fletecheri*.

Canopy traits, viz., number of primary shoots, secondary shoots, terminal shoots and the density of terminal shoots, were found to be higher in the susceptible cv. Deanna, where, heavy incidence of stem borer was noticed. Usually, host-preference of herbivourous insects is attributed to their behavioral response to visual, tactile or chemical cues received from the plants when pests encounter (Bernays and Chapman, 1994; Briese and Walker, 2002). This provides the insects with positive and negative signals which enable them to identiy a right host (Bernays, 1989). Earlier studies reported that plant traits such as odour, colour, morphological and anatomical characteristics were also important factors influencing insect host-choice (Bernays and Chapman, 1994). In the present study, the susceptible variety Deanna was found to be highly vigorous, with higher number of secondary shoots and, terminal shoots, leading to a dense canopy structure. This may have attracted the stem borer to cv. Deanna, compared to cv. Poona which was less vigorous, having a less dense canopy architecture. Connections between general host-vigour and herbivore preference have been found, especially in gall-inducing insects (Craig *et al,* 1989; Horner and Abrahamson, 1992; Fritz *et al,* 2003; Price and Hunter, 2005). Plant vigour hypothesis by Price (1991) states that females prefer to oviposit on fast-growing plants because of the plant's better nutritional quality or higher general vigour. Further, it is also reported that some plant genotypes endowed with a higher level of defense chemicals, are more resistant to insects than plants with lower concentrations of the same (Diego *et al,* 2011). We too observed in the present study that cv. Poona with a higher latex-flow index recorded a lower incidence of stem borer. Inherent plant traits, viz., high latex-flow index and plant vigour in cv. Poona may be responsible for the non-preference of stem borer to this genotype. These can be used as marker traits in breeding programs for developing stem-borer resistant varieties. It is clear from the present study that canopy traits that influence stem borer infestation. The density of terminal shoots, and the number of secondary shoots can be managed to develop a less dense canopy in the susceptible variety, Deanna. As reported in earlier studies, herbivorous insect do not attack plants indiscriminately but prefer to feed/ oviposit on specific plant species, or, genotypes of a single species (Jaenike, 1990; Hjalten *et al,* 2007; Crawford *et al,* 2007; Tommi *et al,* 2011). Further, in addition to genetic effects (i.e., species and genotype effects) on host-plant quality, other factors such as shading, soil fertility, etc. may influence suitability of a host (Mutikainen *et al,* 2000; Lower *et al,* 2003; Osier and Lindroth, 2006). Semiochemical cues in successful host-plant location and colonization can be expected to play a role in primary host attraction, and probably provide a basis for future olfaction-based studies.

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