Antixenotic and allelochemical resistance traits of watermelon against *Bactrocera cucurbitae* in a hot arid region of India

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Abstract

Host plant resistance is an important component of integrated pest management of the melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). We studied various antixenotic and allelochemical traits in the fruit for 15 varieties/genotypes of watermelon *Citrellus lanatus* (Thunb.) Matsumara & Nakai (Cucurbitales: Cucurbitaceae) in relation to resistance against *B. cucurbitae* under field conditions in a hot arid region of India. Results showed significant differences in tested varieties/genotypes in levels of fruit infestation and larval density per fruit. The varieties/genotypes 'Asahi Yamato' (12.73%), 'AHW/BR-16' (15.10%), and 'Thar Manak' (18.27%) were found to be resistant; 'Durgapura Lal' (23.03%), 'Sugar Baby' (26.67%), 'AHW/BR-12' (29.73%), 'Arka Manik' (34.15%), 'Charleston Gray' (38.70%), 'AHW-65' (35.80%), and 'AHW-19' (48.97%) were found to be moderately resistant; and 'IC 582909' (53.18%), 'AHW/BR-60' (55.52%), 'BSM-1' (59.10%), 'AHW/BR-137' (60.58%), and 'AHW/BR-9' (67.37%) were found to be susceptible to fruit fly infestation. Significant positive correlation ($r = 0.99$; $P < 0.01$) was observed between percentage fruit infestation and larval density per fruit. Percentage fruit infestation and larval density per fruit were significantly and positively correlated with fruit length ($r = 0.57$ and 0.55, respectively) and with days to first fruit harvest ($r = 0.75$ and 0.76, respectively), but negatively correlated with length of ovary pubescence ($r = -0.91$ and -0.91, respectively), rind hardness ($r = -0.86$ and -0.87, respectively), and rind thickness ($r = -0.77$ and -0.75, respectively). Maximum variation in fruit infestation and larval density were explained by length of ovary pubescence (82.5 and 83.6%, respectively) followed by fruit length (4.3 and 3.0%, respectively) and rind thickness (3.2 and 2.0%, respectively). Free amino acid content was lowest in the resistant 'Asahi Yamato' and highest in the susceptible 'BSM-1', whereas the contents of phenols, tannins, total alkaloids, and flavonoids were highest in resistant and lowest in susceptible varieties/genotypes. Flavonoid and total alkaloid contents explained 88.4 and 92.0%, respectively, of the total variation in fruit fly infestation and in larval density per fruit.

Key Words: flavonoid; alkaloid; phenol; tannin; 'Asahi Yamato'; 'BSM-1'

Resumen

La resistencia de las plantas hospederas es un componente importante para el manejo integrado de plagas de la mosca del melón, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae). Estudiamos varios características antixenoticas y de aleloquímicos en el fruto de 15 variedades/genotipos de sandía *Citrellus lanatus* (Thunb.) Matsumara y Nakai (Cucurbitales: Cucurbitaceae) en relación a la resistencia contra *B. cucurbitae* en condiciones de campo en una región árida y caliente de la India. Los resultados mostraron diferencias significativas en las variedades/genotipos probados en los niveles de infestación de la fruta y de la densidad de larvas por fruto. Las variedades/genotipos 'Asahi Yamato' (12,73%), 'AHW/BR-16' (15,10%) y 'Thar Manak' (18,27%) resultaron ser resistentes; 'Durgapura Lal' (23,03%), 'Sugar Baby' (26,67%), 'AHW/BR-12' (29,73%), 'Arka Manik' (34,15%), 'Charleston Gray' (38,70%), 'AHW-65' (35,80%) y 'AHW-19' (48,97%) resultaron ser moderadamente resistente; y se encontraron 'IC 582909' (53,18%), 'AHW/BR-60' (55,52%), 'BSM-1' (59,10%), 'AHW/BR-137' (60,58%) y 'AHW/ BR- 9' (67,37%) susceptibles a la infestación de mosca de la fruta. Se observó una correlación positiva significativa ($r = 0{,}99$; $P < 0{,}01$) entre el porcentaje de infestación de fruta y la densidad de larvas por fruto. Se correlacionaron significativamente y positivamente el porcentaje de infestación de frutas y la densidad de larvas por fruto con la longitud del fruto ($r = 0{,}57$ y 0,55, respectivamente) con el número de días hasta la primera cosecha de la fruta ($r = 0{,}75$ y 0,76, respectivamente), pero fueron negativamente correlacionados con la duración de la pubesencia de ovario ($r = -0{,}91$ y $-0{,}91$, respectivamente), la dureza de corteza ($r = -0{,}86$ y $-0{,}87$, respectivamente), y el grueso de la corteza ($r = -0{,}77$ y $-0{,}75$, respectivamente). Se explica la variación máxima de la infestación de frutas y la densidad larval por la longitud de pubescencia del ovario (82,5 y 83,6%, respectivamente) seguido de la longitud del fruto (4,3 y 3,0%, respectivamente) y el grueso de la corteza (3,2 y 2,0%, respectivamente). El contenido de aminoácidos libres fue más bajo en el resistente 'Asahi Yamato' y más alto en el susceptible 'BSM-1', mientras que el contenido de fenoles, taninos, alcaloides totales y flavonoides fue más alto en las variedades/genotipos resistentes y menor en las variedades susceptibles. El contenido de alcaloides y flavonoides totales explicaron el 88,4 y 92,0%, respectivamente de la variación total de la infestación por la mosca de la fruta y de la densidad de larvas por fruta.

Palabras Clave: flavonoides; alcaloide; fenol; taninos; 'Asahi Yamato'; 'BSM-1'

Watermelon (*Citrullus lanatus* [Thunb.] Matsumara & Nakai; Cucurbitales: Cucurbitaceae) is a popular dessert crop throughout the tropics and the Mediterranean regions of the world (Tindall 1983). Because of its antioxidant properties, the fruit is being rated equal to apple, banana, or orange. Fruits contain diverse carotenoids that are responsible for the different flesh colors. Different carotenoid patterns

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have been associated with distinct cultivars and cultivated environments (Zhao et al. 2013). Fruits also vary in size, shape, and rind pattern (Choudhary et al. 2012); are rich in lycopene and have a total antioxidant capacity similar to tomato (Djuric & Powell 2001; Perkins-Veazie et al. 2001); and are a rich source of β-carotene, vitamins (B, C, and E), minerals (K, Mg, Ca, and Fe), amino acid (citrulline), and phenols (Perkins-Veazie & Davis 2007). Plants generally are exposed to a variety of biotic and abiotic factors that may alter their genotypic and/or phenotypic properties resulting in expression of different mechanisms of resistance to pest attack (Gogi et al. 2010). Such mechanisms of plant resistance have been used effectively against insect pests in many field and horticultural crops (Dhillon et al. 2005a; Gogi et al. 2010). Mechanisms of resistance in plants are either constitutive or induced (Traw & Dawson 2002) and are grouped into 3 main categories: antixenosis, antibiosis, and tolerance (Painter 1951). Plants responsible for antibiosis resistance may cause reduced insect survival, prolonged development time, decreased size, and reduced fitness of new-generation adults (Sarfraz et al. 2006, 2007; Gogi et al. 2010). Antixenosis refers to the potential plant characteristics/traits, either allelochemical or morphological, that impart or alter insect behavior towards the host (Moslem et al. 2011; War et al. 2012; Haldhar et al. 2013).

Insect pests are a major constraint for increasing the production and productivity of the watermelon crop. The melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), is a serious pest of watermelon in India, and its outbreaks cause substantial crop losses to the growers. The melon fly has been observed on 81 host plants, with watermelon being a highly-preferred host, and has been a major limiting factor in obtaining good-quality fruits and high yield (Nath & Bhushan 2006). The extent of losses varies between 30 and 100%, depending on the cucurbit species and the season. As the maggots damage the fruits internally, it is difficult to control this pest with insecticides. Hence, development of watermelon varieties/genotypes resistant to the melon fly is an important component of integrated pest management (Panda & Khush 1995), but it has been limited in India owing to inadequate information on the sources of plant traits associated with resistance to pest infestations. The present study was designed to identify various morphological (antixenotic) and biochemical (allelochemical) fruit traits of watermelon varieties/genotypes associated with resistance against the melon fly in terms of fruit infestation and larval density under field conditions.

Materials and Methods

PRELIMINARY SCREENING OF WATERMELON VARIETIES/GENOTYPES (SUMMER 2012)

Twenty-seven varieties/genotypes of watermelon (RSS-1, AHW/BR-18, AHW/BR-8, AHW/BR-21, AHW/BR-20, AHW/YF-4, AHW/BR-19, AHW/BR-96, AHW/YF-5, AHW/YF-7, AHW/BR-10, Durgapura Kesar, AHW/BR-137, Durgapura Lal, AHW/BR-9, Sugar Baby, AHW-65, AHW-19, IC 582909, BSM-1, AHW/BR-16, Charleston Grey, Asahi Yamato, Arka Manik, AHW/BR-60, AHW/BR-12, and Thar Manak) were sown at the experimental farm of ICAR-Central Institute for Arid Horticulture (CIAH), Bikaner (28°06'N, 73°21'E), India. The crop was sown in summer 2012 with 3 replicates (blocks) for each variety/genotype in a randomized block design. The area of each bed was 5 × 2 m, and the plant-to-plant distance was maintained at 50 cm with a drip irrigation system. All the recommended agronomic practices (e.g., weeding, fertilizing, hoeing) were performed equally in each experimental bed according to local practices. Three pickings were done during the entire growing season of watermelon. Five fruits were selected randomly from each picking from each experimental bed (replication) of each variety/genotype and were brought to the laboratory for examination using a stereomicroscope for fruit infestation. The infested fruits were sorted and the percentage fruit infestation was calculated. Five fruits from all infested fruits from each picking of each variety/genotype were then selected randomly for further examination, and the larvae were counted in each infested fruit. The varieties/genotypes were categorized by following the rating system given by Nath (1966) for fruit infestation as: immune (no damage), highly resistant (1–10%), resistant (11–20%), moderately resistant (21–50%), susceptible (51–75%), and highly susceptible (76–100%).

FINAL SCREENING OF THE SELECTED WATERMELON VARIETIES/GENOTYPES (RAINY SEASON 2013 & SUMMER 2014)

Fifteen selected varieties/genotypes from the preliminary screening of watermelon (AHW/BR-137, Durgapura Lal, AHW/BR-9, Sugar Baby, AHW-65, AHW-19, IC 582909, BSM-1, AHW/BR-16, Charleston Grey, Asahi Yamato, Arka Manik, AHW/BR-60, AHW/BR-12, and Thar Manak) were sown at the experimental farm of ICAR-CIAH, Bikaner, India, in Jul 2013 and Feb 2014 using a randomized block design, with 3 blocks for each variety/genotype and each block representing a replication. The area of each bed was 5 × 2 m, and the plant-to-plant distance was maintained at 50 cm with a drip irrigation system. The picking and examination of fruits were performed as described for the preliminary screening.

ANTIXENOTIC FRUIT TRAITS OF THE WATERMELON VARIETIES/GENOTYPES

Ten marketable fresh fruits of each of the 15 varieties/genotypes were used to record data on the biophysical traits (length of pubescence, rind hardness, rind thickness, day to first harvest, fruit length, and fruit diameter). Length of ovary pubescence, rind thickness, fruit diameter, and fruit length were measured at 5 different positions of each fruit using a Digital Vernier Caliper (MITU-TOYO, 300 mm, 0.01 mm reading capacity). The days of first harvesting of fruits were recorded visually in the field. The hardness of fruit rind was assessed at harvesting using a fruit pressure tester (Model FT 327, 0–13 kg/cm^2).

ALLELOCHEMICAL FRUIT TRAITS OF THE WATERMELON VARIETIES/GENOTYPES

Two fresh fruits of each variety/genotype from each replication were selected, cut into small pieces, and dried. For estimation of metabolites, the procedure as published for each metabolite was followed to determine contents of phenols (Malik & Singh 1980), tannins (Schanderl 1970), ascorbic acid (Sadasivam & Balasubraminan 1987), free amino acids (Lee & Takahashi 1966), and flavonoids (Ebrahimzadeh et al. 2008; Nabavi et al. 2008).

STATISTICAL ANALYSES

Transformations (angular and square-root transformed values) were used to obtain normality in the data distribution before analysis (Steel et al. 1997), but untransformed means are also presented in all tables. The data on percentage fruit infestation, larval density per fruit, and biochemical fruit traits were analyzed through 1-way ANOVA using SPSS 16 software (O'Connor 2000). The means of significant parameters, among tested varieties/genotypes, were compared using Tukey's Honest Significant Difference (HSD) test for paired comparisons at a probability level of 5%. Correlations between biophysical and biochemical fruit traits and fruit fly parameters (percentage fruit infestation and larval density per fruit) were determined by correlation analysis and backward stepwise multiple regression analysis at the 95% significance level.

Results

PRELIMINARY SCREENING OF WATERMELON VARIETIES/ GENOTYPES

In the preliminary screening against the melon fly, significant differences were found in percentage fruit infestation and larval density per fruit among the 27 tested varieties/genotypes. The larval density per fruit had a significant positive correlation with percentage fruit infestation ($r = 0.99$; $P < 0.01$). The varieties/genotypes Asahi Yamato, Thar Manak, and AHW/BR-16 were resistant; AHW/BR-12, Arka Manik, Charleston Grey, AHW-65, AHW-19, Sugar Baby, Durgapura Lal, AHW/BR-19, AHW/BR-96, AHW/YF-5, AHW/YF-7, and RSS-1 were moderately resistant; and AHW/BR-18, AHW/BR-8, AHW/BR-21, AHW/BR-20, AHW/YF-4, AHW/BR-10, Durgapura Kesar, AHW/BR-137, AHW/BR-9, IC 582909, BSM-1, and AHW/BR-60 were susceptible (Table 1). The larval density ranged from 9.97 to 19.10 larvae per fruit and was significantly lower in resistant varieties/genotypes than in susceptible ones. It was highest in genotype AHW/BR-9 (19.10 larvae/fruit) followed by AHW/BR-8 (18.33 larvae/fruit). The minimum larval density was found in Asahi Yamato (9.97 larvae/fruit) followed by AHW/BR-16 (10.60 larvae/fruit). The percentage fruit infestation was highest in AHW/BR-9 (66.90%) and lowest in Asahi Yamato (12.60%) followed by AHW/BR-16 (14.73%). The fruit infestation ranged from 12.60 to 66.90% and was significantly lower in resistant and higher in susceptible varieties/genotypes (Table 1).

Table 1. Larval density and percentage fruit infestation by the melon fly on different varieties/genotypes of watermelon during preliminary screening trials (summer season).

Genotype	Larval density per fruit	Fruit infestation (%)[a,b]	Resistance category[c]
Thar Manak	11.00 ab	17.80 (24.85) bc	R
Asahi Yamato	9.97 a	12.60 (20.59) a	R
AHW/BR-16	10.60 ab	14.73 (22.54)ab	R
Arka Manik	14.30 de	33.90 (35.51) fgh	MR
AHW/BR-12	13.60 cde	28.90 (32.49) ef	MR
Charleston Grey	14.57 de	38.03 (38.05) hi	MR
AHW-19	15.23 ef	48.97 (44.39) kl	MR
AHW-65	14.00 de	35.33 (36.46) ghi	MR
Sugar Baby	13.23 cd	26.70 (31.10) de	MR
Durgapura Lal	11.90 bc	22.70 (28.28) cd	MR
AHW/YF-7	14.20 de	31.30 (34.00) efg	MR
AHW/YF-5	13.03 cd	26.90 (31.23) de	MR
AHW/BR-96	14.60 d	41.57 (40.13) ij	MR
AHW/BR-19	15.27 efg	40.90 (39.74) ij	MR
RSS-1	15.17 ef	44.60 (41.88) jk	MR
Durgapura Kesar	18.23 ij	61.53 (51.68) opq	S
AHW/BR-10	17.97 hij	63.33 (52.72) pq	S
AHW/BR-9	19.10 j	66.90 (54.91) q	S
AHW/BR-137	17.70 hij	59.33 (50.37) np	S
AHW/BR-60	16.97 ghi	55.57 (48.18) mno	S
BSM-1	17.73 hij	58.20 (49.70) mnop	S
IC 582909	16.43 fgh	52.70 (46.53) lm	S
AHW/BR-20	17.70 hij	62.43 (52.22) pq	S
AHW/BR-21	17.07 hi	59.03 (50.19) mnop	S
AHW/BR-8	18.33 ij	58.27 (49.74) mnop	S
AHW/BR-18	18.20 ij	63.83 (53.02) pq	S
AHW/YF-4	17.43 hij	55.23 (47.99) lmn	S

[a] Values in parentheses are angular transformed.

[b] Values followed by different letters are significantly different (Tukey's Honest Significant Difference test).

[c] R, resistant; MR, moderately resistant; S, susceptible; and HS, highly susceptible.

FINAL EVALUATION OF WATERMELON VARIETIES/GENOTYPES

The 15 varieties/genotypes selected for final evaluation of melon fly resistance were tested during the rainy season 2013 and summer season 2014. The varieties/genotypes Asahi Yamato, Thar Manak, and AHW/BR-16 were resistant; AHW/BR-12, Arka Manik, Charleston Grey, AHW-65, AHW-19, Sugar Baby, and Durgapura Lal were moderately resistant; and AHW/BR-137, AHW/BR-9, IC 582909, BSM-1, and AHW/BR-60 were susceptible in both seasons (Table 2). The larval density per fruit increased with an increase in percentage fruit infestation, and there was a significant positive correlation ($r = 0.99$; $P < 0.01$) between percentage fruit infestation and larval density per fruit (Table 3).

The larval density ranged from 10.30 to 19.37 and 10.10 to 19.17 larvae per fruit in the rainy season 2013 and the summer season 2014, respectively. Pooled data showed that larval density per fruit in both seasons (10.20–19.20 larvae/fruit) was significantly lower in resistant and higher in susceptible varieties/genotypes. Pooled data showed that fruit infestation in both seasons (12.73–67.37%) was significantly lowest in resistant and highest in susceptible varieties/genotypes. In pooled data, the percentage fruit infestation was highest in AHW/BR-9 (67.37%) and lowest in Asahi Yamato (12.73%) followed by AHW/BR-16 (15.10%) (Table 2).

ANTIXENOTIC FRUIT TRAITS OF THE WATERMELON VARIETIES/ GENOTYPES

Length of ovary pubescence, rind hardness, and rind thickness ranged from 3.82 to 6.20 mm, 8.37 to 12.99 kg/cm^2, and 0.80 to 1.58 cm, respectively. However, days to first fruit harvest (70.33–80.67 d), fruit length (12.23–25.60 cm), and fruit diameter (12.05–20.59 cm) were different among varieties/genotypes of watermelon (Table 4). Length of ovary pubescence, rind hardness, and rind thickness had significant negative correlations, whereas days to first fruit harvest, fruit length, and fruit diameter had significant positive correlations with percentage fruit infestation and larval density per fruit (Table 3). Stepwise regression analysis indicated that length of ovary pubescence, rind hardness, rind thickness, fruit length, days to first harvest, and fruit diameter explained 94% of the total variation in melon fly infestation. The maximum variation in fruit infestation was explained by length of ovary pubescence (82.5%) followed by fruit length (4.3%) and rind thickness (3.2%), whereas the remaining biophysical fruit traits explained < 3.0% variation in the fruit infestation (Table 5). Length of ovary pubescence, rind hardness, rind thickness, fruit length, days to first fruit harvest, and fruit diameter explained 93.3% of the total variation in the larval density per fruit. The maximum variation in the larval density per fruit was explained by length of ovary pubescence (83.6%) followed by fruit length (3.0%) and days to first fruit harvest (2.6%), whereas other traits explained < 2% variation in larval density (Table 5).

ALLELOCHEMICAL FRUIT TRAITS OF THE WATERMELON VARIETIES/ GENOTYPES

The free amino acid content in fruits of different varieties/genotypes ranged from 2.00 to 8.47 mg/g (on dry weight basis) with values significantly lower in resistant and higher in susceptible varieties/geno-

Table 2. Larval density of and percentage fruit infestation by the melon fly on different varieties/genotypes of watermelon during final evaluation trials.

	Larval density per fruit			Fruit infestation (%)			
Genotype	Rainy season	Summer season	Pooled	Rainy season	Summer season	Pooled	Resistance category
Thar Manak	11.17 ab	10.93 ab	11.05 ab	18.57 (25.41) bc	17.97 (24.97) ab	18.27 (25.23) bc	R
Asahi Yamato	10.30 a	10.10 a	10.20 a	12.90 (20.83) a	12.57 (20.55) a	12.73 (20.73) a	R
AHW/BR-16	11.03 a	10.80 ab	10.92 a	15.37 (23.04) ab	14.83 (22.63) a	15.10 (22.84) ab	R
AHW/BR-12	13.90 de	13.77 de	13.83 c	30.83 (33.70) ef	28.63 (32.32) cde	29.73 (33.02) ef	MR
Arka Manik	14.57 ef	14.17 def	14.37 cd	34.70 (36.03) fg	33.60 (35.33) def	34.15 (35.68) fg	MR
Charleston Grey	15.20 f	14.73 ef	14.96 cd	39.23 (38.77) g	38.17 (38.13) f	38.70 (38.45) g	MR
AHW-19	15.60 fg	15.37 fg	15.48 de	49.30 (44.58) h	48.63 (44.20) g	48.97 (44.39) h	MR
AHW-65	14.73 ef	14.20 def	14.47 cd	36.97 (37.43) fg	34.63 (36.03) ef	35.80 (36.74) g	MR
Sugar Baby	12.77 cd	13.10 cd	12.90 ab	26.93 (31.25) de	26.40 (30.90) cd	26.67 (31.07) de	MR
Durgapura Lal	12.33 bc	11.87 bc	12.10 b	23.07 (28.48) cd	23.00 (28.48) bc	23.03 (28.48) cd	MR
AHW/BR-9	19.37 j	19.17 j	19.20 h	67.50 (55.31) k	67.23 (55.11) i	67.37 (55.14) k	S
BSM-1	17.97 hi	17.93 ij	17.95 g	60.37 (50.97) ij	57.83 (49.49) h	59.10 (50.22) ij	S
IC 582909	16.47 gh	16.30 gh	16.39 ef	53.40 (46.93) hi	52.97 (46.68) gh	53.18 (46.81) hi	S
AHW/BR-60	17.27 hi	16.47 ghi	16.87 fg	55.87 (48.35) hij	55.17 (47.95) gh	55.52 (48.15) hij	S
AHW/BR-137	18.10 i	17.47 hi	17.78 g	61.53 (51.65) j	59.63 (50.55) h	60.58 (51.09) j	S

[a] Values in parentheses are angular transformed.
[b] Values followed by different letters are significantly different (Tukey's Honest Significant Difference test).
[c] R, resistant; MR, moderately resistant; S, susceptible; and HS, highly susceptible.

Table 3. Correlation coefficient (*r*) between percentage fruit infestation and larval density per fruit with various antixenotic fruit traits of watermelon varieties/genotypes.

	Percentage infestation	Larval density	Length of ovary pubescence (mm)	Rind hardness (kg/cm^2)	Rind thickness (cm)	Days to first fruit harvest	Fruit length (cm)
Larval density	0.991**						
Length of ovary pubescence	−0.908**	−0.914**					
Rind hardness	−0.856**	−0.872**	0.880**				
Rind thickness	−0.770**	−0.746**	0.728**	0.591*			
Days to first harvest	0.746**	0.763**	−0.669**	−0.763**	−0.423^{NS}		
Fruit length	0.568*	0.545*	−0.453^{NS}	−0.395^{NS}	−0.253^{NS}	0.284^{NS}	
Fruit diameter	0.241^{NS}	0.206^{NS}	−0.095^{NS}	−0.289^{NS}	0.242^{NS}	0.359^{NS}	0.581*

**, significant at *P* = 0.01 (2-tailed); *, significant at *P* = 0.05 (2-tailed); NS, not significant.

Table 4. Antixenotic fruit traits of different varieties/genotypes of watermelon.

Genotype	Length of ovary pubescence (mm)	Rind hardness (kg/cm^2)	Rind thickness (cm)	Days to first fruit harvest[a]	Fruit length (cm)	Fruit diameter (cm)
Thar Manak	5.44 gh	11.23 fg	1.17 cd	70.33 (8.45) a	17.65 c	15.54 cd
AHW/BR-12	5.31 g	10.77 ef	1.13 bcd	73.00 (8.60) abcd	12.23 a	12.05 a
AHW/BR-60	4.70 cde	9.20 ab	0.80 a	80.67 (9.04) e	20.13 d	17.84 e
Arka Manik	5.21 fg	9.97 bcde	1.58 e	79.67 (8.98) de	17.83 c	20.18 h
Asahi Yamato	6.20 i	12.00 g	1.57 e	70.67 (8.47) ab	17.57 c	19.90 gh
Charleston Grey	5.09 efg	10.70 def	1.04 bc	74.00 (8.66) abcde	21.23 d	14.39 bc
AHW/BR-16	5.75h	12.99 h	1.46 e	71.00 (8.48) abc	17.94 c	13.80 b
BSM-1	4.41bc	9.40 abc	1.07 bc	74.67 (8.70) abcde	25.60 g	20.59 h
IC 582909	4.61 cd	9.87 bcde	0.80 a	77.00 (8.83) bcde	15.03 b	14.90 bc
AHW-19	4.83 def	10.07 bcde	1.16cd	75.33 (8.73) abcde	22.13 f	19.39 fg
AHW-65	4.88 def	9.67 bcd	1.49 e	77.33 (8.85) bcde	18.58 c	17.99 e
Sugar Baby	5.03 efg	10.57 def	1.20 cd	75.33 (8.73) abcde	17.75 c	16.47 d
AHW/BR-9	3.82 a	8.37 a	0.80 a	77.67 (8.87) cde	21.70 ef	15.54 cd
Durgapura Lal	4.88 def	10.36 cdef	1.33 de	72.00 (8.54) abc	15.21 b	15.41 cd
AHW/BR-137	4.14 ab	9.77 bcde	0.90 ab	79.67 (8.98) de	20.43 de	18.27 ef

Values in a column followed by different letters are significantly different (Turkey's Honest Significant Difference test).
[a] Values in parentheses are square-root transformed.

Table 5. Backward stepwise regression models showing the effect of different antixenotic fruit traits of watermelon on percentage fruit infestation and number of larvae per fruit.

Model[a]	R^2	Role of individual traits (%)
Percentage fruit infestation		
$Y = 10.68 - 10.06X_1 - 1.21X_2 - 23.33X_3 - 1.18X_4 + 0.96X_5 + 0.62X_6$	94.00	00.10
$Y = 1.29 - 8.49X_1 - 2.01X_2 - 20.70X_3 + 1.34X_4 + 1.27X_5$	93.90	04.30
$Y = 47.49 - 12.84X_1 - 1.95X_2 - 18.07X_3 + 1.28X_4$	89.60	02.50
$Y = 173.75 - 13.11X_1 - 4.86X_2 - 17.21X_3$	87.10	03.20
$Y = 179.98 - 20.33X_1 - 3.94X_2$	83.90	01.40
$Y = 171.77 - 26.89X_1$	82.50	82.50
Larval density per fruit		
$Y = 9.04 - 1.35X_1 - 0.47X_2 - 2.32X_3 + 0.23X_4 + 0.19X_5 - 0.06X_6$	93.30	00.10
$Y = 9.97 - 1.51X_1 - 0.39X_2 - 2.58X_3 + 0.21X_4 + 0.17X_5$	93.20	03.00
$Y = 15.96 - 2.07X_1 - 0.38X_2 - 2.24X_3 + 0.20X_4$	90.20	02.60
$Y = 36.16 - 2.12X_1 - 0.84X_2 - 2.10X_3$	87.60	02.00
$Y = 36.92 - 2.99X_1 - 0.73X_2$	85.60	02.00
$Y = 35.39 - 4.22X_1$	83.60	83.60

[a] X_1, length of ovary pubescence; X_2, rind hardness; X_3, rind thickness; X_4, days to first fruit harvest; X_5, fruit length; X_6, fruit diameter; and R^2, coefficient of determination.

types. Flavonoid, tannin, total alkaloid, phenol, and ascorbic acid contents ranged from 50.43 to 100.93 mg/100 g, 30.84 to 60.83mg/100 g, 0.43 to 1.55%, 14.33 to 21.41 mg/g, and 46.64 to 89.38 mg/10 g, respectively, with values significantly higher in resistant and lower in susceptible varieties/genotypes (Table 6). The free amino acid content of fruit had a significant positive correlation whereas flavonoid, tannin, total alkaloid, phenol, and ascorbic acid contents had a significant negative correlation with percentage fruit infestation and larval density per fruit (Table 7). Backward stepwise regression analysis indicated that flavonoid and total alkaloid contents explained 88.4% of the total variation in fruit fly infestation (Table 8). The maximum variation in fruit infestation was explained by flavonoid content (69.7%) followed by total alkaloid (18.7%), phenol (3.3%), ascorbic acid (1.4%), tannin (1.0%), and free amino acid contents (0.3%). The flavonoid and total alkaloid contents explained 92.0% of the total variation in larval density per fruit. The maximum variation in larval density per fruit was explained by flavonoid content (71.1%) followed by total alkaloid (20.9%), phenol (2.0%), and ascorbic acid contents (1.0%), whereas the rest of the biochemical fruit traits explained < 1% variation in larval density (Table 8).

Discussion

Host plant selection by insects is expressed either by the occurrence of a population of insects on the plant in nature or by feeding, oviposition, or use of the plant for complete offspring development (Rafiq et al. 2008). Plant characteristics influence the herbivores directly by affecting host plant preference or survival and reproductive success (direct defense) and indirectly through influencing the behavior of other species such as natural enemies of the insect pests (indirect defense) (Dudareva et al. 2006; Hower & Jander 2008; Arimura et al. 2009). Direct defenses are mediated by plant characteristics that affect the herbivore's biology such as mechanical protection on the surface of the plants (e.g., hairs, trichomes, thorns, spines, and thick leaves) or production of toxic chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and quinones that either kill or retard the development of the herbivores (Hanley et al. 2007). Inheritance of resistance to the fruit fly was studied in intervarietal crosses of watermelon *C. lanatus* and 2 sources of resistance (J 18-1 and J 56-1) were used. The resistance of watermelon to the fruit fly was controlled by a

Table 6. Allelochemical fruit traits of different varieties/genotypes of watermelon.

Genotype	Flavonoid content (mg/100 g)[a]	Tannin content (mg/100 g)[a]	Total alkaloid content (%)	Phenol content (mg/g)	Ascorbic acid (mg/10 g)[a]	Free amino acids (mg/g)
Thar Manak	67.73 (8.29) cd	48.36 (7.04) d	1.55 i	18.97 efg	79.93 (9.00) g	4.74 cd
AHW/BR-12	70.57 (8.46) de	46.18 (6.87) c	1.06 f	18.54 efg	75.05 (8.72) efg	4.59 cd
AHW/BR-60	55.25 (7.50) ab	34.61 (5.97) a	0.74 b	16.15 abcd	58.44 (7.71) c	7.43 f
Arka Manik	58.70 (7.72) abc	58.10 (7.69) fg	0.89 cde	17.97 def	69.28 (8.38)de	5.19 d
Asahi Yamato	100.93 (10.09)g	59.10 (7.77) fg	1.35 h	21.41 h	89.38 (9.51) i	2.00 a
Charleston Grey	59.77 (7.78) abc	57.13 (7.62) efg	0.82 bc	17.08 bcde	72.21 (8.55) ef	6.13 e
AHW/BR-16	87.27 (9.39) f	51.30 (7.22) def	1.34 h	20.67 gh	85.80 (9.32) hi	2.83 b
BSM-1	53.61 (7.39) a	33.72 (5.89) a	0.48 a	15.65 abc	53.06 (7.35) b	8.47 g
IC 582909	64.53 (8.07) bcd	35.77 (6.06) ab	0.98 def	17.55 cde	63.50 (8.03) cd	6.00 e
AHW-19	55.60 (7.52) ab	35.07 (6.00) a	0.84 bcd	16.86 bcde	62.20 (7.95) c	6.55 e
AHW-65	57.30 (7.63) ab	42.07 (6.56) bcd	1.09f g	16.77 bcde	59.14 (7.75) d	7.30 f
Sugar Baby	86.10 (9.32) f	51.53 (7.24) def	1.02 ef	20.61 gh	77.22 (8.84) gh	4.31 c
AHW/BR-9	50.43 (7.17) a	30.84 (5.64) a	0.52 a	14.33 a	46.64 (6.90) a	8.11 g
Durgapura Lal	80.03 (9.00) ef	60.83 (7.85) g	1.21 gh	20.02 fgh	76.24 (8.79) fg	4.85 cd
AHW/BR-137	53.16 (7.36) a	32.56 (5.79) a	0.43 a	15.12 ab	48.60 (7.04) ab	8.38 g

Values in a column followed by different letters are significantly different (Turkey's Honest Significant Difference test).

[a] Values in parentheses are square-root transformed.

Table 7. Correlation coefficient (*r*) between percentage fruit infestation and larval density per fruit with various allelochemical fruit traits of watermelon varieties/genotypes.

	Percentage infestation	Larval density	PC	FC	TC	AA	FAA
Larval density	0.991**						
PC	−0.930**	−0.933**					
FC	−0.835**	−0.843**	0.946**				
TC	−0.847**	−0.810**	0.794**	0.692**			
AA	−0.953**	−0.954**	0.955**	0.878**	0.821**		
FAA	0.911**	0.914**	−0.955**	−0.919**	−0.824**	−0.967**	
TAC	−0.912**	−0.934**	0.841**	0.730**	0.692**	0.874**	−0.836**

**, significant at $P = 0.01$ (2-tailed); *, significant at $P = 0.05$ (2-tailed); AA, ascorbic acid (mg/10 g); FAA, free amino acids (mg/g); FC, flavonoid content (mg/100 g); PC, phenol content (mg/g); TAC, total alkaloid content (%);TC, tannin content (mg/100 g).

single dominant gene. The symbol *Fwr* has been proposed to denote the resistant gene (Khandelwal & Nath 1978). In the present study, the varieties/genotypes Asahi Yamato, Thar Manak, and AHW/BR-16 were resistant and AHW/BR-9, AHW/BR-137, BSM-1, IC 582909, and AHW/BR-60 were susceptible varieties/genotypes of watermelon against the melon fly. The percentage fruit infestation and larval density were found to be significantly lower in resistant and higher in susceptible varieties/genotypes of watermelon. Numerous studies have shown that genotypes of the same species could differ significantly in their resistance to insect pests (Simmons & Levi 2002a,b; Thies & Levi 2003; López et al. 2005; Kousik et al. 2007; Simmons et al. 2010; Moslem et al. 2011; Haldhar et al. 2013), and that this resistance was influenced by morphological and biochemical traits of plants. Our findings are in line with those of Dhillon et al. (2005b) and Gogi et al. (2010), who observed lower fruit infestation and larval densities on resistant than on susceptible genotypes of bitter gourd.

The antixenotic fruit traits were significantly different among the tested watermelon varieties/genotypes. Fruit length, fruit diameter, and days to first fruit harvest had significant positive correlation whereas rind hardness, rind thickness, and length of ovary pubescence had significant negative correlation with percentage fruit infestation and larval density. In previous studies, biophysical fruit traits also were found significantly different among genotypes (Dhillon et al. 2005b; Gogi et al. 2010; Simmons et al. 2010). Pubescence consists of the layer of hairs (trichomes) extending from the epidermis of the above-ground plant parts including stem, leaves, and fruits, and occurring in several forms such as straight, spiral, stellate, hooked, and glandular (Hanley et al. 2007). Similar to our results, Gogi et al. (2010) documented that fruit length, fruit diameter, number of longitudinal ribs per fruit, and number of small ridges per cm^2, which were significantly lowest in resistant and highest in susceptible genotypes, had a significant positive correlation with percentage fruit infestation and larval density per fruit. In contrast to our results, rind hardness, height of small ridges, height of longitudinal ribs, and pericarp thickness, which were significantly highest in resistant and lowest in susceptible genotypes, had a significant negative correlation with percentage fruit infestation and larval density per fruit (Gogi et al. 2010). These variations in measured biophysical fruit traits may be attributed to differences in the tested genotypes and/or stage of the fruits selected for measuring these traits, as reported in earlier studies (Dhillon et al. 2005b; Kumara et al. 2006; Gogi et al. 2010). Stepwise regression analysis of our data indicated that maximum variation in percentage fruit infestation and larval density per fruit were explained by length of ovary pubescence followed by fruit length. However, Gogi et al. (2010) showed that the tested morphological traits explained 100% of the total variation in percentage fruit infestation and larval density per fruit. The maximum variation, in percentage fruit infestation and larval density per fruit, in their study was explained by rind hardness followed by fruit diameter and number of longitudinal ribs.

The allelochemical compounds in fruit were significantly different among the tested watermelon varieties/genotypes. The free amino acid content was lowest in resistant and highest in susceptible varieties/genotypes, whereas flavonoid, tannin, phenol, alkaloid, and ascorbic acid contents were highest in resistant and lowest in susceptible

Table 8. Backward stepwise regression models showing effects of different allelochemical fruit traits of watermelon on percentage fruit infestation and number of larvae per fruit.

Model[a]	R^2	Role of individual traits (%)
Percentage fruit infestation		
$Y = 182.76 + 0.026X_1 + 0.095X_2 - 16.22X_3 - 3.58X_4 - 0.85X_5 - 2.38X_6$	94.40	00.30
$Y = 145.08 + 0.13X_1 + 0.075X_2 - 16.14X_3 - 3.52X_4 - 0.60X_5$	94.10	01.40
$Y = 163.49 + 0.176X_1 + 0.093X_2 - 21.35X_3 - 6.78X_4$	92.70	03.30
$Y = 99.59 - 0.38X_1 - 0.05X_2 - 34.71X_3$	89.40	18.70
$Y = 100.86 - 0.77X_1 - 0.21X_2$	70.70	01.00
$Y = 103.94 - 0.979X_1$	69.70	69.70
Larval density per fruit		
$Y = 35.83 - 0.015X_1 + 0.014X_2 - 3.42X_3 - 0.42X_4 - 0.12X_5 - 0.396X_6$	96.10	00.30
$Y = 29.55 + 0.003X_1 + 0.01X_2 - 3.41X_3 - 0.41X_4 - 0.077X_5$	95.80	01.00
$Y = 31.86 + 0.009X_1 + 0.013X_2 - 4.07X_3 - 0.825X_4$	94.80	02.00
$Y = 24.14 - 0.059X_1 - 0.005X_2 - 5.70X_3$	92.80	20.90
$Y = 24.35 - 0.124X_1 - 0.03X_2$	71.90	00.80
$Y = 24.798 - 0.154X_1$	71.10	71.10

[a] X_1, flavonoid content (mg/100 g); X_2, tannin content (mg/100 g); X_3, total alkaloid content (%); X_4, phenol content (mg/g); X_5, ascorbic acid (mg/10 g); X_6, free amino acids (mg/g); and R^2, coefficient of determination.

varieties/genotypes. Very little information is available on correlation of the biochemical traits. Ismail et al. (2010) reported that of all tested cantaloupe plant parts, the leaf extracts showed the highest total phenol content (26.4 mg/g extract) and total flavonoid content (69.7 mg/g extract). Others showed that the pH was lowest and tannin, flavanol, and phenol contents were highest in fruit fly–resistant genotypes of bitter gourd (Gogi et al. 2010). Total soluble solids and pH of fruit had a significant positive correlation whereas tannin, phenol, alkaloid, and flavonoid contents had a significant negative correlation with percentage fruit infestation and larval density per fruit (Gogi et al. 2010). Biochemical characters such as total sugar and crude protein were positively correlated whereas total phenols were negatively correlated with fruit borer infestation (Sharma & Singh 2010; War et al. 2012; Haldhar et al. 2013). Similar to our findings, it has been demonstrated that phenols, tannins, and flavonoids enhanced plant defenses against insects (Gogi et al. 2010; War et al. 2012; Haldhar et al. 2013).

Backward stepwise regression analysis of our data indicated that the maximum variation in percentage fruit infestation and larval density per fruit were explained by flavonoid followed by total alkaloid contents. Flavonoids are cytotoxic and interact with different enzymes through complexation. Flavonoids and isoflavonoids protect the plant against insect pests by influencing the behavior, growth, and development of insects (Simmonds 2003). In addition, flavonoids scavenge the free radicals including reactive oxygen species and reduce their formation by chelating metals (Treutter 2006). Tannins are astringent (mouth puckering), bitter polyphenols and act as feeding deterrents to many insect pests. They precipitate proteins non-specifically (including the digestive enzymes of herbivores) by hydrogen bonding or covalent bonding of protein –NH$_2$ groups. Phenolic heteropolymers play a central role in plant defense against insects and pathogens (Barakat et al. 2010). Phenols also play an important role in cyclic reduction of reactive oxygen species such as superoxide anion and hydroxide radicals, H$_2$O$_2$, and singlet oxygen, which in turn activate a cascade of reactions leading to the activation of defensive enzymes (Maffei et al. 2007). Gogi et al. (2010) indicated that the maximum variation in percentage fruit infestation was explained by tannin and flavanol contents whereas other biochemical fruit traits explained < 0.2% variation. The maximum variation in larval density per fruit was explained by tannin followed by flavanol contents whereas other biochemical fruit traits explained < 0.1% variation (Gogi et al. 2010). Haldhar et al. (2013) found in muskmelon that the total alkaloid content and pH explained 97.96% of the total variation in percentage fruit infestation, and alkaloid and total sugar contents explained 92.83% of the total variation in larval density per fruit.

Thus, we suggest that reduction in fruit fly infestations on resistant varieties/genotypes could be due to antixenosis (biophysical properties) and antibiosis (allelochemicals). Certain biophysical traits (e.g., length of ovary pubescence, rind hardness, and rind thickness) and biochemical traits (e.g., flavonoids, tannins, phenols, ascorbic acid, and total alkaloids) described in Fig. 1 and Fig. 2 were linked to resistance of watermelon against *B. cucurbitae* and, therefore, can be used as marker traits in plant breeding programs to select resistant varieties/genotypes.

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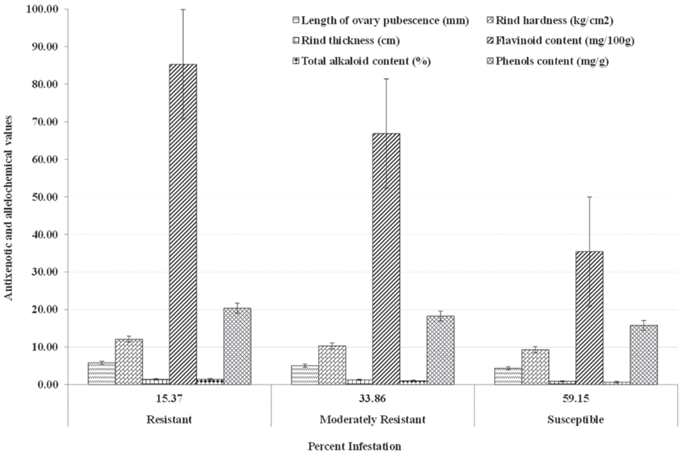

Fig. 1. Associations of major antixenotic and allelochemical fruit traits of watermelon with resistance to the melon fly evaluated by percentage fruit infestation under different infestation categories.

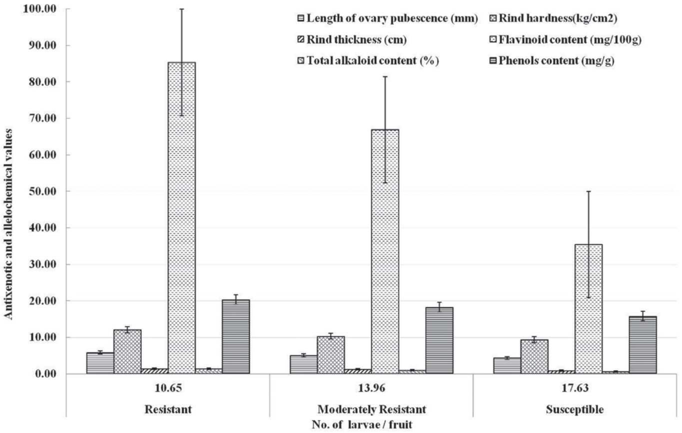

Fig. 2. Associations of major antixenotic and allelochemical fruit traits of watermelon with resistance to the melon fly evaluated by the number of larvae per fruit under different infestation categories.

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