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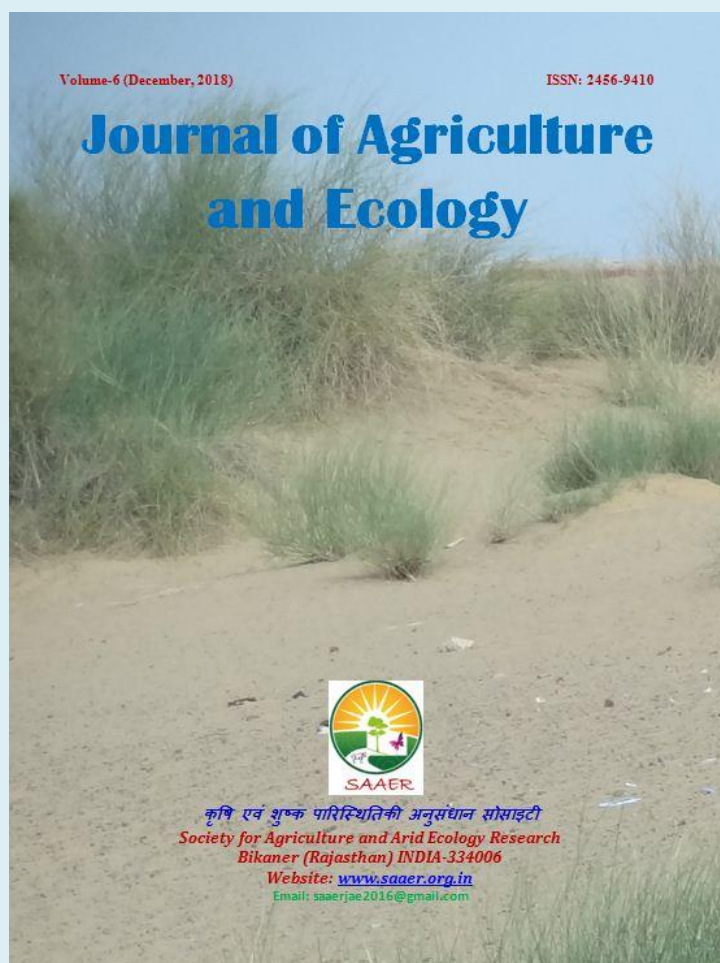
SM Haldhar, MK Berwal, DK Samadia, R Kumar, JS Gora & S Choudhary

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Review Article

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Biochemical basis of plant-insect interaction in arid horticulture crops: a scientific review

SM Haldhar¹, MK Berwal¹, DK Samadia¹, R Kumar¹, JS Gora¹ & S Choudhary²

¹ICAR-Central Institute for Arid Horticulture, Sri Ganganagar Highway, Beechwal Industrial Area, Bikaner (Rajasthan)-334006, India

²Departement of Horticulture, SKNAU, Jobner

✉ Corresponding author: SM Haldhar, E-mail: haldhar80@gmail.com

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Abstract

Plants are persistently confronted to both abiotic and biotic stresses that drastically reduce their productivity. Plant responses to these stresses are multifaceted and involve copious Biochemical, physiological, molecular, molecular and cellular adaptations. Recent evidence shows that simultaneous occurrence of abiotic and biotic stress can have a positive effect on plant performance by reducing the susceptibility to biotic stress which is a positive sign for arid horticulture crops. Some of these adaptations specifically biochemical adaptations become the source of plant defense mechanisms against biotic stresses like insect's pest and diseases. These biochemical adaptations/mechanisms includes production of secondary metabolites of plant defense against the biotic stresses especially against insects are wide spread and highly dynamic, and are mediated the response directly or indirectly in arid horticultural crops. Production of secondary metabolites viz. terpenes, phenolics, flavonoids, alkaloids, N & S containing compounds is constitutive as well as inducible through mild stress caused by insect damage to plants which leads to affect the feeding, growth and survival of the insect. Quality and quantity of constitutive secondary metabolites production is species as well as cultivar specific and can be expressed as signature of particular plant or species and leads to the phenomenon of host-plant interaction or host-plant resistance. This phenomenon of host plant resistance to insect can be exploited for development of crop cultivars which readily produce the inducible response upon mild infestation and can perform as one of the of integrated pest management for sustainable arid horticulture crop production. This review presents overviews about these constitutive and inducible responses towards biochemical adaptations in arid horticulture crops to protect themselves against insects.

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Introduction

Plants and insects have been living together for more than 350 million years. In

co- evolution, both have evolved strategies to avoid each other's defense systems. This evolutionary arms race between plants and insects has resulted in the development of an elegant defense system in plants that has the ability to recognize the nonself molecules or signals from damaged cells, much like the animals, and activates the plant immune response against the herbivores (Howe & Jander 2008; Verhage et al. 2010; Hare 2011). Plant-arthropod interactions are thought to be of utmost importance for understanding the dynamics of ecological communities (Sarmiento et al. 2011; Han et al. 2016; Haldhar et al. 2018). Plant defence strategies against insect herbivores may involve the synthesis of a plethora of biologically active compounds (allelochemicals), which are phylogenetically conserved in specific plant families or genera (Mithofer & Boland 2012). Plants frequently display genetic variation within and between population for traits that influence the preference and non preference of insects on their hosts that is resistance traits (Johnson & Agrawal 2005; Haldhar et al. 2017). It has been widely recognised that biological diversity plays a vital role in structuring community ecosystem processes (Haddad et al. 2011; Sarmiento et al. 2011; Tooker et al. 2012; Muthusamy et al. 2017). The genotypic variation may influence the distribution and damage levels of herbivores on focal plants through processes referred to as associational resistance or susceptibility (Barbosa et al. 2009). Host plants play an important role in determining insect populations in respect to concentrations and proportions of nutrients, which differ among species (Schoonhoven et al. 2005). Plants

having antibiosis characters such as *flavonoid*, phenols, tannins etc. may cause reduced insect survival, prolonged development time, decreased size and reduced fitness of new generation adults (Gogi et al. 2010; Haldhar et al. 2013a) (Figure 1).

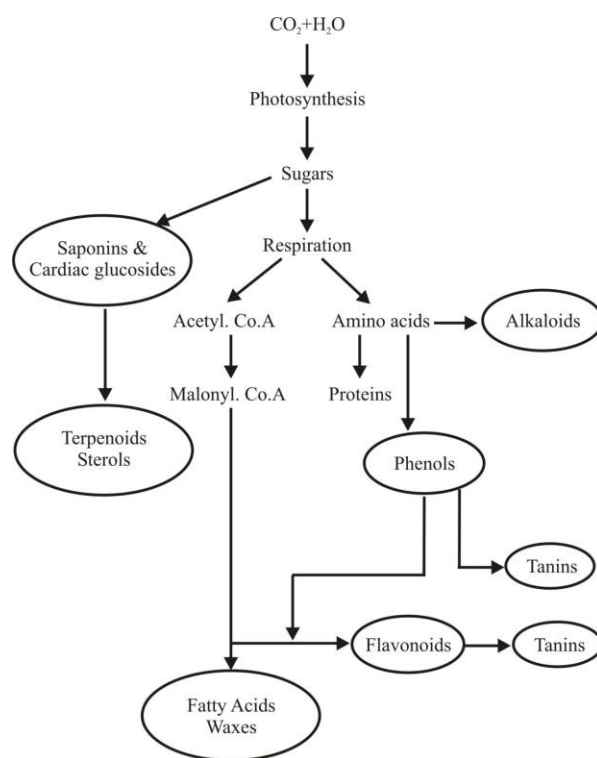


Fig. 1 Biosynthetic relationship among some primary and secondary metabolites. The principal group of secondary metabolites are circled (Mazid et al. 2011).

Hence, such mechanisms of plant resistance have been effectively and widely used for managing insect-pests in horticultural crops (War et al. 2012; Haldhar et al. 2015a; Haldhar et al. 2017a&b). The utilization of native and introduced genetic material of arid horticulture crops for breeding varieties over the long period of time in the country resulted into generation of many new genotypes / lines in the form of selections and to some extent

through hybridization. Thereby, considerable generated material / variations may have exists in targeted species with regards to the plant type, flowering, fruiting, morphological and physiological of fruits, reaction to biotic and abiotic factors and eco-adaptations. Since, detailed evaluation of identified genotype is essential for further breeding programme and to incorporate desirable gene(s) through combination breeding. Wild and relative species gene-pool possesses unique traits and that can be exploited both by direct selection for use in combination breeding or improvement through advanced approaches. They also constitute priceless reservoir that contain gene (s) conferring better adaptations to stressed environment and also resistant to diseases and insects or have more nutritional and medicinal properties. Therefore, there is urgent need to promote systematic utilization of wild genepool in strategic breeding work for developing genotypes having biotic and abiotic stress resistance or tolerance, and their conservation as relative species (Samadia & Haldhar, 2017). In this manuscript reviewed major arid horticulture crops for biochemical basis of plant-insect interaction.

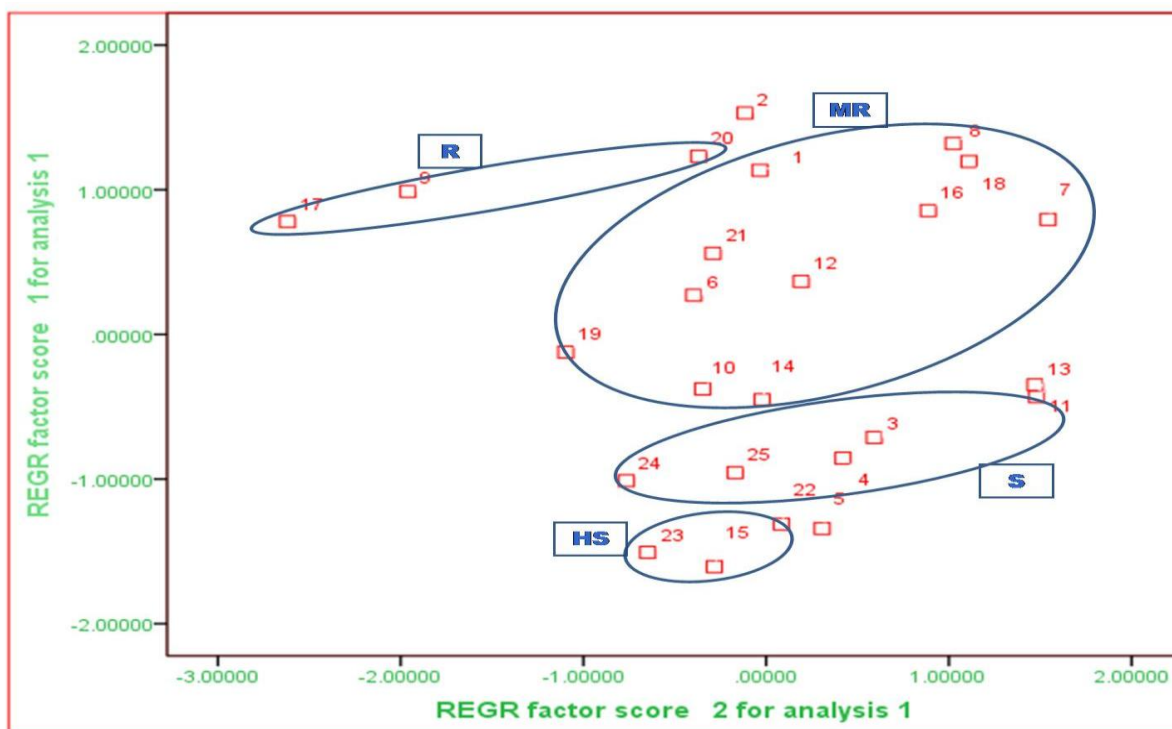
Ber, *Ziziphus mauritiana* Lamark

Ber (*Ziziphus mauritiana*) also called 'desert apple', 'jujube', 'Chinese apple', 'Ber (Hindi)', 'Indian plum' and 'Permsret (Anguilla)' is a tropical fruit tree species, belonging to the family Rhamnaceae (Balikai et al. 2013). Fruit fly, *Carpomyia vesuviana* Costa is the most destructive pest of ber in India. It is a monophagous pest, infests *Zizyphus* species only and contributes towards low yield and poor quality fruits (Haldhar et

al. 2012; Haldhar et al. 2013b; Haldhar et al. 2016a; Dhileepan 2017). The fruit fly causes yield losses of up to 80% under severe infestation when no control measures as taken (Batra 1953). While analyzing the effect of biochemical traits on the fruit fly in different cultivars of ber, significant differences in fruit fly incidence were observed. The cultivars such as Tikadi, Katha and Illaichi were found to be resistant; BS-75-1, Safeda, Dandan, Gola, Goma Kirti, Jogia, Narma, Mundia, Reshmi, Seb, ZG-3, Umran and Akharota were found to be moderately resistant; Banarasi Karaka, Banarasi Pawandi, Chhuhara, Kaithli, Thar Sevika and Thar Bhubraj were susceptible, whereas Sanaur-3, Sanaur-4 and Sanaur-5 were highly susceptible to fruit fly, *C. vesuviana* in both the studied seasons (Haldhar et al. 2018). Hosagoudar et al. (1999) reported that fruit fly, *C. vesuviana* infestation was high in the cultivar Sanaur-2 followed by Umran and Sanaur-6 and the lowest infestation being recorded in Illaichi. The *flavonoid* content (179.0 mg/100 g) was found to be maximum in Safeda followed by Tikadi (176.5 mg/100 g) and minimum in Chhuhara (40.7 mg/100 g). The tannin content (511.6 mg/100 g) was found to be the highest in Safeda followed by Tikadi (502.8 mg/100 g) and the lowest in Chhuhara (264.8 mg/100 g). Phenols content was highest in Safeda (239.0 mg/100 g) followed by Tikadi (232.0 mg/100 g) and lowest in Sanaur-4 (113.0 mg/100 g) with values significantly higher in resistant and lower in susceptible cultivars. The percentage of fruit infestation with flavonoid (-0.914), tannins (-0.914) and phenols (-0.947) had significant negative correlation (Haldhar et al.

2018). Backward stepwise regression analysis indicated that flavonoid and phenols contents explained 89.0% of the total variation in fruit fly infestation. The maximum variation in fruit infestation was explained by flavonoid content (83.5%) followed by phenols (5.5%), and tannin (1.9%) (Haldhar et al. 2018). 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, H₂O₂, and singlet oxygen, which in turn activate a cascade of reactions leading to the activation of defensive enzymes (Maffei et al. 2007). Phenols act as a

defensive mechanism not only against herbivores but also against microorganisms and competing plants. Tannins, flavonoids and isoflavonoids protect the plant against insect pests by influencing the behavior, growth, and development of insects (Simmonds 2003; Barbehenn & Peter 2011; Nath et al. 2017). Two principal components (PCs) were extracted explaining the cumulative variation of 84.7% in ber fruit fly infestation. PC1 and PC2 were plotted and the plot showed four discrete classes of cultivars, which could be grouped into resistant (R), moderately resistant (MR), susceptible (S), and highly susceptible (HS) as shown in Figure 2 (Haldhar et al. 2018).



R: Tikadi, Katha, Illaichi; **MR:** BS-75-1, Safeda, Dandan, Gola, Goma Kirti, Jogia, Narma, Mundia, Reshmi, Seb, ZG-3, Umran, Akharota; **S:** Banarasi Karaka, Banarasi Pawandi, Chuhara, Kaithli, Thar Sevika, Thar Bhubraj and **HS:** Sanaur-3, Sanaur-4 and Sanaur-5.

Fig. 2 Plot of PC1 and PC2 showing clusters of Indian *ber* (*Z. mauritiana* L) varieties/ genotypes show resistance to fruit fly, *C. vesuviana* (Haldhar et al. 2018)

Musk melon, *Cucumis melo* L.

Musk melon (*Cucumis melo* L.) is one of the important horticultural crops worldwide and plays an important role in international trade. Different forms of melon are known that are morphologically different. The melon fruit fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae) is a serious pest of muskmelon in India and its outbreaks cause substantial crop losses to growers. The melon fruit fly has been observed on 81 host plants, but muskmelon is one of the most preferred hosts and has been a major limiting factor in obtaining good quality fruits and high yield (Rabindranath & Pillai 1986; Nath & Bhushan 2006; Haldhar et al. 2014; Choudhary et al. 2015). The extent of losses varies between 30 to 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 varieties resistant to melon fruit fly is an impotent component of integrated pest management (Panda & Khush 1995). Plant varieties/ genotypes have possess biochemical variations due to the environment stress or genetic makeup, which alter the nutritional values for herbivores (Misirli et al. 2000; Rafiq et al. 2008; Gogi et al. 2010; Haldhar et al. 2015c). The genotypes, AHMM/BR-1, RM-50 and AHMM/BR-8 were the most resistant; MHY-5, D. Madhu and P. Sarabati were moderately resistant; AHMM/BR-13, P. Madhuras and Arka Jeet were susceptible whereas Arka Rajhans and GMM-3 were the

highly susceptible varieties/ genotypes of muskmelon (Haldhar et al. 2013). Ismail et al. (2010) reported that the cantaloupe flesh extract afforded the highest yield ($89.6 \pm 0.3\%$) whilst the lowest yield was obtained from the seed ($13.7 \pm 0.5\%$). The leaf extract showed the highest total phenolic content (26.4 ± 0.3 mg GAE/g extract) and total flavonoid content (69.7 ± 3.37 μ g RE/g extract).

Total sugar, reducing sugar and non-reducing sugar of different varieties/ genotypes fruits of muskmelon were ranged from 309 to 553.27, 62.07 to 124.27 and 246.93 to 429 (mg/g on dry weight basis), respectively with values significantly lower in resistant varieties/ genotypes and higher in susceptible varieties/ genotypes. The pH was significantly highest in Arka Rajhans (6.56) and lowest in RM-50 (5.67). Tannins, phenols, total alkaloid and flavonoid contents ranged from 0.02 to 0.12 mg/g, 15.27 to 39.13 mg/g, 0.24 to 1.25 % and 0.40 to 1.05 mg/g, respectively with values significantly higher in resistant varieties/ genotypes and lower in susceptible varieties/ genotypes. Total sugar, reducing sugar, non-reducing sugar and pH of fruit had a significant positive correlation ($P = 0.01$) whereas, tannins, phenols, alkaloids and flavonoid contents had significant negative correlations with the percentage fruit infestation and the larval density per fruit (Figure 3) (Haldhar et al. 2013a; Bhargava et al. 2016).

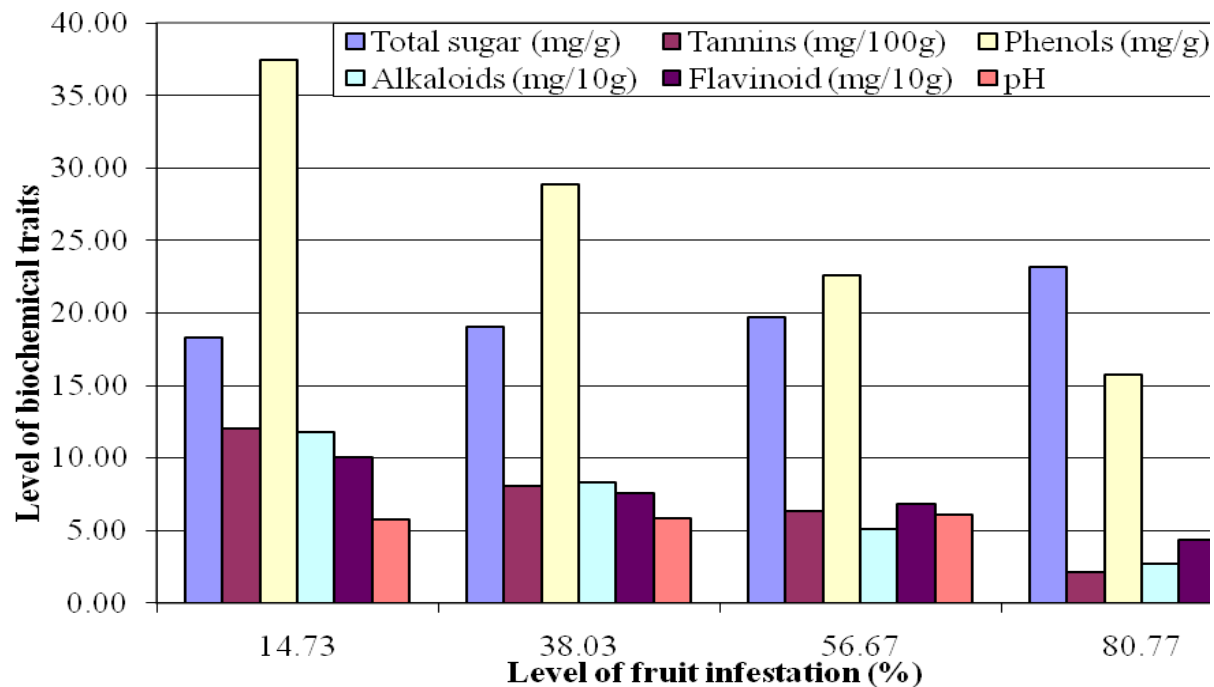


Fig. 3 Associations of biochemical traits with resistance to melon fruit fly infestation under different infestation categories (Haldhar et al. 2013)

Backward stepwise regression analysis indicated that total alkaloid and pH contents explained 97.96% of the total variation in fruit fly infestation. The maximum variation in fruit infestation was explained by total alkaloid contents (97%) followed by pH contents (0.96%), flavonoid (0.88%), total sugar (0.51%), phenols (0.32%), reducing sugar (0.18%), non-reducing sugar (0.10%) and tannins (0.01%) (Haldhar et al. 2013). Similar finding also incorporated that pH was lowest in resistant varieties/ genotypes and tannin, flavanol and phenol contents were highest in resistant varieties/ genotypes (Gogi et al. 2010). Similar to our findings, phenols, tannins, and flavonoids enhanced plant defences against insects (Tomas-Barberan et al. 1988; Mila & Scalbert 1994; Ryan & Robards 1998; Gogi et al. 2010).

Watermelon, *Citrullus lanatus* (Thunb.) Matsumara & Nakai

Watermelon (*Citrullus lanatus*) 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 have been associated with distinct cultivars and cultivated environments (Zhao 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 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 (Figure 4) (Haldhar et al. 2015b).

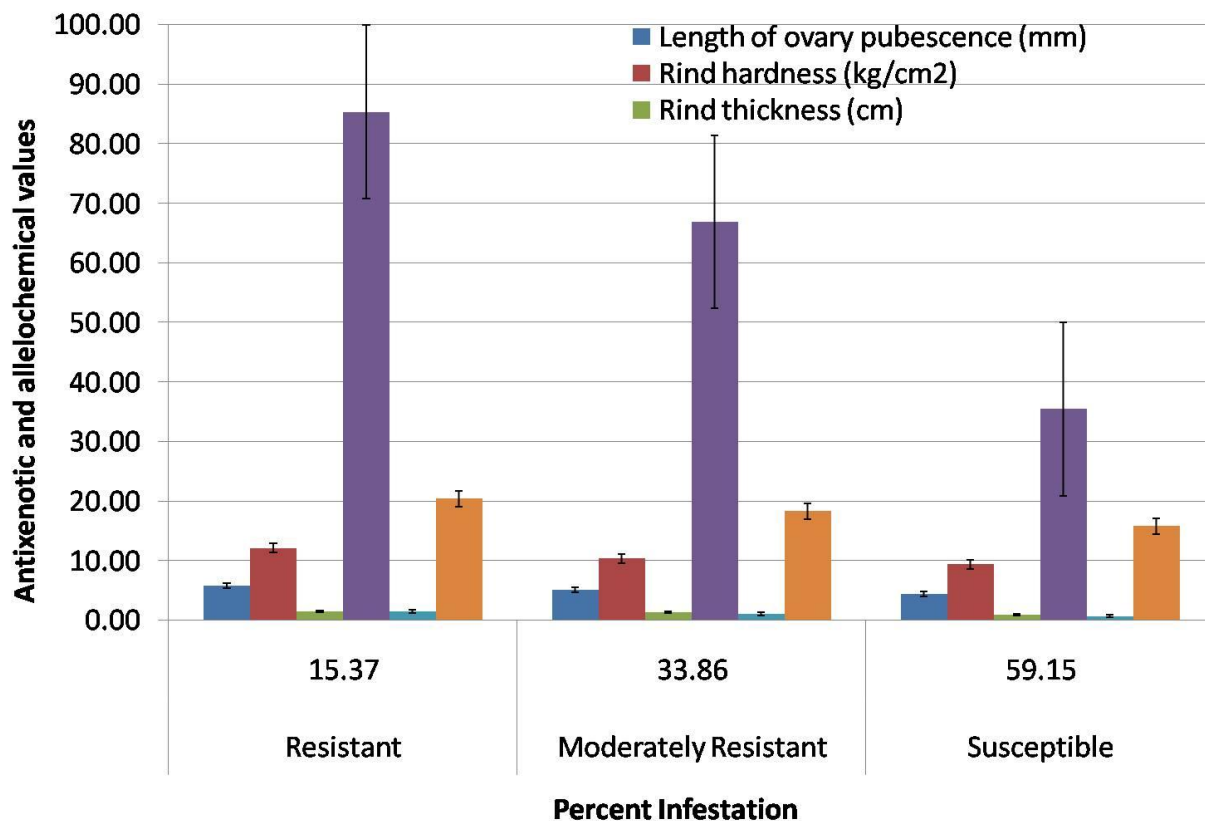


Fig. 4 Associations of major antixenotic and allelochemical fruit traits of watermelon with resistance to the melon fly evaluated by percentage fruit infestation under different infestation categories (Haldhar et al. 2015b).

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 (Haldhar et al. 2015b). Inheritance of resistance to the fruit fly was studied in intervarietal crosses of watermelon *C. lanatus* and two sources of resistance J 18-1

and J 56-1 were used. The resistance of watermelon to the fruit fly was controlled by a single dominant gene. The symbol *Fwr* has been proposed to denote the resistant gene (Khandelwal & Nath 1978). 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. Backward stepwise regression analysis indicated that flavonoid and total alkaloid contents explained 88.4% of the total variation in fruit fly infestation. 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%) (Haldhar et al. 2015b). 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. 2013a). Similar to our findings, it has been demonstrated that phenols, tannins, and flavonoids enhanced plant defenses against insects (Nath et al. 2017; Haldhar et al. 2018).

Ridge gourd [*Luffa acutangula* (Roxb.) L.]

Ridge gourd (*Luffa acutangula*) is an important warm season cucurbitaceous vegetable crop grown in different parts of India and in the tropical countries of Asia and Africa. Its immature fruits are cooked as vegetable and also used in the preparation of chutneys and curries. Being a warm season crop, it has the ability to tolerate hotter conditions, which makes it suitable for widespread cultivation throughout the tropics (Choudhary et al. 2014). Host plant selection by insects is either expressed 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). Direct defenses are mediated by plant characteristics that affect the herbivore's biology such as 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). The ridge gourd varieties/ genotypes; AHRG-57, Pusa Nasdar, and AHRG-29 were resistant; AHRG-35, Arka Sujata, AHRG-41, AHRG-36, S. Manjari, and S. Uphar were moderately resistant; AHRG-49, AHRG-33, AHRG-42, and AHRG-30 were susceptible whereas AHRG-47, and AHRG-31 were the highly susceptible varieties/ genotypes. Pooled data of larval density per fruit in both seasons (13.23- 28.5 larvae per fruit) was significantly lower in resistant and higher in susceptible varieties/ genotypes. The per cent fruit infestation was highest in AHRG-31 (79.72 %) and lowest in AHRG-57 (15.92 %) followed by AHRG-29 (17.67 %) (Haldhar et al. 2013c; Haldhar et al. 2015b).

The allelochemical compounds of fruit were significantly different among the tested ridge gourd varieties/ genotypes. The free amino acid was lowest in resistant and highest in susceptible varieties/ genotypes, whereas flavonoid, tannins, phenols, and ascorbic acid contents were highest in resistant and lowest in susceptible varieties/ genotypes (Haldhar et al. 2015). Total soluble solid and pH of fruit had a significant positive correlation whereas tannins, phenols, alkaloids and flavonoid contents had significant negative correlation

with the percentage fruit infestation and the larval density per fruit. The biochemical characters such as total sugar and crude protein were positively correlated with fruit borer infestation, whereas, total phenols had negative correlation (Sharma and Singh, 2010; War et al., 2012, Haldhar et al. 2013a). Basis on Kaiser Normalization method, two principal components (PCs) were extracted explaining cumulative variation of 90% in melon fruit fly infestation. The PC1 and PC2

were plotted and the plot showed four discrete classes of varieties genotypes which could be grouped into resistant (R), moderately resistant (MR) and susceptible (S) and highly susceptible (HS) as depicted in Figure 5 (Haldhar et al. 2015b). According to Gogi et al. (2010) maximum variation in fruit infestation was explained by tannin and flavanol contents whereas, rest of the biochemical fruit traits explained <0.2% variation in the fruit infestation.

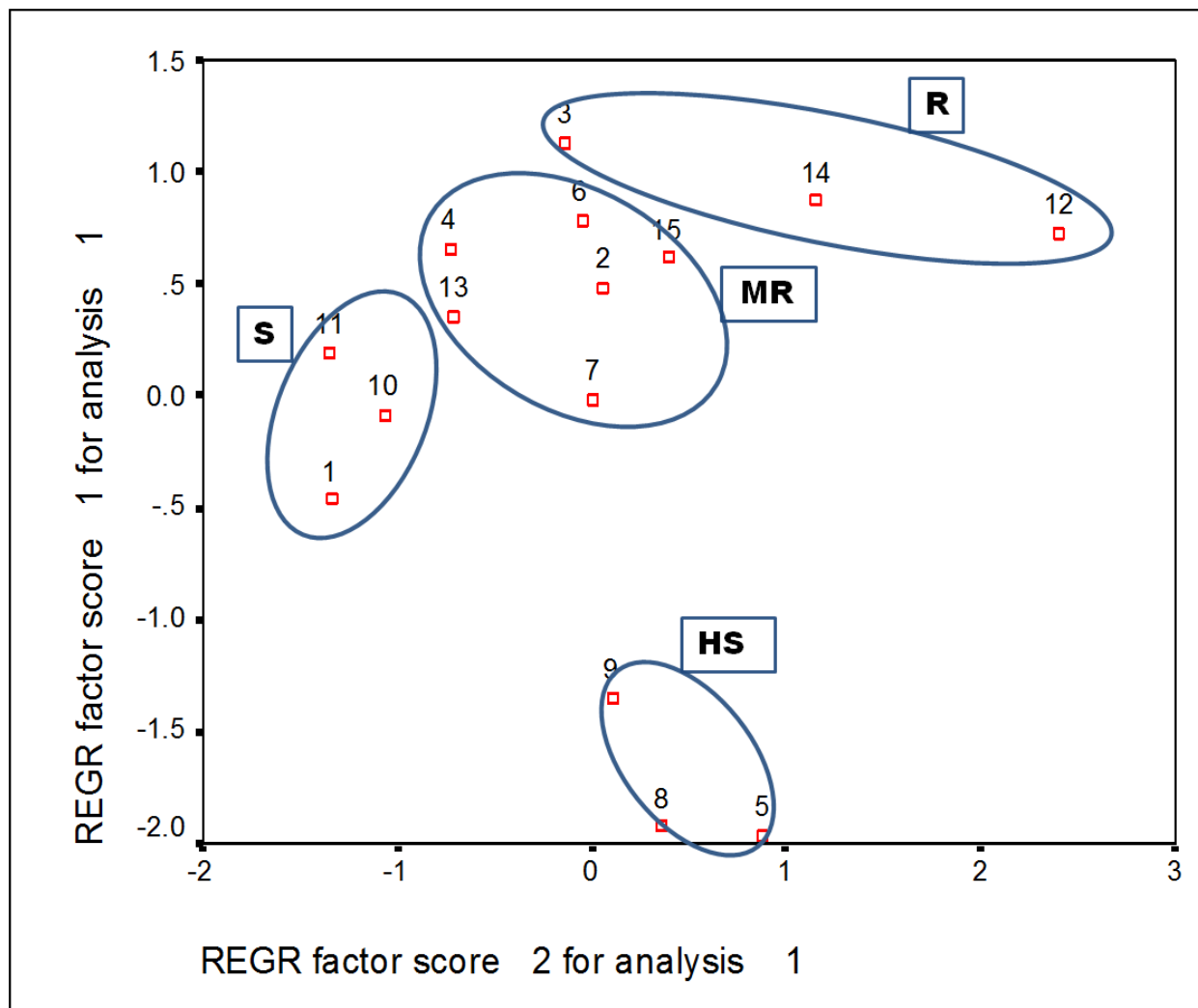


Fig. 5 Plot of PC1 and PC2 showing clusters of ridge gourd varieties/ genotypes showing resistance to melon fruit fly, *B. cucurbitae* (Haldhar et al., 2015).

Kachri, *Cucumis melo* var. *callosus*

Cucumis species is an important genus of cucurbitaceous vegetable crops and is widely grown for their fresh fruits at various stages. Kachri, a non-desertic form of *Cucumis melo* var. *callosus* is an under-exploited drought-hardy cucurbit vegetable of the Indian Thar Desert. Kachri is the Hindi name of the species, which is also known as mango melon in English, and as karkati in Sanskrit belongs to the family Cucurbitaceae which is a widely found in rainy season crop in arid and semi-arid regions of India (Samadia & Pareek 2000). A goal of many integrated pest management (IPM) researchers and practitioners has been to develop sustainable management programmes that are more resilient and less reliant on synthetic pesticides (Sharma & Ortiz 2002; Lin 2011; Bustos-Segura et al. 2017). The bottom-up effects in the crop plant is an economical and environment-friendly method of insect management. The attractive and beneficial feature of bottom up effect is that it is farmer friendly and does not need much financial investment for pest control. The identification and development of crop specific genotypes with resistance to pests is determined by the

nutrients and concentrations of secondary metabolites. Host plants play an important role in determining insect populations in respect to concentrations and proportions of nutrients and differ among species (Schoonhoven et al. 2005). The kachri genotypes IC-350933 and IC-373479 were found to be highly resistant; IC-350953, IC-351005, IC-351088, IC-258131 and DKS 2011/01 were found to be resistant whereas IC-351258, DKS 2011/02 and DKS 2011/03 were highly susceptible to melon fruit fly. The larval densities ranged from 4.87 to 15.50 larvae per fruit and were found to be significantly lower in resistant genotypes than in the susceptible genotypes. The larval density was the highest in genotype DKS 2011/03 (15.5 larvae/ fruit) followed by IC-351258 (15.3 larvae/ fruit). The minimum larval density was found in IC-370479 (4.9 larvae/ fruit) followed by IC-350933 (5.2 larvae/ fruit). The per cent fruit infestation was the highest in IC-351258 (76.9 %) and the lowest in IC-350933 (7.8 %) followed by IC-370479 (8.5 %). The fruit infestation ranged from 7.8 to 76.9 % which was significantly lower in resistant genotypes and higher in susceptible genotypes (Figure 6) (Haldhar et al. 2017a).

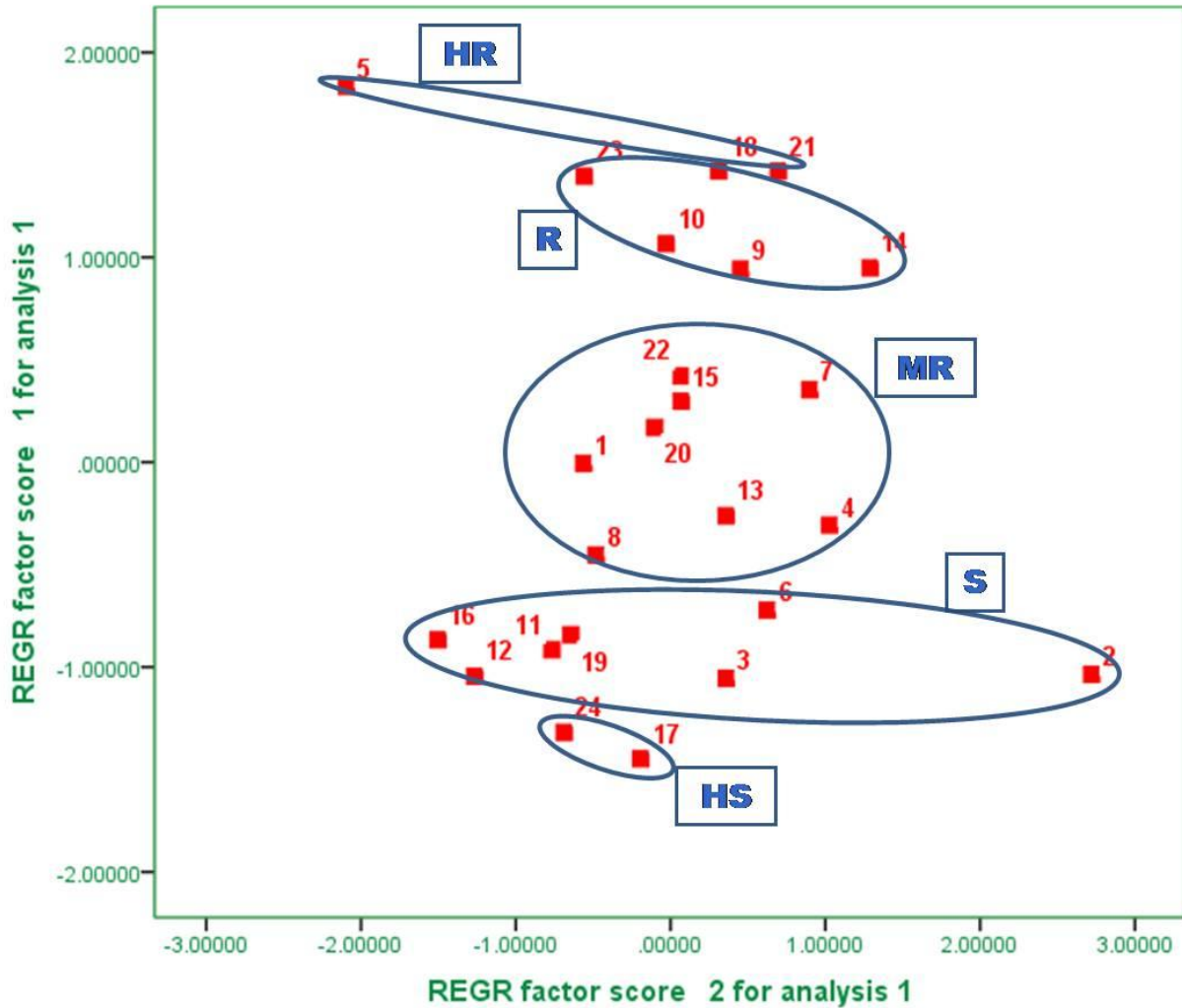


Fig. 6 Plot of PC1 and PC2 showing clusters of kachri, *C. melo* var. *callosus* genotypes show resistance to melon fruit fly, *B. cucurbitae* (Haldhar et al. 2017).

The allelochemical compounds of the fruit differed significantly among the tested kachri genotypes. The flavonoid, tannins, phenols, and total alkaloid contents were the highest in resistant and lower in susceptible genotype of kachri. The percentage of fruit infestation and the larval density per fruit with flavonoid (-0.955 & -0.938), tannins (-0.891 & -0.902),

phenols (-0.903 & -0.896) and total alkaloid (-0.797 & -0.759) had significant negative correlation. Backward stepwise regression analysis indicated that flavonoid and tannins contents explained 93.6% of the total variation in fruit fly infestation. The maximum variation in fruit infestation was explained by flavonoid content (91.2%) followed by tannins (2.4%),

phenols (0.4%), and total alkaloid contents (0.1%) (Haldhar et al. 2017a). Phenols act as a defensive mechanism not only against herbivores but also against microorganisms and competing plants. Tannins, Flavonoids and isoflavonoids protect the plant against insect-pests by influencing the behavior, growth, and development of insects (Simmonds 2003, Barbehenn & Peter 2011). Similar to our findings, it has been demonstrated that phenols, tannins, and flavonoids enhanced plant defenses against insects and had a significant negative correlation with the percentage fruit infestation and the larval density per fruit (Sharma & Singh 2010; War et al. 2012; Haldhar et al. 2013a; Haldhar et al. 2015b; Haldhar et al. 2016b). Based upon the above biochemical characters individually it was impossible to group the entries as variables were not in agreement with each other. Hence, principal component analysis was performed to achieve parsimony and reduce the dimensionality by extracting the smallest number of components that accounted for most of the variation in the original multivariate data. Four principal components (PCs) were extracted with eigenvalue ≥ 1.0 , after varimax rotation with Kaiser Normalization procedure which converged in three iterations. The extraction communalities for all the variables tested were ≥ 0.5 indicating that the variables were well represented by the extracted PCs which together explained a cumulative variation of 88.2 %. PC1 explaining 71.6 % of the variation while PC2 explained 16.6 % of the variation. PC1 had the loadings for flavonoid content (0.92), tannins content (0.94), the total

alkaloid (0.86) and phenols content (0.96) (Haldhar et al. 2017). Gogi et al. (2010) indicated that the maximum variation in percentage fruit infestation was explained by tannin and flavanol contents whereas maximum variation in larval density per fruit was explained by tannin followed by flavanol contents.

Future work

Although host plant resistance has attained a considerable momentum recently, and has attracted the attention of scientists in evolutionary ecology, entomology, plant physiology, and biotechnology, much of the underlying mechanism have still remained unanswered. There is a need to understand the insect specific signal molecules, their identification, mode of action, and further signal transduction pathway. Since a single attribute can affect the insects and/or natural enemies positively and/or negatively, understanding of the multitrophic interactions is important to know the consequences of supposed defensive traits of a plant for use in pest management. Since the biochemical pathways that lead to induce resistance are highly conserved among the plants and elicitors of these pathways could be used as inducers in many crops. The future challenge is to exploit the elicitors of induce defense in plants for pest management, and identify the genes encoding proteins that are up and/or down regulated during plant response to the insect attack, which can be deployed for conferring resistance to the insects through genetic transformation.

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