



Plant-insect interaction in underutilized horticultural crops for sustainable production

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Summary

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 can recognise the non-self-molecules or signals from damaged cells, much like animals. It activates the plant's immune response against the herbivores. Differences in genotypes of plant characters may affect insect-plant herbivore interactions, and variations in genotype traits are responsible for modifying the bottom-up effects. Recent evidence shows that the simultaneous occurrence of abiotic and biotic stress can positively affect plant performance by reducing the susceptibility to biotic stress, a positive sign for pest management. Plant responses to these stresses are multifaceted and involve copious antibiosis, physiological, antixenotic, molecular, molecular and cellular adaptations. Plants with antibiosis characteristics such as flavonoids, phenols, tannins, alkaloids, etc., may cause reduced insect survival, prolonged development time, decreased size and reduced new generation fitness. Quality and quantity of constitutive secondary metabolites production is species and cultivar specific and can be expressed as the signature of a particular plant or species and leads to the phenomenon of host-plant resistance. Hence, such plant resistance mechanisms have been effectively and widely used for managing insect pests in fields of underutilized crops. Natural defences are mediated through plant characteristics that affect insect biology, such as mechanical protection on the surface of the plants (*e.g.*, hairs, trichomes, thorns, spines and thicker leaves) that either kill or retard the development of the herbivores. These phenomena of host plant resistance to insects can be exploited for the development of resistance crop cultivars which readily produce the inducible response upon mild infestation and can perform as one of the integrated pest management for sustainable crop production.

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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 that can recognize the non-self-molecules or signals from damaged cells, much like animals. It activates the plant's immune response against herbivores. Plant-arthropod interactions are of utmost importance for understanding the dynamics of ecological communities^{1,2,3}. Plant defense strategies against insect herbivores may involve synthesizing many biologically active compounds (allelochemicals), which are

phylogenetically conserved in specific plant families or genera. Plants frequently display genetic variation within and between populations for traits that influence the preference and non-preference of insects on their hosts, which is resistance traits⁴. It has been widely recognised that biological diversity plays a vital role in structuring community ecosystem processes. The genotypic variation may influence the distribution and damage levels of herbivores on focal plants through processes referred to as associational resistance or susceptibility (Table 1). Host plants play an essential role in determining insect populations with respect to concentrations and proportions of nutrients, which differ among species. Plants having antibiosis characteristics such as flavonoids, phenols, tannins etc., may cause reduced insect survival, prolonged development time, decreased size and reduced fitness of new generation adults^{5,6}. Several plant characteristics affect the growth and development of arthropods. The plants defend against the attack by pests by producing defensive biochemical compounds for the whole plant system⁷.

Plants are generally exposed to various biotic and abiotic factors that may alter their genotypic and phenotypic properties resulting in different mechanisms

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of resistance which enable plants to avoid, tolerate or recover from the effects of pest attacks. Host plants are essential in determining insect populations concerning concentrations and proportions of nutrients, which differ among species. Natural 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 thicker leaves) that retard the development of the herbivores^{8,9}. Antixenosis refers to the potential plant characteristics/traits or morphological that impair or alter insect behaviour towards the host preference in such a way as to lessen the chances of insects using a host plant for oviposition food, damage or shelter¹⁰.

Table 1. Different genotypes of underutilized horticulture crops resistant to insect-pests in arid and semi-arid regions of India

S. No.	Crop name	Insect species	Resistance genotypes	References
1.	Ber, <i>Z. mauritiana</i>	Stone weevil, <i>A. imalayanus</i>	Resistant: Kali, Katha, Illaichi and Tikadi Moderately resistant: Akharota, Dandan, Gola, Goma Kirti, Sanaur-1, Seb, Umran and ZG-3	11
2.		Fruit fly, <i>C. vesuviana</i>	Resistant: The ber cultivars such as Tikadi, Katha and Illaichi Moderately resistant: BS-75-1, Safeda, Dandan, Gola, Goma Kirti, Jogia, Narma, Mundia, Reshmi, Seb, ZG-3, Umran and Akharota	2
3.		Fruit borer, <i>M. scyroides</i>	Resistant: Safeda, Tikadi, Darakhi and Illaichi Moderately resistant: BS-75-1, Gola, Goma Kirti, Seb and Umran	12
4.	Indian Cherry, <i>C. myxa</i>	Tingid bug, <i>D. cheriani</i>	Resistant: AHCM-22, AHCM-25 and AHCM-34 Moderately resistant: AHCM-14, AHCM-30 and AHCM-31	13
5.	Jamun, <i>S. cumini</i>	Fruit borers, <i>M. scyroides</i> and <i>D. aprobola</i>	Resistant: GJ-26, GJ-27, GJ-19, GJ-17 and GJ-15 Moderately resistant: GJ-3, GJ-6, GJ-7, GJ-9, GJ-13, GJ-16, GJ-18, GJ-20, GJ-23, GJ-24 and GJ-25	14
6.	Datepalm, <i>P. dactylifera</i>	Fruit borers, <i>B. amydraula</i> and <i>A. sabella</i>	Resistant: Migra, Tayer, Javantri and Medjool	15
7.	Pomegranate, <i>P. granatum</i>	Mite, <i>T. punicae</i>	Resistant: HP Collec., Speen Sacarin, Gule Shah Rose Pink and AHPG-C3 Moderately resistant: Sur Sukker, Tujetis EC 4347, Bassin Seedless, Dholka, Uthkal, Agah, Achik Dana and Goma Khata	16
8.	Snampmelon, <i>C. melo</i> L. var. <i>momordica</i>	Fruit fly, <i>B. cucurbitae</i>	Resistant: IC-430190, DKS-AHS 2011/4, and DKS-AHS 2011/3 Moderately resistant: IC-430160, IC-430162, IC-430175, IC-430179, IC-430180, IC-430185, IC-369788, and DKS-AHS 2011/2	17
9.	Musk melon, <i>C. melo</i>	Fruit fly, <i>B. cucurbitae</i>	Resistant: AHMM/BR-1, RM-50 and AHMM/BR-8 Moderately resistant: MHY-5, D. Madhu and P. Sarabati	6
10.	Watermelon, <i>C. lanatus</i>	Fruit fly, <i>B. cucurbitae</i>	Resistant: Asahi Yamato, Thar Manak, and AHW/BR-16 Moderately resistant: AHW/BR-12, Arka Manik, Charleston Grey, AHW-65, AHW-19, Sugar Baby, and Durgapura Lal	18
11.	Ridge gourd, <i>L. acutangula</i>	Fruit fly, <i>B. cucurbitae</i>	Resistant: AHRG-57, Pusa Nasdar, and AHRG-29 Moderately resistant: AHRG-35, Arka Sujata, AHRG-41, AHRG-36, S. Manjari, and S. Uphar	20,19
12.	Kachri, <i>C. melo</i> var. <i>callosus</i>	Fruit fly, <i>B. cucurbitae</i>	Highly resistant: IC-350933 and IC-373479 Resistant: IC-350953, IC-351005, IC-351088, IC-258131 and DKS 2011/01	21

Hence, such plant resistance mechanisms have been effectively and widely used for managing insect pests in horticultural crops^{10,18,21,22}. The utilization of native and introduced genetic material of arid horticulture crops for breeding varieties over a long period in the country resulted in the generation of many new genotypes/ lines in the form of selections and, to some extent, through hybridization. Thereby, considerable generated material/ variations may have existed in targeted species regarding the plant type, flowering, fruiting,

morphological and physiological of fruits, reaction to biotic and abiotic factors and eco-adaptations. Since the detailed evaluation of identified genotypes is essential for further breeding programme and incorporating desirable gene(s) through combination breeding. Wild and relative species gene pool possesses unique traits that can be exploited by direct selection for use in combination breeding or improvement through advanced approaches. They also constitute priceless reservoirs that contain gene (s) conferring better adaptations to

stressed environments and also resistant to diseases and insects or have more nutritional and medicinal properties. Therefore, there is an urgent need to promote the systematic utilization of a wild gene pool in strategic breeding work for developing genotypes having biotic and abiotic stress resistance or tolerance and their conservation as relative species^{23,24}. This manuscript reviewed major underutilized horticultural crops for the morphological and biochemical basis of plant-insect interaction.

1. Ber, *Ziziphus mauritiana* Lamark

The ber, *Ziziphus mauritiana*, is native to the Province of Yunnan in southern China to Afghanistan, Malaysia and Queensland, Australia. It is native to South and Central Asia, found throughout the arid and semi-arid tracts. It is cultivated to some extent throughout its natural range on a commercial scale and has received much horticultural attention in India. *Z. mauritiana* is a gregarious spiny shrub or a small tree ends of branches curved or drooping. Branches and branchlets armed with short stipular spines. The plant is a vigorous grower and has a rapidly-developing taproot. The richness of the pulp in nutritive compounds has been widely recognised. Nonetheless, there are no absolute values for pulp composition. However, ber is a richer protein, phosphorus, calcium, carotene and vitamin C source. The crop is gaining popularity among growers because of its adaptability to adverse climatic conditions and reasonable yield returns. The crop suffered significant losses due to insect pests and diseases, and more than 130 insect pests were found to attach the crops in India. Balikai et al. (2013)²⁵ reported 22 insect and non-insect species; likewise, Kavitha and Savithri (2002)²⁶ documented about 23 insect species on ber.

Stone weevil, *Aubeus himalayanus* resistance study

The ber stone weevil, *Aubeus himalayanus* Voss (Coleoptera: Curculionidae), appeared to be an emerging pest reported from various regions of India (Karuppaiah et al. 2015; Haldhar et al. 2012; Haldhar et al. 2016a)^{27,28,29}. The stone weevil is an emerging threat to beer production in India, especially in Northern India. The ber varieties/ genotypes Kali, Katha, Illaichi and Tikadi were found to be resistant; Akharota, Dandan, Gola, Goma Kirti, Sanaur-1, Seb, Umran and ZG-3 moderately resistant; Badami, Banarasi Karaka, Gularvasi, Jogia, Kaithli, Mundia, Reshmi, Sanaur-3, Thar Bhubhraj, Thar Sevika and Thornless susceptible and Banarsi Pebandi, Chhuhara, Sanaur-2, Sanaur-4 and Sanaur-5 highly susceptible varieties/ genotypes against stone weevil (Haldhar et al. 2018c). The per cent fruit infestation was found highest in Sanaur-2 (49.44 % in retained fruit and 73.77 % in dropped fruits) and the lowest in Tikadi (8.80 % in retained fruits and 13.31 % in fallen fruits), followed by Katha (9.07 % in retained fruits and 13.71 % in dropped fruits). Plant-arthropod interactions are thought to be of utmost importance for understanding the dynamics of ecological communities. Plant defense strategies against insect herbivores may involve synthesizing many biologically active compounds (allelochemicals), which are phylogenetically conserved in specific plant families or genera. Plants frequently display genetic variation within and between populations for traits that influence

the preference of insects on their hosts, that is, resistance traits (Johnson & Agrawal 2005; Haldhar et al. 2013c)^{4,20}.

Tannins, phenols, alkaloids and flavonoid contents had significant negative correlations ($P = 0.01$) with the percentage of fruit infestation on plant fruits and fallen fruits. The antixenotic fruit traits like fruit surface, stone hardness and pulp: the stone ratio was observed for different varieties/ genotypes of ber. The pulp: stone ratio ranged from 2.12 to 27.13. It was significantly high in susceptible and low in resistance varieties/ genotypes—the highest pulp: the stone ratio was found in variety Mundia and least in variety Tikadi. Most resistant varieties had extremely hardy stones, and in susceptible varieties, the stones were slightly hard (Haldhar et al. 2018c)¹¹. Based upon the above morphological and biochemical characters individually, grouping the entities as variables did not agree was impossible. 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 90.75 %. PC1 explained 70.74 % of the variation, while PC2 explained 20.01 %. PC1 had the loadings for flavonoid content (0.91), tannin content (0.71), total alkaloid (0.93) and phenols content (0.95). Pulp: stone ratio of different varieties of ber (0.96) was loaded in PC2 (Haldhar et al. 2018c)¹¹.

Fruit fly, *C. vesuviana* resistance study

The fruit fly, *Carpomyia vesuviana* Costa, is India's most destructive pest of ber. It is a monophagous pest that infests *Zizyphus* species only and contributes towards low-yield and poor-quality fruits (Haldhar et al. 2013b; Haldhar et al. 2016a; Dhileepan 2017)^{29,30,31}. The fruit fly causes yield losses of up to 80% under severe infestation when no control measures as taken. The ber 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 the fruit fly, *C. vesuviana* in both the studied seasons (Haldhar et al. 2018a)². Hosagoudar et al. (1999)³² reported that fruit fly, *C. vesuviana* infestation was high in the cultivar Sanaur-2, followed by Umran and Sanaur-6 and the lowest infestation 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 flavonoids (-0.914), tannins (-0.914) and phenols (-0.947) had a significant negative correlation (Haldhar et al. 2018a)². 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. 2018a)². Phenolic heteropolymers play a central role in plant defense against insects and pathogens. Phenols also play an essential role in the 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)³³. Phenols act as a defensive mechanism against herbivores but also against microorganisms and competing plants. Tannins, flavonoids and isoflavonoids protect the plant against insect pests by influencing insect behaviour, growth, and development (Nath et al. 2017)³⁴. Two principal components (PCs) were extracted, explaining the cumulative variation of 84.7% in ber fruit fly infestation. The fruit length, width, pericarp thickness and pulp: stone ratio ranged from 17.2 to 43.2 mm, 12.8 to 33.4 mm, 0.3 to 1.2 mm and 2.1 to 27.1, respectively. The resistant germplasm accession Tikadi, Katha and Illaichi had pulp texture (hard) and fruit surface (ridge and plain) high in resistant and low in susceptible cultivars. The pericarp thickness (-0.85) had significant negative correlations, and the pulp: stone ratio (0.47) and fruit length (0.42) had a significant positive correlation with the percentage of fruit infestation. The maximum variation in fruit infestation was explained by fruit length (1.90%) followed by pulp: stone ratio (1.60%) and pericarp thickness (0.20%), whereas the remaining biophysical fruit traits explained < 1.0% variation in the fruit infestation (Haldhar et al. 2018a)².

Fruit borer, *Meridarchis scyrodes* resistance study

The ber genotypes under study indicated significantly low incidence of fruit borer, *M. scyrodes* in Safeda (13.27%) followed Tikadi (14.01%). Significantly greater incidence of fruit borer was registered in Sanaur-5, Chhuhara and Sanaur-2 with a magnitude of 75.09, 72.90 and 71.78 %, respectively. Basis of fruit borer, *M. scyrodes* incidence; Safeda, Tikadi, Darakhi and Illaichi were considered as resistant; BS-75-1, Gola, Goma Kirti, Seb and Umran were found moderately resistant; Dandan, Mahawali, Jogia, Sukavani, Narma, Reshmi and ZG-3 were found to be susceptible whereas, Banarasi Karaka, Banarasi Pawandi, Chhuhara, Kaithali, Mundia, Sanaur-2 and Sanaur-5 were highly susceptible to fruit borer (Haldhar et al. 2023)¹². The quality and quantity of resources available for plants triggers on plant-insect herbivore interaction, *i.e.*, plants are affected by environmental factors, which in turn influence the performance of insect herbivores (Han et al. 2016)¹. However, the bottom-up effects are highly variable and may depend on both biotic and abiotic factors, such as plant genotypes (Haldhar et al. 2017a)²¹, insect feeding strategy (Inbar et al. 2001)³⁵, feeding specialization (Gulbrodt et al. 2011)³⁶, resource type (Inbar et al. 2001)³⁵ and environmental stress intensity (Mody et al. 2009)³⁷. Different studies have shown that genotypes of the same species could differ significantly in their resistance to insects (Vir et al. 2015)³⁸ and it is influenced by morphological and biochemical traits of

plants (Visschers et al. 2019)³⁹. Hosagoudar et al. (1999)³² reported that fruit fly infestation was high in cultivar Sanaur-2 followed by Umran and Sanaur-6, and the lowest infestation was recorded in Illaichi.

The percentage of fruit infestation with flavonoid (-0.95), tannins (-0.95) and phenols (-0.96) had a significant negative correlation. The resistant genotypes Safeda, Tikadi and Darakhi had pulp texture (hard) and fruit surface (ridge and plain), high in resistant and low in susceptible genotypes. The pericarp thickness (-0.88) had significant negative correlations, and pulp: stone ratio (0.77) and fruit length (0.49) had significant positive correlations with percentage fruit infestation (Haldhar et al. 2023)¹². Tannic acid and gossypol in cotton have deleterious effects on *A. gossypii* and when concentrations increase, the mortality of cotton aphid (Ma et al. 2019)⁴⁰.

2. Tingid bug resistance study in Indian Cherry (*Cordia myxa* L.)

Cordia myxa L., commonly called Indian cherry (synonyms: clammy cherry, fragrant manjack, lasora, shell, cinnanakkeru, bahubara, chokri, lahsoda, lahsua, gonda, gondi), belongs to Boraginaceae family. This tree is a multipurpose species distributed in hot arid, and semi-arid regions of India, and it originated in the North-Western part of the country. Few studies were made on the bug *D. cheriani* infestation on *Cordia sp.* (India) and the bug *D. monotropidia* infestation on *Cordia verbenacea* (Brazil). AHCM-22, AHCM-25 and AHCM-34 were found to be resistant; AHCM-14, AHCM-30 and AHCM-31 moderately resistant; AHCM-16 and AHCM-09 moderately susceptible; AHCM-33 and AHCM-08 susceptible and AHCM-01 and AHCM-26 highly susceptible germplasm accessions of Indian cherry against tingid bug (Haldhar et al., 2019)¹³.

The allelochemical compounds of the leaf were significantly different among the tested germplasm accessions of Indian cherry. The flavonoid content was positively correlated to tannins, phenols, and total alkaloid content. The negative correlations were observed with the per cent bug infestation, bug density per leaf and free amino acid (Haldhar et al., 2019)¹³. Isoflavonoids (judaicin, judaicin-7-*O*-glucoside, 2-methoxyjudaicin, and maackiain) isolated from the wild relatives of chickpea acted as antifeedant against *Helicoverpa armigera* (Hubner) at 100 ppm. Judaicin and maackiain were also found to be deterrents to *S. littoralis* and *S. frugiperda*, respectively. The tannin content of tested germplasm accession was the maximum in AHCM-22, followed by AHCM-25 and the minimum was found in AHCM-01. The negative correlation was observed with per cent bug infestation, bug density per leaf and free amino acid and positive correlations with flavonoid content, phenols content and total alkaloid content. Tannins had a robust deleterious effect on phytophagous insects, affecting insect growth and development by binding to the proteins, reducing nutrient absorption efficiency, and causing midgut lesions (Barbehenn & Peter Constabel 2011)⁴¹.

The maximum length of the leaf was found in AHCM-22 followed by AHCM-25 and minimum in AHCM-01, and

the high length in resistant and the minimum length in susceptible germplasm accession. A positive correlation was observed between the length and the leaf's width, and negative correlations with the per cent bug infestation and bug density per leaf. The maximum width of the leaf was recorded in AHCM-14 and the minimum in AHCM-26. A negative correlation was observed between the width of the leaf and the per cent bug infestation and bug density per leaf. The resistant germplasm accession of Indian cherry (AHCM-22, AHCM-25 and AHCM-34) had the maximum leaf size, high rough and hairy (Haldhar et al. 2019)¹³. The first line of plant defense against insect pests is the erection of a physical barrier either through forming a waxy cuticle and developing spines, setae, and trichomes (Sharma et al. 2009)⁴². One principal component (PC) was extracted based on the Kaiser Normalization method, explaining the cumulative variation of 90.07% in tingid bug infestation. PC had the loadings for flavonoid content (0.99), tannins content (0.97), total alkaloid (0.99), phenols content (0.88), free amino acid (-0.96), leaf length (0.90) and leaf width (0.86) (Haldhar et al. 2019)¹³.

3. Fruit borers, *Meridarchis scyrodes* and *Dudua aprobola* resistance study in jamun (*Syzygium cumini*)

The jamun is native to India, Burma, Ceylon and the Andaman Islands and available throughout Indian plains as well as in Kumaon hills up to 1,600 m. It is widely distributed in Sri Lanka, the Philippines, Malaysia, Thailand and Australia. The jamun, *Syzygium cumini* Skeels (*Eugenia jambolana*), has vernacular English names such as Jaman, black plum, damson plum, duhat plum and Indian blackberry. It is nutritive fruit with a variety of uses. Both urban and rural peoples have utilized every part of the tree. The jamun fruit has a sub-acid spicy flavour, and squash is a refreshing drink for quenching the thirst in the summer. A small quantity of fruit syrup is much useful for curing diarrhoea. The vinegar prepared from the juice of the slightly unripe fruit of jamun is stomachic, carminative, diuretic, cooling and digestive properties. The fruit borer, *Meridarchis scyrodes* (Lepidoptera: Carposinidae), is a serious pest of jamun. The moths lay eggs on fruits at the pea stage, and upon hatching, the newly emerged caterpillars bore into fruits, feed on the near pulp seed, and accumulate faecal. The borer causes up to 60% yield loss under severe infestation. The leaf roller, *Dudua aprobola* (Lepidoptera: Tortricidae), is reported to be a major pest of jamun in Rajasthan and Gujarat. It mainly damaged tender leaves and inflorescence, but has recently been damaged to fruits of jamun. Eggs were laid in axils of leaves or flowering stalks or on fruits. GJ-26, GJ-27, GJ-19, GJ-17 and GJ-15 were found to be resistant; GJ-3, GJ-6, GJ-7, GJ-9, GJ-13, GJ-16, GJ-18, GJ-20, GJ-23, GJ-24 and GJ-25 moderately resistant; GJ-4, GJ-8, GJ-10, GJ-12, GJ-14, GJ-21 and GJ-22 were susceptible and GJ-1 and GJ-GJ-11 highly susceptible genotypes. The per cent fruit infestation of fruit borer, *M. scyrodes*, was highest in genotype GJ-1 (64.70%) followed by GJ-11 (62.07%). The minimum per cent fruit infestation of fruit borer, *M. scyrodes*, was observed in GJ-27 (8.23%), followed by GJ-17 (10.03%). The per cent infestation of *D. aprobola*

was highest in GJ-1 (76.30 %) and lowest in GJ-27 (10.80 %), followed by GJ-26 (11.13 %) (Haldhar et al., 2016c)¹⁴.

The allelochemical compounds of the fruit differed significantly among the tested jamun genotypes. Tannins, phenols, total alkaloids and flavonoids had significant negative correlations with per cent fruit infestation of fruit borer, *M. scyrodes* and *D. aprobola* (Haldhar et al., 2016c)¹⁴. In wild cabbage (*Brassica oleracea*), the concentrations of glucosinolates, which are secondary metabolites acting as chemical defences to insects, increased from summer to winter (Gols et al. 2018)⁴³. Other plant secondary metabolites such as methyl-ketones and sesquiterpene carboxylic acid derivatives could negatively affect insect pests' population development. Phenol compounds also play the leading role in the cyclic reduction of reactive oxygen species such as superoxide anion and hydroxide radicals, H₂O₂, and singlet oxygen, which turn, activate a cascade of reactions leading to the activation of defensive enzymes (Maffei et al. 2007)³³. Tannins, flavonoids and isoflavonoids protect the plant against insect pests by influencing insect herbivores' behaviour, growth, and development (Barbehenn & Peter 2011; Nath et al. 2017)^{34,41}.

The antixenotic fruit traits were significantly different among the tested jamun genotypes. The fruit length, fruit width, pulp thickness and pulp: stone ratio were found to be minimum in the GJ-27 genotype, but maximum fruit length in GJ-4, fruit width in GJ-8, pulp thickness in GJ-11 and pulp: stone ratio in GJ-11 and GJ-24 genotypes, respectively. The fruit length, width, pulp thickness and pulp: stone ratio showed significant positive correlations with the per cent fruit infestation of fruit borer, *M. scyrodes* and *D. aprobola* (Haldhar et al., 2016c)¹⁴. Glandular trichomes secrete secondary metabolites, including flavonoids, terpenoids, and alkaloids, that could be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defence (Sharma et al. 2009)⁴². Pramanick et al. (2005)⁴⁴ reported that the genotypes differed for all the physical and biochemical traits indicating divergence for them. The genotypic coefficient of variation (GCV) ranged from 65.4 to 8.4 per cent in the biological and biochemical characteristics, respectively. Structural traits such as spines and thorns, trichomes, toughened or hardened leaves, incorporation of granular minerals into plant tissues, and divaricated branching (shoots with wiry stems produced at wide axillary angles) played a leading role in plant protection against herbivory.

4. Datepalm (*Phoenix dactylifera* L.) genotypes screening against fruit borers, *Batrachedra amydraula* and *Arenipses sabella*

Many arthropod species are known as pests of the date palm (*Phoenix dactylifera* L.) worldwide. Carpenter & Elmer (1978)⁴⁵ reported on more than 50 species of insects and mites as pests of date palms in worldwide. In Israel, approximately 25% of these species of insects and mites are considered serious pests. The most dominant and economically important pests are scale insects (*Parlatoria blanchardii*, and *Phoenicococcus marlattii*), a mealy bug (*Dysmicoccus brevipes*), the lesser date moth (*Batrachedra amydraula*), greater date moth (*Arenipses*

sabella), red palm weevil (*Rhynchophorus ferrugineus*), rhinoceros beetle (*Oryctes rhinoceros*) and the termite, *Psammodermes hypostoma* (Blumberg 2008; Haldhar et al. 2015d)^{46,47}. The lesser date moth (*Batrachedra amydraula* Myer) is a pest that damages fruits in both fields and stores (Dowson 1982)⁴⁸.

A total of 32 date palm varieties/ genotypes were evaluated for screening against the fruit borers in hot arid region. The results showed that the percentage of fruit infestation of fruit borers, *B. amydraula* and *A. sabella* on tested varieties/ genotypes of datepalm varied significantly. Pooled data showed that the Migra, Tayer, Javantri and Medjool were found highly tolerant varieties/ genotypes with fruit infestation (5.32%, 8.40%, 8.40%, 8.78% of *B. amydraula* and 4.33%, 5.27%, 5.62%, 5.52% of *A. sabella*, respectively). Whereas, the varieties/ genotypes Zahidi, Suriya, Khasab and Khuneizi had fruit infestation (29.88%, 28.33%, 28.27%, 27.05% of *B. amydraula* and 20.67%, 19.83%, 17.40%, 19.95% of *A. sabella*, respectively) and declared as highly infestation varieties/ genotypes to the fruit borers. Lower values of host plant susceptibility indices based on fruit infestation (HPSI) were recorded on resistance varieties/ genotypes, Migra, Tayer, Javantri and Medjool (31.63%, 49.97%, 49.97%, 52.25% of *B. amydraula* and 40.16%, 48.81%, 52.05%, 51.13% of *A. sabella*, respectively) which could be used as a source of resistance for developing date palm varieties/ genotypes resistant to fruit borers (Haldhar et al. 2021)¹⁵. Faleiro et al. (2014)⁴⁹ revealed that the popular date palm cultivar Khalas had the least antixenotic effect on female RPW adults where a high degree of attraction to palm tissue volatiles was recorded, which was statistically similar to the cultivars Reziz, Sheshi and Hatmi. The cultivars Khasab, Shahal and Gaar exhibited high degree of non-preference (antixenosis). Further, Reziz registered the highest egg lay by red palm weevil and was statistically on par with the cultivars Khalas and Sheshi. Similar and non-significant values for egg hatch and larval tunneling in the cultivars tested indicate no antibiotic effects against RPW in the 7 date palm cultivars. The studies carried out in Qatar (Elmeer et al. 2011)⁵⁰ using new microsatellite markers to assess the genetic diversity among 10 major date palm cultivars (including 5 from our study) revealed 2 distinct groups. Among the cultivars we studied for resistance to RPW, the report from Qatar placed Khalas, Sheshi and Reziz in one cluster of the 6 cultivars while the cultivars Khasab and Shahal in another cluster of 4 cultivars. Since seedling date palms are the original source of most of the present well-established cultivars (Johnson et al. 2013)⁵¹, the RPW susceptible (Khalas, Sheshi and Reziz) and resistant cultivars (Shahal and Khasab) may have evolved from 2 separate seeding date palm progenies with distinctly different genes for resistance to RPW.

It was observed that the genotype Zahidi showed maximum HPSI based on fruit infestation *i.e.*, 177.77% followed by Suriya showing 168.55 % HPSI against fruit borer, *B. amydraula*. The minimum HPSI based on fruit infestation was 31.63% for Migra, which was a tolerant genotype followed by Tayer (49.97% HPSI) against fruit

borer, *B. amydraula*. HPSI was observed that the genotype Zahidi showed maximum HPSI based on fruit infestation *i.e.*, 191.54% followed by Khuneizi showing 184.89 % HPSI against fruit borer, *A. sabella*. The minimum HPSI based on fruit infestation was 40.16% for Migra which was found to be tolerant genotype followed by Tayer (48.81% HPSI) against fruit borer, *A. sabella*. On the basis of percent fruit infestation, the highest HPSI was recorded in Zahidi categorized as highly susceptible to fruit borers and lowest HPSI was found in Migra categorized as resistance to fruit borers (Haldhar et al. 2021)¹⁵. According to Shahid et al. (2014)⁵², the genotype Cool Sun-70 showed 27% HPSI followed by Cauliflower Desi 26%. The minimum HPSI was calculated 9% for Pari F1 and Shumila F1. Cashmere and White Island genotypes were categorized as intermediate with 14% and 15% HPSI, respectively.

5. Mite (*Tenuipalpus punicae*) resistance study in pomegranate, *Punica granatum* L.

Pomegranate (*Punica granatum* L.) is an important fruit crop in arid and semi-arid regions of India. It has the capability to withstand extreme environmental conditions of heat, drought and moisture deficit situations. Pomegranate has very good nutritional and nutraceutical values and is one of the richest sources of plant-based antioxidant compounds. It is grown commercially in the states of Maharashtra, Gujarat, Karnataka, Andhra Pradesh, Tamil Nadu, Madhya Pradesh and Rajasthan (Kumar et al. 2018)⁵³. In the hot arid region of Rajasthan, mite, *Tenuipalpus punicae* Pritchard & Baker, 1958 is the major pest causing severe damage to the leaf, fruit and stem of pomegranate. The *T. punicae* is red or brown in colour, dorsum medially and laterally reticulate; prodorsum with oblique striae and folds laterally; opisthosoma with longitudinal striae laterally. Venter is mostly smooth with weak striae laterally and posteriorly. The spermathecal duct narrows to form proximal constriction, before forming a membranous bulge and narrows again into a slender tube, terminating into a small bulb distally (Ueckermann et al. 2018)⁵⁴. Mite, *T. punicae* is most active during dry spells from April to October. Shiny white or brown patches can be seen on the undersurface of affected leaves, which may further curl and fall. Adults and nymphs nourish on the lower leaf surface by sucking sap. The leaf is reddish on severe infestation (Haldhar and Maheshwari 2021; Nidhi & Haldhar 2021)^{55,56}.

The pomegranate cultivars; HP Collec., Speen Sacarin, Gule Shah Rose Pink and AHPG-C3 cultivars were found to be resistant; Sur Sukker, Tujetis EC 4347, Bassin Seedless, Dholka, Uthkal, Agah, Achik Dana and Goma Khata cultivars were found to be moderately resistant; Jalore Seedless, Jodhpur Red, Saharanpur and Bhagwa were susceptible whereas Dorsata Malus, Kajaki Anar, Saih Sirin, P-23, IC-318712 and Phule Arakta were highly susceptible against *T. punicae*. The leaf infestation ranged from 5.17 to 56.33% in 2019 whereas it was 5.33 to 57.5% during 2020. Pooled data of leaf infestation in both years (5.25- 56.92%) was significantly lower in resistant and higher in susceptible cultivars. In pooled data, the per cent leaf infestation was the highest in

Kajaki Anar (56.92 %) and the lowest in HP Collec. (5.25 %) followed by Gule Shah Rose Pink (7.17 %) and Speen Sacarin (7.33%) (Haldhar et al. 2022)¹⁶. The more closely related study is probably on carob moth susceptibility, which was assessed on 19 pomegranate varieties of Iranian origin (Sobhani et al. 2015)⁵⁷. More recently, a demographic laboratory study on the same insect also revealed significant differences among the 11 Iranian varieties under investigation (Abedi et al. 2019)⁵⁸.

The flavinoid content (4.48 mg cat.Equi./g) was found to be maximum in HP Collec. followed by Speen Sacarin (4.05 mg cat.Equi./g) and minimum in Bassin Seedless (2.47 mg cat.Equi./g). Phenols content was highest in HP Collec. (49.00 GAE/g) followed by Gule Shah Rose Pink (48.94 GAE/g) and lowest in Kajaki Anar (34.10 GAE/g). The tannin content (9.87 mg cat.Equi./g) was found to be the highest in HP Collec. followed by Speen Sacarin (8.89 mg cat.Equi./g) and the lowest in AHPG-C3 (3.45 mg cat.Equi./g). Total antioxidant activity on CUPRAC scale was highest in Gule Shah Rose Pink (571.45 mg AAE/g) followed by HP Collec. (522.14 mg AAE/g) and lowest in IC-318712 (289.71 mg AAE/g) with values significantly higher in resistant and lower in susceptible cultivars (Haldhar et al. 2022)¹⁶. Antibiotics affect herbivores by suppressing growth, development, reproduction, to death and several small molecules of neurotransmitters are known to modulate neuroreceptor activity (Pivovarov et al. 2019)⁵⁹. Antixenosis is a secondary plant metabolite that plays a role in blocking insect colonization or being a deterrent to coming. The orientation of insects to plants includes, among others, food, a place to lay eggs, and take shelter. Plants showing resistance with antixenotic properties were able to reduce the initial number of colonization in one season and reduced population size in each generation compared to susceptible plants. Secondary metabolites fight against microbial and insect attack (phytoalexins) or stored in inactive form (phytoanticipins). One example of antixenosis is the glucosinolate content which gives a distinctive smell and taste to the Brassicaceae family vegetables, which are not favored by pests (Khare et al., 2020)⁶⁰.

The plant height (-0.24), canopy spread (N-S) (-0.19), stem diameter (-0.05) and number of stems (-0.42) had non-significant negative correlations and canopy spread (E-W) (0.008) had non-significant positive correlation with percentage mite leaf infestation (Haldhar et al. 2022)¹⁶. Gladiolus varieties showed the density of papillae was negatively correlated with thrips damage, while the length of mesophylls and epidermal cells was positively correlated with thrips damage. As a rule, an epidermal cell produces one papilla (Wahyuni et al. 2021)⁶¹.

6. Fruit fly resistance study in snap melon (*Cucumis melo* L. var. *momordica*)

Snapmelon (*Cucumis melo* L. var. *momordica* (Roxb.)) belongs to the family *Cucurbitaceae*, which is a native of India and is used as a vegetable in a variety of ways. Snapmelon is rich in nutritional attributes; the 100 g edible fruit of snap melon contains 15.6 g carbohydrates, 18.6 mg vitamin C, and provides 74.0 kcal energy. The melon fruit fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), is a severe pest of snap melon in

India, and its outbreak causes substantial crop losses to the growers. The melon fruit fly has been observed on 81 host plants, but snap melon is one of the most preferred hosts and has been a major limiting factor in obtaining good quality fruits and high yield. The genotypes IC-430190, DKS-AHS 2011/4, and DKS-AHS 2011/3 were resistant; IC-430160, IC-430162, IC-430175, IC-430179, IC-430180, IC-430185, IC-369788, and DKS-AHS 2011/2 were moderately resistant whereas IC-430155, IC-430164, IC-430169, IC-430171, IC-430172 and IC-430184 were found the susceptible genotypes to fruit fly infestation (Haldhar et al. 2016b & 2018b)^{17,71}.

The free amino acid and the total soluble solid were the lowest in resistant and the highest in susceptible genotypes. In contrast, flavonoids, tannins, phenols, and total alkaloid contents were the highest resistant and lowest in susceptible genotypes of snap melon (Haldhar et al. 2018b)¹⁷. Phenols act as a defensive mechanism against herbivores but also against microorganisms and competing plants. Qualitative and quantitative phenol alterations and elevation in oxidative enzyme activities in response to insect attacks were general phenomena. Lignin, a phenolic heteropolymer, plays a central role in plant defense against insects and pathogens (Barakat et al. 2010)⁶². Flavonoids were cytotoxic and interacted with different enzymes through complexation. Both flavonoids and isoflavonoids protect the plant against insect pests by influencing insect behaviour, growth and development. Total soluble solid and pH of fruit had a significant positive correlation. In contrast, tannins, phenols, alkaloids and flavonoid contents had a significant negative correlation with the percentage of fruit infestation and the larval density per fruit. The biochemical characteristics such as total sugar and crude protein were positively correlated with fruit borer infestation, whereas total phenols had a negative correlation (War et al. 2012; Haldhar et al. 2013a; Haldhar et al. 2015b)^{6,10,19}.

Fruit length, flesh thickness and fruit diameter had significant positive correlations. In contrast, rind hardness at an immature stage, rind hardness at a mature stage, pericarp thickness and length of ovary pubescence had significant negative correlations with the per cent fruit infestation and larval density (Haldhar et al. 2018b)¹⁷. In these findings, biophysical fruit traits were also significantly different among genotypes (Simmons et al. 2010; Haldhar et al. 2015b&c)^{19,63,64}. Glandular trichomes secrete secondary metabolites, including flavonoids, terpenoids, and alkaloids, that could be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defense (Sharma et al. 2009)⁴². 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 82.8 %. PC1 explained 53.41 % of the variation, while PC2 explained 29.39 %. PC1 had the loadings for flavonoid content (0.86), tannins content (0.88), a total alkaloid (0.82), phenols content (0.88), free amino acid (-0.83), total soluble solid (-0.66), length of ovary pubescence (0.88), pericarp thickness (0.67) and rind hardness at an

immature stage (0.89). Rind hardness at the mature stage (0.52), flesh thickness (-0.74), fruit length (-0.86) and fruit diameter (-0.68) were loaded in PC2 (Haldhar et al. 2018b)¹⁷.

7. Fruit fly resistance study in musk melon, *Cucumis melo* L.

Musk melon (*Cucumis melo* L.) is one of the essential horticultural crops worldwide and plays a vital 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 severe 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 (Haldhar et al. 2014; Choudhary et al. 2015; Choudhary et al. 2018a)^{65,66,67}. The extent of losses varies between 30 to 100%, depending on the cucurbit species and the season. As maggots damage the fruits internally, controlling this pest with insecticides is difficult. Hence, developing varieties resistant to melon fruit fly is an impotent component of integrated pest management. 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. 2013a)⁶. Ismail et al. (2010)⁶⁸ reported that the cantaloupe flesh extract afforded the highest yield (89.6 ± 0.3%), whilst the lowest yield was obtained from the seed (13.7 ± 0.5%). The leaf extract showed the highest total phenolic content (26.4 ± 0.3 mg GAE/g extract) and entire flavonoid content (69.7 ± 3.37 µg RE/g extract).

Total sugar, reducing sugar, and non-reducing sugar of different varieties/ genotypes fruits of muskmelon ranged from 309 to 553.27, 62.07 to 124.27 and 246.93 to 429 (mg/g on a 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 (Haldhar et al. 2013a; Bhargava et al. 2016)^{6,69}.

The antixenotic mechanisms of fruit traits significantly differed among the tested muskmelon genotypes. Fruit diameter and days to first harvest had significant positive correlations, whereas fruit toughness, rind thickness, flesh thickness and length of ovary pubescence had significant negative correlations with the per cent fruit

infestation and larval density. Biophysical fruit traits were also found to be significantly different among genotypes (Gogi et al. 2010)⁵. Structural characteristics such as spines and thorns (spinescence), trichomes (pubescence), toughened or hardened leaves (sclerophylly), incorporation of granular minerals into plant tissues, and divaricated branching (shoots with wiry stems produced at wide axillary angles) play a leading role in plant protection against insects (Hanley et al. 2007)⁸. Pubescence consists of the layer of hairs (trichomes) extending from the epidermis of the above-ground plant parts, including stem, leaves, and even fruits. It occurs in several forms, such as straight, spiral, stellate, hooked, and glandular (Hanley et al., 2007)⁸. The leaf glossiness, plumule and leaf sheath pigmentation were responsible for shoot fly *Atherigona soccata* (Rondani) resistance in sorghum *Sorghum bicolor* (L.) (Moench). Similar results were documented by Gogi et al. (2010)⁵ that fruit length, fruit diameter, number of longitudinal ribs/fruit and number of small ridges/cm², which were significantly lowest in resistant and highest in susceptible genotypes, had a significant positive correlation with the per cent fruit infestation and larval density per fruit. However, fruit toughness, the height of small ridges, the height of longitudinal ribs and pericarp thickness, which were significantly highest in resistant and lowest in susceptible genotypes, had a significant negative correlation with the per cent fruit infestation and larval density per fruit. These variations in measurements of biophysical fruit traits may be attributed to differences in the tested genotypes and stage of the fruits selected for measuring these traits, as reported in earlier studies (Gogi et al., 2010)⁵.

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 entire 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. 2013b)³¹. Similar findings 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)⁵.

8. Fruit fly resistance study in watermelon, *Citrullus lanatus* (Thunb.) Matsumura & Nakai

Watermelon (*Citrullus lanatus*) is a popular dessert crop throughout the world's tropics and Mediterranean regions. Because of its antioxidant properties, the fruit is rated equal to apple, banana, or orange. Fruits contain diverse carotenoids that are responsible for the different flesh colours. Different carotenoid patterns have been associated with distinct cultivars and cultivated environments. Insect pests are a significant constraint in increasing the production and productivity of the watermelon crop. The melon fly, *Bactrocera cucurbitae* (Coquillett) (Diptera: Tephritidae), is a severe 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)⁷⁰. The watermelon 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 (Haldhar et al. 2015b)¹⁹.

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 the percentage of 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)¹⁹. Total soluble solids and pH of fruit had a significant positive correlation. In contrast, tannin, phenol, alkaloid, and flavonoid contents had a significant negative correlation with the percentage of fruit infestation and larval density per fruit (Gogi et al. 2010)⁵. Biochemical characteristics such as total sugar and crude protein were positively correlated, whereas total phenols were negatively correlated with fruit borer infestation (War et al., 2012; Haldhar et al. 2013a)^{6,10}. Similar to our findings, it has been demonstrated that phenols, tannins, and flavonoids enhanced plant defenses against insects (Haldhar et al. 2018a)².

The antixenotic mechanisms of fruit traits significantly differed among the tested watermelon varieties/genotypes. Fruit length, fruit diameter and days to first fruit harvest had significant positive correlations. In contrast, rind hardness, rind thickness and length of ovary pubescence had significant negative correlations with the per cent fruit infestation and larval density. In these findings, biophysical fruit traits were also significantly different among genotypes (Gogi et al. 2010)⁵. Pubescence consists of the layer of hairs (trichomes) extending from the epidermis of the above-ground plant parts, including stem, leaves, and even fruits. It occurs in several forms such as straight, spiral, stellate, hooked, and glandular (Hanley et al. 2007)⁸. Similar results were documented by Gogi et al. (2010)⁵ that fruit length, fruit diameter, number of longitudinal ribs/fruit and number of small ridges/cm², which were significantly lowest in resistant and highest in susceptible genotypes, had a significant positive correlation with the per cent fruit infestation and larval density per fruit. However, rind hardness, the height of small ridges, the height of longitudinal ribs and pericarp thickness, which were significantly highest in resistant and lowest in susceptible genotypes, had a significant negative correlation with the per cent fruit infestation and larval density per fruit. These variations in measurements of biophysical fruit traits may be attributed to differences in the tested genotypes and stages of the fruits selected for measuring these traits, as reported in earlier studies

(Gogi et al. 2010)⁵. Stepwise regression analysis indicated that maximum variation in fruit infestation and larval density per plant were explained by the length of ovary pubescence followed by fruit length. However, Gogi et al. (2010)⁵ indicated that the tested morphological traits explained 100% of the total variation in fruit infestation and larval density per fruit. The maximum variation in fruit infestation and larval density per fruit was described by rind hardness followed by fruit diameter and number of longitudinal ribs.

9. Fruit fly resistance study in ridge gourd, *Luffa acutangula* (Roxb.) L.

Ridge gourd (*Luffa acutangula*) is an essential 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 vegetables and used to prepare chutneys and curries. Being a warm-season crop, it can tolerate hotter conditions, making it suitable for widespread tropical cultivation (Choudhary et al. 2014; Choudhary et al. 2018b)^{72,73}. 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. Direct defenses are mediated by plant characteristics that affect the herbivore's biology, such as the production of toxic chemicals such as terpenoids, alkaloids, anthocyanins, phenols, and quinones) that either kill or retard the development of 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)^{19,20}.

The phenotypic fruit trait mechanisms significantly differed among the tested ridge gourd varieties/genotypes. Fruit length and fruit diameter had significant positive correlations, whereas rind hardness, rind thickness, fibre content and length of ovary pubescence had significant negative correlations with the per cent fruit infestation and larval density. Biophysical fruit traits were also found to be significantly different among genotypes (Gogi et al. 2010)⁵. Pubescence consists of the layer of hairs (trichomes) extending from the epidermis of the above-ground plant parts, including stem, leaves, and even fruits, and occurs in several forms such as straight, spiral, stellate, hooked, and glandular (Hanley et al. 2007)⁸. Similar results were documented by Gogi et al. (2010)⁵ that fruit length, fruit diameter, number of longitudinal ribs/fruit and number of small ridges/cm², which were significantly lowest in resistant and highest in susceptible genotypes, had a significant positive correlation with the percent fruit infestation and larval density per fruit. However, rind hardness, the height

of small ridges, the height of longitudinal ribs and pericarp thickness, which were significantly highest in resistant and lowest in susceptible genotypes, had a significant negative correlation with the per cent fruit infestation and larval density per fruit. These variations in measurements of biophysical fruit traits may be attributed to differences in the tested genotypes and stage of the fruits selected for measuring these traits, as reported in earlier studies (Gogi et al. 2010)⁵.

The allelochemical compounds of fruit significantly differed among the tested ridge gourd varieties/genotypes. The free amino acid was lowest in resistant and highest in susceptible varieties/genotypes. In contrast, flavonoid, tannins, phenols, and ascorbic acid contents were highest in resistant and lowest in susceptible varieties/genotypes (Haldhar et al. 2015a)¹⁸. Total soluble solid and pH of fruit had a significant positive correlation, whereas tannins, phenols, alkaloids and flavonoid contents had a significant negative correlation with the percentage of 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 a negative correlation (War et al. 2012, Haldhar et al. 2013a)^{6,10}. Basis on the 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)¹⁹. According to Gogi et al. (2010)⁵, maximum variation in fruit infestation was explained by tannin and flavanol contents, whereas, the rest of the biochemical fruit traits explained <0.2% variation in the fruit infestation.

10. Fruit fly resistance study in 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 widely found in rainy season crops in arid and semi-arid regions of India. The bottom-up effects in the crop plant are an economical and environment-friendly method of insect management. The attractive and beneficial feature of the bottom up effect is that it is farmer friendly and does not need much financial investment for pest control. The nutrients and concentrations of secondary metabolites determine the identification and development of crop-specific genotypes with resistance to pests. Host plants play an essential role in determining insect populations with respect to concentrations and proportions of nutrients and differences among species. 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 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 %, significantly lower in resistant genotypes and higher in susceptible genotypes (Haldhar et al. 2017a)²¹.

The phenotypic (antixenotic) fruit trait mechanisms significantly differed among the tested kachri genotype. The length of ovary pubescence, rind hardness, rind thickness, fruit length, and fruit diameter had significant negative correlations with the per cent fruit infestation and larval density. In these findings, biophysical fruit traits were also significantly different among the genotypes (Gogi et al. 2010; Haldhar et al. 2015b)^{5,19}. Glandular trichomes secrete secondary metabolites, including flavonoids, terpenoids, and alkaloids, that could be poisonous, repellent, or trap insects and other organisms, thus forming a combination of structural and chemical defense (Sharma et al. 2009)⁴². Structural traits such as spines and thorns (spinescence), trichomes (pubescence), toughened or hardened leaves (sclerophylly), incorporation of granular minerals into plant tissues, and divaricated branching (shoots with wiry stems produced at wide auxiliary angles) played a leading role in plant protection against herbivory. Similar results were documented by Haldhar et al. (2015b)¹⁹ that the length of ovary pubescence, rind hardness, fibre content, and rind thickness had significant negative correlations, whereas; fruit length and fruit diameter had significant positive correlations with the percentage of fruit infestation and the larval density per fruit in different genotypes of ridge gourd. These variations in measurements of biophysical fruit traits might be attributed to differences in the tested genotypes and stage of the fruits selected for measuring these traits, as reported in earlier studies (Gogi et al., 2010; Haldhar et al., 2015a)^{5,18}. Stepwise regression analysis of our data indicated that the maximum variation in percentage fruit infestation and larval density per fruit were explained by the length of ovary pubescence followed by rind hardness. However, Gogi et al. (2010)⁵ 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 their study, in percentage fruit infestation and larval density per fruit, was explained by rind hardness followed by fruit diameter and a number of longitudinal ribs. Maximum variation in fruit infestation and larval density were presented by the length of ovary pubescence (82.50 and 83.60%, respectively) followed by fruit length (4.3 and 3.0%, respectively) and rind thickness (3.2 and 2.0%,

respectively) in watermelon against fruit fly (Haldhar et al. 2015a)¹⁸.

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 the susceptible genotypes 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 a significant negative correlation. Backward stepwise regression analysis indicated that flavonoid and tannin 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)²¹. Phenols act as a defensive mechanism against herbivores but also against microorganisms and competing plants. Tannins, Flavonoids and isoflavonoids protect the plant against insect pests by influencing insect behavior, growth, and development (Barbehenn & Peter 2011)⁴¹. 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 (War et al. 2012)¹⁰. 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. 2017a)²¹. Gogi et al. (2010)⁵ 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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Declaration of Interests

The authors have no conflict of interest to declare.

Data Sharing

All relevant data are within the manuscript.

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