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Plant morphological traits associated with field resistance to cardamom thrips (*Sciothrips cardamomi*) in cardamom (*Elettaria cardamomum*)

Thuruthumkara K. Jacob[1] | Chellappa M. Senthil Kumar[1] | Selvakaran Devasahayam[1] | Sharon D'Silva[2] | Rathinampillai Senthil Kumar[2] | Chakkiyanickal N. Biju[1] | Ravindran Praveena[1] | Shettahalli K. J. Ankegowda[2]

[1]Division of Crop Protection, ICAR – Indian Institute of Spices Research, Kozhikode, India

[2]Regional Station, ICAR – Indian Institute of Spices Research, Appangala, Madikeri, India

Correspondence
C. M. Senthil Kumar, Division of Crop Protection, ICAR – Indian Institute of Spices Research, Marikunnu P.O., Kozhikode 673 012, India.
Email: senthilkumar.cm@icar.gov.in, cmskm@yahoo.com

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Abstract

Cardamom thrips (*Sciothrips cardamomi*) is a major insect pest of cardamom (*Elettaria cardamomum*) causing severe economic losses to the crop in all cardamom producing countries. The present control measures rely heavily on chemical insecticides, which in addition to increased input costs also lead to pesticide residues in the produce and environmental hazards. Although the crop is of high commercial value, limited efforts have been made to identify sources of resistance to this major pest. Exploiting sources of resistance along with integrated pest management tactics will help to reduce pesticide usage in this crop promoting sustainable production. The present study aimed at identifying sources of resistance against cardamom thrips and the associated plant morphological traits conferring resistance against the pest. Field screening of 180 cardamom germplasm accessions for 3 years at Appangala, Karnataka, India, resulted in identification of eight accessions resistant to cardamom thrips. Differences in panicle type and the nature of adherence of leaf sheath to the pseudostem explained a significant amount of the variance in resistance and therefore are likely to play a major role in conferring resistance against this pest. Multiple regression analysis of the different traits indicated that accessions with prostrate panicles having leaf sheath loosely adhered to the pseudostems were found to have significantly less thrips damage, when compared with other panicle and leaf sheath types. However, persistence of flower bract did not have a significant additive effect on imparting resistance against thrips. Metabolomic analysis of the accessions may provide further insight into the existence of supplementary biochemical mechanisms, if any, in imparting resistance. The identified traits and accessions can be exploited in future breeding programmes for developing thrips resistant cardamom varieties.

KEYWORDS
field screening, flower bract, host plant resistance, leaf sheath, panicle, plant architectural traits, resistance breeding, spices, sucking pest

T. K. Jacob and C. M. Senthil Kumar contributed equally to this study.

1 | INTRODUCTION

Cardamom thrips (*Sciothrips cardamomi* Ramk.) (Thysanoptera: Thripidae) is a major limiting factor in cardamom production (*Elettaria cardamomum* Maton.) (Zingiberaceae), a high-value commercial spice crop, mainly grown in India, Guatemala and Sri Lanka valued for its aroma and medicinal properties (Ravindran, 2002). The insect damages panicles, flowers and developing capsules by sucking the sap, leading to premature shedding of flowers and capsules. The pest infestation also results in scab formation on the capsule surface with poorly developed seeds inside presenting a shrivelled appearance (Figure 1) and lacking the characteristic aroma. Thrips damaged capsules have very low market value causing severe economic losses to growers. The extent of capsule damage by thrips is 30–90%, and the estimated crop loss is up to 48% in major cardamom producing countries (Dharmadasa, Nagalingam, & Seneviratne, 2008; Global Agricultural Information Network, 2014; Gopakumar & Chandrasekar, 2002).

Cardamom thrips reproduce both sexually and parthenogenetically and have a short life cycle leading to rapid multiplication of the insect. The availability of vulnerable plant parts almost throughout the year also facilitates high build-up of thrips populations in the field. Currently, pest management options are limited to application of synthetic chemical insecticides (Dharmadasa et al., 2008; Gopakumar & Chandrasekar, 2002; Jacob et al., 2015) and farmers often resort to 15–20 sprays per year of highly toxic organophosphates and synthetic pyrethroids, which is more than the recommended spray schedules (Shetty, Murugan, & Sreeja, 2008). This often leads to pesticide residues in the produce, mortality of pollinators and other environmental hazards (Murugan, Shetty, Ravi, Subbiah, & Hiremath, 2011). Pesticide residues are a major concern in cardamom and this has led to drastic decline in export of cardamom to other countries (Beevi et al., 2014; Shetty et al., 2008). Over-dependence on insecticides needs to be brought down for a residue-free safe produce that is widely used in food and medicine. Hence, development of alternate strategies for the management of this pest is important. Recently, we have isolated an entomopathogenic fungus *Lecanicillium psalliotae* (Treschew) Zare & W. Gams (Ascomycota: Hypocreales), which offers scope for biological control of the pest (Senthil Kumar, Jacob, Devasahayam, D'Silva, & Krishna Kumar, 2015; Senthil Kumar, Jacob, Devasahayam, Stephy, & Geethu, 2018). However, solely relying on biological control will not be a viable strategy for the management of the pest.

Development of management strategies based on host plant resistance offers an attractive alternative to the use of synthetic chemical pesticides. The extent of expression of defensive traits against arthropod pests may vary among the wild relatives or within the cultivated accessions of a plant and identification of resistant genotypes is an important step towards development of resistant varieties (Eyidozehi, Fanooj, & Mokhtari, 2015). Host plant resistance forms an important component in developing integrated pest management strategies being compatible with other management strategies (Panda & Khush, 1995). Thrips resistance in many crops has been attributed to plant morphological characters (Kirk, 1997; Srinivasan et al., 2018). Limited attempts have been made so far to identify and exploit natural sources of resistance of cardamom lines to cardamom thrips. Earlier attempts to exploit the natural variation in resistance of cardamom germplasm and cultivars to thrips included only limited number of accessions (Chandrasekar & Balu, 1993; Parvathi & Chandrappa, 1993; Singh, Sudarshan, & Kumaresan, 1996).

In the present study, we evaluated 180 cardamom accessions, maintained at the Regional Station of ICAR – Indian Institute of Spices Research at Appangala, Karnataka, India, under field conditions to identify sources of resistance against cardamom thrips. We screened the accessions based on capsule damage by the insect and studied three plant architectural traits: erectness of panicle, persistence of flower bract, and the nature of adherence of leaf sheath to the pseudostem to know their influence on pest damage. We predict that accessions with prostrate panicles and loosely attached leaf sheath are less prone to thrips attack because these factors increase the vulnerability of thrips to several biotic and abiotic factors.

FIGURE 1 Thrips damaged cardamom capsules with scab formation on the capsule surface

2 | MATERIALS AND METHODS

2.1 | Study area

The study was conducted at the National Active Germplasm Site (NAGS) for cardamom in India, established in the experimental farm of the Regional Station (12°26′N, 75°45′E) of ICAR – Indian Institute of Spices Research, Kozhikode at Appangala, Karnataka. The farm is situated in a high altitude (920 m above MSL) and high rainfall region. The annual total rainfall received during the study period (2011–2012 to 2013–2014) ranged from 2,049 to 3,677 mm.

2.2 | Plant material

Cardamom accessions collected from various agroclimatic zones of India and maintained ex-situ in the NAGS for cardamom were used for the study. In total, 443 cardamom accessions available in the germplasm collection identified by their indigenous collection (IC) number with other passport details as described in the IPGRI Manual on descriptors for cardamom (International Plant Genetic Resources Institute, 1994) were used. However, because of inconsistency in the yield of some of the cultivars, the number of accessions used for final analysis was reduced to 180.

2.3 | Screening of germplasm against thrips

Experiments were conducted for three seasons (2011–2012; 2012–2013; 2013–2014) to screen the cardamom accessions against the natural population of cardamom thrips under field conditions. The observations were carried out on five clumps of each accession (5–6 years old and yielding) maintained with a plant to plant spacing of 3 m × 3 m. Each

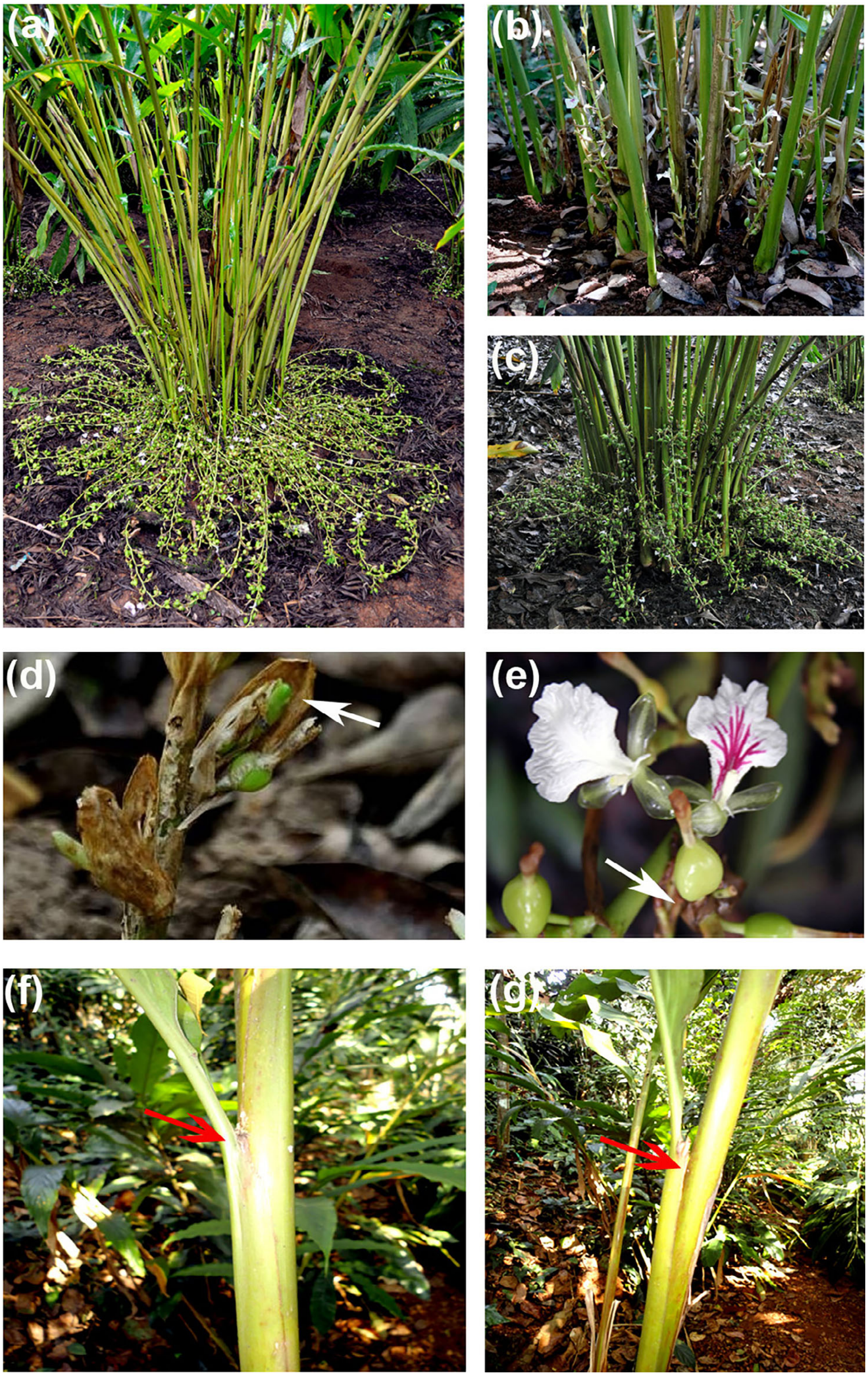

FIGURE 2 Cardamom accessions with different types of panicle ((a) prostrate panicle, (b) erect panicle and (c) semi-erect panicle), flower bract ((d) persistent bract and (e) nonpersistent bract) (arrow indicates presence or absence of flower bract) and leaf sheath ((f) tight leaf sheath and (g) loose-leaf sheath) (arrow indicates the nature of adherence of leaf sheath to the pseudostem)

clump was considered as a replication. The plants were raised following the standard agronomic practices for cardamom (ICAR – Indian Institute of Spices Research, 2015) except for nonapplication of pesticides throughout the study period.

2.4 | Scoring for thrips damage

Cardamom capsules after attaining physiological maturity were harvested separately from each clump during July, September and December each year and cured following standard procedures (ICAR – Indian Institute of Spices Research, 2015). The cured capsules were pooled clump-wise and stored in polythene bags at ambient room temperature for further observations. Capsule damage by thrips was assessed by drawing 100 g of sample from each clump of every accession. The total number of capsules and number of capsules that showed characteristic scab formation because of thrips infestation were visually recorded for calculating the per cent capsule damage. The mean per cent capsule damage for an accession in a year was calculated, pooling the plant-wise harvest data.

2.5 | Plant morphological traits

To study the influence of plant morphological traits imparting resistance against thrips, the cardamom accessions were scored for three different morphological traits: (a) panicle type ("*Malabar*" – prostrate panicle; "*Mysore*" – erect panicle and "*Vazhukka*" – semi-erect panicle) (International Plant Genetic Resources Institute, 1994); (b) flower bract (persistent or nonpersistent); and (c) attachment of the leaf sheath to pseudostem based on the level of adherence (tight, loose and intermediate) (Figure 2). The accessions were grouped based on these characters along with corresponding thrips damage for further analysis.

2.6 | Data analysis

Yearly mean per cent capsule damage for individual accessions were calculated by pooling the plant-wise data. Data on thrips damage from an accession pooled together per year were considered as a single replication and accordingly there were three replications considering the data from 3 years. The overall mean capsule damage (M) and SD for all the accessions were calculated to determine the thresholds for resistance and the accessions were categorised as resistant, moderately resistant, moderately susceptible, susceptible and highly susceptible to thrips following Bhumannavar, Singh, and Sulladmath (1989) with slight modification. Accessions with capsule damage less than $M{-}2SD$ were classified as highly resistant; between $M{-}2SD$ and $M{-}1.5SD$ as resistant; between $M{-}1.5SD$ and M as moderately resistant; between M and $M{+}1.5SD$ as moderately susceptible; between $M{+}1.5SD$ and $M{+}2SD$ as susceptible and higher than $M{+}2SD$ as highly susceptible to thrips. Association between the three plant morphological traits: panicle type, persistence of bract, tightness of leaf sheath were analysed by chi-square tests. The influence of panicle type and the nature of adherence of leaf sheath on thrips damage were subjected to one-way analysis of variance and the influence of persistence of flower bract on thrips damage was compared by unpaired t-test with Welch's correction. The data were transformed to arcsine $[(x + 0.5)/100]^{½}$ prior to analysis. The mean comparison for all pairs was carried out by Fisher's LSD ($\alpha = .05$). To assess the magnitude of variation in thrips damage because of various factors, a multiple regression with categorical variables and dummy coding was attempted with thrips damage (y) as a function of panicle type (PT), bract (B) and leaf sheath (LS) characters. The analyses were carried out in GraphPad Prism® Version 7.0 for Windows, GraphPad Software, La Jolla, CA, and SPSS Version 25.0.

3 | RESULTS

3.1 | Screening of cardamom accessions for resistance

The mean capsule damage in the accessions for 3 years was 37.2% ± 12.7 (*SD*). The resistance threshold values for different categories namely, highly resistant, resistant, moderately resistant, moderately susceptible, susceptible and highly susceptible were <11.8, 11.9–18.2, 18.3–37.2, 37.3–56.2, 56.3–62.5 and >62.5%, respectively. Among the 180 accessions screened, none of them were found to be highly resistant; eight accessions (IC 349370, IC 349606, IC 349588, IC 349363, IC 349362, IC 349364, IC 349455 and IC 547167) were resistant to thrips. The average capsule damage by thrips for these accessions ranged from 13.7 to 16.7%. Based on the threshold values for different categories, 96, 60, 9 and 7 accessions were rated as moderately resistant, moderately susceptible, susceptible and highly susceptible, respectively, to the pest (Table S1).

3.2 | Association between plant morphological traits

Among the accessions with prostrate panicles, majority of them were found to have nonpersistent bract, whereas accessions with semi-erect and erect panicles were found to possess more of persistent bract than nonpersistent bract. The proportion of plants with semi-erect and erect panicles having loose-leaf sheath was comparatively lesser when compared with accessions with prostrate panicles. Accessions with loose and intermediate leaf sheath tend to have a higher proportion of nonpersistent bract than accessions with tight leaf sheath. Chi-square analysis to the study the association between morphological traits revealed existence of significant association between the traits studied (Table 1).

3.3 | Influence of plant morphological traits and thrips damage

3.3.1 | Panicle type

Among the 180 accessions screened for thrips resistance, 125 accessions belonged to prostrate panicle type, 30 accessions to erect

TABLE 1 Association between plant morphological traits

Traits		*n* (%)	Chi-square test
Panicle type versus presence of bract			
Panicle type	Presence of bract		
Prostrate	Yes	2 (1.6%)	χ^2 = 111.83, p < .0001; Pearson contingency coefficient = 0.62
	No	123 (98.4%)	
Semi-erect	Yes	19 (76.0%)	
	No	6 (24.0%)	
Erect	Yes	22 (73.3%)	
	No	8 (26.7%)	
Panicle type versus leaf sheath type			
Panicle type	Adherence of leaf sheath		
Prostrate	Loose	109 (87.2%)	χ^2 = 45.43, p < .0001; Pearson contingency coefficient = 0.45
	Intermediate	11 (8.8%)	
	Tight	5 (4.0%)	
Semi-erect	Loose	11 (44.0%)	
	Intermediate	6 (24.0%)	
	Tight	8 (32.0%)	
Erect	Loose	14 (46.7%)	
	Intermediate	3 (10.0%)	
	Tight	13 (43.3%)	
Leaf sheath versus presence of bract			
Adherence of leaf sheath	Presence of bract		
Loose	Yes	17 (12.7%)	χ^2 = 45.20, p < .0001; Pearson contingency coefficient = 0.45
	No	117 (87.3%)	
Intermediate	Yes	7 (35.0%)	
	No	13 (65.0%)	
Tight	Yes	19 (73.1%)	
	No	7 (26.9%)	

panicle type and the remaining 25 accessions to semi-erect panicle type. There were significant differences in thrips damage among the cardamom panicle types (F = 30.61; df = 2, 177; p < .0001). The prostrate panicle type had significantly less thrips damage when compared with erect and semi-erect panicle types. The erect and semi-erect panicle types also differed significantly in terms of thrips damage. The mean per cent thrips damage in prostrate panicle type was 32.9% ± 1.0 (*SE*), whereas it was 49.3% ± 2.0 and 44.5% ± 2.2, respectively, for erect and semi-erect panicle types (Figure 3).

3.3.2 | Persistence of flower bract

Significant difference in thrips damage was observed between the accessions with persistent bract and nonpersistent bract (t = 6.152; df = 66.47; p < .0001). Among the 180 accessions screened, 43 accessions had persistent bract, whereas 137 accessions had nonpersistent bract. Cardamom accessions with nonpersistent bract had significantly

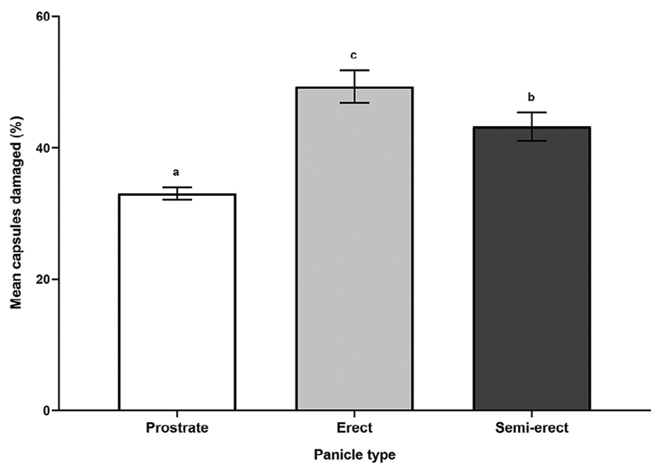

FIGURE 3 Influence of panicle type on capsule damage (mean ± *SE*) by thrips. Bars represent original data. For analysis, data were transformed to arcsine $[(x + 0.5)/100]^{1/2}$. Means followed by different letters are significantly different by Fisher's LSD

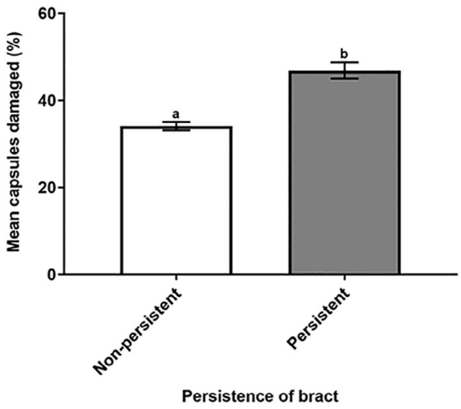

FIGURE 4 Influence of flower bract type on capsule damage (mean ± *SE*) by thrips. Bars represent original data. For analysis, data were transformed to arcsine $[(x + 0.5)/100]^{1/2}$. Means followed by different letters are significantly different by Student *t*-test

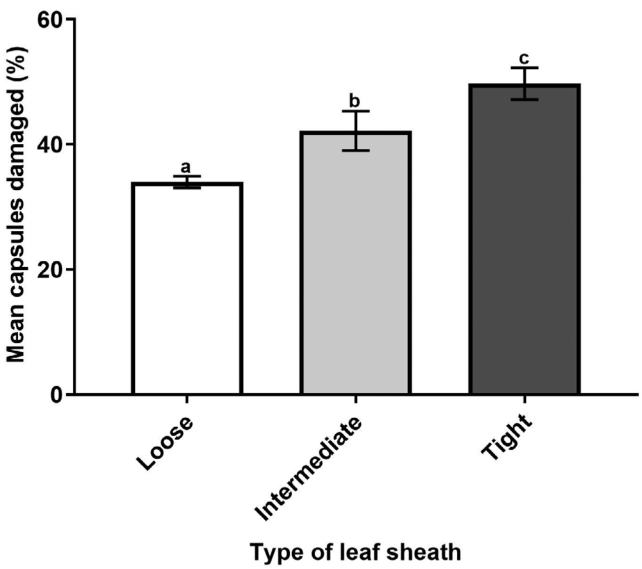

FIGURE 5 Influence of leaf sheath character on capsule damage (mean ± *SE*) by thrips. Bars represent original data. For analysis, data were transformed to arcsine $[(x + 0.5)/100]^{1/2}$. Means followed by different letters are significantly different by Fisher's LSD

less thrips damage (34.1% ± 1.0) in comparison with accessions having persistent bract (46.9% ± 1.9) (Figure 4).

3.3.3 | Adherence of leaf sheath

Among the accessions screened for resistance, 134 accessions had loose-leaf sheath, whereas 20 and 26 accessions had intermediate and tight leaf sheath, respectively. The level of adherence of leaf sheath to the pseudostem of cardamom plants showed significant differences in thrips damage among the accessions ($F = 21.39$; df = 2, 177; $p < .0001$). Plants with loose-leaf sheath had significantly less

TABLE 2 Regression estimates of different morphological traits with respect to thrips damage

Parameter	Estimate	Significance
Intercept (β0)	32.129	0.000
PT1 (β1)	5.890	0.072
PT2 (β2)	11.849	0.000
B (β3)	1.106	0.720
LS1 (β4)	6.140	0.020
LS2 (β5)	9.059	0.001

Note: $R^2 = 0.322$; $F = 16.536$; $p < .0001$.
Abbreviations: B, Bract dummy variable; LS1, leaf sheath dummy variable 1; LS2, leaf sheath dummy variable 2; PT1, panicle type dummy variable 1; PT2, panicle type dummy variable 2.

thrips damage (34.0% ± 0.9) compared with plants with either intermediate (42.2% ± 3.2) or tight (49.7% ± 2.6) leaf sheath (Figure 5).

3.3.4 | Regression analysis

A regression model of the form $Y = β0 + β1*PT1 + β2*PT2 + β3*B + β4*LS1 + β5*LS2 + e$ was fitted to the data and the parameters estimated are indicated in Table 2. Here, β0 represents the thrips damage of accessions with prostrate panicle type, loose-leaf sheath and no bract. β1 and β2 are the incremental thrips damage of accessions with semi-erect and erect panicles, respectively, over prostrate types. Similarly, β4 and β5 represent the additional damage of accessions with intermediate and tight leaf sheath as compared with loose types. β3 is the difference in thrips damage between accessions with bract and without bract and 'e' represents error term. Estimates reveal that there is no significant difference between accessions with and without bract. Similarly, plants with semi-erect panicles are not having any significant difference in tolerance when compared to plants with prostrate panicles. However, plants with erect panicles have a significantly higher thrips damage (11.85%) than the other two types. Accessions with intermediate and tight leaf sheath are significantly more susceptible to thrips (6.14% and 9.06%, respectively) than those with loose leaf sheath.

4 | DISCUSSION

In systems where herbivores are potent agents of natural selection, phenology, growth rate, thickness and hairiness of leaves, and size and architecture of plants, may evolve as adaptive defences against herbivory and these traits have larger effects on the preference and performance of herbivores than secondary metabolites (Carmona, Lajeunesse, & Johnson, 2011). It was reported earlier that there were no intraspecific variations among the cardamom thrips occurring all over the cardamom tracts in India based on molecular studies (Asokan et al., 2013). Locating sources of resistance in cardamom cultivars to cardamom thrips assumes significance in developing ecologically sound management programmes against a serious and persistent pest of the crop. In our studies, we screened 180 accessions of cardamom, which varied in different traits for thrips resistance based on capsule damage continuously for 3 years. We considered only the thrips damage to capsules as a measure of resistance because in cardamom, the direct economic loss is caused by scab formation on the capsules because of feeding injury by thrips leading to rejection of the produce in the market. Moreover, feeding damage on capsule is a reliable factor rather than thrips population density because lower thrips population per plant is unreliable, if that accession suffers severe feeding damage (Miyazaki, Stiller, & Wilson, 2017). We could observe large differences in the degree of thrips damage between the accessions, based on different morphological traits. Because the variation in the per cent capsule damage between various accessions was wide, it was not possible to fix the upper and lower limits of each group as constant values. Hence, the mean and standard deviation of the mean capsule damage was used for fixing various categories of resistance and susceptibility. The categorisation based on the extent of variation from the mean reduced the probabilities of inclusion of pseudo resistant and susceptible accessions (Bhumannavar et al., 1989). Based on the degree of capsule damage, we could identify eight accessions, which were found to be resistant to thrips.

Cardamom is a highly cross-pollinated plant, which express high degree of variability in qualitative and quantitative characters. This variability is also reflected in their susceptibility to thrips. Our studies reveal that there exists a close association between various morphological traits (see Table 1). In general, plant types with erect panicles are the most susceptible followed by plants with semi-erect panicle type. However, plant types with prostrate panicles were relatively resistant to thrips (Chandrasekar & Balu, 1993). In the present study, we observed a similar pattern of thrips damage according to the plant types. Out of the eight accessions showing resistance to thrips, seven accessions belonged to the prostrate panicle type (except Acc. No. IC 349606 having semi-erect panicle) with a combination of morphological characters: loose-leaf sheath and nonpersistent flower bracts. The relationship between panicle type and lower thrips damage could be linked to high rainfall in cardamom growing areas. Rainfall is one of the major limiting factors for the existence of thrips (Kirk, 1997). Cardamom flowering coincides with heavy rainfall in regions where they are grown. The reason for plants having prostrate type panicles being more resistant to thrips could be because of the fact that the insects are more vulnerable to washing off and drowning by heavy rains as they remain submerged in water for some time after heavy rains. The chances of infection of thrips by soil borne entomopathogenic fungi and other antagonistic organisms are also higher when the panicles are close to the soil surface thus exposing the thrips populations to these organisms. In case of plants having erect and semi-erect panicles, thrips can take relative advantage of the panicle architecture by moving to the floral parts thereby escaping heavy rains and the chances of being infected by soil borne pathogens is also low.

In general, cardamom accessions with nonpersistent bract exhibited evidence of resistance to thrips with significantly less capsule damage, when compared with accessions having persistent bract. However, when analysed by multiple regression, persistence of the bract did not show a significant extra amount of the variance in resistance. This could be because of the reason that more than 98% of the plant types with prostrate panicles have nonpersistent bract and hence it is difficult to discern the individual contribution or extra variation in resistance caused by this morphological trait. Apart from other plant parts, thrips also colonise and prefer to breed on flower bracts of cardamom (Gopakumar & Chandrasekar, 2002). Persistent flower bracts may provide ideal spaces for feeding and breeding of thrips and protect them from natural enemies, heavy rain and other abiotic factors. The preference of flower bracts as preferred feeding and breeding sites has also been reported in *Frankliniella occidentalis* and *F. tritici* infesting field pepper (Hansen et al., 2003), *Scirtothrips dorsalis* in grapes (Niranjana, 2008) and *Thrips hawaiiensis* in banana (Yu et al., 2018). Conversely, nonpersistent flower bract will expose the insects to rain or direct sunlight resulting in washing off by rain splashes or dehydration of the insect.

Cardamom plants whose leaf sheath attachment is either tight or intermediate were more prone to thrips attack than compared with those having loose-leaf sheath. Phytophagous thrips are known to prefer tightly enclosed and concealed spaces of plants (thigmotactic behaviour) which provides a conducive microcosm with high relative humidity protecting them from solar radiation preventing desiccation during summer and washing off during rainy season. Such small spaces also protect them from large predators and parasitoids and hence thrips populations thrive well on plants with narrow enclosed spaces (Alimousavi, Hassandokht, & Moharramipour, 2007; Kirk, 1997). This may also provide thrips a safe haven during off-season period of the crop. Alimousavi et al. (2007), Biritha et al, (Birithia, Subramanian, Muthomi, & Narla, 2014), da Silva, Bettoni, Bona, and Foerster (2015) and Njau et al. (2017) observed a significant negative correlation between leaf angle and thrips damage in onion. They argued that onion accessions with semi-erect leaves and wider angles were avoided by thrips because they are more exposed to the natural enemies and hence plants possessing these traits can be considered as resistant entries.

Plants deploy multiple defence strategies to protect themselves against herbivory (Agrawal, 2011) and hence multiple resistance traits may provide a higher level of resistance than could be predicted from their independent action (Romeo, Saunders, & Barbosa, 1996). In our studies, multiple regression analysis indicated that panicle type and nature of adherence of leaf sheath to the pseudostem explained a significant amount of the variance in resistance and therefore are likely to cause resistance against thrips. We could identify eight resistant accessions, which had consistently low thrips damage throughout the study period. These accessions are good sources of host plant resistance, which can be used for future breeding programmes and the morphological traits, which were found to play a role in resistance against cardamom thrips can be used as phenotypic markers for indirect selection of resistance (Gharalari, Smith, Fox, & Lamb, 2009). However, the conclusion about these traits need to be drawn cautiously because some of the accessions with similar morphological traits vary in their degree of resistance and hence there may be some plant secondary metabolites which may also play a covert role in imparting resistance against thrips. Hence, these accessions must be studied for the production of secondary metabolites, if any, which delineate them from the rest of the accessions with similar morphological traits. A detailed metabolomic profiling using modern analytical tools is required to identify biochemical constituents which may play a supplementary role in imparting resistance against thrips. Accessions with erect type panicle and tight leaf sheath were found to be susceptible to the pest and hence need to be avoided. Future breeding programmes, which aim for developing thrips resistant varieties, underpin the need for selection of genotypes having prostrate type panicles with loose-leaf sheath as phenotypic markers to introgress thrips resistance in commercial varieties. However, the plants need to be simultaneously selected for other agronomically important traits such as yield, essential oil content, and so forth before being considered in breeding programmes.

Our findings provide a scope for noninsecticidal management of a highly devastating pest. Future defence strategies against this pest will aim at the use of varieties with defensive morphological traits, exploitation of its bacterial endosymbiont, *Wolbachia* sp. (Jacob et al., 2015) and its naturally occurring entomopathogen, *L. psalliotae* (Senthil Kumar et al., 2015) for organic production of this high-value spice crop of global importance.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

ORCID

Chellappa M. Senthil Kumar https://orcid.org/0000-0001-7336-5447

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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