Research Article

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Dwarf-cashew resistance to whitefly (*Aleurodicus cocois*) linked to morphological and histochemical characteristics of leaves

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Abstract

BACKGROUND: The cashew whitefly (CW), *Aleurodicus cocois*, is an important pest of cashew in Brazil. The use of resistant plants may be an effective strategy for the control of this pest. In a preliminary assay, we found that dwarf-cashew clones show different levels of resistance to CW. Here, we hypothesized that such resistance is associated with morphological characteristics of cashew leaves and their content of phenolic compounds.

RESULTS: We determined (i) the attractiveness and suitability for oviposition of five dwarf-cashew clones towards CW, (ii) the leaf morphology and chemistry of those clones, and (iii) the relationship between leaf characteristics and resistance to CW. In greenhouse multiple-choice assays, PRO143/7 and CCP76 showed, respectively, the lowest and highest counts of both CW adults and eggs. Scanning electron microscopy (SEM) analysis revealed that PRO143/7 and EMBRAPA51 have, respectively, the highest and lowest numbers of leaf glandular trichomes. We found a negative correlation between number of trichomes in the abaxial surface of cashew leaves and CW oviposition. In addition, confocal microscopy analysis and histochemical tests with ferrous sulfate indicated a higher accumulation of phenolic compounds in the resistant clone PRO143/7 relative to the other clones. Dwarf-cashew clones did not significantly differ based on the number of leaf epicuticular striations, and the thickness of both leaf lamina and the epidermal layer.

CONCLUSION: The resistance of dwarf-cashew plants to CW is associated with an elevated number of trichomes and accumulation of high levels of phenolics in leaves. Additionally, the contribution of epicuticular striation density and thickness of leaf lamina/epidermal layer are insignificant.

Keywords: *Anacardium occidentale*; leaf glandular trichomes; leaf phenolic compounds; leaf lamina; leaf surface; Aleyrodidae; Antixenosis; deterrence

1 INTRODUCTION

The cashew whitefly (CW), *Aleurodicus cocois* Curtis (Hemiptera: Aleyrodidae), is a sap-sucking insect that causes direct damage to crops by puncturing leaves during feeding, and indirect damage by promoting the proliferation of sooty molds and viruses.[1] CW is a major pest of dwarf-cashew (*Anacardium occidentale* L.) and is widespread in all growing areas of northeastern Brazil, occurring in the form of episodic but intensive outbreaks that cause significant losses in productivity.[2,3]

Despite the agricultural losses caused by CW, there is a scarcity of cashew-specific pesticides registered in the Brazilian Ministry of Agriculture to control this pest. Under these circumstances, the adoption of an integrated pest management (IPM) strategy involving resistant cashew genotypes is an appealing option. The advantages of such an approach include the reduction of pest populations to levels that do not cause economic damage, positive impacts on the environment, compatibility with other pest control methods, cost-effectiveness, and lasting results.[4,5] Despite the plethora of cashew clones that are commercially available in Brazil,[6] little is known about their resistance to CW and respective mechanisms of resistance. Identification of cashew genotypes expressing traits associated with insect resistance could be valuable for breeding and IPM programs.[7,8]

Plant resistance to whiteflies has been associated with a number of factors, including increased epidermal thickness, type and size of trichomes, production of secondary metabolites, and color of the leaves.[9–12] According to Aoyama and Labinas,[13] enhanced epidermal thickness confers rigidity to leaves owing to increased numbers of overlapping *cellulose microfibrils* incrusted with lignin. Sap-sucking insects need to insert their mandibular stylets deep into plant tissues in order to access the vascular bundles, and a thickened leaf epidermis hinders this process by increasing

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energy demand.[14] Moreover, an increase in the number of tector trichomes on the leaf surface may act as a physical barrier by limiting the mobility of nymphs and larvae,[15–17] while the release of secondary compounds from glandular trichomes may affect food preference, oviposition, and survival.[18,19]

Here, we hypothesized that the resistance of cashew plants to CW is associated with morphological characteristics of leaves and their content of phenolic compounds. We determined (i) the relative attractiveness and suitability for oviposition of five dwarf-cashew clones towards CW, (ii) the leaf morphology and chemistry of those clones, and (iii) the relationship between leaf characteristics and resistance to CW.

2 MATERIAL AND METHODS

2.1 Plant material

The dwarf-cashew clones CCP76, BRS226, EMBRAPA51, BRS274 and PRO143/7, originating from the germplasm bank of Embrapa Agroindústria Tropical (Fortaleza, CE, Brazil), were selected for investigation of the characteristics associated with resistance to *A. cocois*. This selection was based on preliminary experiments where the infestation rates of *A. cocois* on 25 dwarf-cashew genotypes was assessed in the field. The clones that stood out as the most susceptible or resistant to *A. cocois* were selected.[20]

2.2 Attraction and oviposition assays

The objective of this multiple-choice assay was to correlate leaf characteristics with attraction and oviposition preferences of CW females. The experimental design was completely randomized with five replicates, each involving one dwarf-cashew seedling featuring mature leaves (120 days old) selected from each of the studied clones. The plants were distributed randomly inside a 1.0 m cube screen cage and spaced at least 15 cm apart in order to prevent contact between the leaves. One hundred adult female whiteflies (20 insects per plant) were released into the cage and the attraction of insects to plants was evaluated after 24 h by counting, with the aid of a mirror, the number of insects present on the abaxial surfaces of the leaves. The insects were carefully removed in tubes. Subsequently, the eggs laid on leaves were counted. Seedlings were used as an exception to adult plants in this assay because it required plant confinement in cages, which would not be feasible with adult plants. However, adult 3-year-old plants were used in the next three microscopy experiments.

2.3 Scanning electron microscopy

Morphological analyses were carried out by scanning electron microscopy (SEM) using a Tescan (São Bernardo do Campo, Brazil) Vega 3 microscope under an acceleration voltage of 15 kV. The experimental design was completely randomized with three replicates each involving five leaf fragments removed from three different individuals of each dwarf-cashew clone. The leaves were collected from 3-year-old adult plants in the experimental station of Embrapa Agroindústria Tropical (Pacajus, CE, Brazil). Plant material was treated with Karnovsky fixative for 48 h, washed three times (10 min each) with phosphate buffer, post-fixed with 1% osmium tetroxide for 1 h, washed in distilled water, dehydrated by treatment with ethanol solutions of increasing concentration (20, 30, 40, 50, 60, 70, 80, 90%) (15 min each) and finally washed three times (15 min each) in 100% ethanol. Samples were submitted to critical point drying, mounted on stubs, sputter coated with platinum, and examined by SEM. For each sample, we determined the number of glandular trichomes in 1.05 mm^2 areas of abaxial surface, the number of epicuticular striations between stomata, the thickness of the leaf lamina (μm), and the thicknesses of the epidermal layers on the abaxial and adaxial surfaces (μm).

2.4 Confocal microscopy

Histochemical analyses of leaves of the selected dwarf-cashew clones were performed in order to detect the presence of phenols. In the first assay, six leaf fragments were removed from each of the clones and submitted to paradermic and longitudinal sectioning. Samples were separated into two groups, one of which was retained as non-treated control and the other was treated with Neu's reagent [2-aminoethyl diphenylborinate (10 g L^{-1}) and polyethylene glycol 4000 (50 g L^{-1}) in 95% ethanol], which binds to specific chemical groups and enhances the fluorescence of flavonoids.[21] Treated and non-treated samples were mounted

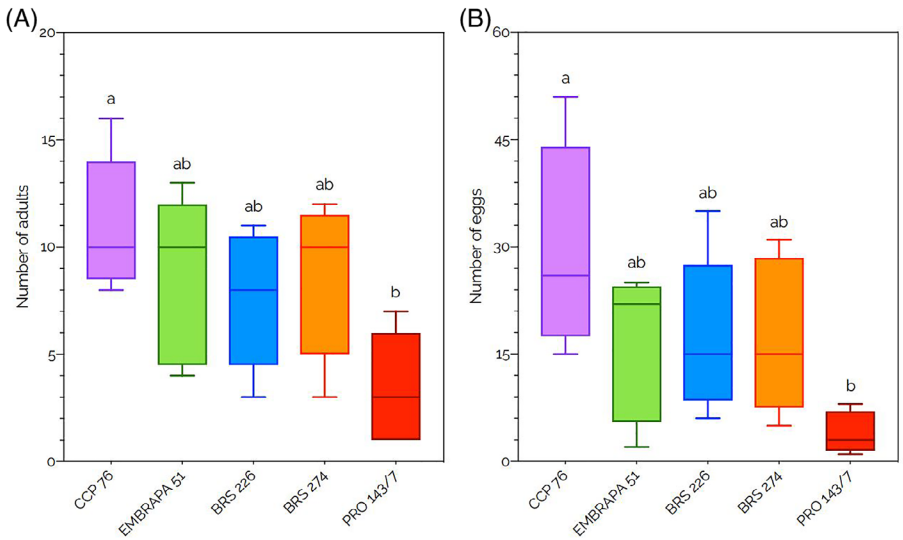

Figure 1. Resistance of dwarf-cashew clones to cashew whitefly (CW), *Aleurodicus cocois*, in greenhouse, multiple-choice tests. (A) Number of CW adults on leaves. (B) Number of CW eggs on leaves. $N = 5$. Adults: $F_{4,20} = 3.47$, $P = 0.0262$. Eggs: $F_{4,20} = 3.70$, $P = 0.0207$. Boxes with different letters significantly differ from each other according to Tukey's test ($\alpha = 0.05$).

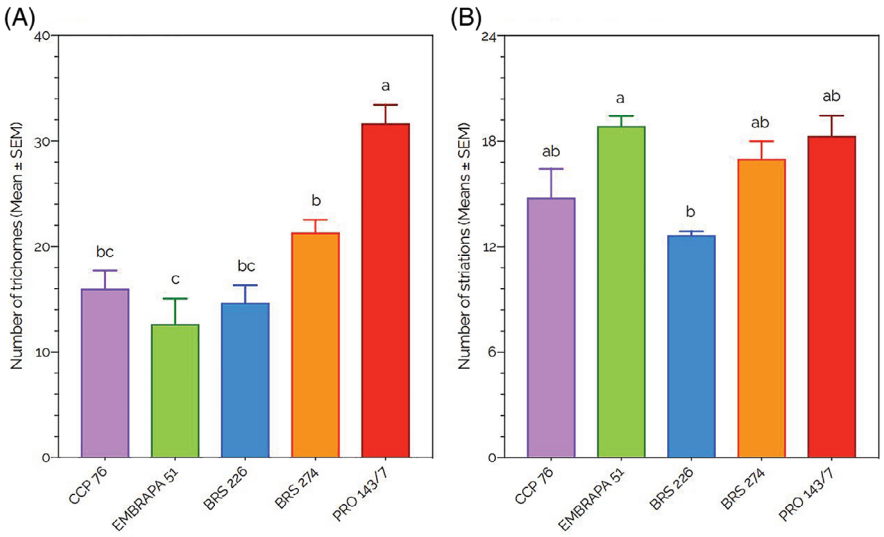

Figure 2. Morphological characteristics (mean ± SEM) of leaves of five dwarf-cashew clones with different levels of resistance to the cashew whitefly, *Aleurodicus cocois*, from scanning electron micrographs. (A) Number of glandular trichomes on the abaxial leaf surface. (B) Number of epicuticular striations between stomata. $N = 3$ plants, each donating five leaf fragments for analysis. Trichomes: $F_{4,10} = 18.11$, $P = 0.0001$. Striations: $F_{4,10} = 6.21$, $P = 0.0089$. Columns with different letters significantly differ from each other according to Tukey's test ($\alpha = 0.05$).

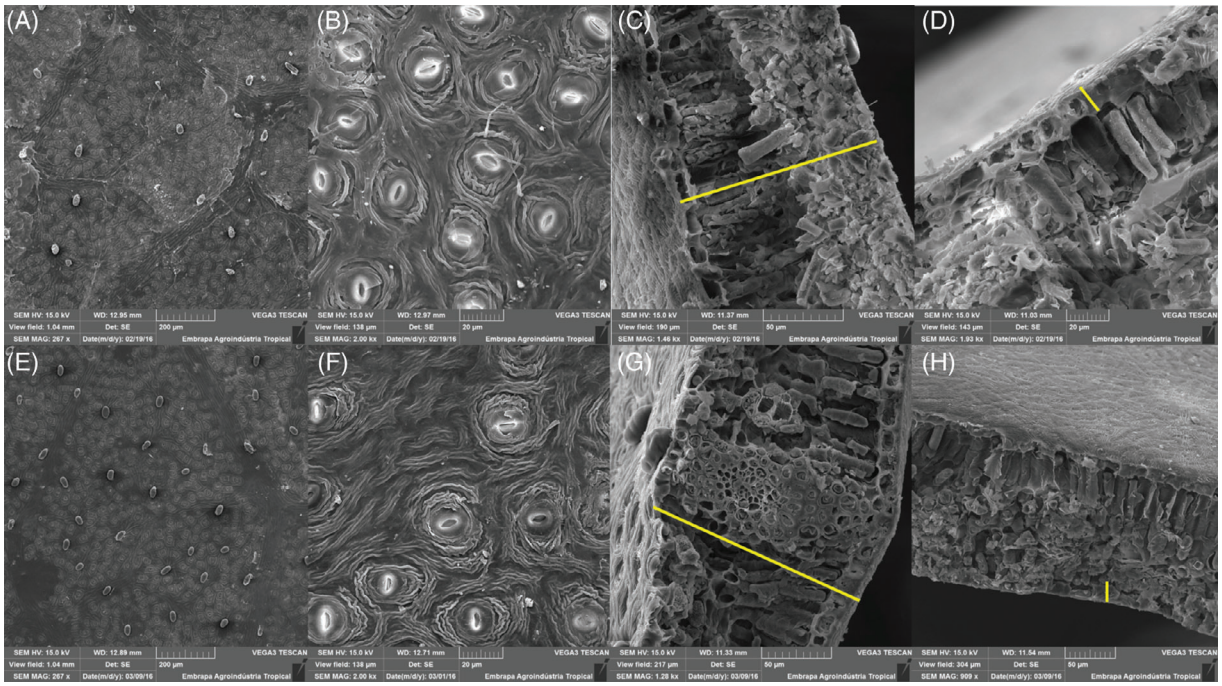

Figure 3. Scanning electron micrographs of leaves of dwarf-cashew clones that are susceptible (A–D, CCP76) and resistant (E–H, PRO143/7) to the cashew whitefly, *Aleurodicus cocois*. (A) and (E) Density of glandular trichomes on the abaxial leaf surface (267× magnification). (B) and (F) Epicuticular striations between stomata (2000× magnification). (C) and (G) Cross-section of the leaf lamina with leaf thickness indicated by yellow line (1460× magnification). (D) and (H) Abaxial epidermis with epidermal thickness indicated by yellow line (1930× magnification). Micrographs: C.R. Muniz.

on semi-permanent slides and examined/photographed using a Zeiss (Oberkochen, Germany) model LSM710 confocal laser scanning microscope (CLSM) with a 40× objective, an ultraviolet filter (450–490 nm) and a barrier filter (520 nm) for fluorescence viewing.

2.5 Optical microscopy

In the second assay, leaf fragments from each of the clones were fixed in ferrous sulfate solution (0,002 g L^{-1}) for 48 h to determine the presence of total phenols.[22] Treated and non-treated (control) samples were washed with distilled water, cross-sectioned, mounted onto slides under water and examined by light microscopy using a Leica (Wetzlar, Germany) model DM4000 B digital microscope with light emitting diode (LED) illumination coupled with a digital camera.

2.6 Statistical analysis

After confirmation of normality (Shapiro–Wilk, D'Agostino & Pearson, and Kolmogorov–Sminorv's tests) and homoscedasticity (Barllet's and Brown–Forsythe's tests), one-way ANOVA

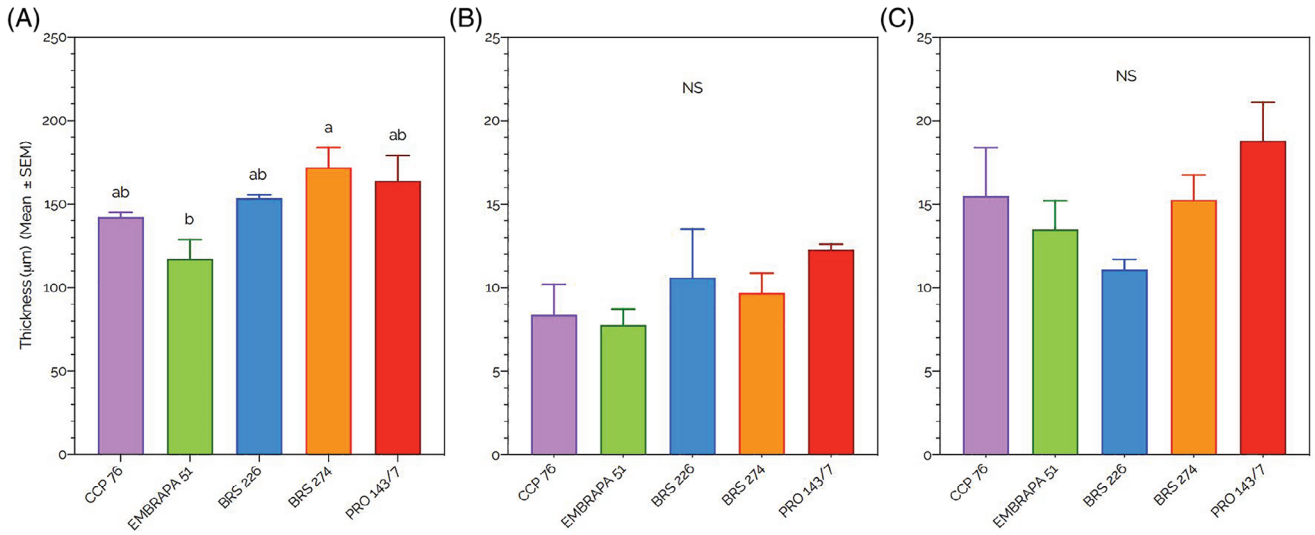

Figure 4. Morphological characteristics (mean ± SEM) of leaves of five dwarf-cashew clones with different levels of resistance to the cashew whitefly, *Aleurodicus cocois*, from scanning electron micrographs. (A) Leaf thickness across the leaf lamina. (B) Thickness of the abaxial epidermal layer. (C) Thickness of the adaxial epidermal layer. $N = 3$ plants, each donating five leaf fragments for analysis. Leaf lamina: $F_{4,10} = 4.43$, $P = 0.0257$. Abaxial epidermal layer: $F_{4,8} = 1.93$, $P = 0.1982$. Adaxial epidermal layer: $F_{4,8} = 2.02$, $P = 0.1843$. Columns with different letters significantly differ from each other according to Tukey's test ($\alpha = 0.05$). NS = non-significant difference among clones.

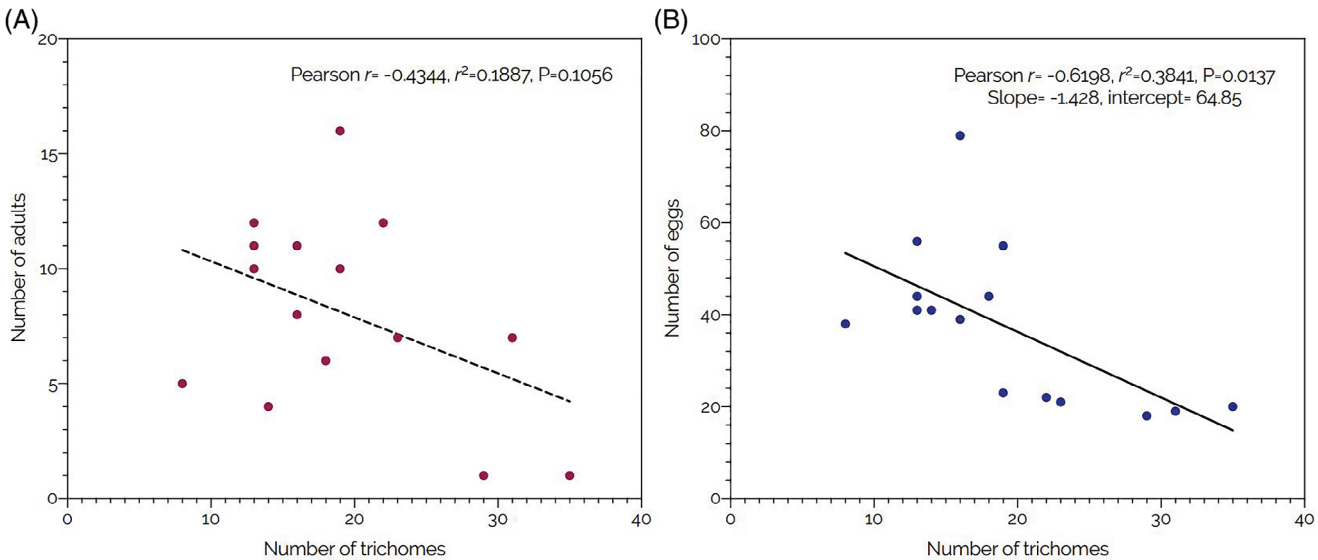

Figure 5. Correlation between number of glandular trichomes on the abaxial leaf surface of dwarf-cashew plants and number of individuals of cashew whitefly (CW), *Aleurodicus cocois*. (A) CW adults. (B) CW eggs. Pearson's correlation coefficient (r) ($\alpha = 0.05$).

followed by Tukey's test ($\alpha = 0.05$) was applied to test the effects of dwarf-cashew clone on the number of CW adults and eggs, the number of leaf trichomes and epicuticular striations, and the thickness of leaf lamina, the abaxial epidermal layer, and the adaxial epidermal layer. Additionally, we tested for correlations between numbers of CW adults and eggs versus the plant trichome density using the Pearson's correlation coefficient (r) ($\alpha = 0.05$). All analyses were performed using GraphPad Prism version 8.0.2 for Mac OS X (GraphPad Software, La Jolla, CA, USA).

3 RESULTS

3.1 Attraction and oviposition assays

We observed significant differences among the five dwarf-cashew clones tested regarding both number of CW adults ($F_{4,20} = 3.47$, $P = 0.0262$) and eggs ($F_{4,20} = 3.70$, $P = 0.0207$) on leaves. PRO143/7 had significantly fewer adults and eggs than CCP76, but no significant differences were found between either of these two clones and all the other tested clones (Fig. 1) regarding both adults and eggs.

3.2 Scanning electron microscopy

Densities of leaf trichome were strongly different among dwarf-cashew clones ($F_{4,10} = 18.11$, $P = 0.0001$). PRO143/7 and EMBRAPA51 showed the highest and lowest trichome densities of all tested clones, respectively. However, no significant differences were found among EMBRAPA51, CCP76, and BRS226 (Figs 2(A) and 3(A,E)). The number of epicuticular striations between stomata was affected by dwarf-cashew clone ($F_{4,10} = 6.21$, $P = 0.0089$). Striations were highest and lowest, respectively, in EMBRAPA51 and BRS226.

However, we found no significant differences between either of these two clones and all the other tested clones (Figs 2(B) and 3(B,F)). In addition, we observed that the vascular system in the leaves of the resistant PRO143/7 comprised broad and highly lignified cell walls compared to the susceptible CCP76. A significant effect of dwarf-cashew clone was found on thickness of leaf lamina ($F_{4,10} = 4.43$, $P = 0.0257$). BRS274 and EMBRAPA51 showed the highest and lowest thickness, respectively. However, we found no significant differences among either of these two clones and all the other tested clones (Figs 3(C,G) and 4(A)). Dwarf-cashew clone did not significantly affect the thickness of epidermal layer, either in the abaxial ($F_{4,8} = 1.93$, $P = 0.1982$) or in the adaxial ($F_{4,8} = 2.02$, $P = 0.1843$) surface (Figs 3(D,H) and 4(B,C)). There was no significant correlation between the number of adults on plants and trichome density (Pearson $r = -0.4344$; $r^2 = 0.1887$, $P = 0.1056$). However, we observed a negative correlation between the number of eggs and trichome density (Pearson $r = -0.6198$; $r^2 = 0.3841$, $P = 0.0137$, slope = −1.428, intercept = 64.85) (Fig. 5).

3.3 Confocal microscopy

Longitudinal sections of leaf fragments that had been treated with Neu's reagent exhibited a greenish fluorescence, especially in the epidermal cells (Fig. 6), when examined by CLSM under UV illumination, while non-treated samples showed no such fluorescence. Although we observed fluorescence in the samples of all clones, its intensity was particularly strong in PRO143/7 (Fig. 6(J)). In samples from CCP76 and EMBRAPA51, the fluorescence was less intense (Fig. 6(F,H)).

3.4 Optical microscopy

Microscopic examination of cross-sections of leaf fragments that had been treated with ferrous sulfate confirmed the presence of phenols in the epidermal and mesophyll layers of all clones, as demonstrated by the black–brown areas in the micrographs (Fig. 7). The reaction was more intense in leaf samples from PRO143/7 (Fig. 7(J)) in comparison with the other clones, especially CCP76 (Fig. 7(F)).

4 DISCUSSION

With the attraction and oviposition assays, we demonstrated that the dwarf-cashew clone PRO143/7 is resistant to CW relative to CCP76 in semi-field conditions, as it had been observed in field in a preliminary assay.[20] Our morphological and histochemical analysis revealed that the leaves of such a resistant clone featured higher glandular trichome density, as well as higher intensity of phytochemicals (aromatic amino acids, flavonoids, and phenolic compounds) relative to the other clones, showing that these leaf characteristics are associated with resistance of PRO143/7 to CW.

The presence of glandular trichomes in plants decreases attack by herbivores and indicates resistance to whiteflies.[12,23–25] Hasanuzzaman *et al.*[11] reported that varieties of eggplant that contained high densities of glandular trichomes negatively affected the landing, feeding, and oviposition preferences of *B. tabaci*. The abaxial surfaces of cashew leaves are preferred for feeding and oviposition by CW,[6] thus a high density of glandular trichomes in this area represent a physical barrier for the pest. Our data on oviposition and glandular trichome density support this hypothesis as it shows that the number of CW eggs on leaves decreases as trichome density increases.

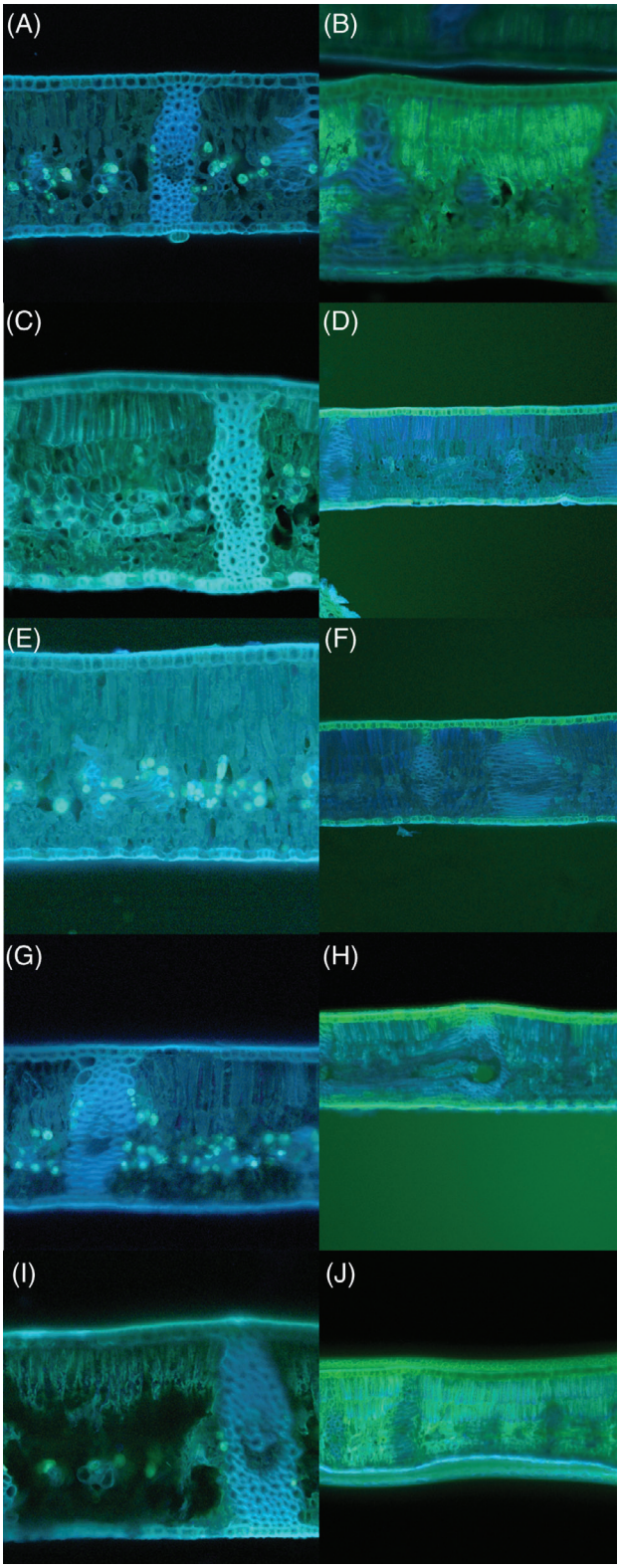

Figure 6. Confocal laser scanning micrographs of the longitudinal sections of leaves of dwarf-cashew clones treated with Neu's reagent and corresponding non-treated controls. Clone BRS226, (A) non-treated and (B) treated; BRS274, (C) non-treated and (D) treated; CCP76, (E) non-treated and (F) treated; EMBRAPA51, (G) non-treated and (H) treated; PRO143/7, (I) non-treated and (J) treated. The greenish fluorescence observed in all clones and with higher intensity in PRO143/7 is typical of phenols. Micrographs: C.R. Muniz.

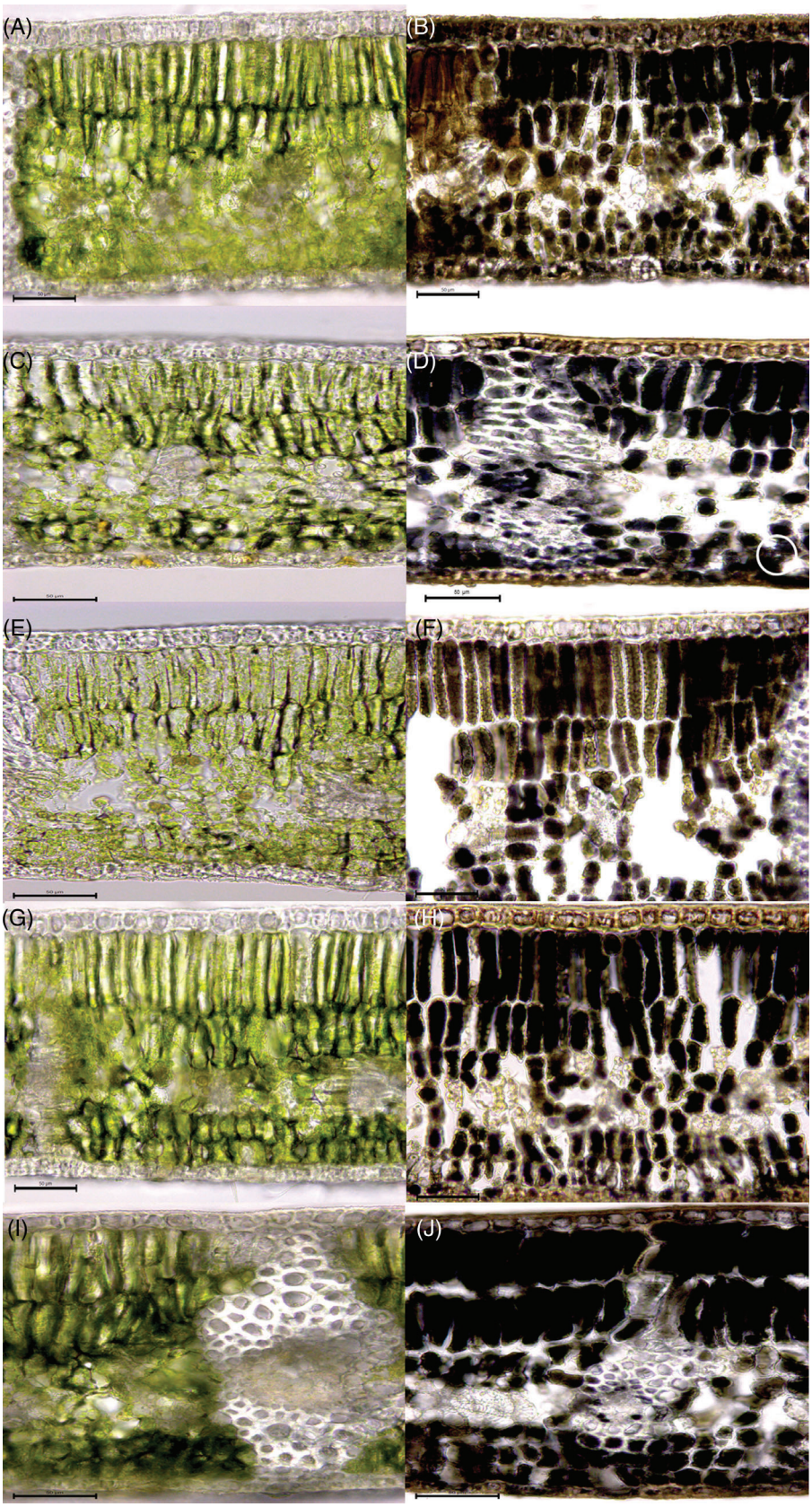

Figure 7. Optical micrographs of cross-sections of leaves of dwarf-cashew clones treated with ferrous sulfate solution and corresponding non-treated controls. Clone BRS226, (A) non-treated and (B) treated; BRS274, (C) non-treated and (D) treated; CCP76, (E) non-treated and (F) treated; EMBRAPA51, (G) non-treated and (H) treated; PRO143/7, (I) non-treated and (J) treated. The black–brown color indicates the presence of phenols. Micrographs: A.A. Soares and C.R. Muniz.

Another possible mechanism of resistance afforded by glandular trichomes is chemical protection since these leaf structures can excrete lipids, terpenoids, and polyphenols.[26,27] Previous reports have shown negative correlations between glandular trichome density and attraction/oviposition preference of whiteflies.[10,28,29] According to Simmons and Gurr,[30] the glandular trichomes of *Lycopersicon* species release exudates containing ketones, such as 2-tridecanone and 2-undecanone, which act to deter or repel arthropod pests. Glandular trichomes can store volatile terpenoids such as 7-epizingiberene, p-cymene, a-terpinene, and a-phellandrene, which confer antixenotic resistance to whiteflies.[31,32] In the young shoots of birch (*Betula*), phenolics from the glandular trichomes act as defense mechanisms and have important roles in the plant's resistance against insect pests.[33,34] It is possible that phenolics in the glandular trichomes of *B. pubescens* may be as important in birch resistance against herbivores as foliar phenolics.[35,36] In our study, confocal and optical microscopy analysis showed that PRO143/7 accumulates higher amounts of aromatic amino acids, flavonoids, and other phenolic compounds relative to CCP76 and EMBRAPA51, which is consistent with the higher density of glandular trichomes observed in the resistant clone (PRO143/7). However, we observed a lack of correlation between number of CW females and trichome density, while dwarf-cashew clone affected both number of females and of trichomes, as previously discussed. This implies that trichome-related chemicals most likely play an insignificant role in the repellent potential of dwarf-cashew clones to CW adults, and suggests that the negative impact of trichomes on CW oviposition is based on deterrence by chemical and physical mechanisms.

Epidermal thickness can be augmented by the deposition of lignin, cellulose, and hemicellulose, hence leaf cells with augmented epidermal layers are far more rigid and, therefore, more resistant to the attack of herbivores.[13] Cuticle and cell wall thicknesses, as well as epicuticular wax deposition, act as physical barriers by hindering movement, feeding, and oviposition of herbivores that feed directly from the epidermal cells. In onion plants, these structural characteristics were associated with resistance of different cultivars to *Thrips tabaci*.[37] Populations of the whitefly *B. tabaci* have been positively correlated with the thickness of leaf lamina in cotton,[38] black gram (*Vigna mungo*),[39] and eggplant.[11] In our study, the five dwarf-cashew clones tested showed similar thickness of both abaxial and adaxial epidermal layers despite displaying different levels of resistance to CW based on both attraction and oviposition trials. In addition, the impact of dwarf-cashew clone on thickness of leaf lamina and epicuticular striations strongly differed from the clone impact on number of adults and eggs found on leaves. Therefore, the thicknesses of leaf lamina and the epidermal layer, as well as epicuticular striations, do not contribute significantly to the resistance of dwarf-cashew clones to CW.

Phenolic compounds are the most common group of plant defense secondary metabolites and include simple phenols and phenolic acids, hydroxycinnamic acid derivatives, and flavonoids, all of which play an important role in host plant resistance against herbivorous insects.[40] Indeed, the presence of high concentrations of phenolics has been negatively correlated with the resistance of eggplant,[12] cotton,[41–43] and mung beans (*Vigna radiata*)[44] towards *B. tabaci*. Within this class of natural compounds, the condensed tannins (polyphenols) have significant insect resistance properties since they bind to proteins, inhibiting digestion and delaying growth of the herbivores. In this regard, cashew plants are very rich sources of tannins.[45] However, in agreement with the morphological analysis previously discussed, the fluorescence technique carried out in our study revealed that the five dwarf-cashew clones here tested differ in their contents of amino acids and phenolic compounds, with the resistant clone PRO143/7 showing higher contents relative to the susceptible CCP76 and EMBRAPA51. It is worth noting that EMBRAPA51 and CCP76 are extensively grown by farmers in northeastern Brazil, where the latter is intensively attacked by CW.[46] In a breeding program that aims at incorporating mechanisms of resistance to biotic factors such as pests and diseases, PRO143/7 arises as a source of interesting characteristics that will contribute to the development of CW-resistant varieties of dwarf-cashew.

The present study focused on the role of physical and chemical barriers in the previously reported resistance of PRO143/7 to CW. First, we confirmed that PRO143/7 is resistant to CW. Second, we demonstrated that the presence of large numbers of trichomes and epicuticular striations, as well as the accumulation of high levels of phenolics in the leaves, are factors that discourage CW landing and oviposition, consequently conferring resistance of PRO143/7 to CW. Third, we showed that thickness of leaf lamina and thickness of epidermal layer of leaves do not contribute to such a resistance. Hence, the presence of large numbers of trichomes and epicuticular striations, as well as the accumulation of high levels of phenolics in the leaves, should be considered as resistance factors in future breeding programs of dwarf-cashew. Additionally, the resistance of PRO143/7 to CW makes this clone the most appropriate candidate for further investigation within our genetic improvement program at Embrapa Agroindústria Tropical, especially if we consider that besides the resistance to CW, PRO143/7 produces better quality cashew nuts than CCP 76. A trichome/phenolic-based resistance approach could be further investigated in PRO143/7 with the aim of creating healthier plants thus reducing pesticide usage, although the commercialization of this genotype still depends on the improvement of its agronomical and industrial attributes.

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AUTHOR CONTRIBUTION STATEMENT

ESSG, CRM, and NDSDP conceived and designed research. ESSG, CRM, JCA, and AAS conducted experiments. NDSDP and FCVN contributed with reagents and/or analytical tools. CSBDS analyzed data. ESSG, CRM, NDSDP, and CSBDS wrote the manuscript. All authors read and approved the manuscript.

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