



Structural plasticity in roots of the hemiepiphyte *Vanilla phaeantha* Rchb.f. (Orchidaceae): a relationship between environment and function

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Abstract

The aerial environment appears to structurally modify roots, which frequently show specializations for absorbing water and nutrients. Among those specializations are the velamen, a multiseriate epidermis generally composed of dead mature cells, and greater degrees of lignification in the endodermis, exodermis, and pith. *Vanilla phaeantha* is a hemiepiphyte used here as a model of study to determine which root characteristics demonstrate the most plasticity in response to aerial and terrestrial environments. It produces roots growing under three conditions: (1) aerial and free, growing from the highest branches towards the ground; (2) aerial roots attached to the phorophyte; and (3) terrestrial. Samples taken 3 cm from the apices were used to prepare histological slides. The tissues and other anatomical structures were measured and histochemically characterized. The most plastic characteristics were the external periclinal thicknesses of the exodermis and the total area occupied by the aerenchyma lacunae. The free roots were the longest, did not evidence root hairs, and had the largest number of the aerenchyma lacunae; they also evidenced greater thicknesses of the exodermis in contact with the epidermis walls that helped maintain their shapes. Terrestrial roots had root hairs around the entire circumference and intense infestations of mycorrhiza, indicating their involvement in nutrient acquisition. The adhering roots evidenced free regions similar to those of aerial roots, as well as adhering regions showed characteristics similar to terrestrial roots (with root hairs and mycorrhiza infestations).

Keywords Orchid · Epiphytic · Phenotypic plasticity · Root anatomy · Velamen

Introduction

There are various advantages to the epiphytic lifestyle, especially the greater access to sunlight in the upper canopy. Those advantages, however, are accompanied by significant limitations in acquiring water and nutrients (Benzing 1990; Coxson and Nadkarni 1995; Holbrook and Putz 1996a, b, c; Swagel et al. 1997). Epiphytic plants are notably subject to deficits in access to those resources, although they exhibit compensatory morphological and physiological strategies through their vegetative organs (Silva and Milaneze-Gutierrez

2004). Examples of those strategies can be seen in their specialized root systems, with aerial roots exhibiting adaptive anatomical characteristics designed to capture and absorb water and minerals, and perform photosynthesis (Benzing 1990; Black 1973; Moreira et al. 2013).

Approximately 75% of all orchid species are epiphytes (Zotz et al. 2021). Their root systems comprise adventitious roots whose tissues are covered by a simple or multiple epidermis composed of dead cells, called velamen (Dycus and Knudson 1957). The term “velamen radicum” was coined by Chatin (1856) and Schleiden (1843) to refer to a multiseriate epidermis. Subsequently, Engard (1944) and Dycus and Knudson (1957) reinforced the concept of velamen as a multiple epidermis, but encountered a single layer of epidermal cells in *Vanilla planifolia* (synonym of *Vanilla fragans*), and consequently accepting the possibility of velamen as a tissue composed of only a single layer. Porembski and Barthlott (1988) adopted the term velamen to define a uni- or multiseriate epidermis that comprised of dead cells delimited

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Fig. 1 *Vanilla phaeantha* in a gallery forest in the region of Araguari, Minas Gerais State, Brazil. (a) Overview, showing the hemiepiphyte growing on a phorophyte, from soil level up to 5 m. (b) Detail of the phorophyte adhering roots (arrows). (c) Detail of the terrestrial roots (arrows). (d) Detail of the free roots in their initial stages of development (arrow)

internally by an exodermis, regardless of functional aspects. Those authors described different types of parietal thicknesses at maturity and the presence of an epivelamen (the outermost velamen layer, differentiated from other velamen cells).

Internal to the velamen is the cortical parenchyma, located between the exodermis and the endodermis (the outermost and innermost layer of the cortex, respectively). Endodermal and exodermal cells can be highly lignified and dead at maturity and intercalated by passage cells (alive at maturity) (Pridgeon 1987; Trépanier et al. 2009; Joca et al. 2017). The parenchymatic cortex contains cells that can exhibit different parietal thicknesses, being phi, reticulated, or uniform (Stern & Whitten 1999; Stern and Judd 2001; Moreira et al. 2013; Joca et al. 2017). Internal to the endodermis is the vascular cylinder, which can contain xylem bundles and phloem surrounding the pith (Oliveira and Sajo 1999).

Among the orchids, the genus *Vanilla* Mill comprises 115 predominately hemiepiphyte species distributed in tropical and subtropical regions in North America, South America, Africa, and Asia (Cameron 2011). Hemiepiphytes generally constitute a relevant component of tropical vegetation, with more than 800 species (Zotz 2013). In some cases, as with *Vanilla*, hemiepiphytes germinate in the soil, establishing contact with the trunk of the host plant (i.e., phorophyte), and subsequently climbing using adhering roots to become epiphytes; those plants can reconnect with the soil again through aerial roots (Kress 1989; Putz and Holbrook 1986). Those two types of aerial roots are encountered in the genus *Vanilla* and take on different roles: shorter and non-ramified adhering roots, generally of limited growth, hold the orchid to the phorophyte, while longer and ramified free roots of unlimited growth grow downwards toward the soil (substrate) (Stern and Judd 1999). In *Vanilla*, aerial and terrestrial roots have different structures that physiologically affirm their different functional properties, such as the larger caliber of the metaxylem of the terrestrial roots, which have the function of absorption (Stern and Judd 1999). The aerial environment, therefore, appears to structurally mold those roots, generating morphological characteristics that differentiate them from terrestrial roots. In other genera, greater lignification degrees have been observed in the endodermis, exodermis, and pith of aerial roots of epiphytic plants (Moreira and Isaias 2008). Studies

such as Moreira and Isaias (2008) have been primarily based on comparisons between epiphytic and terrestrial species. *Vanilla phaeantha* has a wide distribution in Brazil, occurring both in dry environments and in semideciduous forests (Karremans et al. 2020). In this way, studies focusing on the structure and functions performed by the roots can help in the understanding of this species establishment in new environments. Here, we sought to measure the phenotypic plasticity of *V. phaeantha* roots to determine which characteristics are most plastic and reflect specializations to either epiphytic or terrestrial environments.

Despite the taxonomic proximity of various genera that have velamen in the roots, and the velamen presence in epiphytic species, the genus *Vanilla* is traditionally associated with a simple epidermis (Engard 1944; Stern and Judd 1999). Stern and Judd (1999) considered the simple epidermis as velamen based on the thickening of the walls in diverse species of the genus (such as *V. poitaei* Rchb.f. and *V. madagascariensis* Rolfe). Velamen is, therefore, characterized by the presence of dead cells at maturity, commonly evidencing thickenings of their cell walls. As such, the present study sought to reevaluate the simple epidermis observed in *V. phaeantha* as velamen, while reconsidering the structural and physiological concept of that tissue.

Material and methods

Study area and the plant species

The present study was undertaken in a gallery forest located in the Permanent Preservation Area of the privately owned Fazenda Quilombo, located in the municipality of Araguari, Minas Gerais State, Brazil (763 m.a.s.l., 18°43'58.5"S 48°02'58.9" W). The local climate is tropical type Aw according to the Köppen classification system (Alvares et al. 2013). The mean annual temperature is near 21.4°C, and the mean monthly precipitation rate is about 127 mm. A rainy season occurs between October and March (with a mean monthly rainfall rate of 220 mm), followed by a dry austral winter from April to September (with a mean monthly rainfall rate of 22 mm). The *V. phaeantha* population studied, however, occurs in a gallery forest with high humidity levels in the soil throughout the year, having only major variations in the relative humidity of the air during the two marked seasons.

The study species is a secondary hemiepiphyte with wide geographic distribution, present in North, Central, and South America, and in the Antilles (Karremans et al. 2020). It can reach heights of 5 m, extending from the soil to the canopy

of a single phorophyte (Fig. 1a). Adventitious roots that adhere to the phorophyte (Fig. 1b), while completely free roots descend towards the soil (Fig. 1c); additional roots grow close to the leaf litter and fix the epiphyte to the soil (Fig. 1d) (Ferreira et al. 2017; Alconero 1968).

Structural analyses

Fragments of each type of root (roots that initiate directly at soil/terrestrial levels, roots adhering to the phorophyte, and completely free roots) were collected for anatomical and histochemical analyses. Root fragments were excised at 3 cm from the apices of each type of root from different five individuals of *V. phaeantha* ($n = 5$). The fragments were then fixed in FAA50 (formaldehyde, acetic acid, 50% ethyl alcohol, 1:1:18 v/v) for 48 h and then stored in 70% ethyl alcohol (Johansen 1940).

To prepare the histological slides, transversal and longitudinal sections were manually prepared using razor blades. Fragments were cleared in 50% sodium hypochlorite, washed in distilled water (Kraus and Arduin 1997), and then stained with 1% aqueous solutions of Astra blue and safranin (9:1 v/v) (Bukatsch 1972, modified). The slides were mounted with glycerinated gelatin (Kaiser 1880) and photomicrographed using an ICC50 HD digital camera coupled to a DM500 microscope (Leica, Germany).

Three sections of each root were utilized for the histometry. We counted the number of protoxylem strands in the vascular cylinder and the number of aerenchyma lacunae in the cortex. The transversal area of the root, the transversal areas occupied by the root cortex and the vascular cylinder, the total area occupied by the aerenchyma lacunae, the areas of the metaxylem vessels, the thicknesses of the epidermis and exodermis, and the thickness of the cell wall of the exodermis in contact with the epidermis were measured using Image J software (version 1.51, National Institute of Health, EUA). The data used for the analyses were based on the means of three measurements of the same section. In terms of the roots adhering to the substrate, the measurements were always performed on free sections of the roots to avoid any deformations resulting from contact with the phorophyte.

Observations of thin sections involved embedding the samples in methacrylate resin, following the manufacturer's recommendations (Historesin® Leica, Germany). Samples were sectioned in transversal and longitudinal planes (10 μm) using a rotary microtome (YD315, ANCAP, Brazil). The sections were then stained with 0.05% toluidine blue in 0.1 M phosphate buffer (pH 6.8) (O'Brien et al. 1964) and photomicrographed using a digital camera coupled to a microscope (Leica, DM1000, Germany).

The parietal thicknesses of the epidermis/velamen and the exodermis were visualized using a scanning electron microscope (Zeiss EVO MA10, Germany). Samples from the three types of roots were fixed in FAA50 (Johansen 1940) and gradually dehydrated in an acetone series (O'Brien and McCully 1981). Sections were then submitted to critical point CO₂ drying and metallized with gold, following Silveira (1989). The material was examined in the Instituto de Química at Universidade Federal de Uberlândia.

Histochemical analyses

Freehand sections were treated with Sudan III and Lugol solution (iodine + potassium iodide) to detect total lipids and starch, respectively (Johansen 1940). Proteins were tested in the sections cut using the rotary microtome to determine if the epidermal cells were alive. The sections were treated with 1% bromophenol blue, and then washed with 0.5% acetic acid, followed by distilled water (Durrum 1950). Temporary slides were mounted in water and immediately inspected under a microscope (Leica, DM1000, Germany).

For the histochemical localization of lignin in the root cell walls, freehand sections were mounted in distilled water and analyzed using a Leica DM500 optical microscope with fluorescence system, coupled with a HD5000 digital camera with a DAPI emission filter (excitement spectrum: 385–400 nm) (Chomicki et al. 2014; Joca et al. 2020). The presence of lignin was confirmed using an alcohol solution of 1% Floroglucin, with the addition of a second solution of 25% HCl (Johansen 1940; Joca et al. 2020).

Quantitative data analysis

The histometric data were compared using JMP software (SAS Institute, EUA). The data that demonstrated normality according to the Shapiro–Wilk test was used to determine the structural differences between the three types of roots through an ANOVA test (JMP, SAS Institute, EUA). The data that did not demonstrate the parametric suppositions of normality were analyzed using the Kruskal–Wallis test. Differences among the factors or parameters were considered significant at a 5% level of probability.

The histometric data were evaluated in terms of their plasticity based on the Relative Distances Plasticity Index (RDPI) as proposed by Valladares et al. (2006). The RDPI was calculated based on a X_{ij} matrix, where i (lines) are the individuals analyzed, and j (columns) refer to environmental conditions (adhering, free, or terrestrial roots). The RDPIs were calculated based on the formula $RDPI = \Sigma$

Table 1 Structural characteristics of the roots of the hemiepiphyte *Vanilla phaeantha* (Orchidaceae) growing adhering to a phorophyte, free, and fixed to the soil (terrestrial). Values with different letters on the same line are different by the Tukey test at a 0.05 level of significance

	Free (aerial root)	Adhering to the phorophyte	Fixed to the soil (terrestrial root)	<i>p</i>
Transversal area of the roots (mm ²)	1.09 ± 0.23b	1.09 ± 0.38b	1.47 ± 0.36a	<0.01
Thickness of the epidermis (µm)	36.76 ± 6.79a	29.75 ± 4.60a	28.79 ± 11.70a	>0.05
Thickening of the cell wall of the exodermis in contact with the epidermis (µm)	6.13 ± 1.68a	7.82 ± 2.65a	4.40 ± 1.76b	<0.01
Thickness of the exodermis (µm)	53.24 ± 10.22a	61.88 ± 8.50a	57.89 ± 18.20a	>0.05
Transversal area of the root cortex + vascular cylinder (mm ²)	1.00 ± 0.22b	1.02 ± 0.36b	1.35 ± 0.35a	<0.01
Transversal area of the cortex (mm ²)	0.87 ± 0.20b	0.88 ± 0.33b	1.24 ± 0.31a	<0.01
Transversal area of the vascular cylinder (µm ²)	0.14 ± 0.03a	0.14 ± 0.04a	0.11 ± 0.05a	<0.05
Number of aerenchyma lacunae	11.47 ± 3.14a	9.20 ± 1.70b	8.87 ± 1.68b	<0.05
Area of aerenchyma lacunae of the cortex in cross section (µm ²)	66,497.5 ± 44,698.6a	49,585.0 ± 29,640.4a	49,871.0 ± 26,388.8a	>0.05
Number of protoxylem strands	12.87 ± 1.36a	11.33 ± 0.90b	9.40 ± 1.24c	<0.0001
Mean area of metaxylem vessels (µm ²)	1239.9 ± 435.2a	1459.9 ± 290.4a	1169.9 ± 599.1a	>0.05

$(d_{ij} \rightarrow i'j' / (x_{ij} + x_{j'i'})) / n$, where $j \rightarrow j'$ represents the number of conditions, $i \rightarrow i'$ the number of individuals, n is the total number of distances, and x is the characteristic to be analyzed. RDPI can vary between 0 (without plasticity)

to 1 (high plasticity). Considering that the data did not demonstrate normality, the differences in plasticity were detected using the Kruskal–Wallis test (at a 5% level of probability).

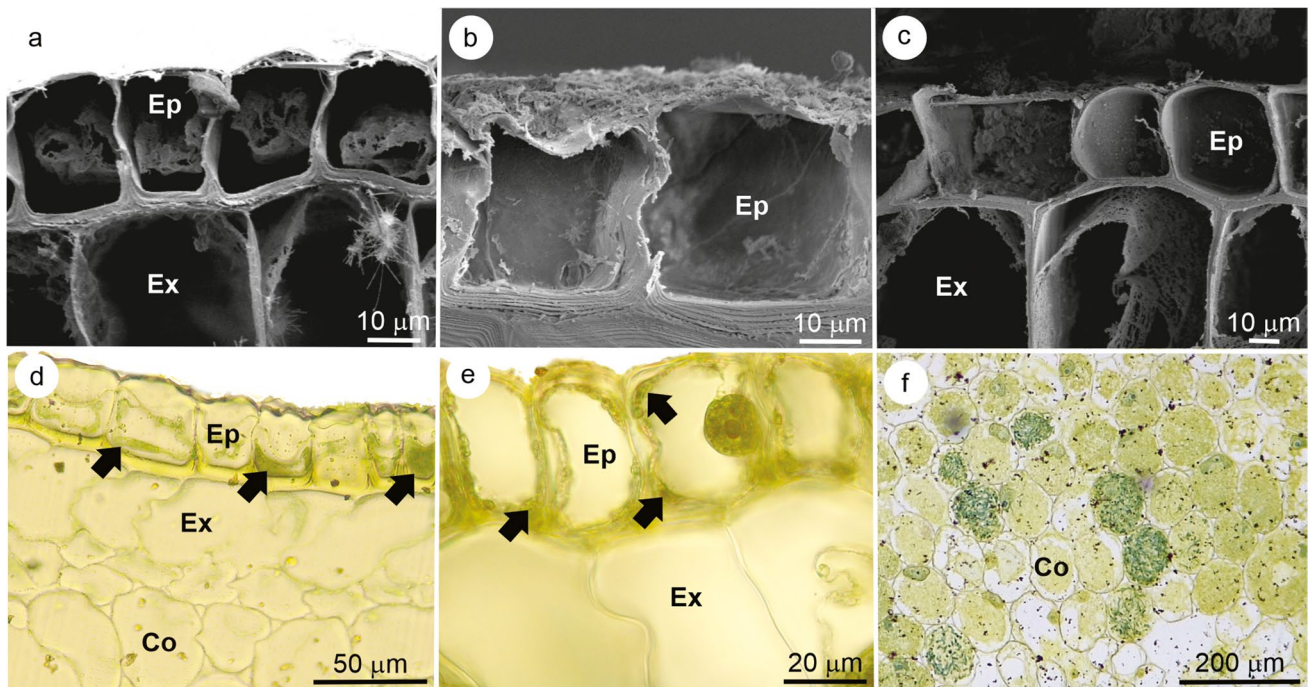


Fig. 2 Detail of the epidermis and protein contents of *Vanilla phaeantha* roots (Orchidaceae). Scanning electron micrograph demonstrating details of the epidermis of the free roots (a), root adhering to the phorophyte (b), and fixed in the soil (c). (d) Transversal section of the free root, demonstrating the exodermis and simple epidermis with live cells at maturity (positive reaction for proteins are

indicated by a blue/green color — arrows). (e) Transversal section of the root in contact with the phorophyte, showing a simple epidermis with conspicuous cellular contents. (f) Transversal section of a root fixed to the substrate, showing the cortical parenchyma infested with mycorrhiza (proteins are indicated by a blue color). Ep=Epidermis; Ex=Exodermis and Co=Cortex

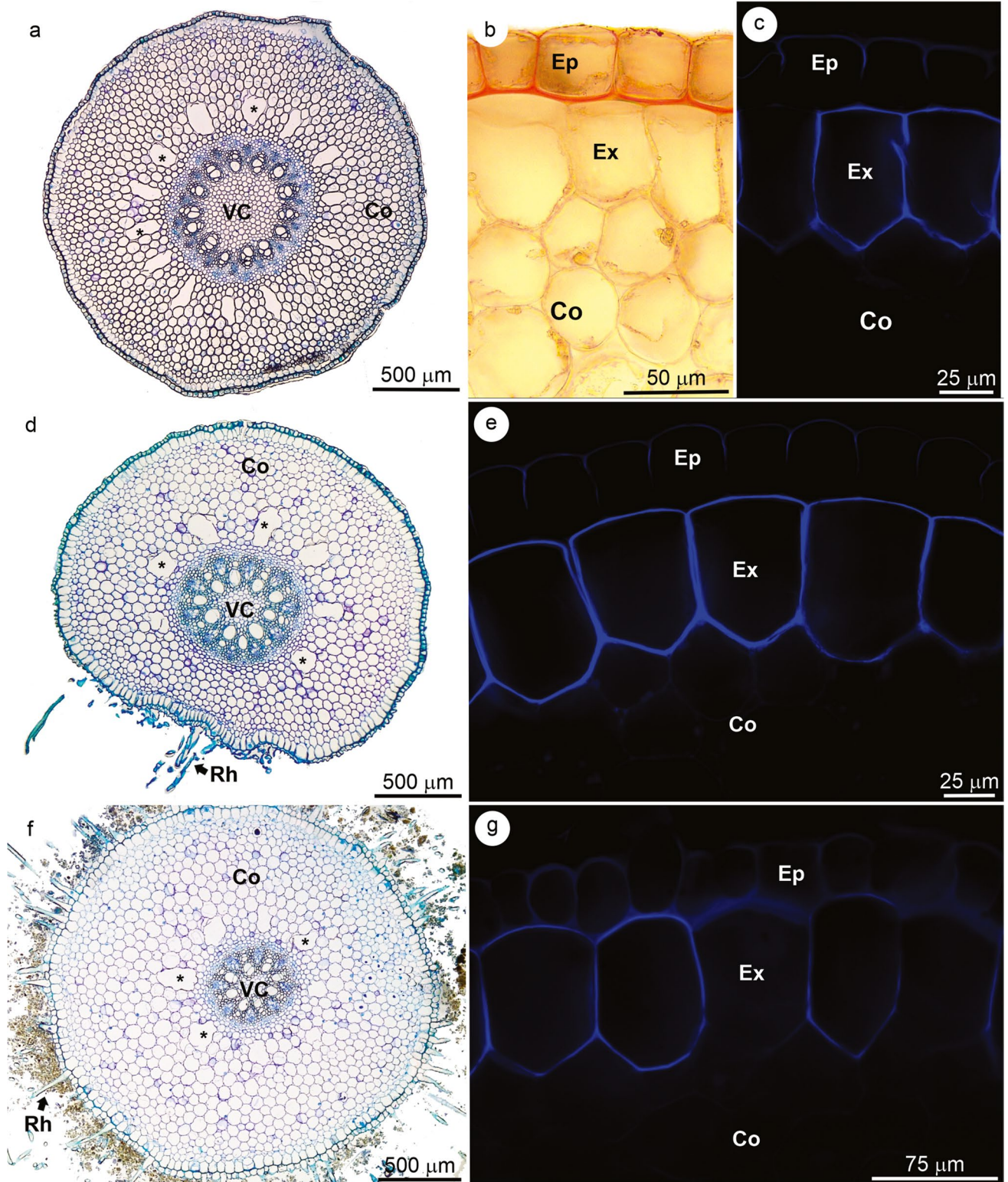


Fig. 3 Internal structure of the roots of *Vanilla phaeantha* (Orchidaceae) growing under different conditions. (a, b and c) Transversal sections of the totally free aerial roots: (a) general view of the root with many aerenchyma lacunae (*), (b) detail of the epidermis showing light impregnations with lipidic substances, (c) detail of the lightly lignified epidermis and more conspicuous fluorescence (more lignin) in the exodermis. (d and e) Transversal sections of the growing roots adhering to the phorophyte; (d) General view demonstrating the epidermis with root hairs (arrows) in contact with the substrate, and aerenchyma lacunae (*), and (e) detail of the lightly lignified epidermis and a more conspicuous fluorescence (more lignin) in the exodermis. (f and g) Transversal sections of the terrestrial roots; (f) Less developed aerenchyma lacunae (*), and root hairs around the entire root, (g) detail of the lightly lignified epidermis. Staining for lipids (Sudan), and lignin (DAPI filter). Ep=Epidermis; Ex=Exodermis; Co=Cortex; VC=Vascular cylinder; and Rh=Root hairs

Results

Morphology and root anatomy

The roots from the three different growth conditions evidenced variable dimensions, with the transversal area of roots fixed to the soil (terrestrial) being greater than the areas of the roots adhering to the phorophyte or those that grew freely towards the ground (Table 1). The roots of all three root types had a simple epidermis, with juxtaposed cells (Fig. 2a–c) that were alive at maturity (demonstrating positive reactions for proteins — Fig. 2d and e). However, the cells of the freely growing roots evidenced lipidic impregnations in their cell walls (Fig. 3b). The epidermis of the aerial roots evidenced slight lignification in their external periclinal walls that gradually extended to the anticlinal walls (Fig. 3c, e and g). Although the three different roots had exodermal cells with similar thicknesses (Table 1), the external periclinal thicknesses of the exodermal cells in contact with the epidermis were approximately 40% thicker in free roots and 75% in the roots adhering to the phorophyte, than those of the terrestrial roots. The roots adhering to the phorophyte evidenced a slightly arched epidermis in the region in contact with the substrate, and the presence of root hairs (Fig. 3d), with no parietal thickenings. Terrestrial roots, on the other hand, evidenced root hairs entirely covering their surfaces (Fig. 3f).

The area occupied by the cortex in terrestrial roots was larger than that observed in the adhering or free roots (Table 1). The thin-walled cortical parenchyma cells are rounded and of varying sizes in the roots under all three environmental conditions, and the cells are compactly arranged with few intercellular spaces (those being small and triangular) (Fig. 3a, d and f), with few raphides. The free roots contain larger numbers of aerenchyma lacunae in the inner cortex region, although no differences were observed in the total areas occupied by those aerenchyma

lacunae (Table 1). Mycorrhizae were observed distributed throughout the cortex of the terrestrial roots (Fig. 2c), with restricted colonization of the cortex adjacent to the phorophyte substrate in the adhering roots.

The exodermis in all root types was composed of a layer of anticlinally elongated cells in the transversal section, with a mean thickness of 53.0 to 62.0 μm . The cells of the exodermis (excepted the passage cells) in all studied root types were impregnated with lipidic substances (Fig. 4a–b). However, those thickenings were more conspicuous in the aerial roots (whether free or adhering to the phorophyte). Passage cells did not evidence lipidic impregnations or lignin (Fig. 4c), although their cellular contents were conspicuous. The roots adhering to the phorophyte evidenced larger numbers of passage cells in the contact region with the substrate (Fig. 4c). The endodermal cells were little differentiated, with Casparian strips and lignin impregnations (Fig. 4d). The endodermal cells in the adhering and terrestrial roots also exhibited an impregnation of lipidic substances (Fig. 4e–g). The passage cells in all root types were directed toward the xylem poles (Fig. 4h and i).

The xylem and phloem strands were intercalated in the vascular cylinders. The xylem was polyarch, with the numbers of poles in roots adhering to the phorophyte and those growing freely (approximately 12 protoxylem poles) (Fig. 3a and d, Table 1) being greater than in roots fixed to the soil (approximately nine poles) (Fig. 3f). In spite of the differences in the number of protoxylem poles, all of the roots demonstrated similar calibers of their vessel elements in the metaxylem.

Phenotypic plasticity index

The RPDI values demonstrate differences among the different root types for all of the parameters analyzed (Table 2). Plasticity was generally greater in roots fixed to the soil than in adhering or free roots. That is, aerial roots demonstrated smaller structural variations than terrestrial roots. The parameters that demonstrated the greatest plasticity were the total area occupied by aerenchyma lacunae in the cortex (values between 0.30 and 0.36), and the thickness of the external periclinal wall of the exodermis in contact with the epidermis (values between 0.23 and 0.30). The most conservative characteristic was the number of protoxylem poles (values between 0.07 and 0.16).

Discussion

A study considering 96 taxa belonging to different families demonstrated that root structures represent essential aspects of plant adaptations to their environments (Kong et al. 2014). According to those authors, thicker roots require

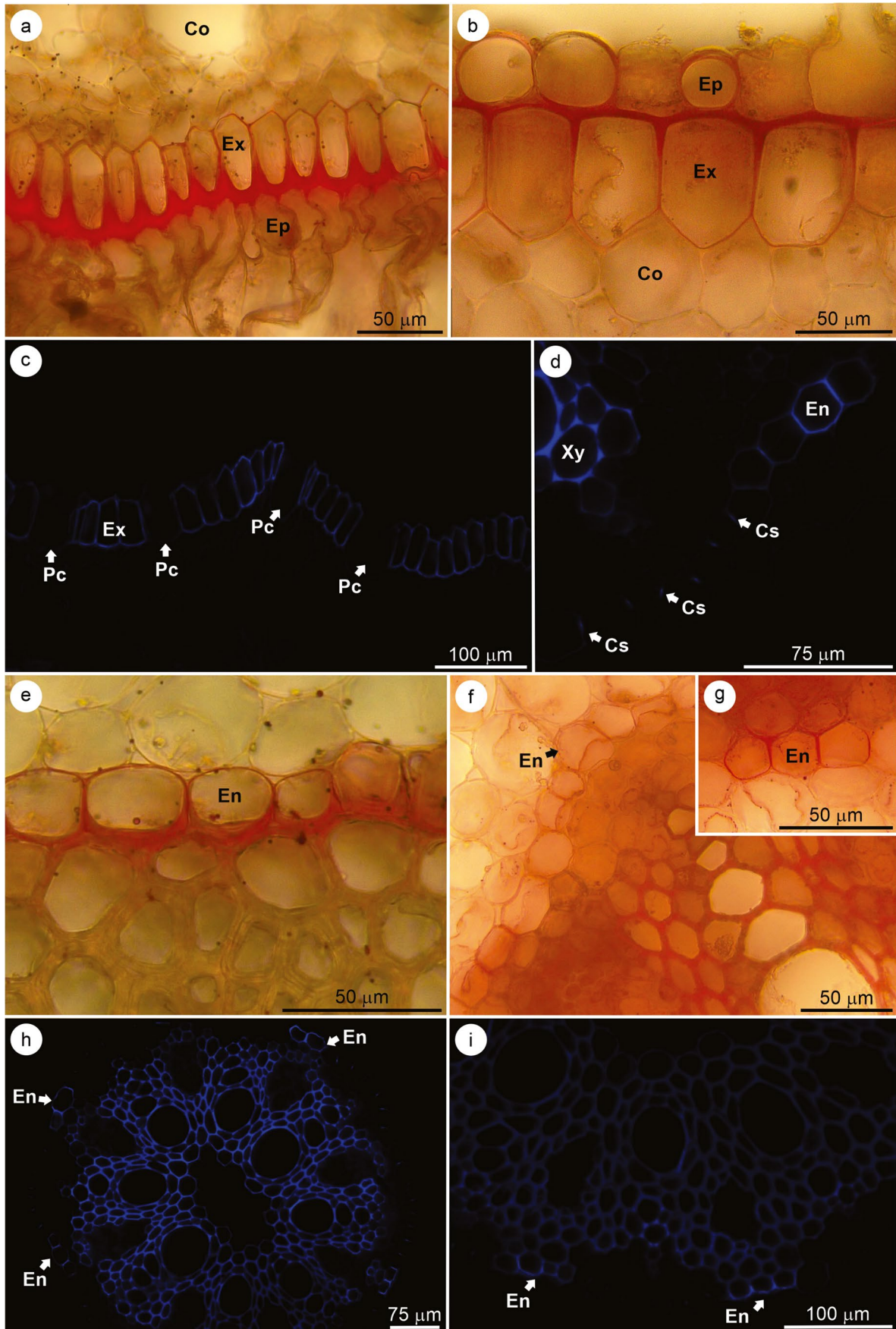


Fig. 4 Presence of lipids and lignin in the root tissues of *Vanilla phaeantha* (Orchidaceae). (a and b) Lipidic impregnations in the exodermal cells of the (a) roots adhering to the phorophyte and (b) roots fixed to the soil. (c) Lignified exodermis and passage cells in the contact region between the phorophyte (arrows) and the adhering roots. (d) Detail of the lignified Casparian strip cells of the endodermis (arrow) of free roots. (e, f and g) Detail of the endodermis with lipidic impregnations in (e) roots adhering to the phorophyte and (f and g) roots fixed to the soil. (h and i) Endodermal cells showing the presence of lignin (arrow) in (h) roots fixed to the soil and (i) roots adhering to the phorophyte. Staining for lipids (Sudan), and lignin (DAPI filter). Ex=Exodermis; En=Endodermis; PC=passage cells; Co=Cortex; Cs=casparian strips; VC=vascular cylinder; Xy=Xylem

more carbon and nutrients per unit area for their construction and are considered less efficient in nutrient investment per surface area. The loss of surface area resulting from greater diameters can be compensated by greater infestations of mycorrhiza and, consequently, increased extra-radicular hyphae density (Kong et al. 2014). Similarly, *V. phaeantha* had terrestrial roots with larger diameters and greater mycorrhiza infestations. Among the aerial roots, only the adhering roots had mycorrhiza infestations, although their colonization was restricted to the cortex adjacent to the substrate. The fungal hyphae in orchids form intracellular fungal coils (pelotons) that can be digested by the host cells, making them essential to plant nutrition (Lesica and Antibus 1990; Senthilkumar et al. 2000).

Root thickness usually correlates positively with cortex thickness, with greater diameters of the stele and the vessel elements (Kong et al. 2014). That same relationship was observed in *V. phaeantha*, but only in the area occupied by the cortex. At the same time, characteristics linked to the vascular cylinder appeared more conservative (to the degree that there were no differences between the three types of roots

studied here in the area occupied by the vascular cylinder and occupied by the vessel elements). The vascular cylinder was formed by polyarch xylem in all of the roots analyzed, evidencing varying numbers of protoxylem poles, as has been reported for other species (Rosso 1966; Singh 1986). The cortex comprises exodermis, cortical parenchyma, and endodermis, all originating from the ground meristem (Engard 1944). The endodermis, the innermost cortex layer, exhibited evident Casparian strips impregnated with lignin. That type of cell wall thickening acts as an apoplastic barrier, influencing the selectivity of nutrients entering the vascular cylinder (Peterson and Enstone 1996; Enstone et al. 2002; Schreiber and Franke 2011).

One of the most plastic characteristics among the three root types analyzed (free, adhering to the phorophyte, and terrestrial) was the external periclinal thickness of the exodermis adjacent to the epidermis. Both impregnation by lipidic substances and the development of secondary walls in the exodermis are strongly influenced by the environment in which the roots develop (Hose et al. 2001; Enstone et al. 2002). The rate at which apoplastic exodermal barriers (Casparian bands and suberin lamellae) are laid down in radial transverse and tangential walls depends on the response to the environment conditions (Hose et al. 2001). Factors such as variations in water availability affect the maturation of both the endodermis and exodermis, with the rapid maturation of the exodermis being associated with interruptions in the apoplastic movements of ions and lower levels of water absorption (Hose et al. 2001; Enstone et al. 2002). An exodermis with secondary thickenings of the cell walls impregnated with lignin and lipidic substances (most conspicuous in the aerial roots — both fixed to the substrate and free) suggests that strong mechanical resistance (as proposed by Enstone et al. 2002) is probably

Table 2 Plasticity of the histometric data of the adventitious roots of the hemiepiphyte *Vanilla phaeantha* (Orchidaceae) growing adhering to the phorophyte, free, and fixed to the soil. The plasticity val-

ues were obtained using the Relative Distance Plasticity Index (RDPI, Valladares et al. 2006). Values with different letters on the same line are different by the Tukey test at a 0.05 level of significance

	Free roots × adhering roots	Free roots × terrestrial roots	Adhering roots × terrestrial roots	<i>p</i>
Transversal area of the root (mm ²)	0.14c	0.18b	0.21a	<0.0001
Thickness of the epidermis (µm)	0.11b	0.20a	0.19a	<0.0001
Thickening of the cell wall of the exodermis in contact with the epidermis (µm)	0.23b	0.22b	0.33a	<0.0001
Thickness of the exodermis (µm)	0.11b	0.17a	0.15a	<0.0001
Transversal area of the root cortex + vascular cylinder (mm ²)	0.14b	0.18a	0.20a	<0.0001
Transversal area of the cortex (mm ²)	0.15b	0.20a	0.23a	<0.0001
Transversal area of the vascular cylinder (µm ²)	0.13b	0.23a	0.24a	<0.0001
Number of aerenchyma lacunae	0.18a	0.19a	0.10b	<0.0001
Area of aerenchyma lacunae of the cortex in cross section (µm ²)	0.36a	0.34ab	0.30b	<0.05
Number of protoxylem strands	0.07a	0.16a	0.10b	<0.0001
Mean area of metaxylem vessels (µm ²)	0.18b	0.23a	0.23a	<0.001

more relevant to aerial roots (which develop subjected to greater variations in water availability, and possibly even desiccation) than contact and friction with soil particles. Additionally, the interruption of apoplastic conduction diminishes root water losses as it increases humidity in the cortex by making the return of water to the external environment more difficult, as Sanford and Adanlawo (1973) and Benzing et al. (1982, 1983) suggested for other orchid species. It is worth noting that even in the region of contact with the substrate (phorophyte), the adhering roots evidenced heavy staining for lipids (see Fig. 4a). Greater numbers of passage cells in the exodermis were also observed in that region. That observation reinforces the substrate's importance in terms of resource acquisition, such as water and mineral nutrients.

In addition to the thickenings of the exodermal parietal cell walls in contact with the epidermis, it should be noted that the characteristic that demonstrated the greatest plasticity was the number of aerenchyma lacunae in the root cortex. According to Stern (1997), the presence of aerenchyma lacunae in the roots of *Vanilla* could indicate the potential storage of oxygen. The greater number of aerenchyma lacunae, and consequently their total area within the transversal section, was the only characteristic that demonstrated high plasticity among roots growing in the aerial environment, or differences between the free-growing aerial roots and terrestrial roots. In this case, the least difference in plasticity was observed between adhering and terrestrial roots, indicating that contact with a substrate could determine for the development of those intercellular spaces (or rather their reduced development). That reduction in the numbers of aerenchyma lacunae in terrestrial roots was not expected, as the study population of *V. phaeantha* grew in a very humid environment, with frequent inundations — which runs contrary to the proposal of Stern (1997) for the need for greater oxidation. In spite of demonstrating the same area occupied by aerenchyma lacunae, the greater number of those intercellular spaces in the aerial and free roots could guarantee an environment favorable for photosynthesis, as those roots do not have stomata and the epidermis remains alive. Photosynthesis in orchid roots has been related to the reduction of hypoxia as a consequence of difficulties for gas exchange under conditions of velamen saturation (Moreira et al. 2009; Roth-Nebelsick et al. 2021), so that the maximization of the control of gases by the presence of intercellular spaces cannot be discarded. Root aeration is key to orchid survival and, in some taxa without leaves, aeration (including through the presence of pneumatophores) is strongly related to the evolution of the group (Carlsward et al. 2006).

Among orchids with leaves, the photosynthesis occurring in the roots could not sustain their metabolism and growth alone, but could aid in the maintenance of the cellular machinery (Moreira et al. 2009). In that case, primary

starch grains in the cortical parenchyma and the pith of the aerial roots were associated only with photosynthetic activity (Moreira et al. 2009), without any indication of a storage function. Apparently, the cortical parenchyma occupies a large volume within the roots of *V. phaeantha*. Still, it does but does not demonstrate any relationship with the accumulation of carbohydrates, as only small lipidic droplets were observed in that region, without any indication of starch. The absence of starch in aerial roots has also been reported in other monocotyledon families. *Dracaena draco* (L.) L. and *D. marginata* Aiton (synonym of *Aloe purpurea* Lam.) (Asparagaceae) evidenced only the presence of soluble (non-structural) carbohydrates in their roots, which may function as osmotically active substances capable of reducing water losses under limiting conditions of humidity (Jupa et al. 2017; Jura-Morawiec et al. 2021).

The adventitious roots of *V. phaeantha* showed a simple epidermis with live cells at maturity with cellular contents. The epidermis appears similar to velamen due to parietal thicknesses impregnated with lipids and lignin, although it is not very conspicuous and does not have channels or pores. Velamen is commonly found in orchids, generally associated with an epiphytic habit in environments considered xeric, although it is also common in terrestrial species (Dycus and Knudson 1957; Benzing 1990; Pedroso de Moraes et al. 2012; Zotz et al. 2017), which probably conserved that character. As mentioned earlier, velamen is generally described in the literature as dead tissue at maturity. Its cells have walls with complex arrangements of pores and lignified grooves that lend it an absorbing nature (by increasing capillarity and the hygroscopic nature of the tissue) and aid its mechanical support functions to avoid cellular collapse when desiccated (Pridgeon et al. 1983; Porembski and Barthlott 1988; Benzing 1990). The presence of velamen is therefore considered an adaptive character, and its importance for acquiring resources is widely treated in the literature (Engard 1944; Benzing et al. 1982; Pridgeon 1986; Silva and Milaneze-Gutierrez 2004; Zotz and Winkler 2013; Chomicki et al. 2015). In that context, the dead velamen at maturity, the taxonomic proximity of species producing that tissue, and the recognition of the epidermis of the genus *Vanilla* as velamen by other authors (Stern and Judd 1999; Zotz 2013), lead us to believe that perhaps *V. phaeantha* only demonstrates velamen maturation at distances greater than 3 cm from the base, or that its epidermis is just a simple epidermis.

In these roots, contact with the phorophyte causes changes in root structure and the formation of root hairs to promote adherence to the substrate in that region. That new dorsiventral configuration, where the dorsal face assumes a protective function and the ventral face develops root hairs that have absorption function and aid in fixation to the substrate, has been observed in other studies (Dycus and Knudson 1957; Sanford and Adanlawo 1973; Benzing et al. 1982;

Moreira et al. 2013; Tomlinson and Metcalf 1969; Almeida et al. 2016; Stern 2014). Corroborating earlier observations by Stern and Carlswald (2009) and Moreira et al. (2013), root hairs were observed on the entire circumferences of terrestrial roots and at the contact surface with the substrate in adhering roots, indicating their role in the absorption of water and nutrients.

Studies of phenotypic plasticity have been essential for predictions about how global climate change will affect species distributions and community compositions (Lande 2009). Phenotypic plasticity can contribute to widening environmental amplitudes that a species can tolerate (and thrive) (Ackerly et al. 2000; Gratani 2014). Specifically, the environment can induce changes in behavior at both morphological and physiological levels (Price et al. 2003). Those variations are crucial for survival in heterogeneous environments or environments with variable conditions, climatic or otherwise (Gratani 2014). *Vanilla phaeantha* is a hemiepiphyte that extends from the soil up to 5 m to the canopy in gallery forests, and thus subject to environmental variations as it grows that are determined by the epiphytic environment, their contact with the substrate, and the terrestrial environment to which they still could be connected. As such, the present study demonstrated how aerial and terrestrial environments strongly influence the structural plasticity of the roots. Most of the parameters evaluated showed remarkable plasticity among aerial roots (free or adhering) compared to terrestrial roots, and less plasticity among free roots compared to adhering. Free aerial roots were longer, do not developed root hairs, showed the largest numbers of aerenchyma lacunae, and had thickenings (composed of lignin) in the exodermis, endodermis, and pith of the vascular cylinder that help maintain their structural integrity. Terrestrial roots (fixed to the soil), on the other hand, developed root hairs and were highly infested with mycorrhiza, indicating their critical role in nutrient acquisition. Adhering roots demonstrate free regions similar to those found on aerial roots, and adhering regions with characteristics similar to terrestrial roots (with root hairs and mycorrhiza).

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