CELLULAR AND MOLECULAR BIOLOGY

Vessel element morphology of *Allagoptera campestris* (Mart.) Kuntze (Arecaceae) belowground organs affected by growing conditions

BEATRIZ APPEZZATO-DA-GLÓRIA, MARCELO RODRIGO PACE, DAIANE DOS S. SOUZA, GABRIELA S. DA SILVA & LUCAS HENRIQUE S. BARBOSA

Abstract: *Allagoptera campestris* is an acaulescent, rhizomatous palm tree that occurs in grassland and savanna areas (Cerrado). In the Santa Bárbara Ecological Station (Águas de Santa Bárbara, São Paulo, Brazil) the species is found growing in three distinct conditions: 1) in the understory of *Pinus* species plantations introduced in the 1970s in formerly open savanna, 2) in an area where *Pinus* species cultivated in the 1970s were later removed and the remaining material burned, and 3) in an open, undisturbed savanna area without the interference of pines. Anatomical studies carried out with *A. campestris* leaves collected in the same three areas indicated leaf plasticity in response to growth conditions. To verify whether there are differences in vessel element morphology in belowground organs, light, and scanning electron microscopy analyses were conducted on portions just below the crown, in the middle of the rhizome, and the median portions of three longer adventitious roots sampled from three plants in each area. The study reveals significant variations in vessel element characteristics of *A. campestris*, with roots consistently displaying longer and larger elements than rhizomes, and environmental conditions, especially in pine understory, influence vessel dimensions, and hydraulic conductivity in a negative manner.

Key words: acaulescent palm, adaptation, rhizome, roots, tracheary elements.

INTRODUCTION

Allagoptera campestris (Mart.) Kuntze (Arecaceae), popularly known in its natural range as buri-do-campo, imburi, pissandó, and ariri, is a slow-growing palm tree with a single underground stem (rhizome) or sometimes an underground stem with a small aerial portion, which occurs in grasslands and savannas (Durigan et al. 2018). The species has a wide distribution covering a large part of the south, southeast, central and northeastern Brazil, being registered in the states of Maranhão, Bahia, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, São Paulo, Paraná, and the Federal District (Moraes & Martins 2019). The leaves of this palm tree are widely used in handicrafts by native-Brazilian communities and its fruits are used in cooking and consumed fresh, as is its palm heart (Martins et al. 2014). Its fruits are also of invaluable importance as a food resource for numerous animal species in the Cerrado (Andreazzi et al. 2009).

At the Santa Bárbara Ecological Station (SBES), located in São Paulo state, Southeast Region of Brazil, the species is found growing in three distinct conditions: 1) in the understory of *Pinus* sp. plantations introduced in the 70s in formerly open savanna, 2) in an area where *Pinus*

sp. cultivated in the 70s was removed and the remaining material burned, and 3) in an open savanna area without the interference of pine. A study carried out by our group showed that long-term pine cultivation in areas previously occupied by open savannas caused a drastic reduction in the bud bank and subterranean structures, affecting the survival of several native species (Ferraro et al. 2021). *Allagoptera campestris* is one of the few species that still occurs on those pine understory areas and presents good performance probably due to the plasticity of its leaves (Barbosa et al. 2022). According to the authors, in pine understory, the leaves have a lower stomatal index and lower values of net CO_2 assimilation, while in the area under regeneration, plants fully exposed to sunlight form leaves with a thicker leaf blade and a higher stomatal index. Nevertheless, it is unknown whether anatomic variations in organs other than leaves occurs, and how their hydraulic conductivity responds to different ecological regimes (e.g., soil and water degradation) such as the ones found in the studied Cerrado area.

Water transport capacity through the xylem is an important functional trait closely linked to the plant water-use strategy and net primary productivity in a given environment (Fonti & Jansen 2012). Transport efficiency is associated with vessel elements whose morphology (i.e., vessel elements of larger diameter with simple perforation plates) compromises safety in cases of embolism (Carlquist 1975, 1989, Baas et al. 1983, 2004, Hacke et al. 2023) although this statement is a matter of debate (Lens et al. 2022, 2023, Isasa et al. 2023, Olson et al. 2023). Carlquist (1975) suggests that in aquatic or mesic environments, monocots tend to have longer, narrower conductive elements with multiple perforation plates, while those growing in seasonal environments, with a well-marked dry season, generally shorter and wider vessel

elements with simple plates are present. Baas et al. (1983) also demonstrated in a broad study of the flora of Israel and surrounding areas that vessel elements tend to reduce in dimensions (length and width) from mesic to xeric environments, a pattern mirrored across the globe (Olson et al. 2023). Nevertheless, the correlation between vessel dimensions and embolism remains a subject of ongoing debate (Isasa et al. 2023). The authors used data from 20 temperate broad-leaved tree species and concluded that there can be variations in the values of the traits analyzed and in the way the data were grouped and examined. But they also observed that embolism-resistant species had thick pit membranes and narrow vessels.

Concerning the diameter of vessel elements in the xylem, which is associated with the plant's hydraulic capacity ensuring the supply of water from roots to leaves, it was shown that the vessel elements have a high degree of phenotypic plasticity in direct response to environmental stimuli (Schreiber et al. 2015). In monocotyledons, the morphology of the xylem conductive cells is an interesting point to be analyzed, as differences exist according to the organ where they occur, and in general the vessels are shorter and wider in the roots, intermediate in the stems, and very long and narrow on leaves, with multiple plates with many bars (Cheadle 1942, 1943a, b, 1944, 1956). Identical patterns of diameter and type of plate were found in palm trees of the genus *Syagrus*, the first being wider on the roots, intermediate on the stems, and very narrow on the leaves, with simple plates on the roots, multiple plates with few bars on the stems, and multiple plates with many bars on the leaves (Pace et al. 2011). However, the data on the length of the vessel elements were inconsistent, as these were as long or longer in the roots than those in the stems and leaves (Pace et al. 2011). Particularly

in the species *Syagrus petraea*, which has an underground rhizomatous stem like *A. campestris*, much shorter vessel elements were observed in the rhizomes than in the other organs, something that was related by the authors to the organ's reserve function (Pace et al. 2011).

Analysis of *Sansevieria* species (currently included in *Dracaena*, Asparagaceae) showed the absence of vessel elements in the rhizomes and leaves, which are only present in the roots (Carlquist & Schneider 2007). In Orchidaceae, tiny vessel elements were found in rhizomes and pseudobulbs (Carlquist & Schneider 2006). Shorter vessel elements in storage organs have been associated with the apparent slowness in their rate of conduction when compared to the faster flow in roots (Carlquist & Schneider 2006).

As plant hydraulic capacity is closely associated with adaptation to the environment and xylem morphology, conductive cells can exhibit a high degree of phenotypic plasticity. Therefore, our objective was to elucidate whether vessel elements show structural and ultrastructural variations in the roots and rhizome of *A. campestris* growing in three distinct conditions in the Cerrado.

MATERIALS AND METHODS
Plant material and studied area

The species *Allagoptera campestris* (Mart.) Kuntze (Arecaceae) is a palm tree with a belowground rhizome-type stem (Fig. 1) that grows in three different sites in the SBES (22°48'59" S; 49°14'12" W): a) a natural Cerrado area (NCE) characterized as an open savanna, excluded from fire for at least 15 years; b) a formerly open savanna under the cultivation of different pine species (UPI) since the 1970s and excluded from fire since then; and c) an area where Cerrado is regenerating (CER) after 40 years of pine cultivation that

underwent the clear-cutting of the pine trees in 2012, followed by a fire treatment in 2014 for the removal of the remaining material. In the three studied areas, three whole plants were collected with the aid of a backhoe for morphological and anatomical analyses. The predominant soils of the SBES are deep and sandy Oxisols (Melo & Durigan 2011). At the UPI site, a substantial layer of needles (approximately 14 cm thick) covers the soil surface, effectively shading it. In contrast, the soil in the other two areas experiences greater exposure to sunlight. The humidity of the soil (%) in the region of 0-20 cm were 5 ± 0.02 in the NCE, 6 ± 0.01 in the CER, and 10 ± 0.02 in the UPI, that is, soil humidity was significantly higher in UPI than in the two other areas. The soil temperature was lower in UPI area (Supplementary Material - Figure S1) and clay content (w/dispersant) (Teixeira et al. 2017) was slightly higher in the UPI (138 g/kg) than in the NCE (100 g/kg) and in the CER (125 g/kg). Species identification was confirmed by specialists and the material was deposited at the ESA herbarium under accession number 140303.

Structural analyses

For structural analyses, the median portion of the rhizome was sampled from each plant, as well as the median portions of the three longest adventitious roots. The rhizome and root samples were fixed separately in FAA 50 (Johansen 1940) for 48h, conserved in 70% ethyl alcohol where they were stored until processing. The methodology for observing the vessel elements of the rhizome and roots was based on the method proposed by Pace et al. (2011). Samples were macerated in a solution of 50% acetic acid and 50% hydrogen peroxide overnight (Franklin 1945), with subsequent staining in 1% Safranin and 50% ethanol, and mounted on semipermanent slides with glycerin.
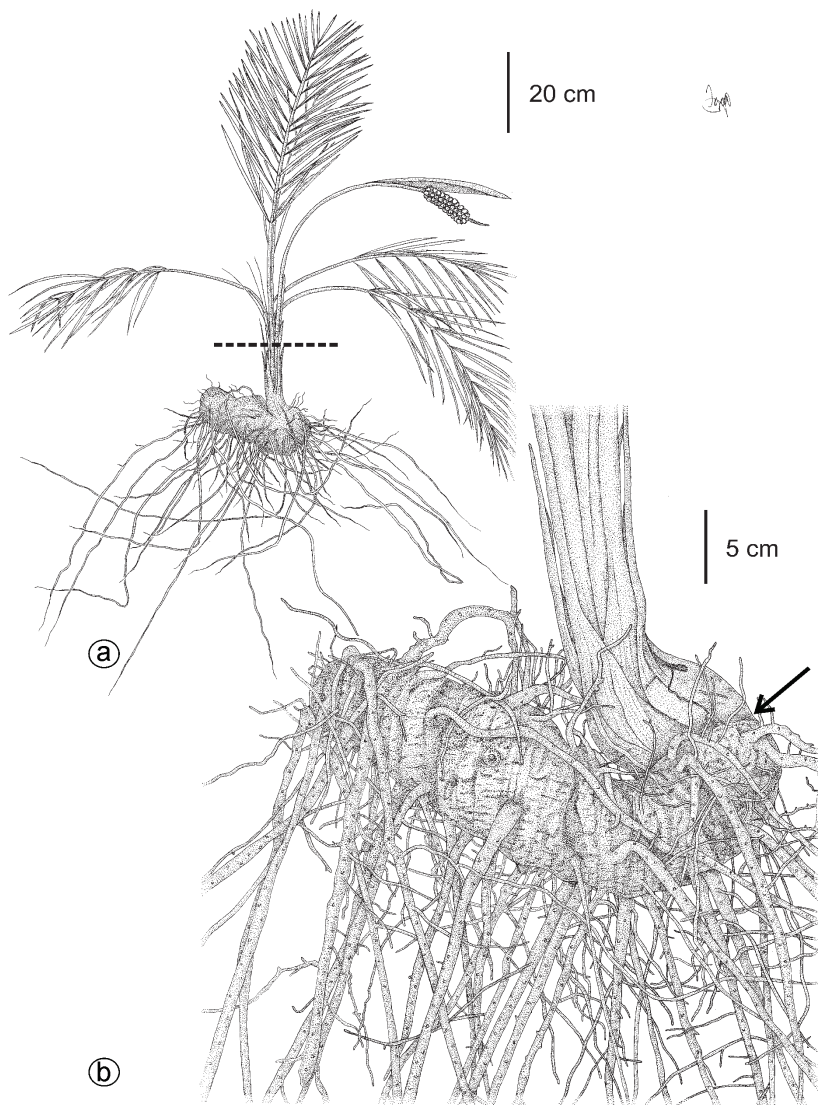
Figure 1. Adult plant of *Allagoptera campestris* is composed of a belowground rhizome (a) with plenty of adventitious roots (b). Dashed line in (a) represents the soil level; Arrow in (b) indicates the crown.

For quantitative analyses under a light microscope, part of the macerated material was used to assemble slides of the roots and rhizomes of the three plants from each area studied. The length and diameter of 50 vessel elements per organ and per plant were measured, totaling 450 measurements per organ and 150 measurements per study area. Measurements were performed using the ImageJ Software (Rasband 2006) after capturing images of the slides using a Leica® DC 300F video camera coupled to the Leica® DM LB microscope and Leica M205C stereomicroscope coupled to the Leica DFC295 camera.

For ultrastructural analyses, the other part of the macerated material was fixed to an adhesive tape on aluminum supports and, after drying at room temperature, covered with a thin gold layer (30–40 nm) in a Sputter Coater (Balzers SCD 050). The analyses and digitalization of the images were carried out in a JSM-IT300 scanning electron microscope (JEOL, Tokyo, Japan), operated at 20 kV with the scales printed directly on the electron micrographs.

Potential hydraulic conductivity

The calculation of potential hydraulic conductivity (K_p; kg m^{-1} MPa^{-1} s^{-1}) was based on the method described in *Elaeis guineenses* Jacq (Waite et al. 2019) using the Hagen–Poiseuille equation: $K_p = (((\pi * \Sigma\ D^4) / 128\eta) * \rho) / (A_{tot})$. In the equation, η is the viscosity of water (1.002 10^{-9} MPa s^{-1}) and ρ is water density (998.2 kg m^{-3}), both at 20 °C, D is the diameter of metaxylem vessels (μm) (n = 50), and *Atot* is the cross-sectional area of the xylem (m^2).

Data analyses

The quantitative results were analyzed and statistically compared among the three areas, being subjected to analysis of variance (ANOVA) and Tukey's test at 5% probability to compare means, using the R program (R Core Team 2019).

RESULTS

Ultrastructural analyses of metaxylem vessel elements

Ultrastructural analyses of the root vessel elements (Fig. 2) and the rhizome (Fig. 3) showed simple (Fig. 2a and 3a) and multiple perforation plates (Figs. 2b, 3b, 3c) in both rhizomes and roots. Concerning multiple perforation plates, the number of bars can vary from 1 to 7 in the root and from 1 to 8 in the rhizome, with multiple
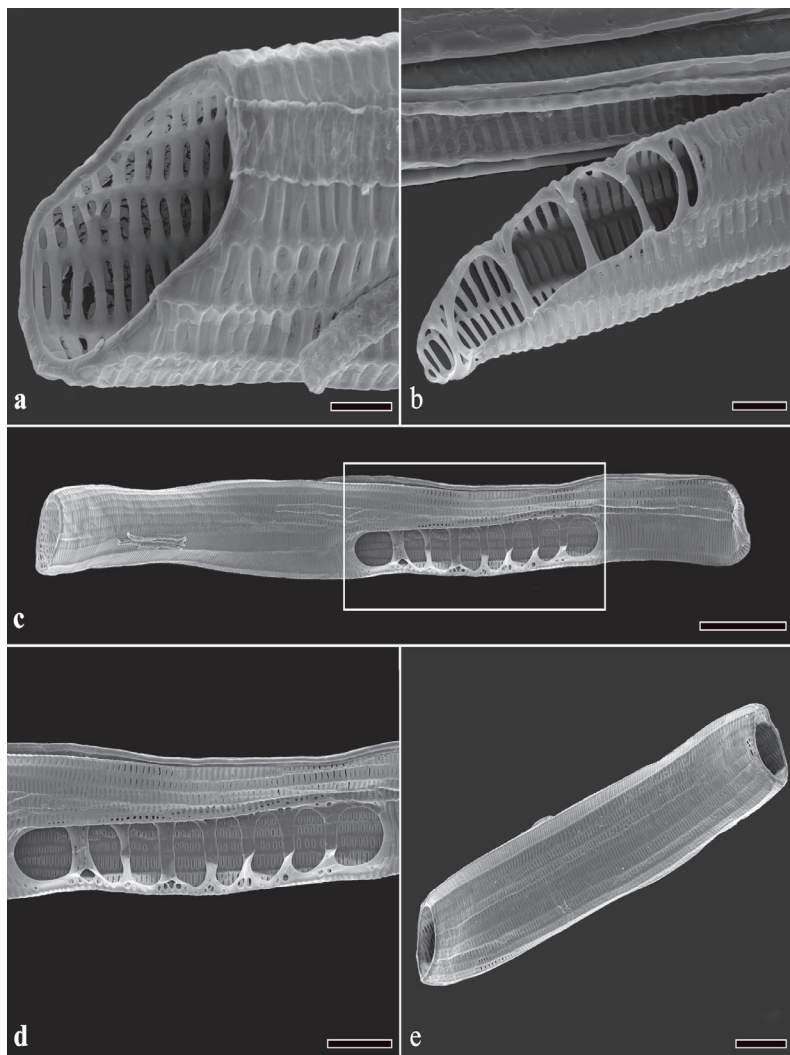

Figure 2. Metaxylem vessel elements of *Allagoptera campestris* root. a) Vessel element with simple perforation plate. b) Vessel element with multiple perforation plates with six bars. c) Vessel element with perforation plate with seven thick bars on the lateral wall. d) Detail of the area delimited in c. e) Vessel element with a simple perforation plate at its ends. Scale bars: a, b = 20 μm, c = 200 μm, d, e = 100 μm.

perforation plates with 1 to 3 bars predominating in all three areas. Vessel elements with the same type of perforation plate at both ends (Fig. 2e, 3d, 3f) or with perforation plates of different types (Fig. 3e) were found. In the root, a perforation plate was observed on the lateral wall of the vessel element (Fig. 2c, d). In the rhizome, short vessel elements predominate (Figs. 3g), but intermediate (Fig. 3f) and long (Fig. 3h) vessel elements also occur, while in the roots they are always long (Fig. 2c, e).

Quantitative analysis of length and diameter of vessel elements

In the three studied areas, the length and diameter of the vessel elements were higher in the roots than in the rhizomes (Table I). Plants from the *Pinus* sp. understory had shorter and narrower vessel elements in both root and rhizome when compared to plants from the natural Cerrado (NCE). The plants in the regenerating area also presented shorter vessel elements compared to the NCE plants for both

Figure 3. Rhizome metaxylem vessel elements of *Allagoptera campestris* with simple perforation plate (a), multiple perforation plates with one (b) and five bars (c). d) Vessel element with simple perforation plates at both ends. e) Vessel element with simple and multiple perforation plates at opposite ends (arrows). f) Medium-sized vessel element showing multiple perforation plates at both ends (arrows). g) Short vessel element, note the presence of two spherical silica bodies (arrow). h) Long vessel elements showing multiple perforation plates at both ends (arrows). Scale bars: a, b = 10 µm, c-e = 20 µm, f, g = 50 µm, h = 100 µm.

organs, with the diameter being greater only in the root, not differing in the rhizome (Table I).

Potential hydraulic conductivity analysis

In the three areas studied, the rhizome with shorter and narrower vessel elements presented the lowest values of potential hydraulic conductivity (Fig. 4). In the understory of *Pinus* sp., where *A. campestris* is subjected to shading and lower soil temperature and higher humidity, the values of potential hydraulic conductivity and the dimensions of the vessel elements were smaller than in the other areas (Fig. 4).

DISCUSSION

Vessel elements are extremely morphologically variable, ranging from wide (700 μm) to narrow (20 μm), and long (2 mm) to short (50 μm) (Baas et al. 2003, 2004, Olson et al. 2023). Perforation plates can vary from multiple (with 100+ bars) to simple plates (Baas et al. 2004). Or, as seen in this study, one side of the vessel element can have a simple perforation plate, while the opposite side has multiple perforation plates. Initially, this enormous variation had been related to phyletic evolution and were considered unidirectional (Bailey & Tupper 1918), while later an ongrowing number of studies showed the contribution of natural selection allowing the evolution of vessel element's morphologies towards any

possible morphology (Carlquist 1975, Maherali et al. 2004) and strongly influenced by allometry (Koçillari et al. 2021, Olson et al. 2021), and climate (Jacobsen & Pratt 2023, Hacke et al. 2023, Olson et al. 2023). A series of trade-offs has been proposed to explain these diverse morphologies and how they derive from plants growing under different conditions or selective pressures (Baas et al. 2003, 2004). For instance, wider vessel elements conduct more water, but are more prone to embolisms both by freezing (Carlquist 2001, Baas et al. 2004) and drought (Jacobsen & Pratt 2023), although the latter is still a matter of debate (Lens et al. 2022, 2023, Olson et al. 2023). Here, we show how *A. campestris*, a palm species of broad distribution growing in the Brazilian Cerrado, varies in vessel element anatomy in both its underground organs, rhizomes and roots. Moreover, we show how these organs respond to three different ecological regimes within a single area, and to what extent this phenotypic plasticity responds to known selective pressures.

Some features of *Allagoptera*, regardless of the environment they were growing in, were consistent with previous data in monocotyledons as a whole and specifically in palms. For instance, the longer, wider vessels with more frequent simple perforation plates in roots than in stems are common in other palms (Cheadle 1943a, b, Pace et al. 2011) and have been associated with

Table I. Length (LE) and diameter (DI) in micrometers (mean ± standard error) of vessel elements in the root and rhizome of *Allagoptera campestris* in the areas of natural Cerrado (NCE), Cerrado under regeneration (CER), and pine understory (UPI).

		AREAS					
		NCE		CER		UPI	
Root	LE	1673.1 ± 139.3	Aa	1414.4 ± 132.1	Ab	1274.9 ± 297.9	Ab
	DI	141.9 ± 3.5	Ab	165.1 ± 4.8	Aa	110.6 ± 2.5	Ac
Rhizome	LE	323.9 ± 25.1	Ba	261.9 ± 12.4	Bb	268.3 ± 31.6	Bb
	DI	45.1 ± 4.6	Ba	45.9 ± 3.4	Ba	34.8 ± 3.7	Bb

Significant differences (ANOVA followed by Tukey's post hoc test, $p < 0.05$) are indicated by letters. Capital letters (in each column) compare each variable between organs in the same area and lowercase letters (in each line) compare each variable of each organ among different areas. When capital and lowercase letters are the same, the values are not statistically different.

the provision of high positive root pressures during the night that can help revert embolisms in the stems (Davis 1961, Ewers et al. 1997).

Vessel element morphology is also influenced by the growth habit. In a comparative study of simple stemmed (*Syagrus romanzoffiana*), suckering (*S. flexuosa*), and rhizomatous (*S. petraea*) palms, the first two species had longer vessel elements when compared to the subterranean stem of *S. petraea* (Pace et al. 2011), whose length values were similar to those of the *A. campestris* rhizome. The presence of much shorter vessel elements in the rhizome has been associated with its storage function and slower water transport (Pace et al. 2011). The absence of vessels or the presence of shorter vessel elements that are supposedly less efficient in water conduction has already been described for other storage organs of monocotyledons, such as rhizomes, bulbs, and pseudobulbs (Cheadle 1942, Carlquist & Schneider 2006).

We observed no qualitative differences among the vessel elements, their morphology varied equally under the three areas studied.

However, we found statistically significant differences at the quantitative level. The vessel elements were always longer in the undisturbed Cerrado (NCE) for both subterranean stems and roots, and their diameters were wider in the stems of NCE and regenerating Cerrado (CER) areas, but only wider in CER roots.

We found slight differences in the soil clay contents between the three areas. These differences were not enough to explain the higher moisture percentage of the pine understory soil. Conversely, the thick layer of pine needles renders higher moisture and lower temperature in the soil compared to the other two areas, where the soil is more exposed to sunlight and, therefore, more subjected to soil water evaporation.

Although higher soil moisture in the pine understory could potentially lead to organ elongation, this phenomenon was not observed in the present study. We believe that the considerably lower length and diameter in plants growing under the pine trees is related to an allelopathic negative effect of pine, which occurs in many understory communities,
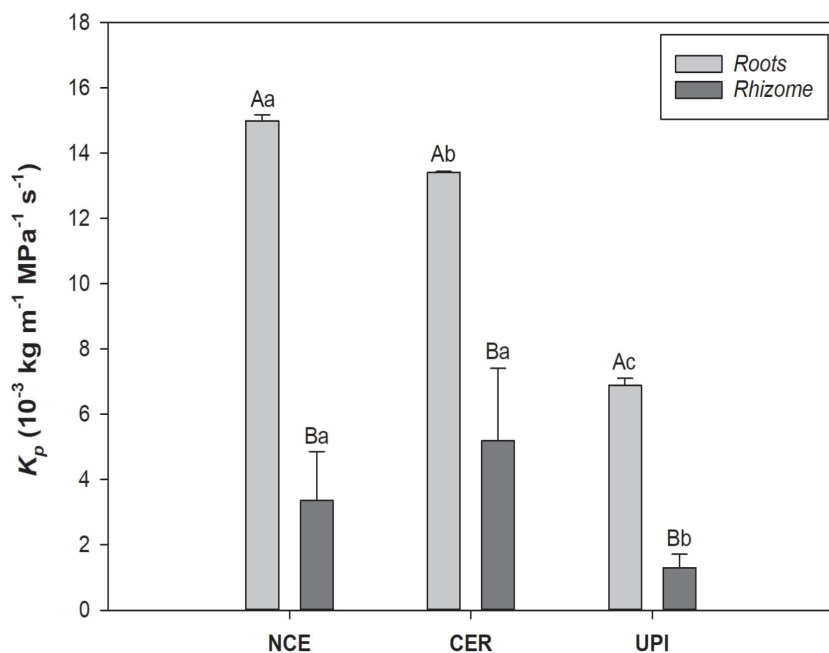

Figure 4. Potential hydraulic conductivity (*Kp*) in the roots and rhizome of *Allagoptera campestris* from the natural Cerrado (NCE), Cerrado under regeneration (CER), and pine understory (UPI) areas. Significant differences (ANOVA followed by Tukey's post hoc test, $p < 0.05$) between organs in each area are indicated by letters. Capital letters compare *Kp* between organs in the same area and lowercase letters compare *Kp* of each organ among different areas.

lowering understory plant performance in general and not only hydraulic conductance (Lodhi & Killingbeck 1982, Kato-Noguchi et al. 2009, Zhang et al. 2021). Nevertheless, pine species have volatile organic compounds such as linalool (Halarewicz et al. 2021, Park & Lee 2011), capable of damaging the cortical parenchyma and inhibiting the development of root hairs and metaxylem cells, which affects the water transport (Jiang et al. 2021). Thus, it is plausible to speculate that this allelopathic effect can also affect the length and width of vessel elements. Potential hydraulic conductivity values were lower in plants growing in the pine understory (Fig. 4) as verified in *Psidium grandifolium* by Faleiro et al. (2022) in the same studied area. In these plants growing in the pine understory, where soil humidity is higher and soil temperature is lower, transpiration would be lower as compared to areas with higher light exposure (Fig. S1). Barbosa et al. (2022) demonstrated that *A. campestris* presents lower rates of net CO_2 assimilation almost throughout the day in this pine understory area.

We can conclude that vessel elements, like other plant elements, have significant phenotypic plasticity, as previously proposed by Schreiber et al. (2015), but here tested for the first time in disturbed and undisturbed areas. The lower and narrower sizes of vessel elements and the lower potential hydraulic conductivity in *A. campestris* plants growing under pine trees are probably due to the allelopathic effect of pine. Our results suggest that studies of pit membrane structure and porosity among the three populations could advance our understanding of how this species avoids embolisms (Lens et al. 2022).

Acknowledgments

REFERENCES

ANDREAZZI CS, PIRES A & FERNADEZ FA. 2009. Mamíferos e palmeiras neotropicais: interações em paisagens fragmentadas. Oecol Bras 13: 555-574.

BAAS P, EWERS FW, DAVIS SD & WHEELER EA. 2004. Evolution of xylem physiology. In: Helmsley AR & Poole I (Eds), The evolution of plant physiology: from whole plants to ecosystems. Academic Press, London.

BAAS P, JANSEN S & WHEELER EA. 2003. Ecological adaptations and deep phylogenetic splits – evidence and questions from the secondary xylem. In: Stuessy F, Mayer V & Hörandl E (Eds), Deep morphology: towards a renaissance of morphology in plant systematics. Gantner Verlag, Liechtenstein.

BAAS P, WERKER E & FAHN A. 1983. Some ecological trends in vessel characters. IAWA J 4: 141-159.

BAILEY IW & TUPPER WW. 1918. Size variation in tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. Am Acad Arts Sci 54: 149-204.

BARBOSA LHB, DA SILVA GS, NOGUEIRA JÚNIOR AF & APPEZZATO-DA-GLÓRIA B. 2022. Leaf phenotypic variation of *Allagoptera campestris* (Mart.) Kuntze (Arecaceae) in response to unnatural disturbances in the Cerrado. Flora 287: 151993.

CARLQUIST S. 1975. Ecological strategies of xylem evolution. Univ of California Press, Berkeley.

CARLQUIST S. 1989. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood, 1st ed., Springer, Berlin.

CARLQUIST S. 2001. Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood, 2nd ed., Springer, Berlin.

CARLQUIST S & SCHNEIDER EL. 2006. Origins and nature of vessels in monocotyledons: 8. Orchidaceae. Am J Bot 93: 963-971.

CARLQUIST S & SCHNEIDER EL. 2007. Origins and nature of vessels in monocotyledons. 9. *Sansevieria*. S Afr J Bot 73: 196-203.

CHEADLE VI. 1942. The occurrence and types of vessels in the various organs of the plant in the Monocotyledoneae. Am J Bot 29: 441-450.

CHEADLE VI. 1943a. The origin and certain trends of specialization of the vessel in the Monocotyledoneae. Am J Bot 30: 11-17.

CHEADLE VI. 1943b. Vessel specialization in the late metaxylem of the various organs in the Monocolyledoneae. Am J Bot 30: 484-490.

CHEADLE VI. 1944. Specialization of vessels within the xylem of each organ in the Monocotyledoneae. Am J Bot 31: 81-92.

CHEADLE VI. 1956. Research on xylem and phloem – progress in fifty years. Am J Bot 43: 719-931.

DAVIS T. 1961. High Root-Pressures in Palms. Nature 192: 277-278.

DURIGAN G, PILON NAL, ASSIS GB, SOUZA FM & BAITELLO JB. 2018. Plantas pequenas do Cerrado: Biodiversidade Negligenciada, 1st ed., Instituto Florestal - Secretaria de Estado do Meio Ambiente, São Paulo.

EWERS FW, COCHARD H & TRUREE MT. 1997. A survey of root pressures in vines of a tropical lowland forest. Oecologia 110: 191-196.

FALEIRO R, DA SILVA GS, PILON NAL, DE AGUIAR CL & APPEZZATO-DA-GLÓRIA B. 2022. Attributes that ensure Cerrado shrub layer resilience after afforestation: The case of *Psidium grandifolium*. S Afr J Bot 149: 6-18.

FERRARO A, FIDELIS A, DA SILVA GS, MARTINS AR, PIEDADE SMDS & APPEZZATO-DA-GLÓRIA B. 2021. Long-term *Pinus* plantations reduce the bud bank in Cerrado areas. Appl Veg Sci 24: e12537.

FONTI P & JANSEN S. 2012. Xylem plasticity in response to climate. New Phytol 195: 734-736.

FRANKLIN L. 1945. Preparation of thin sections of synthetic resin and wood. Resin composites, and a new macerating method for wood. Nature 155: 51.

HACKE UG, JACOBSEN AL & PRATT RB. 2023. Vessel diameter and vulnerability to drought-induced embolism: within tissue and across-species and the issue of survivorship bias. IAWA J 44: 304-319.

HALAREWICZ A, SZUMNY A & BACZEK P. 2021. Effect of *Prunus serotina* Ehrh. volatile compounds on germination and seedling growth of *Pinus sylvestris* L. Forests 12: 846.

ISASA E, LINK RM, JANSEN S, TEZEH FR, KAACK L, SARAMENTO CABRAL J & SCHULDT B. 2023. Addressing controversies in the xylem embolism resistance–vessel diameter relationship. New Phytol 238: 283-296.

JACOBSEN AL & PRATT RB. 2023. Vessel diameter polymorphism determines vulnerability-to-embolism curve shape. IAWA J 44: 320-334.

JIANG C, ZHOU S, LIU L, TOSHMATOY Z, HUANG L, SHI K & SHAO H. 2021. Evaluation of the phytotoxic effect of the essential oil from *Artemisia absinthium*. Ecotoxicol Environ Saf 226: 112856.

JOHANSEN DA. 1940. Plant microtechnique. McGraw-Hill, New York.

KATO-NOGUCHI H, FUSHIMI Y & SHIGEMORI H. 2009. An allelopathic substance in red pine needles (*Pinus densiflora*). J Plant Physiol 166: 442-446.

KOÇILLARI L ET AL. 2021. The widened pipe model of plant hydraulic evolution. PNAS 118: e2100314118.

LENS F, GLEASON SM, BORTOLAMI G, BRODERSEN C, DELZON S & JANSEN S. 2022. Functional xylem characteristics associated with drought-induced embolism in angiosperms. New Phytol 236: 2019-2036.

LENS F, GLEASON SM, BORTOLAMI G, BRODERSEN C, DELZON S & JANSEN S. 2023. Comparative anatomy vs mechanistic understanding: how to interpret the diameter-vulnerability link. IAWA J 44: 368-380

LODHI MA & KILLINGBECK KT. 1982. Effects of pine-produced chemicals on selected understory species in *Pinus ponderosa* community. J Chem Ecol 8: 275-283.

MAHERALI H, POCKMAN WT & JACKSON RB. 2004. Adaptive variation in the vulnerability of woody plants to xylem cavitation. Ecology 85: 2184-2199.

MARTINS RC, FILGUEIRAS TS & ALBUQUERQUE UP. 2014. Use and diversity of palm (Arecaceae) resources in central western Brazil. Sci World J 1: 1-14.

MELO AD & DURIGAN G. 2011. Estação Ecológica de Santa Bárbara Plano de Manejo. Secretaria do Meio Ambiente. Secretaria do Meio Ambiente.

MORAES M & MARTINS RC. 2019. *Allagoptera* in Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro. Available in: <http://reflora.jbrj.gov.br/reflora/floradobrasil/FB15668> (accessed in April 2019).

OLSON ME, ANFODILO T, GLEASON SM & MCCULLOH KA. 2021. Tip-to-base conduit widening as an adaptation: causes, consequences, and empirical priorities. New Phytol 229: 1877-1893.

OLSON ME, PACE MR & ANFODILO T. 2023. The vulnerability to drought-induced embolism-conduit diameter link: breaching the anatomy-physiology divide. IAWA J 44: 334-354.

PACE MR, BOTÂNICO MP & ANGYALOSSY V. 2011. Diversity of metaxylem vessel elements in three *Syagrus* palms (Arecaceae) of different habits. Acta Bot Bras 25: 315-323.

PARK JS & LEE GH. 2011. Volatile compounds and antimicrobial and antioxidant activities of the essential oils of the needles of *Pinus densiflora* and *Pinus thunbergii*. J Sci Food Agric 91: 703-709.

R CORE TEAM. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. URL https://www.R-project.org/.

RASBAND WS. 2006. Image J, U. S. Nacional Institute of Health, Bethesda, Maryland.

SCHREIBER SG, HACKE UG & HAMANN A. 2015. Variation of xylem vessel diameters across a climate gradient: insight from a reciprocal transplant experiment with a widespread boreal tree. Funct Ecol 29: 1392-1401.

TEIXEIRA PC, DONAGEMMA GK, FONTANA A & TEIXEIRA WG. 2017. Manual de métodos de análise de solo, 3rd ed., Brasília: Embrapa, 574 p.

WAITE PA, SCHULDT B, LINK RM, BREIDENBACH N, TRIADIATI T, HENNINGS N, SAAD A & LEUSCGENER C. 2019. Soil moisture regime and palm height influence embolism resistance in oil palm. Tree Physiol 39: 1696-1712.

ZHANG ZJ, LIU YJ, YUAN L, WEBER E & VAN KLEUNEN M. 2021. Effect of allelopathy on plant performance: a meta-analysis. Ecol Lett 24: 348-362.

SUPPLEMENTARY MATERIAL

Figure S1.

BEATRIZ APPEZZATO-DA-GLÓRIA[1]
https://orcid.org/0000-0003-2989-6931

MARCELO RODRIGO PACE[2]
https://orcid.org/0000-0003-0368-2388

DAIANE DOS S. SOUZA[1]
https://orcid.org/0009-0006-7811-988X

GABRIELA S. DA SILVA[3]
https://orcid.org/0000-0002-8756-9317

LUCAS HENRIQUE S. BARBOSA[1]
https://orcid.org/0000-0003-2039-3924

[1]Universidade de São Paulo, Escola Superior de Agricultura Luiz de Queiroz, Departamento de Ciências Biológicas, Laboratório de Anatomia Vegetal, Avenida Pádua Dias, 11, 13418-900 Piracicaba, SP, Brazil

[2]National Autonomous University of Mexico, Institute of Biology, Department of Botany, Circuito Zona Deportiva, s/n, Ciudad Universitaria, 04510 Mexico City, Mexico

[3]Institute of Botany of the Czech Academy of Sciences, Dukelská, 135, 37901 Třeboň, Czech Republic

Correspondence to: **Beatriz Appezzato-da-Glória**
E-mail: bagloria@usp.br

Author contributions

BEATRIZ APPEZZATO-DA-GLÓRIA: Conceptualization, Data curation, Formal analysis, Investigation, Funding acquisition, Methodology, Project administration, Writing – original draft, review & editing. MARCELO RODRIGO PACE: Formal analysis, Investigation, Writing – original draft, review & editing. DAIANE DOS SANTOS SOUZA: Data curation, Formal analysis, Investigation, Methodology, Writing original draft, review & editing. GABRIELA SANTOS DA SILVA: Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. LUCAS HENRIQUE SANTOS BARBOSA: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, review & editing.