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ANATOMICAL CHARACTERIZATION OF THE BARK OF FIVE TREE SPECIES IN A NEOTROPICAL SAVANNA IN THE PERUVIAN AMAZON

Enrique Gianlucca Monteverde-Calderón[1*], Sonia Cesarina Palacios-Ramos[2], Manuel Chavesta-Custodio[3]

[1*]Herbario Forestal MOLF, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina (UNALM), Lima, Perú – gianluccamonteverde@gmail.com

[2] Herbario Forestal MOLF, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina (UNALM), Lima, Perú soniapalacios@lamolina.edu.pe

[3]Laboratorio de Anatomía de la Madera. Departamento Académico de Industrias Forestales, Facultad de Ciencias Forestales, Universidad Nacional Agraria La Molina (UNALM), La Molina, Lima, Perú - mchavesta@lamolina.edu.pe

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Resumo

Caracterização anatômica da casca de cinco espécies de árvores em uma savana neotropical na Amazônia peruana. A casca das árvores desempenha funções vitais como a proteção do ambiente externo, a regulação das trocas gasosas e hídricas e a adaptação a condições diversas. A sua importância ecológica, especialmente nas florestas tropicais, tem sido pouco explorada, embora estudos recentes revelem a sua diversidade estrutural e funcional, destacando-se o seu papel na resistência ao fogo e à seca. As cascas das florestas tropicais secas apresentam adaptações que lhes permitem sobreviver a condições extremas, como a espessura da casca, a densidade básica da madeira e caraterísticas anatómicas que favorecem a resistência ao fogo e ao stress hídrico. O estudo caracteriza a casca de cinco espécies florestais comuns nas florestas subxerófitas de Chanchamayo, Peru: *Astronium fraxinifolium, Curatella americana, Luehea paniculata, Machaerium hirtum* e *Physocalymma scaberrimum*. As amostras foram recolhidas num ecossistema propenso a incêndios com stress hídrico frequente, onde foram realizadas análises microscópicas para identificar caraterísticas anatómicas como fibras, tecidos secretores e floema. Os resultados revelam que essas espécies desenvolveram diversas estratégias adaptativas para suportar as condições ambientais das savanas neotropicais, incluindo a formação de ritidoma, tecido esclerenquimatoso e a disposição dos canais secretores. Além disso, diferenças na espessura da casca interna e externa sugerem variações nas estratégias de armazenamento de água e proteção contra incêndios.
Palavras-chave: floema; características funcionais; fogo; stress hídrico.

Abstract

Tree bark fulfills vital functions such as protection against the environment, regulation of gas and water exchange, and adaptation to diverse conditions. Its ecological importance, especially in tropical forests, has been little explored, although recent studies have revealed its structural and functional diversity, highlighting its role in fire and drought resistance. Tree barks in dry tropical forests demonstrate adaptations, such as thickness, basic wood density, and anatomical characteristics that favor resistance to fire and water stress and allow the trees to survive extreme conditions. This study characterized the barks of five tree species common to the subxerophytic forests of Chanchamayo, Peru: *Astronium fraxinifolium*, *Curatella americana*, *Luehea paniculata*, *Machaerium hirtum*, and *Physocalymma scaberrimum*. The samples were collected in an ecosystem prone to fires and frequent water stress. Microscopic analyses identified the anatomical characteristics such as fibers, secretory tissues, and phloem. The results revealed that these species have developed diverse adaptive strategies, including the formation of rhytidome, sclerenchymatous tissue, and the arrangement of secretory canals to resist the environmental conditions dominating the Neotropical savannas. Additionally, the inner and outer bark thickness differences suggest variations in water storage and fire protection strategies.
Keywords: phloem; functional traits; fire; water stress

INTRODUCTION

Bark works as a protective barrier against the environment; protects the internal system of the trees; and regulates the exchange of gases and water, making it crucial for the survival and adaptability of a species to varied ecosystems (MORRIS; JANSEN, 2017). Although its potential has been studied minimally, its rising availability as industrial processing waste has opened new opportunities to consider it a valuable resource (MOTA *et al.*, 2021). Nevertheless, information on its structure and composition in tropical forest species remains limited.

The ecological significance of bark traits is poorly understood (SHTEIN *et al.,* 2023). Recent characterization of the bark of tropical forest species has revealed their functional and structural diversity, emphasizing their role in adaption to extreme environmental conditions (SALGADO-NEGRET, 2016). Likewise, research in Seasonally Dry Tropical Forests (SDTF) has focused on the mechanisms by which the barks of different species have adapted to prolonged drought and fire, by developing anatomical and chemical characteristics that enhance their resistance (PAUSAS, 2015). Additionally, its role in regeneration, providing protection against pathogens, and potential as an industrial resource have been explored; the last aspect is still underrepresented (MALENGUE *et al*., 2024; ROSELL, 2019).

The extreme environmental conditions of the SDTF impede the survival of many species (BANDA *et al*., 2016). The species distribution in these ecosystems is strongly conditioned by rainfall seasonality and water availability (PENNINGTON *et al.,* 2018). In Peru, differences between SDTFs have been identified, indicating that subxerophilous vegetation formations, also known as subxerophilous forests, share a remarkable floristic similarity with the Brazilian "Cerrado," harboring species characteristic of the Neotropical savannas (LINARES-PALOMINO *et al*., 2022; PALACIOS-RAMOS *et al.,* 2019). These species face constant water stress and the recurrent impact of fire, whether from controlled burning or natural wildfires (ARAUJO & SANTOS, 2019). In the Neotropical savannas, fire and drought are frequent, and the bark of tree species have evolved adaptations to survive these conditions (CORRÊA *et al*., 2020). Tree species in this ecosystem tend to have thicker bark, higher basic wood density, specialized architecture, and specific bark characteristics that can resist fire and water scarcity (MONTEVERDE-CALDERÓN *et al.,* 2023; SANTACRUZ-GARCÍA *et al.,* 2021).

The relationship between forest species and fire reveals various adaptative strategies, such as root sprouts, tree architecture, branching, bark thickness, wood density, and anatomical characteristics of the bark (CORRÊA *et al*., 2020; MONTEVERDE-CALDERÓN *et al*., 2023; SANTACRUZ-GARCÍA *et al.,* 2021). The bark morphology, anatomy, and chemical composition diversify due to the different stresses to which the trees are exposed. However, the relationship between the two remains largely unexplored (SHTEIN *et al.,* 2023).

This research characterized the bark of five forest species abundant in the subxerophilous forest of the Chanchamayo Valley, Peru, focusing on their shared characteristics and adaptations that enable them to thrive in this specific environment. The five species were *Astronium fraxinifolium* Schott, *Curatella americana* L., *Luehea paniculata* Mart., *Machaerium hirtum* (Vell.) Stellfeld, and *Physocalymma scaberrimum* Pohl. They demonstrate significant diversity in anatomical structures, suggesting varied adaptative strategies in response to the environmental conditions of the Neotropical savanna.

MATERIALS AND METHODS

Bark samples were collected from five representative species from the subxerophilous forest, located in the San Ramon district, Chanchamayo, Junin, Peru. The altitudinal range of the area is between 950 and 1100 m above sea level (m.a.s.l.). The average maximum temperature was 22.8°C during September and October, while the average minimum dropped to 11.6°C in July. The average annual temperature is 17.7°C and yearly precipitation is 3,046 mm (CLIMATE-DATA, 2024). The physiography of the area is rugged, with alluvial soils, and dominated by humid forests that host between 90 and 147 tree species per hectare (PALACIOS-RAMOS *et al*., 2019). Additionally, the region exhibits dry-seasonal vegetation formations, including species commonly found in the savannas and dry forests, scarce or absent in rainforest areas like those analyzed in this study.

The five species evaluated were *Astronium fraxinifolium*, *Curatella americana*, *Luehea paniculata*, *Machaerium hirtum*, and *Physocalymma scaberrimum*, with five trees sampled per species. From each tree trunk, an almost rectangular bark fragment was extracted, at a height between 50 and 100 cm above the ground, as this area is the most prone to disturbances such as fire or physical damage (SALGADO-NEGRET, 2016). Trees with tumors, spines, or other irregularities that could compromise the results or hinder the preparation of anatomical sections were avoided. The biometric data, including diameter at breast height (dbh), total height, and bark thickness, are presented in Table 1.

Table 1. The biometric data of the five species studied.
Tabela 1. Dados dasométricos para as cinco espécies estudadas.

Species	Dbh (cm)	Total height (m)	Bark thickness (mm)
Astronium fraxinifolium	11.8–39.5	13–28	5.6–21.9
Curatella americana	10.2–15.4	3.5–7	2.3–12.7
Luehea paniculata	11.3 – 21.3	3.5–14	3.4–19.5
Machaerium hirtum	10.6–23.1	8–18	2.4–5.9
Physocalymma scaberrimum	10.2–25.1	6.5–15	4.6–12.1

The bark samples were stored in a glycerin + water solution and then softened in water to obtain cross-sections, with a thickness ranging between 20 and 30 µm using a microtome (ANGYALOSSY *et al.*, 2016). Samples were prepared following the methods described by ANGYALOSSY *et al.* (2016) and SCHWEINGRUBER *et al.* (2019). This process involved dehydrating the samples with an alcohol gradient. First, they were immersed in 30% alcohol for 10–15 min, followed by 60% alcohol for the same time, and finally in 96% alcohol for 12 h. For final mounting, after removing all the alcohol, three thin sections were placed on microscope slides, and a drop of M-GLAS was added before placing the coverslip. The microscopic characterization of the bark was carried out utilizing a DM500 optical microscope (Leica) with an integrated camera, focusing on identifying the secretory structures, parenchyma, and other vital tissues.

RESULTS

Astronium fraxinifolium

The species had a bark with a poorly developed rhytidome, which appeared as plates that peeled off, leaving a smooth bark with a hammered appearance in adulthood (Figure 1A). The inner bark was sandy in texture and ranged in color from melon to pink (Figure 1B). The inner bark comprised a functional phloem (noncollapsed) and a nonfunctional or collapsed phloem (Figure 1C). Additionally, a network formed by rows of resin secretory channels, parallel to the fiber bands and perpendicular to the rays, with slight dilations, was observed (Figure 1D).

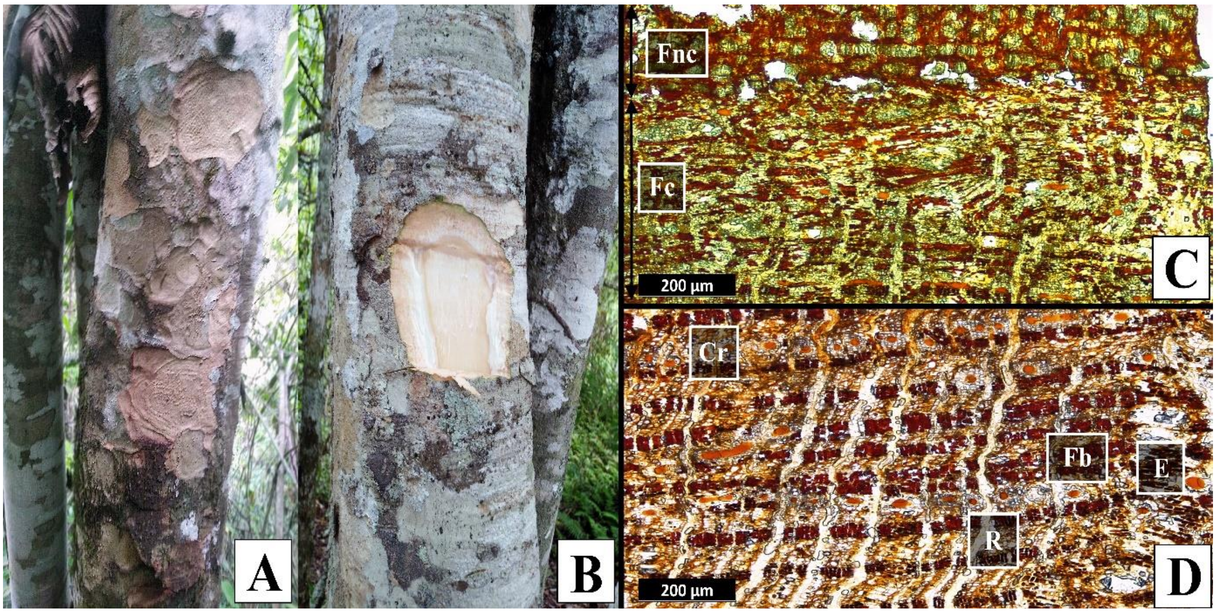

Figure 1. Bark of *Astronium fraxinifolium* (A–D). A: Smooth and yellow outer bark. B: Tree with smooth outer and sandy inner bark. C: Collapsed phloem (Fc) and uncollapsed phloem (Fnc). D: Internal bark with banded fibers (Fb); rays (R); sclereids (E) and resinous canals (Cr).

Figura 1. Casca de *Astronium fraxinifolium* (A–D). A: Casca exterior lisa e amarelada. B: Indivíduo jovem com casca exterior lisa e casca interior arenosa. C: Floema colapsado (Fc) e floema não colapsado (Fnc). D: Casca interna com fibras em faixas (Fb); raios (R); esclereídes (E) e canais resinosos (Cr).

Curatella americana

The outer bark was grayish, with nuances ranging from red to maroon, and exhibited a slightly fissured texture (Figures 2A and B). Its inner bark was thin and inconspicuous (Figure 2B). Microscopically, the peridermal tissue consisted of a very thin phellogen, a poorly defined phelloderm, and a multilayered phellem or cork made up of multiple cell layers (Figure 2C). The inner bark was thin and homogeneous in certain areas, with fiber bands distributed throughout (Figure 2D).

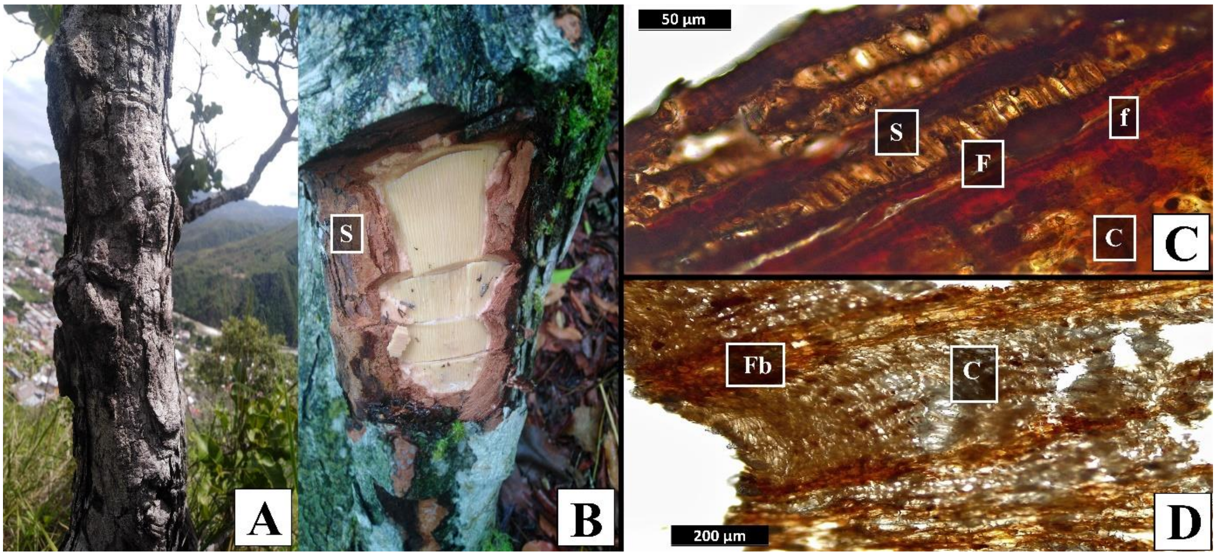

Figure 2. The bark of *Curatella americana* (A–D). A: Outer bark. B: Outer bark and the inconspicuous inner bark. C: Peridermis. Cork (S), telogen (F), exodermis (f) and cortex (C). D: Inner cortex. Banded fibers (Fb).
Figura 2. Casca de *Curatella americana* (A–D). A: Casca externa. B: Casca externa e casca interna pouco visível. C: Periderme. Cortiça (S), felogénio (F), feloderme (f) e casca (C). D: Córtex interno. Fibras em faixas (Fb).

Physocalymma scaberrimum

The outer bark was fissured with a plate-like rhytidome of soft brown color and orange tones (Figure 3A). The inner bark was homogeneous and layered in texture (Figure 3B), with cream-colored collapsed sieve tubes (Figure 3D). Neither the phellogen nor the phelloderm was distinct; however, the phellem consisted of several layers that easily peeled off but were very difficult to cut (Figure 3C). Only the collapsed (nonfunctional) phloem could be observed in the inner bark, along with some additional structures (Figure 3E).

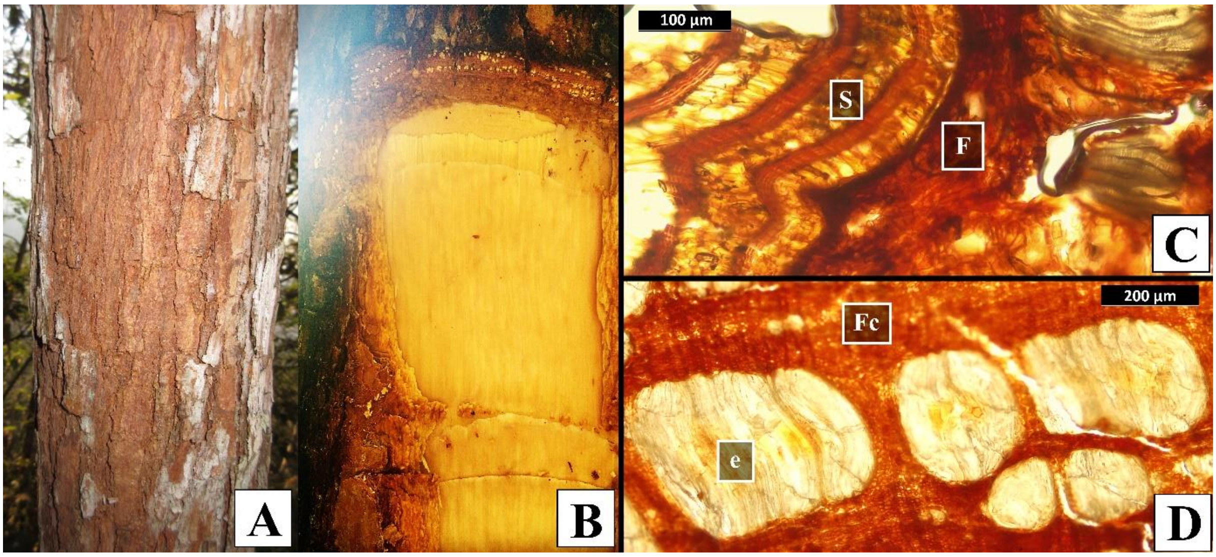

Figure 3. The bark of *Physocalymma scaberrimum* (A–D). A: Outer bark. B: Inner bark of *P. scaberrimum*. C: Peridermis. Cork (S), phellogen (F), and collapsed phloem (Fc). D: Collapsed phloem structures of the inner bark (e).
Figura 3. Casca de *Physocalymma scaberrimum* (A-D). A: Casca externa de *P. scaberrimum*. B: Casca interna de *P. scaberrimum*. C: Periderme. Cortiça (S), felogênio (F) e floema colapsado (Fc). D: Estruturas de floema colapsado da casca interna (e).

Luehea paniculata

The outer bark ranged from gray to black and appeared fissured, with a woody rhytidome (Figure 4A). The inner bark was reddish, turning pinkish internally, with a fibrous texture (Figure 4B). Microscopy identified mucilage-

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secreting cells (Figure 4D). The peridermal tissue was conspicuous, with a phellem consisting of ~12 thin-walled and a phelloderm composed of ~7 thick-walled cells (Figure 4E). In addition, the bark contained abundant sclerenchyma tissue, with fiber bands and dilated rays (Figure 4C).

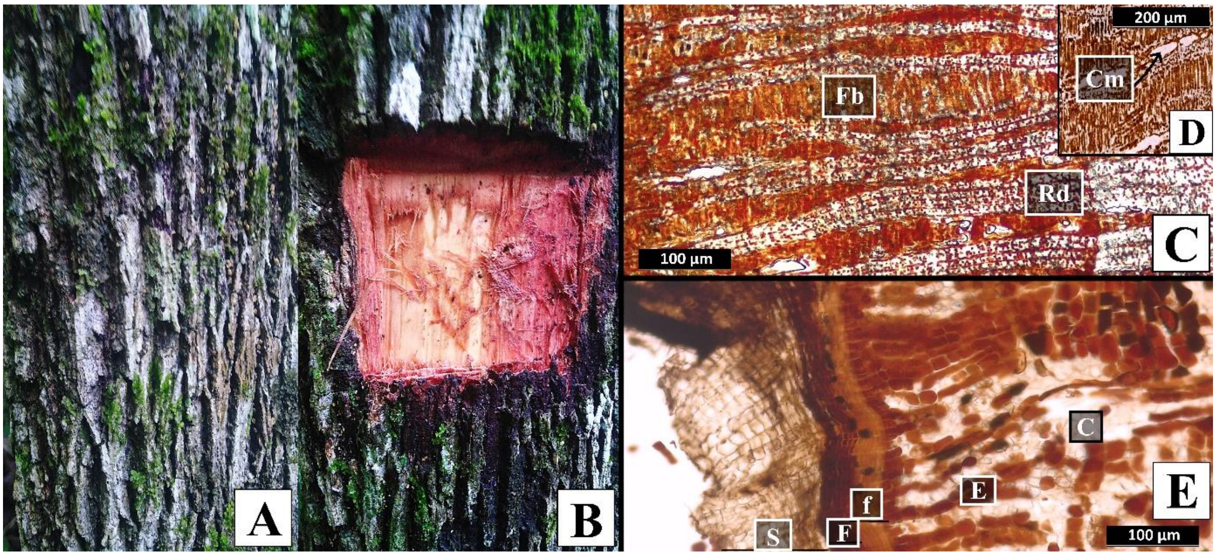

Figure 4. The bark of *Luehea paniculata* (A–E). A: Outer bark. B: inner bark. C: Bark with abundant band-like clarified fibers (fb) and dilated rays (Rd). D: Mucilage-secreting cells (Cm). E: Peridermis tissue; cork (S); telogen (F), exodermis (f), sclereids (E) and cortex (C).

Figura 4. Casca de *Luehea paniculata* (A–E). A: Casca externa. B: Casca interna. C: Casca com presença abundante de fibras esclerificadas (fb) na forma de uma faixa e raios dilatados (Rd). D: Células secretoras de mucilagem (Cm). E: Tecido da periderme; cortiça (S); felogênio (F), feloderme (f), esclereides (E) e córtex (C).

Machaerium hirtum

The outer bark was grayish and had a texture that ranged from smooth to slightly cracked (Figure 5A). In contrast, the inner bark was fibrous, homogeneous, and yellowish. Microscopically, the bark was homogeneous, with a narrow and poorly developed rhytidome (Figure 5B). Sclerenchyma tissue, xylem, and secretory cells were arranged in long tangential lines (Figure 5C). Furthermore, secretory cells with red pigmentation (Figure 5D) were observed at a higher magnification, arranged perpendicular to the rays, which sometimes dilatated (Figure 5E). Figures 5C and E illustrate a layer of secondary xylem, with vessels visible between the inner bark layers, revealing an alternating arrangement of phloem, xylem, and phloem again.

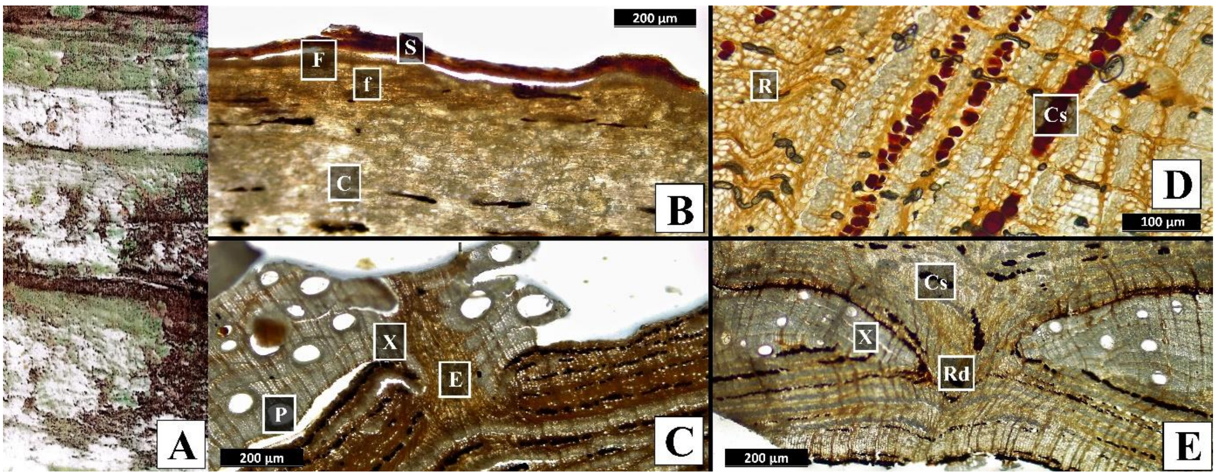

Figure 5. A cross-section of *Machaerium hirtum* (A–E). A: Corteza externa de un individuo arbóreo. B: Peridermis. Cork (S); telogen (F); exodermis (f) and cortex (C). B: Inner cortex with xylem and dilatation of the sclerenchymatous tissue. Pores (P), xylem (X) and sclereids (E). C: Cells with reddish pigmentation (Cs). D: Dilated rays (Rd) and rows of pigmented cells perpendicular to the rays.

Figura 5. Seção transversal de *Machaerium hirtum* (A–E). A: casca externa de uma árvore. B: Periderme. Cortiça (S); felogênio (F); feloderme (f) e córtex (C). C: casca interna com dilatação do xilema e do tecido esclerenquimatoso. Poros (P), xilema (X) e esclereides (E). D: Células com pigmentação avermelhada (Cs). E: Raio dilatado (Rd) e linhas de células pigmentadas perpendiculares aos raios.

DISCUSSION

Anatomical analysis of the species studied revealed a series of fire and water stress resistance-related adaptations, which are crucial for understanding their survival strategies in tropical ecosystems subjected to extreme conditions. These findings were comparable with previous studies reporting similar adaptations in other tropical species.

The cortex of *A. fraxinifolium* has resin-secreting canals, a distinctive feature of its family (MOTA *et al*., 2021; ROTH, 1981). Secretory cells were arranged in tangential rows, a common characteristic of Anacardiaceae. However, the formation of tangential rays was not observed unlike other species (CARMO *et al*., 2016; MOTA *et al*., 2021). Such a protective mechanism is particularly relevant for forest management in fire-prone areas because it may enhance the species' resilience to such adversities. Although resin is a flammable compound, sclerenchymatous and lignified tissue surrounding the secretory cavities suggests a defensive strategy against physical damage, especially that caused by fire (ANGYALOSSY *et al*., 2016).

C. americana, a common species in the neotropical savannas and subxerophytic forests of the Chanchamayo Valley (PALACIOS *et al*., 2019; SIMON; PENNINGTON, 2012), exhibited an outer bark that was significantly thicker than the inner one. This characteristic could be associated with passive defense strategies, where the dead tissue of the outer bark acts as a protective barrier due to its chemical composition and texture (MORRIS; JANSEN, 2017). This type of suberose bark and rhytidome shedding may function as an effective protection mechanism against fire and water stress. *P. scaberrimum* lacks fibers and sclereids; additionally, it contains structures that are likely collapsed phloem elements or small crystals derived from axial parenchyma cells (SCHWEINGRUBER *et al*., 2019). It has a suber composed of many rows of rectangular, thin-walled, nonlignified cells. This could represent an adaptive strategy to tolerate water stress or desiccation in places with alluvial soils, as suggested by the high moisture levels. The formation of a suberose rhytidome indicates a strategy similar to that adopted by *C. americana* to resist mechanical or environmental damage. This finding could imply its potential use as a priority species for restoring areas degraded by recurrent drought or fire. The lack of information on the bark of this species underscores the importance of this study, which opens new avenues for future research on its ecology and adaptations.

The bark of *L. paniculata* is abundant in sclerenchymatous tissue, providing resistance to physical damage and fire (ANGYALOSSY *et al*., 2016). Along with the mucilage secretory channels characteristic of the subfamily Tilioideae (ROTH, 1981), it likely plays a crucial role in protecting the bark from adverse conditions. Moreover, the mucilage appears to be fundamental in modulating plant water stress during drought (KROENER *et al*., 2014), reinforcing its significance in mixed plantations aimed at the sustainable management of tropical forests. This mechanism promotes a more sustainable and productive forest system by contributing to soil moisture retention and enhancing resistance to environmental stresses (OLGUÍN *et al*., 2019).

The bark of *M. hirtum* is characterized by its homogeneity and xylem bands interspersed with phloem, a phenomenon that could be related to phylogenetic adaptation, since this genus, both as trees and lianas, presents an intrusive xylem (ROTH, 1981). This characteristic not only provides greater water transport capacity and adaptability to water stress but also reflects an anatomical plasticity that may be crucial in managing species within ecosystems with high climatic variability (CELIS *et al*., 2024). In addition, the secretory cells of this species could offer a certain degree of fire resistance, although a chemical analysis would be necessary to confirm this (SANTACRUZ-GARCÍA *et al*., 2021). Unlike other species, such as *M. opacum* Vogel, *M. hirtum* does not exhibit collapsed and noncollapsed phloem (COSTA *et al*., 1997).

The relationship between the bark structure and the selective pressures, these species are exposed to, is key to understanding their defense strategies. In species such as *A. fraxinifolium* and *M. hirtum*, the inner bark is thicker than the outer one, providing greater water storage capacity. This trait, which is associated with more dynamic mechanisms where living cells actively respond to water stress and physical damage (DOSSA *et al*., 2016; MORRIS; JANSEN, 2017), is also fundamental for selecting species in reforestation programs in areas prone to forest fires.

This study evaluated five species, with five individuals per species, previewing the anatomical characteristics of their bark. However, expanding the sample size could offer a deeper understanding of the intraspecific variability and its relationship to environmental factors such as water stress. Complementary experiments, including chemical tests, statistical analyses, or experimental simulations, could help confirm the proposed hypotheses regarding functional constraints and their influence on anatomy (CELIS *et al*., 2024).

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Finally, certain additional anatomical features that can be analyzed include cellular hypertrophy, such as the dilated rays observed in *M. hirtum*, *A. fraxinifolium*, and *L. paniculata*. These traits may be associated with radial growth in trees, a process influenced by mechanical and environmental stress, commonly referred to as cellular hypertrophy (ANGYALOSSY *et al*., 2016; SHTEIN *et al*., 2023). Furthermore, banded clarified fibers, as observed in *C. americana*, could also result from an environmental response or resistance to physical damage (ANGYALOSSY *et al*., 2016). These findings contribute to a better understanding of the mechanism by which the bark of these tree species adapts and responds to the extreme conditions of Neotropical savannas.

CONCLUSION

Through this research, it was possible to determine that:

- The anatomical similarities in the bark of the species studied suggest functional convergence under the selective pressure of the sub-xerophilous environment.
- *Curatella americana* and *Physocalymma scaberrimum* exhibit thick outer bark and thin inner bark, a passive defensive strategy to resist fire and reduce dehydration.
- *Astronium fraxinifolium* and *Luehea paniculata* possess secretory channels and sclerenchymatous tissue, indicating an active defense mechanism against physical damage through secretion and structural reinforcement.
- The homogeneous bark of *Machaerium hirtum*, characterized by xylem bands in the phloem and dilated rays, reflects its lianescent adaptation and a potential physiological response to fire, supporting the hypothesis of cellular hypertrophy as a defense mechanism.
- The species studied display key anatomical adaptations that make them suitable for afforestation programs in ecosystems vulnerable to fire and water stress, highlighting their potential to contribute to the restoration and sustainable management of tropical forests.

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