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Analysis of climate adaptability in four tropical fruit trees: Longan (*Dimocarpus longan* Lour.), Lychee (*Litchi chinensis* Sonn.), Pulasan (Nephelium *ramboutan-ake* (Labill.) Leenh.) and Rambutan (*Nephelium lappaceum* L.) through leaf anatomy evaluation

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Abstract
The tropical fruit species *Dimocarpus longan* (Longan), *Litchi chinensis* (Lychee), *Nephelium lappaceum* (Rambutan), and *Nephelium ramboutan-ake* (Pulasan) demonstrate significant ecological adaptability, enabling their cultivation under diverse tropical conditions. This study uses light and scanning electron microscopy to investigate the adaptive significance of leaf micromorphological, anatomical, and histochemical traits in these species. Fresh leaf samples were collected from cultivated habitats in Kerala, India, a tropical monsoon zone. Microscopic evaluations revealed a unique combination of evergreen and xerophytic traits. Evergreen features, including robust internal anatomy, extensive photosynthetic area, and well-developed vein vasculature, support adaptation to high light intensity and fluctuating humidity. Xerophytic characteristics, such as thick abaxial and adaxial cuticles, stomatal index of less than three, and compartmentalised photosynthetic areas, enhance drought resilience. Defensive adaptations like papillated cuticles, trichomes, crystals, phenolic compounds, mucilage, and domatia mitigate herbivory, UV stress, and thermal load. These traits collectively ensure survival in challenging tropical environments. The findings underline the critical role of leaf anatomy in the ecological adaptability and economic viability of these species, providing valuable insights for crop selection and cultivation strategies. Promoting such adaptive traits in tropical horticulture can enhance productivity while minimising environmental impact, contributing to sustainable agriculture and ecosystem stability.

Keywords: Cuticular papillae, Domatia, Heterobaric leaves, Tropical climate, Tropical trees

INTRODUCTION

The perennial plant populations growing in the tropics have mechanisms to effectively harness sunlight and moisture, overcome the water-stressed dry period, and resist herbivores, thereby achieving maximum photosynthetic productivity or yield (Borrell *et al*., 2020; He *et al*., 2020). Several tropical crop plants and fruit trees spread rapidly from their origin to more expansive cultivated areas and become high-yielding crop plants and fruit trees. Longan, Lychee, Pulasan, and Rambutan are extensively cultivated in orchards and home gardens of tropical monsoon zones (at an elevation of 500 m), including parts of South and Southeast Asia, Central America, Northern Australia, and West and Central Africa (Tindall, 1994; Schultz, 2005; Marboh, 2020). Owing to their evolutionary history, Longan, Lychee, Pulasan, and Rambutan share several physiological reactions and morphological and ecological similarities, including limited water stress, rainfall distribution, and an upper limit of temperature for optimum vegetative growth and flower initiation (Marboh, 2020).

Although foliar anatomy has played a significant role in the productivity of plants and provided interesting information regarding their adaptability, there is a dearth of studies on the significance of foliar anatomy in plant breeding (Metcalfe and Chalk, 1950; Evert, 2006; Liu *et al*., 2020). Selecting plant species with characteristics adapted to the specific environment for cultivation is economical and maintains the sustained ecosystem structure by reducing dependence on external chemical sources (Liu *et al*., 2020). Moreover, information on plant characteristics is helpful for farmers not only in choosing plant varieties suited for their region but also in expanding species to new favourable areas (Sthapit *et al*., 2012; Liliane and Charles, 2020).

The Sapindaceae fruit trees, *Dimocarpus longan* Lour. (Longan), *Litchi chinensis* Sonn. (Lychee), *Nephelium lappaceum* L. (Rambutan), *Nephelium ramboutan-ake* (Labill.) Leenh. (Pulasan) have gained popularity in the tropical region not only because of their delicious and nutrient-rich fruits but also their excellent yield, better adaptability to the environment, and comparatively low requirement of water irrigation, fertilisers, and pesticides as a horticulture crop (Tindall, 1994; Vishal *et al*., 2018). These advantages are greatly influenced by anatomical, physiological, and reproductive traits. This study provides a comprehensive overview of how leaf anatomy contributes to the climate adaptability of these tropical plants.

MATERIALS AND METHODS

Site description and sample collection

The tropical fruit trees of Sapindaceae, *Dimocarpus longan* Lour. (Longan), *Litchi chinensis* Sonn. (Lychee), *Nephelium lappaceum* L. (Rambutan), *Nephelium ramboutan-ake* (Labill.) Leenh. (Pulasan), that belong to the tribe Nephelieae (Buerki *et al*., 2021) were selected for the study. The study was conducted during the period from 2021 to 2023. Fully expanded fresh leaf samples, without damage signals, were collected from three individuals chosen for each species. The individuals selected are over 8 cm in diameter at breast height and grow in their cultivated habitats in Kerala, a part of peninsular India (10.1632° N, 76.6413° E). As per 'The *Köppen* climate classification', the zone comes under the tropical monsoon or tropical wet climate, pronounced by summer, rainy wet seasons, and an average annual temperature of 27.05 °C (Gepts, 2008).

Methodology for leaf anatomical study

To prepare temporary paradermal leaf sections, three cm^2-sized portions from the middle part of the mature lamina, including the leaf margin, were selected and soaked in concentrated nitric acid for two days (Dilcher, 1974). Samples were then washed 2–3 times in distilled water. Peeled off-leaf surfaces were stained with safranin O in 50% alcohol for approximately 2 minutes before mounting. The dried leaf surfaces were mounted on aluminium stubs using double-faced adhesive tape, metallized with gold in a high-vacuum evaporator for 1–1.5 min. (Silva *et al*., 2019), and the Scanning electron microscopy (SEM) images were taken using JSM-6390 model SEM.

For the temporary transverse sections, the middle part of the leaves, including the midrib, was preferred; handmade sections of leaf lamia, midrib and petiole were treated in 30% sodium hypochlorite solution (NaOCl) for 3–5 minutes. Sections were stained in 1% Toluidine Blue (TBO) and washed in 50% alcohol to remove the excess stain. They were mounted in 50% glycerine (Vigi and Hari, 2022). Histochemical tests were performed to detect the presence of phenolic compounds and mucilage (Badria and Aboelmaaty, 2019). Five samples of lamina, midrib and petiole from each species were taken, and 15 microscope fields were examined. Measurements and images were taken using a Magnus MLXi Plus microscope equipped with a Magnus camera adapter. The terminology used in this study was adopted from Metcalfe and Chalk (1950) and Dilcher (1974).

RESULTS AND DISCUSSION

Cuticle and epidermis

The paradermal sections of the leaves of four species (*Dimocarpus longan*, *Nephelium lappaceum*, *Nephelium ramboutan-ake* and *Litchi chinensis*) showed thick cuticular covering on both leaf surfaces, but cuticular papillae and striations were present on the lower surface only (Table 1). These papillae on the lower surface joined with the neighbouring striations to form interconnecting ridges with highly fimbriated margins (Fig. 1). All the analysed species had non-glandular trichomes on the abaxial leaf surface, except *L. chinensis,* where trichomes were absent (Table 1). The trichomes were more confined to the veins or on leaf blades closer to them (Fig. 1). The thick and papillated cuticular anatomy, along with non-glandular trichomes in *D. longan*, *L. chinensis*, *N. lappaceum* and *N. ramboutan-ake* (Fig. 1), not only reduces water loss through the nonstomatal areas but also protects these plants by reducing external stresses such as heavy rain, UV radiation, and microbial and pest attacks. Glandular trichomes in *N. ramboutan-ake* were restricted to the veins (Fig. 1H) and are sites of phenolic depositions.

The role of cuticle and trichome as defenders against abiotic stress was reported in earlier research works (Domínguez *et al*., 2017; Liu *et al*., 2020; Wang *et al*., 2021). These structures provide a cooling internal atmosphere by preventing surplus radiation, which benefits the tropical species during heavy radiation exposure (Farfán *et al*., 2020). Moreover, the trichomes in all the species act as defenders against sustained microbial and animal assaults-the reason for the approximately 40% decline in global crop productivity (Farfán *et al*., 2020).

The leaves of four species were hypostomatic and possessed a stomatal index of less than 3 (Table 1). The stomatal index in plants represents the number of stomata in relation to the number of epidermal cells and a

Table 1. Leaf anatomical characteristics studied in the four tropical Sapindaceae fruit trees

Leaf - anatomical traits	*Dimocarpus longan*	*Nephelium lappaceum*	*Nephelium ramboutan-ake*	*Litchi chinensis*
Heterobaric leaves	+	+	+	+
Sclerified bundle sheath extension	Ad	Ad	Ad	ab/ad
Spongy parenchyma	Compact	Loose	loose	loose
Width of adaxial bundle sheath extension	1-celled/2-celled	1-celled	1-celled	1-celled/2-celled
Abaxial cuticle	Papillated	Papillated	papillated	papillated
Cuticle papillae covering the lateral veins	+	-	-	-
Adaxial cuticle	Smooth	Smooth	smooth	smooth
Non-glandular trichomes	+	+	+	+
Glandular trichomes	-	-	+	-
Type of stomata	Cyclocytic	Cyclocytic	cyclocytic	cyclocytic
Presence of stomata	Adaxial	Adaxial	adaxial	adaxial
Mucilage cells	Mc	ad/mc	pc/mc	mc/pc
Phenolic deposition	pc/mc/mir	pc/mc/mir	pc/mc/epi/mir	pc/mc/epi/mir
Prismatic crystals	pc/mc/mir	mc/mir	pc/mc/mir	pc/mc/mir

ab= abaxial epidermis, ad= adaxial epidermis, epi=epidermal cells, mc= mesophyll cells, mir= midrib, pc= palisade cells

Table 2. Measured leaf anatomical characteristics of four tropical Sapindaceae fruit trees (Mean of 15 samples* ±SD)

Taxa	Thickness of midrib vasculature(µm)	Stomatal Index	Adaxial cuticular thickness	Palisade/spongy parenchyma ratio	Mesophyll/leaf thickness ratio
Dimocarpus longan	914.15±253.40	3.32±0.89	5.8±1.72	1.32±0.10	0.83±0.05
Nephelium lappaceum	1022.79±43.43	2.2±0.24	4.93±0.61	0.77±0.085	0.89±0.04
Nephelium ramboutan-ake	1077.25±60.89	2.52±0.329	4.5±0.52	0.91±0.079	0.80±0.029
Litchi chinensis	1227.30±105.05	1.52±0.284	4.6±0.89	0.37±0.03	0.83±0.04

*Refer Supplementary file (ST1 to ST4) for the details of the data selected

value less than 10 is considered to be a xerophytic adaptation as it reduces the rate of dehydration (Ayala-Ramos *et al*., 2024).

Mesophyll

Dorsiventral mesophyll was common with elongated compactly arranged columnar palisade cells (Fig. 2). In the case of *N. ramboutan-ake*, the palisade cells were septate (Fig. 2C). Spongy parenchyma was loosely organised to leave large air cavities, and the compactness varied with species. (Fig. 2E; Table 1) The leaves had a thicker palisade parenchyma ratio (higher than 0.75), except in *L. chinensis* (0.37). The ratios of mesophyll leaf thickness were higher than 0.80 in all the studied species (Table 2), which implies that photosynthetic tissues rather than mechanical tissues occupied a greater part of the leaf area. A high mesophyll leaf thickness ratio provides information regarding the functional aspects of light use strategies (Goncharovska and Iwona, 2023; Somavilla *et al*., 2014). Highly chlorophyllated, thick, and regularly arranged palisade tissue is a characteristic anatomical trait of humid tropical trees with evergreen leaves, offering a high productivity rate (Goldstein *et al*., 2016). This information is very relevant for orchard cultivation, where the development of effective canopy architecture for optimum light interception is a dominant factor in determining productivity (Singh *et al*., 2023).

Bundle sheath extensions (BSEs)

The vein bundles were spaced regularly throughout the mesophyll with a bundle sheath and extensions composed of sclerified parenchyma cells (Fig. 2A, 2B, 2C, 2D). BSEs resulted in the compartmentalisation of the mesophyll area into the so-called heterobaric anatomy (Beyschlag and Eckstein, 2001; Crang *et al*., 2018; Barbosa *et al*., 2019). The width and sclerification of BSEs varied in different species (Table 1; Fig. 2F), and the stomatal patchiness was evident in the sectional view of the lamina (Fig. 2G). The possibility of reduced gaseous exchange rate owing to low stomatal index was compensated by highly aerated spongy parenchymatous tissue in *L. chinensis*, *N. lappaceum* and *N. ramboutan-ake*, enabling rapid diffusion of gases between the internal tissues. In the case of *D. longan*, the compactly arranged and thickly chlorophyllated spongy parenchyma ensure good CO_2 uptake during the sunny season. In short, higher photosynthetic areas in the

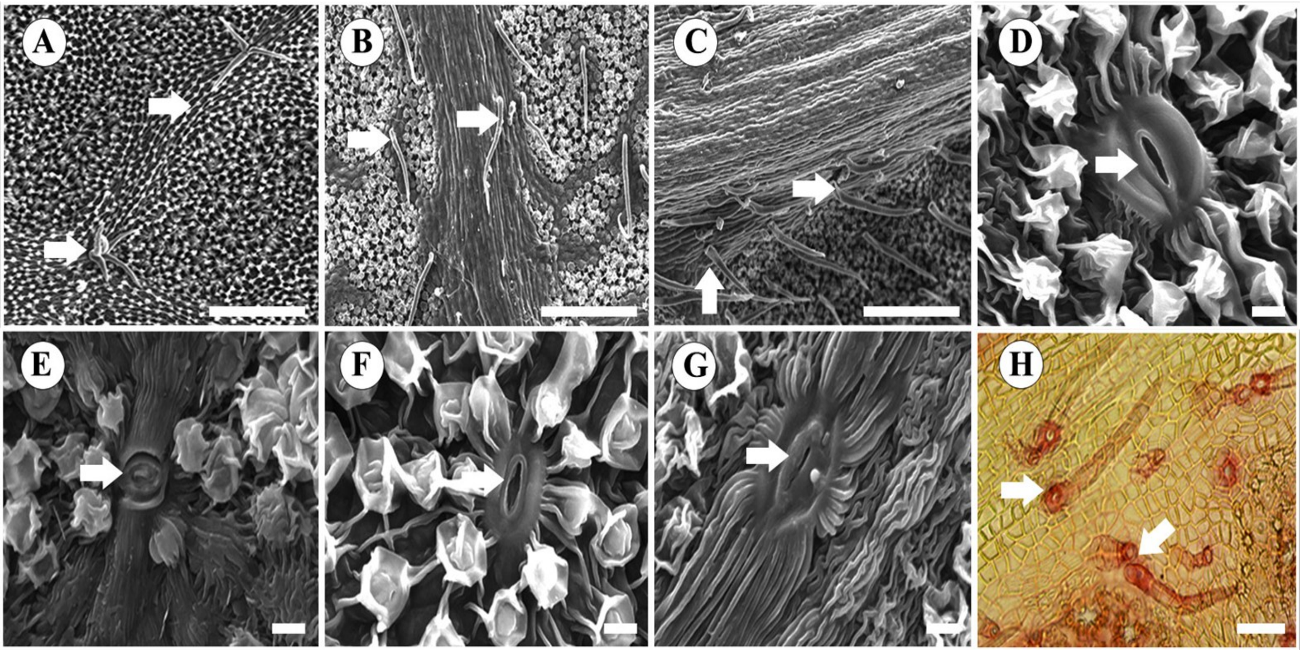

Fig. 1. *Cuticular anatomy - Cuticular striations and the armed non-glandular trichomes in (A) Dimocarpus longan; Non-glandular trichomes in (B) Nephelium lappaceum, (C) Nephelium ramboutan-ake; Abaxial cuticular ridges and stomata with striations on guard cells in (D) Dimocarpus longan, (E) Nephelium lappaceum, (F) Nephelium ramboutan-ake, (G) Litchi chinensis; Glandular trichomes in (H) Nephelium ramboutan-ake. (A, B, C = 100 μm; D, E, F, G = 20 μm; H = 40 μm).*

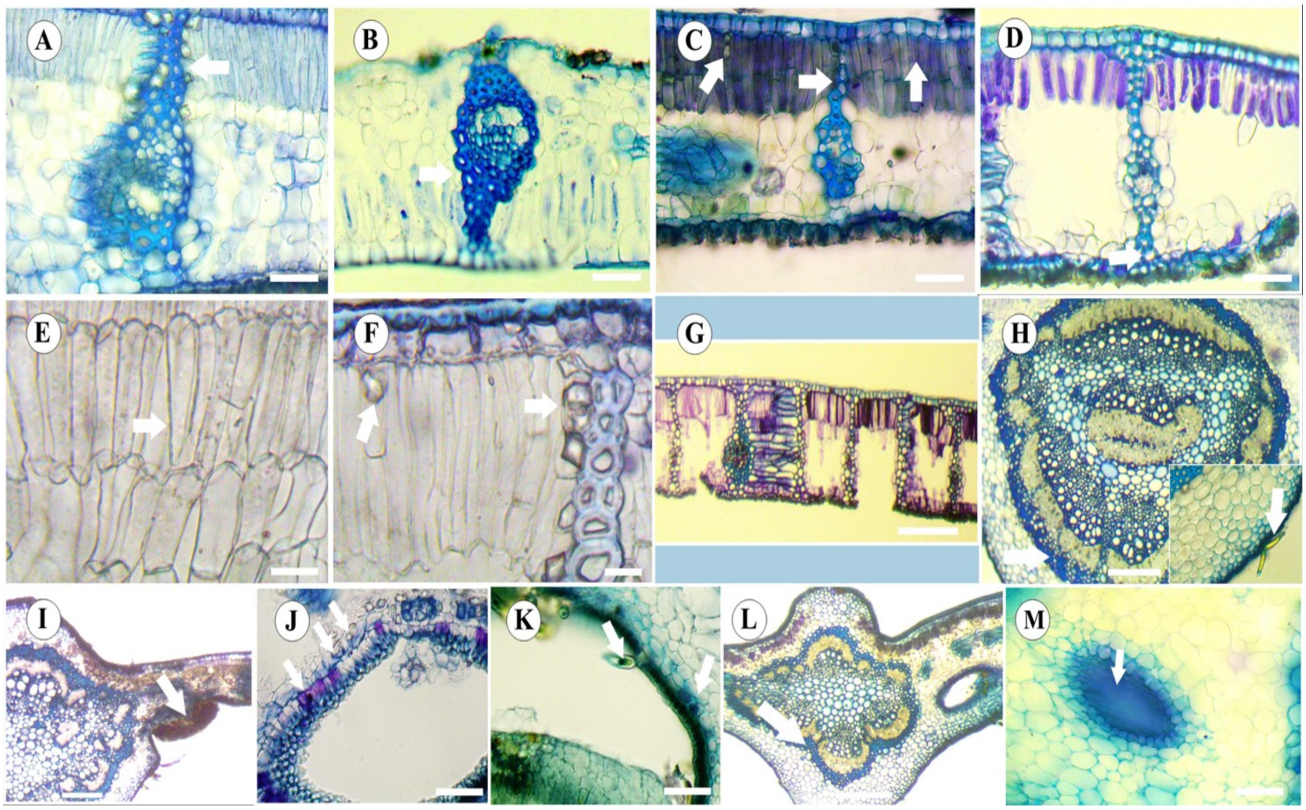

Fig. 2. *Lamina anatomy – Sclerified BSEs in (A) Dimocarpus longan. (B) Nephelium lappaceum. (C) Nephelium ramboutan-ake. (D) Litchi chinensis. Elongated sac-shaped spongy parenchyma in (E) Dimocarpus longan; Prismatic crystals attached to the vein bundle in (F) Dimocarpus longan; Stomatal patchiness in (G) Litchi chinensis; Midrib with sclerenchymatous sheath in (H) Dimocarpus longan. Midrib with domatia of Nephelium lappaceum showing (I) Opened pit (J) Prismatic crystals, secretory tissues (K) Non-glandular trichomes; Midrib with pit-type domatia in (L) Nephelium ramboutan-ake; (M) Young domatia filled with secretions. (A, B, C, D, = 40 μm; E, F, J, K, M = 30 μm; G, H, I, L= 200 μm).*

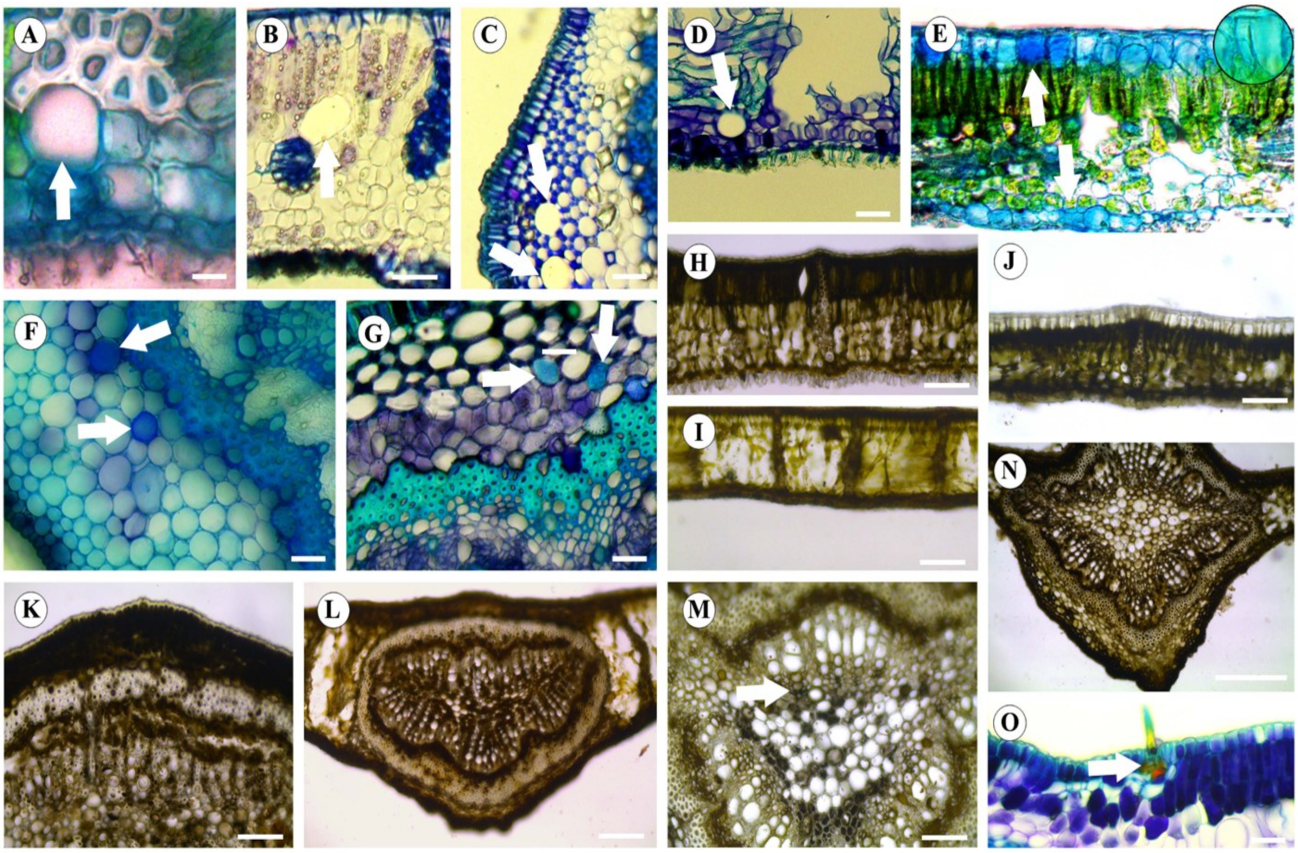

Fig. 3. *Foliar depositions - Secretory cells in (A) Dimocarpus longan (B) Nephelium lappaceum (C) Nephelium ramboutan-ake; Mucilage deposition in (E) Epidermal cells in Nephelium lappaceum, (F) Midrib cortex in Nephelium ramboutan-ake (G) Midrib parenchyma in Litchi chinensis; Lamina T.S positively stained for phenolic deposition in (H) Dimocarpus longan (I) Litchi chinensis (J) Nephelium lappaceum; Midrib showing phenolic compounds in (K) Dimocarpus longan (L) Litchi chinensis (M) Nephelium lappaceum (N) Nephelium ramboutan-ake; Trichome base with phenolic deposition in (O) Nephelium ramboutan-ake. (A = 40 µm; B, C, D, E, H, I, J, K, L, M= 100 µm; F, G, H, O = 50 µm; N = 200 µm).*

four tropical fruit trees adapted them to utilise maximum solar radiation for CO_2 assimilation in a minimum water economy (Sack and Scoffoni, 2013).

Midrib ground tissue and vasculature

The midribs of all the analysed species showed thick cuticle, non-glandular (Fig. 2H) or glandular trichomes, well-developed, medullated, closed, and collateral vascular system (Table 2) surrounded by a sclerenchymatous sheath (Fig. 2H). The presence of mucilage cells, phenolic depositions, and prismatic crystals was prevalent in the ground tissue of midribs (Fig. 3B). The midrib with solid and prominent vasculature present in all four species contributes to faster loading of photosynthates, and the mechanical tissues surrounding the midrib, especially at the corners, also offer protection from physical injuries (Sack *et al*., 2012).

Domatia

Specialised nesting cavities were found on the leaves of tropical plants that host organisms such as ants and mites by a mutualistic association (Romero and Benson, 2004). Among the analysed species, *N. lappaceum* and *N. ramboutan-ake* had domatia in the axils of the midvein and secondary veins on the abaxial leaf surface (Fig. 2 I, 2 L). The rim of leaf tissues associated with domatia showed more glandular trichomes, prismatic crystals and brown-coloured phenolic depositions than other leaf parts (Fig. 2J, 2K, 2 M). Understanding the role of domatia is reasonable, especially in the case of fruit trees, where the chances of herbivory are high, and pesticide use in orchards might remove the natural pest controllers residing in the leaf shelters from their biota. Studies by Nishida *et al*. (2006) proved that differently shaped domatia were associated with different mite taxa, and pit domatia (seen in *N. lappaceum* and *N. ramboutan-ake*) were inhabited by carnivorous mites.

Mucilage and phenolic depositions

Secretory cells were present in the abaxial BSEs and, among the mesophyll tissue and also in the outer cortex of the midrib of *D. longan*, *N. lappaceum* and *N. ramboutan-ake* (Fig. 3A, 3B, 3C, 3D). The adaxial and abaxial epidermises of *N. lappaceum*, palisade cells of *N. ramboutan-ake,* and the outer cortex of the midrib of all the species had mucilage cells (Fig. 3E, 3F, 3G). Phenolic deposition appeared throughout the lamina in all four species. It was more confined to the mesophyll tissues near the epidermis (Fig. 3H-3N) and the glandular trichome base and peripheral leaf tissues in *N. ramboutan-ake* (Fig. 3O). The phenolic depositions in the lamina, domatia, midrib epidermis, and subepidermal tissues act as a repellent for herbivores and protect the internal cells from UV radiation by acting as optical filters (Goldstein *et al*., 2016). The role of mucilage depositions in regulating hydration at the leaf level and the remobilisation of the solutes, serving as an osmotic adjuster, was reported by Somavilla *et al*. (2014).

Prismatic crystals

All the analysed species had prismatic crystals unevenly distributed in the tissues and parts of the leaf blade and midrib (Table 1; Fig. 2, 3). The crystals were associated with vein bundles in *N. lappaceum* and bundle sheath extension in *D. longan* (Fig. 2H). Furthermore, prismatic crystals were arranged in a linear chain of 2–4 in chambered palisade cells in *N. ramboutan-ake* (Fig. 2F, 2J). The distribution of calcium oxalate crystals serves as a defence against herbivory (Farfán *et al.,* 2020) and acts as a means to regulate the internal calcium sink and osmotic potential (Webb, 1999).

Conclusion

This study highlights the adaptive significance of leaf traits in tropical fruit species, showcasing a unique combination of evergreen and xerophytic characteristics that enhance climate resilience. Evergreen anatomical traits, such as robust mesophyll structure, extensive photosynthetic areas, and well-developed vein vasculature, support adaptation to high light intensity and fluctuating humidity. Concurrently, xerophytic features confer resilience to periodic droughts, including thick abaxial and adaxial cuticles, a low stomatal index, and compartmentalized photosynthetic areas. Additionally, defensive adaptations such as papillated cuticles, trichomes, crystals, phenolic compounds, mucilage, and domatia provide protection against herbivory, UV radiation, and heat stress, ensuring survival in challenging tropical environments.

This work underscores the importance of leaf anatomy in understanding the climate adaptability of tropical fruit trees and its implications for sustainable agriculture. By leveraging these adaptive traits in crop selection and breeding, it is possible to reduce reliance on external inputs, such as irrigation and pesticides, while optimizing productivity and preserving environmental health. These findings are a foundation for integrating anatomical insights into cultivation practices, contributing to ecosystem stability and advancing climate-resilient horticulture.

Supplementary Information

The author(s) is responsible for the content or functionality of any supplementary information. Any queries regarding the same should be directed to the corresponding author. The supplementary information is downloadable from the article's webpage and will not be printed in the print copy.

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Conflict of interest

The authors declare that they have no conflict of interest.

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