

# Anatomical Study and Silicon Content of The Foraged Plant Material by Leaf-Cutting Ants

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**Abstract** – A great number of plant species is collected selectively in the habitat by leaf-cutting ants, but it is unknown about anatomy of leaves and silicon content of preferred plants. Thus, our study was investigated the leaf anatomy and silicon content in the foraged plants by grass-cutting and leaf-cutting ants *Atta bisphaerica* and *Atta sexdens rubropilosa*. Food preference differs between the two studied ants, with *A. s. rubropilosa* preferentially foraging on dicotyledons and *A. bisphaerica* on grasses. Our results showed that the leaves of grasses are extremely vascularized and contain large numbers of lignified cells, while in dicot leaves the vascular bundles are more distant and cells with lignified walls are rarer. Furthermore, analysis of the silicon content of preferred plants clearly showed a higher silicon content of grasses compared to most dicotyledons. Our study contributes to a better understanding of the so far unknown anatomy of leaves and silicon content of preferred plants by and leaf-cutting ants *Atta bisphaerica* and *Atta sexdens rubropilosa*.

**Keywords** – Atta, Leaf Anatomy, Leaf-Cutting Ants Silicon Content

## I. INTRODUCTION

The leaf-cutting ants use several alimentary sources for diet composition, provided mainly from plant sap [1]-[3], symbiotic fungus [4], [5] and proctodeal trophallaxis with larvae in the colony [6].

This alimentary structural complex is based on plant selection, used as substrate for the symbiotic fungus cultivation [4], [7]-[9]. Thus, a great number of plant species is collected selectively in the habitat [10]. However, some species of leaf-cutting ants have preferential in certain plants (dicotyledons) and others grasses (monocotyledons) [11].

The leaf of grasses contains lignified cells [12], which are more resistant to cutting, as well as solid particles of silica (SiO<sub>2</sub>nH<sub>2</sub>O) is located in the epidermal cells [13]. These features have been associated with a many functions, including protection against fungal, prevention to water loss, structural support and protection against herbivores [14]-[16]. Moreover, silica accumulation in grasses increases leaf abrasiveness, causing the wear and deterioration of mandibles and impairing insect feeding [17]-[18].

The objective of the present study was to investigate the leaf anatomy and silicon content in the foraged plants

by grass-cutting and leaf-cutting ants *Atta bisphaerica* and *Atta sexdens rubropilosa*.

## II. MATERIAL AND METHODS

### A. Studied Species

Plant materials foraged by the two leaf-cutting ant species (*A. bisphaerica* and *A. s. rubropilosa*) were selected: *Paspalum* sp., *Acalypha* sp., *Ligustrum* sp., *Eucalyptus* sp., *Citrus* sp., and *Gmelina arborea*, respectively.

### B. Anatomical study of the foraged plant material

The anatomical study was conducted at the Laboratory of Plant Anatomy, Department of Botany, Institute of Biosciences, UNESP, Botucatu, SP. Samples of the leaf blade of *Paspalum* sp. were collected across the *A. bisphaerica* trail near the entry holes of the nests, which were located in a pasture area. For *A. s. rubropilosa*, the samples were collected in a laboratory colony. Foraging was performed by opening one of the connections of the colony, providing access to an arena where *Acalypha* sp., *Ligustrum* sp., *Eucalyptus* sp., *Citrus* sp., and *Gmelina arborea* plants were available. The fragments were collected as they were cut by the workers.

After collection, the fragments were fixed in 50% FAA for 24 h and cut transversely with a Ranvier microtome. The sections obtained were cleared in 20% sodium hypochlorite, washed in water-1% acetic acid and distilled water, and stained with Safrablau [19]. Semi-permanent slides were mounted with glycerin jelly and examined under an Olympus BX41 light microscope. Relevant results were documented with an Olympus Camedia C-7070 digital camera coupled to the microscope.

### C. Quantification of silicon in the foraged plant material

For this study, samples of the foraged plants were collected, dried in a forced air circulation oven (65 °C), ground, and sent to the Laboratory of Soil-Plant Relationship, Department of Agriculture, College of Agricultural Sciences (Faculdade de Ciências Agrônomicas - FCA-UNESP), Botucatu, SP. 10 used to analyze silicon in plant tissue. Mean silicon levels were compared by analysis of variance ( $\alpha=0.05\%$ ).



### III. RESULTS

#### A. Anatomical study of the foraged plant material

##### *Acalypha* sp

The leaf blade of *Acalypha* sp. has uniseriate epidermis covered with a moderately thick cuticle (Fig. 1). Stomata occur on the abaxial surface of the leaf blade and are arranged at the same level of the common epidermal cells. The mesophyll is dorsiventral and consists of a layer of palisade parenchyma and four to six layers of spongy parenchyma (Fig. 1). Idioblasts containing calcium oxalate crystals are observed in the mesophyll (Fig. 1). The vascular bundles are small and located distant from one another.

In the midrib region (Fig. 1), the cortex is formed by four or five layers of collenchyma and six to eight layers of parenchyma cells. The vascular system is composed of primary phloem and xylem. The scarcity of lignification is remarkable and the vessel members are the only cells with lignified walls (Fig. 2).

##### *Gmelina* sp.

The leaf blade of *Gmelina* sp. has uniseriate epidermis covered with a thin cuticle (Fig. 3). Stomata are found on the abaxial surface of the leaf blade and are arranged at the same level of the common epidermal cells. Glandular and non-glandular trichomes are found on both leaf blade surfaces, but are more abundant on the abaxial surface (Fig. 3). The mesophyll is dorsiventral and consists of one to two layers of palisade parenchyma cells and three or four layers of shorter parenchyma cells with reduced intercellular spaces (Fig. 3). The vascular bundles are surrounded by a sheath of parenchyma extending in the direction of the epidermis of the abaxial and adaxial leaf blade surfaces (Fig. 3).

In the midrib region, glandular and non-glandular trichomes also occurs in the epidermis (Fig. 4). The cortex is formed by about four layers of collenchyma cells and four to five layers of parenchyma cells (Fig. 4). The vascular system consists of primary phloem and xylem and the scarcity of lignified elements is a notable feature throughout the leaf blade (Fig. 4).

##### *Eucalyptus* sp.

The leaf blade of *Eucalyptus* sp. has uniseriate epidermis covered with a thick cuticle (Fig. 5). Stomata are found on both leaf blade surfaces and are arranged at the same level of the common epidermal cells. The mesophyll is exclusively constituted by five or six layers of elongated parenchyma cells (Fig. 5). Oil cavities are observed in the mesophyll and are more common in the adaxial portion of the leaf blade (Fig. 5). The vascular bundles are surrounded by a sheath of lignified fibers (Fig. 5).

In the midrib region, the cortex consists of three to four layers of collenchyma and four or five layers of parenchyma cells (Fig. 6). A well-established cambial zone is observed between the xylem and phloem (Fig. 6).

##### *Citrus* sp.

The leaf blade of *Citrus* sp. has uniseriate epidermis (Figs. 7 and 8) covered with thick cuticle. Stomata are found on the abaxial leaf surface and are arranged at the

same level of the common epidermal cells. Idioblasts containing prismatic crystals of calcium oxalate are observed in the epidermis on both leaf surfaces (Figs. 7 and 8). The mesophyll is dorsiventral and consists of two to three layers of palisade parenchyma and about 10 layers of spongy parenchyma (Figs. 7). Oil cavities are found in the mesophyll, beneath the epidermis, and are more common on the adaxial surface of the leaf (Fig. 7). Cells containing clusters of raphides are observed in the mesophyll (Fig. 8). The vascular bundles immersed in the mesophyll are constituted by primary phloem and xylem and exhibit a cap of fibers with lignified walls surrounding the phloem (Figs. 7 and 8).

In the midrib region, the cortex is composed of collenchyma and parenchyma cells (Fig. 9). The vascular system is externally surrounded by a sheath consisting of four or five layers of fibers with lignified walls (Fig. 9). An installed cambium zone is observed between the xylem and phloem (Fig. 9).

##### *Ligustrum* sp.

The leaf blade of *Ligustrum* sp. has uniseriate epidermis covered with a moderately thick cuticle (Fig. 10). Stomata are found on the abaxial leaf surface and are arranged at the same level of the common epidermal cells. Sessile and scarce glandular trichomes are observed on both leaf blade surfaces and are inserted into small recesses in the epidermis (Fig. 10). The mesophyll is dorsiventral and consists of one or two layers of palisade parenchyma and five layers of spongy parenchyma (Fig. 10). The vascular bundles immersed in the mesophyll are small and close to each other (Fig. 10).

In the midrib region (Fig. 11), the cortex is formed by three or four layers of collenchyma and about eight layers of parenchyma. A well established cambial zone is observed between the phloem and xylem (Fig. 11). In general, a finding that calls attention is the scarcity of lignification, with the vessel members of the xylem being the only cells with lignified walls (Fig. 11).

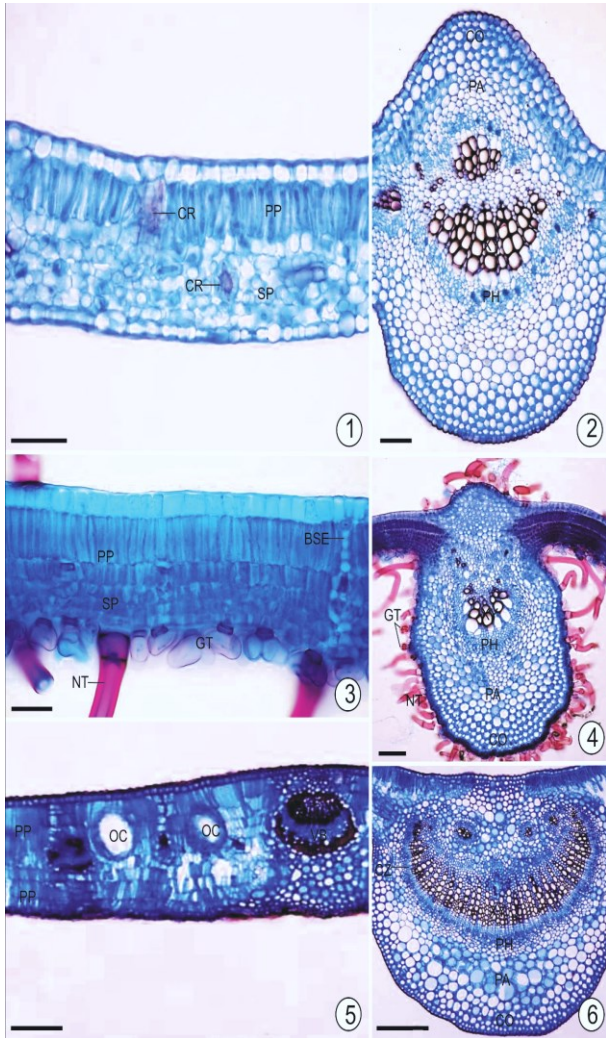
##### *Paspalum* sp.

The leaf blade of *Paspalum* sp. has uniseriate epidermis. The common epidermal cells present thick lignified walls (Figs. 12) Clusters of bulliform cells are found on the adaxial surface of the leaf blade (Fig. 13). Stomata are present on both leaf blade surfaces (Figs. 12 and 13). In the mesophyll, the chlorophyll parenchyma cells extend radially around the vascular bundles characterizing Kranz anatomy (Figs. 12 and 13). Groups of fibers with lignified walls are found beneath the epidermis on both leaf blade surfaces (Figs. 12). A well-delimited endodermis surrounds the vascular bundles, which are numerous and disposed close to each other, (Figs. 12 and 13). Perivascular fibers are present in the vascular bundles with larger caliber (Fig. 13).

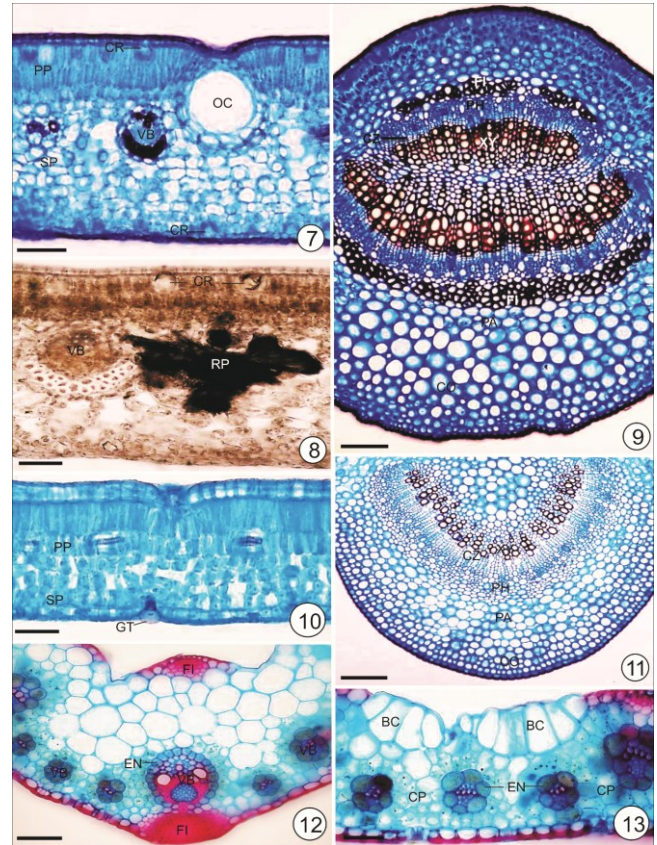
#### B. Quantification of silicon in foraged plant material

A significant difference in mean silicon content was observed between the plant species studied (ANOVA,  $F_{6,14} = 16.6624$ ,  $p < 0.0001$ ). *Paspalum* sp. ( $10515.6 \pm 863.2$  mg kg<sup>-1</sup>) did not differ from *Gmelina* sp. ( $9601.0 \pm 686.0$  mg kg<sup>-1</sup>), but differed from *Ligustrum* sp. ( $6515.0 \pm 343.0$

mg kg<sup>-1</sup>), *Citrus* sp. (7887.0±686.0 mg kg<sup>-1</sup>), *Acalypha* sp. (6858.0±343.0 mg kg<sup>-1</sup>) and *Eucalyptus* sp. (6972.3±523.9 mg kg<sup>-1</sup>) (Tukey post-test,  $p < 0.001$ ). The silicon content of *Gmelina* sp. differed from that of *Ligustrum* sp., *Acalypha* sp. and *Eucalyptus* (Tukey post-test,  $p < 0.001$ ), but not from *Citrus* sp. *Ligustrum* sp. differed from *Acalypha* sp. and *Eucalyptus* sp. (Tukey post-test,  $p < 0.001$ ).



**Figs. 1-6.** Micrographs of cross-sections of the leaf blades. 1-2. *Acalypha* sp. 1. General view showing uniseriate epidermis and dorsiventral mesophyll. Observed idioblasts with calcium oxalate crystals in the mesophyll. 2. Midrib showing epidermis, cortex with collenchyma and parenchyma, and vascular system. 3-4. *Gmelina* sp. 3. Overall view showing uniseriate epidermis with glandular and non-glandular trichomes and dorsiventral mesophyll. Note the extent of the bundle sheath extension. 4. Section of the midrib showing the uniseriate epidermis with trichomes, cortex consisting of collenchyma and parenchyma, and vascular system. 5-6. *Eucalyptus* sp. 5. Overall view showing uniseriate epidermis, mesophyll with palisade parenchyma cells and oil cavities, and vascular bundles. 6. Midrib showing uniseriate epidermis, cortex with collenchyma and parenchyma, and vascular system with well-established cambial zone. BSE: bundle sheath extension; CO: collenchyma; CR: crystal; CZ: cambial zone; NT: non-glandular trichome; OC: oil cavity; PH: phloem; PP: palisade parenchyma; SP: spongy parenchyma; GT: glandular trichome; VB: vascular bundle; XY: xylem. Scale bars: 1, 3, 5 = 100  $\mu$ m; 2, 4, 6 = 150  $\mu$ m.



**Figs. 7-13.** Micrographs of cross-sections of the leaf blades. 7-9. *Citrus* sp. 7-8. Overall view showing uniseriate epidermis with idioblasts of calcium crystals, dorsiventral mesophyll with oil cavities idioblasts with raphides, and vascular bundles. 9. Midrib showing uniseriate epidermis, cortex with collenchyma and parenchyma, and vascular system surrounded by a sheath of lignified fibers. Observe the well-established cambial zone. 10-11. *Ligustrum* sp. 10. Overall view showing uniseriate epidermis with sparse glandular trichomes and dorsiventral mesophyll. 11. Midrib showing uniseriate epidermis, cortex with collenchyma and parenchyma, and vascular system with a well-established cambial zone. 12-13. *Paspalum* sp. Sections showing cells with lignified walls, bulliform cells and stomata in the epidermis; mesophyll with chlorophyll parenchyma arranged radially around vascular bundles. Observe the endodermis with large cells around the vascular bundles and groups of fibers beneath the epidermis. BC: bulliform cells; CO: collenchyma; CP: chlorophyll parenchyma; CR: crystal; CZ: cambial zone; EN: endodermis; GT: glandular trichome; OC: oil cavity; FI: fibers; PA: parenchyma; PH: phloem; PP: palisade parenchyma; RP: raphides; SP: spongy parenchyma; VB: vascular bundle; XY: xylem. Scale bars: 7, 8, 10, 12, 13 = 100  $\mu$ m; 9, 11 = 150  $\mu$ m.

#### IV. DISCUSSION

Food preference differs between the two studied ants, with *A. s. rubropilosa* preferentially foraging on dicotyledons and *A. bisphaerica* on grasses [21]. This fact is due to the biome that these species inhabit. The morphological structure of the leaf blades of the preferred plants supports the differences in the behavior of leaf cutting and cultivation of the symbiotic fungus by the workers. The leaves of grasses are extremely vascularized and contain large numbers of lignified cells, while in dicot leaves the vascular bundles are more distant and cells

with lignified walls are rarer (see anatomical description). These results corroborate the fact that grass-cutting ants perform a less thorough processing of the plant material compared to leaf-cutting ants because of the greater hardness and shear strength of these leaves, which impair their digestibility by the animals. In grasses, the presence of epidermal cells with lignified walls is the first mechanical barrier that protects the leaves against herbivory and pathogen attack [21]. Thus, although it is known that glandular and non-glandular trichomes, calcium crystals and structures producing secondary metabolites play an important role in the defense of plants against the attack of herbivores and pathogens [23]. In the present study the abundance of cells with lignified walls exerted a greater influence on the degree of processing of plant fragments by leaf-cutting ants.

Furthermore, analysis of the silicon content of preferred plants clearly showed a higher silicon content of grasses compared to most dicotyledons. The presence of silicon in plant tissues is a mechanism to reduce herbivory by vertebrates [24] and invertebrates [25] by means of an increase in shear strength and its abrasive effect on mandibles, acting as a food deterrent [26]. One way to reduce the abrasive effect on mandibles is the incorporation of inorganic components in the latter, which renders them more resistant when interacting with the environment. For example, a high correlation between mandibular tooth hardness and zinc content has been observed in *A. s. rubropilosa* [27], but this mineral enrichment is unknown for grass-cutting species which forage plants with a high silicon content.

Thus, our study contributes to a better understanding of the so far unknown anatomy of leaves and silicon content of preferred plants by and leaf-cutting ants *Atta bisphaerica* and *Atta sexdens rubropilosa*.

## V. ACKNOWLEDGMENT

R.S. Camargo thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the Postdoctoral fellowship. L.C. Forti thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico for the research assistance (301917/2009-4).

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