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Are the Species of the Genus *Avicennia* L. (Acanthaceae) a “Superhost” Plants of Gall-Inducing Arthropods in Mangrove Forests?

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Additional information is available at the end of the chapter

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1. Introduction

Some plant species, especially angiosperms, present infestation by invertebrates that modify the general appearance of their vegetative and/or reproductive parts, known as galls. The galls are the result of abnormal growth of cells, tissues or organs due to an increase in cell volume (hypertrophy) and/or in the number of cells (hyperplasia) in response to feeding or to stimuli caused by foreign bodies, except for other inducing agents such as fungi and bacteria, which lead to amorphous tumor formation (Rohfritsch & Shorthouse 1982; Dreger-Jauffret & Shorthouse 1992; Raman *et al.* 2005; Raman 2007).

Gall-inducing arthropods have a highly specific relationship with their host plants, and normally attack only a single or a few closely-related plant species (Dreger-Jauffret & Shorthouse 1992). This degree of specialization facilitates the recognition of the diversity of gall-inducing insects, for example, in a given locality or plant species (Carneiro *et al.* 2009). The presence in some plant communities of species that support a relative rich fauna of gall-inducing insects has resulted in these plants being referred to as “superhost”, whose local and regional distribution have a decisive influence on the local and regional galling diversity (Veldtman & McGeoch, 2003; Espírito-Santo *et al.*, 2007; Mendonça, 2007).

Some plant species, from a range of biogeographic regions and ecosystems, present a wide variety of gall morphotypes (Fernandes & Price 1988; Waring & Price 1989; Blanche 2000; Stone *et al.* 2002; Cuevas-Reyes *et al.* 2003). In the Neotropical region, for example, “superhosts” have been identified in a number of different habitat types, such as highland rocky grassland (“campo rupestre”), involving the species *Baccharis concinna* (Carneiro *et al.* 2005) and *Baccharis pseudomyriocephala* (Lara *et al.* 2002), and *Copaifera langsdorffii* (Oliveira *et al.*

2008), associated with litholic habitats (“canga”), as well as halophytic formations, where examples include *Eugenia umbelliflora* (Maia 2001b; Monteiro *et al.* 2004) and *Guapira opposita* (Oliveira & Maia 2005). In the temperate zone, Waring & Price (1989) and Gagné & Waring (1990) have also identified the creosote bush (*Larrea tridentata*) as a “superhost” for Cecidomyiidae (Diptera) species of the *Asphondylia auripila* group.

The vast majority of the studies of herbivory by insects in mangrove forests have focused on leaf-chewing species (Cannicci *et al.* 2008), adding the fact that little is known about interactions involving endophytic forms such as leaf miners or gall-inducing species (Gonçalves-Alvim *et al.* 2001; Burrows 2003; Menezes & Peixoto 2009).

The genus *Avicennia* has pantropical distribution, comprising the following species: *A. alba* Blume, *A. bicolor* Standley, *A. eucalyptifolia* (Zipp. ex Miq.) Moldenke, *A. germinans* (L.) Stearn, *A. integra* Duke, *A. lanata* Ridley, *A. marina* (Forks.) Vierh., *A. officinalis* L., *A. rumphiana* Hallier f. e *A. schaueriana* Stapf and Leechman ex Moldenke (WORMS 2010). Based on the fact that the genus *Avicennia* presents a great variety of gall morphotypes and hence many gall-inducing arthropods, the present study aims to review this plant-gall association describing what is known so far, and to verify whether the species of *Avicennia* are “superhost” plants of tropical mangrove forests.

2. Gall-inducing arthropods and their hosts in mangrove worldwide

Of the nine species of gall-inducing arthropods described for mangrove plants in different parts of the world, two species (Acari: Eriophyidae) were described in the genus *Laguncularia* L. (Combretaceae) (Flechtman *et al.* 2007) and seven species (Diptera: Cecidomyiidae) in the genus *Avicennia* L. (Acanthaceae) (Cook 1909; Felt 1921; Gagné & Law 1998; Gagné & Etienne 1996). Besides, there are twenty-two morphotyped already described, totalizing 29 species of Cecidomyiidae recorded on four species of *Avicennia* (Table 1). Table 1 also presents three other groups of arthropods (Acari, Hemiptera, and Hymenoptera), which have been registered associated with mangroves around the world, and the family Cecidomyiidae stands out as the main group of galling in this ecosystem.

In fact, the species of the genus *Avicennia* have been identified as hosts of gall-inducing cecidomyiids in the Neotropical region since the beginning of the twentieth century. Gagné & Etienne (1996) reviewed the data on this phenomenon and proposed that the insect *Cecidomyia avicenniae* (Diptera, Cecidomyiidae), described by Cook in 1909 in *Avicennia nitida* in Cuba and Central America, should be reassigned to the species *Meunieriella avicenniae* (Cook). They also emphasized the fact that Tomlinson (1986) considered *A. nitida* to be a synonym of *A. germinans*.

Galls similar to those described by Cook at the beginning of the century were also identified subsequently in *A. tomentosa* in the Brazilian state of Bahia (Tavares 1918), and in *Avicennia officinalis* in French Guiana (Houard 1924). However, the two mangrove species identified in these studies were in fact *A. germinans* or *Avicennia schaueriana*, given that *A. tomentosa* is a synonym of *A. germinans* and *A. officinalis* is found only in the Old World (Tomlinson 1986).

Plant host	Inducing taxon	Reference
<i>A. germinans</i> (6 spp.)	CECIDOMYIIDAE	
	<i>Meunieriella avicenniae</i>	Tavares 1918; Houard 1924; Gagné & Etienne 1996
	Undet. sp. A	Jiménez 2004
	Undet. sp. B	
	Undet. sp. B	Jiménez 2004
	Undet. sp. C	Jiménez 2004
	PSYLLIDAE	
	<i>Telmasylla minuta</i>	Jiménez 2004
	ACARI	
	Undet. sp. A	Jiménez 2004
<i>A. marina</i> (16 spp.)	CECIDOMYIIDAE	
	<i>Actilasioptera coronata</i>	Gagné & Law 1998
	<i>Actilasioptera falcaria</i>	Kathiresan 2003
	<i>Actilasioptera pustulata</i>	Gagné & Law 1998
	<i>Actilasioptera subfolium</i>	Gagné & Law 1998
	<i>Actilasioptera tuberculata</i>	Gagné & Law 1998
	<i>Actilasioptera tumidifolium</i>	Gagné & Law 1998
	Undet. sp. A	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	Undet. sp. B	
	Undet. sp. C	
	Undet. sp. D	
	Undet. sp. E	
	Undet. sp. B	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	Undet. sp. C	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	Undet. sp. D	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	Undet. sp. E	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	Undet. sp. F	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	ERYOPHYIDAE	
	Undet. sp. A	Gagné & Law 1998
	COCCIDAE	
	Undet. sp. A	Gagné & Law 1998
	ACARI or INSECTA	
	Undet. sp. A	Gagné & Law 1998
	HYMENOPTERA	

Plant host	Inducing taxon	Reference
<i>A. officinalis</i> (4 spp.)	Undet. sp. A	Sharma & Das 1994; Sharma <i>et al.</i> 2003
	CECIDOMYIIDAE	
	<i>Actilasioptera falcaria</i>	Raw & Murphy 1990
	Undet. sp. A	Raw & Murphy 1990
	Undet. sp. B	Raw & Murphy 1990
	ERYOPHYIDAE	
<i>A. schaueriana</i> (3 spp.)	<i>Eriophyes</i> sp.	Raw & Murphy 1990
	Undet. sp. A	Maia <i>et al.</i> 2008
	<i>Meunierilla avicenniae</i>	Menezes & Peixoto 2009
	Undet. sp. B	Present study

Table 1. Gall-inducing arthropods on species of *Avicennia*

In addition, Gagné (1994) identified rounded and smooth galls in *A. germinans* in Florida (USA) and Belize, while Gagné & Etienne (1996) identified the same gall morphotypes in specimens of *A. germinans* in Guadalupe and San Martin, in Central America. In Belize, Central America, Farnsworth & Ellison (1991) identified two gall morphotypes in *A. germinans*, but without identifying the inducing agent. Jiménez (2004) highlighted the presence of leaf galls induced by *Telmapsylla minuta* (Psyllidae: Homoptera), by three undetermined species of Cecidomyiidae, and an unidentified mite species in *A. germinans*, in Costa Rica.

In Ranong, Thailand, the occurrence of four gall-inducing insects in *A. officinalis* was recorded, being two induced by undetermined species of Cecidomyiidae, one by an unidentified mite species belonging to the family Eriophyidae and another by *Stefaniella falcaria* Felt (Diptera: Cecidomyiidae) (Rau & Murphy, 1990). Subsequently, Gagné & Law (1998) reviewed a material from Java and redescribed and transferred the species *Stefaniella falcaria* to the new genus *Actilasioptera*.

Regarding *A. schaueriana*, at least three species of Cecidomyiidae are involved in leaf gall-inducing in this species, two in southeastern Brazil, *Meunieriella avicennae* (= *Cecidomyia avicennae*) and an undetermined (Maia *et al.*, 2008; Menezes & Peixoto, 2009), and another in the northern region (present study).

Gagné & Law (1998) described from Queensland, Australia, five gall-inducing insects of the family Cecidomyiidae in *A. marina*, all of which belong to a new genus, *Actiolasioptera* (*A. coronata* Gagné, 1998; *A. pustulata* Gagné, 1998; *A. subfolium* Gagné, 1998; *A. tuberculata* Gagné, 1998; *A. tumidifolium* Gagné, 1998). In addition to these midge species, a eriophyid mite (Acari), a coccid (Homoptera), and an unknown arthropod gall were identified in *A. marina* in Australia. In addition, Sharma & Das (1984) and Sharma *et al.* (2003) recorded six undetermined species of Cecidomyiidae (leaf gall) and an unidentified species of

Hymenoptera (stem gall) for *A. marina*, from the coastal region of Andaman and Vikhroli, Maharashtra, India. Kathiresan (2003) also recorded *Stephaniella falcaria* (= *Actilasioptera falcaria*) in the mangrove forests of Pichavaram, southeastern coast of India. Burrows (2003), investigating herbivory in mangroves near Townsville, Queensland, Australia, recorded at least ten gall morphotypes to this mangrove species, without identifying, however, the gall-inducing agents.

3. Gall morphotypes in *Avicennia*

The vast majority of gall-inducing arthropods is restricted to a single host plant species, thus corroborating the idea that the gall morphotype can be used as reliable substitutes of gall-inducing species. In addition, polymorphism of galls, which could lead to the occurrence of failures in the identification of galls, appears to be a rather rare phenomenon (Carneiro *et al.* 2009).

Numerous surveys have been conducted in different regions of Brazil in an attempt to identify the diversity of gall-inducing agents in different ecosystems (Fernandes & Price 1988; Gonçalves-Alvim & Fernandes 2001; Fernandes & Negreiros 2006; Araújo *et al.* 2007; Maia *et al.* 2008; Carneiro *et al.* 2009). Given that some species of the genus *Avicennia* support many gall-inducing arthropods throughout their geographic distribution, it is expected a greater diversity of gall-inducing arthropods and a wide variety of gall morphotypes growing on their organs (Table 2).

4. New records of gall morphotypes in *Avicennia* of the north coast Brazil

Given the wide distribution of the genus *Avicennia* around the world, it is clear that the interaction between galls and *Avicennia* species is an import gap in our understanding of the role of these trees in the mangrove system. At this topic, in addition to the literature review, new records of gall morphotypes found in *Avicennia* on the Ajuruteua Peninsula (00°57,9'S-46°44,2'W), on Brazil's Amazon coast (Fig. 1) will be also presented. Data collection was carried out in October/2010 and leaves from 20 individuals of *A. germinans* were collected simultaneously.

A total of 11,448 leaves were counted on the 20 specimens of *A. germinans*. Of this total, only 17% (n=1,970) had galls, which were classified in 14 distinct morphotypes, based on their coloration and morphological features (Fig. 2 and Table 3).

Among 4,787 morphotyped galls, conical ones were the most common (n=1,101 – 23%), while disc galls were the rarest (n=9 – 0.2%). The number of galls per leaf varied from one to 41, with an average of 4.7 ± 1.5 galls. Table 3 also indicates that an additional 2,313 galls – almost a third of the total of 7,100 recorded in the study – were not identified, due to be either damaged (DAM) or in an initial stage of development (ISD). The total number of galls in the individuals of *A. germinans* sampled at the Furo do Taici must be higher, although stem galls have been observed in different branches, they were not counted in the present study.

Plant host	Organ	Form	Geographic location	Reference
<i>A. germinans</i> or <i>A. schaueriana</i>	Leaf	Round and smooth on the upper surface and warty on the lower surface, a craterlike exit hole eventually develops	Cuba	Cook 1909; Tavares 1918; Houard, 1924
<i>A. germinans</i>	Leaf	No description	Belize	Farnsworth & Ellison 1991
<i>A. germinans</i>	Leaf	No description	Costa Rica	Jiménez 2004
<i>A. germinans</i>	Leaf	No description	Costa Rica	Jiménez 2004
<i>A. germinans</i>	Leaf	No description	Costa Rica	Jiménez 2004
<i>A. officinalis</i>	Leaf	Gregarious small gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf	No description	India	Katherisan 2003
<i>A. officinalis</i>	Leaf	Small globular gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf, Petiole and/or shoot	Large globular gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf (abaxial surface of midvein)	Keel-like gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf	Large flattened gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf	Small, widely scattered pouch gall	Thailand	Rau & Murphy 1990
<i>A. officinalis</i>	Leaf	The gall is a 1 cm diameter swelling situated on or very near leaf midvein, is unevenly round and apparent both leaf surfaces	Java	Gagné & Law 1998
<i>A. germinans</i>	Leaf	Round and smooth on the upper surface and warty on the lower surface, a craterlike exit hole eventually develops	Belize and USA	Gagné 1994
<i>A. germinans</i>	Leaf	Round and smooth on the upper surface and warty on the lower surface, a craterlike exit hole eventually develops	Guadeloupe and Saint Martin	Gagné & Etienne 1996

Plant host	Organ	Form	Geographic location	Reference
<i>A. germinans</i>	Leaf	Spheroid on the abaxial and adaxial surfaces	Brazil	Gonçalves-Alvim <i>et al.</i> 2001
<i>A. marina</i>	Leaf	No description	India	Katherisan 2003
<i>A. marina</i>	Leaf	Small, unevenly hemispheroid and warty on the upper surface, craterlike on the lower surface	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	Circular and flat on the upper surface, nearly evenly hemispherical on the lower surface	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	Large, mostly soft, simple leaf swelling, apparent on only the lower surface	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	Circular basally, with one or more elongate, conical projections arising from it on the upper surface	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	Large, simple, convex leaf swelling, apparent on both leaf surfaces	Australia	Gagné & Law 1998; Burrows 2003
<i>A. marina</i>	Leaf	No description	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	No description	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	No description	Australia	Gagné & Law 1998
<i>A. marina</i>	Leaf	Edge gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Tower/Spike gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Cabbage gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Yellow lamp gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Marble gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Midvein gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Acne gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Raised-pit gall	Australia	Burrows 2003
<i>A. marina</i>	Leaf	Pimple gall	Australia	Burrows 2003
<i>A. marina</i>	Stem	Stem gall	Australia	Burrows 2003
<i>A. schaueriana</i>	Leaf	Unilocular globoid gall	Brazil	Maia <i>et al.</i> 2008;
<i>A. schaueriana</i>	Leaf	No description	Brazil	Menezes & Peixoto 2009
<i>A. schaueriana</i>	Leaf	No description	Brazil	Present study

Table 2. Gall morphotypes of *Avicennia*

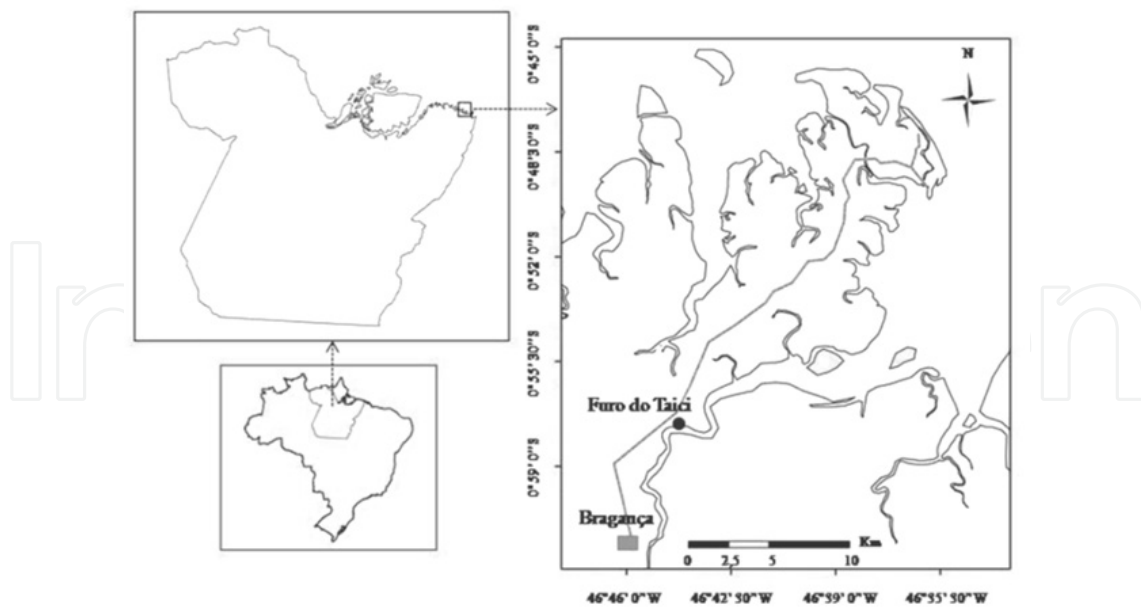


Figure 1. Location of the study area (Furo do Taíci) on the Ajuruteua Peninsula, Bragança, Pará.

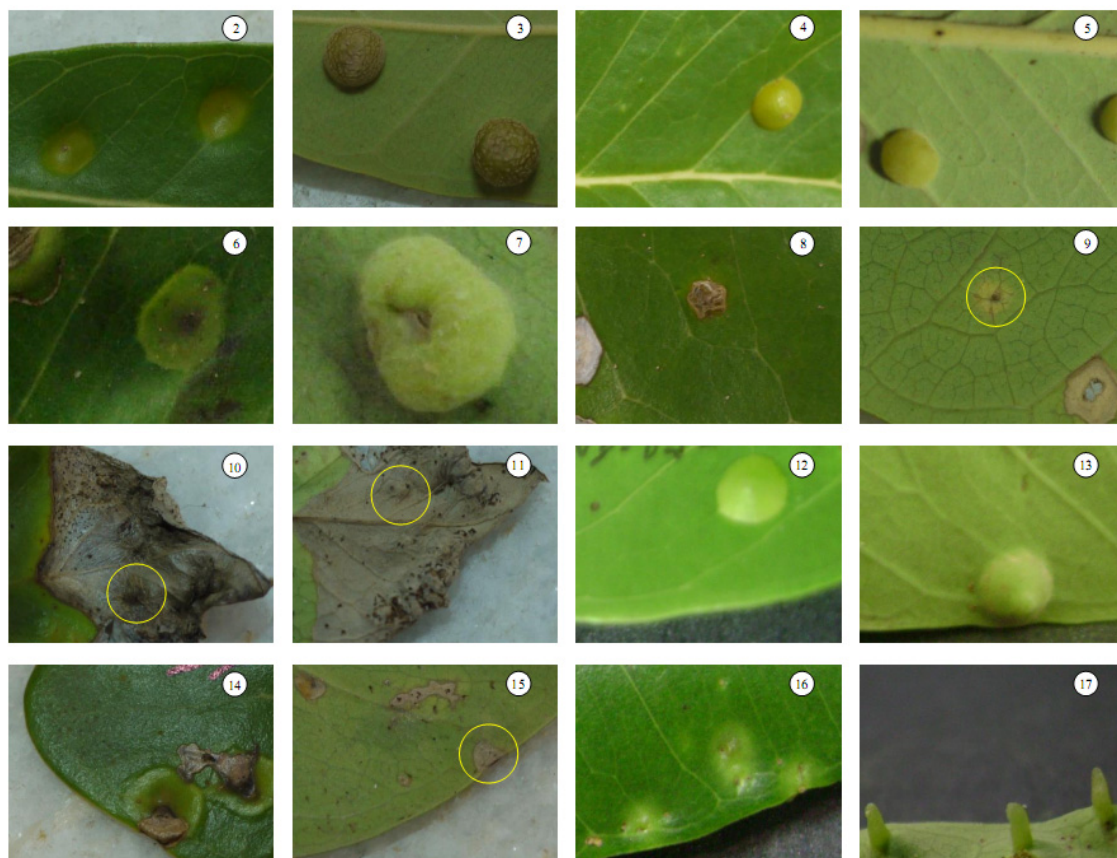


Figure 2. 2-17. Gall morphotypes observed on the leaves of *A. germinans*: GAB: Globular - 2) adaxial surface, 3) abaxial surface; GBD: Globular - 4) adaxial surface, 5) abaxial surface; GCC: Globular with a central concavity - 6) adaxial surface, 7) abaxial surface; GAD: Globular - 8) adaxial surface, 9) abaxial surface; GLO: Globoid - 10) adaxial surface, 11) abaxial surface; GTA: Globular with a tapering free portion - 12) adaxial surface, 13) abaxial surface; FLA: Flattened - 14) adaxial surface, 15) abaxial surface; CYL: Cylindrical - 16) adaxial surface, 17) abaxial surface.

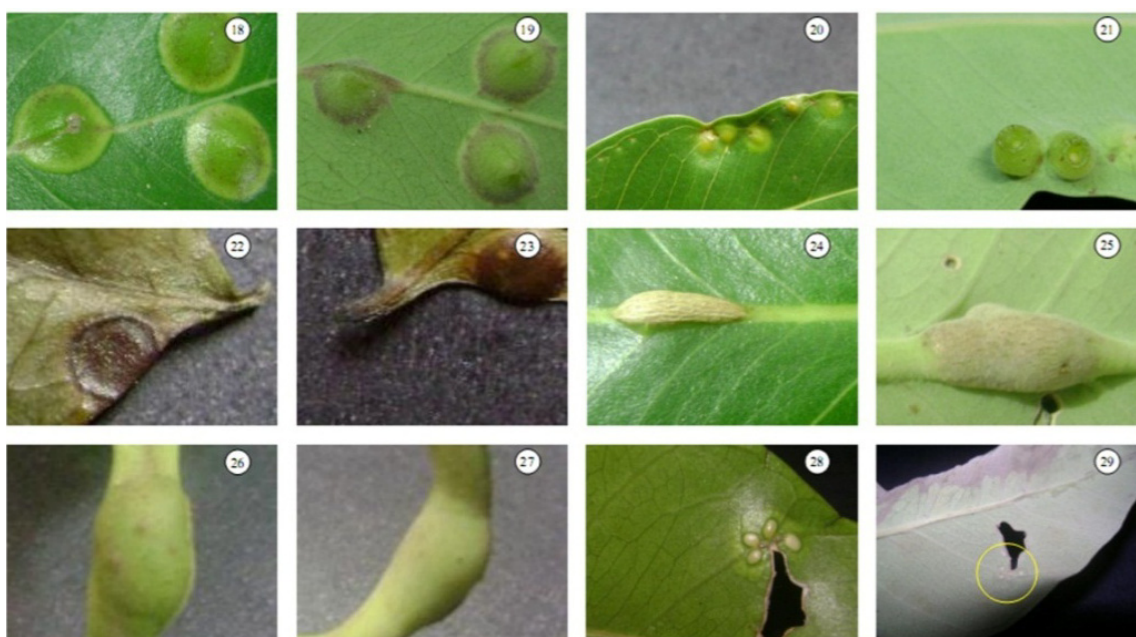


Figure 3. 18-29. Gall morphotypes observed on the leaves of *A. germinans*: CON: Conical - 18) adaxial surface, 19) abaxial surface; VLC: Volcanic crater - 20) adaxial superficie, 21) abaxial surface; DIS: Discoid - 22) adaxial surface, 23) abaxial surface; MDR: Midrib - 24) adaxial surface, 25) abaxial surface; PET: Petiolar - 26: adaxial surface, 27) abaxial surface; AOV: Aggregated Ovoid Gall - 28) adaxial surface, 29) abaxial surface.

Six of the 14 morphotypes identified during the study were globular in shape (to varying degrees): i) lobular gall on the abaxial surface of the leaf – monolocular, with opening on the adaxial surface (GAB); ii) globular gall on the abaxial and adaxial surfaces – globular on both surfaces, with opening on the adaxial surface (GBD); iii) globular gall with central concavity – monolocular, with opening on the adaxial surface (GCC); iv) globular gall on the adaxial surface of the leaf – monolocular (GAD); v) globoid gall – monolocular, normally very close to one another and more globular on the adaxial surface (GLO); vi) globular gall – monolocular, globular base on the abaxial surface with a tapering free portion (GTA); vii) flattened gall with a slit-like opening – monolocular, globoid on the adaxial surface, with opening on the adaxial surface (FLA); viii) cylindrical gall – globoid on the adaxial surface, with opening at the base of the cylindrical portion, on the abaxial surface (CYL); ix) conical gall – monolocular gall with a conical shape on both surfaces of the leaf and opening on the adaxial surface, coloration changes from greenish to purplish during senescence (CON); x) volcanic crater gall – globoid on the adaxial surface, opening in the tubular portion on the abaxial surface, often grouped (VLC); xi) discoid gall – monolocular, globoid only on the adaxial surface (DIS); xii) gall on the midrib of the leaf – appears as a thickening of the midrib, often individually but also in closely-spaced agglomerations, opening on the adaxial surface (MDR); xiii) petiolar gall – appears as a thickening of the petiole (PET); xiv) aggregated ovoid gall – distributed very close together in circular, flower-shaped groups (AOV) (Table 4).

Finally, a subsample of the fourteen morphotyped galls were separated and placed in plastic pots to await the emergence of gall-inducing arthropods. Of the gall-inducing insects

isolated from the leaves of *A. germinans*, seven morphotypes were identified as belonging to the family Cecidomyiidae (Table 3).

	Morphotype	Number of galls	Mean galls per plant ($\pm$ SD; n=20)	%
Identified	CON	1,101	55.1 $\pm$ 42.8	15.5
	AOV	922	46.1 $\pm$ 43.9	13.0
	GAB	685	34.3 $\pm$ 32.4	9.6
	GCC	591	29.6 $\pm$ 28.5	8.3
	MDR	398	19.9 $\pm$ 17.2	5.6
	GLO	397	19.9 $\pm$ 34.3	5.6
	PET	237	11.9 $\pm$ 29.7	3.3
	GBD	146	7.3 $\pm$ 9.9	2.1
	CYL	141	7.1 $\pm$ 16.8	2.0
	VLC	55	2.8 $\pm$ 4.3	0.8
	GAD	54	2.7 $\pm$ 4.9	0.8
	GTA	36	1.8 $\pm$ 2.5	0.5
	FLA	15	0.8 $\pm$ 2.0	0.2
	DIS	9	0.5 $\pm$ 0.6	0.1
Subtotal		4,787		
Unidentified	ISD	1,837	91.9 $\pm$ 71.9	25.8
	DAM	476	23.8 $\pm$ 23.5	6.7
Subtotal		2,313		
Total		7,100	355.4 $\pm$ 244.6	100

Table 3. Number (total, mean $\pm$ standard deviation) and relative frequency (%) of galls by morphotype found on 1,970 leaves of *Avicennia germinans* (L.) Stearn (Acanthaceae), in the Furo do Taici of the Ajuruteua Peninsula in Bragança, in the Brazilian state of Pará. IDENTIFIED: CON = Conical gall; AOV = Aggregated Ovoid gall; GAB = Globular gall – Abaxial surface; GCC = Globular gall with a Central Concavity; MDR = Midrib gall; GLO = Globoid gall; PET = Petiolar gall; GBD = Globular gall – Abaxial and Adaxial surfaces; CYL = Cylindrical gall; VLC = Volcanic Crater gall; GAD = Globular gall – Adaxial surface; GTA = Globular gall with a tapering free portion; FLA = Flattened gall; DIS = Discoid gall. UNIDENTIFIED: ISD = Initial stage of development; DAM = Damaged; SD = Standard Deviation.

Morphotype	shape	Organ/Location	Color	Pusbescence	Chamber	Ocurrence
CON	Conical	Leaf	Green/Purple	Glabrous	One	Isolated
AOV	Aggregated ovoid	Leaf	Green	Glabrous	One	Coalescent
GAB	Globular concavity	Leaf	Green	Glabrous	One	Isolated
GCC	Globular with central concavity	Leaf	Green	Glabrous	One	Isolated
MDR	Midrib	Leaf	Green	Glabrous	Several	Isolated
GLO	Globoid	Leaf	Green	Glabrous	One	Coalescent
PET	Petiole	Leaf/Petiole	Green	Glabrous	Several	Isolated
GBD	Globular	Leaf	Green	Glabrous	One	Isolated
CYL	Cylindrical	Leaf	Green	Glabrous	One	Isolated
VLC	Volcanic crater	Leaf	Green	Glabrous	One	Isolated/ Coalescent
GAD	Globular woody	Leaf	Green	Glabrous	One	Isolated
GTA	Globular with tapering free portion	Leaf	Green	Glabrous	One	Isolated
FLA	Flattened	Leaf	Green	Glabrous	One	Isolated
DIS	Discoid	Leaf	Green	Glabrous	One	Isolated

Table 4. Description of the gall morphotypes identified on the leaves of *Avicennia germinans* (L.) Stearn (Acanthaceae), in the Furo do Taici of the Ajuruteua Peninsula in Bragança, in the Brazilian state of Pará. CON = Conical gall; AOV = Aggregated Ovoid gall; GAB = Globular gall – Abaxial surface; GCC = Globular gall with a Central Concavity; MDR = Midrib gall; GLO = Globoid gall; PET = Petiole gall; GBD = Globular gall – Abaxial and Adaxial surfaces; CYL: Cylindrical gall; VLC = Volcanic Crater gall; GAD = Globular gall – Adaxial surface; GTA = Globular gall with a tapering free portion; FLA = Flattened gall; DIS = Discoid gall;

5. Conclusions

The genus *Avicennia* presents a pioneer group of species which is highly tolerant of salinity (Hogarth 1999), and has leaves with high levels of total nitrogen (Medina *et al.* 2001), low levels of secondary compounds (Roth 1992), and high leaf productivity with less energy

investment (Cannicci *et al.* 2008). In addition to the wide distribution of this genus, where *Avicennia* species occur they are often abundant and the dominant species. These characteristics, together with the reduced plant diversity of the mangrove ecosystem on a regional scale (Menezes *et al.* 2008), are probably among the key factors to determine the preference of endophytic herbivores for this species.

However, Blanche (2000) notes that the available studies have reported different effects of plant species richness on the diversity of gall-inducing insects, and according to Veldtman & McGeoch (2003), in some areas taxonomic composition of the vegetation appears to be more important than species richness.

At present, of the ten currently recognized species of *Avicennia*, four have already been registered with galls: *A. germinans*, *A. marina*, *A. officinalis*, and *A. schaueriana*. In total, 44 gall morphotypes have already been recorded for species of *Avicennia* (Table 2), and therefore it must be considered as a “superhost” genus. The terminology “superhost” for a botanical genus has been previously proposed by Mendonça (2007).

Avicennia germinans and *A. marina* are, by far, the mangrove species with the greatest known variety of gall-inducing arthropods, with 22 and 19 galls, respectively, which doubtless characterizes both species as “superhost” plants. In the case of *A. germinans*, the categories DAM and ISD, together with the stem galls, suggest that this particular species may have an even larger number of gall morphotypes. In addition, *A. officinalis* and *A. schaueriana*, may also be considered potential “superhost” plants, since available records showed four and three species of gall-inducing arthropods associated with both species, respectively (Table 1 and 2). The species of *Avicennia* are similar with respect to their chemical, morphological, anatomical and ecological traits, which favor its infestation by several species of galling arthropods in different geographic regions (Tomlinson, 1986; Burrows, 2003). This fact becomes even more pronounced in areas that have low mangrove plant diversity and where other plant species have characteristics that prevent colonization by arthropods (e.g. sclerophyllous leaves and high amounts of secondary compounds), as in the genus *Rhizophora*.

Thus, it is important to bear in mind that *Avicennia* species appears to have a similar role in the trophic chain of the endophytic herbivores of the mangrove forest. Of the ten species of the genus *Avicennia*, only four have been recorded on the literature. Thus, it is likely that with the increasing progress the work on the interaction of arthropods with this botanical genus, it also increases the number of records of the endophytic herbivores.

The effect of arthropod herbivore activities may negative and positively impact both the mangrove trees and the ecosystem. Cannicci *et al.* (2008) pointed out that herbivory is usually considered to be a negative impact, due to the fact that they are more apparent and readily measured than positive ones. Regarding the fact that many gall-inducing organisms are associated with the genus *Avicennia*, it may be a considerable positive contribution to the overall diversity of herbivores in mangroves. Likewise, the premature abscission of a large quantity of leaf material (Burrows 2003) and the conversion of leaves into frass by caterpillars (Fernandes *et al.* 2009) may cause positive impacts on either individual or

ecosystem, respectively, by providing high leaf yield for the trees and rich nutrient supply for the mangrove *per se*.

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