External seminal analysis of the Inga alliance (Ingeae-Caesalpinioideae-Leguminosae) and its taxonomic implications

Análisis externo seminal de la alianza Inga (Ingeae-Caesalpinioideae-Leguminosae) y sus implicaciones taxonómicas

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Abstract: The Inga alliance belongs to the tribe Ingeae, subfamily Caesalpiniodeae, family Leguminosae. It comprises eight genera: Archidendron, Calliandra, Cedrelinga, Cojoba, Inga, Macrosamanea, Viguieranthus and Zygia, approximately 600 species; particularly diverse in the Neotropics. The external morphology of seeds was studied in 42 species corresponding to the genera of the Inga alliance with the objective of identifying the taxa and establishing similarities and differences among them by using seminal characters. Seeds were obtained from field collections and material from the herbaria COL, HUA, HUEFS, JBSD, MEXU, MY, NY, US and VEN. The collected specimens were identified by dissections and specialized botanical literature; subsequently deposited in the HUA, HUEFS, MY, NY and VEN herbaria. We selected 10-15 seeds per species. Characters such as shape, size, thread (position, shape), raphe (shape), funiculus, existence of aril, characters of the seed coat including surface, color, presence of pleurogram were analyzed. The seeds were observed and photographed with a stereoscopic microscope. With the information obtained a matrix was elaborated and a cluster analysis was performed. In the phenogram obtained, two major groupings were observed, where the characters analyzed as presence/absence of pleurogram, shape, size and color of the seed were the most relevant for their possible use as taxonomic criteria. External seed morphology data were useful for analyzing the taxonomy of the Inga alliance at intrageneric and generic levels. Our analyses supported previous phylogenetic data indicating that the Inga alliance is not a monophyletic group. Keyword: cluster analysis, mimosoid clade, seed coat, seeds, taxonomy.

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Resumen: La alianza Inga pertenece a la tribu Ingeae, subfamilia Caesalpiniodeae, familia Leguminosae. Comprende ocho géneros: Archidendron, Calliandra, Cedrelinga, Cojoba, Inga, Macrosamanea, Viguieranthus y Zygia, aproximadamente 600 especies; particularmente diversas en el Neotrópico. Se estudió la morfología externa de las semillas en 42 especies correspondientes a los géneros de la alianza Inga con el objetivo de identificar los taxones y establecer similitudes y diferencias entre ellos mediante el uso de caracteres seminales. Las semillas

se obtuvieron de colecciones de campo y material de los herbarios COL, HUA, HUEFS, JBSD, MEXU, MY, NY, US y VEN. Los ejemplares recolectados se identificaron mediante disecciones y literatura botánica especializada; posteriormente se depositaron en los herbarios HUA, HUEFS, MY, NY y VEN. Se seleccionaron entre 10 y 15 semillas por especie. Se analizaron caracteres como la forma, el tamaño, la rosca (posición, forma), el rafe (forma), el funículo, la existencia de arilo, los caracteres de la cubierta de la semilla incluyendo la superficie, el color, la presencia de pleurograma. Las semillas fueron observadas y fotografiadas con un microscopio estereoscópico. Con la información obtenida se elaboró una matriz y se realizó un análisis de cluster. En el fenograma obtenido se observaron dos grandes agrupaciones, donde los caracteres analizados como presencia/ausencia de pleurograma, forma, tamaño y color de la semilla fueron los más relevantes por su posible uso como criterio taxonómico. Los datos de la morfología externa de las semillas fueron útiles para analizar la taxonomía de la alianza Inga a nivel intragenérico y genérico. Nuestros análisis apoyan los datos filogenéticos anteriores que indican que la alianza Inga no es un grupo monofilético. Palabra clave: análisis de conglomerados, clado de mimosoides, cubierta de semillas, semillas, taxonomía. Introduction

Palabras clave: análisis de conglomerados, clado de mimosoides, cubierta de semillas, semillas, taxonomía.

Introduction

The Inga alliance belongs to the tribe Ingeae, relocated as part of the mimosoid clade, in the new delimitation of the subfamily Caesalpinioideae of the family Leguminosae (LPWG, 2017). It is considered as an informal group described by Barneby and Grimes (1996) and confirmed by Lewis et al. (2005), consisting of the genera Archidendron F. Muell. , Calliandra Benth. Cedrelinga Ducke, Cojoba Britton & Rose, Inga Mill., Macrosamanea Britton & Rose ex Britton & Killip, Viguieranthus Villiers and Zygia P. Browne, and approximately 600 species worldwide, with special diversity in the Neotropics (Lewis and Rico, 2005). Barneby and Grimes (1996) included Zapoteca H.M. Hern. in the Inga alliance; however, Lewis and Rico (2005) placed this genus as a sister group of the alliance. Phylogenetic studies (Souza et al., 2013; Ferm et al., 2019) based on molecular data support Lewis and Rico's proposal, suggesting that Zapoteca does not belong to the Inga alliance.

In recent years, taxonomic research has shown interest in studies on seed morphology, because they provide characters of great diagnostic value and play an important role in modern classification systems (Dahlgren, 1980; Heneidak and Kadry, 2015). This is largely due to the fact that seeds show very little phenotypic plasticity (Von Teichman and Van Wyk, 1991).

In the Leguminosae, seed morphology has been of great importance in classification (De Candolle, 1825; Capitaine, 1912; Corner, 1951; Lersten, 1992). In this sense, in the most recent taxonomic study (LPWG, 2017) the family Leguminosae was divided into six subfamilies, based on molecular and morphological evidence; in the latter case, open or closed pleurogram on both seed faces were included as a seminal diagnostic character of the mimosoid clade of the subfamily Caesalpinioideae.

The importance of seed morphology in the mimosoid clade has been confirmed in some works; Boelcke (1946) compared seeds of Mimosoideae and Caesalpinioideae of agronomic interest in Argentina. Bravato

(1974) found in seeds of Mimosoideae (now a mimosoid clade within Caesalpiniodeae) that the variability in characters supports their use for application in the taxonomy of the subfamily, which was later supported by Gunn (1981) and Escala (1999). In the Inga alliance of the mimosoid clade, seminal studies have been conducted for taxonomic purposes in species and/or species groups (Bravato, 1974; Leython and Jáuregui, 2008; Leython, 2010), but there has not been a comparative treatment that includes all genera.

Based on the above, the present study aims to contribute to identify genera and species of the Inga alliance, to establish similarities and differences between them by using seminal characters that can be easily observed, either with a stereoscopic microscope or with a hand-held magnifying glass.]

Materials and methods

Ten to fifteen mature seeds were analyzed for each of the 42 species (Table 1), representative of the genera that make up the Inga alliance. The samples were collected during four years (2008-2012) in different localities or, taken from herborized specimens from the following herbaria: Herbarium of the Universidad Nacional de Colombia (COL), Herbarium of the Universidad de Antioquia (HUA), Herbarium of the Universidade Estadual de Feira de Santana (HUEFS), Herbarium Dr. Rafael M. Moscoso (JBSD), Herbarium of the Universidade Estadual de Feira de Santana (HUEFS), Herbarium of the Universidade Estadual de Feira de Santana (HUEFS), Herbarium Dr. Rafael M. Moscoso (JBSD), Herbarium of the Universidad Nacional Autónoma de México (MEXU), Herbarium of the Universidad Central de Venezuela Dr. Víctor Manuel Badillo (MY), New York Botanical Garden (NY), Herbarium Smithsonian Institution (US), Herbarium Nacional de Venezuela (VEN). Herbarium acronyms are cited based on Index Herbariorum (Thiers, 2020). Supporting specimens were deposited in the herbaria HUA, HUEFS, MY, NY and VEN. Also, the MO Missouri Botanical Garden (Tropicos, 2020) and NYBG (NYBG, 2020) databases were reviewed.

Morphological characterization

Seed dimensions were measured with a vernier (Fowler 52-085-012) considering length, width and thickness (l × a × g) expressed in millimeters. The description of the shape and external structure was made based on Gunn16. Color was determined using the Methuen Handbook of Colour by Konerup and Wanscher (Konerup and Wanscher, 1983). The pleurogram or fissural line was described following the terminology proposed by Gunn16, while the shape and position of the thread and shape of the raphe were characterized according to Boelcke (Boelcke (1946), Bravato (1974), Gunn (1981) and Escala (1999). Observations in the field were made with a hand magnifying glass with magnifications of 20× and 40×; detailed study and photographs were taken with a stereoscopic microscope (Nikon SMZ-745T) with integrated camera.

Analysis of morphological characters.

Nine characters were observed in the 42 species (operational taxonomic units or OTU); three quantitative and six qualitative. A cluster analysis was performed using the UPGMA unweighted average linkage method. For this purpose, a matrix of qualitative characters was elaborated, coding them as binary (absence (0) and presence (1) and multi-state. The analyses were carried out with the program NTSYS pc v. 2.11a24. In order to include continuous variables in the cluster analysis, they were transformed into discrete characters according to the homogeneous subset coding methodology (Rae, 1998).

Result

Identification key for genera of the Inga alliance, based on morphological characters of the seeds.

1a. Elliptical seeds, compressed..... 2

1b. Seeds oblong, rounded or ovate, if elliptic then teretes or sub teretes 3

2a. longitudinally arranged on fruit, not covering contiguous seed; 7-35 × 20-25 × 1-2 mm; funiculus 4-5 mm long .... Cedrelinga

2b. Arranged transversely on the fruit, superimposed one on top of the other, covering ..longitudinally at least 2/3 of the contiguous seed; 14-20 × 8-12 × 0.8-1.2 mm; funiculus 15-20 mm long .... Macrosamanea

3a. Sarcotesta soft and fleshy, white, enveloping the whole seed..... ..... Inga

3b. Sarcotesta absent..... 4

4a. Rafe not visible or less than 0.1 mm diameter 5

4b. Visible raphe 0.1-1 mm in diameter..... 6

5a. Seeds oblong in cross section; microcilium orbicular or as a deltoid depression .... Archidendron

5b. Seeds teretes in transverse section; micropyle indistinguishable..... Cojoba

6a. Monochromatic light or dark brown or ocher colored seminal cover; raphe up to 0.5 mm diameter without central white line 7

6b. Seminal cover monochromatic brown or variegated; raphe 0.5-1 mm diameter with central white line 8

7a. seeds 6-12 × 4-9 mm, 0.5-1 mm thick; smooth seed coat; orbicular micropyle, 0.4 mm diameter ..... Viguieranthus

7b. Seeds 12-25 × 9-25 mm, 1.5-3mm thick; seed coat porous, rough, warty, sometimes smooth; micropyle oblong or orbicular, 0.3-0.5 mm in diameter..... ..... Zygia

8a. Pleurogram present on both sides of the seminal envelope ..... Calliandra Group I

8b. Pleurogram absent on both sides of seminal sheath..... Calliandra Group II

External seminal morphology

Inga Alliance

Seeds 3-40 per fruit; located transversely or longitudinally; ovate, oblong, elliptic, suborbicular to orbicular; faces convex or flat, margins rounded or compressed, usually narrow at the hilar end, rounded at the calcareous end, 4-50 × 3-27 × 0.5-18 mm; predominantly monochromatic, brownish, light or dark brown, black, also bichromatic or variegated, with dark irregular spots; surface smooth, rough, porous, warty or with fracture lines, concentric and transverse, opaque or lustrous; sarcotesta absent or present of soft, fleshy consistency (Inga); pleurogram absent or present on both sides, either horseshoe-shaped or completely closed (Calliandra); funiculus of uniform thickness or thickened in the vicinity of the thread, long or short, straight, slightly spiral, white, yellowish, brownish, dry and filamentous; micropyle apical, subapical, close to or in contact with thread, oblong or orbicular, 0.4-0.5 × 0.3-0.5 mm or indistinguishable; thread sparsely exposed, sometimes hidden by funiculus itself or remnant of it, when evident, 0.5-1.2 mm, circular, ellipsoid, linear, whitish or yellowish, apical, subapical or sparsely lateral; raphe lateral to thread and usually elongate or inconspicuous.

Genera of the Inga alliance

Archidendron F. Muell, Fragm. 5: 59. 1865

Seeds 3-8 per fruit; transversely placed; subterete; oblong or orbicular; faces convex; margins rounded; hilar end rounded; calazal end rounded; 11-35 × 10-35 × 4-15 mm; seed coat monochromatic dark brown or black, smooth, rough, porous, lustrous or opaque; pleurogram absent; funiculus short, 4-7 mm long, straight, dark brown, uniform relative to thickness; micropyle apical or subapical, proximal or in contact with thread, orbicular, as a deltoid depression, 0.5 × 0.5 mm; thread oblong or orbicular, 1.1-1.2 × 0.5 mm; raphe not visible or less than 0.1 mm wide.

Calliandra Benth, J. Bot. (Hooker) 2(11): 138. 1840.

Seeds 3-8 per fruit; located transversely or longitudinally; elliptic, ovate, oblong or orbicular; faces convex to flat; margins rounded, compressed; hilar end acute, rounded, punctate; calazal end rounded, oblong, punctate; 4-14 × 3-11 × 0.8-4 mm; seminal cover monochromatic dark or light brown, also variegated with dark or light brown spots on light or dark brown ground (Figs. 1A and C), surface smooth, rough, porous, with fracture lines, lustrous or opaque; pleurogram absent or present on both faces and, in the latter case, covering 70-90% of the seed surface (Fig. 1A), arms of equal length close to the hilar end, sometimes positioned above it, large areole; funiculus short, straight, whitish, white or dark brown, uniform in relation to the thickness or thicker at the attachment to the fruit; micropyle apical to subapical, close to or in contact with the thread, oblong or orbicular, 0.5 × 0.3 mm; thread oblong or orbicular, 0.5-1.2 × 0.4-0.5 mm; raphe prominent to sunken, oblong or orbicular, 1 × 0.5-1 mm, light or dark brown, with central white line (Figs. 1B and D).

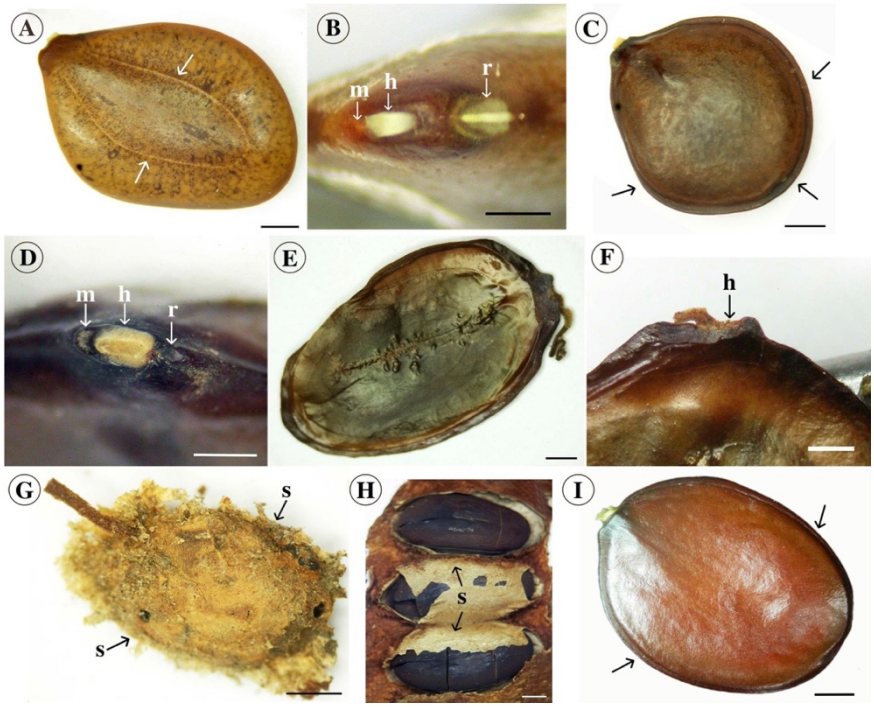
The genus Calliandra can be divided into two groups, based on the presence or absence of the pleurogram.

Group I. Consisting of species with seeds showing pleurogram on both sides (Fig. 1A). Group II. Consisting of taxa with seeds without pleurogram (Fig. 1C).

Cedrelinga Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 70. 1922

Seeds 1-7 per fruit; placed longitudinally; elliptic; faces compressed; margins strongly compressed; hilar end obtuse, with plumule and radicle of embryo pronounced above surface of seed coat; calazal end obtuse; 27-35 × 20-25 × 1.5-2 mm; seed coat dark brown, smooth, with longitudinal lines without becoming protruding, membranaceous, very fragile and brittle when dry, surface lustrous (Fig. 1E); pleurogram absent; funiculus short, 4-6 mm long, straight, uniform relative to thickness; apical micropyle, oblong, 0.5-1 × 0.5 mm; thread oblong or elliptic, 1-1.2 × 0.5 mm (Fig. 1F); raphe not visible; germination often occurs in fruit (viviparous seeds).

Figure 1. A-B. Calliandra falcata. A. frontal view, variegated surface with pleurogram. B. hilar end. C-D. C. coriacea. C. frontal view, edges strongly compressed. D. hilar end. E-F. Cedrelinga cateniformis. E. frontal view. F. detail of the hilar end, note the thread. G. Inga alba, seed with funiculus and remains of sarcotesta. H. I. laurina, seeds placed transversely in the fruit, note remains of the sarcotesta. I. Viguieranthus pervillei, frontal view, surface smooth, margins strongly compressed. Scale= A, C, E, H=2 mm, B, F=1mm, D, G=0.5 mm, I=1.5 mm; m= micropyle, h= thread, r= raphe.



Cojoba Britton & Rose, N. Amer. Fl. 23(1): 29. 1928.

Seeds 7-10 per fruit; located transversely or longitudinally; teretes, elliptic or orbicular; faces convex; edges rounded; hilar end acute to rounded; calacal end

acute or rounded; 9-30 × 5-17 mm diameter; seminal sheath monochromatic dark brown or black, smooth, porous, venous, surface lustrous or opaque; pleurogram absent; funiculus short, straight or whorled, white or dark brown, uniform in relation to thickness, also thicker at attachment to fruit; micropyle indistinguishable; thread oblong or orbicular, 1.0-1.2 × 0.5 mm; raphe not visible or less than 0.1 mm wide.

Inga Mill, Gard. Dict. Apr. (ed. 4) vol. 2. 1754.

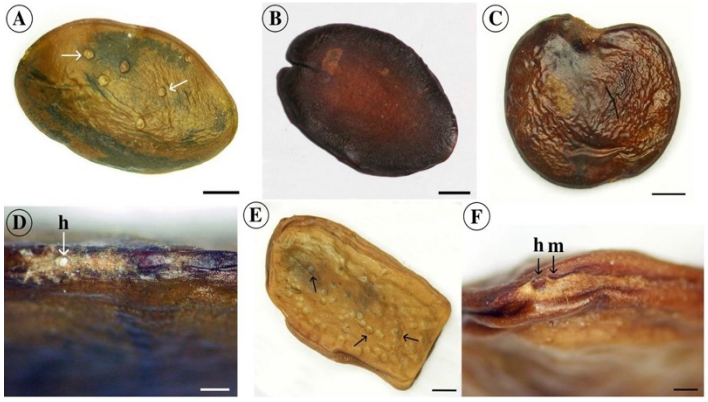
Seeds 6-40 per fruit; placed transversely or longitudinally; teretes or subteretes, elliptic, ovate or oblong; faces convex; margins rounded; hilar end acute, rounded to pointed; calazal end acute, rounded or pointed; 8-50 × 7-20 × 2-7 mm; seed coat monochromatic medium or dark brown or black, surface smooth, rough, porous, lustrous or opaque; sarcotesta enveloping entire seed (1G and H), white, less common yellowish, densely fibrous, soft and fleshy consistency; pleurogram absent; funiculus straight or whorled, cream or dark brown, uniform in relation to thickness or thicker at attachment to fruit; micropyle indistinguishable; thread oblong, elliptic or orbicular, 0.5-1.2 × 0.4-0.5 mm, often sunken and covered by sarcotesta; raphe not visible.

Macrosamanea Britton & Rose ex Britton & Killip, Ann. New York Acad. Sci. 35(3): 131. 1936.

Seeds 18-35 per fruit; placed transversely, superimposed one over the other, longitudinally covering at least 2/3 parts of the adjoining seed; elliptic; faces compressed; margins rounded; hilar end slightly acute to rounded, with plumule and radicle of embryo pronounced on the surface; calazal end rounded; 14-20 × 8-12 × 0.8-1.2 mm; seminal cover monochromatic dark brown or variegated with large, irregular, light brown spots on dark brown ground (Figs. 2A and B); surface smooth, rough, warty (Fig. 2A), opaque; pleurogram absent; funiculus filamentous, 15-20 mm long, white, whitish, most commonly chestnut, uniform relative to thickness, straight to partially spiral; micropyle inconspicuous, observed as orbicular depression, usually closed, close to thread; thread apical or subapical, oblong or elliptical, 0.5-1.1 × 0.5 mm; raphe not conspicuous.

Figure 2. A. Macrosamanea discolor var. discolor, frontal view, see the difference in color of the seminal sheath. B. M. pubiramea var. lindsaeifolia, frontal view. C-D. Zygia latifolia, C. frontal view, note the lustrous,

rough surface. D. spinning end, thread slightly visible. E-F. Z. ocumarensis, E. front view, note warty surface. F. view of spinning end with thread detail. Scale= A, B, F=2mm, C=3 mm, D, E=1mm; m= micropyle, h= thread, f= funiculus.



Viguieranthus Villiers, Legum. Madagascar, p. 271-285. 2002

Seeds 6-10 per fruit; obliquely placed; elliptic, ovate or orbicular; faces convex; margins compressed (Fig. 1I) or rounded; hilar end acute or orbicular; calazal end rounded; 6-12 × 4-9 × 0.5-2 mm; seminal coat monochromatic dark brown or light brown; surface smooth, lustrous (Fig. 1I) or opaque; pleurogram absent; funiculus usually short, 4-5 mm long; subapical micropyle, proximal to thread, orbicular, 0.4 mm wide; thread oblong, elliptic or orbicular, 1-1.1 × 0.5 mm; raphe slightly sunken, oblong or orbicular, 0.5-1 × 0.5 mm, light brown.

Zygia P. Browne, Civ. Nat. Hist. Jamaica, p. 279. 1756

Seeds 5-18 per fruit; located transversely or longitudinally; elliptic, ovate, oblong or orbicular; faces convex or compressed; margins rounded, compressed, acute; hilar end obtuse, subtruncate or emarginate, sometimes with plumule and radicle of embryo pronounced above surface; calazal end broadly obtuse (Fig. 2C), truncate (Fig. 2E) or subtruncate; 10-25 × 6-25 × 1-15 mm; seminal sheath monochromatic dark brown or light brown, sometimes ochre; surface smooth, rough, porous, warty (Fig. 2E), lustrous or opaque; pleurogram absent; funiculus short, 3-8 mm long, straight, whitish or dark brown, uniform relative to thickness; apical or subapical micropyle, sometimes lateral, proximal or in contact with the thread (Fig. 2F), oblong or orbicular, dark brown, 0.3-0.5 × 0.3 mm or indistinguishable (Fig. 2D); thread minute, prominent, also sunken, oblong or commonly orbicular (Figs. 2D and F), 1-1.2 × 0.5 mm; raphe orbicular, 0.5 mm wide, light brown or not visible.

Phenetic analysis

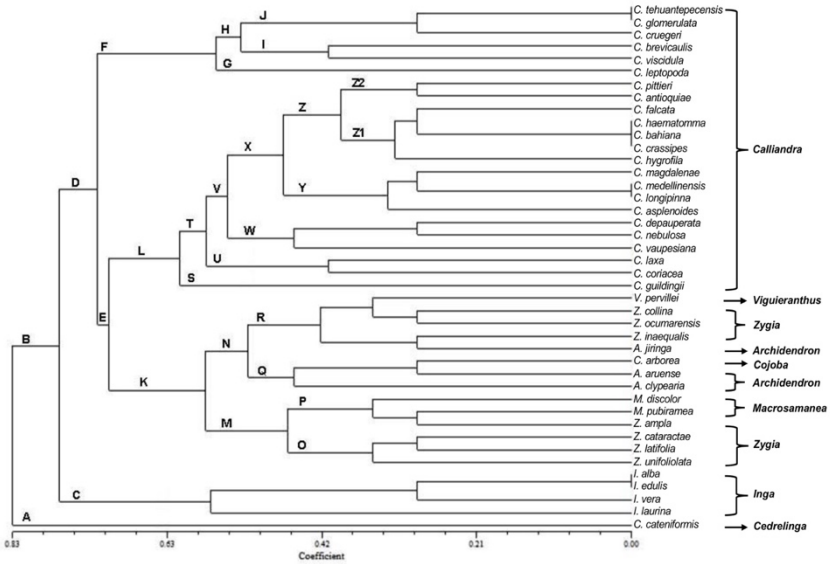
The phenogram obtained (Fig. 3) shows a main OTU group (B) and an isolated OTU Cedrelinga cateniformis, which separates from group B at the greatest distance of similarity (0.83). Group B comprises a large subgroup D and a small one (C) formed by the species of the genus Inga, which is characterized by larger seeds (8-50 × 7-20 mm) than the rest of the genera of the alliance, elliptical terete shape and the sarcotesta of soft and fleshy texture.

Cluster D is in turn constituted by subsets E and F, the first includes six Calliandra species characterized by the shape and presence of the pleurogram. The second comprises two sets, L and K. The first one groups the rest of the Calliandra species related by the size of the seeds larger than in group F and also by the presence of pleurogram, as in F group. However, within this group L there are two subgroups, S and U, with fewer Calliandra species, which have common seminal characters such as shape, color and absence of pleurogram.

Group K comprises two subsets N and M. Subgroup N is formed mainly because the species share five characters: seed size, lustrous seed surface, with variant in Zygia ocumarensis (opaque), rounded margins, absence of pleurogram and sarcotesta, species Viguieranthus pervillei, Zygia collina, Z. ocumarensis, Z.

inaequalis, Archidendron jiringa, Cojoba arborea, A. aruense and A. clypearia. The subgroup M, is grouped mainly by the characters: shape, rounded edges, membranaceous seminal cover, dark brown, without pleurogram and without sarcotesta, microphyll, thread and raphe tiny or imperceptible, in which the species M. discolor var. discolor, M. pubiramea, Z. ampla, Z. cataractae, Z. latifolia and Z. unifoliolata are found.

Phenogram of taxonomic distances illustrating the relationships between 42 investigated species of the Inga alliance, based on seminal morphometric characters.



The results obtained show the importance of seminal characters in the taxonomy of the Inga alliance, which is part of the mimosoid clade, within the new circumscription of the subfamily Caesalpinioideae. Being the shape, size and surface or ornamentation of the seminal cover, the most diverse characters, which in turn fall within the breadth of morphological characters of the subfamily Caesalpinioideae (Gunn, 1981) and in particular terms with that indicated for genera of the Inga alliance (Boelcke, 1946; Bravato, 1974; Leython and Jáuregui, 2008).

The shape of the seeds is influenced by the space available during their development. Although in the mimosoid clade it has been little studied and it is not known which is the most common. Gunn (1981) indicated that the silhouette of the seeds of this clade is regular and symmetrical, as was observed in the studied species of the members of the Inga alliance in the present study. Werker (1997) pointed out that this character is genetically determined, but is ultimately shaped by the space available within the fruit, and further indicated that shape may play a crucial role in their dispersal. Lindorf et al. (2006) mentioned that, in case there are few seeds in large locules, these tend to be spherical, a pattern observed in some members of the Inga alliance, where seeds are convex (Archidendron, Cojoba, Inga, Viguieranthus and Zygia (pro parte), developed in large fruits.

Regarding size, Lindorf et al. (2006) noted that small seeds are generally present in most grasses, while in woody plants the size is larger, which coincides with what is observed here in members of the Inga alliance, since large seeds can measure up to 50 mm in length, mostly belonging to woody species. Some records indicate Kirkbride that in the mimosoid clade, some seeds are larger than in other subfamilies of Leguminosae (Kirkbride et al., 2003).

Regarding color, Werker (1997) and Lindorf et al. (2006) noted that most mature angiosperm seeds have various shades from brown to black. Likewise, Werker (1997) indicated that those seeds that are similar to the color of the soil where they grow may contribute camouflage to protect them from predators. Leython (2010) used color as a discriminating character to establish two groups within the genus Calliandra,

separating between monochromatic (brown) and variegated. In the present study, in most members of the Inga alliance, the color of the seed coat was monochromatic with a predominance of dark brown, as previously reported by Boelcke (1946) and Escala (1999) for members of the mimosoid clade, with the exception of some species of the genus Calliandra and the species Macrosamanea discolor var. discolor, whose surfaces are variegated, showing a combination of light and dark brown.

The pleurogram has been considered as a structure present in 65-70% of the seeds of the genera of the mimosoid clade, with defined patterns and usually open (Gunn, 1981, 1991). This character was rated of great taxonomic value by Boelcke (1946), Gunn (1981), Escala, (1999), Corner (1976) and Irwin and Barneby (1981). In the present study, pleurograms were observed only in some species of the genus Calliandra, equivalent to 20% of the total number of genera that make up the Inga alliance. Maumont (1993) mentions that in the Ingeae and probably in the Mimosoideae (Corner, 1951), the absence of pleurogram is particular in large seeds. Boelcke (1946) pointed out that those seed covers without pleurogram within the subfamily Mimosoideae (now the mimosoid clade) had a series of uncommon or exclusive characteristics on the testa, such as a rough or porous surface or with fracture lines, characters observed in most of the species of the Inga alliance studied that did not have pleurograms.

The thread, micropyle and raphe have been constant characters in species of the Inga alliance. Ubiergo and Lapp (2007) considered their position as taxonomically relevant characters to differentiate some members of the tribe Cassineae. Escala (1999) indicated that the thread is of little diagnostic value in representatives of the mimosoid clade, while in Papilionoideae it constitutes one of the most important characters for identification. Regarding the raphe, Corner (1951) and Gunn (1981) considered that it is an attribute not very noticeable in the mimosoid clade; however, Escala (1999) considered that the raphe is of great taxonomic importance in this clade. In the Inga alliance, seeds presented thread, micropyle and raphe in apical or subapical position; in Calliandra a great variation was registered for these characters; nevertheless, for the Inga alliance, these characteristics provide relevant taxonomic information when considering and comparing the whole group of species.

Similarity relationships and analysis of morphological characters

The phenogram obtained shows that seminal characteristics are useful to distinguish species and confirm in some cases, proposals for generic classification of the Inga alliance (Barneby and Grimes, 1996; Lewis et al., 2005; Souza et al., 2013; Ingnaci et al., 2016; Ferm et al., 2019). In the present study, the classification of Souza et al. (2013) for Calliandra was maintained, with the inclusion of Guinetia (genus monospecific) in Calliandra (C. tehuantepecensis). Viguieranthus was related to Calliandra because of the similarity in leaves and inflorescences (Du Puy et al., 2002), but the phenogram obtained does not show any similarity. In the present study, a main group and an isolated species were obtained, delimited by the combination of characters size and shape of the seed, which are of taxonomic value for classifying the genera of the tribe Ingeae (Lewis and Rico, 2005). Barneby and Grimes (1996) highlighted the importance of these characters in Cedrelinga, being Inga the most similar genus in seed size, but the results of the phenogram show them slightly distant (similarity distance 0.60 to 0.83) because additional characters were considered.

The genera Archidendron, Cojoba and Zygia are phylogenetically related (Lewis et al., 2005; Ignaci et al., 2016). Based on morphological characters of fruits (spiral pods with red endocarp) and seeds (partially translucent seed coat), these genera appear to have evolved independently several times within the tribe Ingeae (Ignaci et al., 2016). Results of the phenetic analysis indicate that external seminal morphology allows Archidendron, Cojoba and Zygia (pro parte) to be recognized as taxa similar to each other.

Regarding Macrosamanea and some members of Zygia that formed groups with a similarity (0.47), there is agreement with Souza et al. (2013) and Ignaci et al. (2016), who placed some members of Zygia in the same subgroup as Macrosamanea, with which it can be inferred that the similarity analysis of seminal characteristics corroborates molecular phylogenetic studies.

Seed morphology and general seed coat characteristics provide one set of taxonomic information on the genera of the Inga alliance, while other characteristics are apparently associated with particular habitats. The systematic value of the seminal characters of the alliance needs to be evaluated in a phylogenetic context.

Characterization of external seed morphology also provided evidence of intrageneric classification for some genera coinciding with phylogenetic results supporting the polyphyly of the Inga alliance (Souza et al., 2013; Ignaci et al., 2016; Ferm et al., 2019). Likewise, the similarity analysis performed supports phylogenetic data, which indicate the existence of distinct lineages within Archidendron (Ingaci et al., 2016) and Zygia (Ferm et al., 2019) and evidence that these genera are not monophyletic, as both Archidendron and Zygia form distinct groups. The external morphology of the seeds confirmed that variation in characters is taxonomically useful, not only because it gives us a better understanding of the structure, but also because it allows us to recognize the genera of the Inga alliance, and is useful for constructing an identification key at the generic level.

Conclusions

The external morphology of seeds provides taxonomically valuable characters that allow differentiation at the genus level. Those genera of the Inga alliance with great variability of seminal characters (monochromatic or variegated seminal cover, presence or absence of pleurogram, presence or absence of sarcotesta), represent heterogeneous genera; furthermore, these characters indicate the possibility of intrageneric classifications (sections, subgenera or series).

Silk tree, Guanacaste, Monkey's earring: A generic system for the synandrous Mimosaceae of the Americas

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