

The “Lianescent Vascular Syndrome” statistically supported in a comparative study of trees and lianas of Fabaceae subfamily Papilionoideae

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Lianas are one of the most iconic elements of tropical forests and their presence is a major feature of these biomes. Here we aim to describe and compare the wood of key genera of Fabaceae subfamily Papilionoideae comprising both trees and lianas. Thirty-eight species from the genera *Machaerium*, *Dalbergia*, *Clitoria* and *Dioclea* were sampled to establish the main quantitative features that differentiate lianas and trees, the so-called “Lianescent Vascular Syndrome”. Variance analyses were carried out to diagnose the anatomical differences between trees and lianas. Whereas most studies focused on qualitative features, this study focused on a statistical, quantitative comparison of lianas and trees of Papilionoideae, some not previously analysed anatomically. Our results show that lianas are quantitatively different from trees in having wider and more frequent vessels, a higher percentage of axial and radial parenchyma relative to fibres, greater ray height and width and longer fibres, statistically corroborating the “Lianescent Vascular Syndrome”.

ADDITIONAL KEYWORDS: climbers – *Clitoria* – *Dalbergia* – *Dioclea* – Leguminosae – *Machaerium* – self-supporting – vessel diameter – vessel density – wood anatomy – xylem.

INTRODUCTION

Climbing plants, both herbaceous and woody, the latter being referred to as “lianas”, comprise plants of unrelated lineages that use external mechanical supports to ascend towards light. Lianas germinate in the soil, and their stems grow towards the canopy using the stems of other species or objects as support (Putz & Mooney, 1991; Cabanillas & Hurrell, 2012; Sperotto *et al.*, 2020; Souza-Baena *et al.*, 2021).

The lianescent habit is not restricted to a single geographical region; however, c. 90% of all liana species occur in tropical forests (Hegarty, 1989; Schnitzer *et al.*, 2012, 2014). Lianas have great value as a functional and structural component interconnecting treetops in a range of forest ecosystems, particularly in

the Tropics (Gentry, 1983, 1991; Putz, 1984; Schnitzer *et al.*, 2014), contributing 9–35% of the woody species diversity (Schnitzer & Bongers, 2002, 2011; Schnitzer *et al.*, 2014). They are an important source of food, shelter and interconnecting bridges between trees for tropical fauna; however, they also compete with trees for space, light, water and nutrients, exerting a strong selective pressure on tropical trees reducing growth, fecundity, physiological performance and tree survival rates (Gentry, 1991; Kurzel *et al.*, 2006; Schnitzer *et al.*, 2014; Álvarez-Cansino *et al.*, 2015; Dias *et al.*, 2017).

Lianas circumnate in search of support, and once a support is found, lianas undergo a rapid modification in anatomy and morphology, frequently developing structures that facilitate their ascent to the canopy, including tendrils, spines, hooks and adventitious adhesive roots (Darwin, 1867; Isnard & Silk, 2009; Cabanillas & Hurrell, 2012;

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Souza-Baena *et al.*, 2018, 2021). A set of anatomical vascular features has been proposed to distinguish the wood of lianas from that of self-supporting plants. These features include the presence of wider and more frequent vessels for any given stem diameter, a larger amount of axial parenchyma and higher rays, with a consequent reduction in the amount of fibres, and the presence of cambial variants (Schenk, 1892–1893; Pfeiffer, 1926; Obaton, 1960; Putz, 1980; Metcalfe & Chalk, 1983; Carlquist, 1991; Gasson & Dobbins, 1991; Carlquist *et al.*, 1993; Fisher & Ewers, 1995; Angyalossy *et al.*, 2012, 2015; Pace & Angyalossy, 2013; Morris *et al.*, 2016; Gerolamo & Angyalossy, 2017). The sum of these features was coined the “Lianescent Vascular Syndrome” by Angyalossy *et al.* (2015). However, quantitative analyses comparing trees and lianas under the same taxonomic groups are rare, with Bignoniaceae being the sole exception (Gasson & Dobbins, 1991; Pace & Angyalossy, 2013; Pace *et al.*, 2015; Gerolamo & Angyalossy, 2017; Gerolamo *et al.*, 2020). Other studies typically focus on a single species/genus (Pelissari *et al.*, 2018; Ganthaler *et al.*, 2019; Chery *et al.*, 2020) or on just one of the habits [e.g. those of Brandes & Barros (2008), Brandes *et al.* (2011), and Tamaio *et al.* (2011) focused on lianas].

The presence of the lianescent habit was reported in 133 families by Gentry (1991), scattered across angiosperm lineages. They are, however, especially frequent in Fabaceae, the second largest family of angiosperms in Neotropical forests (Lewis & Owen, 1989) and often the largest family in number of trees, shrubs and lianescent species in floristic surveys (Gentry, 1982, 1988, 1991; Hegarty, 1989; Ribeiro *et al.*, 1994; Gei *et al.*, 2018). Thus, given the importance of lianas for tropical forest diversity and the importance of Fabaceae in this biome, combined with the lack of formal statistical studies comparing trees and lianas in this important family and of studies with large datasets, we aimed to compare the wood between these two plant habits. statistically characterizing the “Lianescent Vascular Syndrome”, trees and lianas in *Machaerium* Pers., *Dalbergia* L.f., *Clitoria* L. and *Dioclea* Spreng., all belonging to Fabaceae subfamily Papilionoideae.

MATERIAL AND METHODS

Thirty-eight species (92 specimens) of Papilionoideae were sampled, including 19 trees and 19 lianas. These included 22 *Machaerium* spp. and six *Dalbergia* spp. (Dalbergieae), and six *Clitoria* spp. and four *Dioclea* spp. (Phaseoleae) (Appendix).

Histological sections were performed according to techniques adapted from Johansen (1940) and Sass

(1951) on samples taken from the outermost region of the stem of fully-grown individuals. Transverse and longitudinal sections (tangential and radial), 20–120 µm thick, were stained (Gerlach, 1984). The Franklin method for cellular element dissociation was used, modified according to Berlyn & Miksche (1976). The wood anatomy terminology and recommendations for measurements followed the IAWA Committee (1989). Since the scope of this article was a statistical comparison, full descriptions of species were not given.

Morphological variables present in all species were recorded, including percentage of overall parenchyma (axial and radial combined), vessel element diameter and length and fibre length (all in µm), vessels per mm², ray width (number of cells and µm), ray height (µm), rays per mm² and percentage of fibres. Lianas typically have two vessel classes, those that are very wide and those that are very narrow. Here, following the recommendations of the IAWA Committee (1989) for plants with vessel dimorphisms we measured only the diameter of wide vessels, which are those that contribute to the bulk of water conduction. One to five individuals were analysed per species, as listed in the Appendix.

The statistical test employed to differentiate lianas and trees was analysis of variance (ANOVA). This analysis considered ten variables present in all the species where the sample unit was each species' variable mean. Variables for which residues did not satisfy the requirements of normal distribution (as determined by a Lilliefors test) and equal variances were log, arcsine or square-root transformed. Differences were considered statistically significant when $P < 0.05$ and highly significant when $P < 0.001$. The statistical analyses were conducted using Microsoft Excel 97 SR-2 and Statistic 5.1 for Windows software (Statsoft Inc., 1997).

RESULTS

Visually trees and lianas of the studied genera are different (Fig. 1). However, the main goal of this work was to test if these observed differences were statistically significant. Thus, Table 1 summarizes the ANOVA results for quantitative wood anatomical features of trees and lianas (mean ± standard deviation, range). Lianas had highly significant differences related to the percentage of fibres, vessels and overall parenchyma (axial and radial combined), vessel diameter (µm), vessel per mm², ray width (µm) and ray height (µm).

All trees considered, vessels were predominantly solitary (55%), with an average diameter of 151 µm, vessel element length of 230 µm, frequency of six

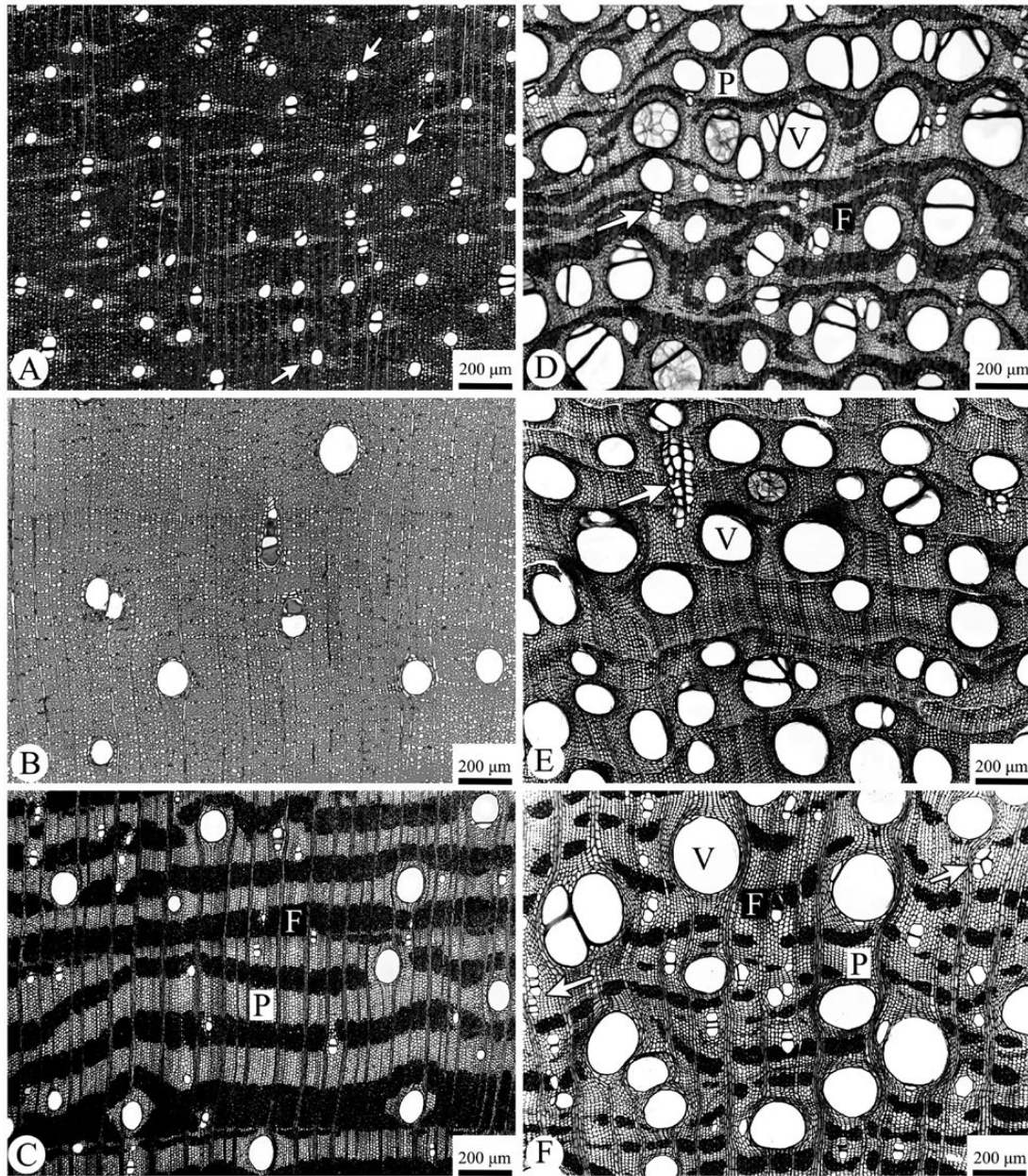


Figure 1. Transverse wood sections of trees and lianas. Trees (A-C): axial parenchyma aliform (A, arrow), aliform forming short confluences (A), in bands (C, P) and diffuse-in-aggregates. Lianas (D-F): axial parenchyma mainly in bands (P), vessel dimorphism [wide vessels (V) accompanied by narrow vessels – arrow] and fibres in a smaller percentage of the total secondary xylem area (F). A, *Machaerium incorruptible*, tree. B, *Dalbergia retura*, tree. C, *Clitoria arborea*, tree. D, *Machaerium ferox*, liana. E, *Dalbergia monetaria*, liana. F, *Clitoria arborescens*, liana.

vessels/mm², occupying 6% of the total wood area. The axial parenchyma was predominantly aliform, aliform forming confluences, and in bands, with diffuse-in-aggregates (lines or bands) also present. Overall, parenchyma occupied 27% of the total wood area. The rays were homocellular and/or heterocellular and were on average two cells and 26 µm wide with a height of 29 µm. The fibres had a

length of 1202 µm, occupying 67% of the total wood area (Fig. 1A-C).

All lianas considered, vessel dimorphism was present (wide vessels accompanied by narrow vessels), with vessels predominantly in groups (40% solitary), wide vessels with an average of diameter of 289 µm, vessel element length of 271 µm, frequency of 17 vessels/mm² and the vessels occupied 25% of the total wood area.

Table 1. Analysis of variance summary for quantitative wood anatomical features of trees and lianas (mean \pm standard deviation, range)

Features/ variables	Trees	Lianas	<i>P</i>
Fibres (percentage)	67 \pm 7 (57–81)	20 \pm 15 (4–61)	0.000**
Vessels (percentage) ¹	6 \pm 4 (2–14)	25 \pm 17 (6–79)	0.000**
Axial parenchyma (percentage) ²	27 \pm 8 (15–42)	56 \pm 14 (17–72)	0.000**
Vessel length (μm)	230 \pm 43 (169–315)	271 \pm 78 (135–425)	0.074
Vessel diameter (μm)	151 \pm 48 (64–210)	289 \pm 86 (114–437)	0.000**
Vessel frequency (per mm ²) ¹	6 \pm 6 (2–23)	17 \pm 14 (3–60)	0.000**
Ray width (μm) ³	26 \pm 1 (14–64)	45 \pm 23 (17–81)	0.009**
Ray width (number of cells) ¹	2 \pm 1 (1–4)	3 \pm 1 (1–5)	0.041*
Ray height (μm) ¹	291 \pm 293 (105–1116)	917 \pm 856 (83–2686)	0.012**
Fibre length (μm)	1202 \pm 355 (685–1866)	1723 \pm 741 (671–3302)	0.017*

Variables transformed to logarithm¹, arcsine² or square root³.

* = Significant difference.

** = Highly significant difference.

The axial parenchyma was mainly banded, and the overall parenchyma (axial and radial) occupied 56% of the total wood area. The rays varied from homo- to heterocellular and were on average three cells and 45 μm wide, with a height of 917 μm . The fibres had a length of 1723 μm and occupied 20% of the total wood area (Fig. 1D–F).

DISCUSSION

Whereas most comparative studies between trees and lianas have focused on qualitative data or the quantitative data for single taxa or a single habit, this study innovates by showing statistically how lianas and trees of one of the most abundant Neotropical families, Fabaceae, are statistically different. Bignoniaceae are the only family previously thoroughly investigated in this matter (Gasson & Dobbins, 1991; Pace *et al.*, 2015; Gerolamo & Angyalossy, 2017; Gerolamo *et al.*, 2020). Statistical support for the “Lianescent Vascular Syndrome” (Angyalossy *et al.*, 2015) was found in this study, with a lower percentage of fibres, higher percentage of vessels, parenchyma (axial and radial); wider and more frequent vessels, wider and taller rays and longer fibres.

Differences between liana and tree wood types probably reflect known different functional roles related to water conductivity, storage and mechanical support for the plant (Baas *et al.*, 2004; Pratt *et al.*, 2007; Carlquist, 2013; Ziemińska, 2018). Thus, xylem is subject to adaptive selection and diverse arrangements of cell types can be configured for the plant to assume a safety-efficiency trade-off (Bittencourt *et al.*, 2016; Ganthaler *et al.*, 2019).

For the vessel dimensions, our results show the same trend of increased vessel diameter and/or frequency in

the lianas. It corroborates with the conductive ability of lianas as observed in other lineages of eudicots, outside core eudicots [Menispermaceae (Mennega, 1982)] and among core rosids [Euphorbiaceae, Celastraceae (Mennega, 1997); Sapindaceae (Klaassen, 1999; Ménard *et al.*, 2009; Tamaio, 2011; Pelissari *et al.*, 2018)] and asterids [Bignoniaceae (Gasson & Dobbins, 1991; Pace *et al.*, 2015; Gerolamo & Angyalossy, 2017)] of core eudicots, as well as in entire floras (Baas & Schweingruber, 1987; Gartner *et al.*, 1990; Ewers *et al.*, 1990; Gutierrez *et al.*, 2009). The width of the vessels and tracheids in plants has been showed to be correlated to the total plant length; therefore, taller plants have wider vessels (Olson *et al.*, 2014). Lianas are among the longest in the plant kingdom, which would explain their extremely wide vessels (Field *et al.*, 2012; Rosell & Olson, 2014; Angyalossy *et al.*, 2015). These wider vessels combined with their higher frequency in lianas promote a greater water-carrying capacity in these plants (Ganthaler *et al.*, 2019). It has been shown experimentally that larger diameter vessels in lianas offer less friction and conduct more water when compared to the same tissue area for tree species, making the lianas efficient in water conduction and capable of supporting leaf biomass comparable to that of the larger trees in tropical forests (Ewers & Fisher, 1989; Jacobsen *et al.*, 2012; Rosell & Olson, 2014; Carvalho *et al.*, 2015). Under the same climatic conditions, vessels twice as wide in diameter will carry 16 times more water (Ewers & Fisher, 1989; Tyree & Zimmermann, 2002), and this greater efficiency in water conduction should compensate for the limited transverse area of the liana stem.

A liana conducting system composed of vessels of wider diameter guarantees greater water conduction efficiency. However, these characteristics make the system vulnerable to embolism, representing a huge

loss to the plant water system (Tyree & Zimmermann, 2002; Hacke *et al.*, 2006). On the other hand, smaller vessel diameter with the addition of intervacular pit structure more frequently guarantees greater safety in conduction, since these together reduce the chance of rupture of the water column when bubbles are formed, as those that do form are smaller and dissolve more easily (Ewers, 1985; Tyree & Zimmermann, 2002; Lens *et al.*, 2011; Li *et al.*, 2016), and in lianas the occurrence of narrow vessels side by side with wide vessels is ubiquitous (Carlquist, 1985; Angyalossy *et al.*, 2015), a phenomenon called “vessel dimorphism” by Carlquist (1981). Carlquist (1985) reported that many lianas occur in areas where freezing and extreme drought are either absent or moderate, and most occur in wetlands where water stress and freezing never occur. Global studies on liana abundance in forests, on the other hand, showed that lianas endure longer drought periods better than trees, something that would explain their increase in recent years [(Schnitzer, 2005; Schnitzer & Bongers, 2011); but see Gerolamo *et al.* (2018) for contrasting results]. It is likely that behind this higher endurance, the larger amount of parenchyma in lianas plays a pivotal role, since it has been proposed that vessel-associated parenchyma can prevent and repair events of embolism (Braun, 1984; Salleo *et al.*, 2004, 2009; Morris & Jansen, 2016; Morris *et al.*, 2016, 2018a, b).

Lianas seem to expend more energy in elongation than in growth in diameter of the stem. Studies on cambial seasonality and dendrochronology of lianas have shown that they form annual growth rings (Brandes *et al.*, 2011), although with a shorter cambial activity span than trees growing in the same environment (Lima *et al.*, 2010), and therefore less wood is formed. The reduced diameter of the stem is compensated by an external mechanical support used by the plant to reach the canopy. In this way, the cylinder is modified and more efficient in water conduction, presenting more conducting (vessels) than supporting cells (fibres), something that had been already suggested qualitatively and is here statistically corroborated for Fabaceae.

Fabaceae subfamily Papilionoideae are known for having abundant axial parenchyma. However, here we also found that parenchyma is more abundant in lianas than in trees. The same trend has been suggested for other taxa (Carlquist, 1995, 1996) and revealed in a global analysis of parenchyma abundance (Morris *et al.*, 2016). Since lianas use external mechanical support, parenchyma is considered as an alternative tissue to occupy the place of fibres (Carlquist, 1988; Gasson & Dobbins, 1991; Ewers *et al.*, 1991), an anatomical case of homeosis (*sensu* Sattler, 1988), since the space occupied by fibres in the ancestral plant is substituted by another cell type in the

descendant. In fact, we found a clear increase in axial and ray parenchyma in liana stems. Higher and wider rays and more abundant axial parenchyma have been shown to increase the ability of lianas to withstand torsions, making their stems more flexible (Rowe & Speck, 1996; Gallenmüller *et al.*, 2001; Rowe *et al.*, 2004). Other known functions of the more abundant parenchyma are related to injury repair (Dobbins & Fisher, 1986; Fisher & Ewers, 1989), the protection of conducting elements from events of cavitation, probably acting in embolism repair by the presence of vessel-associated parenchyma (Braun, 1984; Carlquist, 1988; Ewers & Fisher, 1989; Salleo *et al.*, 2004, 2009; Clearwater & Goldstein, 2005; Morris & Jansen, 2016; Morris *et al.*, 2018a, b), in avoiding pathogen entrance by the formation of tyloses and gum secretion in cases of pathogen attack, and in the formation of heartwood (Chattaway, 1949; De Micco *et al.*, 2016).

Here it was observed that liana fibres were longer than those of trees, with significant differences in the analysis of variance. Although Mennega (1982, 1997) recorded shorter fibre tracheids in lianas in Menispermaceae and Celastraceae, there is currently no hypothesis for the influence of fibre length influencing mechanical attributes. Here, we saw that vessel elements were slightly longer in the lianas (although not statistically significant), and this difference, although small, probably also reflects the convergence for longer fusiform cambial initials in the lianas.

CONCLUSIONS

Our results describe statistically the features of the “Lianescent Vascular Syndrome” for four of the most representative lianescent Neotropical genera of Fabaceae, *Machaerium*, *Dalbergia*, *Clitoria* and *Dioclea*, representatives of Papilionoideae tribes Dalbergieae and Phaseoleae. Our paper brings a quantitative view adding to the qualitative approach for the study of lianas, and evidence that the wood of lianas has statistically wider, and more abundant vessels, more axial and ray parenchyma and longer fibres, a case of evolutionary convergence. We expect that similar statistical significance is to be found in other lianescent lineages, evidencing the convergent evolution of wood anatomy and habit.

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AUTHOR CONTRIBUTIONS

C.L.D.L. and V.A. designed the study; C.L.D.L. conducted the laboratory work, data analyses and wrote the manuscript with significant contributions from V.A. and M.R.P.; all authors commented and approved the final version of the manuscript.

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APPENDIX

Information on analysed samples of *Machaerium* Pers., *Dalbergia* L.f., *Clitoria* L. and *Dioclea* Spreng. including species/taxa, voucher information (wood collection and/collector-herbarium number), geographical origin, habit and circumference of the stem in centimetres. The Wood Collections cited are: Naturalis Biodiversity Center (Uw), Leiden, The Netherlands; Forest Products Laboratory Wood Collection and Samuel J. Record Memorial (MADw and SJRw), Madison, Wisconsin, USA; Dr. Calvino Mainieri Xylarium at the Institute of Technological Research, São Paulo, Brazil (BCTw), the Reserva Natural Vale Herbarium, Brazil, and the Royal Botanic Gardens Xylarium, Kew (Kw), England.

***Machaerium aculeatum* Raddi:** BCTw 1577/Hoehne-236, Brazil, tree, > 15 cm. BCTw 1619/-, Brazil, tree, > 15 cm. ***Machaerium acutifolium* Vogel:** Uw 13591/Lindeman e Haas-2204, Brazil, tree, > 15 cm. BCTw 12692/- PR-Brazil, tree, > 15 cm. ***Machaerium affine* Benth.:** Uw 30672/Jansen *et al.*-538, Guyana, tree, > 15 cm. ***Machaerium angustifolium* Vogel:** SJRw 23827/Hoehne-28802, Brazil, tree, > 15 cm; SJRw 1797/Curran50-1915, Brazil, tree, > 15 cm; MADw 13156/Maguire, Brazil, tree, > 15 cm. ***Machaerium biovulatum* Micheli:** MADw 31637/Maguire, Brazil, tree, > 15 cm. ***Machaerium capote* Dugand:** MADw 24884/Darien Holdridge-6284, Panamá, tree, > 15 cm.

SJRw 55086/Stern *et al.* 890, Panamá, tree, > 15 cm. SJRw 29609/D. Dugand-136, Colombia, tree, > 15 cm. ***Machaerium ferox* (Benth.) Ducke:** Uw 23138/Heyde 1976-455, Suriname, liana, 12 cm. Uw 17084/Maguire *et al.*-51483, Brazil. Liana, 10.5 cm. Uw 33425/Ursem e Potters-132, Suriname, liana, 15 cm. ***Machaerium floribundum* Benth.:** SJRw 52677/Maguire-42652, Venezuela, liana, 12 cm. MADw 21597/Maguire-51936, Brazil, tree, > 15 cm. Uw 9662/Pires 1961–51936, Brazil, liana, > 15 cm. ***Machaerium hoehneanum* Ducke:** Xylarium of the University of São Paulo (SPFw)/Dias-Leme 1995-CDL45, Brazil, liana, 12 cm. SPFw/Dias-Leme 1995-CDL69, Brazil, liana, 8.5 cm. SPFw/Dias-Leme 1995-CDL85, Brazil, liana, 9 cm. ***Machaerium incorruptibile* (Vell.) Benth.:** MADw1 3147/Maguire, Brazil, tree, > 15 cm. SJRw 39525/Hutchison, Brazil, tree, > 15 cm. BCTw 11550/Mattos Filho-SBG-2166, Brazil, tree, > 15 cm. ***Machaerium inundatum* (Benth.) Ducke:** Uw 3877/Lindeman '53-'55-5608, Suriname, liana 10.5 cm. Uw 26435/Lindeman '53-'55-L6409, Suriname, tree, > 15 cm. ***Machaerium legale* (Vell.) Benth.:** BCTw 11548/Mattos Filho-SBG2216, Brazil, tree, > 15 cm. ***Machaerium leucopterum* Vogel:** BCTw 11549/Kuhlmann, Brazil, tree, > 15 cm. BCTw 11006/-, ES-Brazil, > 15 cm. ***Machaerium macrophyllum* Benth.:** Uw 11308/Van Donselaar 1966–2378, Suriname, liana, 11 cm. Uw 11985/Van Donselaar 1965–3066, Suriname, liana, 13 cm. Uw 23329/-, liana, 13.5 cm. ***Machaerium madeirense* Pittier:** Uw 21821/Lindeman – Stoffers-450, Suriname, liana, 4 cm. Uw 22772/Lindeman e Heyde-141, Suriname, liana, 14 cm. Uw 12123/Van Dorselaar 1966–3501, Suriname, liana, 12 cm. ***Machaerium multifoliolatum* Ducke:** SPFw 826/Dias-Leme 1995-CDL15, AM-Brazil, liana, 13 cm. SPFw 827/Dias-Leme 1995-CDL51, AM-Brazil, liana, 10.5 cm. SPFw 828/Dias-Leme 1995-CDL87, AM-Brazil, liana, 7 cm. ***Machaerium ovalifolium* Rudd:** BCTw 18474/Herbário CVRD cod.068, Brazil, tree, > 15 cm. ***Machaerium pedicellatum* Vogel:** BCTw 11005/-, tree, > 15 cm. BCTw 6352/Kuhlmann SBG1353, Brazil, tree, > 15 cm. BCTw 6352/Kuhlmann SBG1353, Brazil. Tree, > 15 cm. ***Machaerium polyphyllum* (Poir.) Benth.:** Uw 13853, liana, 10 cm. ***Machaerium robinifolium* (DC.) Vogel:** Uw 17598/Steyermark-86545, Venezuela, tree, > 15 cm. Uw 35331/Williams-W10977, Venezuela, tree, > 15 cm. Uw 35240/Williams-W10326, Venezuela, tree, > 15 cm. ***Machaerium scleroxylon* Tul.:** Uw 13689/Lindeman e Haas-2345, PR-Brazil, tree, > 15 cm. Uw 13507/Lindeman e Haas-2102, PR-Brazil, tree, > 15 cm. Uw 13465/Lindeman e Haas-2027, PR-Brazil, tree, 9 cm. BCTw 8592/Mattos Filho, MG-Brazil, tree, > 15 cm. ***Machaerium villosum* Vogel:** BCTw 1599/Navarro, SP-Brazil, tree, > 15 cm. BCTw 4452/-, tree, > 15 cm. BCTw 1590/Navarro, SP-Brazil, tree, > 15 cm.

- Dalbergia glauca* Wall:** Uw 1587/Heyde 1976-454, Suriname, liana, 6.5 cm. Uw 22863/Lindeman e Heyde-302, Suriname, liana, 8.5 cm. ***Dalbergia inundata* Benth.:** Uw 32570/Maas *et al.*-7609, Guyana, liana, 9.5 cm. Uw 7546/Krukoff, 1961- 6671, Brazil, liana, > 15 cm. Uw 7861/Krukoff, 1961-6195, Brazil, tree, 14 cm. ***Dalbergia monetaria* L.f.:** Uw 3918/lind '53-'55, 5710, Suriname, liana, 2.5 cm. Uw 11300/via Donselaar 1965-2370, Suriname, liana, 12 cm. Uw 12138/via Donselaar 1966-3744, Suriname, liana, 11 cm. ***Dalbergia nigra* (Vell.) Benth.:** Uw 23538/via Reinbek BFA-6229, Brazil, tree, > 15 cm. Uw 23006/via Reinbek BFA-13201, Brazil, tree, > 15 cm. ***Dalbergia paniculata* Roxb.:** Kew 6286/via Km Bhat, Kerala, India, tree, > 15 cm. Kew 21254/Forest India 40 India, tree, > 15 cm. Uw 3283/via Km Bhat, Kerala Forest India 40, India, tree, > 15 cm. ***Dalbergia retusa* Hemsl.:** Uw 11080/USW9, Panamá, tree, > 15 cm. Uw 7018/U. Smiths. Nat. herb. -678561-2, Panamá, tree, > 5 cm. ***Clitoria arborea* Benth.:** Uw 19911/Krukoff-5335, Brazil, tree, > 15 cm. Uw 20996/Maguire *et al.*-51990, Brazil, tree, > 15 cm. Uw 16124/Krukof-6125, Brazil, tree, > 15 cm. Uw 7499/Krukof, 8208, Brazil, tree, > 15 cm. Uw 20150/-. ***Clitoria arborescens* R.Br.:** Uw 22849/Lindeman e Heyde-272, Suriname, liana, 9.5 cm. Uw 22754/Lindeman e Heyde-119a, Suriname, liana, 8 cm. Uw 13875/Pulle-467, Suriname, liana, 6.5 cm. ***Clitoria brachycalyx* Harms:** Uw 21640/Smith-3128, Guyana, tree, > 15 cm. Uw 30476/Jansen-Jacobs *et al.*-80, Guyana, tree, 9 cm. Uw 33881/Jansen-Jacobs *et al.*-2984, Guyana, tree, 6 cm. ***Clitoria dendrina* Pittier:** Uw 35471/Williams-11638, Venezuela, tree, 14 cm. ***Clitoria javitensis* (Kunth) Benth.:** Uw 31268/Schumke-4339, Peru, liana, 8.5 cm. Uw 31281/Schumke-4926, Peru, liana, 5 cm. ***Clitoria pendens* Fantz:** Uw 2028/Florschütz-1344, Suriname, liana, 7 cm. ***Dioclea macrocarpa* Huber:** Uw 13892/Boschwchem-3870, Suriname, liana, 2.5 cm. Uw 30163/Stoffers *et al.*-SG327, Guyana, liana, 6 cm. Uw 9705a/-, liana, 8 cm. ***Dioclea megacarpa* Rolfe:** Uw 22751/Lindeman and Heyde-303, Suriname, liana, 8 cm. ***Dioclea scabra* (Rich.) Maxwell:** Uw 23186/Heyde-533, Suriname, liana, 3.5 cm. Uw 23309/Heyde, 697, Suriname, liana, 5 cm. Uw 33395/Ursem e Potters-30, Suriname, liana, 2.5 cm. ***Dioclea virgata* (Rich.) Amshoff:** Uw 22886/Lindeman and Heyde-340, Suriname, liana, 4 cm. Uw 32209/Jansen and Jacobs-1075, Guyana, liana, 4.5 cm.