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Monomer composition of polysaccharides of seed cell walls and the taxonomy of the Vochysiaceae

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Abstract

The distribution of polysaccharides from the seed cell walls of 57 samples of Vochysiaceae native to Brazil were studied, comprising 16 species distributed among the genera *Callisthene, Qualea, Salvertia* and *Vochysia*. The polysaccharides were extracted with hot water, then hydrolyzed with the resulting monomers analyzed by HPLC. All samples yielded arabinose, galactose, glucose, mannose and rhamnose, the relative amounts of each monomer, however, varying from one sample to another. Arabinose was always the predominant component, which implies that it might possibly be used as a marker of the Vochysiaceae. The quantitative distribution of monosaccharides was similar between the species of *Qualea* and *Callisthene*, characterized by the predominance of arabinose and mannose, and between the species of *Salvertia* and *Vochysia*, which contained higher amounts of arabinose and galactose. Such results are consistent with affinities inferred from floral morphology, wood anatomy and molecular data. Substantial intraspecific variation was observed for some species. UPGMA analysis based on the distribution of the monosaccharides reveals two main clusters, according to the links commented above. The resultant phenogram is not coherent with the current sectional classification of the Vochysiaceae, but the differences in the monosaccharides distribution between the two clusters are strongly supported by ANOVA.

Keywords: *Callisthene*; *Qualea*; *Salvertia*; *Vochysia*; Vochysiaceae; Seed cell wall polysaccharides; Chemotaxonomy

1. Introduction

The Vochysiaceae are tropical trees and shrubs comprising two tribes, six genera and approximately 200 species. Of these, tribe Erismeae contains two genera, namely *Erismadelphus* (3 species, Western Africa) and *Erisma* (20 species, South America), whereas tribe Vochysieae is composed of 4 genera, namely *Callisthene* (10 species), *Qualea* (60 species), *Salvertia* (1 species) and *Vochysia* (105 species); they are all neotropical (Heywood, 1993).

Vochysiaceae genera are distinguished by their floral and fruit characters. In all taxa, the flowers are zygomorph, with a sole stamen, but the number of petals can vary from one group to another. Within the tribe Erismeae, *Erismadelphus* has five petals and *Erisma*, one petal (Stafleu, 1948, 1952, 1953, 1954). Within the tribe Vochysieae, however, *Salvertia* with five petals presents flowers with characters presumably more archaic, whereas *Vochysia* has three petals, and *Callisthene* and *Qualea* have only one petal. The fruit is a trilocular capsule in these genera with a superior ovule in the *Callisthene, Qualea, Salvertia* and *Vochysia*. In *Callisthene*, the exocarp sets apart irregularly from the endocarp; in the other genera with dehiscent fruits, the exocarp is adherent to the endocarp. *Erisma* has indehiscent alate fruits and one seed per fruit. *Callisthene, Qualea, Salvertia* and *Vochysia* have alate seeds, one per locule in *Salvertia* and *Vochysia* and more than one in *Callisthene* and *Qualea* (Barroso, 1991). A thick and hairy tegument covers the seeds of *Salvertia*. Seeds of Vohysiaceae have little or no endosperm and two cotyledons (Cronquist, 1981), that are foliaceous in *Callisthene, Qualea* and *Salvertia* and convolute in *Vochysia* (Barroso, 1991). *Qualea* seeds collected for analyses in the present work ranged from 31 to 52 mm, those of *Salvertia*, from 40 to 65 mm and those of *Vochysia*, from 21 to 36 mm; in comparison, *Callisthene* seeds were much smaller, 8–9 mm.

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While phytochemical studies of Vochysiaceae have been carried out, none have addressed taxonomy. Of those phytochemical studies, ellagic acid derivatives were reported for *Erisma calcaratum, Salvertia convallariodora, Vochysia acuminata, V. thyrsoidea* (Barros Correa et al., 1975) and *Callisthene major* (Correa et al., 1985), whereas 5-deoxyflavones were isolated from leaves of species of *Qualea, Salvertia* and *Vochysia* (Lopes et al., 1979). *C*-Methylated flavanones and benzophenones were also found in *Qualea labouriauana* and simple flavanones accumulated in *Q. paraensis* (Correa et al., 1981), whereas vochysine, a pyrrolydoflavane, was isolated from stems of *Vochysia guianensis* (Baudouin et al., 1983). Additionally, vismiaefolic acid, a triterpenoid, was found in stems of *Vochysia vismiaefolia* (Araújo et al., 1990).

Seed fatty acids have been frequently investigated for both economic and taxonomic purposes. For example, the studies on the fatty acids of *Cuphea* and related taxa (Graham et al., 1981a,b; Wolf et al., 1983; Graham and Kleiman, 1987; Knapp et al., 1991; Santos and Salatino, 1998) deserve mentioning because of the taxonomic and economic significance of the *Cuphea* saturated and short-medium chain fatty acids. In comparison with seed fatty acids, however, fewer studies have been carried out with seed polysaccharides. Apparently, no information is available about seed sugars of the Vochysiaceae, except for the work by Blanche et al. (1991) who reported sugar contents of seeds of *Vochysia hondurensis*.

Different groups of plants can be distinguished on the basis of the composition of their cell wall polysaccharides (Carpita, 1996). Although the composition of the cell wall of the whole plant is thought to be relatively constant, it may vary according to either its function or the physiological state of the tissue. It is more variable in growing tissues, where the cell wall is changing dynamically, but it is quite constant in the vascular system and quiescent seeds for example.

Comparative studies of seed storage cell wall polysaccharides have been performed only with species of the Fabaceae (Buckeridge et al., 2000). Most species of this family store galactomannan (a water soluble polysaccharide) in the thick endosperms. In other species, either xyloglucan or galactan is present as the main storage compound. The composition of galactomannan (notably the ratio between mannose and galactose) has been demonstrated to be useful for taxonomic purposes, since the three subfamilies (Caesalpinioideae, Faboideae and Mimosoideae) can be distinguished by galactomannan composition and, in certain cases, taxonomic problems have been approached at the species level (Reid and Meier, 1970).

In the present work, the seed polysaccharides of 57 samples, comprising 16 species of Vochysiaceae, were extracted with hot water and their monosaccharide compositions examined, with the aim to evaluate their potential as taxonomic markers.

2. Results and discussion

2.1. Seed cell wall polysaccharides of Vochysiaceae compared with other plant families

The extraction of seed polysaccharides with hot water was carried out with the purpose to obtain cell wall polymers bound weakly to the seed cell wall. According to Buckeridge et al. (2000), such polymers normally correspond to pectins, although in seeds (e.g. Fabaceae) they may be hemicellulosic in character, although often more branched (usually with galactose). Indeed, these authors classified the seed storage polysaccharides into mannans, xyloglucans and arabinogalactans. These general classifications are not mutually exclusive and seeds, such as coffee, contain mannans along with arabinogalactans. In *Coffea arabica* mannans are β-1,4-linked and contain very little branching with galactose. Coffee arabinogalactans correspond to β-1,3 linked galactans branched with β-1,6 residues of galactose. Arabinose is always present as an α-1,5 polymer which is believed to be linked to the galactan chain.

The monosaccharides released by the water soluble polysaccharides of seeds of the Vochysiaceae were arabinose, galactose, glucose, mannose and rhamnose (Table 1). Arabinose and mannose were the predominant monosaccharides, followed by galactose. Rhamnose was always present, but in lower proportions, this being a strong indication of the presence of pectin in the extracts.

On the basis of the current knowledge on the plant (especially seed) cell walls (see Carpita and Gibeaut, 1993, and Buckeridge et al., 2000 for reviews), it can be suggested that seeds from different species of Vochysiaceae contain a variable mixture of polysaccharides of the arabinogalactan and mannan types. It is well known that mannans from plants are always of the β-type as opposed to the fungal ones that are α-linked (Carpita and Gibeaut, 1993). Thus, it can be proposed with a high degree of confidence that the mannose found in Vochysiaceae is derived from a β-linked mannan. A distinctive characteristic of the β-mannans is that they are practically insoluble in water, unless they are branched with galactose (usually α-1,6 linked) to more than 10% of the mannose residues in the main chain. In other words, seeds of Vochysiaceae almost certainly contain a galactomannan and probably also an arabinogalactan with higher amounts of arabinan in its composition.

It is important to note that our data do not bring any clarification as to the sugar linkage types, and although the presence of a β-mannan can be inferred with a

Table 1
Distribution of constituents of polysaccharides from seed cell walls of the Vochysiaceae[a]

Taxa	Polysaccharide constituents (%, w/w)							
	Rha	Ara	Gal	Glc	Man	Ara/Glc	Man/Glc	Man/Gal
Callisthene								
Sect. *Callisthene*								
Callisthene minor Mart.								
1	4.9	39.6	18.3	7.7	29.4	5.1	3.8	1.6
Qualea								
Subg. *Amphilochia*								
Qualea cordata Spreng								
2	2.4	38.4	22.5	4.3	32.4	8.9	7.6	1.4
3	2.8	49.1	18.9	6.3	22.8	7.7	3.6	1.2
4	3.1	47.3	21.1	6.0	22.4	7.9	3.7	1.0
Q. dichotoma Warm.								
5	3.1	42.7	20.0	4.2	30.0	10.2	7.1	1.5
6	2.8	51.5	13.2	6.1	26.4	8.4	4.3	2.0
Q. cryptantha (Spreng) Warm.								
7	6.7	46.7	19.9	6.1	20.5	7.6	3.4	1.0
Subg. *Qualea*								
Sect. *Costatifolium*								
Q. grandiflora Mart.								
8	1.6	63.6	12.1	4.9	17.7	12.9	3.6	1.4
9	2.3	53.0	8.0	8.8	27.8	6.0	3.1	3.4
10	–	58.4	12.8	12.9	15.8	4.5	1.2	1.2
11	1.7	57.1	16.4	8.5	16.2	6.6	1.9	1.0
12	1.8	45.6	14.6	8.3	29.6	5.5	3.5	2.0
13	3.4	42.7	17.1	13.2	23.5	3.2	1.8	1.3
14	2.7	52.8	12.9	7.2	24.3	7.3	3.3	1.9
15	2.4	45.4	14.1	6.7	31.3	6.7	4.6	2.2
16	1.2	58.8	12.6	12.3	15.0	4.8	1.2	1.2
Q. multiflora Mart.								
17	2.5	42.6	22.0	4.8	28.0	8.8	5.8	1.2
18	1.0	61.3	16.5	8.2	13.0	7.4	1.5	0.8
Q. parviflora Mart.								
19	3.0	42.8	18.7	5.2	30.3	8.2	5.8	1.6
20	3.0	31.1	16.1	7.0	22.8	7.3	3.2	1.4
21	3.1	44.5	18.8	6.2	27.4	7.2	4.4	1.4
22	3.8	54.4	10.0	6.6	25.0	8.2	3.7	2.5
23	2.6	47.3	15.6	3.2	31.3	14.9	9.8	2.0
24	–	62.4	15.6	8.6	13.4	7.2	1.6	0.8
Salvertia								
S. convallariodora St. Hil.								
25	6.4	46.8	26.4	14.7	5.6	3.1	0.4	0.2
26	7.9	32.4	30.3	17.9	11.4	1.9	0.6	0.3
27	12.9	35.2	22.7	15.0	14.2	2.3	0.9	0.6
28	12.4	34.2	37.0	7.2	9.2	4.7	1.2	0.2
29	4.6	35.2	34.5	17.7	7.8	2.0	0.4	0.2
Vochysia								
Sect. *Vochysiella*								
Subsect. *Decorticantes*								
Vochysia elliptica Mart.								
30	7.3	34.9	33.6	11.7	12.4	3.0	1.0	0.3
31	6.8	31.3	27.7	21.9	12.2	1.4	0.5	0.4
32	7.6	37.3	28.6	15.8	10.5	2.3	0.6	0.3
33	6.7	32.6	36.3	10.6	13.5	3.1	1.3	0.3
34	8.3	37.3	29.9	10.5	13.8	3.5	1.3	0.4
V. gardneri Warm.								
35	6.2	49.1	24.6	14.3	5.6	3.4	0.4	0.2
36	5.0	40.1	31.8	16.2	6.8	2.4	0.4	0.2
37	5.9	46.8	25.7	15.8	5.6	2.9	0.3	0.2
V. rufa Mart.								
38	8.6	35.5	28.2	16.4	11.2	2.1	0.7	0.4
39	7.6	48.0	27.1	11.1	6.1	4.3	0.5	0.2

(*continued on next page*)

Table 1 (*continued*)

Taxa	Polysaccharide constituents (%, w/w)							
	Rha	Ara	Gal	Glc	Man	Ara/Glc	Man/Glc	Man/Gal
40	6.1	47.9	25.5	14.8	5.7	3.2	0.4	0.2
41	–	44.7	32.6	17.5	5.1	2.5	0.3	0.1
Sect. *Ciliantha*								
Subsect. *Micranthae*								
V. lucida Presl.								
42	6.0	35.1	28.9	15.3	14.3	2.3	0.9	0.5
43	1.7	30.4	29.9	23.2	14.6	1.3	0.6	0.5
44	7.6	25.6	29.5	21.1	16.2	1.2	0.7	0.5
Subsect. *Lutescentes*								
V. pygmaea Bongard								
45	6.8	48.4	23.9	7.4	13.3	6.5	1.8	0.5
V. thyrsoidea Pohl.								
46	5.7	35.7	32.4	19.3	6.7	1.8	0.3	0.2
47	8.0	37.5	28.8	14.2	11.4	2.6	0.8	0.4
48	7.7	37.4	29.5	15.3	10.0	2.4	0.6	0.3
V. tucanorum Mart.								
49	9.3	39.0	29.7	12.7	9.3	3.1	0.7	0.3
50	4.1	39.0	26.9	22.2	7.6	1.7	0.3	0.3
51	6.2	46.1	26.2	15.6	5.7	2.9	0.3	0.2
Subsect. *Ferrugineae*								
V. pyramidalis Mart.								
52	5.6	36.7	33.1	8.7	15.7	4.2	1.8	0.4
53	-	54.2	26.6	9.8	9.2	5.5	0.9	0.3
54	7.5	36.8	31.5	10.3	13.8	3.5	1.3	0.4
55	8.8	40.7	23.4	10.8	16.2	3.7	1.5	0.7
56	5.1	34.3	31.2	10.0	19.1	3.4	1.9	0.6
57	3.5	32.6	35.2	22.8	5.8	1.4	0.2	0.1

[a] Rha = rhamnose; Ara = arabinose; Gal = galactose; Glc = glucose; Man = mannose.

reasonable degree of certainty, the type of galactan (type I or II) and the linkages in the arabinan may be revealed only after complete chemical analysis (i.e. methylation followed by GC–MS). In spite of this lack of evidence on the exact chemical linkages, the proportions of monosaccharides in the inferred polymers (arabinan, galactan and mannan) can be used for taxonomic comparisons within the Vochysiaceae.

2.2. The importance of the water soluble seed polysaccharides for the taxonomy of the Vochysiaceae

All samples analyzed contained arabinose, galactose, glucose, mannose and rhamnose as monomer constituents (Table 1). Arabinose predominates in samples of the four genera (means of quantitative distribution: *Callisthene*, 39.6; *Qualea*, 49.5; *Salvertia*, 36.8; *Vochysia*, 39.1). The predominance of arabinose as the main constituent of seed polysaccharides, indicating a higher proportion of arabinan, may be assumed as a chemical characteristic of the Vochysiaceae. It is possible that it may help clarifying the position of the Vochysiaceae, either along with the Polygalales (Hutchinson, 1967; Takhtajan, 1969; Dahlgren, 1980; Cronquist, 1988) or with the Myrtales. The latter view is supported by studies of vascular anatomy (van Vliet and Baas, 1984) and DNA sequencing (Conti et al., 1996; Conti, Wilson, Graham et al., 1997). As to the second most important monosaccharide, in samples of *Callisthene* and *Qualea* this rank is held by mannose (means: *Callisthene*, 29.4; *Qualea*, 23.8; *Salvertia* 9.6; *Vochysia*, 10.6), while in samples of *Salvertia* and *Vochysia* by galactose (means: *Callisthene*, 18.3; *Qualea*, 16.1; *Salvertia*, 30.2; *Vochysia*, 29.2). Other data linking *Callisthene* to *Qualea* and *Salvertia* to *Vochysia* are the larger amounts of glucose and rhamnose in *Salvertia–Vochysia* (means: glucose — *Callisthene*, 7.7; *Qualea*, 7.2; *Salvertia*, 14.5; *Vochysia*, 14.8; rhamnose — *Callisthene*, 4.9; *Qualea*, 2.5; *Salvertia*, 8.8; *Vochysia*, 6.1). Such chemical affinities are consistent with floral morphology, wood anatomy and molecular biology (see Section 1). Parameters determined by the ratios between the abundance of certain monomers relative to glucose (Table 1) strengthens the establishment of affinity relationships between the Vochysiaceae taxa. For example, the ratios correspondent to arabinose (ara/glc) are generally larger than 5.0 for *Callisthene*/*Qualea* and smaller than 4.0 for *Salvertia*/*Vochysia*. Ratios relative to mannose (man/glc) are also larger for *Callisthene*/*Qualea*, whose values lie generally above 1.0, in lieu of the values below 1.0 of *Salvertia*/*Vochysia*. The ratios between mannose and galactose (man/gal) are also larger than 1.0 in

Callisthene/*Qualea* and much smaller (0.7 at most) in *Salvertia*/*Vochysia* (Table 1). In the Fabaceae, where seed cell wall polysaccharides have more often been studied, the ratios of man/gal have been shown to have both taxonomic and phyletic meaning. A decrease in the values of the ratio man/gal is observed comparing Caesalpinioideae with Faboideae. It has been suggested that an increase in the relative amounts of galactose has run parallel to the evolution of the Fabaceae (Bailey, 1971; Buckeridge and Dietrich, 1990; Buckeridge et al., 1995; Buckeridge et al., 2000). Contrary to the trend observed in the latter family, it seems that evolution in the Vochysiaceae led to a decrease of the relative amounts of galactose. In fact, in the purported more archaic genera *Salvertia* and *Vochysia*, the amounts of galactose are larger (26–37% and 23–36%, respectively) than in the more advanced *Callisthene* and *Qualea* (18 and 8–23%, respectively, Table 1).

2.3. Cluster analysis

Fig. 1 presents the affinity relationships between the samples studied. A major divergence gives rise to two main clusters: cluster A-1 combining samples of *Callisthene*/*Qualea*, characterized by the predominance of arabinose and mannose, and cluster A-2 combining samples of *Salvertia*/*Vochysia*, characterized by the predominance of arabinose and galactose. As commented above, such links between the genera of Vochysiaceae are consistent with other evidence. However, inconsistencies at subgeneric levels characterize the smaller groupings within the major clusters. Indeed, inside

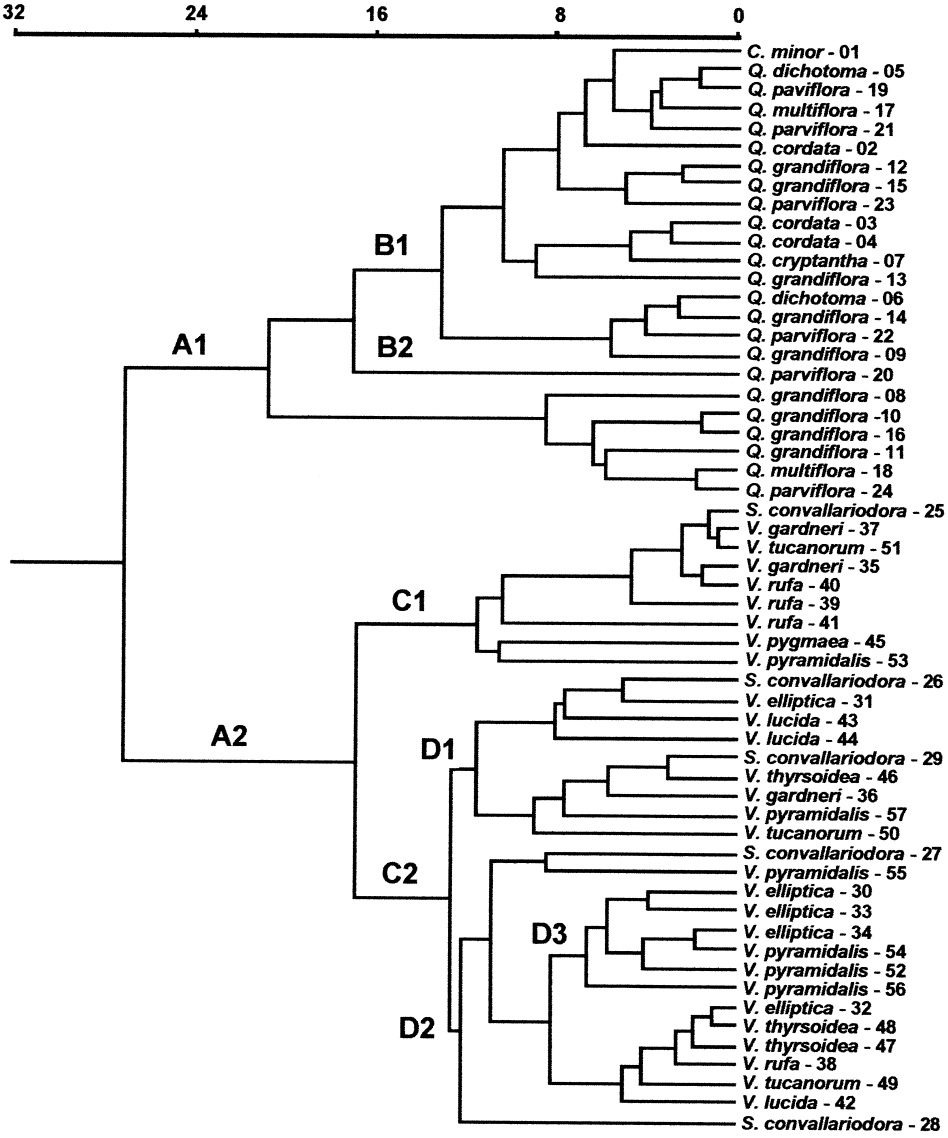

Fig. 1. Affinity relationships among taxa of Vochysiaceae based on the distribution of sugar constituents of polysaccharides from seed cell walls, and determined by Euclidean distances and UPGMA. Digits following scientific names correspond to samples in Table 1.

cluster B-1 close relationships are suggested between species of different subgenera, for example *Q. dichotoma* (subg. *Amphilochia*) and *Q. parviflora* (subg. *Qualea*). Substantial infraspecific variation (Table 1), sometimes larger than the differences between subgenera, precludes not only the clustering of samples taxonomically akin, but also the clustering of samples corresponding to the same species. This holds not only for cluster B-1, but also for clusters B-2–D-2. The outcome of the large infraspecific variation in *S. convallariodora* is the positioning of each of the four studied samples in a different cluster of Fig. 1. Similar to *Qualea*, samples of *Vochysia* fail to cluster according to the corresponding sections, subsections and species. A conclusion may thus be put forward that, with the exception of the main clusters A-1 and A-2, most of the more subordinate clusters have in general little or no taxonomic significance.

Given the obvious infraspecific variability, it may be argued that the main clusters of Fig. 1 (i.e. *Callisthene*/*Qualea, Salvertia*/*Vochysia*) also lack taxonomic significance. For this reason, a statistical approach testing the significance of the differences observed between the two main groupings is pertinent. The F_s values calculated for the percentages of each monosaccharide and the ratios between monosaccharides corresponding to *Callisthene*/*Qualea* and *Salvertia*/*Vochysia* (taking into consideration 1 degree of freedom for the numerator and 55 for the denominator) were as follows: rhamnose, 60.19; arabinose, 47.50; galactose, 174.08; glucose, 55.54; manose, 91.10; arabinose/glucose, 89.02; manose/glucose, 67.01; manose/galactose, 124.69. Since the F critical values are 4.03 for $\alpha = 0.05$ and 7.17 for $\alpha = 0.01$ (given the above mentioned degrees of freedom), $P > > > 0.01$ for all the parameters tested. Thus, the observed differences between the quantitative distribution of monosaccharides and ratios between the contents of monosaccharides are highly significant. In spite of the relatively high infraspecific variability, above, the composition of the polysaccharides is different enough between the major groups of the Vochysiaceae to warrant a taxonomic significance to the distribution of monosaccharides at higher hierarchic levels within the family.

Cluster B-1 combines samples with contents of mannose above 20%; cluster B-2, contents of mannose ranging from 13 to 18%; cluster C-1, contents of galactose ranging from 22 to 27%; cluster C-2, contents of galactose above 28%; cluster D-1, contents of glucose above 16%; and cluster D-2, contents of glucose below 15%.

Some groupings inside the more subordinate clusters may reflect some taxonomic coherence: cluster D-3 gathers three of the six studied samples of *V. pyramidalis* and three of the five studied samples of *V. elliptica* (Fig. 1). This observation strengthens evidence from the distribution of seed fatty acids of Vochysiaceae, which suggest that *V. pyramidalis* is more akin to members of section *Vochysiella* (*V. gardneri, V. elliptica* and *V. rufa*) than to members of section *Ciliantha* (*V. lucida, V. pygmaea* and *V. thyrsoidea*) where it is currently positioned (Mayworm and Salatino, unpublished results).

The results of the present work calls attention to the taxonomic meaning of the distribution of monomers of seed cell wall polysaccharides. With the exception of the Fabaceae it seems that in all other taxa such potentialities have so far been overlooked.

3. Experimental

A total of 57 seed samples from 16 species of Vochysiaceae (tribus Vochysieae) were collected in different ecosystems and states of Brazil, ranging from Tocantins and Bahia (Central and Northern Brazil, respectively) to São Paulo (Southeast). Voucher specimens were deposited in the herbaria of the Institute of Biosciences, University of São Paulo (SPF) and Feira de Santana State University (HUEFS). The fruits collected were left under the shade until dehiscence and the seeds released were kept in a freezer.

Seeds were dried in an oven at 80°C for 48 h and ground. The polysaccharides were extracted from 100 mg of dry seed powder with distilled water at 80°C for 3 h. After extraction, the supernatant was collected by centrifugation (13 000 ***g*** for 7 min), the extraction procedure was repeated three times and the supernatants of each extraction were combined and precipitated with 3 vols of EtOH. After 15 h at −18°C, the precipitate was collected by centrifugation (13 000 ***g*** at 5°C for 5 min). The residues were re-suspended in hot water and freeze dried.

Acid hydrolysis of the polysaccharides was performed by a pre-incubation of 10 mg of the freeze-dried material in 100 μl of 72% H_2SO_4 at 30°C for 45 min followed by dilution to 1.7 ml with distilled water and hydrolysis in autoclave for 1 h at 120°C (Buhl and Harris, 1945; Saeman et al., 1945). After hydrolysis, the solution was centrifuged (13 000 ***g*** for 15 min) and the supernatants were neutralized with NaOH (50%), and desalted in anionic (Dowex 1×8–200) and cationic (Dowex 50×8–200) ion exchange columns. The resulting monosaccharides were analyzed by High Performance Anion Exchange Chromatography (HPAEC) on a CarboPac PA10 anion-exchange column (250×4 mm; Dionex Corporation, Sunnyvale, CA, USA), by isocratic elution with 20 mM NaOH for 30 min. Sugars were detected by a pulsed amperometric detector (PAD/Dionex). Detector responses were determined using the appropriate standards, these being used to calculate correction factors. Data are expressed as percentages (w/w) of each neutral monosaccharide.

Multivariate analysis was carried out using the percentages of the distribution of the monosaccharides

released after hydrolysis of the polysaccharides as characters and the seed samples analyzed as Operational Taxonomic Unities (OTUs). The software NTSYS-pc (Crisci and Armengol, 1983) was used for the determination of Euclidean distances and Unweighted Pair Group Method with Arithmetic Averages (UPGMA) cluster analysis. The significance of the differences observed between the distributions of the monosaccharides from the pairs of genera *Callisthene*/*Qualea* and *Salvertia*/*Vochysia* was evaluated by Analysis of Variance (ANOVA).

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