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Rachis of the genus *Paspalum* L. (Poaceae: Panicoideae: Paniceae): Anatomy and taxonomic significance of the primary branches of the inflorescences

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Abstract

Infrageneric classification of *Paspalum* is mainly based on characters of the inflorescence and spikelets. Some of the inflorescence characters usually used are the width and external morphology of the rachises of the racemes. Nevertheless, morphological terminology used in the literature is frequently imprecise. We examine the internal structure of the rachises of the racemes in *Paspalum* to: (a) compare it with the anatomy of a vegetative culm, (b) precisely describe its variation within the genus to search for features that could be used in taxonomy or phylogeny. Species representative of all subgenera and informal groups were studied. Serial transversal sections were made and analyzed using light microscopy.

Many distinctive characters from the central keel and lateral wings allow to distinguish six anatomical types of rachises: Type I is the most frequent in the genus, being present in species of all subgenera; Type II characterizes Conjugata, Dissecta and Disticha groups; Type III is exclusive of subgenus *Harpostachys*; Type IV is common in *Ceresia* subgenus and it is also present in two species of Gardneriana group and in *Paspalum guttatum* of Erinatha group; Type V is present in Bonplandiana and Racemosa groups, and Type VI is exclusive of *Paspalum falcatum* of Falcata group. Rachises of the racemes are undoubtedly caulinar structures although many species present flat rachises, with vascular bundles arranged in one only row and with abundant photosynthetic tissues. This study permits to differentiate, by means of anatomical characters, rachises that are morphologically similar or undistinguishable. Some anatomical types of rachises are related to taxonomic groups or subgenera, stressing their taxonomic value. Using anatomical characters of the rachis of the *Paspalum* raceme can improve phylogenetic analyses.

Keywords: *Paspalum*; Poaceae; Inflorescence; Rachis; Anatomy; Taxonomy

Introduction

Paspalum L. is one of the largest genus of the Poaceae, with about 330 species (Zuloaga and Morrone, 2005) of which 308 grow in tropical, subtropical and template

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regions of America (Zuloaga et al., 2003). The species prevail in open fields but also are found in a variety of habitats as sandy coast, marshes, forested or brushy slopes, occurring from sea level to 4600 m elevation in the Andes, such as *Paspalum pygmaeum* and *Paspalum candidum*.

The genus belongs to subfamily Panicoideae, tribe Paniceae, subtribe Paspalinae. Because of the large number of species and the morphological variation, *Paspalum* has been divided into subgenera, sections, or informal groups by diverse authors, based on characters of inflorescences and spikelets (Chase, 1929, unpublished; Cialdella et al., 1995; Clayton and Renvoize, 1986; Denham, 2005; Denham et al., 2002; Döll, 1877; Morrone et al., 1995, 1996, 2000, 2004; Nees van Esenbeck, 1829; Pilger, 1929, 1940; Rodríguez, 1992, 1998; Rua and Aliscioni, 2002; Zuloaga et al., 2004). Most of these authors recognize the informal groups established by Chase (1929). Zuloaga et al. (2004) accepted 4 subgenera: *Anachyris* (Nees) Chase, *Ceresia* (Pers.) Rchb., *Harpostachys* (Trin.) S. Denham and *Paspalum,* the latter with ca. 265 species distributed in 25 informal groups. While subgenera *Anachyris* (Morrone et al., 2000), *Ceresia*, including sections *Ceresia* and *Pectinata* (Denham et al., 2002), and *Harpostachys* (Denham and Zuloaga, 2006) seem to be monophyletic, relationships within species in subgenus *Paspalum* are controversial. Synapomorphies have been established for some of these informal groups: Notata (Zuloaga et al., 2004), Dissecta (Morrone et al., 1996), Racemosa (Morrone et al., 1995), Eriantha (Morrone et al., 2004), Bonplandiana (Cialdella et al., 1995); but others groups need to be studied.

Paspalum is distinguished by inflorescences with unilateral racemose branches, the spikelets are usually plano-convex, with the lower glume generally lacking, the lower flower and lower palea also generally absent, upper glume and lower lemma herbaceous to membranous, and the upper floret indurate or membranous, with the margins of the upper lemma inrolled over its palea. Regarding to the photosynthetic pathway, the whole genus is C_4, "panicoid type", with Kranz anatomy of the MS (X and MS-) subtype (Brown, 1977; Hattersley and Watson, 1976; Ellis, 1977) and NADP-me biochemical type, characterized by the presence of a mestomatic Kranz sheath with centrifugal specialized chloroplasts around the vascular bundles direct in contact with the metaxylem vessels. The basic chromosome number in *Paspalum* is $x = 10$ and its species present sexual and apomictic reproduction.

Inflorescences in *Paspalum* are commonly, but not always, truncate (i.e. without main florescence) and homocladic (i.e. all flowers sustained by axes of the same branching order), composed exclusively of long paraclades or racemes (Rua and Weberling, 1995), which are primary branches on a main axis. Racemes are typically unilateral and can end in a spikelet or in a naked point. Inflorescences vary in number of racemes (1–60 or more), the arrangement of them along the main axis (solitary, conjugate, digitate or alternate) and the development of the rachis of the racemes (triquetrous or flat). A triquetrous rachis is the most frequent condition in the genus, but in numerous species the rachis of the racemes becomes flat and develops lateral "wings". These wings can be foliaceous, membranaceous or hyaline.

The presence of a flat or a winged rachis is one of the major characters considered for the taxonomy of *Paspalum*. Thus, subgenus *Ceresia* and Racemosa, Bonplandiana, Disticha, Dissecta, Fasciculata and Falcata groups of subgenus *Paspalum* are identify by the winged rachis of the racemes. In subgenus *Anachyris* the rachises are triquetrous; in *Harpostachys* there are many species with a flat rachis; and in the remaining groups of *Paspalum* rachises are triquetrous with some isolated species with a flat or narrowly broad rachis (i.e. *Paspalum gardnerianum*, *Paspalum erianthum*, *Paspalum fimbriatum*). Summarizing, three of a total of four subgenera present species with winged rachises.

The presence of winged or foliaceous rachises is not an exclusive feature of *Paspalum*, being found also in other genera of Paniceae, as *Baptorhachis* Clayton and Renvoize, *Chlorocalymma* Clayton, *Echinolaena* Desv., *Mesosetum* Steud., *Ophiochloa* Filgueiras, Davidse and Zuloaga, *Thrasyopsis* Parodi, and *Trachys* Pers.

Despite the importance the rachis of the racemes has in the taxonomy of the genus *Paspalum*, the terminology used in taxonomic reviews to describe the rachis is frequently imprecise or conflicting.

While external morphology of the inflorescence and its development have been much considered in Poaceae as sources of diagnostic characters and for phylogenetic inferences, there is a reduced number of studies concerned with the anatomy of the inflorescences. Studies about the anatomy of culms were made in Poaceae, but only describing the distal part of the flowering axis, below the inflorescence (Arriaga and Sánchez, 1992; Sánchez, 1979, 1981a, b). Arriaga (1990) described the development of the Kranz structure in the main axis and branches of *Eriochloa* Kunth. inflorescences. Ramos et al. (2002) studied the reproductive shoots of *Bromus auleticus* Trin. ex Ness and outlined the anatomical variations among them.

With respect to the anatomy of *Paspalum*, many studies were focussed with taxonomic purposes on the internal structure of the leaves including anatomical characters of this organ (Aliscioni and Arriaga, 1998; Cialdella et al., 1995; Denham, 2005; Ellis, 1974; Morrone et al. 1995, 1996, 2000; Türpe, 1967). The anatomy of culms was described for *Paspalum commersonii* Lam. (= *Paspalum scrobiculatum* var. *commersonii*