

Inflorescence patterns in the woody Brazilian genus *Diplusodon* (Lythraceae)

Taciana B. Cavalcanti^{a,*}, Gabriel H. Rua^{b,c}

^a*Departamento de Botânica, Embrapa Recursos Genéticos e Biotecnologia, PqEB, Final W-5 Norte, Caixa Postal 02372, CEP 70770-900, Brasília, DF, Brazil*

^b*Cátedra de Botánica Agrícola, Facultad de Agronomía, Universidad de Buenos Aires, Buenos Aires, Argentina*

^c*Investigador Adjunto, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina*

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Abstract

The Brazilian genus *Diplusodon* is the second largest genus within Lythraceae. Their 85 species occupy diverse habitats within the ‘cerrado’ vegetation, and range from shrubs and treelets to dwarf, xylopodium-bearing subshrubs. A comparative-morphological survey of their inflorescence structures using Trollian typology is here presented, as well as some evolutionary considerations drawn from mapping inflorescence characters onto a preliminary phylogeny. The inflorescences of *Diplusodon* are mostly polytelic, ranging from single racemes to more or less complex double-, triple-, and multiple-racemes. Frondose, compound racemes are plesiomorphic within the genus. Nevertheless, an array of derived features has been found among their species, including production of lateral cymes, proliferation of the main axis, diverse patterns of internode elongation, reduction of subtending leaves to bracts, development of accessory branches, paedomorphic flowering, and, in three species, reversion to monotelic.

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Introduction

The woody genus *Diplusodon* is one of eight Brazilian genera of the mostly pantropical family Lythraceae, and, with 85 species, is the second largest genus in the family. Their species occupy diverse habitats within the ‘cerrado’ biome, and range from shrubs and treelets to dwarf, xylopodium-bearing subshrubs. Since 1985, expeditions in Brazil have been undertaken to increase the knowledge of the Brazilian Lythraceae (Cavalcanti,

1987, 1988, 1990, 2004; Cavalcanti and Graham, 2005; Graham and Cavalcanti, 2001), and they found the basis for the taxonomic revision of the genus *Diplusodon* (Cavalcanti, 1995). This contribution attempts to further expand the current knowledge of the genus by surveying inflorescence patterns and their variations, and discussing inflorescence diversification in the light of available phylogenetic data.

Materials and methods

Inflorescences of all species of *Diplusodon* were dissected and observed using a standard stereoscopic

*Corresponding author. Tel.: +55 61 3448 4651; fax: +55 61 3340 3668.

E-mail address: taciana@cenargen.embrapa.br (T.B. Cavalcanti).

microscope. Observations were made mainly on herbarium material (Appendix A), although living plants were also examined when available. Inflorescence descriptions were based on the typological system proposed by Troll (1964, 1969), see also Weberling (1965, 1988, 1989), Weberling et al. (1993), and the used terminology was according to it (see a glossary to Trollian terms and some another descriptive terms that were used in Appendix B). Inflorescence characters were mapped onto topologies representing preliminary phylogenetic hypotheses (Cavalcanti et al., unpublished), in order to assess their putative evolution within the genus.

Results

Comparative inflorescence morphology

In most species of *Diplusodon* the synflorescences are polytelic (see below). Both simple (Fig. 1A) and compound (Fig. 1B–D) synflorescences were found, i.e. synflorescences in which paracladia (hereafter ‘Pc’) do or do not develop below the main florescence (MF). Leaves of *Diplusodon* are always opposite, and normally paracladia arise from both axils in each node.

Variations in relative development of the enrichment and the inhibition zones along the inflorescence axes

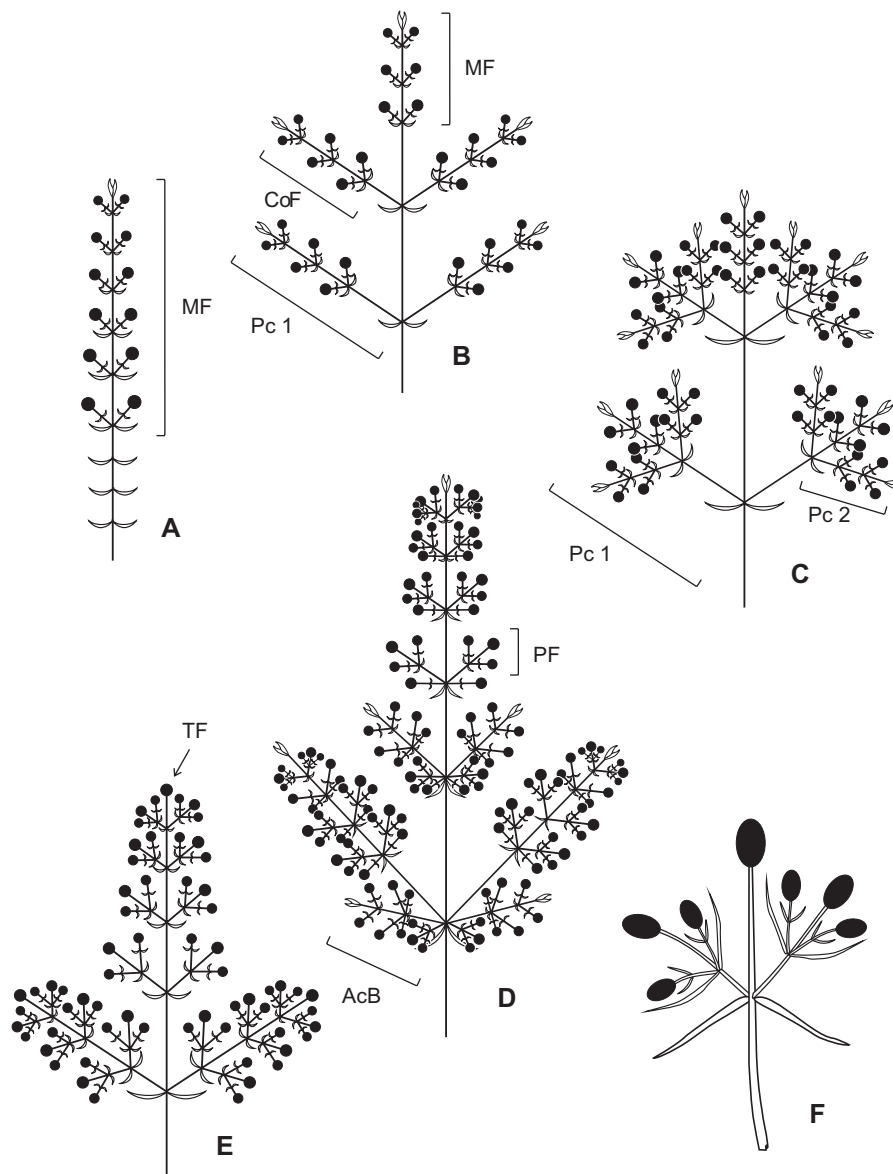


Fig. 1. Inflorescence in *Diplusodon*: (A) raceme; (B) double-raceme; (C) triple-raceme; (D) double-thyrse; (E) double-thyrsoid; (F) dichasial cyme. AcB – accessory branch; Pc 1 – paracladium of first order; Pc 2 – paracladium of second order; MF – main florescence; PF – parcial florescence; TF – terminal flower.

(Troll, 1964) are largely responsible for inflorescence diversity in *Diplusodon*. Troll (1970) has already pointed out that in some species, as *Diplusodon thymifolius* and *Diplusodon virgatus* var. *virgatus*, the MF remains very small in relation to the paracladial zone, while in other ones, such as *Diplusodon villosissimus* and *Diplusodon villosus*, the MF predominates over the paracladial zone, although this can be well developed too. Although it could not be tested under homogeneous environmental conditions for all species, the extent to which paracladia develop seems to be species specific to some degree. Indeed, individuals belonging to separate species growing together in a same ‘campo-rupestre’ area behave differently regarding number and extent of Pc development.

In some species of *Diplusodon*, flowering can occur precociously after regrowth, so that flowering synflorescences 3–10 cm tall stick out from the ground whereas the rest of the plant remains as an underground xylopodium. This is the case with *Diplusodon ciliiflorus*, a population of which was found in full flowering in ‘campo-rupestre’ areas around Diamantina (state of Minas Gerais, Brazil), a region subject to frequent fires.

As well as the relative extent of branching, the branching degree of the synflorescences (i.e. the maximum branching order the paracladia are able to reach) varies considerably within the genus. Double-racemes (first order Pc only, Fig. 1B) are found besides triple-racemes (Pc of first and second branching order, Fig. 1C), and multiple-racemes (three or more Pc orders). This character is rather polymorphic in most species, and seems to be associated with environmental conditions.

The MF is always present in the polytelic synflorescences of *Diplusodon*. Truncate synflorescences without MF have been so far not found within the genus, although abortion of the MF was occasionally observed in isolated individuals of different species. Besides the paracladia, the MF itself can show a good deal of variation. In most species of *Diplusodon*, the MF are racemes, i.e. they are composed of an indeterminate, auxotelic axis bearing single lateral flowers (Fig. 1A–C). Nevertheless, as the floral axes of *Diplusodon* are provided with two prophylls each, additional flowers can develop in some species from the axils of these prophylls, producing dichasial cymes. As a result, the florescences become thyrses (Fig. 1D), as occurs in *Diplusodon ulei* and *Diplusodon bradei*.

Within the domain of the florescence, another source of variation is the relative length of pedicels (see below), so that the florescences can be racemes (sometimes spike-like racemes, with reduced pedicels ca. 1 mm long) to true spikes when the flowers are sessile, as for example in *Diplusodon alatus* (Fig. 2A). Proliferation of the main axis beyond the MF was observed in *Diplusodon glaucescens*, *Diplusodon rotundifolius*

(Fig. 2B) and *Diplusodon sordidus*, so that the same apical meristem can produce successive synflorescences during several growing seasons.

Within each florescence, anthesis occurs always from the base to the apex (acropetally), so recapitulating the sequence of floral differentiation, as generally expected in such structures (cf. Sell, 1980). Secondary alterations of such a sequence have been so far not noticed. Flowering of MF and coflorescences is synchronous.

In addition to the polytelic type, which has been mentioned as the general pattern for *Diplusodon* and other Lythraceae (Graham et al., 1994; Weberling, 1988), three species were found, i.e. *Diplusodon nitidus*, *Diplusodon ovatus* and *Diplusodon panniculatus*, which possess monotelic synflorescences, i.e. the apical meristem of the main axis produces a terminal flower, and this behavior is reproduced by each paracladium below it (Figs. 1E, 3A–D). In these inflorescences, the differentiation, development, and anthesis of the terminal flowers always precede those of paracladia, whereas paracladia of the same branching order develop basipetally. The distal paracladia (‘short paracladia’, cf. Troll, 1965; Weberling et al., 1993) of such inflorescences are cymose-dichasial, so that the whole structure is a thyrsoid-like inflorescence with a terminal flower, hence a ‘thyrsoid’ (Briggs and Johnson, 1979; Troll, 1969; Weberling, 1988, 1989). Such cymose short paracladia are initially triads, but they are able to produce further lateral flowers in the axils of the two prophylls of each new axis (Fig. 1F). A similar behavior occurs in the partial florescences of *D. bradei* and *Diplusodon petiolatus*, two species with polytelic synflorescences, where very short axes continuously produce flowers from the prophyllar axils, resulting in dense glomerules.

An additional feature of the inflorescences of some species of *Diplusodon*, i.e. *D. virgatus* var. *virgatus* (Fig. 2C), *D. ulei* (Fig. 2D), *D. bradei*, and *D. petiolatus*, is the presence of accessory branches (AcB) that are originated from serial buds located immediately below the main paracladium buds (Fig. 1D). In *D. bradei* and *D. petiolatus*, they can reach up to the third branching order and can form both solitary flowers and dichasial cymes of variable branching order, as occurs in the regular paracladia. In *D. ulei*, accessory branching was also observed within the florescence domain, so that axillary cymes (parcial florescences-PF) are generally accompanied by additional solitary flowers (Fig. 2D).

Bracts, prophylls, and pedicels

Inflorescence foliation shows a considerable variation within *Diplusodon*, ranging from completely frondose

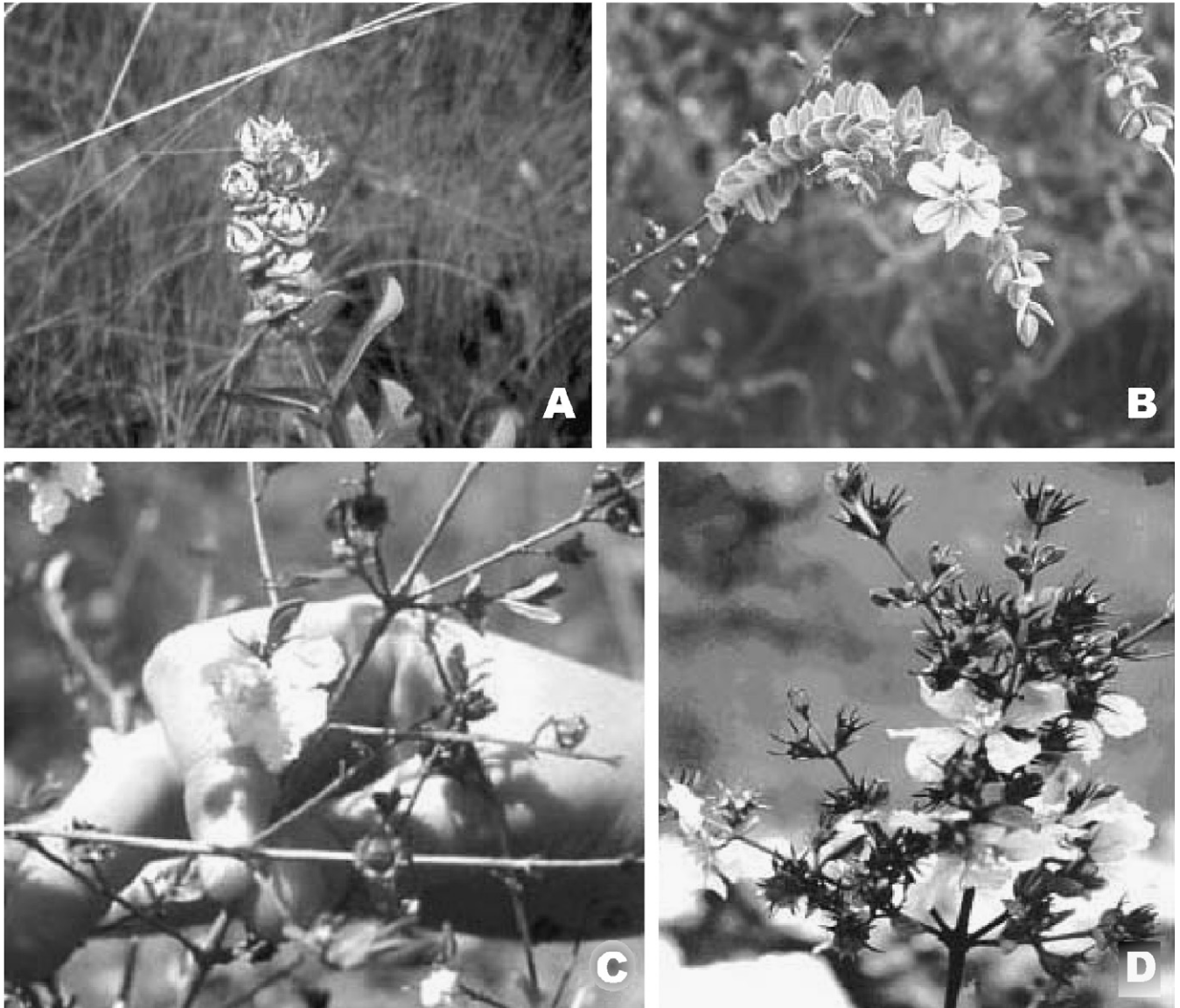


Fig. 2. Some inflorescence features in species of *Diplusodon*: (A) spike of *D. alatus*; (B) proliferation of the main axis beyond the main florescence in *D. rotundifolius*; (C) accessory branch in *D. virgatus* var. *virgatus*; (D) accessory branch in *D. ulei*.

through frondose–bracteose to wholly bracteose inflorescences. In all species of *Diplusodon* with simple synflorescences they are frondose, whereas species with compound synflorescences can have either frondose, frondose–bracteose, and, not so often, bracteose inflorescences, as occurs in *D. panniculatus* (Fig. 3A), *D. bradei* and *Diplusodon ramosissimus*, among others. Bracteose inflorescences show a sharp disruption between the flowering and the vegetative regions, as leaf primordia suddenly shift from foliage leaf to bract production.

Floral axes are always provided of a pair of prophylls, which can be opposite or subopposite, and in the majority of cases distinct in form from the foliage leaves and from the bracts. They are extremely variable in form

and indument showing the same diversity as foliage leaves and bracts.

The prophyllar node divides the pedicel in a proximal portion or ‘hypopodium’ (the ‘peduncle’ of Briggs and Johnson, 1979) and a distal portion or ‘epipodium’ (the ‘anthopodium’ of Briggs and Johnson, 1979) (Fig. 4A). When the prophylls are subopposite, a short mesopodium occurs between them. In *Diplusodon*, the relative length of hypopodium and epipodium is highly variable, and has taxonomic value (Cavalcanti, 1995). Frequently the hypopodium, the epipodium or both remain undeveloped rather than being elongated, so that the pedicel is respectively composed of the epipodium (Fig. 4B) or the hypopodium (Fig. 4C) only, or the flowers are sessile (Fig. 4D).

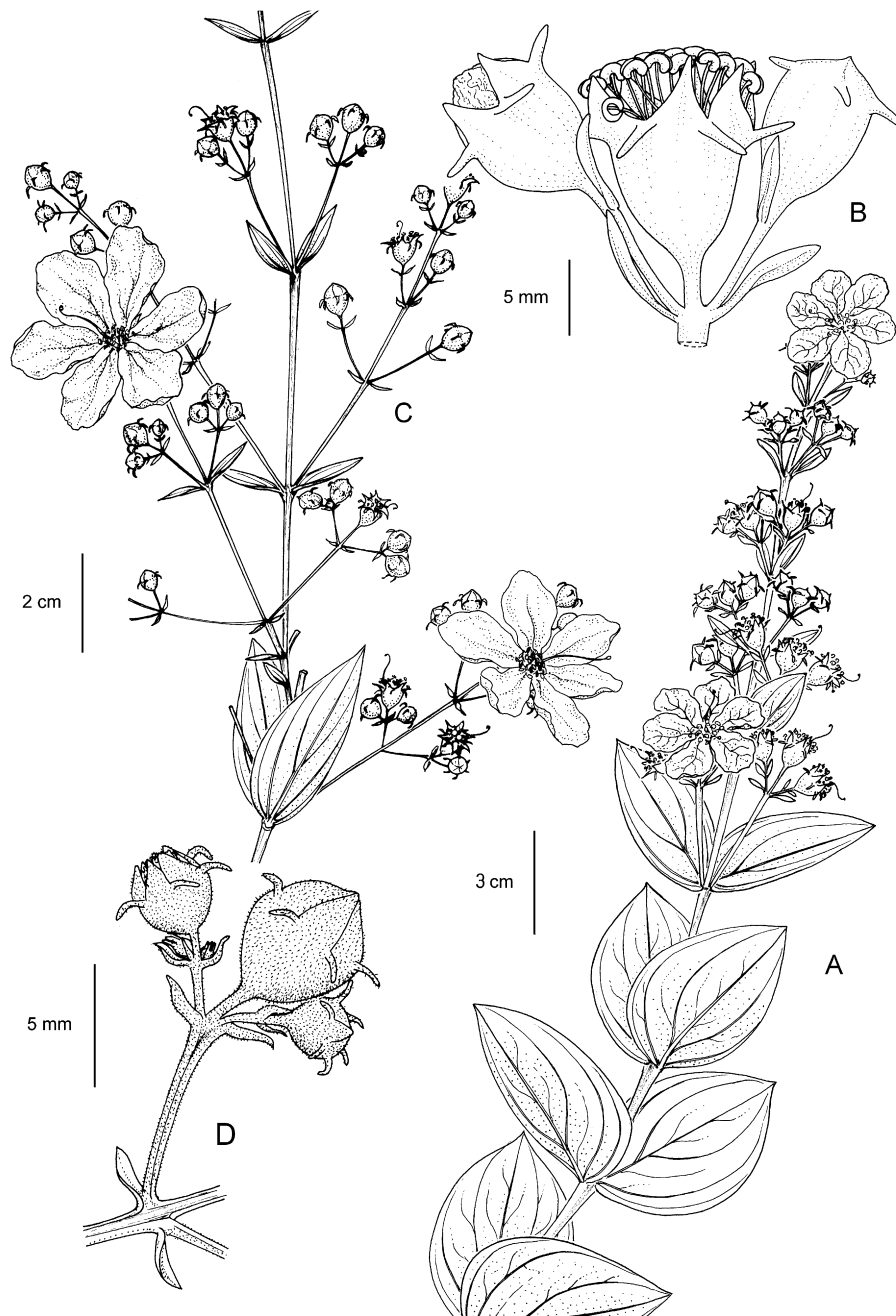


Fig. 3. Monotelic inflorescences in species of *Diplusodon*. (A, B). *D. panniculatus*: (A) flowering branch; (B) detail of a cyme (from Mori et al. 16947, CEN). (C, D). *D. ovatus*: (C) flowering branch; (D) detail of the terminal flower and two distal lateral ones (from Hatschbach & Koczicki 33061, MBM).

Plant architecture and synflorescence arrangement

All species of *Diplusodon* are woody perennials with rhythmic, seasonally growth, with a resting period during the dry season (May–September in Central Brazil). Most of them are subshrubs or shrubs ranging from a few centimeters to ca. 3 m tall, and showing a variable degree of branching. A few species are treelets 2–4 m tall. In all cases, synflorescence axes develop from

innovation buds located immediately below the flowering shoot that died at the end of the preceding growth season. In most species only the distal, flowering region of such innovation axes dies at the end of the growing season, whereas the proximal, vegetative portion remain as a constructional axis (cf. Bell, 1994), i.e. it becomes part of the plant architecture. Their most distal axillary buds will produce the innovation shoots of the next growth season. In contrast with them, there is a group of

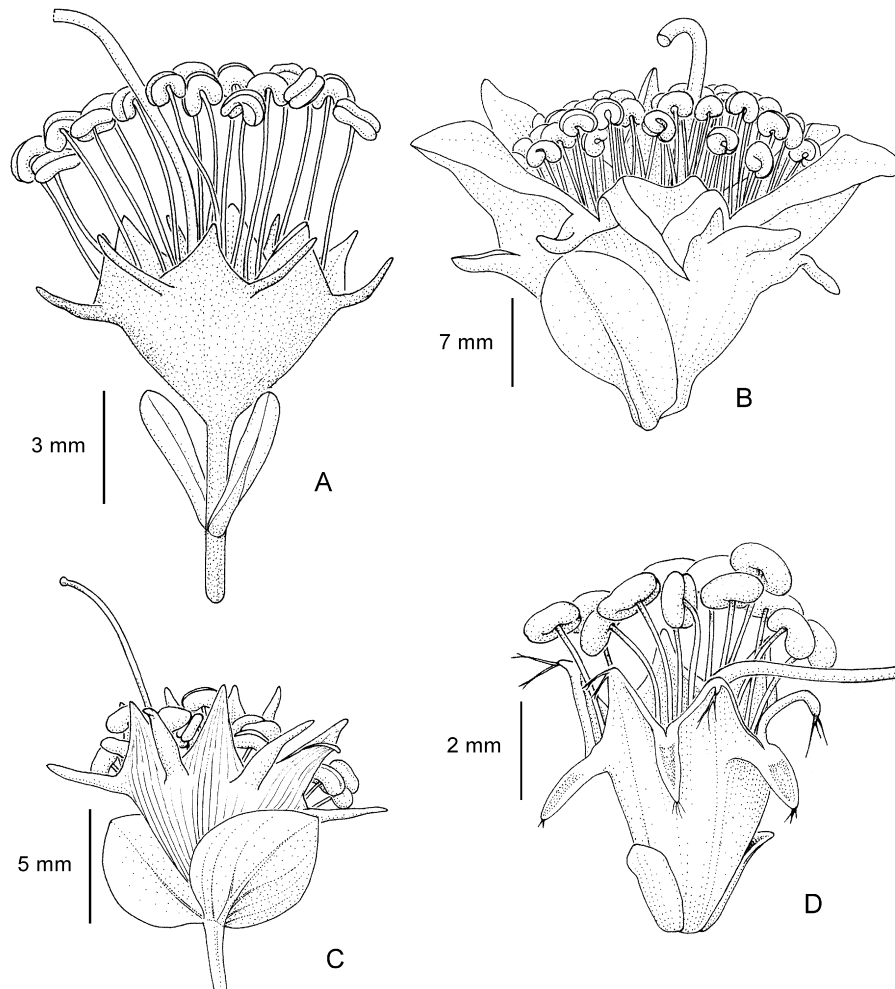


Fig. 4. Variation in flowers, pedicels and prophylls within *Diplusodon*: (A) *D. epilobioides*; (B) *D. alatus*; (C) *D. glaucescens*; (D) *D. helianthemifolius* var. *helianthemifolius*.

species in which the basal portion of the plant forms an underground xylopodium, from which innovation shoots arise. In these cases, the whole synflorescence axis dies at the end of the growth season, with exception of the very base, which becomes part of the xylopodium and bears the innovation buds for the next growth season.

Phylogeny and character mapping

The phylogeny of *Diplusodon* has been hitherto poorly explored. Nevertheless, phylogenetic analyses of the genus based on both morphological and molecular data (Cavalcanti et al., unpublished) are currently being carried out. Furthermore, the family-level phylogenetic analysis by Graham et al. (2005) provides some information on outgroup relationships.

The sister group of *Diplusodon* seems to be *Lourtella* (Graham et al., 2005), a woody monotypic genus from Peru and Bolivia with thyrse inflorescences. The next

most related genus is the tropical South American *Physocalymma*, which includes trees with leafless double- or triple-racemes. When characters from the inflorescence are mapped onto the topologies resulted from morphologic and molecular analyses, it becomes evident that frondose, compound racemes are plesiomorphic within the genus. Cymose branching, accessory paracladia, bracteose inflorescences, proliferating inflorescences, pedicel reduction, paedomorphic flowering and, remarkably, monotely seem to have been derived several times during the evolutionary history of the genus.

Discussion

Monotely and polytely in *Diplusodon*

As stated above, most genera of Lythraceae, including *Diplusodon*, have polytelic synflorescences (Graham

et al., 1994; Weberling, 1988), which represents the plesiomorphic condition of the family (Graham et al., 2005). Six genera, *Duabanga*, *Sonneratia*, *Punica*, *Lawsonia*, *Lagerstroemia* and *Galpinia*, have monotelic inflorescences, a condition that seems to have been evolved at least four times within the family (Graham et al., 2005). Secondary monotelic synflorescences are here reported for three species of *Diplusodon*, i.e. *D. nitidus*, *D. panniculatus* (Fig. 3A and B) and *D. ovatus* (Fig. 3C and D), which represent one or more additional transitions from polytely to monotely. This fact certainly challenges the general view of polytelic inflorescences as derived from monotelic ones (Sell, 1969, 1976; Weberling, 1985, 1989). Such transition has been hypothesized to be the outcome of a rather complex evolutionary process, involving the specialization of distal paracladia (homogenization) together with the onset of acropetal flowering (racemization) and the loss of the terminal flower (truncation) (Sell, 1969, 1976). Thus, re-gain of monotely has been implicitly considered by classical morphologists to be a very improbable evolutionary event. Nevertheless, current evidence from developmental genetics suggests the transition from monotely to polytely and vice versa is mediated by a simple regulatory genetic system (Angenent et al., 2005; Kellogg, 2000; Reinhardt and Kuhlemeier, 2002), so that a single mutation in the proper regulatory gene could suffice to explain the multiple reversions to monotely in Lythraceae.

Paedomorphic flowering

Paedomorphosis takes place when adults of one species resemble juveniles of their ancestors (Raff and Wray, 1989). It can be the morphological expression of at least three different forms of heterochrony (Alberch et al., 1979; Raff and Wray, 1989, and references therein). Among them, ‘progenesis’ occurs when reproductive maturation is accelerated while somatic development remains the same. Plants are modular organisms; thus developmental terms usually refer to particular meristems rather than whole organisms (Porras and Muñoz, 2000, and references therein). *Diplusodon ciliiflorus* and *D. pygmaeus* are able to flower with a minimal production of vegetative growth. Such paedomorphic flowering is the result of an earlier initiation of the inflorescence development with respect to related species, and the extent to which the onset of the reproductive phase is anticipated seems to be controlled by environmental factors, as fire disturbances. A similar behavior has been observed in other plants of the campos rupestres and cerrados, for instance with species of *Euphorbia* (Cordeiro, 1986) and *Camarea* (Mamede, 1988).

Accessory branches

As multiple buds occur in the leaf axils, accessory branches can freely develop. In the domain of the inflorescence, they usually represent additional paracladia that develop after the main inflorescence branching process has taken place. Accessory branching has been described in several families of plants and, according to Weberling (1988), it is very common in Lythraceae. Nevertheless, its occurrence in species of *Diplusodon* is reported here for the first time. Accessory branching contributes to the inflorescence enrichment (Weberling, 1988), increasing the total number of flowers a given inflorescence is able to produce.

Inflorescence evolution and diversification

In spite of the available phylogenies being preliminary, some hypotheses can be suggested regarding inflorescence evolution and diversification within *Diplusodon*. The plesiomorphic inflorescence pattern, i.e. frondose or frondose-bracteose compound racemes, seems to have been highly conserved. Alternative patterns, as thyrses and thyrsoids, are restricted to a few species.

Changes involving meristem-identity genes (Angenent et al., 2005; Coen and Nugent, 1994) are probably responsible for several striking features in inflorescences of some species of *Diplusodon*, such as the switch to monotely, the production of high-order lateral cymes, and the proliferation, i.e. the return to vegetative growth, of the apical meristem of the racemes. On the other hand, paedomorphic flowering seems to be the outcome of a change in flowering-time genes (Angenent et al., 2005; Coen and Nugent, 1994).

Another set of modifications involves variations in internodes elongation and in relative development of subtending leaves. At the time a shoot apical meristem is induced to flowering, some internodes, leaf primordia and axillary meristems are already differentiated, whereas the very meristematic apex remains undifferentiated. Both preformed and neoformed (after induction) internodes can either elongate or remain short. Differences in the distribution pattern of elongated and short internodes are largely responsible for striking variations in inflorescence appearance, yet without deep structural modifications. The same is true for the hypopodium/epipodium elongation pattern. The plesiomorphic condition of elongated internodes has been repeatedly lost during inflorescence evolution of *Diplusodon*, and reduced (strictly, not-elongated) internodes are widespread within the genus. In most radical cases, highly congested inflorescences arose.

Development of leaf primordia can be more or less altered after flowering induction, generally leading to

a gradual reduction of inflorescence leaves: the more incipient the development of a leaf primordium at induction, the less developed the resulting mature leaf. It seems to be the case of most species of *Diplusodon*, in which a gradual reduction from foliage leaves to bracts can be observed along the synflorescence main axis. The occurrence of strictly bracteose synflorescences is apomorphic within *Diplusodon*. In such synflorescences, the transition between foliage leaves and bracts is abrupt. Whether it results from a sudden suppression of pre-existing leaf primordia, or from the fact that the flowering region is entirely produced from previously undifferentiated meristematic tissues is so far to be explored.

Appendix A

Representative herbarium specimens of the species of *Diplusodon* Pohl (Lythraceae) examined for inflorescence analysis.

- Diplusodon adpressipilus* Lourteig-Cavalcanti et al. 3159 (CEN, MO);
Diplusodon aggregatifolius T.B.Cavalc.-Cavalcanti et al. 2320 (CEN, MO, NY);
Diplusodon alatus T.B.Cavalc.-Cavalcanti et al. 2507 (CEN, MO);
Diplusodon appendiculosus Lourteig-Cavalcanti et al. 3538 (CEN, SPF);
Diplusodon argenteus Lourteig-Cavalcanti et al. 3627 (CEN, MO);
Diplusodon argyrophyllus T.B.Cavalc.-Ganev 11 (SPF, HUEFS, K, NY);
Diplusodon astictus Lourteig-Cavalcanti et al. 3161 (CEN, MO);
Diplusodon bolivianus T.B.Cavalc. & S.A.Graham-Cavalcanti et al. 2381 (CEN, MO, NY);
Diplusodon bradei Pilg.-Cavalcanti et al. 2301 (CEN, MO);
Diplusodon burchellii Koehne-Cavalcanti et al. 1824 (CEN, MO);
Diplusodon buxifolius (Cham. & Schltdl.) DC.-Cavalcanti et al. 3100 (CEN);
Diplusodon canastrensis T.B.Cavalc.-Nakajima et al. 2694 (CEN, HUFU);
Diplusodon candollei Pohl ex DC.-Cavalcanti et al. 3130 (CEN, MO);
Diplusodon capitalensis T.B.Cavalc., Pereira-Silva et al. 7905 (CEN, MO);
Diplusodon capitatus (A.St.-Hil.) Koehne-Saint-Hilaire s.n. (P);
Diplusodon chapadensis T.B.Cavalc.-Cavalcanti et al. 2185 (CEN, K, MO, NY, RB, SPF);
Diplusodon ciliatiflorus T.B.Cavalc.-Cavalcanti et al. 1046 (CEN, K, NY, SPF, UB);
Diplusodon ciliiflorus Koehne-Cavalcanti et al. 253 (CEN, SPF);
Diplusodon cordifolius Lourteig-Cavalcanti et al. 3168 (CEN, MO);
Diplusodon cryptanthus T.B.Cavalc.-Cavalcante et al. 3509 (CEN, SPF);
Diplusodon decussatus Gardn.-Cavalcanti et al. 2248 (CEN);
Diplusodon divaricatus Pohl-Cavalcanti et al. 1686 (CEN, MO, NY);
Diplusodon epilobioides Mart. ex DC.-Cavalcanti et al. 3142 (CEN, MO);
Diplusodon ericoides Lourteig-Cavalcanti et al. 2721 (CEN, MO);
Diplusodon fastigiatus Lourteig-Cavalcanti et al. 3603 (CEN);
Diplusodon floribundus Pohl-Cavalcanti & Pereira-Silva 3728 (CEN);
Diplusodon foliosus (Koehne) T.B.Cavalc.-Cavalcanti et al. 3599 (CEN, MO);
Diplusodon glaucescens DC.-Cavalcanti et al. 2284 (CEN, MO, NY);
Diplusodon glaziovii Koehne-Cavalcanti et al. 2305 (CEN, MO, NY);
Diplusodon glocimarii T.B.Cavalc.-Cavalcanti et al. 2513 (CEN, MO, NY, RB);
Diplusodon gracilis Koehne-Cavalcanti et al. 3148 (CEN);
Diplusodon grahamae T.B.Cavalc.-Hatschbach & Barbosa 59326 (MBM);
Diplusodon hatschbachii Lourteig-Cavalcanti et al. 3757 (CEN);
Diplusodon helianthemifolius Mart. ex DC. var. *helianthemifolius*-Cavalcanti et al. 2296 (CEN, NY);
Diplusodon helianthemifolius var. *pemphoides* (DC.) Koehne-Cavalcanti et al. 230 (CEN, K, SPF);
Diplusodon heringeri Lourteig-Cavalcanti et al. 2205 (CEN, MO);
Diplusodon hexander Mart. ex DC.-Cavalcanti et al. 2293 (CEN, NY);
Diplusodon hirsutus (Cham. & Schltdl.) DC.-Cavalcanti et al. 2270 (CEN, MO, NY);
Diplusodon imbricatus Pohl-Cavalcanti et al. 2225 (CEN, MO, NY);
Diplusodon incanus Gardn.-Cavalcanti et al. 3616 (CEN, MO);
Diplusodon kielmeyeroides A.St.-Hil.-Cavalcanti et al. 2268 (CEN, MO, NY);
Diplusodon lanceolatus Pohl-Cavalcanti et al. 414 (CEN, NY, SPF);
Diplusodon leucocalycinus Lourteig-Cavalcanti et al. 2204 (CEN, MO);
Diplusodon longipes Koehne-Pereira-Silva et al. 4422 (CEN, MO, NY);
Diplusodon macrodon Koehne-Cavalcanti et al. 684 (CEN, MO, NY, SPF);

Diplusodon marginatus Pohl-Cavalcanti et al. 1000 (CEN, K, NY, SPF);
Diplusodon mattogrossensis T.B.Cavalc.-Ratter et al. 1574 (K, MO, NY);
Diplusodon microphyllus (Pohl)-Cavalcanti et al. 2581 (CEN, MO, NY);
Diplusodon minasensis Lourteig-Cavalcanti et al. 220 (CEN, K, NY, SPF);
Diplusodon mononeuros Pilg.-Cavalcanti et al. 3125 (CEN, MO);
Diplusodon myrsinites Mart. ex DC.-Cavalcanti et al. 3088 (CEN, MO);
Diplusodon nigricans Koehne-Barroso et al. 624 (CEN, P, UB);
Diplusodon nitidus Mart. ex DC.-Tameirão-Neto 4018 (CEN, BHCB);
Diplusodon oblongus Pohl-Cavalcanti et al. 2181 (CEN, MO, NY);
Diplusodon orbicularis Koehne-Cavalcanti et al. 2271 (CEN, MO, NY);
Diplusodon ovatus Pohl-Pohl 589 = D940 (W, BR, G, K, M, W);
Diplusodon panniculatus Koehne-Cavalcanti et al. 3649 (CEN, MO);
Diplusodon parvifolius Mart. ex DC.-Cavalcanti et al. 3141 (CEN, MO);
Diplusodon petiolatus (Koehne) T.B.Cavalc.-Cavalcanti et al. 2220 (CEN, MO);
Diplusodon plumbeus T.B.Cavalc.-Cavalcanti et al. 3648 (CEN, MO);
Diplusodon puberulus Koehne-Harley 21299 (CEPEC, K, NY, P, SPF);
Diplusodon punctatus Pohl-Cavalcanti et al. 1015 (CEN, K, NY, SPF);
Diplusodon pygmaeus T.B.Cavalc.-Cavalcanti et al. 2194 (CEN, MO, NY);
Diplusodon quintuplinervius (Nees) Koehne-Sevilha et al. 4229 (CEN);
Diplusodon ramosissimus Pohl-Cavalcanti et al. 2712 (CEN, MO);
Diplusodon retroimbricatus Koehne-Pereira-Silva et al. 5951 (CEN);
Diplusodon rosmarinifolius A.St.-Hil.-Cavalcanti et al. 2716 (CEN, MO);
Diplusodon rotundifolius Mart. ex DC.-Cavalcanti et al. 3122 (CEN, MO);
Diplusodon rupestris T.B.Cavalc.-Nakajima et al. 1941 (CEN, HUFU, MO);
Diplusodon saxatilis Lourteig-Hatschbach et al. 28923 (P, MBM, MO);
Diplusodon sessiliflorus Koehne-Cavalcanti et al. 1233 (CEN, SPF);
Diplusodon sigillatus Lourteig-Cavalcanti et al. 2198 (CEN, MO, NY);
Diplusodon sordidus Koehne-Cavalcanti et al. 662 (CEN, MO, NY);

Diplusodon speciosus (Kunth) DC.-Cavalcanti et al. 2237 (CEN, MO);
Diplusodon strigosus Pohl-Cavalcanti & Pereira-Silva 2719 (CEN, MO);
Diplusodon thymifolius Mart. ex DC.-Irwin et al. 31343 (NY);
Diplusodon thysanosepalus Lourteig & Sandwith-Glaziou 21548 a (P);
Diplusodon ulei var. *ciliatus* T.B.Cavalc.-Cavalcanti et al. 2456 (CEN);
Diplusodon ulei Koehne var. *ulei*-Cavalcanti et al. 2456 (CEN);
Diplusodon uninervius Koehne-Cavalcanti et al. 3126 (CEN, MO);
Diplusodon vidalii Lourteig-Cavalcanti et al. 3063 (CEN, MO);
Diplusodon villosissimus Pohl-Cavalcanti et al. 2584 (CEN, MO, NY);
Diplusodon villosus Pohl-Cavalcanti et al. 3579 (CEN, MO);
Diplusodon virgatus var. *virgatus* Pohl-Cavalcanti et al. 1432 (CEN, NY);
Diplusodon virgatus var. *occidentalis* T.B.Cavalc. & S.A.Graham-Hatschbach 31981 (MBM, MO)

Appendix B

Glossary of Trollian terms and another descriptive terms for inflorescences used across the text.

Auxotelic: Condition of vegetative axes in which apical meristems remain active.
Coflorescence: The florescences at the top of paracladia.
Cyme: Partial [lateral] inflorescence composed of a central flower accompanied of further flowers on the axil of prophylls, wich can bear further prophyllar flowers and so on.
Dichasium/dichasial: Cyme in which flowers axillary of both prohylls develop at each branching event/ Condition of such cymes.
Enrichment zone: Paracladial zone, portion of the synflorescence bearing [floriferous] paracladia.
Epipodium: First internode above the prophylls.
Florescence: Raceme- or thyrses-like inflorescence unit composed of an indeterminate axis bearing lateral flowers or lateral cymes (see). It is the minimal inflorescence unit in polytelic synflorescences.
Glomerule: Every globular, dense inflorescence unit, regardless of it branching pattern. Thus, glomerules can be dense cymes, panicles, etc.
Hypopodium: Portion of a lateral branch between its insertion and the [first] prophyllar node.
Inflorescence: Every shoot system bearing flowers.

Inhibition zone: Portion of the synflorescence, generally below the enrichment zone, in which the buds remain repressed.

Innovation buds/shoots: Lateral buds/shoots which [re]-produce whole synflorescences after a resting period.

Long paracladium: In certain inflorescences, each proximal paracladium bearing short paracladia as subunits.

MF: The florescence at the top of the synflorescence main axis.

Mesopodium: Internodium between the prophylls, when they are subopposite.

Monotelic: Synflorescence type in which the main axis is determinate as well as the paracladia, so that all axes bear terminal flowers.

Paracladium: Each lateral axis of the synflorescence [generally] repeating the structure of the main axis.

Polytelic: Synflorescence type in which the main axis is indeterminate as well as the paracladia, and the [lateral] flowers are grouped into florescences.

Proliferation: return of the apical meristem of an inflorescence to a vegetative condition, after production of lateral flowering branches.

Prophyll: Each of the two first leaves (in Dicots, Monocots have only one) of a lateral shoot, which are generally [sub] opposite and differ in form and position from the subsequent leaves.

Short paracladium: In certain inflorescences, each homogeneous paracladium locate along the distal portion of the main axis and repeated as subunits of the long paracladia.

Synflorescence: A system of floriferous branches composed of a main axis bearing either a terminal flower or a terminal florescence (see), and a variable number of paracladia that reproduces the pattern of the main axis. Synflorescences develop either from seedling apical buds or from innovation buds.

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