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ORIGINAL ARTICLE

Inflorescence diversity and evolution in the PCK Clade (Poaceae: Panicoideae: Paniceae)

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Abstract The PCK Clade, represented by six to nine genera, is a monophyletic group situated within the Paniceae tribe. The highly diverse inflorescences within the PCK Clade provide an interesting system for the study of morphological evolution and also may aid in better understanding its unclear systematics. The inflorescence structure of 110 members of the PCK Clade has been investigated. Inflorescences are polytelic showing different levels of truncation. At least 21 different inflorescence subtypes were identified. Fourteen variable inflorescence characters were found, among which some have supra-generic or infrageneric value and others are polymorphic. A key for the identification of inflorescence types is presented. Nine processes have been identified as responsible for inflorescence diversification. Highly branched inflorescences with different internode lengths are present in the basal genus whereas truncated inflorescence morphologies appear late in the history of the clade. The precise timing of morphological changes is impossible to assess until we have a well supported phylogeny for the PCK Clade.

Keywords PCK Clade · Grasses · Inflorescence morphology · Evolution · Typology · SEM

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Introduction

The Poaceae (grass) family is one of the most important groups among the angiosperms in terms of its morphological diversity, systematics, ecology and economic importance (Clayton and Renvoize 1986; Grass Phylogeny working Group 2001). The family includes about 10,000 species divided into 12 subfamilies and over 700 genera (Tzvelev 1989; Renvoize and Clayton, 1992; Watson and Dallwitz 1992; Jacobs et al. 1999; Grass Phylogeny working Group 2001). The grasses are widespread all over the world and are the principal component of human intake since among its species are sugar cane and cereal crops (such as maize, rice, oats, wheat, etc.) (Tzvelev 1989; Renvoize and Clayton 1992; Watson and Dallwitz 1992; Jacobs et al. 1999; Grass Phylogeny working Group 2001).

Morphologically, the grasses diverge from the rest of the monocots by having a unique fruit (caryopsis), a highly differentiated lateral embryo, the pollen wall without scrobiculi and a unique floral morphology. The typical grass flower consists of a pistil, three stamens and two lodicules (second whorl organs) subtended by a palea and a lemma (outer second whorl), the whole unit being known as a floret (Irish 1998; Schmidt and Ambrose 1998; Soreng and Davis 1998; Ambrose et al. 2000; Grass Phylogeny working Group 2001). A spikelet may bear one to forty florets subtended by two sterile bracts (the lower and upper glumes). The spikelets are placed on extensively variable inflorescence ramification systems, which were classically but inaccurately named as “spikes”, “spicate racemes” or “panicles”. The grass inflorescence is considered as a novel structure among the angiosperms and many authors have emphasized its agronomic, taxonomic and phylogenetic importance (Pensiero and Vegetti 2001; Rua 1993, 1996, 2003a, b; Vegetti and Anton 1995, 2000; Friedman and Harder 2005).

The PCK Clade is a well supported monophyletic group of grasses situated within the subfamily Panicoideae and more specifically inside the $x = 9$ clade of the Paniceae tribe (Gómez-Martinez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001; Giussani et al. 2001). All members of the PCK Clade are C_4 plants; the leaf anatomy reflects a PEP-ck physiology (*phosphoenol pyruvate carboxykinase*, PCK), which is a synapomorphy for the clade (Gómez-Martinez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001; Giussani et al. 2001). Also, species of the clade share a mucronate or aristulate upper lemma and different ornamentation patterns and textures of the upper anthecium (Morrone and Zuloaga 1992, 1993).

The PCK Clade is represented by six to nine genera [*Brachiaria* (Trin.) Griseb., *Chaetium* Nees, *Eccoptocarpha* Launert, *Eriochloa* Kunth, *Megathyrsus* (Pilg.) B.K. Simon and S.W.L. Jacobs, *Melinis* P. Beauv., *Thuarea* Pers., *Urochloa* P. Beauv. and *Yvesia* A. Camus] depending on the author of the revision (Clayton and Renvoize 1986; Frank 1998; Gómez-Martinez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001; Giussani et al. 2001; Torres González and Morton 2005). Among them, *Brachiaria* and *Urochloa* are the most important, in terms of number of species.

The *Brachiaria-Urochloa* complex includes about 100 species distributed across the Old and the New World (Frank 1998; Torres González and Morton 2005). The majority of the species are found in Tropical Africa, with some in America and Asia; the group is rare in Europe (Clayton and Renvoize 1982 1986; Watson and Dallwitz 1992; Morrone and Zuloaga 1992, 1993; Veldkamp 1996a, 2004; Frank 1998; Torres González and Morton 2005).

Other genera in the group have one or only a few species. *Thuarea* is paleotropical and represented by two species, *T. perrieri* A. Camus, an annual species from Madagascar and *T. involuta* (G. Forst.) R. Br. ex Sm., an important perennial weed that grows in Indomalesia, Northern Australia and New Guinea (Watson and Dallwitz 1992). *Yvesia* is monotypic, represented by the annual species *Y. madagascariensis* A. Camus, originally from Madagascar. *Eccoptocarpha* is also monotypic, containing only the annual caespitose species *E. obconiciventris* Launert, which is found in Tropical African savannas (Watson and Dallwitz 1992). *Chaetium* is an American genus with three perennial caespitose species found from México, Central America and Cuba, to Northern South America (Morrone et al. 1998). *Megathyrsus maximum* (Jacq.) B.K. Simon and S.W.L. Jacobs (also known as *Panicum maximum* Jacq. or *Urochloa maxima* (Jacq.) R.D. Webster) (Giussani et al. 2001; Aliscioni et al. 2003; Simon and Jacobs 2003) is an African forage species but also a weed, widely cultivated in tropical and subtropical regions around the World.

Eriochloa is a pantropical genus that includes about 25–30 annual and perennial species (Clayton and Renvoize 1986; Nicora and Rúgolo de Agrasar 1987; Arriaga 2000). *Melinis* is a paleotropical genus with about 12 annual or perennial species, among which one or two grow in South America and West India and the rest are found in South Africa and Madagascar (Clayton and Renvoize 1986; Nicora and Rúgolo de Agrasar 1987; Zizka 1988; Watson and Dallwitz 1992).

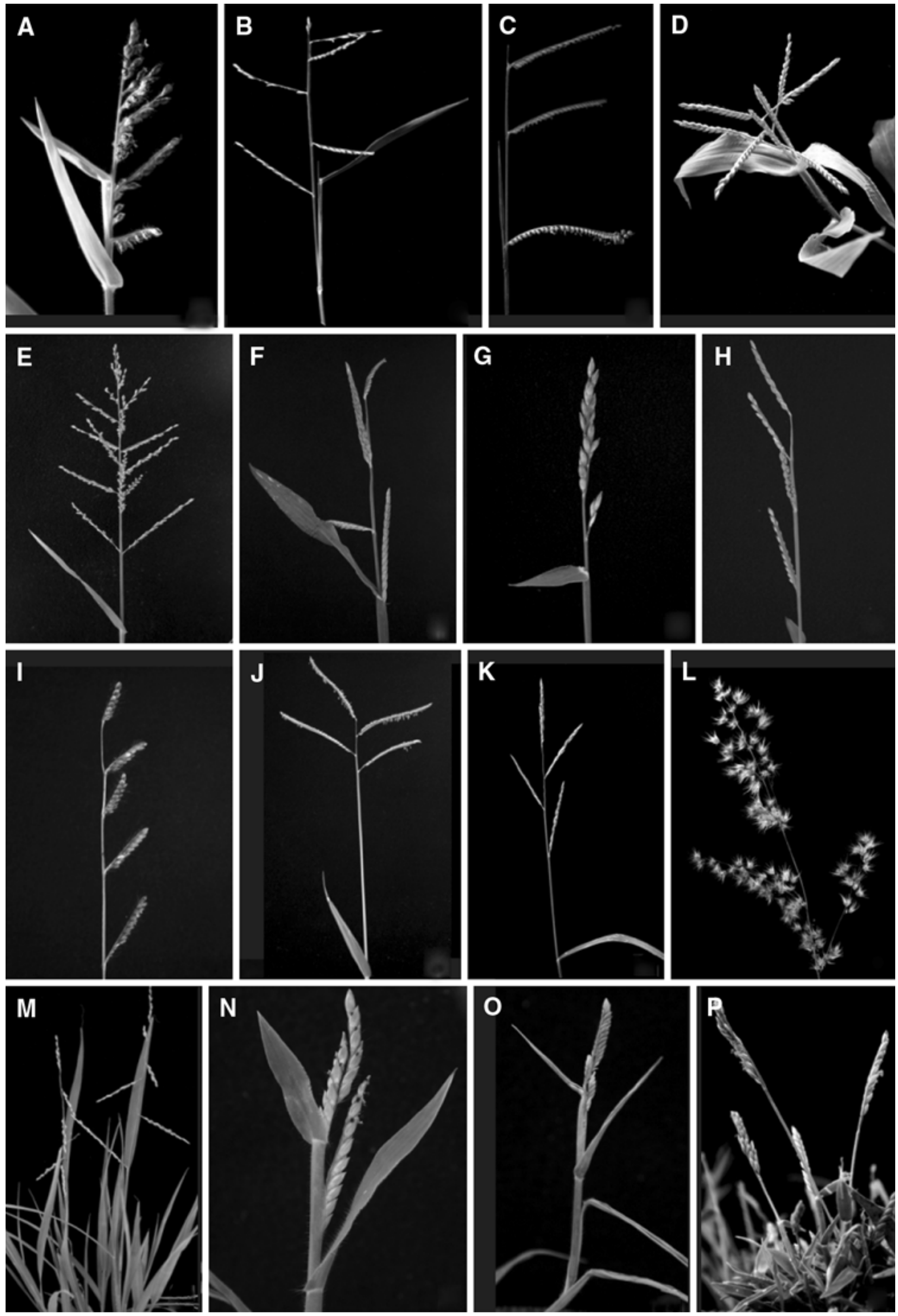
Despite efforts by many authors, the phylogeny of the PCK clade remains poorly resolved (Frank 1998; Gómez-Martinez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001; Giussani et al. 2001; Aliscioni et al. 2003; Torres González and Morton 2005). Moreover, the taxonomic delimitation of *Brachiaria* and *Urochloa* is not clear, with no evidence to support the monophyly of either genus (Beauvois 1812; Trinius 1826; Grisebach 1853; Nash 1903; Stapf 1920; Hughes 1923; Henrard 1941; Clayton and Renvoize 1982; Webster 1987, 1988; Davidse 1993; Morrone and Zuloaga 1991, 1992, 1993; Veldkamp 1996a, 1996b, 2004; Frank 1998; Nelson and Fernández 1998; López-Ferrari and Espejo Serna 2000; Giussani et al. 2001; Wunderlin and Hansen 2001; Sharp and Simon 2002; Zuloaga and Morrone 2003; Torres González and Morton 2005).

The PCK Clade exhibits extensive morphological variation. The inflorescences are highly diverse and several genera have unique inflorescence characters (Fig. 1). Within the clade, the inflorescence varies from lax panicles to simple inflorescences made up of a few racemes (Shaw and Smeins 1984; Clayton and Renvoize 1986; Davidse 1987; Nicora and Rúgolo de Agrasar 1987; Thompson et al. 1990; Morrone and Zuloaga 1992; Watson and Dallwitz 1992; Frank 1998; Morrone et al. 1998; Arriaga 2000).

The morphological diversity of the PCK Clade provides an interesting system for study the evolution of morphology and also may aid in better understanding of the phylogeny and taxonomy of the genera. Inflorescence characters have been used successfully in multiple studies, in which the main goals were to understand evolution and taxonomy (Rua 1993, 1996; Vegetti and Anton 1995, 2000; Kellogg 2000; Pensiero and Vegetti 2001; Doust and Kellogg 2002a, 2002b; Rua 2003a; Doust and Drinnan 2004; Kellogg et al. 2004; Bess et al. 2005; Liu et al. 2005).

In this study, we investigated inflorescence structure in the PCK Clade as a part of a larger project addressing morphological evolution in the clade using the study of adult morphology, development and its genetic bases (Reinheimer 2007). We had four goals: (1) to describe inflorescence structure in the PCK Clade; (2) to identify new characters to include in future phylogenetic studies,

Fig. 1 Mature inflorescence variation in the PCK Clade. **a** *U. mollis*; **b** *U. distachya*; **c** *U. ruziziensis*; **d** *U. lata*; **e** *U. xantholeuca*; **f** *U. plantaginea*; **g** *U. paucispicata*; **h** *U. platyphylla*; **i** *U. jubata*; **j** *U. mosambicensis*; **k** *E. punctata*; **l** *M. repens*; **m** *U. leucacrantha*; **n** *U. panicoides*; **o** *U. lachnantha*; **p** *B. eruciformis*



(3) to discuss their implications in relation to taxonomy in the clade and, (4) to suggest some processes responsible for inflorescence diversity in the group.

Materials and methods

Live plants from field collections and seed banks (CIAT) (cultivated at the greenhouse of the Agronomy School of the University of Litoral, Argentina) and herbarium specimens from eight different herbaria [CTS, J, LIL, SI, y SF, NY, MO, US (abbreviations from Index Herbariorum, ref.)] were studied under a stereoscopic microscope (Table 1). One-hundred and ten species were selected; among which 91 belong to the *Brachiaria*-*Urochloa* complex, while 19 are members of other genera in the clade (*Megathyrsus*, *Eriochloa*, *Melinis*, *Chaetium*, *Yvesia* and *Thuarea*). *Eccoptocarpha obconiciventris* was not

Table 1 Material studied and the most common synonyms for each species

Species	Synonyms	Voucher
Brachiaria ambigens Chiov. ex Chiarugi	_	Bojdan AB–300; Richards 23564 (MO)
Brachiaria chusqueoides (Hack.) Clayton	*Panicum chusqueoides* Hack	Gillett 13143 (MO)
Brachiaria clavipila (Chiov.) Robyns	*Panicum clavipilum* Chiov.	Milne-Redhead 2692 (US); Robison 3390 (US)
Brachiaria coronifera Pilg.	_	Schlieben 768 (US)
Brachiaria dimorpha A. Camus	_	13565 (LIL); Humbert 3879 (US)
Brachiaria epacridifolia (Stapf) A. Camus	*Panicum epacridifolium* Stapf	Bosser 2714 (MO)
Brachiaria eruciformis (Sm.) Griseb.	*Brachiaria erucaeformis* (Sm.) Griseb.; *Brachiaria isachne* (Roth ex Roem. and Schult.) Stapf; *Echinochloa eruciformis* (Sm.) Koch; *Echinochloa eruciformis* (Sm.) Rchb.; *Milium alternans* Bubani; *Moorochloa eruciformis* (Sm.) Veldkamp; *Panicum anisostachium* Bojer; *Panicum caucasicum* Trin.; *Panicum cruciforme* Sibth. ex Roem. ex Schult.; *Panicum eruciforme* Sm.; *Panicum isachne* Roth ex Roem. and Schult.; *Panicum isachne* var. *mexicana* Vasey ex Beal; *Panicum pubinode* Hochst. ex A. Rich.; *Panicum wightii* Nees	Velez I. 3039; Hitchcock 708 (LIL) (MO); 813806 (MO); 1906505 (MO); 2875544 (MO); 2876668 (MO); 2876671 (MO); 2876672 (MO); 2876789 (MO); 3940159 (MO); 3943569 (MO); 04984290 (MO); Abbas et Mokntar 95 (MO); Aellen 13/08/1948, 26/06/1948 (MO); Ament 482 (MO); Aretto 8529 (MO); Bosser 10549 (MO); Brain 944 (MO); Bush 390 (MO); Collenette 8375 (MO); Davidse 6708 (MO); Davidse et Simon 6451 (MO); De Wilde c.s. 5682, 6010 (MO); du Toit 522 (MO); Faden et Faden 74/739 (MO); Fasberg 39198, 59654 (MO); Giffen s/n (MO); Gonde 150, 287 (MO); Gould 15016 (MO); Herbst 46 (MO); Hunttey 14832 (MO); Jermy s/n (MO); Kemp 6650 (MO); Kiriken 448 (MO); Leistner 1243 (MO); Loutfy 1 Nov. 1976, 10312 (MO); Mackee 196, 30762, 42883, 43764 (MO); Pappi 1355, 2436 (MO); Parrignahi 5761 (MO); Phillipson 1050 (MO); Rattray 1649 (MO); Roemer s/n (MO); Russell 2744 (MO); Sáenz et Morrone 260 (MO) (SI); Sandwith 24 (MO); Schimper 1855, 1868 (MO); Smith 3072, 3375, 3497 (MO); Smook 1545, 2143, 2842, 6246, 6296, 6463, 622 (US); 8407 (US)
Brachiaria grossa Stapf	*Panicum nudiglume* var. *major* Rendle	Mitchell 14/22 (US)
Brachiaria humbertiana A. Camus	_	Decary 8546 (US); Humbert 14162 (US)
Brachiaria longiflora Clayton	_	Faden et Faden 71/807 (US); Robertson 6142 (US)
Brachiaria malacodes (Mez and K. Schum.) H. Scholz	*Brachiaria poaeoides* Stapf; *Moorochloa malacodes* (Mez and K. Schum.) Veldkamp; *Panicum malacodes* Mez and K. Schum.	Seydel 3141 (MO)
Brachiaria marlothii (Hack.) Stent	*Panicum marlothii Hack.*	Mennell Feb.1930 (US); Smook 2882 (US); Wilman s/n (US), 7109 (US)
Brachiaria ovalis Stapf	*Brachiaria glauca* Stapf; *Brachiaria somalensis* C.E. Hubb; *Panicum nudiglume* var. *major* Balf. f.; *Panicum ovale* R. Br.	Gilbert et Gilbert 2324 (MO)
Brachiaria pseudodichotoma Bosser	_	Phillipson et Rabesihanaka 3180 (US)
Brachiaria pubifolia Stapf	*Brachiaria xantholeuca* (Hack. ex Schinz) Stapf; *Panicum pubifolium* Mez; *Panicum pubifolium* Nash	Greenway et Kamuri 13529, 13940 (MO)
Brachiaria pungipes Clayton	_	Williamson 1865 (MO)
Brachiaria rugulosa Stapf	*Brachiaria umboensis* Stent and Rattray	Robertson 3238 (MO)
Brachiaria scalaris Pilg.	*Brachiaria heterocraspeda* (Peter) Pilg.; *Brachiaria pilgerana* H. Scholz; *Panicum heterocraspedum* Peter; *Panicum scalare* Mez; *Panicum scalarum* Schweinf.	Chongo 14 (LIL); Junifer et Gefford 201 (LIL); Schlieben 643, 768, 1031 (LIL); Bogdan AB-5306 (US); Webster McCallum 119 (US)
Brachiaria schoenfelderi C.E. Hubb. and Schweick.	*Moorochloa schoenfelderi* (C.E. Hubb. and Schweick.) Veldkamp	Dinter 7438 (US); Giess et al. 6438 (MO); Schuwrickedt 2051 (US); Volk s/n (US)

Table 1 continued

Species	Synonyms	Voucher
Brachiaria serrata (Thunb.) Stapf	*Brachiaria brachylopha* Stapf; *Holcus serratus* Thunb.; *Brachiaria serrata* var. *gossypina* (A. Rich.) Stapf; *Brachiaria serrata* var. *serrata* Stapf; *Panicum gossypinum* A. Rich.; *Panicum nigropedatum* var. *basipiliferum* Chiov.; *Panicum scopuliferum* Trin.; *Panicum serratum* (Thunb.) Spreng.; *Panicum serratum* var. *brachylophum* (Stapf) A. Chev.; *Panicum serratum* var. *gossypinum* Hack. ex T. Durand and Schinz; *Panicum serratum* var. *hirtum* Kuntze; *Panicum serratum* var. *holosericeum* Hack. ex T. Durand and Schinz; *Sorghum serratum* (Thunb.) Roem. and Schult.; *Tricholaena abbreviata* K. Schum. ex Engl.	Pappi 50, 460 (LIL); Bogdan AB-4165 (US); Godfrey SH-1571 (US); Golddamith 6/56 (US)
Brachiaria serrifolia (Hochst.) Stapf	*Panicum serrifolium* Hochst.	Aliyssimia 10 83 (US); HItchcock 24680 (US); Schimper 1083 (US)
Brachiaria stigmatisata (Mez) Stapf	*Panicum stigmatisatum* Mez	Menzirgen et Conert 343, 586 (LIL); Adam 15072 (US); Mensah SLUS/565 (US)
Brachiaria tsiafajavonensis A. Camus	_	Humbert 13447a, 13447b (LIL); Decary et al. s/n (US)
Brachiaria umbelata (Trin.) Clayton	*Panicum nossibense* Steud.; *Panicum umbellatum* subsp. *nossibense* (Steud.) A. Camus; *Panicum umbellatum* Trin.	Robinson 5365 (US); Vaughan A-11 (US)
Brachiaria umbralitis Napper	_	Hitchcock 25024 (US)
Brachiaria urocoides S.L.Chen and Y.X.Jin	_	Volk 501, 510 (US)
Chaetium bromoides (J. Presl) Benth. ex Hemsl.	*Berchtoldia bromoides* J. Presl; *Panicum berchtholdiae* Döll	Arséne 39359 (LIL); Hitchcock s/n (LIL); Pringle 11736 (LIL); Hitchcock 8440 (SI); Matuda et al. 29718 (SI)
Chaetium cubanum (C. Wright) Hitchc.	*Perotis cubana* C. Wright	Ekman 796 (LIL); Clark L. G. s/n (ISC)
Eriochloa aristata Vasey	*Eriochloa boxiana* Hitchc.; *Eriochloa punctata* var. *aristata* (Vasey) M.E. Jones	Warren 23060 (SI)
Eriochloa distachya Kunth	*Eriochloa tridentata* (Trin.) Kuhlm.; *Helopus brachystachys* Trin.; *Paspalum brachystachyum* (Trin.) Trin.; *Paspalum tridentatum* Trin.	Beck 6961 (SI); Killeen 244 (SI); Scolnik et Luti 738 (SI)
Eriochloa grandiflora (Trin.) Benth.	*Helopus grandiflorus* Trin.; *Paspalum ctenostachyum* Trin.	Dusén 16865 (SI); Fontana 117-7 (SI); Jorgensen 4783 (SI)
Eriochloa mollis (Michx.) Kunth	*Eriochloa michauxii* (Poir.) Hitchc.; *Eriochloa michauxii* var. Michauxii; *Panicum molle* Michx.	Fredholm 6097 (SI)
Eriochloa montevidensis Griseb.	*Eriochloa montevidensis* fo. *subcolorata* Hack.; *Eriochloa punctata* var. *montevidense* (Griseb.) Herter; *Eriochloa punctata* var. *montevidensis* (Döll) Herter; *Helopus annulatus* var. *montevidensis* Döll	Covas et Ragonese 3904 (SF); Pensiero et Marino 3574 (SF); Pire et Nisensohn 191 (SF); Ragonese 2118, 3188, 3310 (SF); Vegetti 24 (SF); Burkart 18405 (SI); Burkart et Troncoso 11432 (SI); Cabrera 7482 (SI); Cabrera et al. 27530 (SI); Nicora 4688 (SI); Rosengurtt B-5483, B-5503 (SI); Schinini 6283 (SI); Werdermann 715 (SI); Zuloaga 3027 (SI); Zuloaga et Deginani 3693a (SI)

Table 1 continued

Species	Synonyms	Voucher
Eriochloa polystachya Kunth	*Eriochloa punctata* var. *subglabra* (Nash) Urb.; *Eriochloa subglabra* (Nash) Hitchc.; *Helopus polystachys* (Kunth) Trin. ex Steud.; *Milium polystachyon* (Kunth) Spreng.; *Monachne subglabra* Nash; *Paspalum polystachyum* (Kunth) Raspail	Burkart 16298 (SI); Laegaard et Norsangsni 21788 (SI); Otero 238 (SI)
Eriochloa procera (Retz.) C.E. Hubb.	*Agrostis procera* Retz.; *Agrostis ramosa* (Retz.) Poir.; *Eriochloa annulata* (Flüggé) Kunth; *Eriochloa hackelii* Honda; *Eriochloa polystachya* Hook. f.; *Eriochloa polystachya* var. *annulata* (Flüggé) Maiden & Betche; *Eriochloa ramosa* (Retz.) Kuntze; *Eriochloa ramosa* var. *barbata* Peter; *Helopus annulatus* (Flüggé) Nees; *Helopus laevis* Trin.; *Helopus pilosus* Trin.; *Milium ramosum* Retz.; *Paspalum annulatum* Flüggé; *Piptatherum annulatum* (Flüggé) J. Presl; *Thysanolaena procera* (Retz.) Mez.	Angulo et Ridoutt 208 (SI); Kreucker 608 (SI); Laegaard 21748 (SI); Pappi 3890 (SI); Probst 2834 (SI); Ramos 125 (SI)
Eriochloa punctata (L.) Desv. ex Ham.	*Agrostis decipiens* Salzm. ex Steud.; *Agrostis punctata* (L.) Lam.; *Eriochloa* kunthii G. Mey.; *Eriochloa montevidensis* Griseb.; *Eriochloa polystachya* var. *punctata* (L.) Maiden & Betche; *Eriochloa punctata* f. *intermedia* Parodi; *Eriochloa punctata* Hochst. ex Steud.; *Eriochloa punctata* var. *montevidense* (Griseb.) Herter; *Eriochloa punctata* var. *parodii* Herter; Eriochloa *punctata* var. *punctata*; *Helopus cognatus* Steud.; *Helopus kunthii* (G. Mey.) Trin. ex Steud.; *Helopus punctatus* (L.) Nees; *Helopus punctatus* var. *cognatus* (Steud.) Döll; *Milium punctatum* L.; *Monachne punctata* (L.) Nash; *Oedipachne punctata* (L.) Link; *Paspalum punctatum* (L.) Flüggé; *Paspalus punctatus* (L.) Flüggé; *Piptatherum punctatum* (L.) P. Beauv.	Bernasconi 5614 (SF); D'Angelo 185 (SF); Lewis 651 (SF); Pensiero 5173[a], 5214 (SF); Pensiero et Exner 5635, 6211 (SF); Pensiero et Marino 3669, 3727, 3773, 3777 (SF); Pensiero et Tivano 3029 (SF); Pire et Nisensohn 312 (SF); Boelcke 6786, 6794 (SI); Burkart 16169, 17160 (SI); Dusén 13688 (SI); Fortunato et al. 2690 (SI); Guaglianone et al. 269, 432 (SI); Krapovickas et al. 25571 (SI); Morrone et al. 2005 (SI); Muñoz 5464 (SI); Romanczuk et al. 131 (SI); Runyon 717 (SI); Schinini et Martinez Crovetto 12906 (SI); Zuloaga et al. 3294 (SI)
Eriochloa setosa (A. Rich.) Hitchc.	*Eriochloa filifolia* Hitchc.; *Piptatherum setosum* A. Rich.;	Brother 991 (SI)
Eriochloa villosa (Thunb.) Kunth	*Eriochloa villosa* var. *stenantha* Ohwi; *Helopus villosus* (Thunb.) Nees ex Steud.; *Helopus villosus* (Thunb.) Nees; *Panicum tuberculiflorum* Steud.; *Paspalum distichum* Houtt.; *Paspalum villosum* Thunb. ex A. Murria; *Paspalum villosum* Thunb.	Chase 16782 (SI)
Megathyrsus maximus (Jacq.) B.K. Simon & S.W.L. Jacobs	*Panicum gongylodes* Jacq.; *Panicum hirsutissimum* Steud.; *Panicum jumentorum* Pers.; *Panicum laeve* Lam.; *Panicum maximum* Jacq.; *Panicum maximum* var. *gongylodes* (Jacq.) Döll; *Panicum maximum* var. *pubiglume* K. Schum. ex Peter; *Panicum maximum* var. *pubiglume* K. Schum.; *Panicum maximum* var. *trichoglume* Robyns; *Panicum polygamum* Sw.; *Panicum polygamum* var. *gongylodes* (Jacq.) E. Fourn.; *Panicum praticola* Salzm. ex Döll; *Panicum scaberrimum* Lag.; *Panicum trichocondylum* Steud.; *Urochloa maxima* (Jacq.) R.D. Webster; *Urochloa maxima* var. *trichoglumis* (Robyns) R.D. Webster	Legname et al. 6964 (LIL); Bianchi 1646 (MCNS); Del Castillo 1146 (MCNS); Juarez 1812, 1869 (MCNS); Juarez et Varela 1968 (MCNS); Legname et al. 10140 (MCNS); Novara 3690, 5796, 7698, 7791, 8378,10986, 11430 (MCNS); Palací 724 (MCNS); Tolaba 92 (MCNS);Woodburry et al. W-I108 (NY); Horubeck DW7 (NY); D'Angelo 266 (SF); Pensiero et Kiverling 6304 (SF)

Table 1 continued

Species	Synonyms	Voucher
Melinis leucantha (Hochst. ex A. Rich.) Chiov.	*Tricholaena teneriffae* (L. f.) Link; *Tricholaena teneriffae* subsp. *teneriffae*	Pappi 3884 (LIL)
Melinis minutiflora P. Beauv.	*Muhlenbergia braziliensis* Steud.; *Agrostis glutinosa* Fisch. ex Nees; Agrostis glutinosa Fisch. ex Schrank; *Agrostis polypogon* Salzm. ex Steud.; *Melinis* maitlandii fo. mutica (Chiov.) Robyns; *Melinis maitlandii* Stapf & C.E. Hubb.; *Melinis minutiflora* f. *inermis* (Döll) Stapf & C.E. Hubb.; *Melinis minutiflora* f. *mutica* Chiov.; *Melinis minutiflora* var. *glutinosa* (Nees) Kuntze; *Melinis minutiflora* var. *inermis* (Döll) Rendle; *Melinis minutiflora* var. *inodora* Kuntze; *Melinis minutiflora* var. mutica Hack.; *Melinis minutiflora* var. *pilosa* Staff; *Melinis minutiflora* var. *setigera* Clayton; *Melinis purpurea* Stapf & C.E. Hubb.; *Melinis tenuinervis* f. *mutica* Stapf & C.E. Hubb. ex Peter; *Melinis tenuinervis* Staff; *Melinis tenuinervis* var. *parvispicula* C.E. Hubb. ex Peter; *Muhlenbergia brasiliensis* Steud.; *Panicum melinis* Trin.; *Panicum melinis* var. *inerme* Döll; *Panicum minutiflorum* (P. Beauv.) Raspail; *Suardia picta* Schrank; *Tristegis glutinosa* Nees	Andersson 9776 (LIL); Barkley et al. 1542 (LIL); Bro. Apolinar 688 (LIL); Castellanos 1435, 5767 (LIL); Dusén 17050; Gonzalez 64666 (LIL); Hunziker 2573 (LIL); Irwin et al. s/n (LIL); Klevens et Barkley 17C353 (LIL); Leojnoldo 18 (LIL); Lufantes 1228 (b) (LIL); Pabst 20 (LIL); Palacios et al. 3309 (LIL); Rambo 42026, 43557 (LIL); Ruit C-1130 (LIL); Schulz 12258 (LIL); Schunke 8171(LIL); Stürpe 617 (LIL); Barbosa 664 (SI)
Melinis monachne (Trin.) Pilg.	*Panicum monachne* Trin.; *Tricholaena monachne* (Trin.) Stapf & C.E. Hubb.	Godfrey et Meeuse SH-1596 (US); Gossweilerii 10627 (US); Smook 7067 (US)
Melinis repens (Willd.) Zizka	*Erianthus repens* (Willd.) P. Beauv.; *Melinis argentea* Mez; *Melinis brachyrhynchus* Mez; *Melinis rosea* (Nees) Hack.; *Monachyron roseum* (Nees) Parl.; *Monachyron tonsum* (Nees) Parl.; *Monachyron villosum* Parl.; *Panicum braunii* Steud.; *Panicum roseum* (Nees) Steud.; *Panicum roseum* fo. *hirtum* Kuntze; *Panicum sphacelatum* (Benth.) Steud.; *Panicum teneriffae* var. *roseum* (Nees) F.M. Bailey; *Panicum* tonsum (Nees) Steud.; *Rhynchelytrum dregeanum* Nees; *Rhynchelytrum dregeanum* var. *annuum* Chiov.; *Rhynchelytrum dregeanum* var. *intermedium* Chiov.; *Rhynchelytrum repens* (Willd.) C.E. Hubb.; *Rhynchelytrum repens* var. *roseum* (Nees) Chiov.; *Rhynchelytrum roseum* (Nees) Stapf & C.E. Hubb. ex Bews; *Rhynchelytrum roseum* (Nees) Stapf & C.E. Hubb.; *Rhynchelytrum tonsum* (Nees) Lanza & Mattei; *Rhynchelytrum villosum* (Parl.) Chiov.; *Saccharum* repens Willd.; *Saccharum sphacelatum* (Benth.) Walp.; *Tricholaena dregeana* (Nees) T. Durand & Schinz; *Tricholaena fragilis* A. Braun; *Tricholaena repens* (Willd.) Hitchc.; *Tricholaena repens* var. *rosea* (Nees) Alberts.; *Tricholaena rosea* Nees; *Tricholaena sphacelata* Benth.; *Tricholaena tonsa* Nees; *Tricholaena tonsa* var. *submutica* Schweinfurth	Smook 9270 (LIL); Dalla Fontana s/n (SF); Morrone et Pensiero 222, 378, 436 (SF); Pensiero 4093 (SF); Tivano 513 (SF); Vegetti 1123 (SF); Alonso 970 (SI); Bogdon 4562 (SI); Romanczuk et al. 426 (SI)
Thuarea involuta (G. Forst.) R. Br. ex Sm.	*Ischaemum involutum* G. Forst.; *Thuarea latifolia* R. Br.; *Thuarea media* R. Br.; *Thuarea sarmentosa* Pers.	Edaño 56725 (US); Smith 9508 (US); Williams 220 (US)

Table 1 continued

Species	Synonyms	Voucher
Urochloa acuminata (Renvoize) Morrone and Zuloaga	*Brachiaria tatianae* Zuloaga and Soderstr.; *Panicum megastachyum* Nees; *Streptostachys acuminata* Renvoize	Zuloaga et al. 4766, 4843 (SI)
Urochloa adspersa (Trin.) R.D. Webster	*Brachiaria adspersa* (Trin.) Parodi; *Brachiaria adspersa* (Trin.) S.T. Blake; *Brachiaria echinulata* (Mez) L.R. Parodi; *Panicum adspersum* Trin.; *Panicum adspersum* var. *exile* Lindm.; *Panicum adspersum* var. *neesi* Lindm.; *Panicum echinulatum* Mez; *Panicum echinulatum* var. *boliviense* Henrard; *Panicum keyense* Mez; *Panicum thomasianum* Steud. ex Döll	Parodi 14594 (BAA); Rua et al. 22994 (BAA); Saravia Toledo 283 (BAA); Venturi 1587 (BAA); Krapovickas et Schinini 30505 (CTES);Schulz?? 3869 (CTES) (MCNS); Ahumada et al. 9379, 9383 (JUA); Cabrera et al. 23323 (LIL); Legname et Cuezo 8193 (LIL); Norrman et al. 192 (LIL); Saravia Toledo et Parada 17 (MCNS); Britton et Shaper 334 (NY); Hansen 2473 (NY); Luna 981 (NY); Nee 44580, 44835 (NY); Pierotti 201 (NY); Tonell 2630 (NY); Pensiero et al. 5053 (SF); 13466 (SI); Ahumada 4464 (SI); Alonso 6 (SI); Burkart 20144, 20200, 20378 (SI); Burkart et Troncoso 11442 (SI); Cabrera et al. 26408, 26479, 27477, 31440, 34016 (SI); Guaglianone et al. 612 (SI); Job 13463 (SI); Krapovickas et Schinini 30779 (SI); Lewis et Pire 800 (SI); Pire 1343 (SI); Schinini et Bordas 15141 (SI); Schinini et Mroginski 4602 (SI); Schulz 3329 (SI); Stofella 107 (SI); Stuckert 12792 (SI); Zuloaga et al. 2989 (SI); Zuloaga et Deginani 3703 (SI); Zuloaga et Morrone 3031, 3049, 3050, 3056 (SI)
Urochloa advena (Vickery) R.D. Webster	*Brachiaria advena* Vickery	Killick 4541 (MO)
Urochloa arrecta (Hack. Ex T. Durand and Schinz) Morrone and Zuloaga.	*Brachiaria arrecta* (Hack. ex T. Durand and Schinz) Stent; *Brachiaria* radicans Napper; *Panicum arrectum* Hack. ex T. Durand and Schinz	López 64 (CTES); Borgo et al. 447 (NY); Zuloaga et al. 5618 (NY)
Urochloa atrisola R.D. Webster	*Brachiaria atrisola* (R.D. Webster) B.K. Simon	Blake 17776 (MO)
Urochloa bovonei (Chiov.) A.M. Torres and C.M. Morton	*Brachiaria viridula* Stapf; *Brachiaria bovonei* (Chiov.) Robyns; *Brachiaria hians* Stapf; *Panicum bovonei* Chiov.	Maas Greesteranus 4925 (MO); Wiehe 391 (MO)
Urochloa brachyura (Hack. ex Schinz) Stapf	*Panicum brachyurum* Hack. ex Schinz; *Urochloa geniculata* C.E. Hubb; *Urochloa novemnervia* C.E. Hubb; *Urochloa novemnervia* C.E. Hubb.	Jahogens 6702 (US); Mott 918 (NY); Moss et Ottley 3480 (NY); Seiner 462 (US); Volk 6696 (NY)
Urochloa brizantha (Hochst. Ex A. Rich.) R.D. Webster	*Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf; *Panicum brizanthum* Hochst. ex A. Rich.; *Urochloa decumbens* (Stapf) R.D. Webster	Bhorai Kalloo et Centeno 6 (NY); Heringer et al. 2077 (NY); Mori et al. 10560 (NY); Plowman et al. 8695 (NY); Smith et al. 15775 (NY); Morrone et Pensiero 366 (SF)
Urochloa ciliatissima (Buckley) R.D. Webster	*Brachiaria ciliatissima* (Buckley) Chase; *Panicum ciliatissimum* Buckley	Brant et al. 2222 (MO); Correll et Johnston 18116 (MO)
Urochloa comata (Hochst. ex A. Rich.) Stapf	*Brachiaria epaleata* Stapf; *Brachiaria kotschyana* (Hochst. ex Steud.) Stapf; *Brachiaria secernenda* (Hochst. ex Mez) Henrard; *Panicum comatum* Hochst. ex A. Rich.	Thomas 4343 (LIL) (US); Hitchcock 24974 (US); Mearns 3044, 3046 (US); Shantz 921 (US); Snowden 1202 (US)
Urochloa decidua Morrone and Zuloaga	_	Zuloaga 6942 (SI)
Urochloa decumbens (Stapf) R.D. Webster	*Brachiaria decumbens* Stapf	Honfi 73 (CTES); Cirón et al. 3427 (NY); Davidse et Gonzáles 21954 (NY); Filgueiras 441 (NY); Heringer et al. 1756, 5063 (NY); Nee 45181, 45182, 45992, 46063, 46392, 47388, 47415, 47451, 47853, (NY); Nee et Sundue 51915 (NY); Morrone et Pensiero 117, 315, 371, 497 (SF)

Table 1 continued

Species	Synonyms	Voucher
Urochloa deflexa (Schumach.) H. Scholz	*Brachiaria regularis* (Nees) Stapf; *Brachiaria deflexa* (Schumach.) C.E. Hubb. ex Robyns; *Panicum deflexum* Schumach.	Meinzingen et Conert 336, 599, 755, 796 (LIL); De Leeuw 1088 (US); Godfrey H-1731 (US); Schinker 1653 (US);Thorold CB-28, sws/28 (US)
Urochloa dictyoneura (Fig. and De Not.) Veldkamp	*Brachiaria dictyoneura* (Fig. and De Not.) Stapf; *Brachiaria dictyoneura* subsp. *dictyoneura*; *Brachiaria humidicola* (Rendle) Schweick.; *Panicum dictyoneurum* Fig. and De Not.; *Panicum humidicolum* Rendle; *Urochloa humidicola* (Rendle) Morrone and Zuloaga	Hitchcock 24816 (US); Greenway 10115 (US); Snowden 1219 (US)
Urochloa distachya (L.) T.Q. Nguyen	*Brachiaria subquadripara* (Trin.) Hitchc.; *Brachiaria miliiformis* (J. Presl) Chase; *Brachiaria distachya* (L.) Stapf; *Digitaria distachya* (L.) Pers.; *Panicum distachyon* L.; *Panicum miliiforme* J. Presl; *Panicum subquadriparum* Trin.; *Urochloa subquadripara* (Trin.) R.D. Webster	Andersson s/n (LIL); Adams 13975, 14313, 14700 (NY); Fosberg 24795 (NY); Fosberg et Stoddart 54884 (NY)
Urochloa dura (Stapf) A.M. Torres and C.M. Morton	*Brachiaria dura* Stapf	Mitchell 12/62 (US); Verboom 1319 (US)
Urochloa echinolaenoides Stapf	_	Shauty 586 (US)
Urochloa eminii (Mez) Davidse	*Brachiaria eminii* (Mez) Robyns; *Panicum eminii* Mez.	Stuhlmann 3842 (US)
Urochloa foliosa (R. Br.) R.D. Webster	*Brachiaria foliosa* (R. Br.) Hughes; *Panicum foliosum* R. Br.	Collins 46642 (MO); Snow et Simon 7332 (MO); Blake 20087 (US)
Urochloa fusca (Sw.) B.F. Hansen and Wunderlin	*Brachiaria fasciculata* (Sw.) Parodi; *Brachiaria fasciculata* (Sw.) S.T. Blake; *Brachiaria fasciculata* var. *carthaginense* (Sw.) Beetle; *Brachiaria fasciculata* var. *fasciculata;* *Brachiaria fasciculata* var. *reticulata* (Torr.) Beetle; *Brachiaria fasciculata* var. *reticulata* (Torr.) Vickery; *Brachiaria fasciculata* var. *stricta* (Döll) Beetle; *Panicum carthaginense* Sw.; *Panicum chartaginense* Sw.; *Panicum fasciculatum* Sw.; *Panicum fasciculatum* var. *chartaginense* (Sw.) Döll; *Panicum fasciculatum* var. *flavescens* (Sw.) Döll; *Panicum fasciculatum* var. *fuscum* (Sw.) Döll; *Panicum fasciculatum* var. *genuinum* Döll; *Panicum fasciculatum* var. *reticulatum* (Torr.) Beal; *Panicum fasciculatum* var. *strictum* Döll; *Panicum fastigiatum* Poir.; *Panicum flavescens* Sw.; *Panicum fuscatum* J. Presl ex Nees; *Panicum fusco-rubens* Lam.; *Panicum fuscum* Sw.; *Panicum fuscum* var. *fasciculatum* (Sw.) Griseb.; *Panicum fuscum* var. *fuscum*; *Panicum fuscum* var. *reticulatum* (Torr.) Scribn. and Merr.; *Panicum illinoniense* Desv.; *Panicum nigrica* Willd. ex Spreng.; *Urochloa fasciculata* Kunth	Agostini et al. 1848 (NY); Ahumada et al. 9375 (JUA); Breteler 3998; Buting 5399, 5669, 7598, 7664, 9398 (NY); Byron et Smarino 20981 (NY); Burkart 16991, 20370 (SI); Curtiss 748 (SI);Eiten et Eiten 10315, 10439 (NY); Garber 36 (NY); Holm-Nielsen et al. 2020, 2482 (NY); Krapovickas et Schinini 30945 (CTES); Krapovickas 1544 (LIL, SI); Lieser et González 12154 (NY); Molina 24272 (BAA); Santa Cruz 3500 (BAA); Small 10515 (NY); Stuckert 21603; West s/n (NY)
Urochloa fusiformis (Reeder) Veldkamp	*Brachiaria fusiformis* Reeder; *Brachiaria fusiformis* var. *pilicoronata* (Ohwi) Jansen; *Brachiaria villosa* var. *pilicoronata* Ohwi	Ramos 8214 (US); Ramos et Edaño 44646 (US); Williams 1963 (US)
Urochloa gilesii (Benth.) Hughes	*Brachiaria gilesii* (Benth.) Chase; *Panicum gilesii* Benth.	Hubbard 6011, 7051 (MO)

Table 1 continued

Species	Synonyms	Voucher
Urochloa glumaris (Trin.) Veldkamp	*Brachiaria ambigua* (Trin.) A. Camus; *Brachiaria paspaloides* (J. Presl) C.E. Hubb.; *Panicum ambiguum* Trin.; *Panicum glumare* Trin.; *Panicum urochloa* Steud.; *Urochloa ambigua* (Trin.) Pilg.; *Urochloa glabra* Brongn.; *Urochloa paspaloides* J. Presl	Clayton 5073 (US); Evans 629 (NY); Gould 13445 (US); Gould et Cooray 13733 (US); Hosaka 3143 (NY); Hürlimann 551, 620 (NY); Kajewski 279 (NY); Main et Aden 1563 (US); Procten 4526 (NY); Samlumgen von Otto Kuntze's Weltreise 75 (NY); St. John 16681 (NY); Taylor P-2788-E; Vera Santos 4489, 5018 (US); Wray 334 (NY); Yunker 9114, 9486, 15414, 15820 (NY)
Urochloa holosericea (R. Br.) R.D. Webster	*Brachiaria holosericea* (R. Br.) Hughes; *Panicum holosericeum* R. Br.	Brass 5910, 7810 (US)
Urochloa humidicola (Rendle) Morrone and Zuloaga	*Brachiaria dyctioneura* Stapf; *Brachiaria dictyoneura* subsp. *humidicola* (Rendle) Catasús, *Brachiaria rautanenii* (Hack.) Stapf; *Panicum humidicolum* Rendle; *Urochloa dictyoneura* (Fig. and De Not.) Veldkamp	Ballèe 3503 (NY); Bhorai Kalloo et Centeno 5 (NY); Nee 46051 (NY)
Urochloa jubata (Fig. and De Not.) Sosef	*Brachiaria jubata* (Fig. and De Not.) Stapf; *Panicum jubatum* Fig. and De Not.	Pilz 2061 (LIL); Meinzinger et Conert 352, 556, 816 (LIL)
Urochloa kurzii (Hook. f.) T.Q. Nguyen	*Brachiaria kurzii* (Hook. f.) A. Camus; *Brachiaria lanceata* Ohwi; *Brachiaria lanceata* var. *timorensis* (Ohwi) Jansen; *Brachiaria timorensis* Ohwi; *Panicum kurzii* Hook. f.; *Urochloa kurzii* (Hook. f.) R.D. Webster	Monod de Froideville 1448 (US)
Urochloa lachnantha (Hochst.) A.M. Torres and C.M. Morton	*Brachiaria lachnantha* (Hochst.) Stapf; *Panicum lachnanthum* Hochst.; *Panicum lachnanthum* Torr.	16212 (CIAT)
Urochloa lata (Schumach.) C.E. Hubb.	*Brachiaria lata* (Schumach.) C.E. Hubb.; *Panicum amplexifolium* Hochst.; *Panicum hamadense* Mez; *Panicum insculptum* Steud.; *Panicum latum* Schumach.; *Urochloa insculpta* (Steud.) Stapf	26886 (CIAT)
Urochloa leucacrantha (K. Schum.) Stapf	*Brachiaria leucacrantha* (K. Schum.) Stapf; *Panicum leucacranthum* K. Schum.	16546 (CIAT); Schlieben 6488 (LIL)
Urochloa lorentziana (Mez) Morrone and Zuloaga	*Brachiaria lorentziana* (Mez) Parodi; *Panicum lorentzianum* Mez; *Panicum velutinosum* f. *violascens* Stuck.; *Panicum velutinosum* f. *viride* Stuck.	Nicora 7108 (BAA); Parodi 14600 (BAA); Saravia Toledo 252 (BAA); Saravia Toledo 1522 (CTES); Schulz 1683 (CTES); Jaime 8 (LIL); Zuloaga et Deginani 310 (LIL); Navarro 174 (MCNS); Maruña et al. 598 (NY); Stuckert 18759a (NY); 25398 (SI); Ahumada et Castellon 4763, 4781 (SI); Burkart 12263 (SI); Burkart et al. 25246 (SI); Burkart et Troncoso 11482, 11992 (SI); Cabrera et al. 30236, 30606 (SI); Cuellar 3 (SI); Esteban 10682 (SI); Marquez 16 (SI); Nicora 1910, 17531, 18472 (SI); Nicora et al. 9020 (SI) (SF); Perez 210 (SI); Schulz 3250, 17828 (SI); Stuckert 366, 11070 (SI); Ulibarri 335, 358 (SI); Venturi 1676 (SI); Zuloaga et al. 2678 (SI); Zuloaga et Deginani 3496 (SI); Zuloaga et Morrone 3051 (SI)
Urochloa meziana (Hitchc.) Morrone and Zuloaga	*Brachiaria meziana* Hitchc	Davidse 9928 (LIL); Fisher 35224 (LIL); Hitchcok 402 (LIL); Davidse et Davidse 9928 (MO); Kral 27444 (MO)
Urochloa mollis (Sw.) Morrone and Zuloaga	*Brachiaria mollis* (Sw.) Parodi; *Panicum didistichum* Mez; *Panicum molle* Griseb.; *Panicum molle* Sw.; *Panicum moritzii* Mez; *Panicum polytrichum* Mez; *Panicum velutinosum* Nees ex Trin.; *Panicum velutinosum* Nees	Alain et al. 34441 (NY); Bunting 7963, 8214 (NY); Madsen 63390 (NY); Weberbauer 7714 (NY)

Table 1 continued

Species	Synonyms	Voucher
Urochloa mosambicensis (Hack.) Dandy	*Echinochloa notabilis* (Hook. f.) Rhind; *Panicum mosambicense* Hack.; *Panicum notabile* Hook. f.; *Urochloa pullulans* Stapf; *Urochloa pullulans* var. *mosambicensis* (Hack.) Stapf; *Urochloa rhodesiensis* Stent	Banda et Kananji 3822 (NY); Liogier et Martorell 34441 (NY); Pensiero et Marino 4446 (NY); Sinclair 26 (NY)
Urochloa mutica (Forssk.) T.Q. Nguyen	*Brachiaria glabrinodis* (Hack.) Henrard; *Brachiaria mutica* (Forssk.) Stapf; *Brachiaria numidiana* (Lam.) Henrard; *Brachiaria purpurascens* (Raddi) Henrard; *Panicum amphibium* Steud.; *Panicum barbinode* Trin.; *Panicum equinum* Salzm. ex Steud.; *Panicum glabrinode* Hack.; *Panicum guadaloupense* Spreng. ex Steud.; *Panicum muticum* Forssk.; *Panicum numidianum* Lam.; *Panicum paraguayense* Steud. ex Döll; *Panicum pictigluma* Steud.; *Panicum purpurascens* Raddi; *Paspalum glabrinode* (Hack.) Morrone and Zuloaga; *Urochloa mutica* (Forssk.) R.D. Webster ex Zon	Bartlett 20315 (BAA); Hirschhorn 7356 (BAA); Parodi 14790 (BAA); Carnevali 1180 (CTES); Quarín 2387 (CTES); Asplund 19241 (NY); Degener 11501 (NY); Duke 9728 (NY); Hekking 945 (NY); Herrera 461 (NY); Hoock-Cayenne 196 (NY); Kazuto 10594, 10728 (NY); Lee and Weller 119 (NY); McDaniel et Rimachi 23369 (NY); Rimachi 5913 (NY); Steyermark et al. 121232 (NY); Yuncker T.G. 9659 (NY)
Urochloa nigropedata (Munro ex Ficalho & Hiern) Stapf	*Brachiaria nigropedata* (Munro ex Ficalho and Hiern) Stapf; *Brachiaria melanotyla* (Hack.) Henrard; *Panicum melanotylum* Hack.; *Panicum nigropedatum* Munro ex Ficalho and Hiern	Bogdan 5144 (US); Burtt 1285 (US); Liebenberg 4505 (US)
Urochloa notochthena (Domin) Hughes	*Brachiaria notochthona* (Domin) Stapf; *Brachiaria gilesii* (Benth.) Chase; *Urochloa gilesii* (Benth.) Hughes; *Panicum notochthonum* Domin; *Urochloa gilesii* subsp. *gilesii*.	Hourigan 21 (US)
Urochloa oblita (Swallen) Morrone and Zuloaga	*Brachiaria oblita* (Swallen) Tovar; *Panicum oblitum* Swallen	Holm-Nielsen et al. 4926 (MO); Peterson et al. 8909 (MO)
Urochloa oligotricha (Fig. and De Not.) Henrard	*Brachiaria bulawayensis* (Hack.) Henrard; *Eriochloa bolbodes* (Hochst. ex Steud.) Schweinf.; *Helopus bolbodes* Hochst. ex Steud.; *Panicum bolbodes* (Hochst. ex Steud.) Asch. and Schweinf.; *Panicum bulawayense* Hack.; *Panicum oligotrichum* Fig. and De Not.; *Urochloa bolbodes* (Hochst. ex Steud.) Stapf; *Urochloa bolbodes* (Steudel) Stapf	Liebenberg 11 (US); Pappi 274 (US); Robinson 1425 (US); Shantz 475 (US)
Urochloa ophryodes (Chase) Morrone and Zuloaga	*Brachiaria ophryodes* Chase	Hitchcock 401 (LIL)
Urochloa panicoides P. Beauv.	*Panicum borzianum* Mattei; *Panicum controversum* Steud.; *Panicum helopus* f. *glabrescens* K. Schum.; *Panicum helopus* Trin.; *Panicum helopus* var. *glabrescens* (K. Schum.) Stapf; *Panicum hochstetterianum* A. Rich.; *Panicum oxycephalum* Peter; *Panicum panicoides* (P. Beauv.) Hitchc.; *Panicum setarioides* Peter; *Panicum trichopus* subsp. *breviglume* Chiov.; *Panicum trichopus* var. *glaberrimum* Chiov.; *Panicum trichopus* var. *trichophorum* Chiov.; *Panicum urochloa* Desv.; *Setaria pilifera* Spreng.; *Urochloa* helopus (Trin.) Stapf; *Urochloa helopus* var. *hochstetteriana* (A. Rich.) Chiov.; *Urochloa panicoides* var. *pubescens* (Kunth) Bor; *Urochloa pubescens* Kunth; *Urochloa ruschii* Pilg.	Krapovickas et al. 27906 (CTES); Vanni et al. 4166 (CTES); Ahumada et al. 9376, 9382 (JUA); Ahumada 5166 (MCNS); Del Castillo 269, 588, 599 (MCNS); Del Castillo et al. 475 (MCNS); Del Castillo et Neuman 374 (MCNS); Falce s/n (MCNS); Nicora et al. 9016 (MCNS) (SF); Novara et al. 682, 710, 728 (MCNS); Novara et Bruno 8798 (MCNS); Saravia Toledo 849 (MCNS); Bates 20671 (NY); Johnson 707 (NY); Pinkava 14365 (NY); Sinclair 25 (NY); Smith 3041 (NY); Ahumada 4709 (SI); Ahumada et Castellon 5021 (SI); Cabrera et al. 26171, 31886 (SI); Deginani et Cialdella 233 (SI); Garcia et Grenni 524 (SI); Novara 3348 (SI); Vignale et Breglia 176 (SI); Volk 6500 (NY); Zuloaga et Morrone 3032, 3036, 3052 (SI)

Table 1 continued

Species	Synonyms	Voucher
Urochloa paucispicata (Morong) Morrone and Zuloaga	*Acroceras paucispicatum* (Morong) Henrard; *Brachiaria paucispicata* (Morong) Clayton; *Panicum paucispicatum* Morong	Quarín 94 (CTES); Saravia Toledo 1523 (CTES); Cuezzo et al. 4486 (LIL); Nee 42287 (LIL); Falce HG1145 (MCNS); Karlsson 20 (MCNS); Novara 10121 (MCNS); Ragonese 2539 (SF); Ahumada 4466 (SI); Cantino 735 (SI); Hauman s/n (SI); Ibarrola 225 (SI); Insfrán 1030 (SI); Nicora 18427 (SI)
Urochloa piligera (F. Muell. ex Benth.) R.D. Webster	*Brachiaria piligera* (F. Muell. ex Benth.) Hughes; *Brachiaria piligera* var. *intercedens* (Domin) Hughes; *Brachiaria subquadripara* var. *piligera* (F. Muell. ex Benth.) Reeder; *Panicum intercedens* Domin; *Panicum piligerum* F. Muell. ex Benth.	Carr 11398 (MO); Hubbard et Winders 6345 (MO); Lazarides 4168 (MO)
Urochloa plantaginea (Link) R.D. Webster	*Brachiaria plantaginea* (Link) Hitchc.; *Panicum disciferum* E. Fourn.; *Panicum distans* Salzm. ex Döll; *Panicum distans* Salzm. ex Steud.; *Panicum leandri* Trin.; *Panicum plantagineum* Link; *Urochloa discifera* (E. Fourn.) Morrone and Zuloaga	MacDonald 12465; Dusén 14761 (BAA); Parodi 6422 (BAA); Ahumada 4142 (CTES); Schulz 11052 (CTES); Ahumada et al. 9374, 9378, 9385 (JUA); Türpe 3055 (LIL); Morrone et Pensiero 358 (SF); Nicora et al. 9018 (SF); Ragonese 2128 (SF) (BAA); Ahumada et Rotman 4397 (SI); Cabrera et al. 26152, 26414, 30176, 30262, 34694 (SI); Deginani et Cialdella 16 (SI); Guaglianone et al. 1983 (SI); Zuloaga et al. 1466, 2889 (SI); Zuloaga et Morrone 3005, 3014, 3016, 3018, 3030 (SI)
Urochloa platynota (K. Schum.) Pilg.	*Urochloa bifalcigera* (Stapf) Stapf; *B. platynota* (K. Schum.) Robyns	Lab Stapf 1926 (US); Lienberg May 1930 (US); Snowden 1222 (US)
Urochloa platyphylla (Munro ex C. Wright) R.D. Webster	*Brachiaria extensa* Chase; *Brachiaria platyphylla* (Munro ex C. Wright) Nash; *Panicum platyphyllum* Munro ex C. Wright; *Paspalum platyphyllum* Griseb.; *Urochloa extensa* (Chase) C. Nelson and Fern. Casas; *Urochloa platyphylla* (Griseb.) R.D. Webster	Bartlett 20299 (BAA); Lewis et Collantes 139 (BAA); Quarin 648 (BAA); Rosengurt B4898 (BAA); Ahumada 1506, 1642 (CTES); Lazarte s/n (LIL); Del Castillo et Varela 42 (MCNS); Banks D.J. 2571 (NY); Galvan et al. 27 (NY); Halse 6125 (NY); Hunziker 13808 (NY); Rojas 12644 (NY); Venturi 2384 (NY); Brollo 238 (SF); Brollo et Tivano 604 (SF); D'Angelo 149 (SF); Pensiero 135, 141, 833, 1957, 5213 (SF); Pensiero et al. 1443, 5151 (SF); Pensiero et Kiverling 6382 (SF); Pensiero et Marino 3561 (SF); Pensiero et Tivano 2964, 3032 (SF); Ragonese 2284, 3198 (SF); 25560 (SI); Ahumada 615 (SI); Bartlett 19718, 19719 (SI); Bissio 832 (SI); Burkart 12759 (SI); Burkart et Bacigalupo 21028 (SI); Cabrera et al. 26492 (SI); Gomez 187 (SI); Job 755 (SI); Lewis 1492 (SI); Meyer 388 (SI); Nicolini 20767 (SI); Parodi 563a (SI); Pedersen 4671 (SI); Quarin et al. 2007 (SI); Scipione 268 (SI); Venturi 2384, 7526 (SI); Zuloaga et al. 2694, 2991, 3346 (SI); Zuloaga et Deginani 3668 (SI)
Urochloa platytaenia (Stapf) Crins	*Brachiaria platytaenia* Stapf; *Brachiaria oligobrachiata* (Pilg.) Henrard Kartesz; *Panicum oligobrachiatum* Pilg.; *Urochloa oligobrachiata* (Pilg.)	Leleum 983 (US); Shauty 5941/2; Verboon 1193 (US)
Urochloa praetervisa (Domin) Hughes	*Brachiaria praetervisa* (Domin) C.E. Hubb.; *Brachiaria windersii* C.E. Hubb.; *Panicum kochii* Mez; *Panicum praetervisum* Domin	Badman 5230 (NY)
Urochloa pubigera (Roem. and Schult.) R.D. Webster	*Brachiaria holotricha* Ohwi; *Brachiaria pubigera* (Roem. and Schult.) S.T. Blake; *Brachiaria ramosa* var. *grandiflora* Hughes	Begnin 198 (US)

Table 1 continued

Species	Synonyms	Voucher
Urochloa ramosa (L.) T.Q. Nguyen	*Brachiaria ramosa* (L.) Stapf; *Brachiaria reptans* (L.) C.A. Gardner and C.E. Hubb.; *Echinochloa ramosa* (L.) Roberty; *Panicum helopus* var. *glabrior* Benth; *Panicum pubescens* R. Br.; *Panicum pubigerum* Roem. and Schult.; *Panicum ramosa* L.; *Panicum ramosum* L.; *Urochloa reptans* (L.) Stapf	Brown et Brown 98 (US); Brittom et al. 476; Buting 7694 (NY); Hitchcock 16605 (NY); Hoock 753, 754 (NY); Jemman 6024 (NY); Faulkner 3769 (US); Michelnome 4-9-30 (US); William 3479 (US)
Urochloa rudis Stapf	*Panicum holtzii* Peter; *Urochloa gorinii* Chiov.	Wingfield 3145 (US)
Urochloa ruziziensis (R. Germ. and Evrard) Crins	*Brachiaria decumbens* var. *ruziziensis* (R. Germ. and Evrard) Ndab.; *Brachiaria ruziziensis* R. Germ. and Evrard; *Urochloa ruziziensis* (R. Germ. and Evrard) Morrone and Zuloaga	654 (CIAT); Ramos s/n (SF); Reinheimer et al. 8 (SF); Reinheimer et Guarise 105 (SF)
Urochloa sclerochlaena Chiov. ex Chiarugi	*Urochloa sclerochlaena* var. *commelinoides* Chiov.	Graham 83 (US)
Urochloa setigera (Retz.) Stapf	*Brachiaria setigera* (Retz.) C.E. Hubb.; *Panicum euryphyllum* Peter; *Panicum setigerum* Retz.; *Panicum trichopodioides* Mez and Schum.; *Urochloa trichopodioides* (Mez and Schum.) S.M. Phillips and S.L. Chen	Davidse et Sumithraarachchi 8996 (NY); Mueller-Dombois et Cooray 67121011 (US); Milne-Redhead et Taylor 7270 (US); Faulkner 3293 (US); Gould et Cooray 13712 (US); Kabuye et al. TPR-50 (US)
Urochloa subulifolia (Mez) A.M. Torres and C.M. Morton	*Brachiaria subulifolia* (Mez) Clayton; *Brachiaria filifolia* Stapf; *Panicum subulifolium* Mez	H.B.G. 27322 (LIL); Laegaard 15786 (US); Milne-Redheard et Taylor 8034 (US)
Urochloa texana (Buckley) R.D. Webster	*Brachiaria texana* (Buckley) S.T. Blake; *Panicum texanum* Buckley; *Panicum texanum* Vasey	Bryson et Wayne Morris 6906 (MO); Richard II 1352 (MO); Thomas 146055 (MO); Coston 61 (NY)
Urochloa trichopus (Hochst.) Stapf	*Eriochloa trichopus* (Hochst.) Benth.; *Eriochloa trichopus* var. *glabrata* Schweinf.; *Helopus trichopus* (Hochst.) Steud.; *Panicum papillosum* Fenzl ex Steud.; *Panicum trichopodon* A. Rich.; *Panicum trichopus* Hochst.; *Panicum trichopus* var. *chiovendae* Mattei; *Urochloa brachyphylla* Gilli; *Urochloa engleri* Pilg.	Ash 2564 (US); Madsen s/n (NY); Swaziland 15251 (US)
Urochloa venosa (Swallen) Morrone and Zuloaga	*Panicum venosum* Swallen	Leavenworth 481 (MO)
Urochloa villosa (Lam.) T.Q. Nguyen	*Brachiaria distichophylla* (Trin.) Stapf; *Brachiaria villosa* (Lam.) A. Camus; *Brachiaria coccosperma* (Steud.) Stapf ex Reeder; *Brachiaria villosa* f. *glabriglumis* (Ohwi) Ohwi; *Brachiaria villosa* var. *glaberrima* Basappa and Muniy.; *Brachiaria villosa* var. *glabrata* S.L. Chen and Y.X. Jin; *Panicum coccospermum* Steud.; *Panicum villosum* Lam.; *Urochloa coccosperma* (Steud.) Stapf ex Reeder	Beale 2168 (LIL); Meinzingen and Conert 55, 402, 438, 468, 616 (LIL); Praia Varela 2285 (MO); Sihvonen 247 (MO); Clemens 16216 (NY); Ramos 80569 (NY); Adjanohoum 385A (US; MO); Haperup O. 413 (US); Hitchcock 24936 (US); Maitland 892A (US); Pobeguin 1734 (US)
Urochloa whiteana (Domin) R.D. Webster	*Brachiaria whiteana* (Domin) C.E. Hubb.; *Panicum whiteanum* Domin	Hubbard 2749, 8092 (MO)
Urochloa xantholeuca (Hack. ex Schinz) H. Scholz	*Brachiaria xantholeuca* (Hack. ex Schinz) Stapf; *Panicum xantholeucum* Hack. ex Schinz	Burlt 4553 (US); Dyson-Hudson 56 (US); Liebenberg 9 (US); Williams 238 (US)
Yvesia madagascariensis A. Camus	_	Bathie 11055 (US); Perroi 11055 (US)

CIAT Centro Internacional de Agricultura Tropical; *CTES* Herbario del Instituto de Botánica del Nordeste; *ISC* Ada Hayden Herbarium; *LIL* Herbario Fanerogámico de la Fundación Miguel Lillo; *MCNS* Herbario del Museo de Ciencias Naturales de Salta; *MO* Missouri Botanical Garden; *NY* New York Botanical Garden; *SF* Herbario "E. A. Ragonese"; *BAA* Herbario "Gaspar Xuarez"; *SI* Herbario del Instituto de Botánica "Darwinion"; *US* Smithsonian Institution included because of lack of material. The botanical nomenclature for the species of the PCK Clade is highly diverse and confuse. For that reason, in Table 1 we also provided the most common synonyms for each species.

We studied the branch system of the entire plant using the terminology proposed by Troll and Weberling (Troll 1964; Weberling 1989; Vegetti and Weberling 1996; Rua and Weberling 1998) based on the comparison of plant forms (Rua 1999). Observations were recorded according to the different zones of the synflorescence (shoot system of the plant originated from the apical meristem or axillary buds, (innovations), Troll and Weberling 1989) and schematic drawings have been made accompanying the descriptions. The figures have been prepared with the intention to reflect as closely as possible the shape and architecture of the inflorescence as seen in nature or herbarium material.

For SEM observations, inflorescences were collected from plants of *Megathyrsus maximus* (Reinheimer 129, SF) and *Urochloa lata* (Schumach.) C.E. Hubb. (CIAT # 26886) growing at the Agronomy School of the University of Litoral (Esperanza, Argentina), after which they were fixed in FAA (formalin:acetic acid:70% ethanol, 10:5:85, v/v), and dehydrated in an alcohol series plus two final changes of 100% acetone. Dehydrated material was critical point dried using CO_2 as transitional fluid and coated with gold–palladium using a Thermo VG Scientific POLARON SC7620 SPUTTER COATER (Balzers, Switzerland). All samples were observed and photographed using a PHILIPS XL30 series (Eindhoven, The Netherlands) scanning electron microscope from the Electron Microscopy Service of the "Bernardino Rivadavia" Natural Science Museum (Buenos Aires, Argentina).

Results

Synflorescence zones

In the PCK Clade, the main inflorescence axis of the plant and each innovation can be considered as a synflorescence of a different degree. Each synflorescence has a distal region, the anthotagma (region that bears the floral axis) and a proximal region, the trophotagma (region that usually has a vegetative function) (Figs. 2–4). In all genera analyzed in this work, the anthotagma region is represented by the terminal inflorescence (IF) which develops above the last formed leaf along the main axis or innovation. In the PCK Clade the inflorescence is a paniculodium, that is, a panicle that has spikelets in place of flowers. In general, the inflorescence has flowering branches (paracladia or branches of the inflorescence, B) which lack well developed leaves or bracts, except for those that form the spikelet (Figs. 2–4).

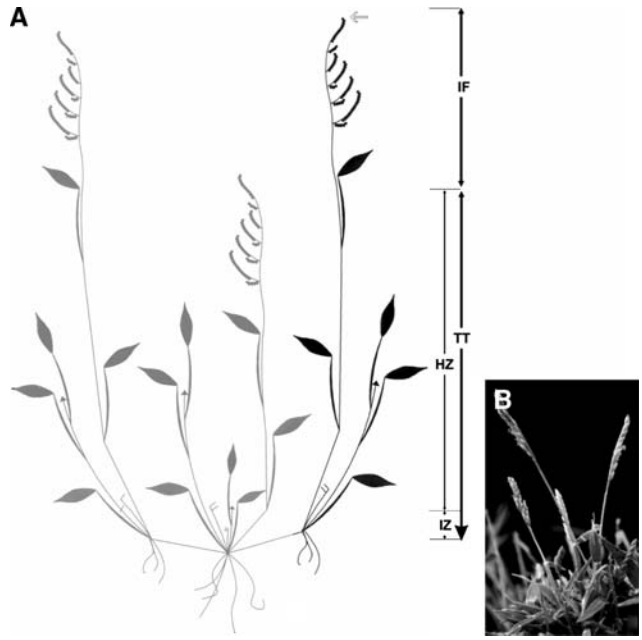


Fig. 2 *Brachiaria eruciformis* synflorescence (shoot system originated from the apical meristem or axillary buds of the whole plant). **a** simplified scheme; **b** photograph of the synflorescence. *HZ* inhibition zone; *IZ* innovation zone; *TT* trophotagma region; *IF* inflorescence. The *arrow* indicates the terminal spikelet on the main florescence

In the PCK Clade, the inflorescence begins with the most proximal primary branch (B^1) and extends to the most distal primary branch. Distal to the uppermost primary branch, the main axis of the inflorescence continues its development and, depending on the species, ends in a main florescence or terminal spikelet (TS), or aborts (Figs. 2–4).

The trophotagma region (TT) is the region of the synflorescence that bears well-developed leaves, sometimes preceded by proximal cataphylls (Figs. 2–4). Usually, the trophotagma region shows a proximal area of short internodes (the innovation zone, IZ) where the innovation axis (IN) originates from axillary buds, and a distal area of long internodes, that could be the inhibition zone (HZ) or may also behave partially as an enrichment zone (EZ).

Presence of an enrichment zone in the trophotagma region

Among the studied species, the area of long internodes in the trophotagma region commonly shows an enrichment zone and an inhibition zone. That is, the axillary buds of the most distal vegetative leaves of the trophotagma region (just below the inflorescence), often develop branches that bear well developed leaves (paracladia of the trophotagma or branches of the trophotagma, B_{TT}) and eventually may end in a terminal inflorescence (Fig. 4). In these cases, the enrichment zone of the trophotagma region is represented by branches of the trophotagma that repeat the ramification

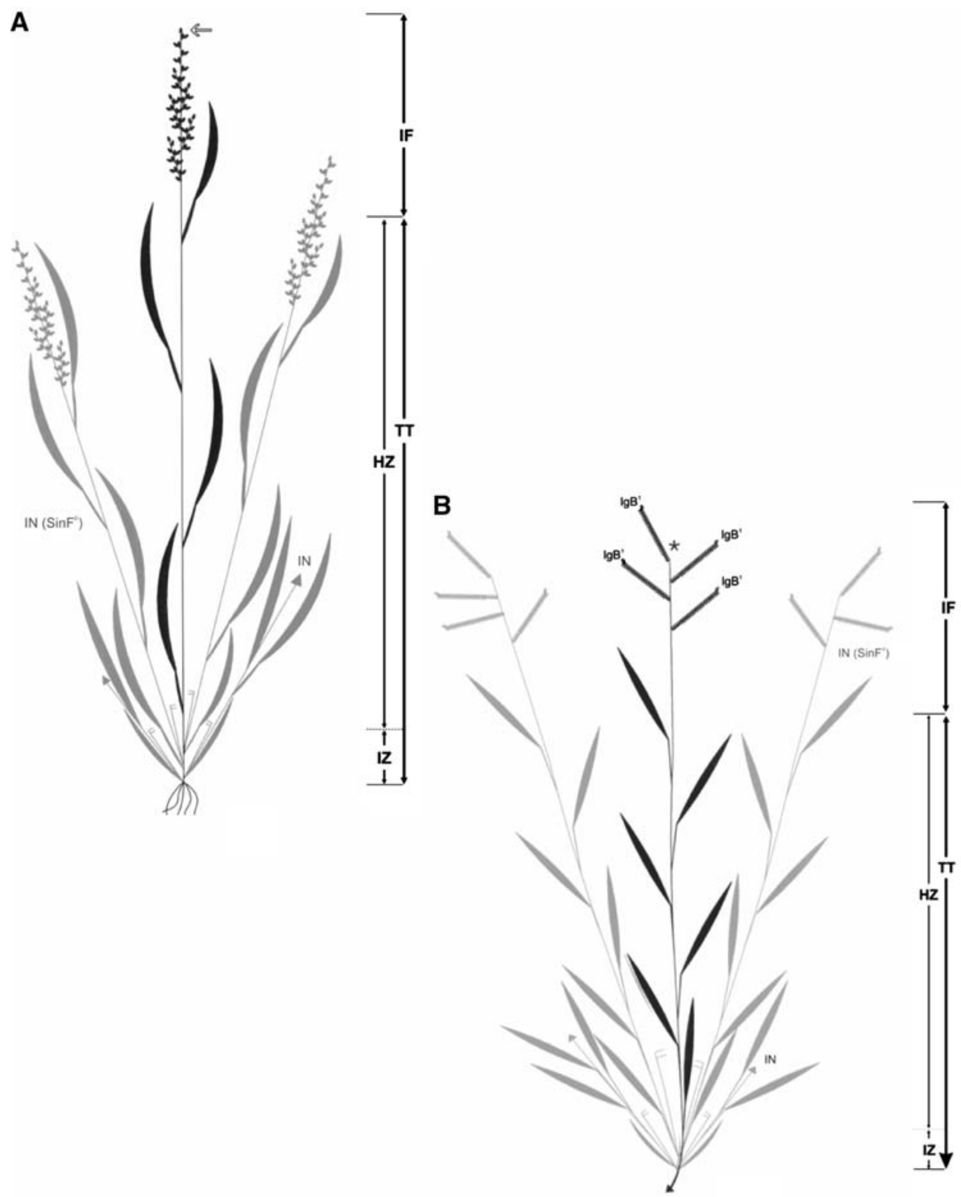


Fig. 3 Simplified scheme of the *Urochloa* synflorescence without branches of the trophotagma. **a** *Urochloa paucispicata*; **b** *Urochloa brizantha*. *HZ* inhibition zone; *IN* innovation; *IN(SinF^{II})* synflorescence of second order; *IZ* innovation zone; *lgB^1* long primary branch; *TT* trophotagma region; *IF* inflorescence. The *arrow* indicates the terminal spikelet of the main axis. The *asterisk* indicates the absence of the terminal spikelet on the main axis

pattern of the main axis. In *Brachiaria*, *Chaetium*, *Eriochloa*, *Megathyrsus*, *Melinis*, and *Urochloa* the enrichment zone in the trophotagma region may be present or not depending on the studied species. In contrast, synflorescences of *Thuarea* and *Yvesia* never develop an enrichment zone in the long internode region (Table 2).

Variation of the inflorescence

The inflorescence is the most variable region of the synflorescence among the studied species. Morphological differences include: (1) presence or absence of a bract entirely surrounding the inflorescence; (2) different degrees of homogenization of the primary branches (morphological similarity of inflorescence branches); (3) presence or absence (truncation) of the distal part of the main axis and distal parts of the branches; (4) orientation of primary branches along the main axis (inflorescence symmetry); (5) number and maximum branch degree of the primary branches; (6) differences in main axis internode length and disposition of the primary branches; (7) differences in the internode length of branches; (8) spikelet distribution and organization on the branch; and (9) total number, ramification degree and phyllotaxis of the most distal primary branch of the inflorescence.

Presence of foliage leaves in the inflorescence

Thuarea involuta (G. Forst.) R. Br. ex Sm. is the only species that has a spathaceous bract that encloses and presumably

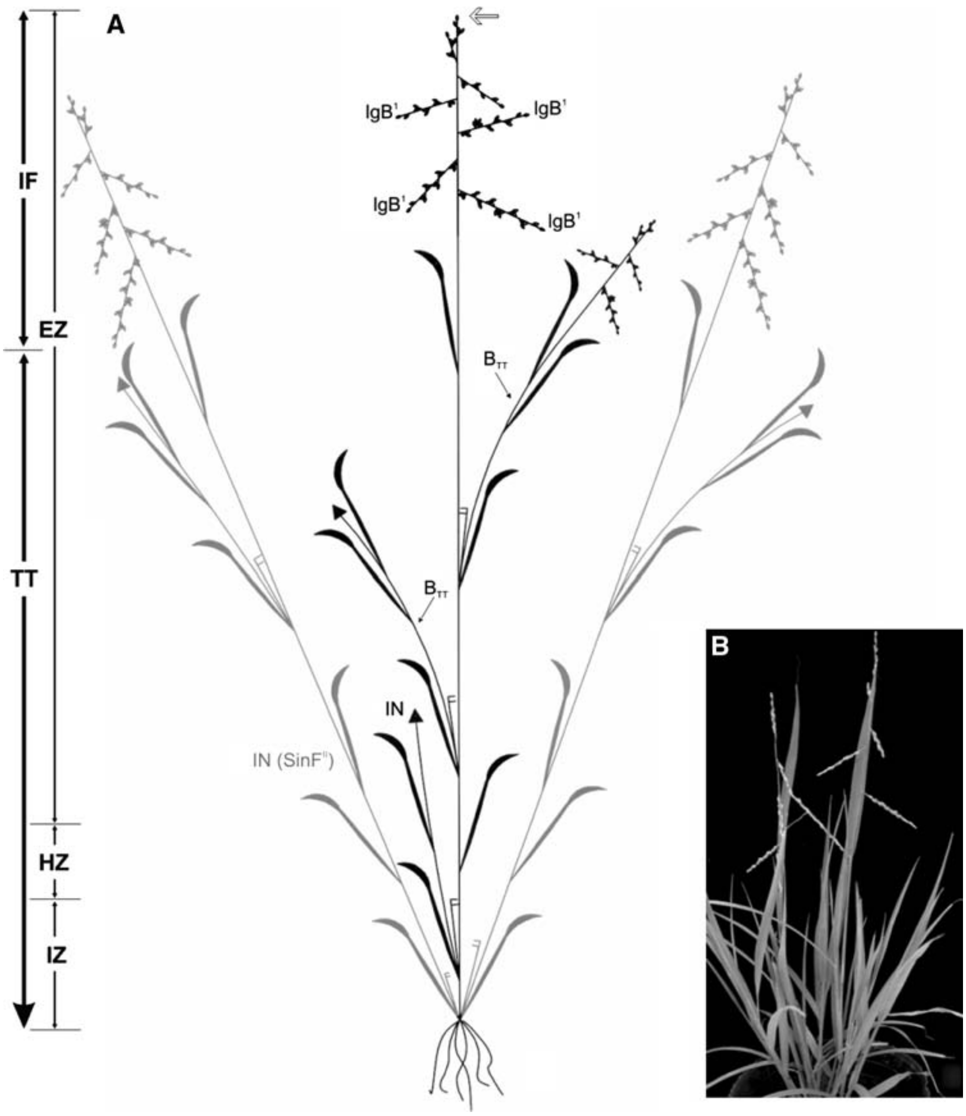


Fig. 4 Synflorescence of *Urochloa leucacrantha* with branches of the trophotagma. **a** simplified scheme; **b** photograph of the synflorescence. B_{TT} trophotagma branch; *EZ* enrichment zone; *HZ* inhibition zone; *IN* innovation; *IN(SinF^{II})* synflorescence of second order; *IZ* innovation zone; *lgB^{1}* long primary branch; *TT* trophotagma region; *IF* inflorescence. The *arrow* indicates the terminal spikelet on the main florescence

protects the inflorescence. This bract subtends the single primary branch that makes up the inflorescence (Fig. 8a).

Homogenization degree of the inflorescence

We found three different homogenization degrees among the inflorescences of the PCK Clade: (1) fully homogenized, (2) partially homogenized, and (3) non-homogenized. In the fully homogenized inflorescence, the maximum degree of ramification (in general, second or third order; B^2, B^3) is the same along the branch and for all primary branches, independent of position on the inflorescence (Figs. 5, 8; Table 2, 3). The partially homogenized inflorescence has primary branches with ramification from third to fifth order (B^3, B^4 and B^5) located at the proximal region, while the primary branches in the middle and distal regions all show the same branch ramification pattern (usually of second or third order) (Figs. 6, 9; Tables 2, 3). In homogenized inflorescences it is possible to recognize two different types of primary branches in the same inflorescence, short paracladia or short primary branches (shB^1) and long paracladia or long primary branches (lgB^1) (Figs. 5, 6, 8, and 9; Tables 2, 3). In contrast, the non-homogenized inflorescence does not show specialization of branches (Fig. 7).

The inflorescence of the PCK Clade presents different degrees of homogenization depending on the species. For example, the inflorescences of *Megathyrsus*, *Melinis*, *Yvesia* and a few species of *Urochloa* are non-homogenized; the proximal primary branch may have up to fifth or sixth order ramifications (B^5 and B^6) (e.g. *Megathyrsus* and *Melinis*), which gradually decrease in the primary branches located at the middle and distal regions of the inflorescence (Fig. 7; Tables 2, 4). In contrast, the inflorescences of

Table 2 Presence of the enrichment zone along the synflorescence and different degree of inflorescence homogenization and truncation in the PCK Clade

Species	Presence/ absence of B_{TT}	Trunc. of TS	Degree of H	Trunc. of shB[1]	Trunc. of lgB[1]	Trunc. of ts
Brachiaria ambigens	Absence	No	Fully	No	No	No
Brachiaria chusqueoides	Absence	No	Non homogenized	No	No	No
Brachiaria clavipila	Absence	No	Fully	No	No	No
Brachiaria coronifera	Presence	No	Fully	No	No	No
Brachiaria dimorpha	Absence	No	Fully	No	Yes	No
Brachiaria epacridifolia	Absence	No	Fully	No	Yes	No
Brachiaria eruciformis	Absence	No	Partially	No	No	No
Brachiaria foliosa	Absence	No	Partially	No	No	No
Brachiaria grossa	Presence	No	Partially	No	No	No
Brachiaria humbertiana	Absence	No	Fully	No	No	No
Brachiaria leucophyrs	Absence	No	Partially	No	No	No
Brachiaria longiflora	Absence	?	Non homogenized	?	No	No
Brachiaria malacodes	Absence	No	Partially	No	No	No
Brachiaria marlothii	Absence	Yes	Fully	Yes	No	No
Brachiaria ovalis	Presence	No	Fully	No	No	No
Brachiaria pseudodichotoma	Presence	Yes	Fully	Yes	No	No
Brachiaria pubifolia	Absence	Yes	Fully	Yes	No	No
Brachiaria pungipes	Absence	No	Fully	Yes	No	No
Brachiaria rugulosa	Absence	Yes	Fully	Yes	No	No
Brachiaria scalaris	Presence	No	Fully	No	No	No
Brachiaria schoenfelderi	Absence	No	Partially	No	No	No
Brachiaria serrata	Presence	No	Fully	No	No	No
Brachiaria serrifolia	Absence	No	Fully	No	No	No
Brachiaria stigmatisata	Presence	Yes	Fully	Yes	No	No
Brachiaria tsiafajavonensis	Presence	No	Partially	No	No	No
Brachiaria umbelata	Presence	No	Non homogenized	No	No	No
Brachiaria umbralitis	Presence	No	Partially	No	No	No
Brachiaria urocoides	Absence	No	Fully	No	No	No
Chaetium bromoides	Presence	No	Partially-fully	No	No	No
Chaetium cubanum	Absence	No	Fully	No	No	No
Eriochloa aristata	?	Yes	Fully	Yes	No	No
Eriochloa distachya	?	Yes	Fully	Yes	No	No
Eriochloa grandiflora	?	Yes	Fully	Yes	No	No
Eriochloa mollis	?	Yes	Fully	Yes	No	No
Eriochloa montevidensis	Presence	Yes	Partially	Yes	No	No
Eriochloa polystachia	?	Yes	Partially	Yes	No	No
Eriochloa procera	?	Yes	Partially	Yes	No	No
Eriochloa punctata	Presence	Yes	Fully	Yes	No	No
Eriochloa setosa	?	Yes	Fully	Yes	No	No
Eriochloa villosa	?	Yes	Fully	Yes	No	No
Megathyrsus maximus	Presence	No	Non homogenized	No	No	No
Melinis leucantha	?	No	Non homogenized	No	No	No
Melinis minutiflora	Presence	No	Non homogenized	No	No	No
Melinis monachne	Absence	No	Non homogenized	No	No	No
Melinis repens	Presence	No	Non homogenized	No	No	No
Thuarea involuta	Absence	Yes	Fully	Yes	No	No

Table 2 continued

Species	Presence/ absence of B_{TT}	Trunc. of TS	Degree of H	Trunc. of shB[1]	Trunc. of lgB[1]	Trunc. of ts
Urochloa acuminata	Presence	No	Partially	No	No	No
Urochloa adspersa	Presence	Yes	Partially	Yes	No	No
Urochloa advena	Absence	No	Fully	No	No	No
Urochloa arizonica	Presence	No	Partially	No	No	No
Urochloa arrecta	?	No	Partially	No	No	No
Urochloa atrisola	Presence	Yes	Fully	Yes	No	No
Urochloa bovonei	Absence	Yes	Fully	Yes	No	No
Urochloa brachyura	Presence	Yes	Fully	Yes	No	No
Urochloa brizantha	Absence	Yes	Fully	Yes	No	No
Urochloa ciliatissima	Presence	No	Fully	No	No	No
Urochloa comata	Absence	No	Non homogenized	No	No	No
Urochloa decidua	Absence	No	Partially	No	No	No
Urochloa decumbens	Absence	Yes	Fully	Yes	No	No
Urochloa deflexa	Presence	No	Partially	No	No	No
Urochloa dictyoneura	Absence	Yes	Fully	Yes	No	No
Urochloa distachya	Absence	Yes	Fully	Yes	No	Yes
Urochloa dura	Absence	Yes	Fully	Yes	No	No
Urochloa echinolaenoides	Absence	Yes	Fully	Yes	No	No
Urochloa eminii	Absence	No	Fully	No	No	No
Urochloa fusca	Presence	No	Partially	No	No	No
Urochloa fusiformis	Presence	No	Fully	No	No	No
Urochloa gilesii	Presence	Yes	Fully	Yes	No	No
Urochloa glumaris	Absence	Yes	Fully	Yes	No	No
Urochloa holosericea	Absence	No	Fully	No	Yes	No
Urochloa humidicola	Absence	Yes	Fully	Yes	No	No
Urochloa jubata	Absence	Yes	Fully	Yes	No	No
Urochloa kurzii	Presence	No	Fully	No	No	No
Urochloa lachnantha	Absence	No	Fully	No	No	No
Urochloa lata	Presence	Yes	Fully	Yes	No	No
Urochloa leucacrantha	Presence	No	Partially-fully	No	No	No
Urochloa lorentziana	Presence	No	Partially	No	No	No
Urochloa meziana	Presence	Yes	Fully	Yes	No	No
Urochloa mollis	Absence	No	Partially	No	No	No
Urochloa mosambicensis	Presence	Yes	Fully	Yes	No	No
Urochloa mutica	Presence	No	Partially	No	No	No
Urochloa nigropedata	Absence	Yes	Partially	Yes	No	No
Urochloa notochthena	Presence	Yes	Fully	Yes	No	No
Urochloa oblita	Presence	No	Fully	No	No	No
Urochloa oligotricha	Absence	No	Fully	No	No	No
Urochloa ophryodes	?	Yes	Fully	Yes	No	No
Urochloa panicoides	Presence	Yes	Fully	Yes	No	No
Urochloa paucispicata	Absence	No	Fully	No	No	No
Urochloa piligera	Presence	Yes	Fully	Yes	No	No
Urochloa plantaginea	Presence	Yes	Partially	Yes	No	No
Urochloa platynota	Absence	Yes	Fully	Yes	No	No
Urochloa platyphylla	Presence	Yes	Fully	Yes	No	No
Urochloa platytaenia	Presence	Yes	Fully	Yes	No	No

Table 2 continued

Species	Presence/ absence of B_{TT}	Trunc. of TS	Degree of H	Trunc. of shB[1]	Trunc. of lgB[1]	Trunc. of ts
Urochloa pratervisa	Presence	No	Fully	No	No	No
Urochloa pubigera	Absence	No	Partially	No	No	No
Urochloa ramosa	Absence	No	Partially	No	No	No
Urochloa rudis	Absence	Yes	Fully	Yes	No	No
Urochloa ruziziensis	Absence	Yes	Fully	Yes	No	Yes
Urochloa sclerochleaena	Presence	No	Fully	No	No	No
Urochloa setigera	?	Yes	Fully	Yes	No	No
Urochloa subulifolia	Absence	Yes	Fully	Yes	No	No
Urochloa texana	Absence	No	Fully	No	No	No
Urochloa trichopus	Presence	Yes	Fully	Yes	No	No
Urochloa venosa	Absence	No	Partially	No	No	No
Urochloa villosa	Absence	No	Partially	No	No	No
Urochloa whiteana	Absence	Yes	Fully	Yes	No	No
Urochloa xantholeuca	Absence	No	Partial	No	No	No
Yuesia madagascariensis	Absence	No	Non homogenized	No	No	No

B_{TT} branch of the trophotagma; *H* homogenization; *shB*[1] short primary branch; *lgB*[1] long primary branch; *Trunc.* truncation; *TS* terminal spikelet of the main axis; *ts*, terminal spikelet at the tip of the primary branch;? missing data

Brachiaria, *Chaetium*, *Eriochloa* and *Urochloa* may be, in general, partially or fully homogenized depending on the species (Figs. 5, 6, 8, and 9; Tables 2, 3), while *Thuarea* has only completely homogenized inflorescences (Fig. 8a; Tables 2, 3). Usually, the degree of homogenization does not vary within a species, but in *Chaetium bromoides* (J. Presl) Benth. ex Hemsl. and *Urochloa leucacrantha* (K. Schum.) Stapf this character is polymorphic, varying between partially and fully homogenized depending on the sample studied (Tables 2, 3).

Presence or absence of the main axis terminal spikelet

In *Chaetium*, *Megathyrsus*, *Melinis* and *Yvesia* the main axis ends in a terminal spikelet (Fig. 7; Tables 2–4). In contrast, the main axis in *Eriochloa* and *Thuarea* may end in a sterile prolongation, in a dome or the most distal primary branch can adopt the terminal position of the main axis as a continuation of it (Figs. 8a, 9c; Tables 2–4). *Brachiaria* and *Urochloa* vary in the presence or absence of the terminal spikelet depending on the species (Figs. 5, 6, 8, and 9, 10a, b, e, i; Tables 2–4).

Presence or absence of different types of inflorescence branches

Among the homogenized inflorescences, all species that lack the terminal spikelet also lack short primary branches, and in consequence those inflorescences are represented only by long primary branches (Figs. 8, 9; Table 3). In contrast, in species that are homogenized and have a terminal spikelet, the inflorescence is formed by both long and short primary branches (Figs. 5, 6; Table 3), except for *Brachiaria pungipes* Clayton, which has the terminal spikelet and long primary branches, but lacks short primary branches (Fig. 5a). Moreover, some inflorescences that are completely homogenized are made up of short primary branches and the terminal spikelet exclusively, and do not develop long primary branches (e.g. *B. dimorpha* A. Camus, *B. epacridifolia* (Stapf) A. Camus and *U. holosericea* (R. Br.) R.D. Webster, Fig. 5b).

Presence of a terminal spikelet on the primary branch

Like the inflorescence main axis, the primary branches may or may not end in a coflorescence or terminal spikelet (ts). In *U. ruziziensis* (R. Germ. and Evrard) Crins, we observed that the most distal spikelets on the primary branches, including the terminal spikelet, are abnormally developed and are also sterile at maturity (Fig. 8c). This phenomenon was also observed in some samples of *U. brizantha* (Hochst. ex A. Rich.) R.D. Webster and *U. decumbens* (Stapf) R.D. Webster (Fig. 10c, d).

Presence of a terminal spikelet on the third order branches

Some species of *Eriochloa*, *Brachiaria* and *Urochloa* (e.g. *B. grossa* Stapf, *B. ovalis* Stapf, *U. deflexa* (Schumach.)

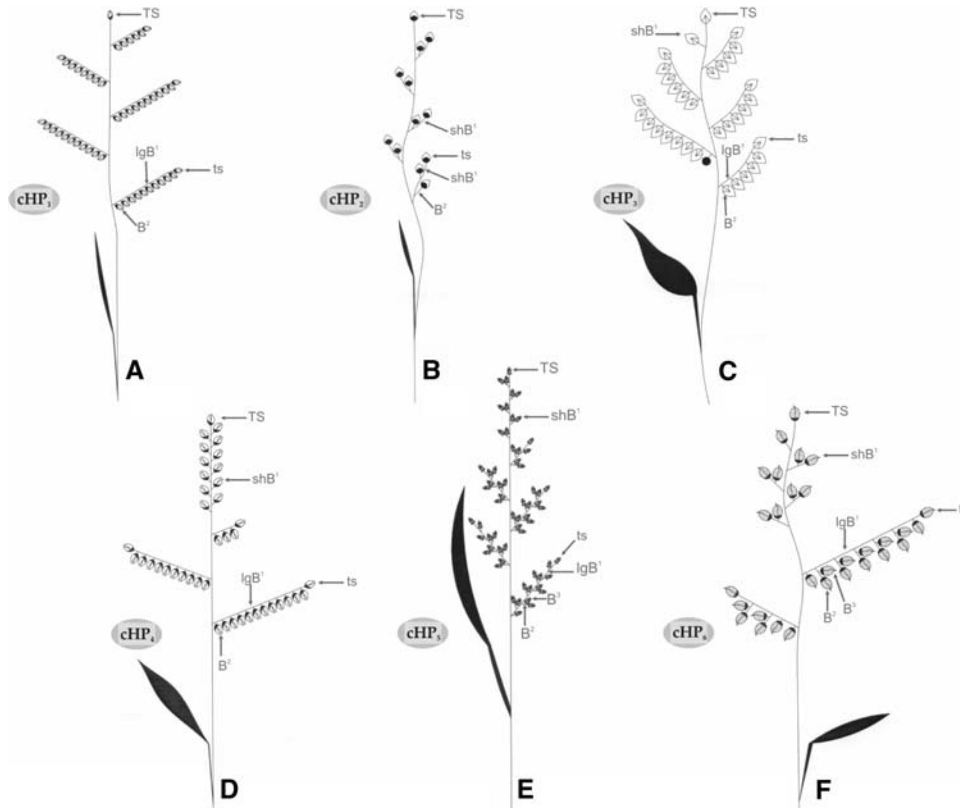


Fig. 5 Fully homogenized paniculodium (cHP-Type). **a** cHP_1-Subtype (*Brachiaria pungipes*); **b** cHP_2-Subtype (*Brachiaria dimorpha*); **c** cHP_3-Subtype (*Brachiaria scalaris*); **d** cHP_4-Subtype (*Urochloa advena*); **e** cHP_5-Subtype, (*Urochloa paucispicata*); **f** cHP_6-Subtype (*Urochloa sclerochlaena*). B^2 branch of second order; B^3 branch of third order; *TS* terminal spikelet of the main axis; *ts* terminal spikelet at the end of the primary branch; lgB^1 long primary branch; shB^1 short primary branch. The *black circle* indicates an aborted spikelet

H. Scholz, *U. lata*, *U. leucacrantha*, *U. meziana* (Hitchc.) Morrone & Zuloaga, *U. oligotricha* (Fig. & De Not.) Henrard, *U. panicoides* P. Beauv, *U. texana* (Buckley) R.D. Webster and *U. trichopus* (Hochst.) Stapf) show, at the tip of the third order branches, spikelets that develop abnormally and are sterile at maturity (Fig. 11a).

Inflorescence symmetry

Members of the PCK Clade show different inflorescence symmetries depending on the orientation of the primary branch along the main axis. The inflorescence may be unilateral (when the inflorescence has only one plane of symmetry, Fig. 1a, c, h, i, o, p), bilateral (with two planes of symmetry, Fig. 1b, f, j, k, n) or radiate (with more than two planes of symmetry, Fig. 1d, e, g, l, m).

Number and maximum degree of branch ramification

The total number of primary branches and the maximum degree of branch ramification vary extensively among members of the clade and also among different individuals of each studied species. Tables 3 and 4 document the variation in these characters for each species.

Orientation of the second order branches on the primary branch

This character is easy to interpret in species that have inflorescences with short second order branches and in which the primary branches are more or less flat (Fig. 10h–j). However, it is hard to assess in species that have mature inflorescence with long second order branches and with primary branches that are rounded in cross section. SEM studies show that, early in development and before the elongation of internodes, the second order branches are abaxial on the primary branches (Fig. 11b).

Differences in main axis internode length and disposition of the primary branches

In *Chaetium*, *Melinis* and many species of *Brachiaria*, *Eriochloa* and *Urochloa*, primary branches are always alternate along the main axis. However, because of differences in internode elongation of the main axis during development, the disposition of the primary branches varies widely across the clade and moreover, among the samples studied for each species. At maturity, therefore, the primary branches may appear subopposite (Figs. 6a, 7c) or pseudoverticillate (Fig. 7c). In Tables 3 and 4 we list the

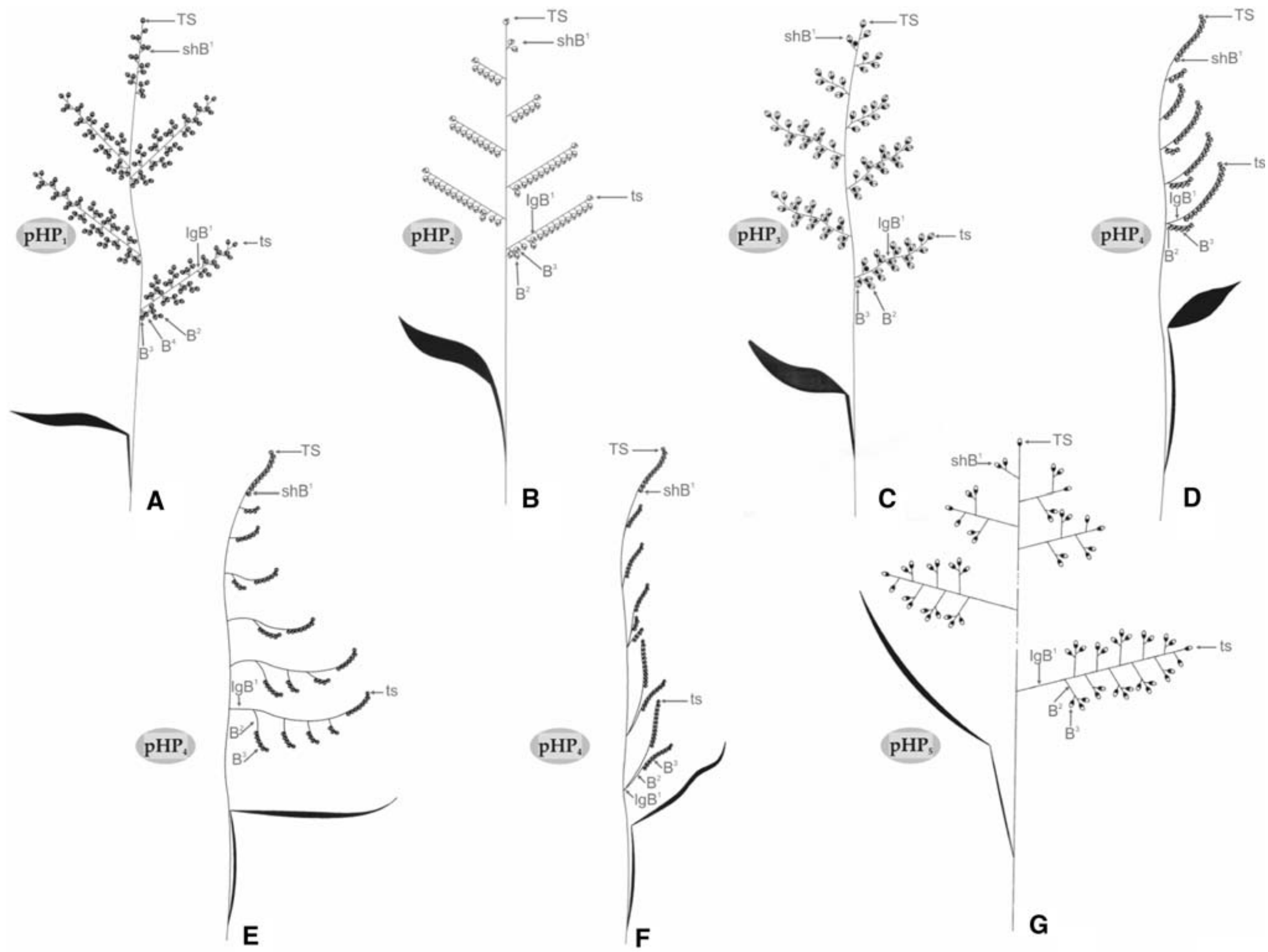


Fig. 6 Partially homogenized paniculodium (pHP-Type). **a** pHP_1-Subtype (*Urochloa fusca*); **b** pHP_2-Subtype (*Urochloa xantholeuca*); **c** pHP_3-Subtype (*Urochloa villosa*); **d** pHP_4-Subtype (*Brachiaria eruciformis*); **e** pHP_4-Subtype (*Brachiaria malacodes*); **f** pHP_4-Subtype (*Brachiaria schoenfelderi*); **g** pHP_5-Subtype (*Urochloa acuminata*). B^2 branch of second order; B^3 branch of third order; B^4 branch of fourth order; *TS* terminal spikelet of the main axis; *ts* terminal spikelet at the end of the primary branch; lgB^1 long primary branch; shB^1 short primary branch. The *black circle* indicates an aborted spikelet

disposition of the primary branches along the inflorescence main axis for each species.

Differences in the internode length of branches

The length of branch internodes varies among members of the clade. In the inflorescence of *Melinis* (Fig. 7b), pseudoverticils are formed by proximal branch internodes that do not elongate. That is, the most proximal branch internodes develop close to the inflorescence main axis and form false pseudoverticils. These false pseudoverticils are formed by the proximity of second to fifth order branches instead of primary branches.

In contrast, in the inflorescences of *Megathyrsus maximus* and *Urochloa acuminata* (Renvoize) Morrone & Zuloaga the proximal internode of each primary branch is the longest in comparison with the rest of the internodes of the same primary branch and in consequence, the second order branches are placed far away from the inflorescence main axis (Figs. 6g, 7c).

The primary branch and second order branch internodes show length variation in *Brachiaria eruciformis* (Sm.) Griseb., *B. malacodes* (Mez & K. Schum.) H. Scholz and *B. schoenfelderi* C.E. Hubb. & Schweick. (Fig. 6d–f). In *B. eruciformis* the primary branch internodes are short except for the second proximal internode which is the longest one (Fig. 6d). In *B. malacodes*, at least the first and the second proximal internodes of the primary branches are long, in comparison with the rest, and also the proximal internodes of the second order branches is the longest one (Fig. 6e). In *B. schoenfelderi*, the second proximal internode is longer than the remaining internodes that form the primary

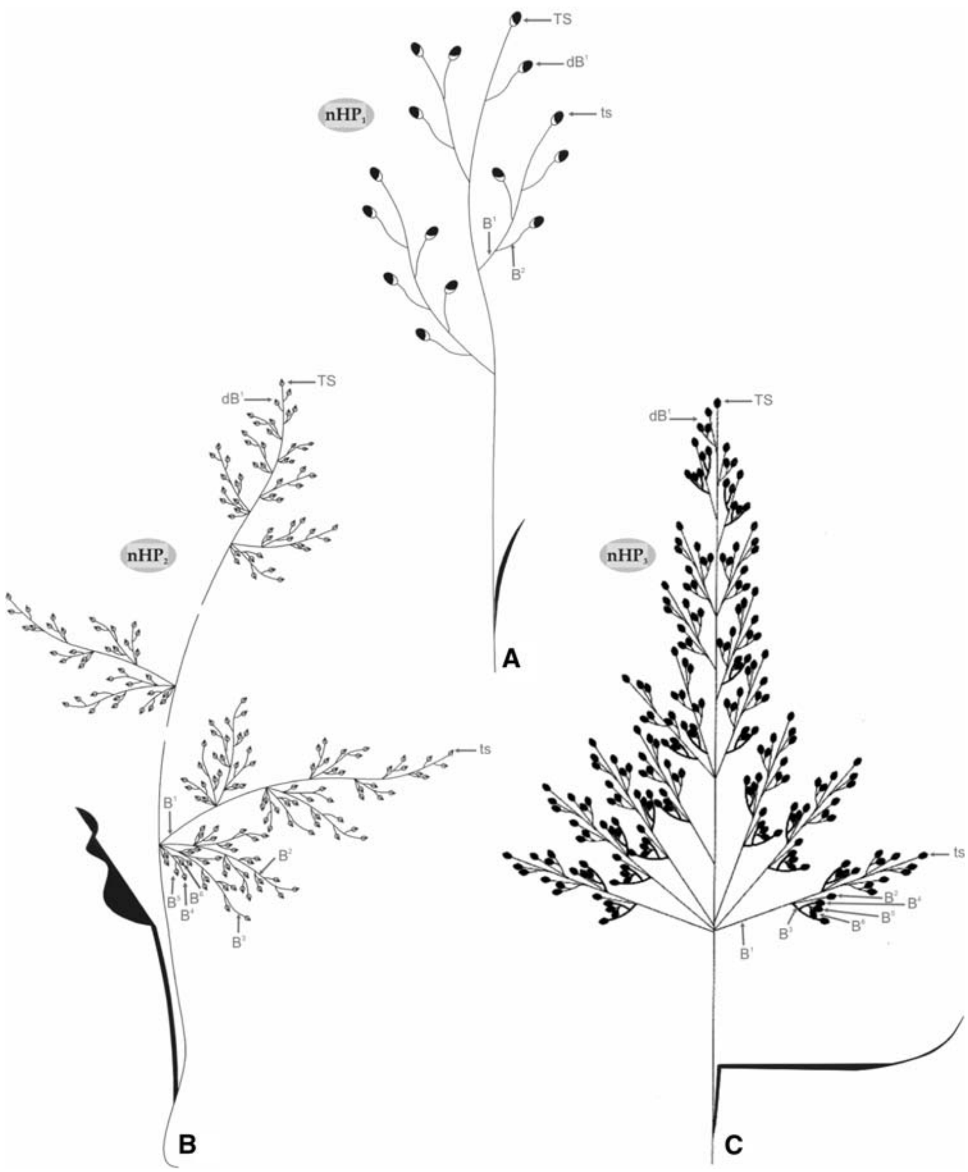


Fig. 7 Non-homogenized paniculodium (nHP-Type). **a** nHP_1-Subtype (*Yvesia madagascariensis*); **b** nHP_2-Subtype (*Melinis repens*); **c** nHP_3-Subtype (*Megathyrsus maximus*) (Reproduced by the authorization of American Journal of Botany, Reinheimer et al. 2005). B^1 primary branch; B^2 branch of second order; B^3 branch of third order; B^4 branch of fourth order; B^5 branch of fifth order; B^6 branch of sixth order; dB^1 distal primary branch; *TS* terminal spikelet of the main axis; *ts* terminal spikelet at the end of the primary branch

branches, while the proximal internode of the second order branches is always longer than the rest of the internodes that form that branch (Fig. 6f).

Spikelet distribution and organization on the branch

In partially or completely homogenized inflorescences, it is easy to assess the distribution and organization of spikelets on the primary branches. In such species the primary branch bears second order branches that may be in one or two rows and may end in a terminal spikelet or may end in a terminal spikelet and have a third order branch at the base. The third order branch may either (1) fail to form a well-developed terminal spikelet; (2) end in a terminal spikelet; or (3) end in a terminal spikelet and develop a new branch (B^4) at its base. As a result, depending on the ramification degree of the primary branch and considering the three patterns described above, the spikelets could be solitary in one row (e.g. *Thuarea involuta*, Fig. 8a), or they could be organized in two rows and be solitary (e.g. some species of *Brachiaria*, *Eriochloa* and many species of *Urochloa*, Fig. 10c, f, g), or solitary with the second spikelet aborted at the base (e.g. *Eriochloa punctata* (L.) Desv. ex Ham., *B. dimorpha*, *U. adpersa* (Trin.) R.D. Webster, *U. bulbodes* (Steudel) Stapf, *U. deflexa* (Schumach.) H. Scholz, *U. lata*, *U. panicoides* and *U. trichopus* (Hochst.) Stapf, Fig. 11a) or be paired (e.g. some species of *Chaetium*, *Brachiaria*, *Eriochloa* and *Urochloa*).

In contrast, for species with a non-homogenized inflorescence with more than three orders of branching, the identification of numbers of rows and spikelet organization becomes hard to assess.

Table 3 Inflorescence variation among members of the PCK Clade with fully or partially homogenized inflorescence

Species	Total *N*° of B^1	*N*° of lgB^1	Disposition of B^1	Max. branch degree of B^1	*N*° of shB^1	Ramification degree of shB^1	Disposition of shB^1	IF type and subtype
Brachiaria ambigens	11–16	9–10	Alt. and subop.	2°	2–3	1°, 2°	Alternate	cHP$_3$
Brachiaria clavipila	8–12	3–4	Alternate	2°	5–8	1°, 2°	Alternate	cHP$_4$
Brachiaria coronifera	5–11	4–10	Alt. and subop.	2°	1	2°	Alternate	cHP$_3$
Brachiaria dimorpha	3–7	0–7	Alternate	2°	1–4	2°	Alternate	cHP$_2$
Brachiaria epacridifolia	3–5	0–2	Alternate	2°	3	1°, 2°	Alternate	cHP$_2$
Brachiaria eruciformis	1–10	3–10	Alternate	3°	9–19	1°	Alternate	pHP$_4$
Brachiaria foliosa	6–11	8–9	Alternate	3°	2–3	1°, 2°	Alternate	pHP$_3$
Brachiaria grossa	6–12	4–10	Alternate	4°	2–3	2°	Alternate	pHP$_1$
Brachiaria humbertiana	5–8	3–4	Alternate	3°	2–4	1°, 2°	Alternate	cHP$_5$
Brachiaria leucophyrs	15	4	Alternate	4°	11	1°, 2°	Alternate	pHP$_1$
Brachiaria malacodes	18–22	8–11	Alternate	3°	9–11	1°	Alternate	pHP$_4$
Brachiaria marlothii	5–9	5–9	Alternate	3°	–	–	–	cHPT$_2$
Brachiaria ovalis	5–8	3–5	Alternate	3°	3–5	1°, 2°	Alternate	cHP$_6$
Brachiaria pseudodichotoma	1–3	1–3	Alternate	2°	–	–	–	cHPT$_4$
Brachiaria pubifolia	2–8	2–8	Alternate	2°	–	–	–	cHPT$_4$
Brachiaria pungipes	5–8	5–8	Alternate	2°	0	–	–	cHP$_1$
Brachiaria rugulosa	3	3	Alternate	2°	–	–	–	cH$_4$PT
Brachiaria scalaris	4–21	2–19	Alternate	2°	1–4	1°, 2°	Alternate	cHP$_3$
Brachiaria schoenfelderi	18–24	8–13	Alternate	3°	5–16	1°	Alternate	pHP$_4$
Brachiaria serrata	5–20	3–16	Alternate	2°	2–6	1°, 2°	Alternate	cHP$_3$
Brachiaria serrifolia	6–12	4–9	Alternate	3°	1–4	1°, 3°	Alternate	cHP$_5$
Brachiaria stigmatisata	2–5	2–5	Alternate	2°	–	–	–	cHPT$_4$
Brachiaria tsiafajavonensis	5–10	3–6	Alt. and subop.	3°	2–5	1°, 2°	Alternate	pHP$_3$
Brachiaria umbralitis	10–12	6–8	Alternate	3°	3–4	1°, 2°	Alternate	pHP$_2$
Brachiaria urocoides	15–21	3–5	Alternate	2°	11–16	1°	Alternate	cHP$_4$
Chaetium bromoides	9–13	1–6	Alternate	3°–4°	6–12	1°, 2°	Alternate	cHP$_6$/pHP$_1$
Chaetium cubanum	10	3	Alternate	3°	7	1°, 2°	Alternate	cHP$_6$
Eriochloa aristata	5–10	5–10	Alternate	2°	–	–	–	cHPT$_4$
Eriochloa distachya	1–2	1–2	Alternate	2°	–	–	–	cHPT$_4$
Eriochloa grandiflora	4–6	4–6	Alternate	2°	–	–	–	cHPT$_4$
Eriochloa mollis	6	6	Alternate	2°	–	–	–	cHPT$_4$
Eriochloa montevidensis	3–13	3–13	Alt. and subop.	3°	–	–	–	pHPT$_3$
Eriochloa polystachia	6–20	6–20	Alt. and subop.	3°	–	–	–	pHPT$_3$
Eriochloa procera	5–14	5–14	Alternate	3°, 4°	–	–	–	pHPT$_1$
Eriochloa punctata	5–17	5–17	Alt. and subop.	2°	–	–	–	cHPT$_4$
Eriochloa setosa	2	2	Alternate	2°	–	–	–	cHPT$_4$
Eriochloa villosa	2	2	Alternate	2°	–	–	–	cHPT$_4$
Thuarea involuta	1	1	–	2°	–	–	–	cHPT$_1$
Urochloa acuminata	28	24–27	Alt., subop. and pseudov.	3°	1–4	1°, 2°	Alternate	pHP$_5$
Urochloa adspersa	2–10	2–10	Alt., subop. and pseudov.	4°	–	–	–	pHPT$_1$
Urochloa advena	15–18	3	Alternate	2°	12–15	1°	Alternate	cHP$_4$
Urochloa arizonica	9–12	5–8	Alternate	4°	4–5	1°, 2°	Alternate	pHP$_1$
Urochloa arrecta	?	?	Alt. and subop.	4°	?	?	?	pHP$_1$
Urochloa atrisola	2	2	Alternate	2°	–	–	–	cHPT$_4$
Urochloa bovonei	1–5	1–5	Alternate	2°	–	–	–	cHPT$_4$
Urochloa brachyura	3–9	3–9	Alternate	3°	–	–	–	cHPT$_2$
Urochloa brizantha	4	4	Alternate	2°	–	–	–	cHPT$_4$/cHPT$_3$

Table 3 continued

Species	Total *N*° of B[1]	*N*° of lgB[1]	Disposition of B[1]	Max. branch degree of B[1]	*N*° of shB[1]	Ramification degree of shB[1]	Disposition of shB[1]	IF type and subtype
Urochloa ciliatissima	5–7	3–4	Alternate	2°	3–4	1°, 2°	Alternate	cHP_3
Urochloa decidua	30	27	Alt., subop. and pseudov.	4°	3	1°, 2°	Alternate	pHP_1
Urochloa decumbens	3–7	3–7	Alternate	2°	_	_	_	$cHPT_4$/$cHPT_3$
Urochloa deflexa	6–17	5–15	Alt., subop. and pseudov.	3°, 4°	1–3	1°, 2°	Alternate	pHP_1
Urochloa dictyoneura	3–7	3–7	Alternate	2°	_	_	_	$cHPT_4$
Urochloa distachya	4–7	4–7	Alternate	2°	_	_	_	$cHPT_4$
Urochloa dura	1–2	1–2	Alternate	2°	_	_	_	$cHPT_4$
Urochloa echinolaenoides	1–2	1–2	Alternate	3°	_	_	_	$cHPT_2$
Urochloa eminii	9–10	7	Alt. and subop.	3°	2–3	1°, 2°	Alternate	cHP_5
Urochloa fusca	4–29	3–27	Alt., subop. and pseudov.	4°	1–7	1°, 2°	Alternate	pHP_1
Urochloa fusiformis	5–10	3–8	Alternate	2°	1–3	1°	Alternate	cHP_3
Urochloa gilesii	2–3	2–3	Alternate	2°	_	_	_	$cHPT_4$
Urochloa glumaris	2–9	2–9	Alt. and subop.	3°	_	_	_	$cHPT_2$
Urochloa holosericea	5–7	3–4	Alternate	2°	2–3	1°, 2°	Alternate	cHP_2
Urochloa humidicola	1–4	1–4	Alternate	2°	_	_	_	$cHPT_4$
Urochloa jubata	3–8	3–8	Alternate	2°	_	_	_	$cHPT_4$
Urochloa kurzii	5–6	3–4	Alternate	3°	2–3	1°	Alternate	cHP_5
Urochloa lachnantha	16	3	Alternate	3°	13	2°		cHP_6
Urochloa lata	4–7	4–7	Alt., subop. and pseudov.	3°	_	_	_	$cHPT_2$
Urochloa leucacrantha	1–11	1–6	Alternate	2°, 3°	1–5	1°, 2°	Alternate	cHP_5/pHP_2
Urochloa lorentziana	4–31	4–30	Alt., subop. and pseudov.	4°, 5°	1–5	1°, 2°	Alternate	pHP_1
Urochloa meziana	4–8	4–8	Alt. and subop.	2°	_	_	_	$cHPT_4$
Urochloa mollis	5–14	3–9	Alternate	3°	1–6	1°, 2°	Alternate	pHP_2
Urochloa mosambicensis	2–15	2–15	Alternate	2°	_	_	_	$cHPT_4$
Urochloa mutica	5–31	8–27	Alt., subop. and pseudov.	3°, 4°	3–7	1°, 2°	Alternate	pHP_1
Urochloa nigropedata	3–8		Alternate	3°	_	_	_	$pHPT_2$
Urochloa notochthena	2–3	2–3	Alternate	2°	_	_	_	$cHPT_4$
Urochloa oblita	6–12	3–6	Alternate	3°	3	2°	Alternate	cHP_5
Urochloa oligotricha	52–62	14–18	Alternate	3°	36–44	1°, 3°	Alternate	cHP_6
Urochloa ophryodes	2–3	2–3	Alternate	2°	_	_	_	$cHPT_4$
Urochloa panicoides	2–9	2–9	Alt. and subop.	2°	_	_	_	$cHPT_4$
Urochloa paucispicata	9–12	4–8	Alternate	3°	1–5	1°, 2°	Alternate	cHP_5
Urochloa piligera	2–4	2–4	Alternate	2°	_	_	_	$cHPT_4$
Urochloa plantaginea	2–14	2–14	Alternate	2°, 3°	_	_	_	$pHPT_2$
Urochloa platynota	2–3	2–3	Alternate	2°	_	_	_	$cHPT_4$
Urochloa platyphylla	2–6	2–6	Alternate	2°	_	_	_	$cHPT_4$
Urochloa platytaenia	2–9	2–9	Alternate	2°	_	_	_	$cHPT_4$
Urochloa pratervisa	8–13	8–9	Alternate	3°	4–5	1°, 2°	Alternate	cHP_5
Urochloa pubigera	22	15	Alternate	3°	7	1°, 2°	Alternate	pHP_2
Urochloa ramosa	10–12	7–10	Alt. and subop.	4°	2–3	1°, 2°	Alternate	pHP_1
Urochloa rudis	4	4	Alternate	2°	_	_	_	$cHPT_4$
Urochloa ruziziensis	1–5	1–5	Alternate	2°	_	_	_	$cHPT_3$
Urochloa sclerochleaena	7	1–2	Alternate	3°	5–6	1°, 2°	Alternate	cHP_6
Urochloa setigera	3–6	3–6	Alternate	3°	_	_	_	$cHPT_2$
Urochloa subulifolia	2–3	2–3	Alternate	2°	_	_	_	$cHPT_4$
Urochloa texana	9–14	8–11	Alternate	3°	2–5	1°, 2°	Alternate	cHP_5
Urochloa trichopus	4–13	4–13	Alternate	2°	_	_	_	$cHPT_4$

Table 3 continued

Species	Total N° of B[1]	N° of lgB[1]	Disposition of B[1]	Max. branch degree of B[1]	N° of shB[1]	Ramification degree of shB[1]	Disposition of shB[1]	IF type and subtype
Urochloa venosa	10–14	8–10	Alt. and subop.	4°	3–4	1°, 2°	Alternate	pHP_1
Urochloa villosa	5–11	3–9	Alt. and subop.	2°, 3°	1–3	1°	Alternate	pHP_3
Urochloa whiteana	2	2	Alternate	2°	_	_	_	$cHPT_4$
Urochloa xantholeuca	3–14	2–13	Alternate	3°	1–3	2°	Alternate	pHP_2

1° ramification up to first order; *2°* ramification up to second order; *3°* ramification up to third order; *4°* ramification up to fourth order; *5°* ramification up to fifth order; *alt.* alternate; *B[1]* primary branch; *IF* inflorescence; *lgB[1]* long primary branch; *Max.* maximum; *N°* number; *pseudov.* pseudoverticillate; *shB[1]* short primary branch; *subop.* subopposite; ? missing data

Total number, ramification degree and phyllotaxis of the most distal primary branch of the inflorescence

In species that have a terminal spikelet on the main axis, the primary branches below the terminal spikelet vary extensively in number and ramification among the species and even among the samples of each species. In species with homogenized inflorescences, the primary branches located below the terminal spikelet are short primary branches, which, in general, may not have ramification or may have ramifications up to second order (Figs. 5, 6) (exceptionally, third order, e.g. *Brachiaria serrifolia* (Hochst.) Stapf and *Urochloa oligotricha*). In contrast, for inflorescences that are non-homogenized we used the term distal paracladia or distal branches (dB) to describe the branches that are located under the terminal spikelet. In these cases, the distal primary branch may not have ramification or may have ramifications up to fouth order (Fig. 7).

In all species studied, the most distal branches (short primary branch or distal primary branch) have an alternate disposition on the inflorescence main axis. In Tables 3 and 4 we describe in detail the range of variation shown by the distal primary branches across the PCK Clade.

Types and subtypes of the PCK Clade inflorescences

Based on the characters described above, we identify different inflorescence types in the clade, all of which are variations of a basic paniculodium. The inflorescences of the PCK Clade can be classified in two main groups: (a) inflorescences with a terminal spikelet (Paniculodium Type, P) and, (b) inflorescence without a terminal spikelet (Truncated Paniculodium Type, TP). Within the P Type group, the inflorescence may be: (a′) a completely Homogenized paniculodium (cHP), (a″) partially Homogenized Paniculodium (pHP), and (*a‴*) non-Homogenized Paniculodium (nHP). Within the TP Type we observed that the inflorescences are (b′) completely (cHPT) or (b″) partially Homogenized (pHPT). In consequence, we found five different, basic inflorescence types, among which we recognized at least 21 different inflorescence subtypes across the clade based on the rest of the characters selected. Inflorescences types and subtypes found are described in the following key:

1	Inflorescence without a terminal spikelet	2
1′	Inflorescence with a terminal spikelet	13
2(1)	Inflorescence completely homogenized (cHP)	3
2′	Inflorescence partially homogenized (pHP)	7
2″	Inflorescence not homogenized (nHP)	11
3(2)	Inflorescence represented by long primary branches and short primary branches	4
3′	Inflorescence represented exclusively by long primary branches	cHP_1-Subtype (eg. *B. pungipes*, Fig. 5a)
3″	Inflorescence represented exclusively by short primary branches	cHP_2-Subtype (eg. *B. dimorpha*, Fig. 5b)
4(3)	Ramifications up to second order, solitary spikelets	5
4′	Ramifications up to third order, paired spikelets	6
5(4)	Equal or higher number of long primary branches than short primary branches	cHP_3-Subtype (eg. *B. scalaris* Pilg., Fig. 5c)
5′	Higher number of short primary branches than long primary branches	cHP_4-Subtype (eg. *U. advena* (Vickery) R.D. Webster, Fig. 5d)
6(4′)	Equal or higher number of long primary branches than short primary branches	cHP_5-Subtype (eg. *U. paucispicata* (Morong) Morrone & Zuloaga, Fig. 5e)
6′	Higher number of short primary branches than long primary branches	cHP_6-Subtype (eg. *U. sclerochlaena* Chiov. ex Chiarugi, Fig. 5f)

7(2′)	Primary branches and second order branches with equal internode lengths	8
7′	Primary branches and second order branches with different internode lengths	10
8(7)	Ramifications up to third order	9
8′	Ramifications up to fourth or exceptionally fifth order	pHP_1-Subtype (eg. *U. fusca* (Sw.) B.F. Hansen and Wunderlin, Fig. 6a)
9(8)	Higher number of solitary spikelets than paired spikelets on long primary branches	pHP_2-Subtype (eg. *U. xantholeuca* (Hack. ex Schinz) H. Scholz, Fig. 6b)
9′	Higher number of paired spikelets than solitary spikelets on long primary branches	pHP_3-Subtype (eg. *U. villosa*(Lam.) T.Q. Nguyen, Fig. 6c)
10(7′)	Equal or higher number of short primary branches than long primary branches	pHP_4-Subtype (eg. *B. eruciformis*, Fig. 6d)
10′	Higher number of long primary branches than short primary branches	pHP_5-Subtype (eg. *U. acuminata*, Fig. 6g)
11(2″)	Ramifications up to second order	nHP_1-Subtype (eg. *Yvesia*, Fig. 7a)
11′	Ramifications up to fifth or sixth order	2
12(11′)	Presence of short proximal internodes on primary branches	nHP_2-Subtype (eg. *Melinis*, Fig. 7b)
12′	Presence of long internodes on primary branches	nHP_3-Subtype (eg. *Megathyrsus*, Fig. 7c)
13(1′)	Completely homogenized inflorescence (cHPT)	14
13′	Partially homogenized inflorescence (pHPT)	17
14(13)	Presence of a spathaceous bract.	$cHPT_1$-Subtype (eg. *Thuarea*, Fig. 8a)
14′	Absence of a spathaceous bract	15
15(14′)	Ramifications up to second order (solitary spikelets)	16
15′	Ramifications up to third order (pared spikelets)	$cHPT_2$-Subtype (eg. *B. marlothii* (Hack.) Stent, Fig. 8b)
16(15)	With truncation of the Cof	cHPT $_3$-Subtype (eg. *U. ruziziensis*, Fig. 8C)
16′	Without truncation of the Cof	$cHPT_4$-Subtype (eg. *U. platyphylla* (R. Br.) R.D. Webster, Fig. 8d)
17(13′)	Ramifications up to third order	18
17′	Ramifications up to fourth order	$pHPT_1$-Subtype (eg. *U. adspersa*, Fig. 9a)
18(17)	Higher number of solitary spikelets than paired spikelets on long primary branches	$pHPT_2$-Subtype (eg. *U. plantaginea* (Link) R.D. Webster, Fig. 9b)
18′	Higher number of paired spikelets than solitary spikelets on long primary branches	$pHPT_3$-Subtype (eg. *E. montevidensis* Griseb., Fig. 9c)

Each subtype may include more than one species; within a subtype, species may differ from each either by the number and disposition of the primary branches and by the number and ramification degree of the short primary branches or distal primary branches (Tables 3, 4).

Discussion

The synflorescence

The limits of what an inflorescence should be are a complex and confused matter and are still somewhat subjective (Weberling 1965, 1989; Rua 1999; Buzgo et al. 2004). In the first work of Troll (1964), that controversy was already considered when the author proposed the term synflorescence in place of the term inflorescence. Troll's model assumes that the inflorescence in the context of the whole shoot system originated from the apical bud of the main axis or from axillary buds (innovations) located along the main axis (Troll and Weberling 1989).

The synflorescence of the PCK Clade has different zones already described for other grasses (Troll 1966, 1969; Troll and Weberling 1989; Rua 1999): (1) the innovation zone, (2) the inhibition zone, (3) the enrichment zone (not present in some species), and (4) the terminal inflorescence. Nowadays it is well known that the architecture of the grass synflorescence is controlled by the expression of several genes, for example *ramosa1* (*ra1*), *teosinte branched1* (*tb1*), *barren stalk1* (*ba1*), *indeterminate spikelet1* (*ids1*), *branched silkless1* (*bd1*), *liguleless2* (*lg2*), *fascinated ear2* (*fea2*), *thick tassel dwarf1* (*td1*) and *knotted1* (*kn1*) among others. All these genes encode transcription factors that affect synflorescence architecture, modifiying the temporal development of the different zones or by regulating meristem sizes (Poeting 1990; Doebley et al. 1997; Chuck et al. 1998, 2002; Walsh and Freeling 1999; Vollbrecht et al. 2000; Taguchi-Shiobara et al. 2001; Gallavotti et al. 2004; Bommert et al. 2005; Vollbrecht et al. 2005).

The grass synflorescence may or may not have branches of the trophotagma along the enrichment zone (Vegetti and Müller-Doblies 2004). In the PCK Clade, this character varies among the different species, is not exclusive for one

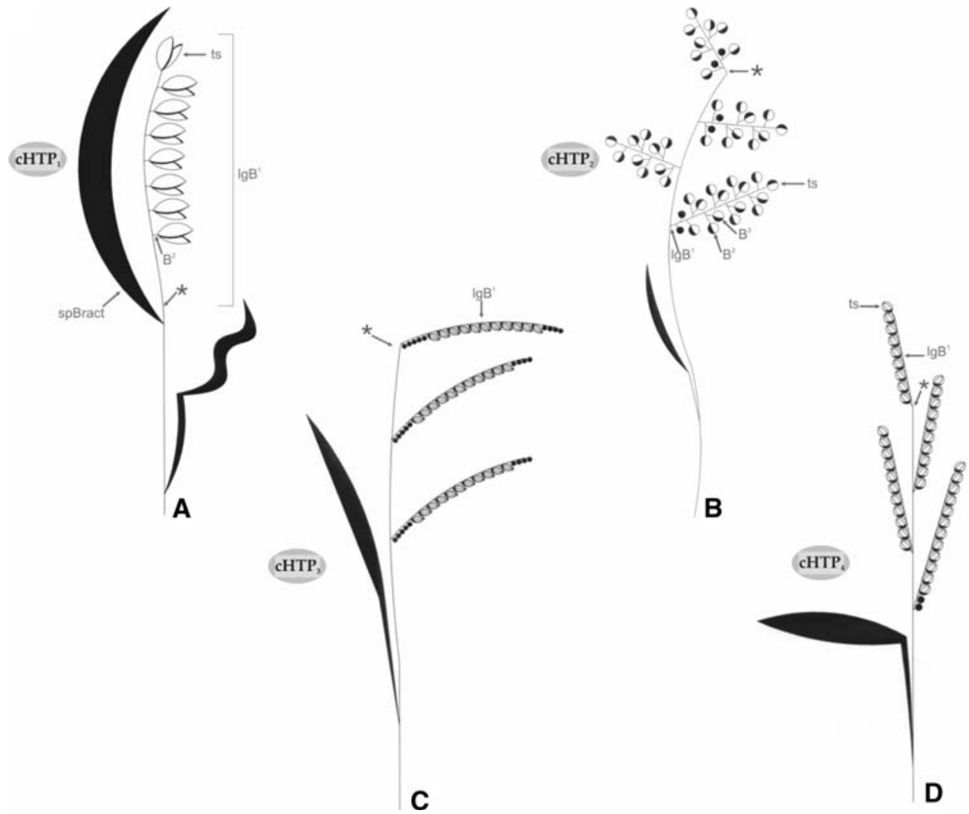


Fig. 8 Fully homogenized truncated paniculodium (cHPT-Type). **a** cHPT$_1$-Subtype (*Thuarea involuta*); **b** cHPT$_2$-Subtype (*Brachiaria marlothii*); **c** cHPT$_3$-Subtype (*Urochloa ruziziensis*); **d** cHPT$_4$-Subtype (*Urochloa platyphylla*). *B*^{2} branch of second order; *B*^{3} branch of third order; *ts* terminal spikelet at the end of the primary branch; *lgB*^{1} long primary branch; *shB*^{1} short primary branch. The *asterisk* indicates absence of a terminal spikelet on the main florescence. The *black circle* indicates an aborted spikelet

genus and does not correlate with plant life history; within the clade, there are perennial and annual plants that may or may not have branches of the trophotagma. Frank (1998) analyzed the correlation between the presence of branches of the trophotagma and the climate in which the plant grows, and concluded that the absence of branches of the trophotagma correlated with tropical climate or arid and dry habitats (e.g. steppe). Also, those species that lack branches of the trophotagma do not grow in regions with high variation in temperature and humidity. Thus, the development of branches of the trophotagma may be directly correlated with humidity gradients.

The structure of the adult inflorescence

The inflorescence in the PCK Clade is polytelic (lacking the terminal flower) as was described also for the Poaceae (Troll 1966, 1969; Cámara Hernández and Rua 1991; Vegetti 1991a, b) and for several monocotyledonous inflorescences. In the PCK Clade, the main axis of the polytelic inflorescence may or may not end in a terminal spikelet. When the main axis develops a terminal spikelet, the inflorescence is a non-truncated paniculodium (P), while when the main axis lacks the terminal spikelet the inflorescence became a truncated paniculodium (TP).

The PCK Clade is a well-supported monophyletic group (Gómez-Martinez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001; Giussani et al. 2001) but is surprisingly diverse in inflorescence structure. We have identified at least 21 different mature inflorescence subtypes within the clade; in addition, some genera exhibited more than one inflorescence type.

We found fourteen characters that vary across the different genera and species in the clade: (1) presence or absence of a spathaceous bract, (2) inflorescence symmetry, (3) total number of the primary branches, (4) maximum branch degree of the primary branches, (5) phyllotaxis of the primary branches, (6) differences in branch internode length, (7) spikelet distribution and organization on branches, (8) total number of the most distal primary branches, (9) ramification degree of the most distal primary branches of the inflorescence, (10) degree of homogenization of the inflorescence, (11) presence or absence of the terminal spikelet of the main axis, (12) presence or absence of the terminal spikelet at the end of primary branches, (13) presence or absence of the terminal spikelet at the tip of third order branches, and (14) presence or absence of different types of branches. Among these characters, some are unique for one species, others vary among species and others are polymorphic in the same species as we describe below. In contrast, the orientation of the second order

Table 4 Inflorescence variation among members of the PCK Clade with non-homogenized inflorescence

Species	Total N° of B[1]	Disposition of B[1]	Max. branch degree of B[1]	N° of dB[1]	Ramification degree of dB[1]	Disposition of dB[1]	IF type and subtype
Brachiaria chusqueoides	4–6	Alternate	2°	2	1°, 2°	Alternate	nHP_1
Brachiaria longiflora	3–5	Alternate	2°	2	1°	Alternate	nHP_1
Brachiaria umbelata	4–17	Alternate	2°	2–3	1°	Alternate	nHP_1
Megathyrsus maximus	18–56	Alt., subop. and pseudov.	5°	1–3	1°, 4°	Alternate	nHP_3
Melinis leucantha	9–12	Alternate	5°	2–3	1°, 2°	Alternate	nHP_2
Melinis monachne	7–10	Alternate	5°	2	1°	Alternate	nHP_2
Melinis minutiflora	9–21	Alternate	6°	2–3	1°, 2°	Alternate	nHP_2
Melinis repens	8–22	Alternate	6°	2–3	1°, 2°	Alternate	nHP_2
Urochloa comata	11–19	Alternate	5°	1	1°	_	nHP_2
Yvesia madagascariensis	3–6	Alt. and subop.	2°	1	1°	_	nHP_1

1° ramification up to first order; *2°* ramification up to second order; *4°* ramification up to fourth order; *5°* ramification up to fifth order; *6°* ramification up to sixth order; *alt.* alternate; *B[1]* primary branch; *dB[1]* distal primary branch; *IF* inflorescence unit; *Max.* maximum; *N°* number; *pseudov.* pseudoverticillate; *subop.* subopposite

branches on the primaries does not show variation in the clade. All the species have second order branches abaxially orientated on primary branches, as was also reported by Reinheimer (2007).

Thuarea involuta is the only species that develops a spathaceous bract subtending the unique primary branch that forms its inflorescence. In general, the grass inflorescence has branches usually subtended by bracts that fail to develop. Whether the bract in *Thuarea* is one that fails to be repressed may be elucidated by ontogenetic studies.

Inflorescence symmetry has been used as one of the most important characters in the taxonomic delimitation of the American species of *Brachiaria* and *Urochloa* (Morrone and Zuloaga 1992, 1993). However, developmental studies show that the symmetry is an intricate character to assess within the PCK Clade because it is directly correlated with the initiation pattern of the primary branches. In the group, the development of primary branches and with that, the specification of inflorescence symmetry, are diverse and complex processes that will be treated in a separate work (Reinheimer 2007).

Inflorescences in the PCK Clade vary extensively in the number of primary branches and maximum branch degree. These characters diverge among different genera, among species within the same genus, and among specimens of the same species. In general, the total number of primary branches varies from 1 to 24 in *Brachiaria*, 1–62 in *Urochloa*, 1–20 in *Eriochloa*, 9–13 in *Chaetium*, 18–56 in *Megathyrsus*, 8–22 in *Melinis*, 3–6 in *Yvesia* and only 1 in *Thuarea*. In most cases, the maximum branch degree correlates with the homogenization level of the inflorescence.

Usually, the primary branches are alternate along the inflorescence main axis. However, depending on the degree of internode elongation of the main axis during development, some primary branches appear subopposite or pseudoverticillate in many species.

The variation in internode length has been observed also along the inflorescence branches of some members of the Clade. Thus, some species may present differential internode elongation only along the main axis (e.g. *Urochloa fusca*), some may have different internode lengths only along the branches (e.g. *Brachiaria eruciformis*), or some may show variation of internode length on the main axis and branches of the inflorescence (e.g. *Megathyrsus maximus*). Furthermore, in some species (e.g. *Melinis*) since the proximal internode of each branch does not elongate, false pseudoverticels are formed by the proximity of second to fifth order branches intead of primary branches. As was already mentioned by Malcomber et al. (2006) and based on several ontogenetic studies (Fraser and Kokko 1993; Doust and Kellogg 2002a, b; Ikeda et al. 2004; Bess et al. 2005; Kellogg et al. 2004; Reinheimer et al. 2005; Sörenson et al., unpublished data), in grasses the elongation of internodes of the main inflorescence axis is independent of that of primary branches and secondary branches. Moreover, in grasses the elongation of the internodes occurs late in development when branches, spikelets and flowers are already formed (Reinheimer 2007). These results suggest that the elongation of the internodes is thus genetically distinguishable from the specification of branch and spikelet identity. Until now, a few genes (e.g. *panicle phytomer1*) and several QTL have been identified as responsible for differences in internode elongation (Takahashi et al. 1998; Doust et al. 2005).

In some members of the PCK Clade we identified inflorescences that bear solitary spikelets along the primary branches and others that have paired spikelets, placed in one or two rows. That organization can be easily assessed in those mature inflorescences that have somewhat

Fig. 9 Partially homogenized truncated paniculodium (pHTP-Type). **a** $pHTP_1$-Subtype (*Urochloa adspersa*); **b** $pHTP_2$-Subtype (*Urochloa plantaginea*); **c** $pHTP_3$-Subtype (*Eriochloa montevidensis*). B^2 branch of second order; B^3 branch of third order; B^4 branch of fourth order; *ts* terminal spikelet at the end of the primary branch coflorescence; lgB^1 long primary branch; shB^1 short primary branch. The *asterisk* indicates absence of a terminal spikelet on the main florescence. The *black circle* indicates an aborted spikelet

flattened primary branches and short secondary branches, while it is hard to evaluate in inflorescences that are profusely branched and with long branches. Developmental studies, certainly, will help us to determine the spikelet organization along the primary branches early in development before the elongation of the internodes.

In the P Type inflorescence, we found short primary branches or distal primary branches placed immediately below the terminal spikelet of the main axis (except in *B. pungipes*). Depending on the species and the specimen studied, these types of branches are high variable in number and may not have ramifications or may have up to fourth order branches. In consequence, the ramification degree of the most distal branches of the inflorescence is polymorphic even among samples of the same species.

Among the different structures found in the inflorescence of the PCK Clade, we identified at least nine different evolutionary trends that have already been described for Poaceae (Vegetti and Anton 1995, 2000). These trends are, at least in part, responsible for the diversity in the inflorescences of the clade: (1) presence or absence of the terminal spikelet of the main axis, (2) presence or absence of the terminal spikelet at the end of the primary branches, (3) presence or absence of long branches, (4) presence or absence of short primary branches, (5) branch homogenization, (6) increase or decrease in inflorescence ramification, (7) differential elongation of main axis internodes, (8) differential elongation of branch internodes, and (9) presence or absence of a spathaceous bract.

The absence of distal structures along the main axis and primary branches (also called truncation) and the

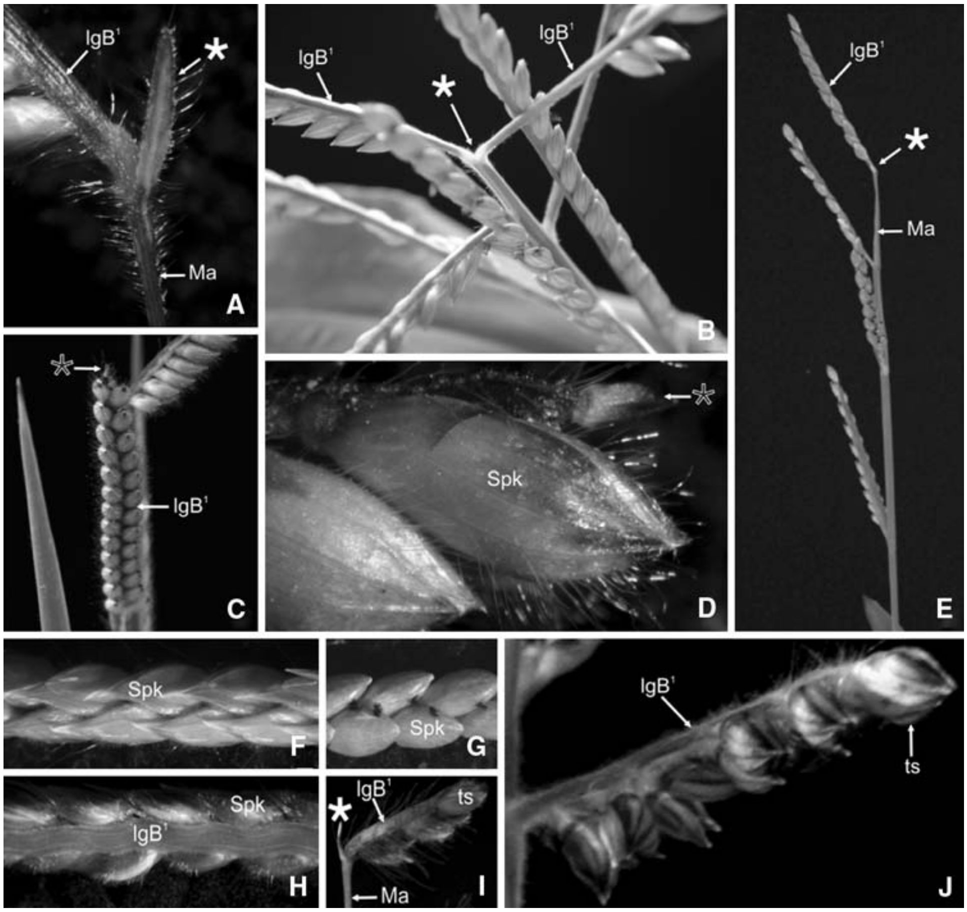


Fig. 10 Photograph of the inflorescence of *Urochloa*. **a** sterile main axis prolongation in the truncated paniculodium of *U. decumbens*; **b** truncated paniculodium of *U. lata*; **c** abnormal coflorescence of a long primary branch in *U. decumbens*; **d** detail of the abnormal coflorescence in **c**; **e** truncated paniculodium in *U. platyphylla*; **f** solitary spikelets in two rows on the abaxial side of a long primary branch of *U. mosambicensis*; **g** solitary spikelets in two rows on the abaxial side of a long primary branch of *U. brizantha*; **h** flat primary branch in *U. mosambicencis*; **i** sterile main axis prolongation in the truncated paniculodium and spikelets with abaxial orientation on the long primary branch *U. jubata*; **j** spikelets with abaxial orientation on the long primary branch *U. mollis*. *ts* terminal spikelet at the end of the primary branch; lgB^1 long primary branch; *Ma* main axis; *Spk* normal spikelet. The *white asterisk* indicates absence of a terminal spikelet on the main axis. The *black asterisk* indicates the abnormal terminal spikelets at the tip of a long primary branch

morphological similarity of inflorescence branches (called homogenization) have been proposed as common evolutionary processes in the angiosperms (Troll 1964, 1969; Weberling 1965, 1985; Maresquelle 1970; Sell 1976; Kunze 1989; Vegetti and Anton 1995, 2000). Moreover, these trends have been considered responsible, at least in part, for the great inflorescence diversity seem among the angiosperms (Troll 1964, 1969; Maresquelle 1970; Sell 1976; Weberling 1965, 1985; Kunze 1989; Vegetti and Anton 1995, 2000).

Truncation

The grasses show different levels of truncation (loss of different inflorescence structures). For example, several grass species lack the terminal flower of the spikelet (Goebel 1931; Troll 1966, 1969; Cámara Hernández and Rua 1991; Vegetti 1991a, b; Cámara Hernández and Miante–Alzogaray 1994) or even more, the distal flower systems (spikelet) of the main axis or branches and may also entire branches. Kunze (1989) suggested different types of polytelic inflorescences according to the different levels of truncation mentioned.

In the PCK Clade, we found non-truncated inflorescences, and inflorescences that lack different parts. Among the latter, we observed truncation of (1) the terminal spikelet of the inflorescence main axis, (2) the entire primary branches (including long primary branches or short primary branches) and (3) distal parts of the primary branches. These patterns are not restricted to the PCK Clade; they have also been recorded for other members of subfamily Panicoideae, as well as members of subfamily Chloridoideae among

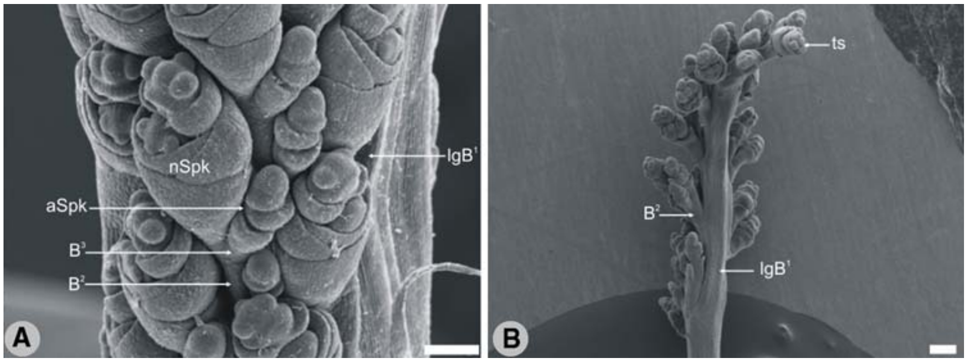


Fig. 11 Scanning electron micrographs. **a** Primary branch of *Urochloa lata* showing the aborted spikelets at the base of branch of third order. **b** Primary branch of *Megathyrsus maximus* showing the abaxial disposition of secondary branches. *aSpk* aborted spikelet; B^2 secondary branch; B^3 branch of third order; *ts* terminal spikelet at the end of the primary branch; lgB^1 long primary branch; *nSpk* normal spikelet

others (Vegetti 1987; Vegetti and Pensiero 1990; Vegetti 1991a; Rua 1993, 1996; Rua and Boccaloni 1996; Perreta and Vegetti 1998; Rua and Weberling 1998; Vegetti 1999; Giraldo-Cañas 2000; Cámara Hernández 2001; Pensiero and Vegetti 2001; Liu et al. 2005).

The inflorescence of *Chaetium*, *Melinis*, *Megathyrsus* and *Yvesia*, are P type paniculodia, while *Eriochloa* and *Thuarea* are always TP type paniculodia. In constrast, *Brachiaria* and *Urochloa* showed P and TP type paniculodia depending on the species examined. All species of *Brachiaria* that have TP inflorescence are African, except for *B. rugulosa*, which is Australian. Also, the majority of the *Urochloa* species that have TP are originally from Africa (except for *U. adpersa*, *U. meziana*, *U. ophryodes* (Chase) Morrone & Zuloaga and *U. platyphylla* which are American species).

When the inflorescence P and TP are compared, we observed that in all the inflorescences that lack the terminal spikelet the distal branches (which should be immediately below the terminal spikelet) are also not developed.

We found two morphologies that were novel for the PCK Clade (the subtype cHP_1 and the subtype cHP_2) and also for the tribe Paniceae. *Brachiaria pungipes*, an African species, has a P type inflorescence made up by the terminal spikelet and long primary branches exclusively. When we compared this subtype with other cHP type inflorescence, we noticed that the inflorescence of *B. pungipes* lacks short primary branches. In contrast, the inflorescence of *B. dimorpha*, *B. epacridifolia* and *U. holosericea*, lack the long primary branches, since their inflorescences are only represented by the terminal spikelet and short primary branch. The first two species are originally from Africa, and *U. holosericea* is an Australian species. Future studies should investigate the origin of the terminal spikelet of *B. pungipes*; it could be a true terminal spikelet or a lateral short primary branch which has adopted a terminal position on the main axis. In the same way, new studies should address the origin of the ramification system of *B. dimorpha*, *B. epacridifolia* and *U. holosericea*, since the entire inflorescence could be also considered to be a unique long primary branch which has acquired the position of the inflorescence main axis. However, we observed neither a pulvinulus nor bracts; there is thus no real evidence for the latter hypothesis. Developmental studies may be a useful tool to investigate and corroborate these hypotheses.

Another level of truncation was observed in some species of *Urochloa*, in which the inflorescence presents long primary branches that lack well developed distal spikelets (including the terminal one). This pattern is constant among all examined samples of *U. ruziziensis*, whereas it varies among samples of *U. brizantha* and *U. decumbens*. Possibly in the last two species the truncation of the distal part of the long primary branch may be conditioned by environmental factors rather than being genetically and ontogenetically fixed as in *U. ruziziensis*. Ontogenetic studies in the PCK Clade revealed that the abnormal spikelets follow different and complex patterns of development depending on their position on the inflorescence and the examined species; a full description of such spikelets is treated elsewhere (Reinheimer 2007).

Homogenization

Homogenization, that is similarities among the inflorescence branches, is an evolutionary process which determines, in part, the general appearance of the inflorescence. Such process has been found in different groups of Poaceae, as in subfamily Panicoideae (Rua 1993, 1996; Rua and Weberling 1998; Vegetti 1991a; Pensiero and Vegetti 2001) as well as in other subfamilies, for example in Chloridoideae (Perreta and Vegetti 1998; Cámara Hernández 2001; Liu et al. 2005) and Ehrhartoideae (Vegetti and Pensiero 1999; Vegetti 2000).

Different degrees of homogenization are found among species of the PCK Clade. We found three levels of homogenization: non-homogenized inflorescence, partially homogenized inflorescence, and completely homogenized inflorescence. The partially homogenized inflorescence has been considered as a transition or intermediate form between the non-homogenized inflorescence and the fully homogenized inflorescence (Rua 1996; Rua and Weberling 1998; Reinheimer and Vegetti 2004). An intermediate form of homogenization has been also observed in other genera of Paniceae (e.g. *Panicum* L. and *Paspalum* L.) (Rua 1996; Rua and Weberling 1998; Reinheimer and Vegetti 2004).

As a direct consequence of the different degrees of homogenization, the inflorescence may or may not be disjunct. Non-homogenized inflorescences do not show disjunction, while partially or fully homogenized inflorescences are disjunct, such that it is possible to identify long primary branches and short primary branches.

Many authors have observed a correlation between homogenization and truncation (Vegetti 1991a; Rua and Weberling 1998; Vegetti and Anton 2000). In this study, however, we found that the correlation is asymmetric. In the PCK Clade, we observed that all truncated inflorescences are also homogenized, but all inflorescences that are homogenized are not necessarily truncated. For example, many species of *Brachiaria*, *Urochloa* and *Chaetium* have homogenized inflorescences without any sign of truncation. In contrast, all species of *Eriochloa*, *Thuarea involuta* and some species of *Brachiaria* and *Urochloa* show a direct correlation between homogenization and truncation as was observed in other members of Panicoideae (e.g. *Setaria* P. Beauv., the majority of *Paspalum* species, and members of Andropogoneae) (Rua 1993, 1996; Rua and Weberling 1998, Vegetti 1999; Pensiero and Vegetti 2001), and species of Chloridoideae (e.g. *Leptochloa* P. Beauv. and *Digitaria* Haller) (Perreta and Vegetti 1998; Cámara Hernández 2001; Liu et al. 2005).

Inflorescence structure and taxonomy of the PCK Clade

Chaetium presented a cHP_6-Subtype inflorescence (fully homogenized paniculodium with higher number of short primary branches than long primary branches) or rarely a pHP_1-Subtype inflorescence (partially homogenized paniculodium with ramifications up to fourth order). All the species of *Melinis* studied in this work have inflorescences that are nHP_2-Subtype (non-homogenized paniculodium with short proximal internodes of the primary branches). Also, the inflorescence of *Megathyrsus* is an nHP_3-Subtype (non homogenized paniculodium with the first proximal internode longer than the rest of the internodes that form the branch), the inflorescence of *Thuarea* belongs to the $cHPT_1$-Subtype (truncated and fully homogenized paniculodium with a spathaceous bract), and the inflorescence of *Yvesia* fits into the nHP_1-Subtype (non-homogenized paniculoidium with ramifications up to second order). We were unable to find any inflorescence characters that allowed us to distinguish *Brachiaria* clearly from *Urochloa*. Moreover, the nHP_1-Subtype is also present in three species of *Brachiaria* (*B. chusqueoides* (Hack.) Clayton, *B. longiflora* Clayton and *B. umbelata* (Trin.) Clayton). The nHP_2-Subtype characteristic of *Melinis* is also present in one *Urochloa* species, *U. comata* (Hochst. ex A. Rich.) Stapf. The cHP_6-Subtype represented by *Chaetium* was also found in *Brachiaria ovalis* Stapf and some species of *Urochloa* (*U. lachnantha* (Hochst.) A.M. Torres & C.M. Morton, *U. oligotricha* and *U. sclerochlaena*).

Inflorescence evolution in the PCK Clade

The most recent phylogeny of the PCK Clade, based on the nuclear ITS and 5.8S regions, suggests that *Brachiaria* and *Melinis* may be sister to each other, and the *Brachiaria*/*Melinis* clade may be sister to the rest of the PCK species. *Urochloa* may be paraphyletic and associated with *Megathyrsus* and *Eriochloa* (Torres González and Morton 2005). If this phylogeny is correct, then inflorescence morphology tends to become simpler during the evolution of the clade. That is, highly branched, non-truncated inflorescences with differences in internode lengths (e.g. pHP_4, nHP_2, nHP_3) are present in the genera *Brachiaria* and *Melinis*, and also in *Megathyrsus* which is sister to the *Urochloa*, and *Eriochloa* group. Truncated inflorescence morphologies (e.g. $pHPT_3$, $cHPT_4$, $cHPT_3$, $pHPT_2$), appear late in the history of the clade. The phylogeny of Torres Gonzalez and Morton is not well-supported, however, and thus a reliable assessment of changes in the inflorescence is still lacking. Furthermore, inflorescence development in the PCK Clade shows considerable variation among its members (Stür 1986; Reinheimer et al. 2005; Reinheimer 2007). As a consequence, further studies—including ontogenetic and gene expression studies—will be necessary to understand how, when and where modifications during development occur to create the extensive adult inflorescence variation described in this work.

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