

Growth Form and Inflorescence Typology in *Bothriochloa* (Poaceae: Panicoideae: Andropogoneae)

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Summary

Growth form and inflorescence typology of American species of *Bothriochloa* (Poaceae: Panicoideae: Andropogoneae) were studied.

Plants of the genus *Bothriochloa* are perennial, with rhizomatose or stoloniform growth; the ramification is concentrated at the base of the plant or dispersed along the stem.

All the species have truncate-polytelic inflorescences with variation in the number and the degree of paracladia ramification. Two basic types of inflorescences are described: a typical paniculodium, with long paracladia bearing paracladia of consecutive order (P'c; P'c and P''c; or exceptionally P'c, P''c and P'''c) and a flabelate paniculodium with long proximal paracladia exceptionally branched (P'c).

Zusammenfassung

VEGA, A. S.: Wuchsformen und Typologie der Infloreszenzen der amerikanischen Arten von *Bothriochloa* (Poaceae: Panicoideae: Andropogoneae).

Wuchsformen und Typologie der Infloreszenzen der Gattung *Bothriochloa* sind immergrün; sie bilden ein Rhizom und Ausläufer. Die Verzweigung erfolgt aus einer gestauchten Basalzzone sowie zerstreut entlang den blühenden Sprossen.

Alle Arten besitzen trunckate polytele Infloreszenzen; Zahl und Ramifikationsgrad der Parakladien wechseln. Es werden zwei Haupttypen von Infloreszenzen beschrieben: Ein typisches Paniculodium mit verlängerten Paracladien in der Reihenfolge P'c, P'c und P''c; ausnahmsweise P'c, P''c und P'''c, sowie ein vereinfachtes Paniculodium mit verlängerten, gedrängten und sehr stark verzweigten Paracladien (P'c).

Introduction

The genus *Bothriochloa* Kuntze, belongs to the subfamily Panicoideae and tribe Andropogoneae. It is mainly distributed in tropical and subtropical regions of both hemispheres and comprises nearly 35 species throughout the world (WATSON & DALLWITZ 1992) with 23 species, two subspecies and a variety in America (VEGA 1997).

Bothriochloa comprises perennial plants of varied height, with two types of inflorescences: oblong to lanceolate panicle, with the main axis notoriously longer than the ramifications, which have a decreasing length toward the apex of the inflorescence and obconic panicles with the main axis of the same length or hardly longer than the ramifications; rachis joints and pedicels are furrowed by a central and longitudinal membranous or hyaline channel; the spikelets are in pairs, one of them basal, sessile and perfect, and the other one pedicelled, neuter or staminate; the glumes are chartaceous: the lower glume often pitted at the back, the lower lemma is lanceolate and hyaline, the lower palea is absent, the upper lemma is generally transformed into an awn and the upper palea is reduced (VEGA 1997).

SCHNEIDER and VEGETTI (1992) initiated the typological study of *Bothriochloa* inflorescence in *B. laguroides* (DC.) Herter and subsequently VEGA (1995) in *B. edwardsiana* (Gould) Parodi and *B. springfieldii* (Gould) Parodi; the present work extends this analysis to all American taxa.

Only a consideration of both the growth form and inflorescence structure together yields an accurate morphological picture of the plant. Moreover, growth form and inflorescence characters have considerable value for taxonomy and phylogenetic interpretations of the genus in particular and for the grass family, in general (RUA & WEBERLING 1995).

The aim of this paper is to study the structural plan of American taxa of the genus *Bothriochloa* through the analysis of the growth form and typology of the inflorescence.

Materials and Methods

The material examined belongs to the following herbaria: BAA, BAB, CORD, CTES, G, LD, LIL, LINN, MA, MO, NY, P, SI, TAES, US and W (in accordance with the abbreviations cited in the Index Herbariorum, HOLMGREN et al. 1990).

Taxa included in this study are: *Bothriochloa alta* (Hitcch.) Henrard, *B. barbinodis* (Lag.) Herter, *B. bladhii* (Retz.) S.T. Blake, *B. campii* (Swallen) de Wet, *B. edwardsiana* (Gould) Parodi, *B. eurylemma* M. Marchi & Longhi-Wagner, *B. exaristata* (Nash) Henrard, *B. hirtifolia* (J. Presl.) Henrard, *B. hybrida* (Gould) Gould, *B. imperatoides* (Hack.) Herter, *B. insculpta* (Hochst. ex A. Rich.) A. Camus, *B.*

ischaemum (L.) Keng var. *ischaemum*, *B. ischaemum* (L.) Keng var. *songarica* (Rupr.) Celarier & Harlan, *B. laguroides* (DC.) Herter subsp. *laguroides*, *B. laguroides* (DC.) Herter subsp. *torreyana* (Steud.) Allred & Gould, *B. longipaniculata* (Gould) Allred & Gould, *B. meridionalis* M. Marchi & Longhi-Wagner, *B. palmeri* (Hack.) Pilg., *B. perforata* (Fourn.) Herter, *B. pertusa* (L.) A. Camus, *B. reevesii* (Gould) Gould, *B. saccharoides* (Sw.) Rydb. subsp. *saccharoides*, *B. saccharoides* (Sw.) Rydb. subsp. *parvispiculus* (Hitchc.) Davidse, *B. springfieldii* (Gould) Parodi, *B. velutina* M. Marchi & Longhi-Wagner and *B. wrightii* (Hack.) Henrard.

Results and Discussion

1. The formation of the plant shoot

In *B. laguroides* once the caryopsis has germinated, there is a rapid elongation of the mesocotyl, so the coleoptile emerges through the soil surface (Fig. 1: A). The primary seminal root is reduced, compared to the length of the mesocotyl, and produces absorbent hairs during the underground growth (Fig. 1: B, C). In young seedlings with developing and mature leaves, the root forms primary ramifications (Fig. 1: D).

In mature seedlings, there is an incipient development of adventitious roots from the mesocotyl (mesocotylar roots) and a strong proliferation of lateral ramifications of the root and adventitious roots from the coleoptile node. The last ones perforate the hyaline coleoptile which has a bifid apex and two dark and longitudinal nerves, and also the sheath of the first leaf. The aspect of the first leaf is similar to that of a mature leaf, with differentiation of sheath, ligule and blade. The internode between the coleoptile node and the first leaf node is short and it is practically disposed at the soil level (Fig. 1: E).

The characteristics of the seedling in the species studied corresponds with the "Panicoid" type (HOSHIKAWA 1969). This type is distinguished by the absence of transitionary node roots in the embryonic root, the elongation of the mesocotyl and the presence of adventitious mesocotylar roots. The scarce development of the mesocotyl is considered a primitive character, while its elongation is characteristic of the subfamilies Chloridoideae, Panicoideae and the majority of the Arundinoideae (STEBBINS 1982). The caryopsis of these subfamilies have larger sized embryos and less proportions of endosperm.

The caespitose growth in this species is the result of the proximity between the rhizome nodes and the strong proliferation of the innovation shoots from them (Fig. 1: F) in addition to the development of adventitious roots. In each innovation shoot there is a gradual transition (foliar succession) from cataphylls to mature leaves with developed sheaths and blades (Fig. 1: G).

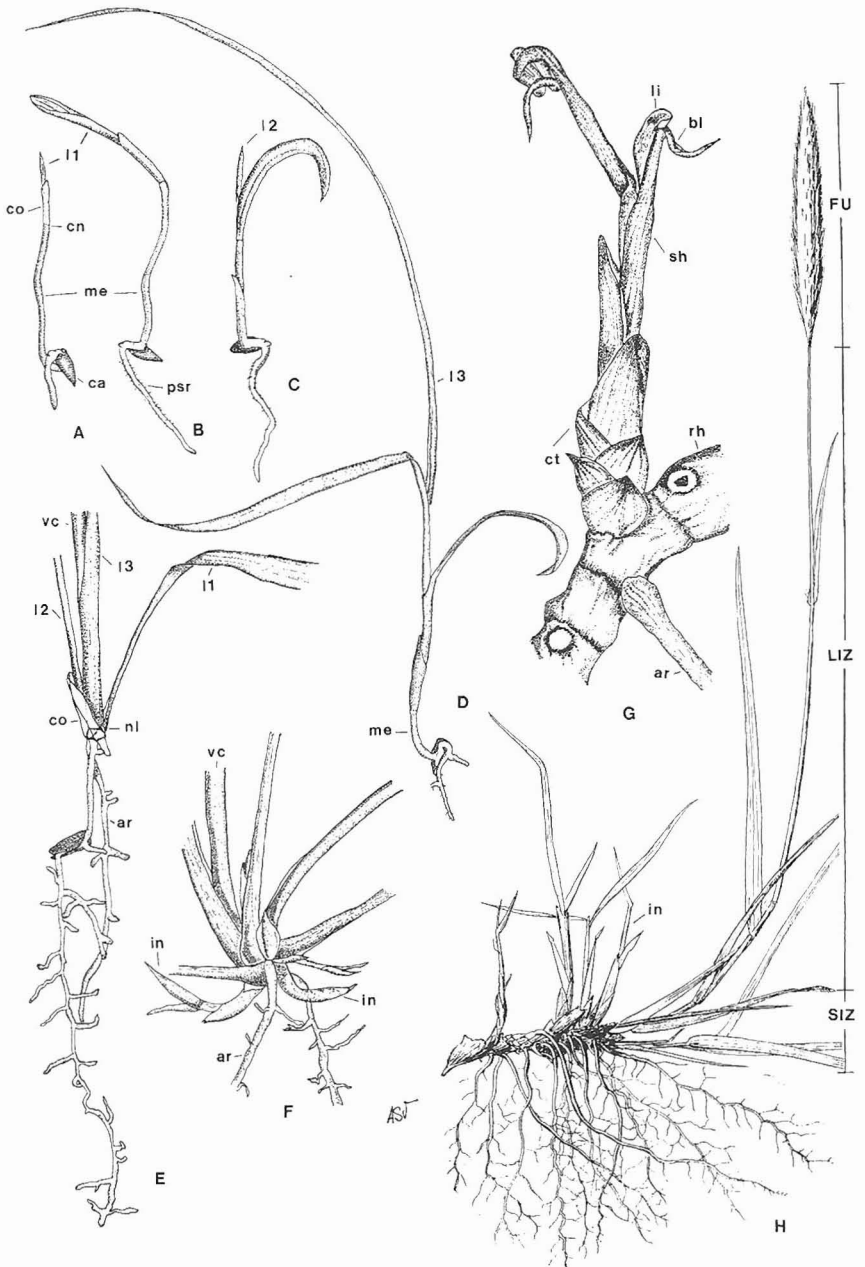


Fig. 1. Growth form in *Bothriochloa laguroides* (DC.) Herter. A-E, stages of development in the seedling; F, beginning of the ramification system in the caespitose growth; G, development of shoots from the rhizome; H, ramification system in a mature plant.

The different zones distinguished in the structural plan of *Bothriochloa* plants, in accordance with the terminology proposed by TROLL (1964) and WEBERLING (1965), present their equivalence with those used in the growth forms in Poaceae by RUA & GRÓTTOLA (1996). This terminology can be applied to the ramification system of a mature plant in this species (Fig. 1: H), recognizing the short internode zone (SIZ), long internode zone (LIZ) and the flowering unit (FU). In this way the following parallelism is established between the terms used: innovation zone (= short internode zone), inhibition zone (= long internode zone) and paracladial zone (= flowering unit).

2. The general growth pattern

Bothriochloa plants are perennial and the majority of the species has vegetative propagation by sympodial rhizomes with close nodes. The dense aspect of the plants is due to the development of several innovation shoots originating at these nodes. In the literature, this type of growth has usually been designated as "caespitose".

In the species studied it is possible to recognize the following structural plan (Fig. 2: A-C):

Innovation zone (JZ): The sympodial rhizomes have short internodes, covered and protected by the hairs of the nodes. These rhizomes develop adventitious roots at the nodes. Innovation shoots have short internodes protected by distichous sheaths and prophylls, the latter are the first leaves situated at the base of the innovation; these are hyaline, bi-keeled and sharpened toward the apex.

Inhibition zone (HZ): This zone is situated above the innovation zone and it is characterized by the presence of long internodes and mature leaves but devoid of lateral shoots.

Paracladial zone (BZ): Above the inhibition zone there are branches with pairs of spikelets and finally, in the distal region there are pairs of spikelets directly disposed on the main axis. The paracladial zone is composed of the subzone of short (sPZ) and long paracladia (lPZ).

As a consequence of modular growth branching systems of *Bothriochloa* plants are composed of modular units, each of them corresponding

References: ca, caryopsis; psr, primary seminal root; me, mesocotyl; cn, coleoptile node; co, coleoptile; nl, node of the first leaf; l1, first leaf; l2, second leaf; l3, third leaf; vc, vegetative culm; ar, adventitious root; in, innovation; ct, cataphyll; rh, rhizome; sh, sheath; bl, blade; li, ligule; SIZ, zone of short internode; LIZ, zone of long internode and FU, flowering unit.

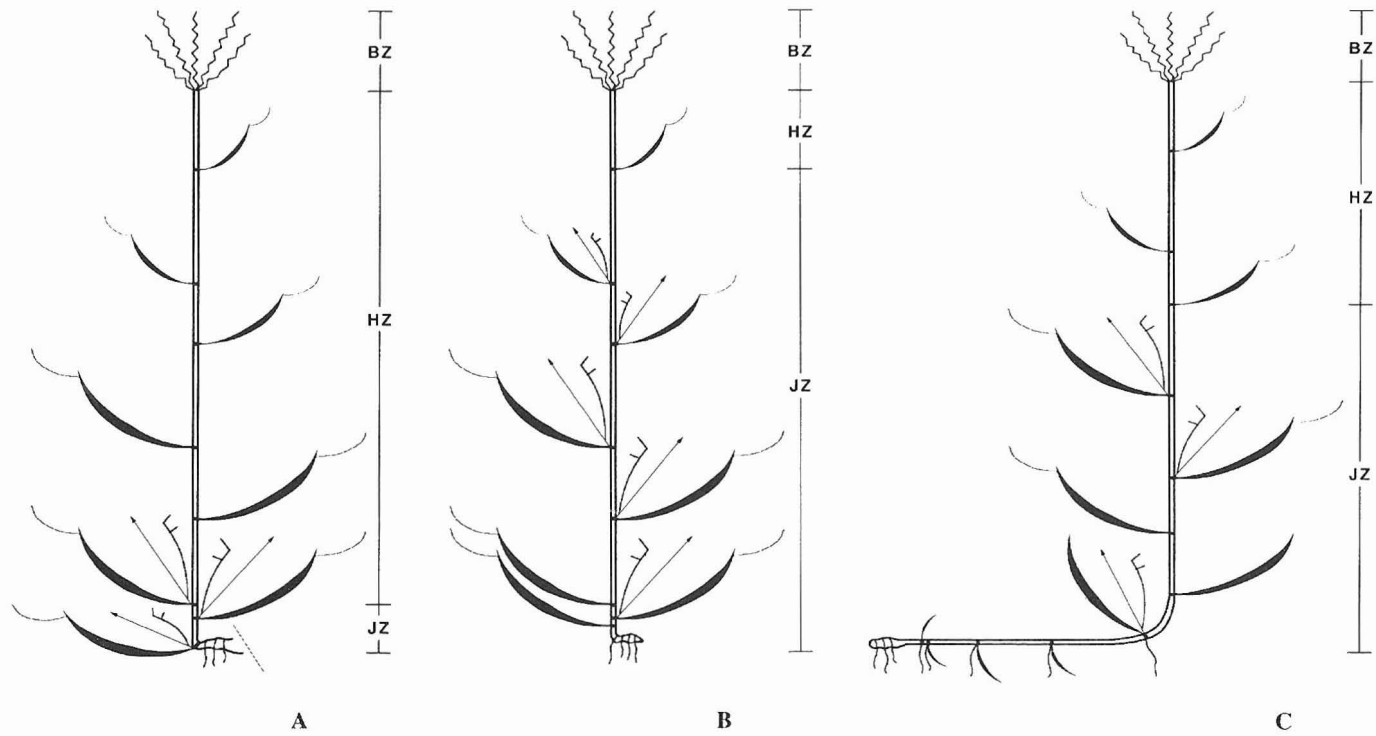


Fig. 2. A, Structural plan in *Bothriochloa edwardsiana* (Gould) Parodi (caespitose growth and basal foliage); B, *Bothriochloa hybrida* (Gould) Gould (caespitose growth and caulinar foliage); C, *Bothriochloa pertusa* (L.) A. Camus (stoloniform growth).
References: JZ. innovation zone, HZ. inhibition zone, BZ. paracladial zone.

to a synflorescence (CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1991; VEGETTI & ANTON 1995). Considering the different possibilities of combinations of vegetative traits, a series of growth types can be characterized. For the recognition of these growth types RUA & GRÓTTOLA (1996) and RUA & WEBERLING (1995) used the term growth form models.

The morphological character set comprises: duration, number of both short and long internodes, growth direction axes, leaf type sequence along them, position and relative strength of branches and presence of adventitious roots.

In *Bothriochloa* we recognize three growth form models. These are all perennials models and they are the following:

Growth form model 1:

The propagation of these plants is based on sympodial rhizomes with short internodes. They develop a basal foliage with thin stems, whose lower nodes are very closely in relation to the upper ones and innovation shoots are concentrated at the base of the plant (concentrated ramification, Fig. 2: A). This type of structural plan is characteristic of *Bothriochloa edwardsiana*, *B. springfieldii* (VEGA 1995), *B. imperatoides*, *B. laguroides* subsp. *laguroides*, *B. meridionalis*, *B. reevesii*, *B. saccharoides* subsp. *saccharoides* and *B. wrightii*.

Growth form model 2:

The structural plan is similar to the former but in this case the foliage is caulinar with robust stems of greater diameter. Ramification occurs in the innovation zone (short internode zone) and along the stem at the long internode zone (dispersed ramification, Fig. 1: B). Ramifications do not always end with a flowering unit.

Growth form model 3:

In this case the plants are reproduced by stolons (*B. pertusa*, Fig. 1: C; occasionally present in *B. ischaemum* var. *ischaemum* and *B. ischaemum* var. *songarica*). Lower stems are rooting at the nodes and conserve remnants of lacerated sheaths. Ramification occurs at innovation zones and along the stem at the long internode zone. In the last zone, the innovation shoots end in a flowering unit similar to the one of the main axis.

3. Inflorescence typology

The inflorescences in species of the genus *Bothriochloa* were traditionally described as "terminal panicles" with spikelets disposed in scarce or numerous spicate primary branches, moderately branched in species with long panicles (GOULD 1967). Subsequently, ALLRED (1982) defined them as "a panicle of racemose branches", a more appropriate definition because the inflorescences bear both sessile and pedicelled spikelets.

Bothriochloa species have two basic types of inflorescences in accordance with the terminology proposed by ALLRED (1982): "typical panicle" composed of a long main axis with branches of consecutive order in which the spikelets are borne in these ones, and a variant of this, denominated "panicle of racemose branches". According to TROLL (1969), this type of inflorescence corresponds with a paniculodium and not a panicle, because it does not have terminal flowers.

There are no bracts in *Bothriochloa* inflorescences, except those that belong to the spikelets (lower and upper glumes, lower and upper lemma and upper palea) and the bract that encloses the inflorescence ("inflorescence bract"). The last one is similar to a vegetative leaf but it has a reduced blade and a well developed sheath. In some inflorescences, a rudimentary bract was observed besides the inflorescence bract. The rudimentary bract shows variable degrees of development (1,5–2,5 mm long.) or is completely absent and is found at the level of the basal node related to only one long paracladium (Fig. 3).

The first type of inflorescence was observed in most of the species studied, with certain degree of variation cited in table 1. In this type of inflorescence the main axis is notoriously longer than the branches. The last ones are appressed to the main axis during the first stages of development and show a decreasing length toward the apex of the inflorescence.

Variation in the form of the paniculodium is due to the degree of branching of the long paracladia (1Pc). In some species, long paracladia develop first and second order paracladia (1P'c and 1P''c; Fig. 4: A), while in other species they only develop first order paracladia (1P'c; Fig. 4: B). Exceptionally they develop first, second and third order paracladia (1P'c, 1P''c y 1P'''c) in *B. eurylemma* and *B. velutina* inflorescences.

B. bladhii (Fig. 4: C) and *B. campii* inflorescences are composed of paracladia branched in the lower nodes (1P'c) and generally they are verticillately disposed by the shortening of the internodes on the main axis and basal portion of paracladia.

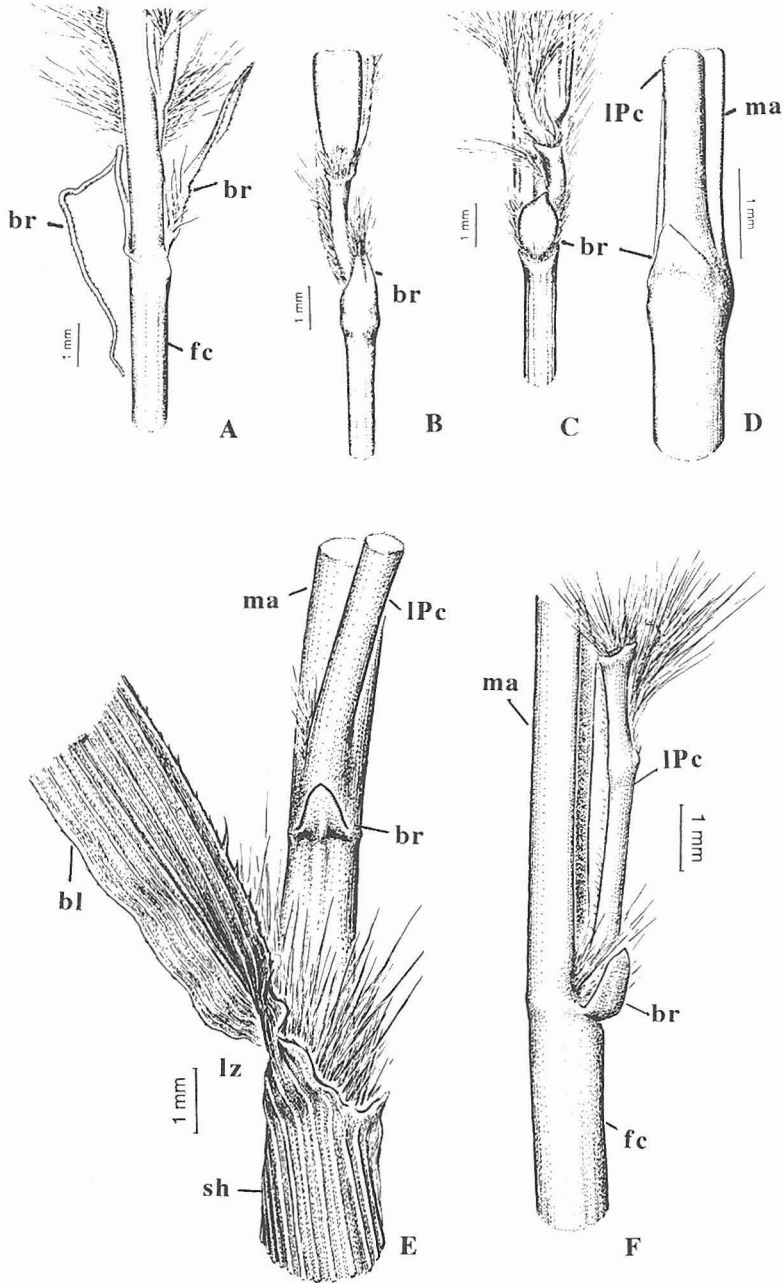


Fig. 3: Rudimentary bracts of the inflorescences: A, D: *B. springfieldii*: Gould 6642 (TAES), Boelcke 16649 (SI); B-C: *B. edwardsiana*: Burkart 3065, 25862 (SI); E-F: *B. barbinodis*: Saravia Toledo 12451 (SI), Ulibarri 228 (SI).
References: br. bract, lPc. long paracladium, ma. main axis, sh. sheath, lz. ligule zone, bl. blade, fc. flowering culm.

Table 1
Comparative table of the species with typical paniculodium.

Species	Inflorescence length (cm)	lPc ramification	Number of pairs of spikelets in each branch	Paracladia length (cm)
<i>B. barbinodis</i>	9,5-15,5	1-3 lP'c	6-11	3-5,5
<i>B. bladhii</i>	7-10,5-(12)	(-)-1 lP'c	13-24	5-6,5
<i>B. imperatoides</i>	7-10,5-(12)	1-2 lP'c	3-9	2-7
<i>B. laguroides</i>	6-10	1-4 lP'c	6-13	2,5-4
<i>B. laguroides</i> subsp. <i>torreyana</i>	6,5-7,5-(10,5)	1-4 lP'c	3-8	2-5
<i>B. meridionalis</i>	6,5-11,5	1 lP'c	7-13	3,5-6
<i>B. saccharoides</i>	6-10,5	1-3 lP'c	6-15	2,5-6
<i>B. alta</i>	10-25	1-8 lP'c 1-2 lP''c	7-14	2-8,5
<i>B. campii</i>	12-14	2-3 lP'c 1 lP''c	7-11	4,5-8,5
<i>B. eurylemma</i>	12-16	1-6 lP'c 1-3 lP''c (1-2 lP'''c)	7-9	3-6
<i>B. exaristata</i>	11-14	1-8 lP'c 1-2 lP''c	5-12	2-3,5-(-4,5)
<i>B. longipaniculata</i>	(9)-14-20	1-6 lP'c 1-2 lP''c	3-10	2,5-5
<i>B. saccharoides</i> subsp. <i>parvispiculus</i>	(6)-8,5-20	1-6 lP'c 1-2 lP''c	5-10	2-8
<i>B. velutina</i>	(9,5-10)-14-16	1-7 lP'c 1-3 lP''c (-1 lP'''c)	7-9	3-7

References: lPc, paracladium; lP'c, first order paracladium; lP''c, second order paracladium; lP'''c, third order paracladium.

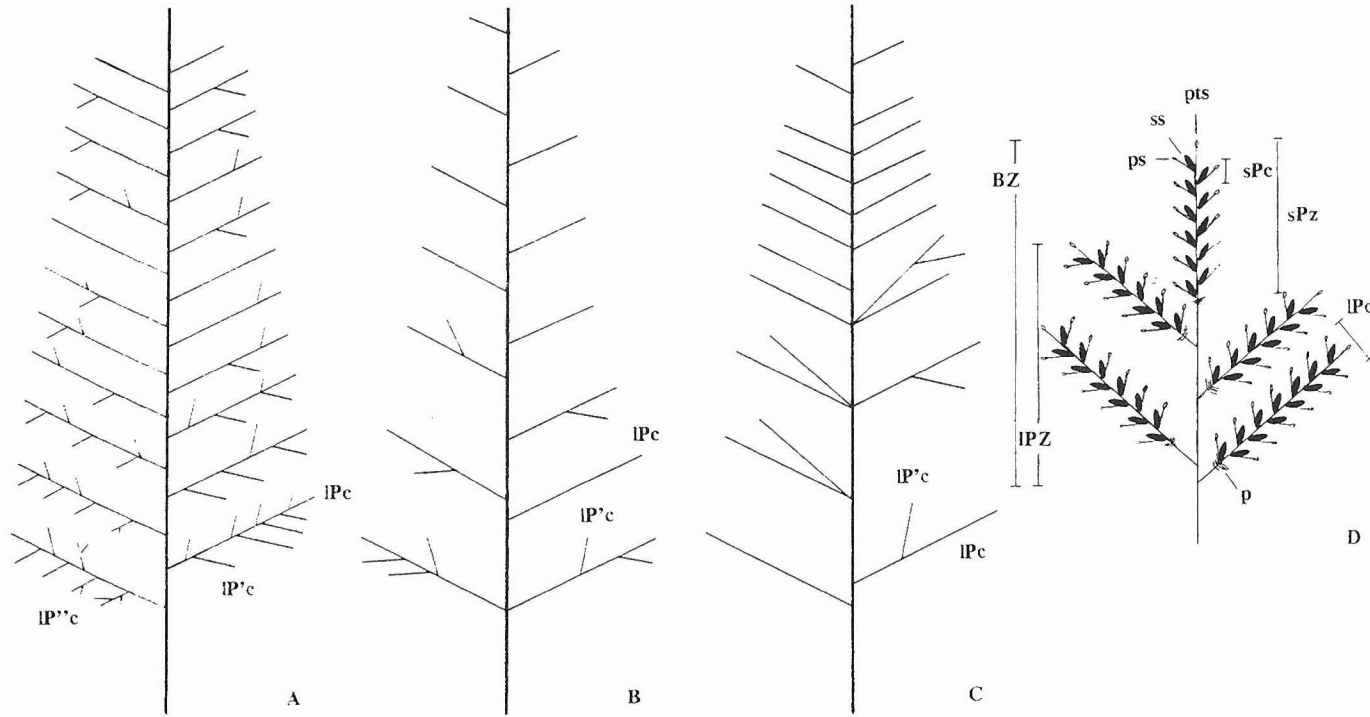


Fig. 4. Variation in the inflorescences of *Bothriochloa*. A, *B. exaristata* (Nash) Henrard; B, *B. saccharoides* (Sw.) Rydb.; C, *B. bladhii* (Retz.) S. T. Blake; D, *B. springfieldii* (Gould) Parodi.
 References: BZ. paracladial zone, sPZ. subzone of short paracladia, lPZ. subzone of long paracladia, lPc. long paracladium, sPc. short paracladium, ss. sessile spikelet, ps. pedicelled spikelet, pts. pseudoterminal spikelet.

In the second type of inflorescences the main axis also exceeds the length of the branches, although the last ones nearly have the same length as the main axis, so the inflorescence has a "flabellate" aspect (Fig. 4: D). Branches (IPc) are simple and "subdigitate"; infrequently branched again and in this case, only in lower paracladia (Table 2). This type of inflorescence was specifically analyzed in *Bothriochloa edwardsiana* and *B. springfieldii* (VEGA 1995) and represents the maximum degree of reduction in number and branching of long paracladia.

The inflorescences analyzed in *Bothriochloa* are polytelic as in all Poaceae (TROLL 1966, 1969; CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1991). The main axis is glabrous and "ends" in a single, axillar and pseudo-

Table 2
Comparative table of the species with flabellate paniculodium.

Species	Inflorescence length (cm)	Number of paracladia	IPc ramification	Number of pairs of spikelets in each branch
<i>B. edwardsiana</i>	4-8	3-6	- (-1 IP'c)	12-20
<i>B. hirtifolia</i>	10-15	7	-	12-23
<i>B. hybrida</i>	4,5-6,5-(-8,5)	4-6	-	9-14
<i>B. insculpta</i>	4-8,5	5-7	-	14-17
<i>B. ischaemum</i> <i>var. ischaemum</i>	5-7,5	1-6	-	16-23
<i>B. ischaemum</i> <i>var. songarica</i>	5-6	2-6	-	9-16
<i>B. palmeri</i>	9	11	-	8-16
<i>B. perforata</i>	6-10,5-(-12)	8-9	- (-1-2 IP'c)	7-14
<i>B. pertusa</i>	4,5-7	4	-	16-20
<i>B. reevesii</i>	5-6	5	-	8-12
<i>B. springfieldii</i>	5-8	(-2)-3-8	- (-1 IP'c)	5-13
<i>B. wrightii</i>	4,5-9	3-4	-	8-10

* The paracladia (IPc) number includes the main axis (subzone of short paracladia, sPZ).

References: IPc, paracladium; IP'c, first order paracladium; IP''c, second order paracladium; IP'''c, third order paracladium.

terminal spikelet, because it lacks the main florescence (truncation), a condition reported in other Andropogoneae (SCHNEIDER & VEGETTI 1992; VEGETTI & WEBERLING 1996; VEGETTI 1997a, 1997b, 1998). This truncate inflorescence is exclusively composed of a paracladial zone. The last one is formed by a subzone of short paracladia and a subzone of long paracladia. The subzone of short paracladia comprises an aggregation of pairs of spikelets in addition to the single and pseudoterminal spikelet, disposed on the distal portion of the main axis of the inflorescence. A short paracladium is composed of a pair of axillary spikelets, one of them basal and perfect and the other one pedicelled, neuter and reduced; except for the distal short paracladium. The last one is formed by a sessile and reduced spikelet, exomorphologically similar to the pedicelled spikelet of each pair. The subzone of long paracladia is composed of paracladia that repeat the structure previously described for the main axis. Each paracladium has a distal portion equivalent to the subzone of short paracladia and occasionally it is possible to observe long paracladia of consecutive order. As there are no bracts and prophylls associated with long paracladia, these are named long paracladia without trophotagma (VEGETTI & WEBERLING 1996).

Long paracladia are racemose branches, glabrous in their basal portion, with pilosity similar to that observed in rachis joints and pedicels below the subzone of short paracladia. Abundant pilosity was also observed in rachis internodes of the subzone of short paracladia, the pedicels, the callus and on the back of the lower glume of the spikelets. The length of the hairs increases toward the apex.

The reduced spikelet of each "terminal" triad on the main axis and the distal portion of the long paracladia can be homologued with the sessile spikelet of each pair of the subzone of short paracladia (VEGETTI & ANTON 1991; VEGETTI 1992). The axillar character of the distal spikelet in the main axis and long paracladia has already been shown in Andropogoneae (CÁMARA HERNÁNDEZ & GAMBINO 1990; VEGETTI & ANTON 1991; SCHNEIDER & VEGETTI 1992; VEGETTI 1992, 1997a, 1997b, 1998).

The processes involved in the evolution of the Poaceae inflorescence have affected the main florescence and the paracladial zone (VEGETTI & ANTON 1995): *truncation* (lack of main florescence and co-florescences), *homogenization* (in the subzone of short paracladia and distal portions of long paracladia), *reduction of the number of long paracladia without trophotagma and decrease in the degree of ramification of the paracladia*. Great diversity in Poaceae inflorescence is principally owed to truncation and homogenization processes (VEGETTI & WEBERLING 1996).

CLAYTON (1987) agrees with the concept of a reductive tendency in reproductive shoots of Andropogoneae and shows that it is accompanied

by an increment in the number of inflorescences as a result of axillary branching.

According to the reductive processes that originate the variation in Poaceae (CÁMARA HERNÁNDEZ & RUA 1991; VEGETTI 1994; VEGETTI & ANTON 1995) it is possible to explain the variation in the genus *Bothriochloa*, based on the most primitive inflorescence of Poaceae. STEBBINS (1982) described the last one as a small panicle with primary and secondary branches, each one originating singly at the nodes.

Variation in *Bothriochloa* inflorescences can be interpreted on the basis of the inflorescence with more primitive characters, which reduces the number and degree of paracladia ramification, originating the most reduced type composed of long paracladia which are exceptionally branched (Fig. 4: D).

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