



Synflorescence analysis in South American species of *Andropogon* section *Leptopogon* (Andropogoneae, Poaceae): a tool to identify different ploidy levels

NICOLÁS NAGAHAMA^a, ABELARDO C. VEGETTI^b, ANA M. ANTON^a
& GUILLERMO A. NORRMANN^c

^a Instituto Multidisciplinario de Biología Vegetal (IMBIV) - CONICET, C.C. 495, X5000JJC, Córdoba, Argentina.

E-mail: nagahama@imbiv.unc.edu.ar

^b Morfología Vegetal, Facultad de Ciencias Agrarias, Instituto de Agrobiotecnología UNL-CONICET, Kreder 2805, S3080HOF, Esperanza, Santa Fe, Argentina.

^c Facultad de Ciencias Agrarias (FCA-UNNE) and Instituto de Botánica del Nordeste (IBONE)-CONICET, Casilla de Correo 209 – 3400, Corrientes, Argentina.

Abstract

In southern South America, *Andropogon* sect. *Leptopogon* is represented by both diploid and hexaploid species. In order to compare the synflorescence structures and floral arrays in relation to ploidy levels in species of *Andropogon*, the section *Leptopogon* was used as model. In this study, the synflorescence structure was typologically characterized. The structural analysis was based on the typology system developed by Troll and Weberling, which has proved useful in describing inflorescences. A comparative analysis of the variations observed in the structure of the synflorescence and a morphometric analysis using principal component analysis were carried out. These results revealed that diploid and hexaploid species present differences mainly in the following parameters: synflorescence length, number of internodes of the enrichment zone main axis, number of internodes and length of paracladia of the trophotagma, number of long paracladia per unit of inflorescence, length of hairs on articulated rachis internodes, pedicellate spikelet length, pedicellate spikelet width, pedicel width, length of hairs on pedicel, sessile spikelet length, awn length and floral system arrangements. This study provides a useful tool to distinguish between diploid and hexaploid species of *Andropogon* sect. *Leptopogon*. We propose naming the group of diploid species from Central and South America as the *Andropogon selloanus* complex.

Key words: grass inflorescence structure; multivariate analysis; taxonomy.

Introduction

Within the tribe Andropogoneae, one of the major sources of variation is the inflorescence (Clayton & Renvoize 1986, Clayton 1987, Vegetti 1994, 1999). Clayton (1987), in his revision of Andropogoneae, identified the need for a detailed exploration of the range of variation in the architecture of the compound panicle in the tribe. Since then, several studies have been performed on *Bothriochloa* Kuntze (1891: 762) (Vegetti 1994, 1999, Vega 2000), *Hyparrhenia* Andersson ex E. Fournier (1886: 51) (Vegetti 1994, 1999), *Schizachyrium* Nees (1829: 331) (Vegetti & Tivano 1991, Vegetti 1992, 1994, Peichoto & Vegetti 2007). In general, the typology-based system developed by Troll (1964, 1969) and Weberling (1989) has proved to be useful for describing inflorescences (Rua 1999).

Most genera in Andropogoneae have spikelets arranged in pairs, one sessile and the other pedicellate, the sessile being bisexual and the pedicellate male or barren (Clayton & Renvoize 1986); rarely, they are solitary as in *Dimeria ornithopoda* Trinius (1820: 167) or form triads as in the genus *Polytrias* Hackel (1887: 24) and in some species of *Lasiurus* Boissier (1859: 145) (Clayton & Renvoize 1986). Although in

Andropogon Linnaeus (1753: 1045) the sessile spikelet is morphologically bisexual, in some species the anthers are non-functional (Norrman 2009). These variations occur among different species, and are considered characters of taxonomic value (Clayton & Renvoize 1986).

Andropogon is a pan-tropical genus of grasses estimated to contain 100 (Clayton & Renvoize 1986) to 120 (Campbell & Windisch 1986) species, which are mainly distributed in the grasslands of Africa and the Americas. Most African species are diploids or tetraploids ($2n = 2x = 20$ or $4x = 40$) (Campbell 1983, Norrman 2009), whereas American *Andropogon* species are usually diploids or hexaploids ($2n = 2x = 20$ or $6x = 60$) (Gould 1967, Norrman 1985, Campbell & Windisch 1986, Galdeano & Norrman 2000, Norrman & Scarel 2000), with only a few exceptions (see Boe *et al.* 2004).

Stapf (1919) proposed four sections for the African species of the genus: (1) section *Andropogon* Stapf (1919: 208), (2) section *Leptopogon* Stapf (1919: 208), (3) section *Notosolen* Stapf (1919: 208) and (4) section *Piestium* Stapf (1919: 208). Gould (1967) suggested the incorporation of the American species into the first three taxonomic sections mentioned above. These sections were recognized by Clayton & Renvoize (1986), with section *Leptopogon* being considered the most derived within the genus (Campbell & Windisch 1986, Norrman 1999). In the Americas, the section *Leptopogon* comprised ca. 45 species, half of them are represented by two complexes: *A. virginicus* Linnaeus (1753:1046) (diploids), distributed in North America (Campbell 1983) and the *A. lateralis* Nees in Campbell & Windisch (1986: 411) complex (hexaploids) covering South and Central America. Documented American diploids of this section are represented by 12 species, 9 of them belong to the *A. virginicus* complex. The other three species do not belong to any complex and are distributed in South and Central America.

Andropogon section *Leptopogon* in Central and South America encompasses ca. 25 species; 11 of them have chromosome counts, and are mainly diploids or hexaploids, with the exceptions of the triploid *A. ternatus* Sprengel (1825: 283) Nees (1829: 326) ($2n = 3x = 30$) (see Nagahama & Norrman 2012) and the octoploid *A. urbanianus* Hitchcock (1912: 424) ($2n = 8x = 80$). *Andropogon leucostachyus* Kunth (1816: 187), *A. macrothrix* Trinius (1832: 270) and *A. selloanus* Hackel (1889: 420) Hackel (1904: 266) are diploids ($2n = 2x = 20$). On the other hand, the hexaploid species within section *Leptopogon* in Central and South America are included in the *A. lateralis* complex [*A. arenarius* Hackel (1885: 134), *A. bicornis* Linnaeus (1753: 1046), *A. glaziovii* Hackel (1883: 286), *A. hypogynus* Hackel (1883: 290) and *A. lateralis* Nees (1829: 329)]. This is considered to be a natural group of allohexaploid species ($2n = 6x = 60$), in which anther size and the number of pollen grains per anther in the fertile sessile spikelets are strongly reduced compared with those of pedicellate spikelets. This discriminant character (dimorphism of anthers) defines the *A. lateralis* complex (Campbell 1983, Campbell & Windisch 1986). Most of these species (*A. arenarius*, *A. bicornis*, *A. glaziovii*, *A. hypogynus*, *A. lateralis*, *A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus*) inhabit in southern South America (Argentina, Bolivia, Brazil, Paraguay and Uruguay).

The present study deals with diploid and hexaploid species of the section *Leptopogon* from southern South America. The purposes of the study were to: (1) clarify the synflorescence structure within the section using the typology-based system proposed by Troll (1964) and Weberling (1989), and (2) compare the degree of development of synflorescences and the floral system arrangement among diploid and hexaploid species of *Andropogon* sect. *Leptopogon*.

Material and methods

Plant material

The living collection of *Andropogon* species held at the Instituto de Botánica del Nordeste (IBONE), Corrientes, Argentina was used for the purposes of the study. Additionally, collection trips were undertaken from 2008 to 2012 covering north-eastern Argentina (Corrientes, Entre Ríos, Formosa, Misiones, Santa Fe), Brazil (Rio Grande do Sul, Santa Catarina), and Paraguay. Each field collection from natural populations included live samples and synflorescences. Plants were transplanted in clay pots to the IBONE experimental

garden where individuals from each species were cultivated. Vouchers were deposited at the CORD and CTES herbaria. Also, other voucher specimens from CORD, CTES, ICN, LIL, MBM, MO, SI, US and W were analyzed.

At least 20 plants were studied per species. Live samples and herbarium specimens were analyzed using a stereoscopic microscope and measured using digital calipers (Electronic IP65, 797B Series, Starrett®). Samples were identified on the basis of morphological and ecological characters listed in Norrmann (1999) and Zanin (2001).

Analysis of the synflorescence structure

We used the typology-based system to interpret the synflorescences of the following species: *A. arenarius*, *A. bicornis*, *A. glaziovii*, *A. hypogynus*, *A. lateralis*, *A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus*. The abbreviations used for the references of the figures are the same as in Vegetti & Müller-Doblies (2004) and for spikelet analysis we relied on the floral arrays proposed by Connor (1979).

Principal component analysis

Analyses were performed using a data set (data available upon request) composed of 19 morphological quantitative characters (Table 1) that were scored for 253 specimens of *Andropogon* sect. *Leptopogon* (Appendix 1). The synflorescences were treated as operational taxonomic units (OTUs). Quantitative characters were either measured or counted and scored as continuous characters. To reduce the experimental error, we considered the variability of the spikelets within the same plant. To do this, 10 pairs of spikelets were measured per plant (units of inflorescences of different paracladia of the trophotagma) and average values were used for morphometric analyses.

TABLE 1. Morphological characters analyzed.

Characters	
(SL)	Synflorescence length
(NI)	Number of internodes of the EZ main axis
(LFB)	Length of first branch on the EZ main axis
(IFB)	Number of internodes of the first branch
(LSB)	Length of second branch on the EZ main axis
(ISB)	Number of internodes of the second branch
(SPL)	Spatheole length
(NFB)	Number of floriferous branches per unit of inflorescence
(FBL)	Floriferous branch length
(IL)	Length of articulated rachis internodes
(LHI)	Length of hairs on articulated rachis internodes
(SSL)	Sessile spikelet length
(SSW)	Sessile spikelet width
(AL)	Awn length
(PSL)	Pedicellate spikelet length
(PSW)	Pedicellate spikelet width
(PL)	Pedicele length
(PW)	Pedicele width
(LHP)	Length of hairs on pedicele

The data set was analyzed on the basis of the correlation matrix through Principal Components Analysis (PCA) using the Pearson correlation coefficient (Michener & Sokal 1957) with the Infostat v. 2010 program (Di Rienzo *et al.* 2010). Before performing PCA, correlation matrix was standardized. The length of the

enrichment zone was excluded from the PCA due to the fact that in previous analyses it was highly correlated with the synflorescence length. The values of the characters measured were averaged and the mean values for each variable were used in the PCA. All the variables were tested for normality with the Shapiro-Wilks test (Mahibbur & Govindarajulu 1997).

Results

Synflorescence zones

In *Andropogon* sect. *Leptopogon* species, the plant is composed of a group of shoots of consecutive branching order: these shoots are the synflorescences. In each synflorescence (Figs. 1–3) we recognize the trophotagma (TT) and the unit of inflorescence (UIF). The trophotagma zone bears proximal cataphylls and foliage leaves; it usually comprises a proximal zone with short internodes (short internodes zone, SIZ) and a distal zone with elongated internodes (long internodes zone, LIZ). The axillary buds of the SIZ develop intra-vaginal lateral shoots (innovations) and consequently the SIZ represents an innovation zone (IZ). In this zone the leaves are formed by sheath and blade, in which the sheath is longer than the internodes. The LIZ is represented by a proximal inhibition zone (HZ), in which the axillary buds of leaves do not develop, and a distal enrichment zone (EZ), in which the buds can generate floriferous shoots (Figs. 1–3). These floriferous shoots are the enrichment axes or paracladia of the trophotagma (Pc_{TT}).

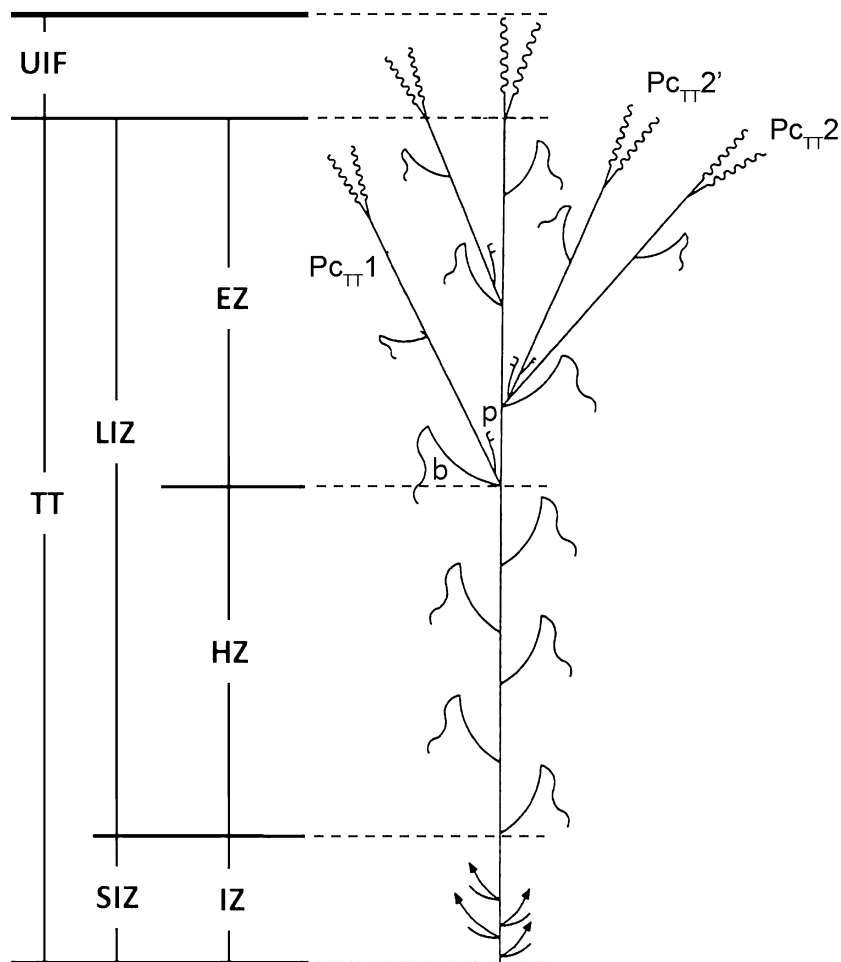


FIGURE 1. Diagram of the synflorescence of *Andropogon selloanus* (Norrman 73). Figure abbreviations: TT: trophotagma; UIF: unit of inflorescence; SIZ: short internodes zone; LIZ: long internodes zone; IZ: Innovation zone; HZ: Inhibition zone; EZ: Enrichment zone; Pc_{TT1} : first paracladium of the trophotagma; Pc_{TT2} : second paracladium of the trophotagma; $Pc_{TT2'}$: paracladium of the trophotagma of second degree in the Pc_{TT2} ; b: bract; p: prophyll.

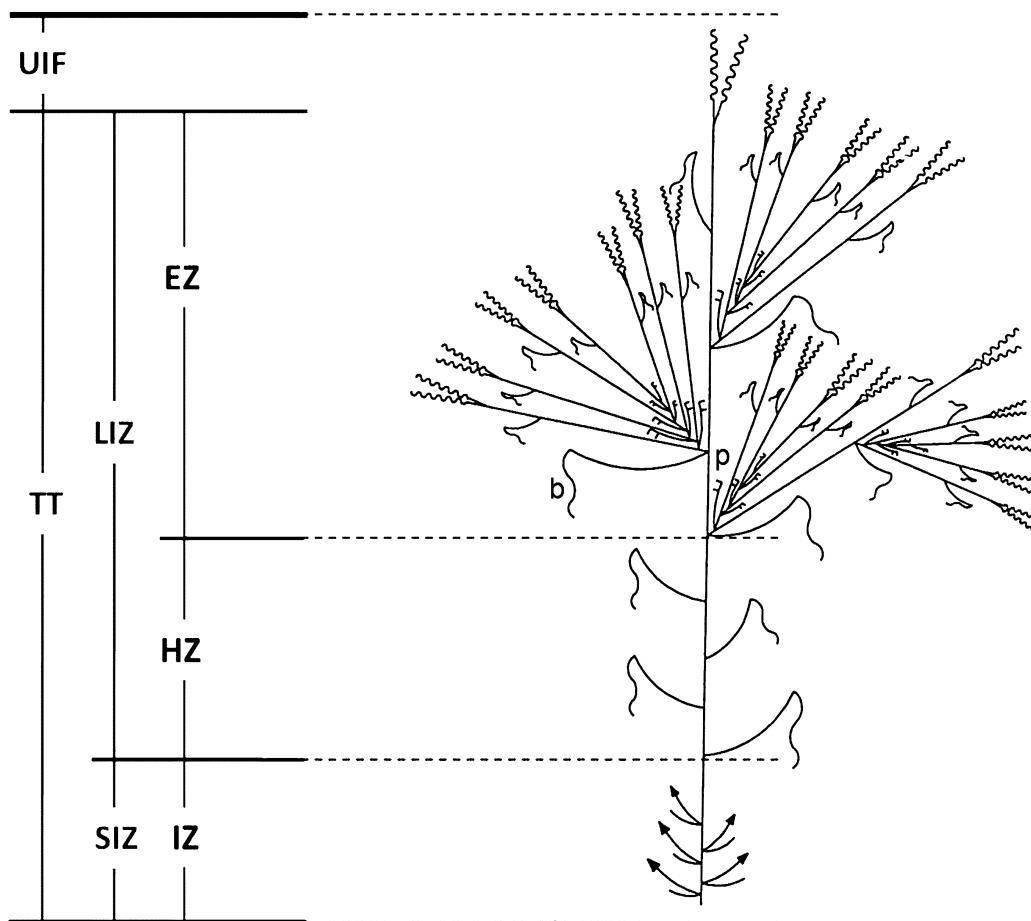


FIGURE 2. Diagram of the synflorescence of *Andropogon lateralis* (Norrmann 71). Figure abbreviations: TT: trophotagma; UIF: unit of inflorescence; SIZ: short internodes zone; LIZ: long internodes zone; IZ: Innovation zone; HZ: Inhibition zone; EZ: Enrichment zone; b: bract; p: prophyll.

The number of internodes in the innovation zone is similar in all species studied (3–6 internodes in *A. arenarius*, 3–7 in *A. bicornis*, 3–8 in *A. glaziovii*, 4–7 in *A. hypogynus*, 3–7 in *A. lateralis*, 3–7 in *A. leucostachyus*, 3–6 in *A. macrothrix*, 3–7 in *A. selloanus* and 3–6 in *A. ternatus*). In the inhibition zone, diploid species present up to 6 internodes, and hexaploid species present usually up to 11–13 internodes, with the only exception being *A. arenarius* with up to 6 internodes.

Analysis of enrichment zone

The variability among synflorescences within the section is mainly due to the degree of development of the enrichment zone. Analysis of length and number of internodes of the enrichment zone main axis in diploid species (*A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus*) shows that these present short enrichment zone and are constituted by few internodes (Table 2). *Andropogon ternatus*, though a triploid species, is closely linked to the diploids both morphologically and genetically (Norrmann 1985, Norrmann & Quarín 1987) and was included in this study in the diploid group.

In hexaploid species, *A. arenarius* shows a short enrichment zone (20.1–32.2 cm), comprising 4–7 internodes; in *A. lateralis* and *A. hypogynus* the enrichment zone is long and is composed of few internodes (Table 2). As a result, the synflorescences are scarcely branched (Fig. 2). In *A. bicornis* and *A. glaziovii* the enrichment zone is long and this is composed of numerous internodes (Table 2). In both species, the internodes of the EZ main axis are shortened upwards and consequently the synflorescence, that is branched and foliose, appears as a dense and profusely branched false panicle in *A. bicornis*.

TABLE 2. Comparison of the most important characters in synflorescences of diploid and hexaploid species of *Andropogon* sect. *Leptopogon*. Values represent the total range of measurements observed from all specimens analyzed per species. Extreme values are shown in brackets. $P_{C_{TT}1}$ = first paracladia of the trophotagma, $P_{C_{TT}2}$ = second paracladia of the trophotagma.

Species	Enrichment zone (Main axis / $P_{C_{TT}1}$ / $P_{C_{TT}2}$)										
	Synflorescence length (cm)	Number of internodes in HZ	Length of the EZ main axis (cm)	Number of internodes of the EZ main axis	Number of bracts in $P_{C_{TT}1}$	Length of $P_{C_{TT}1}$ (cm)	Number of internodes of $P_{C_{TT}1}$	Ramification degree in $P_{C_{TT}1}$	Length of $P_{C_{TT}2}$ (cm)	Number of internodes of $P_{C_{TT}2}$	Ramification degree in $P_{C_{TT}2}$
<i>A. leucostachyus</i>	45–110	3–6	21–51	2–4	1 (Only the distal bract)	16–37.3	2	2 nd –4 th	5–15.9	2	1 st –2 nd
<i>A. macrothrix</i>	30–100	3–4	10.1–44.5	1–2	1 (Only the distal bract)	3.6–21.9	2	1 st	–	–	–
<i>A. selloanus</i>	20–110	3–6	14.6–39.8	2–5	1 (Only the distal bract)	3–21.4	2	1 st –2 nd	5–20.1	2	1 st –2 nd (–3 rd)
<i>A. ternatus</i>	20–75(–100)	3(–4)	12–43.3	1–2(–3)	1 (Only the distal bract)	3–9.5	2	1 st	–	–	–
<i>A. arenarius</i>	20–120(–150)	3–6	20.1–32.2	4–7	1–3	15.2–22.8	2–4	2 nd –3 rd	9.6–13.6	2–3	1 st –3 th
<i>A. bicornis</i>	(130–)150–180	6–12	31.5–73.2	11–16	4–10	35.5–44.8	5–11	(1 st –)2 nd –3 rd	27.7–46	6–10	(1 st –)2 nd –3 rd
<i>A. hypogynus</i>	(80–)100–220	5–12	64.4–102.4	5–9	1–5(–6)	28.5–69.8	2–7	5 th –6 th	28.5–59.8	2–6	4 th –5 th
<i>A. lateralis</i>	(70–)90–170	3–11	51.7–108.4	3–7	1–3(–5)	22.3–44.1	1–3(–4)	5 th –6 th	13.6–54	1–3	3 rd –5 th
<i>A. glaziovii</i>	140–250	8–13	54.9–123.7	9–13	4–8(–9)	22.3–60.6	5–9	(1 st –)3 rd –6 th	20–27.6	4–6	(1 st –)2 nd –4 th

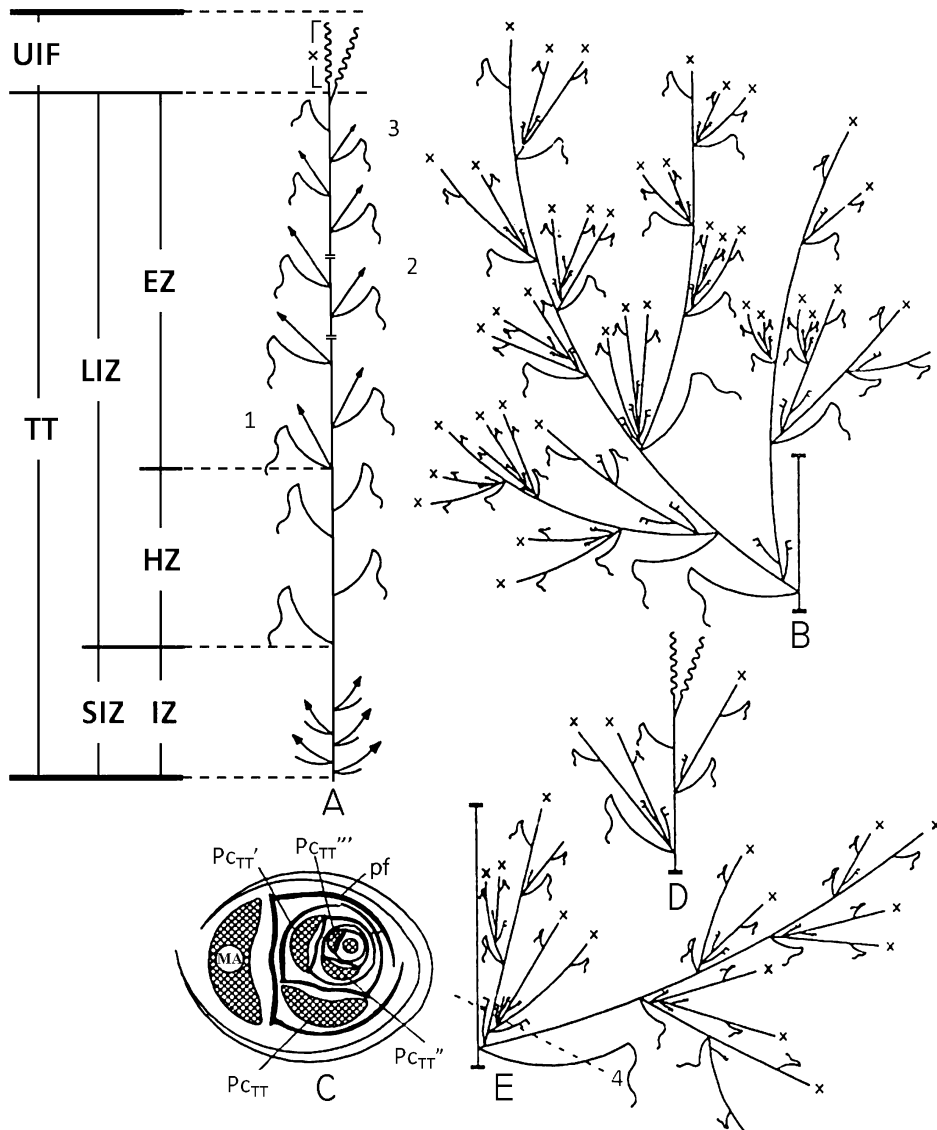


FIGURE 3. *Andropogon bicornis* (Normann & Quarín 91). **A.** synflorescence structure; **B.** basal axillary paracladium (Pc_{TT1}) (1 in A); **C.** cross-section (level 4 in E); **D.** distal zone of the synflorescence (3 in A); **E.** Pc_{TT} of middle zone of the synflorescence (2 in A). Figure abbreviations: TT: trophotagma; UIF: unit of inflorescence; SIZ: short internodes zone; LIZ: long internodes zone; IZ: Innovation zone; HZ: Inhibition zone; EZ: Enrichment zone; Pc_{TT} : paracladium of the trophotagma of first degree; Pc_{TT}' : paracladium of the trophotagma of second degree; Pc_{TT}'' : paracladium of the trophotagma of third degree; Pc_{TT}''' : paracladium of the trophotagma of fourth degree; MA: main axis; pf: prophyll. Crosses represent units of inflorescence.

In the enrichment zone, axillary buds generate floriferous shoots (Pc_{TTs}), which repeat the structure observed on the main axis. These Pc_{TTs} reduce acropetally and finally a sterile distal leaf (= flag leaf) appears in the main axes of the enrichment zone and Pc_{TTs} . Each Pc_{TT} is composed of a short hypopodium, an adaxial prophyll, one or more bracts (Table 2) and terminates in units of inflorescences (Fig. 4). From the axillary buds of prophylls and bracts of these Pc_{TTs} , a variable number of branches of a higher order (Pc_{TT} Pc_{TT}' ; see Fig. 1) will be generated. The exception is the sterile distal leaf of each Pc_{TT} , whose axillary buds do not generate any shoots (see Figures 1–4). Examining the degree of development of Pc_{TTs} , we observed considerable variation among the species of the section *Leptopogon* studied (Table 2). In *A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus* (Table 2, Figs. 5A, B and 6A, B) each Pc_{TT} possess only the distal leaf (whose axillary bud does not develop); consequently, it is not ramified (*A. macrothrix* and *A. ternatus*) (Fig. 5A), or is ramified only from the axillary bud of the prophylls (*A. leucostachyus* and *A. selloanus*) (Fig.

5B). *Andropogon macrothrix* and *A. ternatus* present Pc_{TTs} of first ramification degree (Table 2). In *A. leucostachyus* and *A. selloanus* the Pc_{TTs} are more ramified at the level of the prophylls, generating Pc_{TTs} up to the third and fourth ramification degree (Table 2). On the other hand, in *A. arenarius*, *A. bicornis*, *A. hypogynus*, *A. lateralis* and *A. glaziovii* (Table 2, Figs. 5 C–F and 6 C–F) each Pc_{TT} is ramified from axillary buds of prophylls and bract/s. In *A. arenarius*, each Pc_{TT} presents 1–3 bracts, whose axillary buds produce more Pc_{TTs} , and these are also ramified at the level of the prophyll, generating Pc_{TTs} up to the second and third degree (Table 2, Fig. 5C). *Andropogon lateralis* (Fig. 5D) and *A. hypogynus* usually present 1–3 and 1–5 bracts in Pc_{TTs} respectively, and they can generate Pc_{TTs} up to fifth and sixth degree from axillary buds of the prophylls. These two species have similar branching patterns in the lower portion of the Pc_{TTs} but distally, *A. hypogynus* develops an increased number of bracts and Pc_{TTs} . *Andropogon bicornis* (Figs. 3, 5F and 6F) and *A. glaziovii* (Figs. 5E and 6E) develop up to 10 bracts in the Pc_{TTs} and are also ramified at the level of the prophyll. *A. bicornis* is constituted by up to 3 (normally one) Pc_{TTs} of prophyllar origin, whereas *A. glaziovii* is constituted by 1–3 Pc_{TTs} in the proximal region and up to 5 in the distal region of branches. From both the prophylls and bracts of each Pc_{TT} , new Pc_{TTs} of consecutive order are generated and therefore the synflorescences are profusely branched.

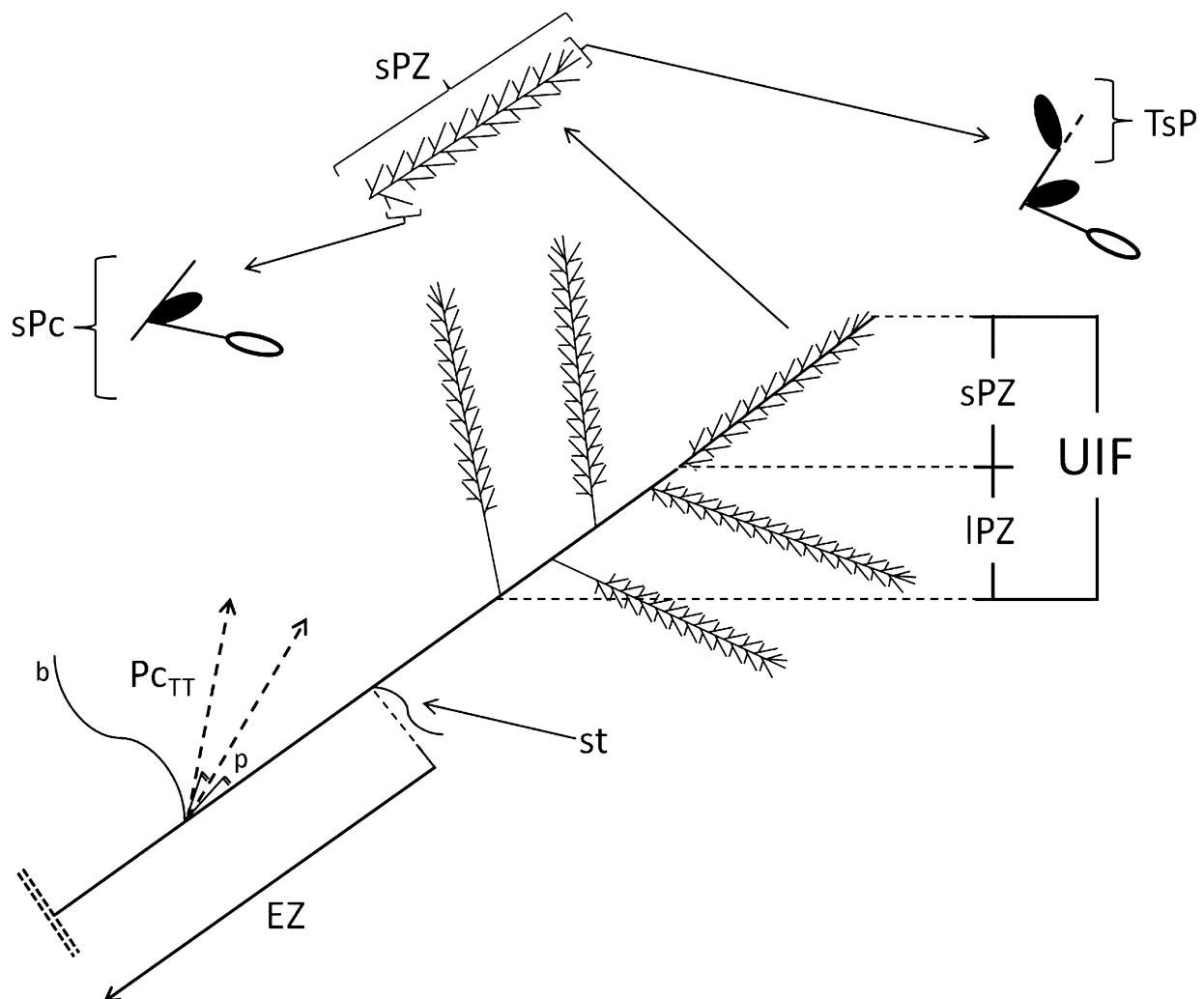


FIGURE 4. Diagram of the distal region of the EZ main axis and Pc_{TTs} in *A. hypogynus* (*Krapovickas 12081*). Figure abbreviations: EZ: enrichment zone; UIF: Unit of inflorescence; IPZ: long paracladia of the unit of inflorescences subzone; SPZ: short paracladia subzone; TsP: terminal short paracladium; st: sterile distal leaf (= spatheole); Pc_{TT} : paracladium of the trophotagma; b: bract; p: prophyll; filled ellipses: sessile spikelets; open ellipses: pedicellate spikelets.

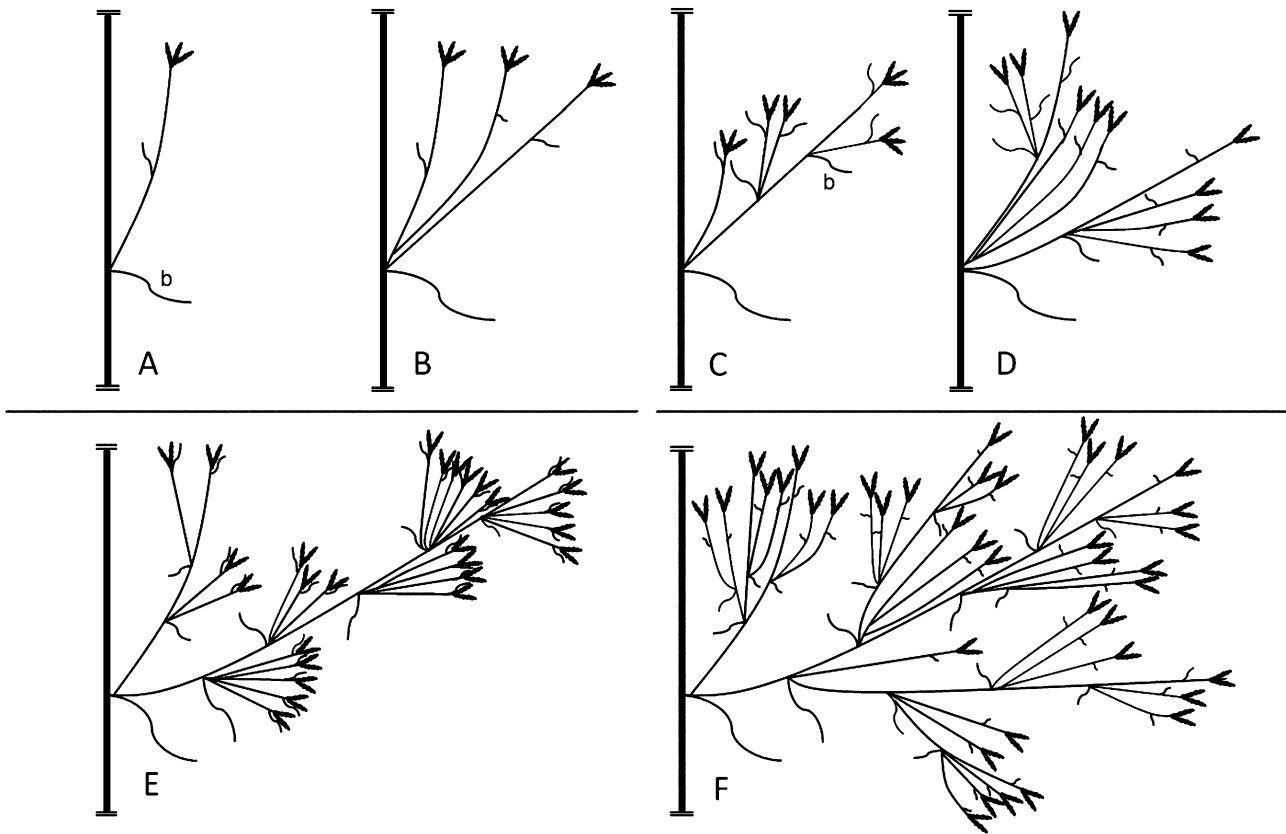


FIGURE 5. Variations of Pc_{TTs} in the section *Leptopogon*. **A–B.** Diploid species. **A.** Not ramified Pc_{TT} in *A. macrothrix* (Norrman 115) and *A. ternatus* (Norrman 74); **B.** Pc_{TT} showing a second ramification degree in *A. leucostachyus* (Norrman 46) and *A. selloanus* (Norrman 229); **C–F.** Hexaploid species. **C.** Pc_{TT} ramified from axillary buds of bracts and prophylls in *A. arenarius* (Nagahama & Norrmann 29a); **D.** Pc_{TT} ramified from axillary buds of bracts and prophylls in *A. lateralis* (Schinini *et al.* 16842); in this species the Pc_{TT} ramified from axillary buds of prophylls develops new Pc_{TTs} ; **E.** Pc_{TT} showing numerous Pc_{TTs} developed from axillary buds of bracts and prophylls in *A. glaziovii* (Norrman 217a); **F.** Pc_{TT} showing numerous Pc_{TTs} developed from axillary buds of bracts and prophylls in *A. bicornis* (Norrman & Quarín 91).

In the species of *Andropogon* sect. *Leptopogon* analyzed here, the unit of inflorescence has a long paracladia subzone (IPZ) and a short paracladia subzone (sPZ) (Fig. 4). In each species, the units of inflorescences are constituted by a variable number of long paracladia (= floriferous branches, IPc_s). Some variation is observed in the unit of inflorescence length among species, with the shortest UIF in *A. glaziovii* and the longest one in *A. hypogynus*. The number of IPc_s per unit of inflorescence varies from 1 to 22 depending on the species. The variations observed in the unit of inflorescence are shown in Table 3.

Short paracladia (sPc) are represented by a pair of spikelets, one sessile and the other pedicellate, with the exception being the distal short paracladium (terminal short paracladium, TsP), which is reduced to a single spikelet (Fig. 4). Consequently, these constitute short paracladia of the second degree (Weberling *et al.* 1993). The terminal short paracladium corresponds to a sessile spikelet and is functional, except in the case of *A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus* in which this spikelet is underdeveloped and sterile (Table 3). In all species, the short paracladia subzone does not have a terminal spikelet.

With respect to the short paracladia, both the sessile (S) and the pedicellate spikelet (P) have two florets; only the distal one develops a flower, either hermaphrodite (H), male (M), female (F) or neuter (O) (Table 3). The floral arrays in short paracladia differ among *Andropogon* sect. *Leptopogon* species and the following combinations were found: sessile spikelet hermaphrodite and pedicellate reduced sterile S(H) + P(O) (*A. leucostachyus*, *A. macrothrix*, *A. selloanus*, *A. ternatus* and *A. bicornis*); sessile spikelet hermaphrodite and

pedicellate male S(H) + P(M) (*A. glaziovii* and *A. arenarius*); sessile spikelet female and pedicellate male S(F) + P(M) (*A. lateralis* and *A. hypogynus*). The distal sessile spikelets (in TsP) may be different to the sessile spikelets in the medium short paracladia depending on the taxa (Table 3). In the short paracladia subzone as well as in the long paracladia subzone (Fig. 4), the following combinations were found: sessile spikelet hermaphrodite and pedicellate reduced and sterile S(H) + P(O) (*A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus*); sessile spikelet hermaphrodite and pedicellate hermaphrodite S(H) + P(H) (*A. glaziovii*, *A. arenarius*, and *A. bicornis*); sessile spikelet female and pedicellate hermaphrodite S(F) + P(H) (*A. lateralis* and *A. hypogynus*).

TABLE 3. Comparison of unit of inflorescence and the floral arrays in short paracladia among *Andropogon* sect. *Leptopogon* species. Values represent the total range of measurements observed from all specimens analyzed per species. Extreme values are show between brackets.

Species	UIF length (cm)	Number of IPC _s per UIF	Sessile spikelet in sPc	Distal sessile spikelet (TsP)	Pedicellate spikelet
<i>A. leucostachyus</i>	2.2–5.6	2–8	Hermaphrodite	Reduced	Reduced
<i>A. macrothrix</i>	3.5–8.7	2–10	Hermaphrodite	Reduced	Reduced
<i>A. selloanus</i>	3–7.2	2–8	Hermaphrodite	Reduced	Reduced
<i>A. ternatus</i>	4.1–7.4 (–9)	2–3 (–4)	Hermaphrodite	Reduced	Reduced
<i>A. arenarius</i>	2.5–5	1–3	Hermaphrodite	Hermaphrodite	Usually male
<i>A. bicornis</i>	2–4	1–3	Hermaphrodite	Usually hermaphrodite	Reduced
<i>A. hypogynus</i>	6–16	7–23	Functionally female	Hermaphrodite	Male
<i>A. lateralis</i>	2–6.5	2–4	Functionally female	Hermaphrodite	Male
<i>A. glaziovii</i>	1.5–3.5	2–5	Hermaphrodite	Usually Hermaphrodite	Usually male

The distribution of OTUs in multivariate morphometric space based on 19 morphological traits of synflorescences was studied with PCA. The first three components accounted for 69.2% of the total variance (34.3%, 24%, and 10.9%, respectively; Figs. 7 and 8; see Table 4). The cophenetic correlation is high (0.899), indicating a good fit between the euclidean distance among OTUs in the two dimensional plot and the distance in the original multidimensional space.

The variables that contribute most to PC1 are the length of the first branch on the EZ main axis (LFB), the number of internodes of the EZ main axis (NI), synflorescence length (SL), length of the second branch on the EZ main axis (LSB), number of internodes of the second branch (ISB) and number of internodes of the first branch (IFB), while pedicellate spikelet width (PSW), length of hairs on articulated rachis internodes (LHI), pedicellate spikelet length (PSL) and pedicel width (PW) contribute to the second component (PC2, see Table 4). Most of the variation in component 3 (PC3) is provided by the length of hairs on pedicel (LHP), number of long paracladia per unit of inflorescence (NFB), sessile spikelet length (SSL) and awn length (AL) (see Table 4). The scatter diagrams of the results of PCA revealed appreciable separation between diploid and hexaploid species, as well as between species of the same ploidy level (Figs. 7 and 8).

In addition, there are also differences between species in the floral system arrangements.

Discussion

Inflorescence typology

The grass plant is composed of shoots of consecutive branching order (Moore & Moser 1995). Each of these is an innovation shoot that normally terminates in an inflorescence. According to the typological system

of Troll (1964) and Weberling (1989), each of these shoots constitutes a synflorescence (Cámara Hernández & Rua 1991, Vegetti 1991).

TABLE 4. Contribution of variables to the first three principal components, the higher value indicated in bold.

	1	2	3
Eigenvalues	6.51	4.56	2.06
Component loadings			
Synflorescence length	0.34	0.09	0.09
Number of internodes of the EZ main axis	0.35	-0.07	0.18
Length of first branch on the EZ main axis	0.36	0.09	-0.02
Number of internodes of the first branch	0.32	-0.11	0.23
Length of second branch on the EZ main axis	0.33	0.11	-0.03
Number of internodes of the second branch	0.33	-0.16	0.10
Spatheole length	-0.25	0.12	-0.14
Number of floriferous branches per unit of inflorescence	0.07	0.27	-0.39
Floriferous branch length	-0.04	0.27	-0.32
Length of articulated rachis internodes	-0.09	0.24	-0.11
Length of hairs on articulated rachis internodes	-0.20	-0.38	-0.06
Sessile spikelet length	-0.22	0.20	0.39
Sessile spikelet width	-0.07	0.09	-0.09
Awn length	-0.21	0.16	0.35
Pedicellate spikelet length	0.05	0.37	0.26
Pedicellate spikelet width	0.10	0.39	0.19
Pedicele length	-0.19	-0.27	0.08
Pedicele width	-0.20	0.31	0.23
Length of hairs on pedicel	-0.11	-0.21	0.41
Percent of total variance explained	34.3%	24.0%	10.9%

The synflorescence in the species of *Andropogon* studied here represent a complex system of ramification. Differences in the aspect of the synflorescences among species depend on the degree of development of the enrichment zone (length of the enrichment zone and their branching system). From the axillary bud of prophylls and bracts along the enrichment zone, variable numbers of Pc_{TTs} are generated. As occurs in other species of Andropogoneae, the exception is the distal bract of the EZ main axis and Pc_{TTs} , whose axillary buds generate no shoots (Vegetti 1992, 1993, 1994, 1999, Peichoto & Vegetti 2007). This area of inhibition may be considered as an intercalary zone of inhibition, represented by the node of the distal sterile foliose hypsophyll (Vegetti & Müller-Doblies 2004).

The unit of inflorescence in *Andropogon* sect. *Leptopogon* species consists of long and short paracladia; it is polytelic and truncate, distinctive of Andropogoneae and, as a consequence of this truncation, the unit of inflorescence shows a homotelic structure (Vegetti 1999). In the tribe, the inflorescence is also homogenized, a process that generally accompanies the truncation (Vegetti & Anton 1995, 2000, Reinheimer & Vegetti 2008, Perreta *et al.* 2009) and enables to recognize short and long paracladia in the area of the unit of inflorescence.

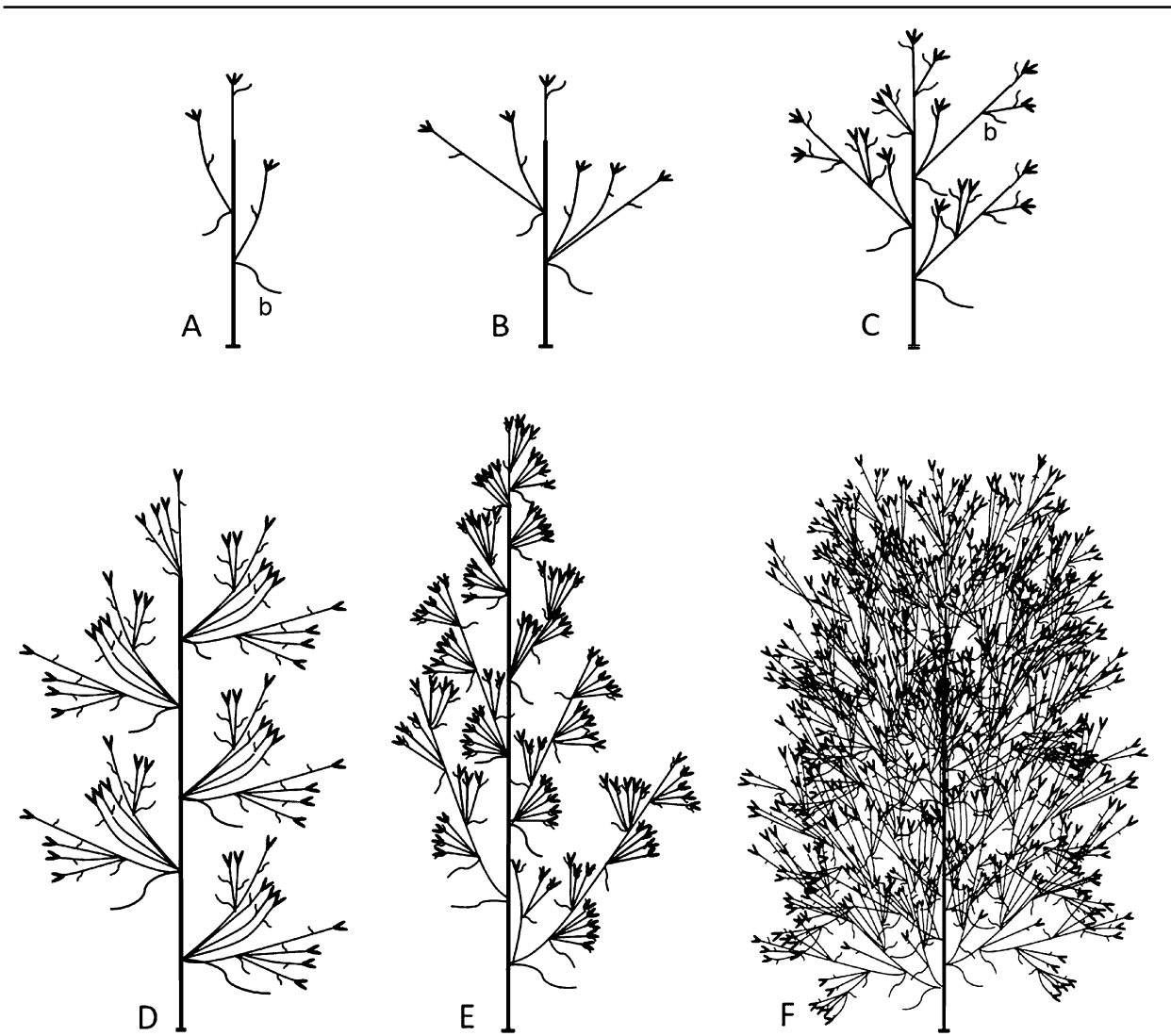


FIGURE 6. Diagrams of the enrichment zone in synflorescences of *Andropogon* sect. *Leptopogon*. **A–B.** Diploid species. **A.** *A. macrothrix* (Normann 115) and *A. ternatus* (Normann 74); **B.** *A. leucostachyus* (Normann 46) and *A. selloanus* (Normann 229). **C–F.** Hexaploid species. **C.** *A. arenarius* (Nagahama & Normann 29a); **D.** *A. lateralis* (Schinini et al. 16842); **E.** *A. glaziovii* (Normann 217a); **F.** *A. bicornis* (Normann & Quarín 91).

The long paracladia (Troll 1964, Cámara Hernández & Rúa 1991, Vegetti & Tivano 1991, Vegetti 1992) are made up of pairs of spikelets, and in the distal paracladium the pair is reduced to a single spikelet. This spikelet has been interpreted as being homologous to the sessile spikelet (Vegetti & Anton 1991) and has an axillary position, as described for other species of Poaceae (Cámara Hernández & Gambino 1990, Vegetti & Anton 1991, Vegetti 1994).

The number of long paracladia in sect. *Leptopogon* is variable as in all the Andropogoneae (Vegetti 1999), and when the reduction of the long paracladia is complete, only the short paracladia subzone remains (Vegetti 1994). Although this feature was manifest in some of the species studied, others present numerous long paracladia per unit of inflorescence (see Table 3).

Variations of inflorescence structure between diploid and hexaploid species

In southern South America, the section *Leptopogon* is segregated into two main groups according to chromosome number: a few species are diploid ($2n = 2x = 20$), small in size, occurring naturally in disturbed

and recently opened spaces, such as crop residues and road edges; another seven species are hexaploid ($2n = 6x = 60$), larger in size and occupying different habitats (Norrman 1985).

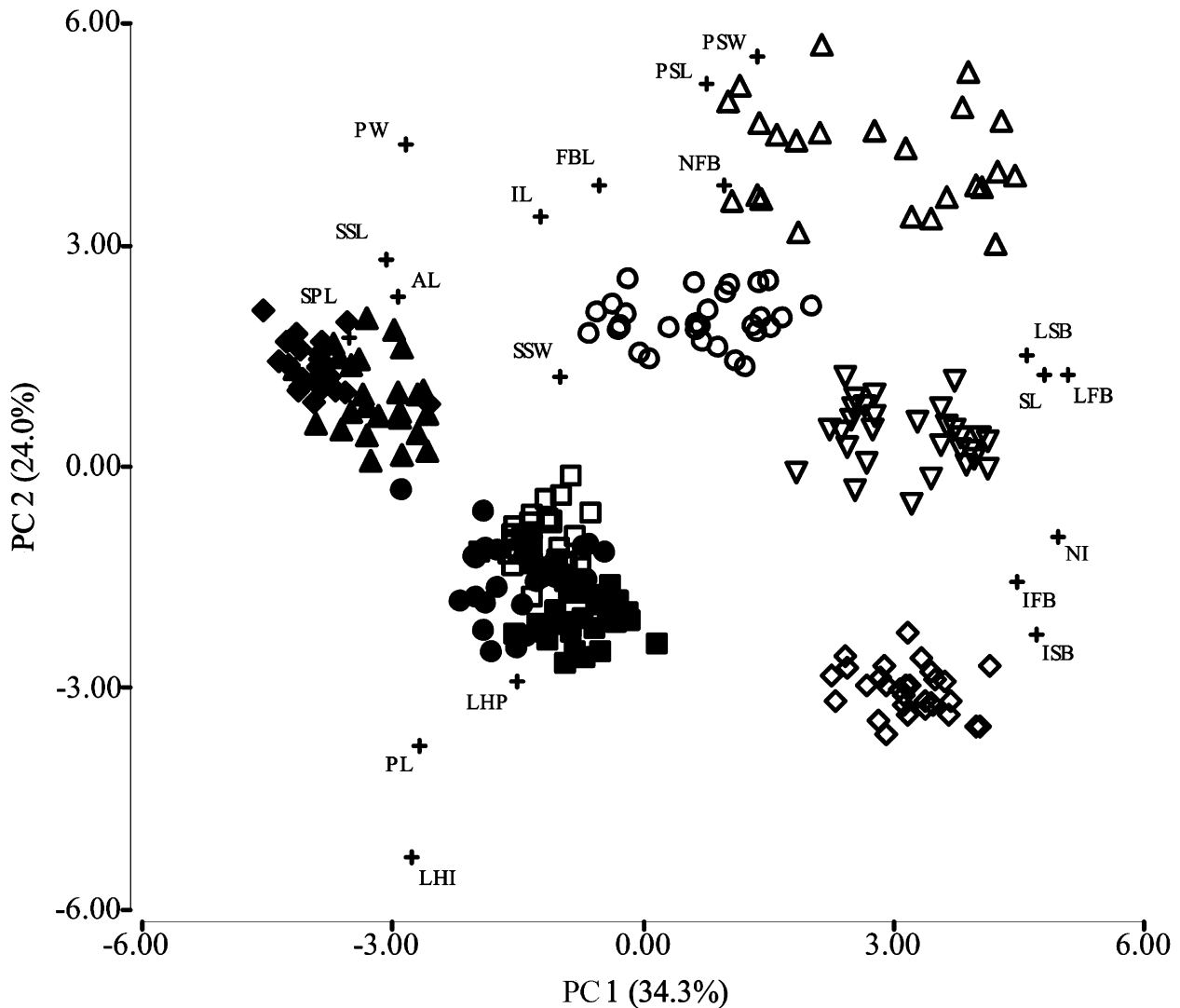


FIGURE 7. Principal component analysis. Plot of scores by principal component axes 1 and 2 from 253 specimens of *Andropogon* sect. *Leptopogon*. *Andropogon arenarius* (\square), *A. bicornis* (\diamond), *A. glaziovii* (∇), *A. hypogynus* (\triangle), *A. lateralis* (\circ), *A. macrothrix* (\blacktriangle), *A. leucostachyus* (\blacksquare), *A. selloanus* (\bullet) and *A. ternatus* (\blacklozenge). PC1= 34.3 %, PC2= 24 %.

Typological and multivariate analysis of synflorescences allows us to recognize the variations of synflorescence structure between diploid and hexaploid species, as well as among taxa within the same ploidy level, according to the level of development of the enrichment zone and characteristics of the pair of spikelets.

In terms of synflorescence structure, hexaploids develop paracladia of the trophotagma from the axillary buds of prophylls and bracts, differing from diploids in which only prophyllary buds are active.

The length and development of synflorescences were used as diagnostic characters in several studies involving species of *Andropogon* (Zanin & Longhi-Wagner 2006, Norrman 2009, Nagahama *et al.* 2012). According to our results, in the studied species of *Andropogon* sect. *Leptopogon* most of the variation observed in the synflorescence occurs in the enrichment zone, and the length and number of internodes in the EZ main axis are good characters to recognize different ploidy levels. Hexaploid species generally present many short internodes or few long internodes, generating in both cases long enrichment zones and synflorescences, in contrast to diploids which present few short internodes in the EZ main axis and therefore

short synflorescences. These differences in size, as well as in overall branching development, are common among different ploidy levels (Stebbins 1971, Raicu *et al.* 1972, Hroudová & Zákřavský 1993, Petit & Thompson 1997). In the *Leptopogon* section, the hexaploid *A. arenarius* presents short synflorescences like the diploid species. However, the small size of *A. arenarius* specimens may be related to the ecological conditions in which they grow (dunes near the sea); in this species the paracladia of the trophotagma may develop up to three bracts in contrast to diploid species, in which the Pc_{TS} only develops the distal bract.

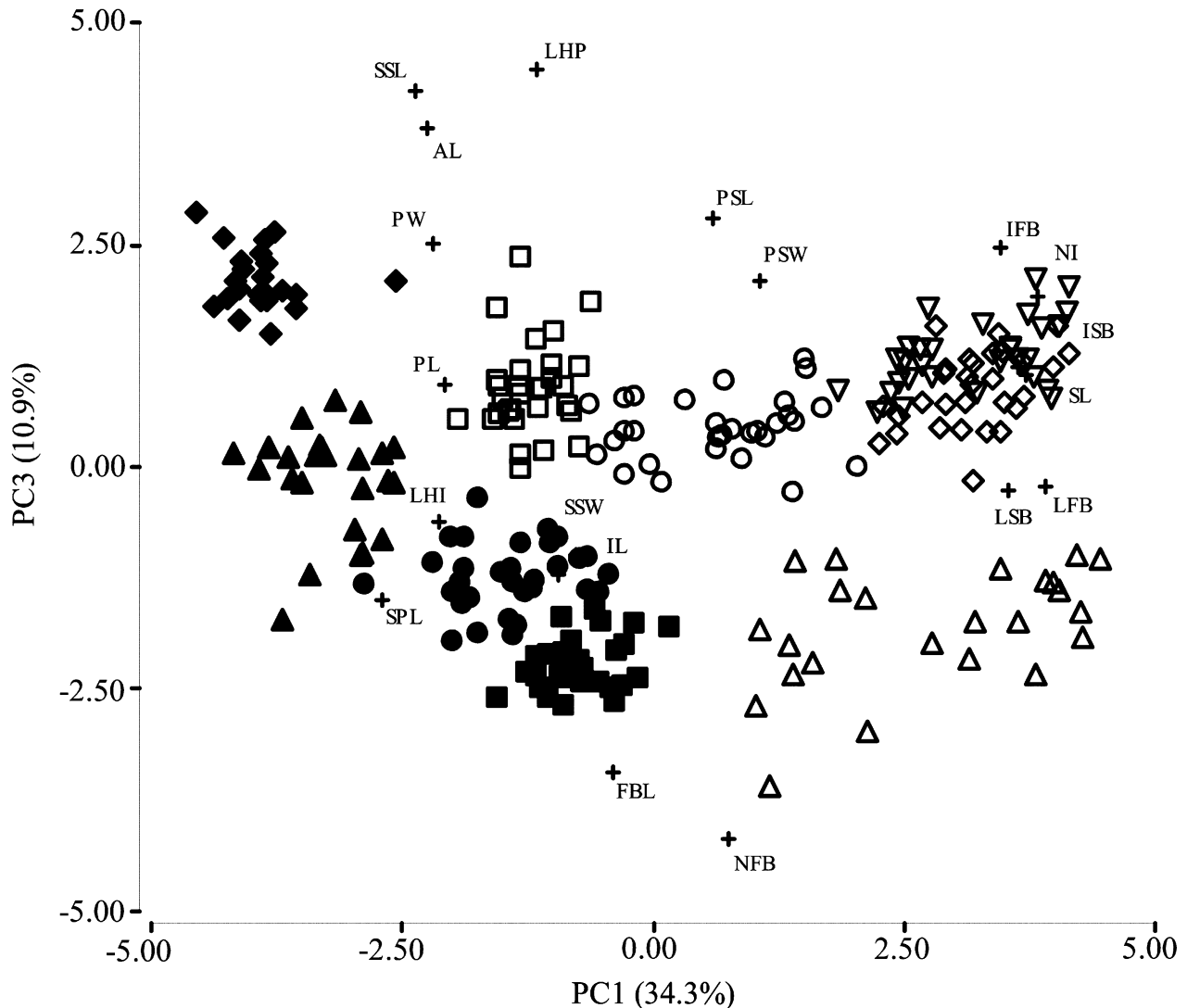


FIGURE 8. Plot of scores by principal component axes 1 and 3 from 253 specimens of *Andropogon* sect. *Leptopogon*. *Andropogon arenarius* (\square), *A. bicornis* (\diamond), *A. glaziovii* (∇), *A. hypogynus* (\triangle), *A. lateralis* (\circ), *A. macrothrix* (\blacktriangle), *A. leucostachyus* (\blacksquare), *A. selloanus* (\bullet) and *A. ternatus* (\blacklozenge). PC1= 34.3 %, PC3= 10.9 %.

Conclusion

Our results provide new elements for the taxonomic treatment of groups such as the *Leptopogon* section, because typological and morphometrical analyses show differences between species of different ploidy levels. The group consisting of *A. leucostachyus*, *A. macrothrix*, *A. selloanus* and *A. ternatus* is well defined by PCA and typological analysis; therefore, we propose that the South American diploid species (and the triploid *A. ternatus*) of the section *Leptopogon* be named as the *Andropogon selloanus* Nagahama & Norrmann complex.

This group of species is related to the *A. virginicus* complex of North America, a closely interrelated group of nine diploid species (Campbell 1982, 1983) that frequently grow together but in which hybrids are apparently rare (Campbell 1983). On the other hand, in the *A. selloanus* complex, interspecific hybrids have been reported (Galdeano & Norrmann 2000) and cytogenetic data suggested a close relationship between species (Galdeano & Norrmann 2000; Norrmann *et al.* 2004). Thus, the section *Leptopogon* in America so far may be divided into three complexes: *A. lateralis* (hexaploid species), *A. virginicus* (North American diploid species) and *A. selloanus* (South and Central American diploid species).

Summing up, the degree of synflorescence ramification, which is variable among *Andropogon* sect. *Leptopogon* species, is mainly associated with: (1) the number of bracts developed in paracladia of the trophotagma, (2) the length and number of internodes in the main axis of the enrichment zone and paracladia of the trophotagma, (3) the number of paracladia of the trophotagma originated from prophylls in the enrichment zone and Pc_{TTS} and (4) the number of long paracladia per unit of inflorescence. In addition, there are also differences in the length of hairs on articulated rachis internodes, in pedicellate spikelet length, pedicellate spikelet width, length of hairs on pedicel, sessile spikelet length, awn length and the floral system arrangements.

How these facts are connected with ploidy levels is still matter of speculation, but it is a useful tool to establish a taxonomic difference among diploid and hexaploid species of *Andropogon* sect. *Leptopogon* from South and Central America.

Specimens examined:

A. arenarius

BRAZIL. **Rio Grande do Sul:** Osorio, praia Atlántida, 2 February 1971, *Valls 1468* (CTES); Osorio, em campo de dunas móveis, 10 October 1972, *Valls 2146* (CTES); Torres, beira da Praia, próximo ao Morro do Farol, 28 February 1970, *Valls 1116* (CTES); Capão da Canoa, 4 March 1992, *Norrmann 104* (BAA, CTES, CEN, US). **Santa Catarina:** Imbituba, Itapirubá, 22 February 2008, *Nagahama & Norrmann 29* [a, b, c, d, e] (CORD), *30* [a, b, c, d, e] (CORD), *31* [a, b, c, d, e] (CORD), *32* [a, b, c, d, e] (CORD), *33* [a, b, c, d, e] (CORD); 2 January 1994, *Norrmann 139* [a, b, c, d] (CTES, MBM, SI, K); Laguna, en dunas, 2 January 1994, *Norrmann 224* (CTES, MBM, US).

A. bicornis

ARGENTINA. **Chaco:** 1 de Mayo, Colonia Benítez, 20 April 1965, *Schulz 15022* (CTES); 21 April 1965, *Schulz 15024* (CTES). **Corrientes:** Bella Vista, 15 km N of Bella Vista, 16 May 1983, *Norrmann & Quarín 89* (CTES). Capital, 18 km SE of Corrientes, Ruta 5, 25 March 1982, *Norrmann 51* (CTES, LIL); Riachuelo, 7 April 1974, *Quarín 2344* (CTES); Campus Universitario, *Schinini 34389* (CTES). General Alvear, ruta 14 y Río Aguapey, 17 May 1983, *Norrmann & Quarín 91* (CTES, BAA, US). Itatí, ruta 12, 47 km. E of Itatí, *Ahumada 775* (CTES). Ituzaingó, ruta 12 y ruta 38, 24 June 1990, *Schinini 26868* (CTES); desembocadura del Arroyo Garapé en el Río Paraná, 24 April 1975, *Schinini 11093* (CTES); Isla Apipé Grande, Puerto San Antonio, 10 December 1973, *Krapovickas 24122* (CTES). Santo Tomé, Laguna la Luna, Galarza, en embalsado, July 1995, *Schinini 6596* (CTES). **Formosa:** Bermejo, Puerto Bermejo, 2 March 1901, *Kermes 634* (CTES). Pilcomayo, Estero Isla Leona, ruta 86, 22 March 1979, *Piccinini & Petetin 3674* (CTES); San Pedro, ruta 20 y Arroyo Piray Guazú, 21 March 1997, *Tressens 5704* (CTES). Monte Carlo, 22 May 1951, *Montes 15388*, (SI, BAA). **Misiones:** Capital, Posadas, 11 June 1912, *Ekman 549* (CORD), *550* (CORD). El Dorado, ruta provincial 17, Pozo Azul, 27 May 2002, *Keller 1832* (CTES). BRAZIL. **Minas Gerais:** Ouro Preto, 22 January 1984, *Schinini & Ferrucci 24590* (CTES). **Paraná:** 11 February 1974, *Anderson, W. 10784* (CTES). **Rio Grande do Sul:** Gramado, estrada Taquara, 7 April 1971, *Valls 11486* (CTES). **Ijuí,** km 346 da BR 285, 24 July 1973, *Valls 2682* (CTES). Torres, colonia Sao Pedro, 28 March 1970, *Valls 1102* (CTES). **Rondônia:** Porto Velho, Estrada Manaus, Castanho Tupana, 7 July 1972, *Silva 184* (CTES). PARAGUAY. **Alto Paraná:** Estancia Santa Elena, 5 km N of Hernandarias, s.d., *Schinini & Caballero 27414* (CTES). **Asunción:** Jardín Botánico, en terrenos modificados, s.d., *Schinini 6230* (CTES). **Cordillera:** Cordillera de Altos, Cerro Tobatí, s.d., *Schinini 24050* (CTES). **Misiones:** Santiago, Estancia La Soledad, s.d., *Pedersen 5941* (CTES). **Paraguarí:** Pirayú, en esteros, s.d., *Mereles 234* (CTES). **Presidente Hayes:** Ruta Trans, Chaco, km. 120, s.d., *Mereles 3019* (CTES).

A. glaziovii

BRAZIL. **Goiás:** 70 km SE of Jataí, 17° 52' S, 51° 42' W, 12 April 1988, *Valls 11712* (CTES); 39 km SW of Gacu, 12 April 1988, *Valls 11720* (CTES). **Mato Grosso do Sul:** 5 km W of Ribas ao Rio Pardo, 14 April 1988, *Valls 11765* (CTES); Campo Grande, s.d., *Norrman 311* (CTES). **São Paulo:** Guzolandia, Route SP 310, km 574, 12 June 1999, *Zanin 793* (SPF). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, ruta 5, 18 April 1995, *Norrman 163*, (CTES), *175a* (CTES), *175b* (CTES). **Concepción:** Ruta 5, 32 km noreste of Concepción, 14 April 2009, *Nagahama 133* (CORD), *134* (CORD), *135* (CORD); 20 April 1995, *Norrman 196* (CTES). **Misiones:** 2 km E of San Juan Bautista por ruta 1, 21 April 1995, *Norrman 217* [a, b, c, d] (CTES); 2,1 km E of San Juan Bautista por ruta 1, 16 April 2009, *Nagahama 87* [a, b, c] (CTES), *88* [a, b, c, d] (CTES), *89* [a, b, c, d] (CTES). **San Pedro:** Ayo. Ipané y ruta 3, 20 April 1995, *Norrman 203* [a, b, c, d, e] (CTES).

A. hypogynus

ARGENTINA. **Chaco:** 1 de Mayo, Colonia Benítez, s.d., *Norrman 342* (CTES); San Fernando, Colonia Florencia, SW of Basail, 23 March 1965, *Schulz 14837* (CTES). **Corrientes:** Ituzaingó, 40 km E of Ituzaingó, s.d., *Norrman 117* [a, b, c, d] (CTES); 36 km E of Ituzaingó, por ruta 12, 29 March 1982, *Norrman 36* [a, b, c] (CTES); ruta 12, 35 km W of border with Misiones, 26 March 1970, *Krapovickas et al. 15703* (CTES). **Misiones:** Candelaria, Cerro Corá, en campos bajos, 8 January 1946, *Bertoni 2599* (LIL). San Ignacio, Ayo. Yabebirí, 16 January 1966, *Krapovickas 12081* (CTES). BOLIVIA. **La Paz,** Abel Iturralde, Lousita, 28 August 1985, *Haase 653* (W). BRAZIL. **Mato Grosso do Sul:** Aquidauana, Fazenda Río Negro, 31 October 1978, *Allem et al. 2309* (CTES). Poconé, Corumbá, Fazenda Bodoquena, Carandazal, 28 October 1978, *Allem et al. 2240* (CTES); Fazenda Ipiranga, km 10 MT3, 12 February 1978, *Allem & Vieira 1692* (CTES). PARAGUAY. **Itapuá:** Ruta 1, 6 km E of Gral. Delgado, 20 April 1995, *Norrman et al. 223* [a, b, c] (CTES); Isla Talavera, 10 April 1992, *Quintana et al. 38* (PY); Sierra de Amambay, s.d., 1907 *E. Hassler 9994* (W).

A. lateralis

ARGENTINA. **Corrientes:** Berón de Astrada, ruta 12 y desvío a Berón de Astrada, 24 February 1993, *Arbo et al. 6027* (CTES). Capital, Barrio Dr. Montaña, s.d., *Norrman 111* (CTES). Concepción, Estancia Tranquera de Hierro, 66 km noroeste de Chavarria, camino de Concepción, 3 December 1996, *Arbo et al. 6950* (CTES); Paso Crucesita, 20 April 1974, *Arbo et al. 631* (CTES); Tabay, 30 January 1971, *Arbo 308* (CTES). General Paz, 29 km S de Caa Catí, ruta 13, 17 March 1978, *Ahumada 1998* (CTES). Goya, Paso Tala, 16 December 1948, *Cabrera 10542* (CTES). Ituzaingó, 20 km NW of Virasoro, ruta 38, 3 March 1982, *Norrman 71* (CTES); Estancia San José del Boquerón, 25 km NE de Playadito, 12 December 1981, *Carnevali 5005* (CTES); Estancia Abelenda, Rincón de Santa María, 9 July 1955, *Carnevali 506* (CTES). La Cruz, costa del Río Uruguay, 20 December 1944, *Ibarrola 1759* (LIL); Mocoretá, 20 February 1945, *Ibarrola 2467* (LIL). Monte Caseros, 8 km S de Labougle, costa río Uruguay, 22 February 1979, *Ahumada 2661* (CTES). Paso de los Libres, Bondpland, 17 January 1945, *Ibarrola 2113* (LIL). San Cosme, 25 km E Corrientes, ruta 12, 25 February 1978, *Ahumada 1573* (CTES); 28 km E de Corrientes, ruta 12, 26 February 1978, *Ahumada 1635* (CTES). San Martín, 8 February 1979, *Schinini et al. 16842* (CEN); Estancia Itá Berá, 25 km N de Carlos Pellegrini, ruta 14, 22 February 1976, *Irigoyen 320* (CTES). San Roque, 1 km de Cañada Mala, sobre camino, 30 June 1980, *Carnevali 6286* (CTES). Santo Tomé, 17 km S of Santo Tomé, ruta 40, 3 March 1982, *Norrman 72* (CTES). **Misiones:** Capital, 11 June 1912, *Ekman 552*, (CORD), *554* (CORD); 12 km W de Posadas por ruta 12, 16 April 2009, *Nagahama 136* (CORD), *137* (CORD), *138* (CORD), *139* (CORD); Pantanos del Arroyo Zaimán, 15 October 1995, *Norrman 46* (MNES). **Formosa:** Laishi, Reserva El Bagual, 15 May 2002, *Di Giacomo 576* (CTES). BOLIVIA. **Santa Cruz:** Andrés Ibanez, 1 km E of Intern. Airport Viru Viru, 17° 40' S, 63° 10' W, 1 January 1986, *Killeen 1550* (CTES); Barrio Florida, zona sur de Santa Cruz, 8 km del centro, 17° 46' S, 63° 11' W, 400 m, 13 February 1992, *Mostacedo 246* (CTES). BRAZIL. **Mato Grosso do Sul:** Corumbá, Nhecolândia, Fazenda Cáceres, 28 November 1979, *Filho 30* (CTES). **Paraná:** Sierra de Sao Luis, Br 277, 19 January 1985, *Ferrucci et al. 217* (CTES). **Rio Grande do Sul:** Dos Irmaos, Santa María do Herval, 26 January 1983, *Bueno et al. 3639* (CTES). PARAGUAY. **Caaguazú:** sur les collines incultes, 19 November 1874 *Balansa 226* (K, SI, as var. *trichocoleus*). **Itapuá:** Isla Yacyreta, 18 March 1992, *Pin et al. 170* (CTES).

A. leucostachyus

ARGENTINA. **Chaco:** Libertador General San Martín, Santa Elisa, 6 December 1903, *Hassler 2697* (SI). **Corrientes:** San Martín, La Cruz, 6 November 1936, *Parodi 12419* (BAA). Ituzaingó, 45 km E de Ituzaingó, 29 March 1982, *Norrman 46* (CTES). Santo Tomé, 50 km NW de Virasoro, ruta 38, 29 March 1982, *Norrman 41*, (BAA, CTES), *43* (BAA, CTES); 40 km NW de Virasoro, ruta 38, 16 January 2012, *Nagahama & Norrmann 170* (CORD), *171* (CORD), *172*, (CORD), *173* [a, b] (CORD); 36 km NW de Virasoro, ruta 38, 16 January 2010, *Nagahama & Norrmann 173*

(CORD), 174 (CORD), 175 (CORD), 176 (CORD), 177 (CORD). **Misiones:** Apóstoles, 29 November 1943, *Burkart 14337* (SI). Capital, Aeródromo, 14 October 1975, *Zuloaga 478* (SI). BRAZIL. **Rio Grande do Sul:** Santa María, 10 km W de Sao Pedro do Sul, 1 April 1982, *Norrman 41* (CTES).

A. macrothrix

ARGENTINA. **Corrientes:** Ituzaingó, Villa Olivarri, 24 km W de Ituzaingó, 15 December 1982, *Norrman 78* (CTES); ruta 12 a 58 km E de Ituzaingó, s.d., *Norrman 115* (CTES); 18 January 2012, *Nagahama 178* [a, b, c] (CORD), *179* [a, b, c] (CORD), *180* [a, b, c] (CORD); 11 km N de San Carlos, *Krapovickas 24950* (CTES). Paso de los Libres, entrada a Estancia Meringá, 3 December 1980, *J.G. Fernández 781* (CTES). San Martín, La Cruz, 10 November 1936, *Parodi 12061* (BAA). San Miguel, 25 km SW de San Miguel, 18 November 1987, *Quarín et al. 3895* (CTES). San Roque, 17 km S de San Roque, 29 January 1983, *Norrman 81* [a, b, c, d] (CTES); 23 km S de San Roque, 16 March 1995, *Quarín et al. 4143* (CTES). Santo Tomé, 17 km S de Santo Tomé, 3 April 1982, *Norrman 76* (CTES); ruta 40 y arroyo Chimiray, 15 December 1982, *Norrman 77* (CTES). **Entre Ríos:** Federación, Camping Drewaus, 18 km E de Chajarí, 17 July 1983, *Norrman 93* (CTES). **Misiones:** San Ignacio, 11 October 1975, *Zuloaga et al. 442* (SI). BRAZIL. s.d., *Glaziou 16590* (K, W); s.d., *Glaziou 18605* (K, W); s.d., *Glaziou 18606* (K, W); s.d., *Glaziou 22392* (K, W).

A. selloanus

ARGENTINA. **Chaco:** Bermejo, Las Palmas, November 1917, *Jorgensen 11940* (BAA). **Córdoba:** 26 November 1950, *Hunziker 8585* (BAA). **Corrientes:** Capital, periferias de Corrientes, 12 March 1994, *Norrman 229* (CTES). Ituzaingó, 5 February 1984, *Norrman 99* (CTES); 9 km W de Ituzaingó, ruta 12, 2 April 1982, *Norrman 45* (CTES); 8 km W de Ituzaingó, ruta 12, 18 January 2012, *Nagahama 181* [a, b, c] (CTES), *182* [a, b, c] (CTES), *183* [a, b, c] (CTES). Monte Caseros, 30 km S of Curuzú Cuatiá, ruta 14, 26 September 1982, *Norrman 73* (CTES). San Cosme, Laguna Totorá, 4 March 1982, *Quarín 3692* (CTES). San Martín, 6 km SW de La Cruz, 8 February 1979, *Schinini et al. 16842* (CTES). **Formosa:** Patiño, Las Lomitas, 24 January 1928, *Parodi 8380* (BAA). **Jujuy:** Capital, Sierra de Zapla, Mina 9 de Octubre, Cerro de la Cruz, 13 November 1980, *Cabrera et al. 31939* (SI). **Santa Fe:** Reconquista, 8 November 1933, *Parodi 11172* (BAA). BRAZIL. **Santa Catarina:** Florianópolis, Autopista BR101, 3 km E hacia Itapirubá, 22 February 2008, *Nagahama & Norrmann 47* [a, b] (CORD).

A. ternatus

ARGENTINA. **Buenos Aires:** Saavedra, Pigué, January 1921, *Ducos F. 3206* (BAA). Salliqueló, 14 March 1941, *Cabrera 6992* (SI). **Córdoba:** Punilla, Rancho Alegre, 8 January 1964, *Giusti & Valle 3708* (BAA); subida de Pampa de la Ollada hacia Pampa de la Esquina, 10 January 1970, *Luti 4946* (BAA); Tanti camino a Carlos Paz, *Nicora 6675* (CORD); W of Tanti at Rancho Alegre, 12 December 1978, *Renvoize 3747* (K); Copina, 10 km del cruce por camino puentes colgantes, 14 April 2012, *Nagahama 184* [a, b, c, d] (CORD), *185* [a, b, c, d] (CORD), *186* [a, b, c, d] (CORD). **Corrientes:** Curuzú Cuatiá, 30 km S de Curuzú Cuatiá, ruta 14, 26 September 1982, *Norrman 74* (MBM). Mercedes, Itá Cabó, 14 October 1961, *Pedersen 6133* (K). Monte Caseros, Estancia La Patala, 27 October 1950, *Nicora 5525* (SI); ruta 22, s.d., *Schinini 18207* (W). **Entre Ríos:** Chajarí, s.d., *Norrman 92* (CTES, BAA). Concepción del Uruguay, 26 November 1876, *Lorentz 822* (CORD); s.d., 12 January 1876, *Lorentz s.n.* (CORD). Concordia, Calabacilla a puerto Yeruá, 18 November 1979, *Troncoso 281* (SI). Santa Ana, 10 km al N, s.d., *Norrman 79* (CTES, US). BRAZIL. Rio Grande do Sul: 60 km W de Porto Alegre, s.d., *Norrman 86* (CTES, US). **Santa Catarina:** Abelardo Luz, 4 km de Abelardo Luz hacia Clevelândia, 1 December 1981, *R.M. Klein et al. 12132* (MBM), 8 January 1974, *Valls et al. 102* (ICN). Curitiba, camino de Curitiba a Lebon Régis, 9 December 1992, *Z. Rúgolo et al. 1600* (ICN). Lages, 15 km na BR 116, norte de Lages, 3 December 1981, *R.M. Klein et al. 12189* (W).

Acknowledgements

We are grateful to the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, PIP 112-200801-01557 and fellowship of the first author), Secretaría de Ciencia y Tecnología de la Universidad Nacional de Córdoba (SECyT-UNC) and Nordeste (SGCy T-UNNE). We thank the curators of CORD, CTES and MO for loan of herbarium specimens. We are grateful to I. Caponio and M. I. Hidalgo for their aid in the collection of plant material. We are grateful to Joss Heywood for helpful suggestions of language and the anonymous reviewers for helpful suggestions that improved earlier versions of our manuscript.

References

- Boe, A., Keeler, K., Norrmann, G. & Hatch, S. (2004) The indigenous bluestems of the western hemisphere and gambagrass. In: Moser, L.E., Burson, B.L. & Sollenberger, L.E. (eds.) *Warm Season Grasses*. American Society of Agronomy: Crop Science Society of America: Soil Science Society of America, Madison, pp. 873–908.
- Boissier, P.E. (1859) *Diagnoses Plantarum Orientalium Novarum, ser. 2*. Herrmann, B., Lipsiae, 146 pp.
- Cámara Hernández, J. & Gambino, S. (1990) Ontogeny and morphology of *Zea diploperennis* inflorescences and the origin of maize (*Zea mays* ssp. *mays*). *Maydica* 35: 113–124.
- Cámara Hernández, J. & Rua, G. (1991) The synflorescence of Poaceae. *Beiträge zur Biologie der Pflanzen* 66: 297–311.
- Campbell, C.S. (1982) Hybridization between *Andropogon glomeratus* var. *pumilus* and *A. longiberbis* (Gramineae) in Central Florida. *Brittonia* 34: 146–150. <http://dx.doi.org/10.2307/2806367>
- Campbell, C.S. (1983) Systematics of the *Andropogon virginicus* complex (Gramineae). *Journal of the Arnold Arboretum* 64: 171–254.
- Campbell, C.S. & Windisch, P. (1986) Chromosome numbers and their taxonomic implications for eight Brazilian *Andropogon* (Poaceae). *Brittonia* 38: 411–414. <http://dx.doi.org/10.2307/2807090>
- Clayton, W.D. (1987) Andropogoneae. In: Soderstrom, T.R., Hilu, K.W., Campbell, C.S. & Barkworth, M.E. (eds.) *Grass systematics and evolution*. Smithsonian Institution Press, Washington DC, pp. 307–309.
- Clayton, W.D. & Renvoize, S.A. (1986) *Genera Graminum. Grasses of the world*. Royal Botanic Gardens, Kew, London, 389 pp.
- Connor, H.E. (1979) Breeding systems in the grasses: a survey. *New Zealand Journal of Botany* 17: 547–74. <http://dx.doi.org/10.1080/0028825X.1979.10432571>
- Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M. & Robledo C.W. (2010) InfoStat software versión 2010. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Fournier, E. (1886) *Mexicanas Plantas 2*. Typographeo Reipublicae, Paris, 160 pp.
- Galdeano, F. & Norrmann, G.A. (2000) Natural Hybridization between two South American diploid species of *Andropogon* (Gramineae). *Journal of the Torrey Botanical Society* 127: 101–106. <http://dx.doi.org/10.2307/3088687>
- Gould, F.W. (1967) The genus *Andropogon* in the United States. *Brittonia* 19: 70–76. <http://dx.doi.org/10.2307/2805085>
- Hackel, E. (1883) Gramineae – Andropogoneae. In: Martius, C.F.P. & Eichler, A.G. (eds.) *Flora Brasiliensis 2*, F. Fleischer, Lipsiae, pp. 245–326.
- Hackel, E. (1885) Andropogoneae novae. *Flora* 68: 131–143.
- Hackel, E. (1887) Gramineae. In: Engler, A. & Prantl, K. (eds.) *Die Natürlichen Pflanzenfamilien 2*. Engelmann, Leipzig, pp. 1–97.
- Hackel, E. (1889) Andropogoneae. In: De Candolle, A.L.P.P. & De Candolle A.C.P. (eds.) *Monographiae Phanerogamarum 6*. Masson, Paris, pp. 1–716.
- Hackel, E. (1904) Gramineae. *Bulletin de L'Herbier Boissier 2 4*: 262–282.
- Hitchcock, A.S. (1912) A new species of *Andropogon*. *Botanical Gazette* 54: 424. <http://dx.doi.org/10.1086/330934>
- Hroudová, Z. & Zákavský, P. (1993) Ecology of two cytotypes of *Butomus umbellatus* II. Reproduction, growth and biomass production. *Folia Geobotanica et Phytotaxonomica* 28: 413–424.
- Kunth, K.S. (1816) *Andropogon*. In: Humboldt, F.W.H.A. & Bonpland, A.J.A. (eds.) *Nova Genera et Species Plantarum 4*. Librairie Gréque-Latine-Allemande, Paris, pp. 184–190.
- Kuntze, C.E.O. (1891) Gramineae. *Revisio Generum Plantarum 2*. Felix, A., Leipzig, 1011 pp.
- Linnaeus, C. (1753) *Species Plantarum 2*. Laurentii Salvii, Stockholm, 1200 pp.
- Mahibbur, R.M. & Govindarajulu, Z. (1997) A modification of the test of Shapiro and Wilks for normality. *Journal of Applied Statistics* 24: 219–235. <http://dx.doi.org/10.1080/02664769723828>
- Michener, C.D. & Sokal, R.R. (1957) A quantitative approach to a problem in classification. *Evolution* 11: 130–162. <http://dx.doi.org/10.2307/2406046>
- Moore, K.J. & Moser, L.E. (1995) Quantifying developmental morphology of perennial grasses. *Crop Science* 35: 37–43. <http://dx.doi.org/10.2135/cropsci1995.0011183X003500010007x>
- Nagahama, N. & Norrmann, G.A. (2012) Review of the genus *Andropogon* (Poaceae: Andropogoneae) in America based on cytogenetic studies. *Journal of Botany* 2012: 1–9.
- Nagahama, N., Anton, A.M., Hidalgo, M.I. & Norrmann, G.A. (2012) Naming hybrids in the *Andropogon lateralis* complex (Andropogoneae, Poaceae) after multivariate analysis. *Darwiniana* 50: 114–123.
- Nees, C.G.D. (1829) Gramineae. In: Martius, C.F.P. (ed.) *Flora Brasiliensis seu enumeratio plantarum 2*. J.G. Cottae, Stuttgartiae et Tubingae, pp. 1–608.
- Norrmann, G.A. (1985) Estudios citogenéticos en especies argentinas de *Andropogon* (Gramineae). *Boletín de la Sociedad Argentina de Botánica* 24: 137–149.
- Norrmann, G.A. (1999) *Biosistemática y relaciones filogenéticas en especies hexaploides sudamericanas de Andropogon*. PhD dissertation, Universidad Nacional de Córdoba, Argentina, 98 pp.

- Norrmann, G.A. (2009) Natural hybridization in the *Andropogon lateralis* complex (Andropogoneae, Poaceae) and its impact on taxonomic literature. *Botanical Journal of the Linnean Society* 159: 136–154. <http://dx.doi.org/10.1111/j.1095-8339.2008.00904.x>
- Norrmann, G.A. & Quarin, C.L. (1987) Permanent odd polyploidy in a grass: *Andropogon ternatus*. *Genome* 29: 340–344. <http://dx.doi.org/10.1139/g87-056>
- Norrmann, G.A. & Scarel, F. (2000) Biología reproductiva de cuatro especies sudamericanas hexaploides de *Andropogon* L. (Gramineae, Andropogoneae). *Kurtziana* 28: 173–180.
- Norrmann, G.A., Hanson, L., Renvoize, S. & Leitch, I.J. (2004) Genomic relationships among diploid and hexaploid species of *Andropogon* (Poaceae). *Genome* 47: 1220–1224.
- Peichoto, M.C. & Vegetti, A.C. (2007) Synflorescences of species related to *Schizachyrium condensatum* (Poaceae). *Flora* 202: 503–512. <http://dx.doi.org/10.1016/j.flora.2006.09.005>
- Perreta, M.G., Ramos, J.C. & Vegetti, A.C. (2009) Development and structure of the grass Inflorescence. *Botanical Review* 75: 377–396. <http://dx.doi.org/10.1007/s12229-009-9038-8>
- Petit, C. & Thompson, J.D. (1997) Variation in phenotypic response to light availability between diploid and tetraploid populations of the perennial grass *Arrhenatherum elatius* from open and woodland sites. *Journal of Ecology* 85: 657–667. <http://dx.doi.org/10.2307/2960536>
- Raicu, P., Staicu, S., Stoian, V. & Roman, T. (1972) The *Phragmites communis* Trin., chromosome complement in the Danube Delta. *Hydrobiologia* 39: 83–89. <http://dx.doi.org/10.1007/BF00047596>
- Reinheimer, R. & Vegetti, A.C. (2008) Inflorescence diversity and evolution in the PCK Clade (Poaceae: Panicoideae: Paniceae). *Plant Systematics and Evolution* 275: 133–167. <http://dx.doi.org/10.1007/s00606-008-0057-4>
- Rua, G. (1999) *Inflorescencias: Bases teóricas para su análisis*. Sociedad Argentina de Botánica, Buenos Aires, 100 pp.
- Sprengel, C.K. (1825) *Systema Vegetabilium editio 16*. Sumtibus Librariae Dieterichianae, Göttingen, 992 pp.
- Stapf, O. (1919) Gramineae. In: Prain, D. (ed.) *Flora of tropical Africa* 9. Reeve, London, pp. 208–265.
- Stebbins, G.L. (1971) *Chromosomal Evolution in Higher Plants*. Edward Arnhold, London, 216 pp.
- Trinius, C.B. (1820) *Fundamenta Agrostographiae: sive Theoria constructionis floris gramineae; adjecta synopsi generum graminum hucusque cognitorum*. J.G. Heubner, Vienna, 227 pp. <http://dx.doi.org/10.5962/bhl.title.15521>
- Trinius, C.B. (1832) Andropogineorum genera. *Mémoires de l'Académie Imperiale des Sciences de St.-Petersbourg. Sixième Série. Sciences Mathématiques, Physiques et Naturelles* 2: 239–337.
- Troll, W. (1964) *Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers 1*. Gustav Fischer, Jena, 615 pp.
- Troll, W. (1969) Botanischer Teil. In: *Kommission für biologische Forschung*. Akademie der Wissenschaften und der Literatur, Jahrbuch, Mainz, pp. 88–105.
- Vega, A.S. (2000) Revisión taxonómica de las especies americanas del género *Bothriochloa* (Poaceae: Panicoideae: Andropogoneae). *Darwiniana* 38: 127–186.
- Vegetti, A.C. (1991) Sobre la politelia en las inflorescencias de Poaceae. *Kurtziana* 21: 267–274.
- Vegetti, A.C. (1992) La sinflorescencia en *Schizachyrium tenerum* y *S. salzmanii*. *Darwiniana* 31: 341–344.
- Vegetti, A.C. (1993) Tipología de la sinflorescencia en *Hemarthria altissima*. *Parodiana* 8: 69–75.
- Vegetti, A.C. (1994) *Tipología de la sinflorescencia en Andropogoneae*. PhD dissertation, Universidad Nacional de Córdoba, Argentina, 205 pp.
- Vegetti, A.C. (1999) Typology of synflorescence of Andropogoneae (Poaceae), additional comments. *Feddes Repertorium* 110: 111–126. <http://dx.doi.org/10.1002/fedr.19991100119>
- Vegetti, A.C. & Anton, A.M. (1991) Interpretación morfológica del par de espiguillas en *Schizachyrium microstachyum* (Poaceae). *Kurtziana* 21: 267–274.
- Vegetti, A.C. & Anton, A.M. (1995) Some trends in the inflorescence of Poaceae. *Flora* 190: 225–228.
- Vegetti, A.C. & Anton, A.M. (2000) The grass inflorescence. In: Jacobs, S.W.L., Everett, J. (eds.) *Grass Systematics and Evolution*. CSIRO Press, Melbourne, pp. 29–31.
- Vegetti, A.C. & Müller-Doblies, D. (2004) Inhibition areas within the synflorescences of Poaceae. *Beiträge zur Biologie der Pflanzen* 73: 51–74.
- Vegetti, A.C. & Tivano, J.C. (1991) Synflorescence in *Schizachyrium microstachyum* (Poaceae). *Beiträge zur Biologie der Pflanzen* 67: 453–473.
- Weberling, F., Müller-Doblies, U. & Müller-Doblies, D. (1993) Zur deskriptiven und vergleichend-morphologischen terminologie komplexer infloreszenzen. *Beiträge zur Biologie der Pflanzen* 67: 453–473.
- Weberling, F. (1989) *Morphology of flowers and inflorescences*. Cambridge University Press, Cambridge, 405 pp.
- Zanin, A. (2001) *Revisão de Andropogon L. (Poaceae–Panicoideae–Andropogoneae) no Brasil*. PhD dissertation, Universidade de São Paulo, São Paulo, 401 pp.
- Zanin, A. & Longhi-Wagner H.M. (2006) Sinopse do gênero *Andropogon* L. (Poaceae–Andropogoneae) no Brasil. *Revista Brasileira de Botânica* 29: 289–299. <http://dx.doi.org/10.1590/S0100-84042006000200010>