



Reproductive biology of South American *Bothriochloa* (Poaceae: Andropogoneae)

Lidia R. Scrivanti^{a,*}, Guillermo A. Norrmann^b, Ana M. Anton^a

^aInstituto Multidisciplinario de Biología Vegetal (IMBIV), Casilla de Correo 495, 5000 Córdoba, Argentina

^bInstituto de Botánica del Nordeste (IBONE), Casilla de Correo 209, 3400 Corrientes, Argentina

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Abstract

The reproductive biology of 13 South American taxa of *Bothriochloa* was studied. All surveyed species reproduce sexually and are self-compatible. Several elements also point to self-pollination as their main breeding system: (i) bud pollination that occurs in most species enhancing cleistogamy, (ii) presence of pits in the glumes that impede the opening of flowers and (iii) reduction in the number of stamens, a trend associated with outbreeding.

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Introduction

Bothriochloa Kuntze (Poaceae: Andropogoneae) is a genus of about 40 species, mainly with tropical distribution though some species extend into temperate areas as well. Species of *Bothriochloa* live in Africa, Asia (India), Europe, Australia, and America (Watson and Dallwitz, 1992). American species are unique since 12 native taxa show a disjunct distribution in North and South America (Allred, 1981; Allred and Gould, 1983; De Wet, 1968; Vega, 2000).

Genus *Bothriochloa* displays diploid ($2n = 2x = 20$) as well as polyploid species ($2n = 40, 50, 60, 120, 180$) (Allred and Gould, 1983; Celarier and Harlan, 1957; De Wet, 1968; De Wet et al., 1963; Faruqi, 1964; Gould, 1956). Diploids are endemic to India and reproduce sexually (De Wet et al., 1963). On the other hand, tetraploids have wide distribution in the Old World and are facultative or obligate apomicts (Celarier and

Harlan, 1957; De Wet et al., 1963; Faruqi, 1964; Harlan and Celarier, 1961; Harlan and De Wet, 1963). Hexaploid species living in Africa, India, and Australia are obligate apomicts (De Wet et al., 1963; Harlan et al., 1964); but a few tetraploids and hexaploids living in Australia also reproduce sexually (De Wet et al., 1963).

Heslop-Harrison (1961) reported the mechanism of cleistogamy in *Bothriochloa decipiens* (Hack.) C.E. Hubbard from Australia. The glume of the fertile spikelet bears a deep depression or pit, which acts as an obturator preventing the emergence of the anther and causing its dehiscence in contact with the stigmas. In addition, cleistogamy commonly results from the retention of an inflorescence within its flag leaf; therefore, the glumes cannot open at anthesis, and the function of the glume pit as an obturator is fulfilled. Yu et al. (2003) studied a combined breeding system in *Bothriochloa biloba* from Australia, where self-pollination and cross-pollination coexist in the same inflorescence.

In America, native species of *Bothriochloa* studied so far are polyploid ($2n = 60, 120, 180, 220$) (Allred and Gould, 1983; De Wet, 1968; De Wet et al., 1963; Gould,

*Corresponding author.

E-mail address: rscrivanti@imbiv.unc.edu.ar (L.R. Scrivanti).

1956). In North America, *Bothriochloa exaristata* (Nash) Henrard, *Bothriochloa laguroides* (DC.) Herter var. *laguroides*, *Bothriochloa laguroides* var. *torreyana* (Steud.) M. Marchi and Longhi-Wagner, *Bothriochloa longipaniculata* (Gould) Allred and Gould, and *Bothriochloa reevesii* (Gould) Gould were reported as sexual and self-compatible (Allred and Gould, 1983). In South America, *Bothriochloa perforata* and *Bothriochloa edwardsiana* have been mentioned as sexual and cleistogamous (Scrivanti and Anton, 2004).

However, the information on the breeding systems of species living in South America is still scarce. This type of data is relevant to understand the reproductive behaviour of native grasses, especially when they have

a reputation as fodder resources, as *B. laguroides* (DC.) Herter, *Bothriochloa barbinodis* (Lag.) Herter and *Bothriochloa springfieldii* (Gould) Parodi (Covas and Steibel, 1968). Therefore, the objective of this work is to report the mode of reproduction and fertility in thirteen taxa of *Bothriochloa* from South America.

Material and methods

Plant material

Thirteen species of *Bothriochloa* were studied (Table 1). The plants were collected at the flowering stage in

Table 1. Species of *Bothriochloa* from South America studied, origin and voucher.

Plant species	Voucher ^a
<i>B. alta</i> (Hitchc.) Henrard	Argentina: Provincia de Córdoba, Santa María, <i>Scrivanti</i> 26, 11-I-2003. Capital, <i>Scrivanti</i> 117, 22-I-2004. Colón, <i>Scrivanti</i> 39, 29-I-2003; 57, 14-III-2003; 99, 07-I-2004. Punilla, <i>Scrivanti</i> 198, 08-II-2005. Tercero Arriba, <i>Scrivanti</i> 55, 12-II-2003. Santa María, <i>Anton</i> 340, 08-II-2003.
<i>B. barbinodis</i> (Lag.) Herter	Argentina: Provincia de Córdoba, Capital, <i>Scrivanti</i> 116, 22-I-2004, 205, 08-II-2005. Punilla, <i>Scrivanti</i> 115, 20-I-2004; 210, 15-II-2005. Río Segundo, <i>Scrivanti</i> 48, 12-II-2003. Tercero Arriba, <i>Scrivanti</i> 52, 12-II-2003.
<i>B. edwardsiana</i> (Gould) Parodi	Argentina: Provincia de Córdoba, Punilla, <i>Scrivanti</i> 110, 111, 113, 20-I-2004; 190, 10-V-2004. Provincia de Entre Ríos, Diamante, <i>Scrivanti</i> 215, 10-III-2005. Gualeguaychú, <i>Scrivanti</i> 224, 11-III-2005.
<i>B. eurylemma</i> M. Marchi & Longhi-Wagner	Argentina: Provincia de Corrientes, Bella Vista, <i>Scrivanti</i> 134, 04-III-2004. Mercedes, <i>Scrivanti</i> 130, 03-III-2004.
<i>B. exaristata</i> (Nash) Henrard	Argentina: Provincia de Entre Ríos, Federación, <i>Scrivanti</i> 243, 15-III-2005. Paraná, <i>Scrivanti</i> 123, 02-III-2004.
<i>B. imperatoides</i> (Hack.) Herter	Argentina: Provincia de Chaco, General Belgrano, <i>Scrivanti</i> 155, 06-III-2004. Provincia de Corrientes, Berón de Astrada, <i>Scrivanti</i> 143, 05-III-2004.- Federación, <i>Scrivanti</i> 169, 29-III-2004. Brazil: Rio Grande do Sul, CORD 33
<i>B. laguroides</i> (DC.) Herter var. <i>laguroides</i>	Uruguay: Maldonado, <i>Scrivanti</i> 239, 13-III-2005.
<i>B. laguroides</i> var. <i>torreyana</i> (Steud.) M. Marchi & Longhi-Wagner	Argentina: Provincia de Córdoba, Capital, <i>Scrivanti</i> 206, 08-II-2005. Punilla, <i>Scrivanti</i> 211, 15-II-2005. Río Segundo, <i>Scrivanti</i> 49, 12-II-2003. Santa María, <i>Scrivanti</i> 56, 14-III-2003. Provincia de Entre Ríos, Gualeguaychú, <i>Scrivanti</i> 218, 11-III-2005.
<i>B. longipaniculata</i> (Gould) Allred & Gould	Argentina: Provincia de Corrientes, Paso de Los Libres, <i>Scrivanti</i> 262, 15-III-2006. Santo Tomé, <i>Scrivanti</i> 280, 15-III-2006. Provincia de Formosa, Clorinda, Km 1200, <i>Scrivanti</i> 157, 07-III-2004. Provincia de Misiones, Bernardo de Irigoyen, <i>Scrivanti</i> 167, 28-III-2004.
<i>B. meridionales</i> M. Marchi & Longhi-Wagner	Uruguay: Maldonado, Punta del Este, <i>Scrivanti</i> 237, 13-III-2005.
<i>B. perforata</i> (Trin. ex Fourn.) Herter	Argentina: Provincia de Chaco, Colonia Benítez, <i>Scrivanti</i> 147, 06-III-2004. Resistencia, <i>Scrivanti</i> 146, 06-III-2004. Provincia de Entre Ríos, Federación, <i>Scrivanti</i> 242, 15-III-2005. Provincia de Misiones, Bernardo de Irigoyen, <i>Scrivanti</i> 166, 27-III-2004.
<i>B. saccharoides</i> (Sw.) Rydb. var. <i>saccharoides</i>	Brazil: Rio Grande do Sul, CORD 30, 37, 40.
<i>B. springfieldii</i> (Gould) Parodi	Argentina: Provincia de Córdoba, Capital, <i>Scrivanti</i> 46, 06-II-2004. Punilla, <i>Scrivanti</i> 100, 103, 105, 106, 107, 07-I-2004. Santa María, <i>Scrivanti</i> 33, 23-I-2003.
<i>B. velutina</i> M. Marchi & Longhi-Wagner	Argentina: Provincia de Córdoba, Colón, <i>Anton</i> 358, 09-IV-2005. Punilla, <i>Scrivanti</i> 45, 29-I-2003, 104, 07-I-2004; 184, 10-V-2004; 202, 08-II-2005. Provincia de Chaco, Vera, <i>Scrivanti</i> 159, 08-III-2004. Provincia de Corrientes, Mercedes, <i>Scrivanti</i> 133, 03-III-2004.
	Argentina: Provincia de Córdoba, Colón, <i>Scrivanti</i> 38, 40, 29-I-2003. Punilla, <i>Scrivanti</i> 43, 44, 29-I-2003; 102, 29-I-2003; 199, 08-II-2005. Río Segundo, <i>Scrivanti</i> 47, 12-II-2003.
	Brazil: Santa Catarina, <i>Scrivanti</i> 163, 24-III-2004.

^aHoused at CORD.

Argentina, Brazil, and Uruguay, during January–May from 2003 to 2006. Therefore, in each flowering season, direct observations were made on natural populations. Selected plants were transplanted and cultivated in the experimental garden of the Instituto Multidisciplinario de Biología Vegetal (IMBIV) at Córdoba, Argentina. Vouchers were on deposit at the Herbarium of the Museo Botánico de Córdoba (CORD).

For embryological analyses, inflorescences at different stages of development were fixed in Carnoy (100% ethanol 6:chloroform 3:glacial acetic acid 1) and stored in 70% ethanol. Entire young spikelets were dehydrated in tertiary butyl alcohol, embedded in paraffin, and sectioned with a rotary microtome at 10 µm. The sections were stained with safranin and fast green (Norrmann et al., 1997).

Phenological observations were carried out during three seasons in the field (summers 2003–2006) and in the experimental garden. The percentage of seed production was determined under self-pollinating and open-pollinated conditions. For self-pollinated conditions, inflorescences were isolated before anthesis with cylinders of translucent sulfite paper sealed at the top with adhesive tape and closed around the pedicel at the bottom. Open pollination was ensured at the field where huge natural populations were screened.

Pollen fertility was estimated by determining the percentage of stainable pollen in Lugol:2% iodine–potassium iodide (I₂–KI) solution. In addition, samples of flowers with mature but undehisced anthers were gathered for each species and preserved in three parts of 70% ethanol and one part of acetic acid. These samples provided the basis for the estimation of pollen/ovule ratios (Cruden, 1977). The pollen grains from an unopened anther were counted and estimated for the whole flower by multiplying the number of pollen grains per anther by the number of anthers per flower. Statistical analyses of the variation in the production of seeds by both pollination pathways and pollen viability data were performed with InfoStat program version 1.1 (Grupo InfoStat, 2002).

Results

Embryo sac development was examined in 57 samples belonging to 13 taxa (Table 1). All plants studied showed a single-embryo sac per ovule. The mature sac always consisted of two synergids, one egg cell, two large polar nuclei, and a cluster of antipodal cells (Fig. 1). This figure is interpreted as a typical monosporic *Polygonum* type, Poaceae variant (Anton and Cocucci, 1984), thus indicating sexual reproduction. No indication of apomictic or irregular megasporogenesis was registered.

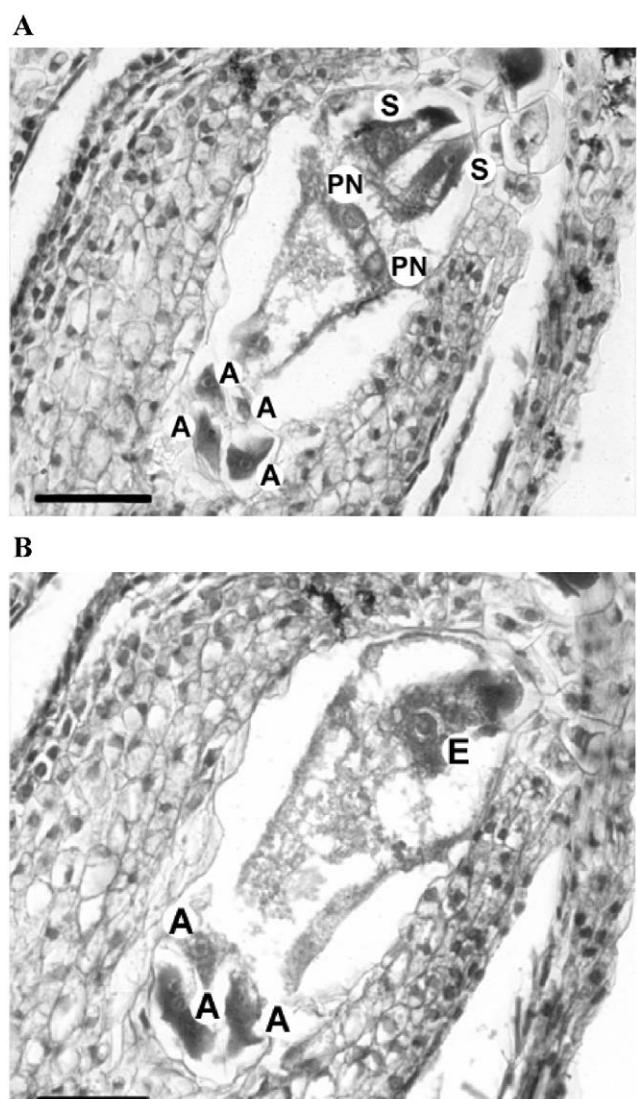


Fig. 1. Photomicrographs of *Bothriochloa perforata* ovules. (A) an ovule with two synergids, two polar nucleus and a group of antipodal cells; and (B) an egg cell and a group of antipodal cells. Bars = 16.2 µm in (A); 12.5 µm in (B).

Self-pollination in plants from all taxa analyzed under greenhouse conditions resulted in an average seed production ranging from 67.88% to 96.88%, indicating self-compatibility (Table 2). In the field, the average percentage of seed production under natural conditions ranged from 39.6% to 83.4%. No significant differences in the percentage of seed set was found between self- and open-pollinated conditions.

In *B. barbinodis*, *B. longipaniculata*, *B. perforata*, and *B. springfieldii*, the florets were unable to open by failure of the inflorescence to emerge from the sheaths prior to anthesis. By remaining enclosed, anthers and stigmas were forced to make contact inside the floret and after fertilization cleistogamous seeds were produced. When most of the caryopses were formed, the inflorescence

Table 2. Pollen/ovule ratio, pollen viability and seed set in different pollination treatments in South American species of *Bothriochloa*.

Species	Pollen/ovule ratio ^a	Pollen viability (%)	Seed set (%)	
			Autogamy	Allogamy
<i>B. alta</i>	711 ^b	95.3±1.0	71.90±9.56	81.58±9.06
<i>B. barbinodis</i>	2133	84.6±1.3	51.45±8.78	76.90±8.38
<i>B. edwardsiana</i>	698 ^b	96.2±2.1	79.23±6.26	85.49±4.84
<i>B. eurylemma</i>	2094	86.5±1.5	59.26±10.10	75.23±7.87
<i>B. exaristata</i>	2214	88.6±1.6	67.88±8.56	90.87±6.53
<i>B. imperatoides</i>	2293	78.6±3.8	59.82±5.20	72.99±8.03
<i>B. laguroides</i> subsp. <i>laguroides</i>	2319	85.1±1.7	63.44±6.83	85.73±9.24
<i>B. laguroides</i> subsp. <i>torreyana</i>	2151	83.3±1.3	56.06±9.85	77.03±7.90
<i>B. longipaniculata</i>	2377	78.8±2.7	66.63±6.78	76.72±9.03
<i>B. meridionalis</i>	2623	88.1±1.5	79.60±4.05	89.71±5.11
<i>B. perforata</i>	735 ^b	96.6±1.9	80.02±7.01	85.00±6.47
<i>B. saccharoides</i> var. <i>saccharoides</i>	1885	84.3±2.3	56.65±10.66	79.21±8.39
<i>B. springfieldii</i>	2392	87.1±2.2	69.22±9.13	79.86±5.75
<i>B. velutina</i>	1985	76.1±3.2	72.29±7.83	81.15±5.68

Date of collection cf. Table 1.

^aThe amount of pollen grains per flower was obtained multiplying the number of grains of pollen per anther and the number of anthers per flower. Pollen/ovule ratio was calculated dividing the number of grains of pollen and the number of ovule per flower.

^bIndicates significant differences ($p \leq 0.05$).

peduncle elongated and the mature panicle was exserted (Fig. 2).

A different scenario applies to *Bothriochloa alta*, *B. edwardsiana*, and *B. perforata*. These species possess a foveola in the lower glume which prevents the emergence of anthers and stigmata, thus provoking its dehiscence inside the floret and in contact with the stigmas (Fig. 3) (Scrivanti and Anton, 2004). This trait seems to be associated with the reduction of the androecium both in size of the anthers as well as in number of stamens, remaining only a single fertile stamen and two staminodes (Fig. 4). The inflorescences of *B. alta* and *B. edwardsiana* are exserted, whereas in *B. perforata* they might be either partially or totally exserted.

In *Bothriochloa eurylemma*, *B. exaristata*, *B. laguroides* var. *laguroides*, *B. laguroides* var. *torreyana*, *Bothriochloa saccharoides* var. *saccharoides* and *Bothriochloa velutina* chasmogamous and cleistogamous spikelets coexist in the same panicle. In these taxa, usually the apical third of the inflorescence emerges from the sheaths; the distal spikelets are then exposed at anthesis, mostly between 7 am and 2 pm. Once the florets open, the stigmas and filaments of the stamens elongate, and dehiscence of the anthers occurs immediately. Below the apical third of the inflorescence, all the spikelets are cleistogamous since they remain hidden in the sheath. In all plants cleistogamy was corroborated histologically, following the events from anthesis to development of mature caryopsis.

The viability of pollen was tested in ca. 40,000 pollen grains; fertility ranged from 76.1% to 96.6% (Table 2).

An analysis of variance (ANOVA) showed no significant differences in pollen viability in the taxa studied. Nevertheless, the pollen–ovule ratio was statistically smaller (ANOVA, $p < 0.05$) in pitted species due to the reduction in the number of stamens.

Discussion

All studied taxa reproduce sexually, these results being in accordance with previous reports for species from North America (Allred and Gould, 1983; De Wet et al., 1963). Therefore, apomictic species are apparently restricted to the Old World (Brown and Emery, 1957; Celarier and Harlan, 1957; De Wet, 1968; De Wet et al., 1963; Harlan et al., 1961) whereas America remains inhabited by sexually reproducing species.

Campbell et al. (1983) established that cleistogamy in grasses is more common within the three most advanced subfamilies, i.e. Panicoideae, Pooideae, and Eragrostioideae. The *Bothriochloa* taxa belong to the Panicoideae–Andropogoneae. Temperate climate seems to favour the expression of cleistogamy (Campbell et al., 1983). Cleistogamous flowers are structurally modified for self-pollination: they never open, and pollination occurs in a bud-like stage that is much reduced compared with a chasmogamous flower. In cleistogamous flowers of the *Andropogon virginicus* complex Campbell (1982) observed that the stamens are reduced in number and in size, with fewer pollen grains than in non-cleistogamous counterparts.

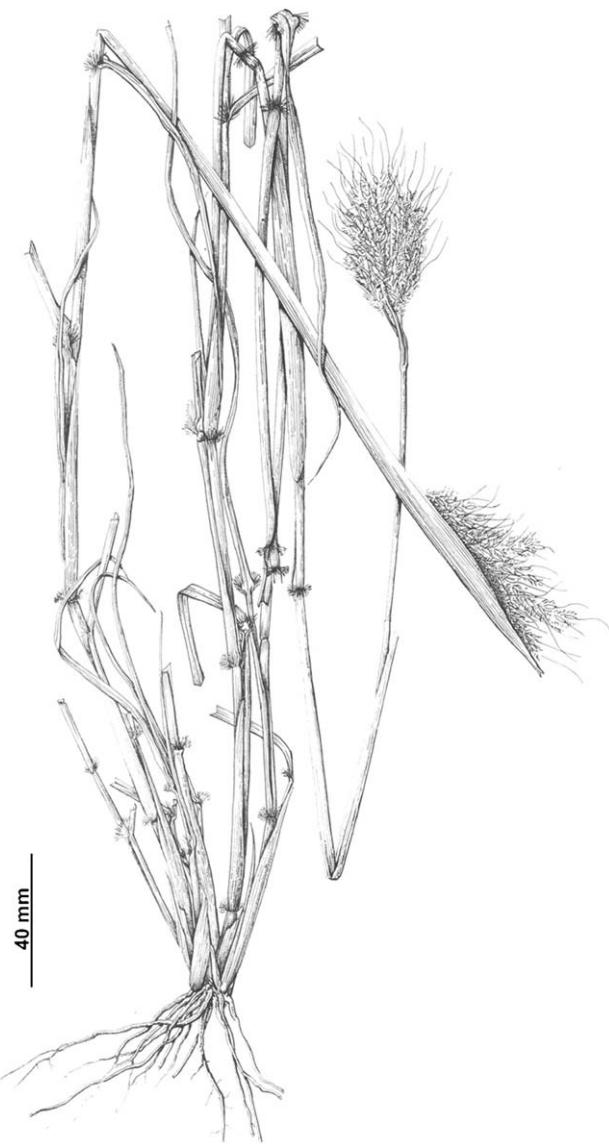


Fig. 2. Flowering and fruiting racemes in *Bothriochloa perforata*. De Anderson 3063 (CORD). Bar = 40 mm.

Cleistogamy in our *Bothriochloa* material is mainly due to the failure of the peduncle to elongate. Thus, several to all of the spikelets within the panicle are hidden inside the sheaths, and therefore unable to undergo anthesis, a situation that was also observed in *B. decipiens* (Heslop-Harrison, 1961) and *A. virginicus* (Campbell, 1982). Cleistogamous grass flowers often mature precociously (Campbell et al., 1983), although the developmental or physiological basis for this heterochrony is generally unknown. Some references show that variation can be associated with environmental variables such as photoperiod, level of soil moisture, and temperature influence (Campbell et al., 1983; Heslop-Harrison, 1961).

Autogamy is common in polyploids and during the initial colonization of new biotypes. It is useful to

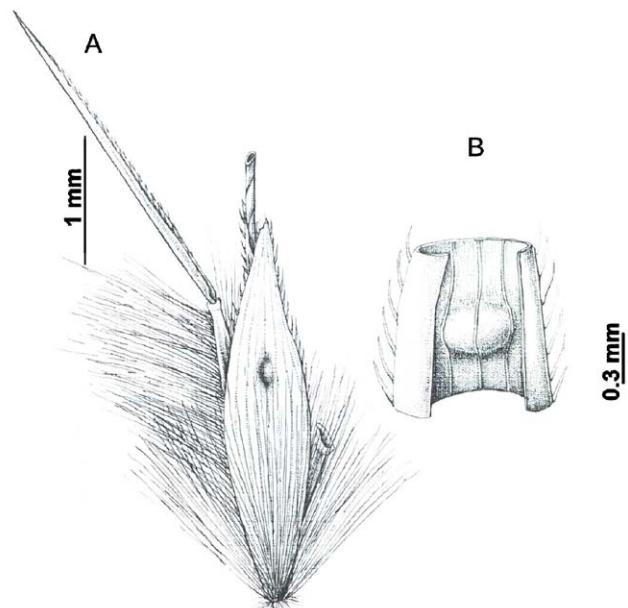


Fig. 3. Cleistogamous spikelet of *Bothriochloa perforata*. (A) sesil and pedicellate spikelets shown to pit on low glume of sesil spikelet, frontal; and (B) detail of (A), internal view. De Anderson 3063 (CORD).

maintain genotypes highly adapted to the habitats (Parker, 1992; Richards, 1986; Stebbins, 1957). In addition, autogamous plants do not require other plants for mating, because a single propagule with viable seeds may lead to an established population (Allred, 1981). The disadvantage of self-pollination is the reduction of effective transference of pollen (Campbell et al., 1983; Harlan and Celarier, 1961). Nevertheless, in those species where cleistogamous and chasmogamous flowers coexist, this is avoided (Valerio and Ramírez, 2003). The *Bothriochloa* species occupy unstable and variable environments. In addition, they present fast development with high-growth rate, precocious reproduction, high productivity and grow in early-succession ecosystems, which characterizes them to be *r* strategists. Furthermore, these grasses show a great ecological advantage, viz. the liberation of allelochemicals, interfering by this way on the growth and development of other plants in the community.

The species of *Bothriochloa* are reportedly aromatic (Gupta and Daniel, 1982). *Bothriochloa* essential oils from Old World and South America taxa are characterised by sesquiterpenes, monoterpenes, hydrocarbons, phenolic compounds, esters, and fatty acids (Kaul and Vats, 1998; Pinder and Kerr, 1980; Scrivanti et al., 2008; Zalkow et al., 1980, and pers. obs.). Most of these compounds are recognized for their allelopathic properties (Einhellig and Leather, 1988; Wójcik-Wojtkowiak, 1992). As reported by Hussain et al. (1982), the essential oil of *Bothriochloa pertusa* – from India – shows allelopathic effects inhibiting the germination of other

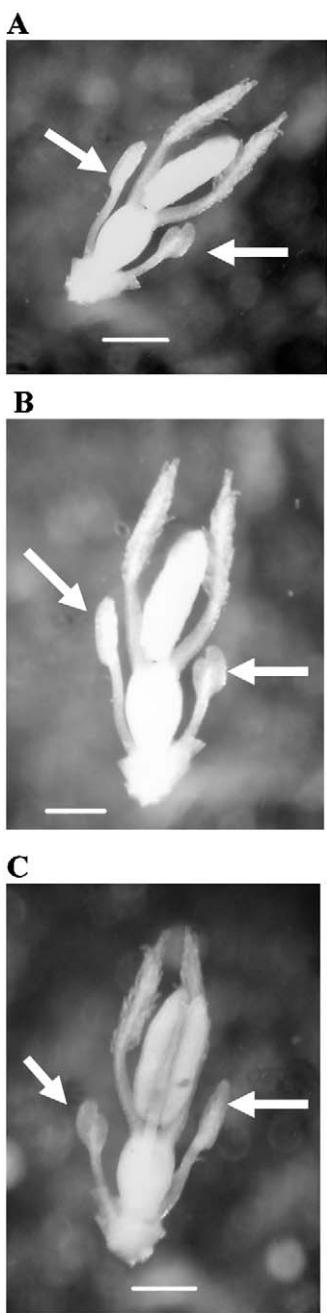


Fig. 4. Cleistogamous flower with a stamen fertile and two stamens reduced (staminoids). (A) *Bothriochloa alta*; (B) *B. perforata*; and (C) *B. edwardsiana*. Arrows indicate the staminodes. Bars = 0.5 mm.

plants. *Bothriochloa* species from South America exhibit great dominance in the area where they live, due to their effective reproduction and mode of colonization. Therefore, the success of these grasses might be attributed to a strategist characteristics, with both outbreeding and selfing reproductive biology and efficient use of resources, and a possible liberation of allelochemicals will allow them to be dominant in their habitats.

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