Plant Syst Evol (2011) 293:111–118
DOI 10.1007/s00606-011-0428-0

ORIGINAL ARTICLE

Reproductive biology of *Setaria magna* Griseb. (Poaceae: Panicoideae: Paniceae)

**Sandra S. Aliscioni · Natalia E. Gómiz ·
Juan P. Torretta · José F. Pensiero**

Received: 20 April 2010 / Accepted: 28 January 2011 / Published online: 12 March 2011

Abstract The genus *Setaria* is economically important because many species are cultivated for grains or forage. *Setaria magna* is an American species, native to North America and introduced in South America. The morphological aspect of this species is similar to *S. italica* (foxtail millet), suggesting its potential value as a crop. The purpose of this work was to understand the breeding system (self-pollination vs. open pollination) of *S. magna*; additionally, the floral development was described. The results of the breeding system analysis indicated that *S. magna* is mainly autogamous and does not appear to have a self-incompatibility mechanism. The floral development observed was similar to that described for other Paniceae; in most of the spikelets only the upper anthecium developed fruit, but a small number of spikelets presented bisexual lower florets. These spikelets produced two caryopses per spikelet. Thus, *S. magna* can produced two types of dispersal units; a few whitish naked caryopses from the lower anthecium that fall without their lemma and palea at maturity; and a high number of brown caryopses protected by the lemma and palea from the upper anthecium. The presence of a normal embryo sac in the upper anthecium suggests that *S. magna* would present normal sexual reproduction, although we can not reject the formation of apomitic seeds in the lower anthecium.

Keywords *Setaria magna* · Paniceae · Breeding system · Floral development · Autogamy

Introduction

Setaria P. Beauv. is a cosmopolitan genus of the family Poaceae, subfamily Panicoideae, tribe Paniceae, subtribe Setariinae (Clayton and Renvoize 1986; Zuloaga et al. 2007). It includes 114 species (Webster 1993), mostly from tropical and subtropical regions of the world, growing in open environments or in woodlands (Rominger 1962; Prasada Rao et al. 1987; Pensiero 1999).

The genus is economically important because many species are cultivated for grains or forage and are used as an important food source for wildlife, whereas other species are noxious weeds (Martin et al. 1961; Rominger 1962; Prasada Rao et al. 1987; Dekker 2003). Most of the cultivated species of *Setaria* are from the Old World, just as *S. italica* (L.) P. Beauv. (foxtail millet) that originates from Asia and is one of the most important cereal and forage plants. This species has been cultivated across southern Europe, and remains an essential human food in some regions of India, China, Korea and Japan (Gao and Chen 1988; Austin 2004). Moreover, the genus has played an important role in the New World; Callen (1967) concluded that *S. parviflora* (Poir.) Kerguélen probably represented the first cereal in America, although neither the origin of this species (Pensiero 1999; Kellogg et al. 2009) nor how its domestication occurred (Austin 2004) is clear.

The successful life histories of locally adapted species of *Setaria* and the evolutionary potential of these species

---

S. S. Aliscioni (✉) · N. E. Gómiz · J. P. Torretta
Cátedra de Botánica Agrícola, Facultad de Agronomía,
Universidad de Buenos Aires, Av San Martín 4453,
C1417DSE Buenos Aires, Argentina
e-mail: aliscion@agro.uba.ar

J. F. Pensiero
Facultad de Ciencias Agrarias, Universidad Nacional del Litoral,
Luis Kreder 2805, S3080HOF Esperanza,
Santa Fe, Argentina

S. S. Aliscioni · J. P. Torretta · J. F. Pensiero
Consejo Nacional de Investigaciones Científicas y Técnicas,
Buenos Aires, Argentina

emphasize the need for accurate predictions of their behavior (Dekker 2003). Knowledge of the reproductive biology of this genus is principally limited to the cultivated species. Several studies have been undertaken in some valuable American native forage species, but results are still scarce (Cáceres and Mazzucato 1995; Pensiero et al. 1995, 2005; Schrauf et al. 1998; Caponio and Pensiero 2002).

Among the wild species from the New World, *S. magna* Griseb. is one of the most morphologically similar to foxtail millet; both species are annuals and have an upper anthecium with a smooth and shining lemma (Pensiero 1999). However, *S. magna* differs because it is much taller (as tall as 4 m) and more robust than *S. italica*, with large, densely flowered panicles that produce many more and smaller spikelets.

Setaria magna is native to North America, with the center of distribution in Florida, radiating northward and westward along the costal regions, but it is rarely found in Mexico and Central America (Rominger 1962). This species has a special affinity for saline marshes, a habit that restricts it to coastal areas and brackish marshes of rivers, generally associated with disturbed areas (Rominger 1962).

The species has been introduced to South America and reported in Bolivia, Brazil, Colombia, French Guiana, Venezuela and northern Argentina (Nicora 1968; Boldrini 1989; Pensiero and Judziewicz 1990; Renvoize 1998; Pensiero 1999; Zuloaga et al. 2003; Nozawa 2006). In Argentina, *S. magna* has been cited in a few localities in the Provinces of Chaco, Corrientes, Formosa, Jujuy and Salta (Pensiero 1999; Zuloaga et al. 2008).

Even though the natural populations of *S. magna* seem to be locally restricted, its very large panicles with an elevated number of spikelets indicate high performance in seed production. This feature, the tolerance for salty soils and the large amount of biomass produced are some attractive characters for the cultivation and economic use of this species. However, our field observations showed that *S. magna* does not grow regularly every year; the natural populations are not frequent or steadily present in the same location year after year. This characteristic represents a disadvantage for cultivating this species; in spite of the huge production of seeds, evidently not all of these are potentially viable or can germinate in the same way, so that the behavior of *S. magna* can be somewhat erratic.

We focused our research on *S. magna* because of its morphological resemblance to *S. italica*, which suggests that it may have economic value. The work was carried out with the purpose of understanding the breeding system of this potential forage or crop species. In addition, we morphologically characterized the cultivated plants, comparing them with wild plants and describing the floral development.

Materials and methods

To assess information about the localities where *S. magna* grows in Argentina, we consulted the following herbarium collections: BA, BAA, BAB, CORD, CTES, LIL, LP, SF and SI (Holmgren et al. 1990). Additionally, we examined the literature to determine the ecological preferences of this species (Hitchcock 1951; Rominger 1962; Nicora 1968; Adams 1972; Beetle 1977; Gould 1979; Pohl 1980, 1994; Boldrini 1989; Pensiero and Judziewicz 1990; Renvoize 1998; Pensiero 1999; Espejo Serna et al. 2000; Barkworth et al. 2003; Nozawa 2006; Funk et al. 2007).

Field trips around northern Argentina were conducted during March 2006 and April 2007 to locate natural populations. One natural site with *S. magna* as the dominant species was situated on the coast of the Arroyo Santa Lucía, Dpto. Mburucuyá, Province of Corrientes (S 28°02′55″, W 58°11′37.5″). In this population, spikelets were harvested from randomly chosen plants and kept in paper bags at room temperature until the time of planting. Voucher specimens were deposited in BAA, SF and SI herbaria (Aliscioni et al. 577; 705; 706; 707).

The spikelets were put in plastic boxes with cotton and absorbent paper saturated with water to germinate in the greenhouse in August 2007. Between September and October 2007, seedlings were individually transplanted to plastic pots with a sterile substrate and kept in the greenhouse. In January 2008, an experimental population was established in the Botanical Garden *"L. Hauman"* at the Faculty of Agronomy, University of Buenos Aires (S 34°35′262″, W 58°28′54″).

We evaluated the breeding system under self- and open-pollination treatments. To enforce self pollination, inflorescences of randomly chosen plants ($n = 28$) were covered with cheesecloth bags before anthesis. The remaining plants ($n = 28$) were used to examine the seed set under open pollination.

Mature inflorescences were harvested, and each one was individually preserved in a paper bag. Five samples of 100 spikelets each were collected per plant. The selected spikelets were examined under a stereomicroscope to determine the presence or absence of a caryopsis; a seed set (i.e. caryopsis set) was expressed as a percentage. Filled spikelets from self- and open pollination were weighted (expressed for 1,000 spikelets). The percentage of filled spikelets and weight of 1,000 spikelets obtained from both treatments (self- and open pollination) were compared with a non-parametric Wilcoxon (Mann-Witney) test for independent samples.

The morphology of the spikelets, florets and fruits was observed using a stereomicroscope. To describe the development of florets, entire spikelets of successive growth stages from cultivated plants were fixed in formalin-acetic alcohol. Thereafter, samples were treated with 25–50% hydrofluoric acid for 24–48 h to dissolve silicates and then embedded in paraffin wax. Serial sections were made using a rotary microtome at 10 µm. The sections were stained with safranin-fast green combinations (D'Ambrogio 1986) and observed using a Wild M20 optical microscope.

Results

The seed set was 57.7% (288.46 ± 225.93, range 0–491) and 66.5% (332.32 ± 137.60, range 15–495) for a total of 500 spikelets for each plant under self- and open pollination, respectively. No statistically significant differences were found for the seed sets between the treatments ($W = 735.50$, $p = 0.7299$). The filled spikelet weight (expressed for 1,000 spikelets) was marginally greater ($W = 874$, $p = 0.0470$) in open pollinated plants (0.25 g ± 0.11, range 0.006–0.428) than in self-pollinated ones (0.23 g ± 0.15, range 0–0.407).

The cultivated plants of *S. magna* were up to 3 m tall and robust, with vigorous culms, rooting at the lower nodes (Fig. 1a). These plants developed intravaginal basal branches and axillary branches, all of which ended in inflorescences leading to as many as nine panicles per plant. The wild plants that grew in their natural environment differed in producing only axillary branches (Fig. 1b, c).

The inflorescences are dense panicles, cylindrical to lobulate, densely flowered, up to 40 cm long, with the rachis densely pilose and the branches bearing the spikelets subtended by one antrorsely scabrous bristle (Fig. 1d).

The spikelets are bi-flowered, ovoid and glabrous, 2.0–2.3 mm long, disarticulating below the glumes; the lower glume is 1/3–1/2 of the spikelet length, 3–5 nerved, and the upper glume is 4/5 of the spikelet length, 7–9 nerved. The lower anthecium bears a staminate or bisexual floret, with the lemma slightly exceeding the upper lemma, apiculate, 5–7 nerved, enclosing a hyaline palea equal in length to the lemma; both the lower lemma and palea are membranaceous. Less than approximately 5% of the mature spikelets produced a caryopsis in the lower anthecium (Fig. 1e). The upper anthecium is ovoid, 2.0–2.2 mm long and 1 mm wide, with the smooth and shiny lemma enclosing a palea of similar texture; the upper floret is bisexual.

Differentiation and maturation of the spikelets are basipetal. Pollen development starts at approximately the same time in both the lower and upper florets, but the stamens of the lower floret develop later than those of the upper one.

In all spikelets that were processed in the anatomical study, the lower and upper florets were initially hermaphroditic, but the gynoecium of the lower floret stopped developing. Thus, at maturity these florets were male (Fig. 2a).

When the pollen mother cells start to differentiate in the upper floret, the gynoecial ridge becomes visible (Fig. 2b); the palea is as long as the stamens, and the lemma is about 1/3 longer, totally covering the floret (Fig. 2c). The external and radial walls of the epidermis of the lemma and palea are very thick, becoming crustaceous at maturity (Fig. 2f). At the same time, the lower floret is totally covered by a thin lemma and palea, and only immature anthers can be distinguished. The upper floret subsequently continues its development; the ovules mature, becoming hemitropous, bitegmic and tenuinucellate (Fig. 2d). When the stamens of the upper floret have anthers with pollen in the three-cell stage, the embryo sac is entirely formed in the ovule and is of the *Polygonum* type (Fig. 2e).

Setaria magna can produced two types of dispersal units: a few whitish naked caryopses from the lower anthecium that fall without their lemma and palea at maturity, and a high number of brown caryopses protected by the lemma and palea from the upper anthecium (Fig. 1f). Both types of caryopsis are ovoid to elliptical and about 1 mm long; the hilum is oval, and the embryo 1/2 or less its length.

Discussion

The results of the breeding system analysis indicate that *S. magna* is mainly autogamous and does not appear to have a self-incompatibility mechanism. Dekker (2003) pointed out that the genus *Setaria* combines self- and open pollination, but that autogamy predominates. Autogamy was also demonstrated for *S. lachnea* (Nees) Kunth, *S. leucopila* (Scribn. & Merr.) K. Schum., *S. macrostachya* Kunth, *S. sulcata* Raddi (Pensiero et al. 1995; Pensiero et al. 2005), *S. italica* (McVicar and Parnell 1941; Li et al. 1945); *S. viridis* (L.) P. Beauv., *S. pumila* (Poir.) Roem. & Schult. (Mulligan and Findlay 1970; Wang et al. 1995; Dekker 2003), *S. pflanzii* Pensiero (Caponio and Pensiero 2002), *S. verticillata* (L.) P. Beauv. and *S. faberi* R. A. W. Herrm. (Dekker 2003). However, Pensiero et al. (2005) showed that *S. fiebrigii* R.A.W. Herrm., *S. oblongata* (Griseb.) Parodi, *S. pampeana* Parodi ex Nicora, *S. parviflora* and *S. vulpiseta* (Lam.) Roem. & Schult. probably are predominantly allogamous, as is *S. sphacelata* (Schumach.) Stapf & C.E. Hubb. ex M. B. Moss (Gildenhuys 1950).

Self-pollination in *Setaria* occurs in wild, weedy and crop species, ensures both long-term stability and novelty, and contributes to a highly diverse collection of locally adapted genotypes and phenotypes ready to exploit any opportunities (Dekker 2003).

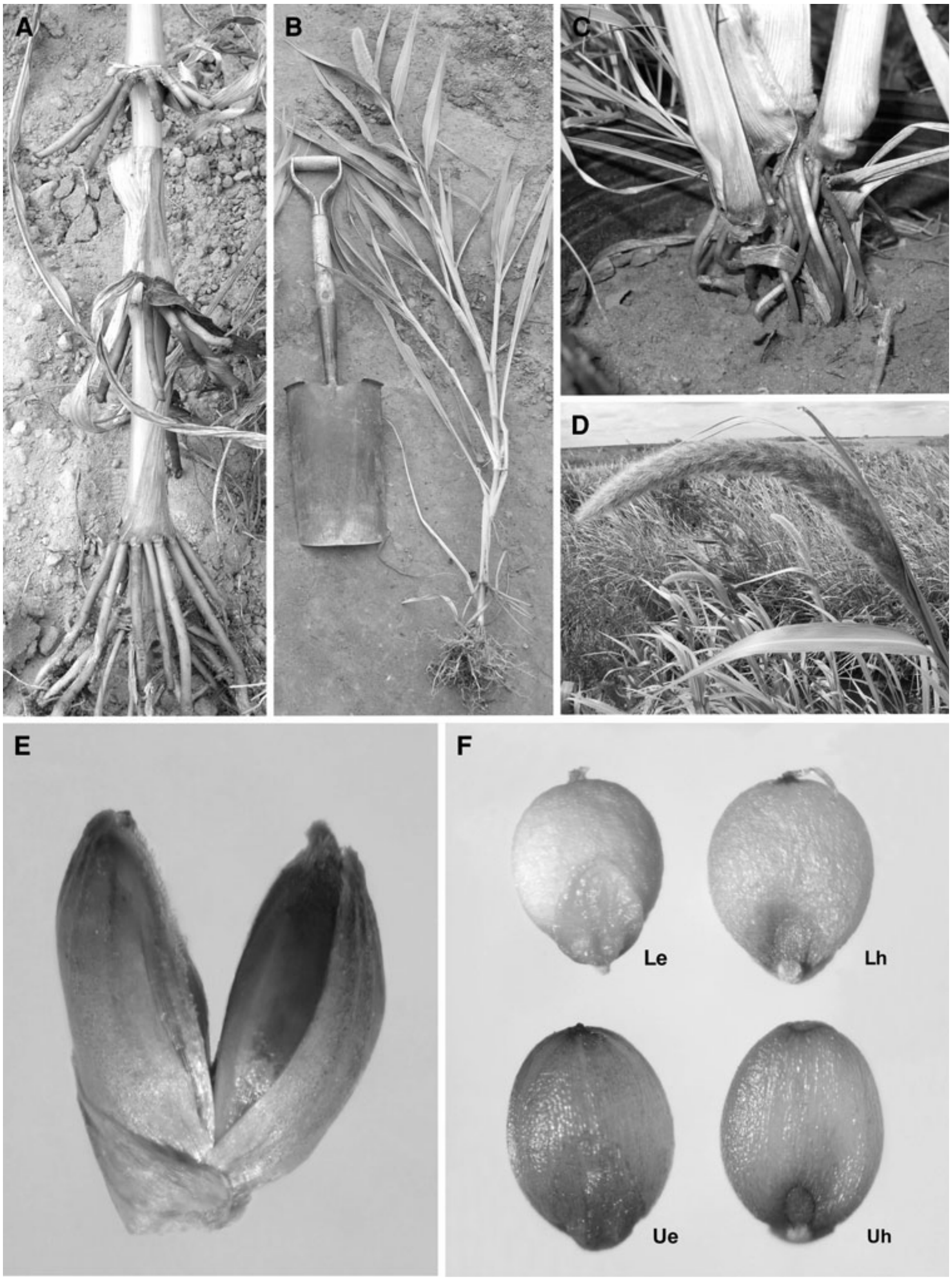

Fig. 1 Morphology of *Setaria magna*. **a** Base of the principal culms rooting at the lower nodes. **b** General aspect of a plant in its natural habitat showing axillary branches. **c** Base of a cultivated plant showing basal branches (tillers). **d** Mature inflorescence. **e** Spikelet with lower and upper caryopses developed. **f** Caryopsis. (*Le*) lower in embryo view, (*Lh*) lower in hilum view, (*Ue*) upper in embryo view, (*Uh*) upper in hilum view

Our results showed that filled spikelets were marginally heavier in open pollination plants. Others authors correlated weight with germination, dormancy and survival of the seedling, depending of self- or open pollination treatments. Pensiero et al. (2005) observed that some species of *Setaria* do not present significant differences in this feature between filled spikelets coming from both self- and open pollination, and that the spikelets are more heavy in open-pollination plants in allogamous species such as *S. fiebrigii*, *S. oblongata*, *S. pampeana* and *S. vulpiseta*. Similar relations were cited for other families of plants (Hamilton and Mitchell-Olds 1994; Maloof 2000; Navarro and Guitián 2003). Our results disagree because, although the spikelets were marginally heavier in open pollination, *S. magna* was autogamous. Therefore, the higher spikelet weight cannot be explained solely by the breeding system, and in *Setaria* this is probably a plastic character not associated with the reproductive system.

The morphological characters observed in live plants of *S. magna* match those of the examined herbarium specimens and descriptions from the literature (Nicora 1968; Rominger 1962; Pohl 1980; Boldrini 1989; Pensiero and Judziewicz 1990; Renvoize 1998; Pensiero 1999; Nozawa 2006), but the observed architectural pattern of the culms

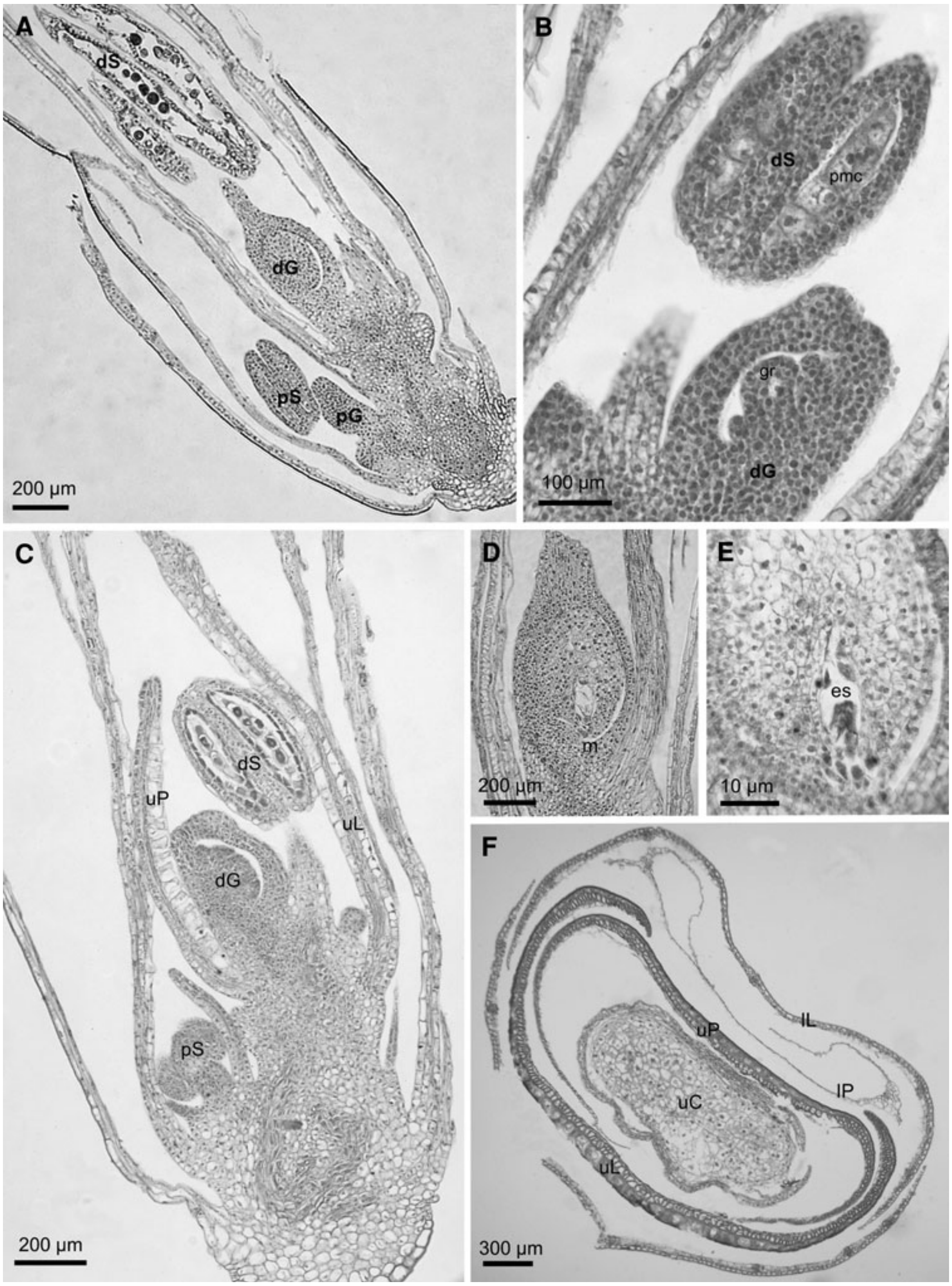

Fig. 2 Light micrographs of sections of spikelets of *Setaria magna*. **a** Longitudinal section of spikelet showing initially hermaphroditic lower and upper florets. **b** Longitudinal section of upper floret at pollen mother cell and gynoecial ridge stages. **c** Longitudinal section of spikelet showing basipetal differentiation. **d** Longitudinal section of a mature ovules. **e** Longitudinal section of an embryo sac. **f** Transverse section of a mature spikelet with a developed caryopsis in the upper anthecium. (*dG*) Upper gynoecium, (*dS*) upper stamen, (*es*) embryo sac, (*gr*) gynoecial ridge, (*m*) micropyle, (*lP*) lower palea, (*lL*) lower lemma, (*pG*) proximal gynoecium, (*pmc*) pollen mother cells, (*pS*) proximal stamen, (*uC*) upper caryopsis, (*uL*) upper lemma, (*uP*) upper palea

varies. Several authors (Pensiero and Judziewicz 1990; Pensiero 1999; Nozawa 2006) described *S. magna* as having unbranched culms; however, we observed plants that were highly branched. Cultivated plants showed more ramifications than wild plants because of the development of basal (tillers) and axillary branches; plants growing in their natural habitat only developed axillary branches. The number of branches directly influences biomass production and the number of caryopses that the plants produce, and is relevant to determining whether a species could be a potential fodder resource. Doust and Kellogg (2006) mentioned that *Setaria viridis* (green millet) produced more than three times as many branches at low density as at high density because weed species are more responsive to environmental differences than domesticated plants. Branch production is controlled by a complex interplay of environmental inputs, hormonal responses and genetic activity (McSteen and Leyser 2005).

The general pattern of floral development observed in *S. magna* was similar to that described for other species of the tribe Paniceae: *Panicum repens* L. (Le Roux and Kellogg 1999), *Megathyrsus maximus* (Jacq.) Simon & Jacobs (*Panicum maximum*) and *Urochloa plantaginea* (Link) R. D. Webster (Reinheimer et al. 2005). In these species, however, cell death is always observed in the gynoecium primordium of the lower florets, which thus develop as male.

The spikelets of *S. magna* that we processed to study the floral development resulted in all cases in male lower florets. Therefore, we could not observe the development of the ovules and embryo sacs in the lower anthecium. However, in the mature material we distinguished a small number of "double spikelets" that produced cariopses from both the lower and upper anthecium.

The presence of spikelets with bisexual lower florets that develop fruits is an unusual character for the tribe Paniceae. This tribe is characterized by the presence of two-flowered spikelets, but with the lower floret staminate or sterile (Nicora and Rúgolo de Agrasar 1987). Cocucci and Anton (1988) postulated that these florets originated from the reduction of a bisexual floret. Spikelets with a bisexual lower floret have been noted in *Setaria lachnea* (Pensiero et al. 1995), *Ocellochloa irregularis* (Swallen) Zuloaga & Morrone (*Panicum irregulare*) and exceptionally in *Dichanthelium sabulorum* (Lam.) Gould (*Panicum sabulorum*) (Cialdella and Vega 1996). Clayton and Renvoize (1986) mentioned the same character for the monotypic genus *Dissochondrus* (Hillebr.) Kuntze, a genus of Paniceae phylogenetically related to *Setaria* (Zuloaga et al. 2000).

We observed the presence of normally developing embryo sacs in the upper florets. Although these data do not provide complete evidence, they suggest that probably the seeds produced would not be apomictic. However, apomixis cannot be rejected in *S. magna* because the development of lower florets when they are bisexual was not observed in this study. Caponio and Pensiero (2002) reported the absence of apomixis in *S. pflanzii*. Contrarily, apomixis was reported in *S. leucopila*, *S. macrostachya, S. villosissima* (Scribn. & Merr.) K. Schum. and *S. texana* Emery (Chapman 1992; Emery 1957a, b).

Regarding the types of ovule and embryo sac observed in the upper florets of *S. magna*, they are the same as those described for *S. cordobensis* R.A.W. Herrm., *S. leiantha* Hack. and *S. pflanzii* (Cáceres and Mazzucato 1995; Caponio and Pensiero 2002), and correspond to the most common types for the family Poaceae.

In the mature inflorescences, we observed spikelets with one caryopsis and a few spikelets with two caryopses in the same inflorescence. Similarly, Pensiero et al. (1995) found spikelets in *S. lachnea* with two fertile anthecia, each containing a caryopsis. Nevertheless, most of the species of the genus produce only one caryopsis per spikelet because the lower floret is reduced to male as in *S. parviflora* and *S. sphacelata*, or is sterile with a rudimentary palea as in *S. viridis* and *S. verticillata* (Pensiero 1999). In these one-caryopsis species, the spikelets disarticulate from the pedicel and fall off entirely; the dispersal unit thus includes glumes that may provide protection to the caryopsis from predators before incorporation into the soil seed bank (Dekker 2003). Schrauf et al. (1998) demonstrated in *S. lachnea* that the main cause of dormancy is the presence of inhibitors in the glumes.

Individual panicles on a single parent plant can produce seeds with different requirements for germination; this attribute was demonstrated in *S. faberi* by Dekker et al. (1996). The two types of caryopses in *S. magna* also produce two kinds of dispersal units with differential germination behavior; a small stock of naked caryopses would have earlier germination, whereas a larger stock is protected by dormancy but could germinate when the glumes are degraded and the environmental conditions are appropriate.

Thus, our observations suggest that the erratic behavior of the natural populations of *S. magna* may explain the production of huge, dormant, protected upper caryopses that will probably not germinate in the next year because of the presence of inhibitors in glumes. Nevertheless, the population remains in the area because of the small number of lower naked, not dormant caryopses, but this will be smaller in the following years. Probably, after of a period of time the stock of the upper caryopses can germinate because the glumes are degraded, and if the environmental conditions are appropriate, the population can resurge, being bigger and increasing the natural area.

Other evidence to support this hypothesis might be the different colors of the lower and upper caryopses because darker caryopses (as the upper one in *S. magna*) seem to be more dormant than lighter colored ones (Dekker 2003).

Information on reproduction is required for future work on genetic improvement and management of potential valuable species. Some of the observed characteristics in *S. magna*, especially its predominant autogamous reproductive system and the high seed set with dormant and not dormant seeds, make it a promising species for future domestication and introduction to cultivation.

Acknowledgments We would like to thank Elizabeth Kellogg, Beatriz Galati and the anonymous reviewers for comments on the manuscript; Juan Valla, Gabriela Zarlavsky and Mariano Bello for technical assistence; and Buenos Aires University (UBACYT-G003; G409) and the Myndel Botanica Foundation for the grants.

References

Adams CD (1972) Flowering plants of Jamaica. University of the West Indies, Kingston

Austin DF (2004) Fox-tail millets (Setaria: Poaceae)—abandoned food in two hemispheres. Econ Bot 60:143–158

Barkworth ME, Capels KM, Long S, Piep MB (2003) Magnoliophyta: Commelinidae (in part): Poaceae. Part 2. In: Flora of North

America Editorial Committee (eds) Flora of North America North of Mexico. Oxford University Press, New York, pp 1–783

Beetle AA (1977) Noteworthy grasses from Mexico V. Phytologia 37:317–407

Boldrini II (1989) Ocorrencia de *Setaria magna* Griseb. e *S. hassleri* Hack. (Gramineae) no Sul Do Brasil. Acta Bot Brasil 2:19–26

Cáceres ME, Mazzucato A (1995) Cytological and embryiological studies in *Setaria cordobensis* Hermann and *Setaria leiantha* Hackel (Poaceae). Caryologia 48:255–263

Callen EO (1967) The first new world cereal. Amer Antiquity 32:535–538

Caponio I, Pensiero JF (2002) Comportamiento citológico y reproductivo de *Setaria pflanzii* (Poaceae). Darwiniana 40:17–23

Chapman GP (1992) Grass evolution and domestication. Cambridge University Press, Cambridge

Cialdella AM, Vega AS (1996) Estudios sobre la variación estructural de las espiguillas en géneros de la Tribu Paniceae (Poaceae). Darwiniana 34:173–182

Clayton WD, Renvoize SA (1986) Genera graminum, grasses of the World. Kew Bull Addit Ser 13

Cocucci AE, Anton AR (1988) The grass flower: suggestions on its origin and evolution. Flora 181:353–362

D'Ambrogio AC (1986) Manual de técnicas en histología vegetal. Hemisferio Sur, Buenos Aires

Dekker J (2003) The foxtail (*Setaria*) species-group. Weed Sci 51:641–656

Dekker J, Dekker BI, Hilhorst H, Karssen C (1996) Weedy adaptation in *Setaria* spp.: IV. Changes in the germinative capacity of *S. faberii* embryos with development from anthesis to after abscission. Am J Bot 83:979–991

Doust AN, Kellogg EA (2006) Effect of genotype and environment on branching in weedy green millet (*Setaria viridis*) and domesticated foxtail millet (*Setaria italica*) (Poaceae). Molec Ecol 15:1335–1349

Emery WHP (1957a) A cyto-taxonomic study of *Setaria macrostachya* (Gramineae) and its relatives in the Southwestern Unites Stated and Mexico. Bull Torrey Bot Club 84:94–105

Emery WHP (1957b) A study of reproduction in *Setaria macrostachya* and its relatives in the Southwestern United Stated and Northern Mexico. Bull Torrey Bot Club 84:106–121

Espejo Serna A, López-Ferrari AR, Valdés-Reyna J (2000) Poaceae monocot mexic. Sinop Flor 10:7–236

Funk V, Hollowell T, Berry P, Kelloff C, Alexander NS (2007) Checklist of the plants of the Guiana shield (Venezuela: Amazonas, Bolivar, Delta Amacuro; Guyana, Surinam, French Guiana). Contr US Natl Herb 55:1–584

Gao MJ, Chen JJ (1988) Isozymic studies on the origin of cultivated foxtail millet. Acta Agron Sin 14:131–136

Gildenhuys PJ (1950) Fertility studies in *Setaria sphacelata* (Schum.) Stapf. & Hubbard. Union Soc Afr Dept Agr Sci Bull 314:1–45

Gould FW (1979) Poaceae. In: Howard RA (ed) Flora of the lesser, vol 3. Leeward, Antilles, pp 25–220

Hamilton MB, Mitchell-Olds T (1994) The mating system and relative performance of selfed and outcrossed progeny in *Arabis fecunda* (Brassicaceae). Am J Bot 81:1252–1256

Hitchcock AS (1951) Manual of the grasses of the United States, edn 2. US Department of Agriculture, Washington

Holmgren PK, Holmgren NH, Barnett LC (1990) Index herbariorum. Part I. The Herbaria of the world. NY Bot Gard, New York

Kellogg EA, Aliscioni SS, Morrone O, Pensiero JF, Zuloaga FO (2009) Phylogeny of *Setaria* (Poaceae, Panicoideae, Paniceae) and related genera, based on the chloroplast gene ndhf. Int J Plant Sci 170:117–131

Le Roux LG, Kellogg EA (1999) Floral development and the formation of unisexual spikelets in the Andropogoneae (Poaceae). Amer J Bot 86:354–366

Li HW, Li CH, Pao WK (1945) Cytological and genetical studies of the interspecific cross of the cultivated foxtail millet, *Setaria italica* (L.) Beauv., and the green foxtail millet *S. viridis* (L.) Beauv. J Amer Soc Agron 37:32–54

Maloof JE (2000) Reproductive biology of a North American subalpine plant: *Corydalis caseana* A. Gray ssp. brandegei (S. Watson) G. B. Owvbey. Plant Spec Biol 15:281–288

Martin AC, Zim HS, Nelson AL (1961) American wildlife and plants: a guide to wildlife food habits. Dover, New York

McSteen P, Leyser O (2005) Shoot branching. Annu Rev Plant Biol 56:353–373

McVicar RM, Parnell HR (1941) The inheritance of plant color and the extent of natural crossing in foxtail millet. Sci Agric 22:80–84

Mulligan GM, Findlay JN (1970) Reproductive systems and colonization in Canadian weeds. Canad J Bot 48:859–860

Navarro L, Guitián J (2003) Seed germination and seedling survival of two threatened endemic species of the northwest Iberian peninsula. Biol Cons 109:313–320

Nicora EG (1968) Las especies anuales del género *Setaria* de la Flora Argentina. Bol Soc Argent Bot 12:373–382

Nicora EG, Rúgolo de Agrasar ZE (1987) Los géneros de gramíneas de América austral. Hemisferio Sur, Buenos Aires

Nozawa S (2006) *Setaria magna* Griseb. (Poaceae), primer reporte para Venezuela. Acta Bot Venez 29:297–302

Pensiero JF (1999) Las especies sudamericanas del género *Setaria* (Poaceae, Paniceae). Darwiniana 37:37–151

Pensiero JF, Judziewicz EJ (1990) 91. *Setaria*. In: Gorts-Ven Rijn ARA (ed) Flora of the Guianas. Koeltz Scientific Books, Koenigstein, pp 583–594

Pensiero JF, Marino GD, Schrauf GE (1995) Características reproductivas de *Setaria lachnea* (Nees) Kunth (Poaceae, Paniceae). Rev Fac Agron (B Aires) 15:59–66

Pensiero JF, Gutiérrez HF, Exner E (2005) Sistema de polinización y su efecto sobre la producción y el peso de semillas en nueve especies sudamericanas del género *Setaria*. Interciencia 30:495–500

Pohl RW (1980) Family 15. Gramineae. In: Burger WC (ed) Flora Costaricensis. Field Museum of Natural History, Chicago, pp 1–608

Pohl RW (1994) 130. *Setaria* P. Beauv. In: Davidse G, Sousa SM, Chater AO (eds) Flora Mesoamericana. Universidad Nacional Autónoma de México, México, pp 359–363

Prasada Rao KE, De Wet JMJ, Brink DE, Mengesha MH (1987) Infraspecific variation and systematics of cultivated *Setaria italica* foxtail millet (Poaceae). Econ Bot 41:108–116

Reinheimer R, Pozner R, Vegetti AC (2005) Inflorescence, spikelet, and floral development in *Panicum maximum* and *Urochloa plantaginea* (Poaceae). Am J Bot 92:565–575

Renvoize SA (1998) Gramíneas de Bolivia. The Royal Botanic Gardens, Kew

Rominger JM (1962) Taxonomy of *Setaria* (*Gramineae*) in North America. IL Biol Monogr 29:1–132

Schrauf GE, Martino A, Giavedoni J, Pensiero JF (1998) Efectos genéticos y ambientales sobre el comportamiento germinativo de poblaciones de moha perenne. Ecol Austral 8:49–56

Wang RL, Wendel J, Dekker J (1995) Weedy adaptation in *Setaria* spp.: I. Isozyme analysis of genetic diversity and population genetic structure in *S. viridis*. Am J Bot 82:308–317

Webster RD (1993) Nomenclature of *Setaria* (*Poaceae: Paniceae*). Sida 15:447–489

Zuloaga FO, Morrone O, Giussani LM (2000) A cladistic analysis of the Paniceae: a preliminary approach. In: Jacobs SWL, Everett J (eds) Grasses: systematics and evolution. CSIRO, Melbourne, pp 123–135

Zuloaga FO, Morrone O, Davidse G, Filgueiras TS, Peterson PM, Soreng RJ, Judziewicz EJ (2003) Catalogue of New World

Grasses (Poaceae): III. Subfamilies Panicoideae, Aristidoideae, Arundinoideae, and Danthonioideae. Contr US Natl Herb 46:443–527

Zuloaga FO, Morrone O, Davidse G, Pennington SJ (2007) Classification and biogeography of Panicoideae (Poaceae) in the new world. Aliso 23:503–544

Zuloaga FO, Morrone O, Belgrano MJ (eds.) (2008) Catálogo de las Plantas Vasculares del Cono Sur. Vol. 1. Pteridophyta, Gymnospermae, Monocotyledoneae. Monogr Syst Bot Missouri Bot Garden 107