Diversity of inflorescences in the Boutelouinae subtribe (Poaceae: Chloridoideae: Cynodonteae)

Vanesa Pilatti [a,b,*], Abelardo Vegetti [a,b]

[a] *Morfología vegetal, Fac. de Ciencias Agrarias, Univ. Nac. del Litoral, Kreder 2805, 3080 Esperanza, Santa Fe, Argentina*
[b] *Instituto de Agrobiotecnología del Litoral (CONICET-UNL), Esperanza, Santa Fe, Argentina*

A B S T R A C T

The Boutelouinae subtribe is comprised of one monophyletic genus, *Bouteloua*, with 57 species inhabiting the semi-arid regions of the New World. The inflorescences show significant structural variations, which provides an interesting system to examine their morphological evolution and identify characters and processes that may help to understand the group systematics. The structure of inflorescences was studied in 25 species of *Bouteloua*. All the species covered under this study have truncated polytelic inflorescences. Structural variations in the inflorescence unit among species may be accounted for by: (1) symmetry of the inflorescence unit, (2) total number of long primary branches, (3) total number of spikelets per branch, (4) number of perfect flowers per spikelet, (5) number of rudimentary flowers, and (6) reproductive system. Homogenization and truncation processes account for the diversity of mature inflorescences that exists in *Bouteloua*. In this work, we discuss the systematic and taxonomic value of the inflorescence in the Boutelouinae subtribe.

© 2014 Elsevier GmbH. All rights reserved.

Introduction

Phylogenetic analyses based on DNA sequencing from chloroplasts (ndhA intron, ndhF, rps16-trnK, rps16 intron, rps3, and rpl32-trnL, matK, ccsA) and nuclear genome (ITS) made it possible to identify four well-supported tribes within the Chloridoideae family (Peterson et al., 2010a, 2011, 2012). The Cynodonteae and Zoysieae tribes are sisters, forming a clade with members of the Eragrostideae tribe and, in turn, the whole set is sister to the Triraphideae tribe (Peterson et al., 2010a, 2011, 2012). Thirteen monophyletic subtribes may be recognized within the Cynodonteae tribe: Aeluropodinae, Triodiinae, Orcuttiinae, Tridentinae, Eleusininae, Tripogoninae, Pappophorinae, Traginae, Hilariinae, Monanthochloinae, Boutelouinae, Scleropogoninae and Muhlenbergiinae, but the relationships between one another are uncertain (Grass Phylogeny Working Group (GPWG), 2012; Peterson et al., 2010a, 2010b, 2011, 2012). However, the clade consisting of the Boutelouinae and Monanthochloinae subtribes shows molecular support in such phylogenies (Peterson et al., 2010a, 2011, 2012).

The Boutelouinae subtribe initially comprised 19 genera, namely: *Chondrosum*, *Neobouteloua*, *Bouteloua*, *Melanocenchris*, *Pentarrhaphis*, *Buchlomimus*, *Cyclostachya*, *Pringleochloa*, *Opizia*, *Schaffnerella*, *Buchloe*, *Cathestecum*, *Griffithsochloa*, *Aegopogon*, *Hilaria* and *Soderstromia* (Clayton and Renvoize, 1986). Recent molecular phylogenetic studies (Columbus, 1999; Columbus et al., 1998, 2000, 2007) have characterized Bouteloua as a paraphyletic group within the subtribe and determined several changes in the composition of Boutelouinae. *Neobouteloua*, *Melanocenchris*, *Schaffnerella*, *Aegopogon* and *Hilaria* were added to other subtribes within the Cynodonteae tribe (Columbus, 1999; Columbus et al., 1998; Hilu and Alice, 2001; Peterson et al., 2010a). The species of the other genera were included within Bouteloua (Columbus et al., 1998). As a consequence of these changes, the Boutelouinae subtribe consists only of Bouteloua, a monophyletic genus with 57 species (Columbus, 1999; Columbus et al., 1998, 2000, 2007).

Bouteloua had its center of origin in the Southwest of the nowadays United States and Mexico, wherefrom it spread naturally to the New World. Presently, most of the species are endemic in Mexico, whereas the rest extends to the Southwest of the United States, six species stretch to South America and three to the West Indies. The four most-widely distributed species (*B. curtipendula, B. gracilis, B. hirsuta, B. repens* and *B. barbata*) are found in grazing lands in North America and South America; one single species (*B. megapotamica*) is restricted to South America; two species (*B.*

* Corresponding author at: Universidad Nacional del Litoral, Morfología vegetal, Facultad de Ciencias Agrarias, Kreder 2805, 3080 Esperanza, Santa Fe, Argentina.
E-mail address: vanesapilatti@hotmail.com (V. Pilatti).

juncea and *B. vaneedenii*) are distributed only in the West Indies; and the *B. kayi* and *B. pectinata* species are known only in Texas (Gould, 1979; Herrera Arrieta and Lemus, 1997; Herrera Arrieta et al., 2004, 2008). *Bouteloua* species inhabit different plant communities, such as tropical rainforests, natural grazing lands, scrublands, temperate forests, NaCl-affected and gypsophile grasslands, and agricultural areas, forming part of the introduced vegetation (Herrera Arrieta et al., 2004).

Bouteloua species are significant components of natural grazing lands, of great importance for ecological balance, and some species (e.g. *B. curtipendula*, *B. gracilis*, *B. hirsuta* and *B. barbata*) are providing high-quality fodder (Gould, 1979; Herrera Arrieta and De la Cerda Lemus, 1997; Herrera Arrieta et al., 2004; Morales Nieto et al., 2007).

Members of *Bouteloua* are annual or perennial plants bearing an inflorescence with 1 – to many – spicate primary branches arranged along the main axis. Branch axes persist or fall entirely. They bear one to several (up to 100) spikelets, which may be bisexual, unisexual (monoecious or dioecious plants) or sterile; single, paired or in triplets; glumes awned or awnless; 3-nerved lemmas, awned or awnless; basic chromosome number $x = 10$; C_4 plants with typical Kranz leaf anatomy (Gould, 1979; Herrera Arrieta et al., 2004, 2008; Peterson et al., 2007; Siqueiros-Delgado, 2007; Watson and Dallwitz, 1992).

Various biosystematics studies have been conducted on *Bouteloua*, which have contributed information related to leaf epidermis (Rosales-Carrillo and Herrera-Arrieta, 1996), leaf blade (Columbus, 1996; 1999) and stem anatomy (Siqueiros-Delgado, 2007; Siqueiros-Delgado and Herrera Arrieta, 1996), lemma micromorphology (Columbus, 1996), flavonoid content in whole plants (Herrera Arrieta and Cháirez Hernández, 2005), morphological (Esparza Sandoval and Herrera Arrieta, 1996; Herrera Arrieta and De la Cerda-Lemus, 1997)and molecular characters (Columbus, 1999; Columbus et al., 1998, 2000, Siqueiros-Delgado et al., 2013). However, studies on the adult inflorescence structure in species of *Bouteloua* have not been carried out.

The characterization of processes and tendencies in the variation of inflorescences, as well as their typological analysis (Troll, 1964; Weberling, 1965, 1989), have been used successfully in many studies mainly intended to understand the evolution of varying inflorescence structures and determine characters and processes to clarify phylogenetic relationships among the studied species (Bess et al., 2005; Doust and Drinnan, 2004; Doust and Kellog, 2002a,b; Kellogg, 2000; Kellogg et al., 2004; Liu et al., 2005; Pensiero and Vegetti, 2001; Reinheimer, 2007; Reinheimer et al., 2005b, 2008, 2009; Rua, 1993, 1996; Vegetti and Anton, 1995, 2000).

In light of the aforementioned, the purpose of this work is to: (1) describe the mature synflorescence structure in species of the Boutelouinae subtribe; (2) identify structural differences at the level of the inflorescence; (3) identify new characters to be included in future phylogenetic research; (4) suggest processes that may account for the diversity of inflorescences within the subtribe; and (5) discuss the implications of such characters and processes in the systematics and taxonomy of the group under study.

Materials and methods

Adult inflorescences from 25 species of the *Bouteloua* genus were examined under a stereoscopic microscope (Table 1) and several structural parameters were recorded (Tables 2 and 3) using the terminology proposed by Troll (1964); Weberling (1989); Vegetti and Weberling (1996); Vegetti and Anton (1995, 2000) and Rua and Weberling (1998). The material studied was obtained from specimens loaned by different herbaria {CTES, KEW, LIL, MACN, MEXU, RSA, SF, SI and UNSL [acronyms of the herbaria according to Holmgren and Holmgren (1998)]} and collected in the field in different trips, specimens which were later left in the herbarium belonging to Universidad Nacional del Litoral (SF).

Results

In plants of the *Bouteloua* species, each shoot originating from the terminal bud (which will bear the main or terminal inflorescence) and from the basal axillary buds is considered a synflorescence of a different degree. Each shoot consists of a proximal portion, "the trophotagma", and a distal portion, "the anthotagma" (Fig. 1).

The trophotagma (TT) is the region of the synflorescence that plays the vegetative role in the plant. It spreads from the basal leaves of the shoot to the most distal leaf and has a short (SIZ) and a long internode zone (LIZ). The SIZ behaves as an innovation zone

Table 1
Material studied.

Species
Bouteloua aristidoides (Kunth) Griseb.
Pilatti, V. et al. 26 (SF); 54 (SF); Morello J. y Cuezzo A.R. 129 (SI); Kiesling R. 4509 (SI); Zuloaga, F. et al. 12,702 (SI); 10,082 (SI); Peterson P.M. et al. 19,322 (SI); 19,473 (SI); 19,313 (SI); Donadio S. et al. 59 (SI); Philip Cantino 652 (SI); Scarpa G.F. 613 (SI); Sanchez E. y Arriaga H. 1281 (SI); Rosa E. y Bianco C. 1614 (UNSL); Sánchez E. 510 (MACN); Isler 3 (MACN); Ledda M s/n (LIL); Morello s/n (LIL); Warnock B.H. 21,021 (LIL); Hitchcook A.S. 381 (LIL); Krapovickas A. y Cristóbal C.L. 20,674 (CTES); Cabrera A. L. et al. 23,311 (CTES); 15,572 (CTES); Esteban E. 10,679 (CTES); Speazzini C. s.n. (CTES); Pedersen T.M. 15,212 (CTES); Brizuela J. 1109 (CTES); Cabrera A.L. y Marchionni J. 13,094 (CTES); Zuloaga F.O. 6395 (CTES); 9462 (CTES); 9427 (CTES); Keller, H.A. 7029 (CTES); Meza Torres E.L. et al. 225 (CTES); Insfrán 754 (CTES); Krapovickas A. y Schinini A. 30,450 (CTES); 30,529 (CTES); Maranta A. 283 (CTES).
Bouteloua barbata Lag.
Pilatti, V. et al. 72 (SF); Ambrosetti J.A. y Cavagnaro J.B. 34,854 (CTES); Huelk 1011 (LIL); Cuezzo A. 2155 (LIL); Till W. 10,315 (LIL); Strother J.L. 1259 (LIL); Ruiz Leal 8751 (LIL); Zuloaga F.O.et al. 12,747 (SI); 11,866 (SI); Nee M. 57,051 (SI); Donadio S. 61(SI); Ulibarri E.A. 357 (SI); Philip Cantino 666 (SI); Reeder J.R. y Reeder C.G. 8604 (SI); 8407(SI); Burkart A. 12,255 (SI); 12,269 (SI); Hunzinker J.H. et al. 13,160 (SI); Covas G. 3583 (SI); 1390 (SI); Gentry H.S.14338 (SI).
Bouteloua chasei Swallen
Jauregui P. y Castillo M. 208 (MEXU); Blanco 2135 (MEXU); Clarkn P. Cowan 3621 (MEXU).
Bouteloua chondrosioides (Kunth) Benth. ex S. Watson
J. Balleza C. 1550 (MEXU); Pringle C.G. 9018 (MEXU); Navarro A.M. 993; Benitez A. 2731 (MEXU).
Bouteloua curtipendula (Michx.) Torr.
Pilatti, V. et al. 7 (SF); 50 (SF); S/N s/n (LIL); Vervoorst F. 8497 (LIL); Castellanos 3167 (LIL); Vliblasvi E.A. 635 (LIL); Leuenberger B. 4969 (BA); Rosa E., Scapinni E., Ocampo 228 (UNSL); Kiesling, R. et al. 5104 (SI); Zuloaga, F.O. et al. 10,719 (SI); 6205 (SI); Prina A. et al. 29,978 (CTES); Roig E. 8591 (CTES); Kiesling, R. et al 10,152 (CTES); Morrone O. et al. 2347 (CTES); Saravia Toledo C. 1910 (CTES); 12,878 (CTES); 12,722 (CTES); Cialdella A.M. et al. 355 (CTES); 331 (CTES); Carnaval R. 307 (CTES); Schulz A.G. 6560 (CTES).

Table 1 (*Continued*)

Species

Bouteloua dimorpha Columbus
Ekman E.L. 13,257 (KEW); Hinton G.B. 133,304 (KEW); Iltis H.H. y Lasseige A. 842 (KEW); Hitckcock A.S. 681 (KEW).

Bouteloua disticha (Kunth) Benth.
Llatas Quiroz S. 1082 (SI); Laegaard S. 19,854 (SI).

Bouteloua diversispicula Columbus
Zuñiga Díaz D. s/n° (MEXU); S/N 126 (MEXU); Navarro Macias A. 1385 (MEXU).

Bouteloua elata Reeder & C. Reeder
Navarrete de la Paz M. 50 (MEXU).

Bouteloua eriopoda (Torr.) Torr.
Bernal M.A. s/n (MEXU); Felger R.S. y Wilson M.F. 93-614 (MEXU); Quiñones Fermán 127 (MEXU).

Bouteloua gracilis (Kunth) Lag. ex Griffiths
Díaz V. I. 272 (MEXU); Flores G. C. 11-76a (MEXU); Reeder J.R. y Reeder C.R. 4295 (MEXU); Artega Saucedo M.C. 771 (MEXU); Chas H.Q. 40 (RSA).

Bouteloua hirsuta Lag.
Palmer E.J. 10,991 (SI); Chase V.H. 5143 (SI); Alcantar A.A. s/n° (MEXU); P. Tenorio L. et al. 7415 (MEXU); Arteaga Saucedo M.C. 773 (MEXU).

Bouteloua johnstonii Swallen
Johnston M.C. et al. 12,114 (MEXU).

Bouteloua karwinskii (E. Fourn.) Griffiths
Alcalá F. 015 México (MEXU); Reeder J.R. y Reeder C.G. 4077 (MEXU); Fuentes R.G. 327 (MEXU); Garza C.J. y Castillo B.M. (MEXU); Henrickson J. 6714 (MEXU).

Bouteloua media (E. Fourn.) Gould & Kapadia
Carrillo Soberón A. 963 (SI).

Bouteloua megapotamica (Spreng.) Kuntze
Pilatti, V. et al. 13 (SF); 48 (SF); 89 (SF); Carletti 9 (SF); Pensiero J. 929 (SF); Pire Nisensohn 5572 (SF); Rosa E. y Scapinni E. 971 (UNSL); Marino 2156 (SI); Burkart, A. 10,193 (SI); Ulibarri, E.A. 855 (SI); Hunziker J.H. 1689 (MACN); Hunziker A. T. 400 d (MACN); Buchinger 29,265 (MACN); Pozzo D. s/n (LIL); Castellanos s/n (LIL); Meyer T. 10,050 (LIL); Krapovickas A. 6418 (LIL); Morello, J. y Cuezzo A.R. 1075 (LIL); Ruiz Huidobro 1250 (LIL); Royo O. 11 (CTES); Martínez Crovetto 4837 (CTES); Pedersen T.M. 5840 (CTES); Saravia Toledo C. et al. 13,438(CTES); Krapovickas A. y Seijo G. 47,528 (CTES); Ragonese A. y Paccinini B. 9415 (CTES); 6490 (CTES); Pertusi L. 169 (CTES); Villamil C. 3263 (CTES); Biurrun F. y Pagliari E. 2704 (CTES); Schinini A. et al. 23,710 (CTES); Carnevali R. 3859 (CTES); Ahumada O. 1418 (CTES); Quarín C. 3339 (CTES); 1642 (CTES); Krapovickas A. et al. 25,918 (CTES); 22,121(CTES); Schulz A.G. 18,672 (CTES); 16,013 (CTES); Mussart P.A s.n. (CTES); Meyer T. 10,050 (CTES); Krapovickas A. Y Cristobal C. L. 14,684 (CTES); Pire E.F. 551 (CTES).

Bouteloua parryi (E. Fourn.) Griffiths
Zamudio S. y Ocampo G. s/n° (MEXU); Franscisco J. y Santana M. 8333 (MEXU); Calzada J.I. 20,440 (MEXU).

Bouteloua radicosa (E. Fourn.) Griffiths
Reeder J.R. y Reeder S.F. 8105 (SI).

Bouteloua repens (Kunth) Scribn.
Díaz Vilchis I. 613 (SI); 152 (SI); Zúñiga D. s/n° (SI); Gould F.W. 12,624 (KEW); 10,020b (KEW); Sohns E.R. 740 (KEW); Duane Isely 10,863 (KEW); Hubert Kruse 87[a] (MEXU); Lizama M.J. 1203 (MEXU).

Bouteloua scorpioides Lag.
Pringle C.G. 8820 (SI)

Bouteloua simplex Lag.
Pilatti, V. et al. 64 (SF); 65 (SF); 82 (SF); Peterson P.M. et al. 19,555 (SI); Candia, D. 11 (SI); Beck, S.G. 342 (SI); Arriaga M. y Aliscioni A. 340 (MACN); Castellanos 20,001 (MACN); Otto Bunchtien 171 (LIL); Schreiter 10,271 (LIL); Lillo 3723 (LIL); Infantes Vera J. 4070 (LIL); Zuloaga F.O. et al. 10,911 (CTES); Saravia Toledo C. et al 13,015 (CTES); Parodi L.R. 9730 (CTES); Ruiz Leal 21 693 (CTES); Kaprovickas A. y Schinini A. 35,763 (CTES); 35,757 (CTES); Murñak A. et al. 223 (CTES); Reales A. 1936 (CTES); Negritto M. et al. 384 (CTES); Jorgensen 1657 (CTES); Meyer T. et al. 21,379 (CTES); Reales A. 1727 (CTES); Nicora E. et al. 8954 (CTES).

Bouteloua triaena (Trin. ex Spreng.) Scribn.
Miranda S.A. 1234 (MEXU); Ernest Lyonnet 1176 (MEXU); Reeder J.R. y Reeder C.G. 4368 (MEXU); Calzada J.I. 20,345 (MEXU); Pringle C.G. 4782 (MEXU).

Bouteloua trifida Thurb.
Tharp B.C. 43A61 (SI); Miller J.S. et al. 5658 (SI); Gálvan G. 480 (MEXU); Encina J.A. 2435 (MEXU); Iribe F. 518 (MEXU); Thorne R.F. et al. 55,569 (RSA); 51,427 (RSA).

Bouteloua uniflora Vasey.
Waller F.R. 2153 (KEW); Peterson P.M. et al. 15,965 (KEW); 10,588 (KEW); Hiriart P. et al. 284 (MEXU); Hinton et al. 19588 (MEXU); Villalpando J.L. 1543 (MEXU).

Bouteloua williamsii Swallen
Benitez A.M. 261 (MEXU); Miranda F. 2982 (MEXU); Aragón L. 127 (MEXU).

MACN: Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"; CTES: Herbario del Instituto de Botánica del Nordeste; KEW: Royal Botanic Gardens; LIL: Herbario Fanerogámico de la Fundación Miguel Lillo; MEXU: Herbario Nacional de México; RSA: Rancho Santa Ana Botanic Graden Herbarium; SF: Herbario "E. A. Ragonese"; SI: Herbario del Instituto de Botánica "Darwinion"; UNSL: Herbario de la Universidad Nacional de San Luis.

Table 2
Trophotagma variations among members of the Boutelouinae subtribe.

Species	Life cycle	Types of shoots	Presence/ Absence of B_{TT}
Bouteloua aristidoides	Annual	Caespitose	Presence
Bouteloua barbata	Annual	Caespitose	Presence
Bouteloua chasei	Perenne	Rhizomatous	Absence
Bouteloua chondrosioides	Perenne	Caespitose	Absence
Bouteloua curtipendula[a]	Perenne	Caespitose	Absence
Bouteloua dimorpha (Female)	Perenne	Stoloniferous	Presence
Bouteloua dimorpha (Male)	Perenne	Stoloniferous	Presence
Bouteloua disticha[a]	Annual	Caespitose/Stoloniferous	Presence
Bouteloua diversispicula	Perenne	Caespitose/Stoloniferous	Absence
Bouteloua elata	Perenne	Caespitose by short rhizomes	Absence
Bouteloua eriopoda	Perenne	Caespitose by short rhizomes	Absence
Bouteloua gracilis	Perenne	Rhizomatous	Absence
Bouteloua hirsuta	Perenne	Caespitose	Absence
Bouteloua johnstonii	Perenne	Caespitose by short rhizomes	Presence
Bouteloua karwinskii	Perenne	Rhizomatous	Absence
Bouteloua media[a]	Perenne	Caespitose	Absence
Bouteloua megapotamica	Perenne	Caespitose/Stoloniferous	Absence
Bouteloua parryi	Perenne	Caespitose	Absence
Bouteloua radicosa	Perenne	Rhizomatous	Absence
Bouteloua repens	Perenne	Caespitose	Presence/Absence
Bouteloua scorpioides	Perenne	Caespitose	Absence
Bouteloua simplex	Annual	Caespitose	Presence
Bouteloua triaena[a]	Perenne	Caespitose	Presence/Absence
Bouteloua trifida	Perenne	Caespitose by short rhizomes	Absence
Bouteloua uniflora[a]	Perenne	Caespitose by short rhizomes	Absence
Bouteloua williamsii	Perenne	Caespitose	Absence

B_{TT} branch of the trophotagma.
[a] Species of the *B. curtipendula* complex according to Siqueiros-Delgado et al., 2013.

(IZ). The LIZ may behave only as an inhibition zone (HZ) or, in certain species, as an enrichment zone as well (EZ): Fig. 1.

The *innovation zone* (IZ) is located at the base of the plant and bears cataphylls with axillary buds that produce new shoots, which will become floriferous shoots, many of which will guarantee the species perennity – i.e. innovations – (Fig. 1). Most of the species of *Bouteloua* are perennial plants with sylleptic and cataleptic shoots, with the latter behaving as innovations. On the other hand, *B. aristidoides, B. barbata, B. disticha* and *B. simplex*, all of which are annual plants, do not have innovations and their shoots are

Table 3
Inflorescence variations among members of the Boutelouinae subtribe.

Species	Truncation of coflorescence	N° of long primary branches	N° of spikelet for branch	N° fertile flowers per spikelet	N° rudimentary flowers per spikelet	Breeding system
Bouteloua aristidoides	Yes	7–16	2–4	1	0–1	M
Bouteloua barabta	No	2–7	19–35	1	1	M
Bouteloua chasei	Yes	2	50–60	1	2	M
Bouteloua chondrosioides	Yes	6	4–10	1	1	M
Bouteloua curtipendula[a]	Yes	17–55	1–5	1	1	M
Bouteloua dimorpha (Female)	Yes	11–14	1	1	1	DM–DD
Bouteloua dimorpha (Male)	Yes	2	11–18	1	0	DM–DD
Bouteloua disticha[a]	Yes	29	?	1	1	M
Bouteloua diversispicula	No	5–10	3	1–2–3	0–1	AD
Bouteloua elata	No	12	?	1	1–2	M
Bouteloua eriopoda	Yes	3–4	4–10	1	1	M
Bouteloua gracilis	No	2–3	47–75	1	1	M
Bouteloua hirsuta	Yes	1–2(4)	30–50	1	2–3	M
Bouteloua johnstonii	No	6	5–9	1	1	M
Bouteloua karwinskii	Yes/No	4–6	20–30	1	2	M
Bouteloua media[a]	Yes	74	?	1	1–2	M
Bouteloua megapotamica	Yes	3–5	3–6	1	1–2	M
Bouteloua parryi	No	4–8	27–70	1	2	M
Bouteloua radicosa	Yes	10	3–7	1	1	M
Bouteloua repens	Yes	5–8(12)	2–8	2	0	M–AM
Bouteloua scorpioides	No	1	43	1	2	M
Bouteloua simplex	Yes	1 (2–3)	(15) 24–60	1	1	M
Bouteloua triaena[a]	Yes	(20) 34–72	1	1	1	M
Bouteloua trifida	No	3–6	13–30	1	1	M
Bouteloua uniflora[a]	Yes	13–43(52)	1	1	0	M
Bouteloua williamsii	Yes	7–9	4–10	1	1	M

N° number; M monocliny; DM monoecy; DD dioecy; AM andromonoecy; AD androdioecious; ? missing data; () outliers.
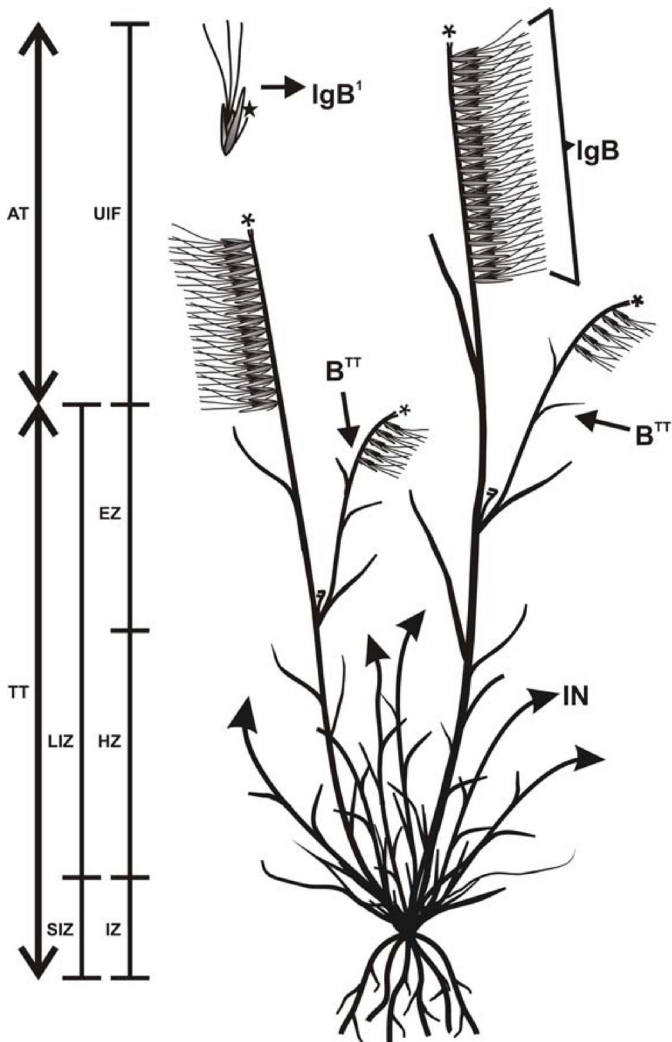[a] Species of the *B. curtipendula* complex according to Siqueiros-Delgado et al., 2013.

Fig. 1. Diagram of the synflorescence of *Bouteloua*. References: AT anthotagma; TT trophotagma; UIF inflorescence unit; EZ enrichment zone; HZ inhibition zone; IZ innovation zone; INinnovations; B^{TT} trophotagma branch; lgB^1 long primary branch, lgB subzone long primary branches; LIZ long internodes zone; SIZ short internodes zone; * truncation of the main florescence, the short branch subzone and some long primary branch; ★ truncation of the coflorescence of the long primary branch.

sylleptic (Table 2). In *Bouteloua*, significant variations occur in the innovation zone, so species can be caespitose (e.g. *B. media, B. simplex, B. megapotamica, B. barbata,* etc.), caespitose with short rhizomes (*B. johnstonii, B. uniflora, B. trífida, B. eriopoda* and *B. elata*), rhizomatous (*B. karwinskii, B. gracilis, B.radicosa* and *B. chasei*) and stoloniferous (*B. dimorpha, B diverspicula* and *B. disticha*). The presence of rhizomes and stolons makes the innovation zone larger (Table 2).

The *inhibition zone* (HZ) is located above the innovation zone and it has leaves with developed sheath and lamina whose axillary buds do not produce any shoots at all (Fig. 1). This zone is present in all the *Bouteloua* species studied.

In certain species (Table 2), the distal region of the long internode zone (LIZ) behaves as the trophotagma *enrichment zone* (EZ). The axillary buds in the EZ develop enrichment axes (paracladia of the trophotagma or branches of the trophotagma, B$_{TT}$). Each of these axes consists of a short hypopodium, an adaxial prophyll, a varying number of leaves, and ends in an inflorescence (lateral inflorescence or lateral unit of inflorescence) (Fig. 1).

The anthotagma (AT) comprises the distal region of the synflorescence which bears only floral axes lacking prophylls

and bracts (except for those that form the spikelets) and is represented by the terminal inflorescence (or terminal unit of inflorescence, UIF). The UIF is composed only of floriferous branches (paracladia or primary branches), which form together the zone of primary branches (B): Fig. 1. The UIF is the region of the synflorescence that shows most morphological variations within the *Bouteloua* genus.

In all the studied species of *Bouteloua*, the UIF is a panicle of alternate spiciform branches with initial bilateral symmetry, which turns dorsiventral as, at a given time of inflorescence growth, the basal internode of the primary branches on one of the sides of the main axis twists to the opposite side. This occurs in most of the species studied, except for *B. chondrosioides* and the female inflorescences of *B. dimorpha*, which show bilateral symmetry.

The *Bouteloua* UIF has a subzone of long primary branches (long primary paracladia, lgB) bearing a definite number of secondary branches reduced to a spikelet (short secondary paracladia or short secondary branches), and it lacks a subzone of short primary branches (shB) and a terminal spikelet (main florescence, MF). Above the distal long primary branch, the UIF main axis ends in a sterile prolongation, which is indicative of the truncation process of the main florescence, the subzone of short primary branches, and some long primary branches (Figs. 1 and 2).

Long primary branches may end in a spikelet (coflorescence = Cof.), as in *B. aristidioides, B. curtipendula, B. eriopoda, B. disticha,* etc., or in a sterile portion of the rachis, as in *B. barbata, B. elata, B. gracilis,* etc., as a result of the coflorescence truncation (Table 3, Figs. 1 and 2).

The number of long primary branches is highly variable within the *Bouteloua* genus. Some species (e.g. *B. triaena, B. uniflora, B. curtipendula,* etc.) have inflorescences with numerous (55–74) long primary branches, while others consist only of one long primary branch (*B. simplex, B. scorpioides* and *B. hirsuta* – Fig. 2). In most species, the number of primary branches is not stable, but varies among different specimens; for instance, *B. aristidoides* may have 7–15 long primary branches (Table 3).

In the UIF of all the studied species, the maximum degree of branching is the same (second order) along each branch and in all primary branches, regardless of the position they have on the inflorescence axis; this determines the UIF in *Bouteloua* to be completely homogenized.

On the long primary branches, 1 -to many- sessile spikelets are inserted in 2 rows along the margins of a flat rachis. The total number of spikelets present in each long primary branch and the number of functional (1–3) and rudimentary (0–2) flowers that comprise them varies among the studied species (Table 3). Flowers may be hermaphrodite or unisexual, and depending on the plant capacity to express one or both sexualities (male/female), different reproductive systems have been identified in the studied species of *Bouteloua* (Table 3).

Discussion

The synflorescence

The structure of the studied synflorescences of *Bouteloua* fits the general model among Poaceae (Cámara Hernández and Rua, 1991; Perreta et al., 2009; Rua, 1999; Troll, 1966, 1969; Troll and Weberling, 1989; Vegetti and Anton, 1996; Weberling et al., 1997). The following zones may be recognized in such synflorescences: (1) innovation zone (IZ), (2) inhibition zone (HZ), (3) enrichment zone (not developed in some species) (EZ), and (4) unit of inflorescence (UIF).

In species of *Bouteloua,* the innovation zone shows several growth models (Table 2) similar to those described for *Paspalum* (Rua and Weberling, 1998). Most of the species are densely
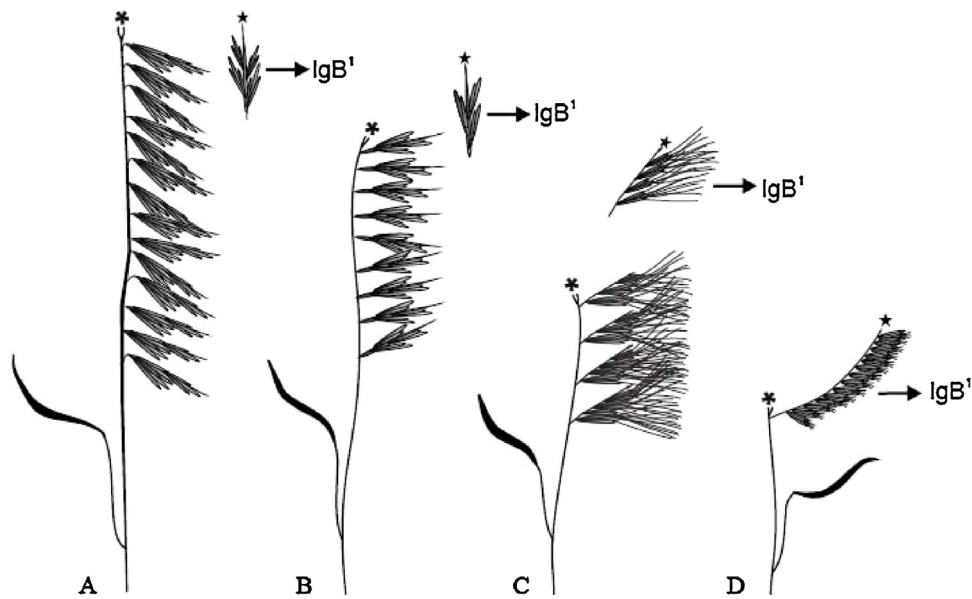
Fig. 2. Variations in the inflorescence structure in *Bouteloua*. A, *B. curtipendula*; B, *B. aristidioides*; C, *B. megapotamic*a y D, *B.simplex*. References: lgB[1] long primary branch; * truncation of the main florescence, the short branch subzone and some long primary branch; ★ truncation of the coflorescence of the long primary branch.

caespitose; this model being the most common growth form among grasses (Rua and Weberling, 1998). Also, some species have stolons and rhizomes in the innovation zone, which help vegetative propagation of the plants as it is the case in species of the *B. curtipendula* complex (Siqueiros-Delgado et al., 2013).

In many members of Poaceae, the long internodes zone behaves as an inhibition zone; however, the axillary buds of the most distal nodes in this zone may produce axes bearing developed leaves and ending in an UIF similar to the main axis (Rua and Weberling, 1998; Vegetti and Weberling, 1996). These axes have been named paracladia of the trophotagma (Vegetti and Muller-Doblies, 2004), second-order long paracladia (Weberling et al., 1993), paracladia with trophotagma (Vegetti and Weberling, 1996) or branches of the trophotagma (Reinheimer and Vegetti, 2008), and their function is related to the increase of floriferous branches in the plant (Rua and Weberling, 1998). In *Bouteloua,* all the annual species studied have branches of the trophotagma, unlike perennial species, most of which are lacking them. Therefore, a correlation may be observed between the presence or absence of the enrichment zone and the life cycle of the plant. This relation could not be confirmed in the inflorescences of the PCK (phosphoenol pyruvate carboxykinase) clade (Reinheimer and Vegetti, 2008). The fact that not all species show such correlation was explained by Frank (1998) and Rua and Weberling (1998). They held that the development of branches of the trophotagma is highly related to the environmental conditions where the plants grow.

Variations in the UIF

In Poaceae, the main florescence, represented by the terminal spikelet, is considered an open branching system. Consequently, grass inflorescences are consistently polytelic (Cámara Hernández and Rua, 1991; Cámara Hernández and Miante-Alzogaray, 1994; Troll, 1966, 1969; Vegetti, 1991; Weberling, 1983). In *Bouteloua*, the main florescence does not develop, so inflorescences are polytelic and truncated (Troll, 1964; Weberling, 1983).

In the studied species of *Bouteloua*, the UIF is represented by a panicle of spiciform primary branches alternately arranged along the main axis. This interpretation of the UIF's shape in the *Bouteloua* genus coincides with the descriptions by Allred (1982) and Gould (1979). However, this inflorescence has been misinterpreted in many works, as it has been described as unilateral racemes of spikelets (Griffiths, 1912), as an inflorescence of spicate branches or a false spike (Watson and Dallwitz, 1992), as an inflorescence of one to several unilateral racemose spikes or racemes of spikelets (Herrera Arrieta and De la Cerda Lemus, 1997; Herrera Arrieta et al., 2004).

The UIF of the studied species showed the following structural variations in terms of: (1) UIF symmetry, (2) total number of long primary branches, (3) total number of spikelets per branch, (4) number of perfect flowers per spikelet, (5) number of rudimentary flowers per spikelet, and (6) reproductive system. Some of these characters were found to be polymorphic in the same species.

In most of the studied species, the long primary branches of the UIF are arranged bilaterally but, at a certain time of growth, the peduncle of the branches on one of the sides twists to the opposite side and then the UIF becomes dorsiventral. Developmental studies are necessary in order to interpret properly this change in the inflorescence branch symmetry. A correct interpretation of the UIF symmetry might allow us to use this character in the taxonomic delimitation of the species as it has been used for the American species of *Brachiaria* and *Urochloa* (Morrone and Zuloaga, 1992, 1993).

The number of long primary branches in the UIF of *Bouteloua* varies significantly among species and among the specimens analyzed from each species. In general, the five species of the *B. curtipendula* complex studied here are the species that produce a high number of long primary branches (55–74), unlike *B. chasei, B. dimorpha, B. hirsuta, B. scorpioides* and *B. simplex*, which bear 1 or 2 long primary branches. The number of primary branches was also found to be a highly variable character in species of *Spartina* (Kern et al., 2008), *Brachiaria, Urochloa, Eriochloa, Chaetium, Megathyrsus, Melinis* (Reinheimer and Vegetti, 2008), *Sporobolus* (Reinheimer et al., 2005a), *Pappophorum* (Tivano and Vegetti, 2004), *Panicum* (Reinheimer and Vegetti, 2005b) and *Melica* (Perreta and Vegetti, 2004).

In *Bouteloua* species, a reverse relationship may be observed between the total number of long primary branches on the main axis and the number of spikelets borne by those branches; this is because the higher the number of long primary branches, the lower is the number of spikelets they bear (*B. curtipendula, B. triaena, B.aristidioides, B. uniflora,* etc.). Conversely, the lower the number of long primary branches, the higher is the number of

spikelets on them, as it occurs in *B. simplex, B. gracilis, B. hirsuta* and *B. scorpioides,* etc. (Table 3, Fig. 2). On the long primary branches, sessile spikelets are inserted alternately in 2 rows along the lower side of the flat rachis, which may or may not extend beyond the insertion point of the distal spikelet (Griffiths, 1912; Herrera Arrieta et al., 2004).

Spikelets of *Bouteloua* are composed of 1–3 functional (male, female or hermaphrodite) flowers in the proximal region, and their distal portion may show rudimentary flowers, sterile flowers or ornamented awns with varying shapes (Griffiths, 1912; Gould, 1979; Herrera Arrieta et al., 2004).

Most angiosperms have bisexual (hermaphrodite) flowers and only 20–30% of the total number of species produce flowers with male organs (stamens) or female organs (pistils) that reach functional maturity, that is, develop unisexual flowers (Richards, 1997; Yampolsky and Yampolsky, 1922). The *Bouteloua* genus shows significant variation in floral sex expression. Out of the 57 species that make up the genus, 13 produce bisexual spikelets and the rest are diclinous (andromonoecious, gynodioecious, monoecious, trimonoecious or dioecious, with more than one of these reproductive systems possibly found in one single species (Kinney et al., 2007)). Molecular phylogenetic analyses indicate that unisexual flowers in *Bouteloua* had at least six independent origins among all species. Therefore, hermaphrodite (bisexual) flowers are deemed to be the ancestral state in the group (Columbus et al., 1999, 2000; Kinney et al., 2007). In turn, those studies suggest that polyploidy and arid environments might be some of the possible factors involved in the evolution and variability of the reproductive systems that occur in *Bouteloua* (Kinney et al., 2007).

The structural variations that display Poaceae inflorescences are due to different processes that may occur in combination or independently, more than once and in several ways. These processes may have taken place at the level of the main florescence and/or in different regions of the primary branch zone (Cámara Hernández and Rua, 1991; Vegetti, 1991; Vegetti and Anton, 1995, 2000). Homogenization (morphological similarity of the primary branches of the inflorescence) and truncation (lack of development of distal structures along the main axis and the primary branches) are reductive processes pointed out as the most important evolutionary processes of the inflorescences of Poaceae (Cámara Hernández and Rua, 1991; Kunze, 1989; Maresquelle, 1970; Perreta et al., 2009; Sell, 1976; Troll, 1964, 1969; Weberling, 1965, 1985; Vegetti and Anton, 1995, 2000).

In the Boutelouinae subtribe, all the examined species show completely homogenized inflorescences, where the maximum branching degree displayed by all the primary branches is that of the second order. This process has been described for different groups of Poaceae, such as species of the Panicoideae (Pensiero and Vegetti, 2001; Rua, 1993, 1996; Rua and Weberling, 1998; Vegetti, 1991), Chloridoideae (Cámara Hernández, 2001; Liu et al., 2005; Perreta and Vegetti, 1998) and Ehrhartoideae subfamilies (Vegetti and Pensiero, 1999; Vegetti, 2000).

In the *Bouteloua* inflorescences, truncation is observed at the level of: (1) the main florescence (terminal spikelet of the inflorescence main axis), (2) short primary branches, (3) long primary branches, and (4) the coflorescence (terminal spikelet) of the long primary branches. All the observed inflorescences show truncation of the main florescence and the subzone of short primary branches, with the inflorescence reduced to the subzone of long primary branches. This subzone may be further reduced because of truncation of the distal long primary branches. Due to such different levels of truncation, the inflorescence may be reduced, in extreme cases, to a single long primary branch, as it occurs in *B. scorpioides* and in some specimens of *B. simplex* and *B. hirsuta* (Fig. 2). Also, in some species, the terminal spikelet (i.e. the coflorescence) is truncated in long primary branches, and a sterile

prolongation of the rachis may be observed above the distal spikelet (Fig 2). The truncation process has also been described for other genera of Poaceae: *Chloris, Cynodon* (Vegetti, 1986; Liu et al., 2005), *Eleusine* (Gasser and Vegetti, 1997), *Leptochloa* (Perreta and Vegetti, 1998), *Paspalum* (Rua and Weberling, 1998), *Digitaria* (Cámara Hernández, 2001), *Setaria* (Pensiero and Vegetti, 2001; Vegetti and Pensiero, 1990), *Urochloa* (Reinheimer, 2007), and has been mentioned as one of the frequent processes in the Chloridoideae and Panicoideae subfamilies (Cámara Hernández and Rua, 1991; Liu et al., 2005; Vegetti and Anton 1995, 2000).

There usually exists a correlation between truncation and homogenization (Perreta et al., 2009). Truncated inflorescences are homogenized inflorescences. However, in species of the PCK (phosphoenol pyruvate carboxykinase) clade (Reinheimer and Vegetti, 2008), there are homogenized inflorescences with no truncation. In this study, we observed that all the species of *Bouteloua* showed a direct correlation between homogenization and truncation, as described for *Setaria* (Pensiero and Vegetti, 2001), *Leptochloa* (Perreta and Vegetti, 1998), *Digitaria* (Cámara Hernández, 2001), for most species of *Paspalum* (Rua, 1996) and for genera of Andropogoneae (Vegetti, 1999).

Systematic and phylogenetic value

In recent phylogenies of the Chloridoideae subfamily based on plastid (ndhA intron, ndhF, rps16-trnK, rps16 intron, rps3, and rpl32-trnL, matK, ccsA) and nuclear (ITS) DNA regions, the Boutelouinae subtribe appears strongly supported as a sister group to the Monanthochloinae subtribe (Peterson et al., 2010a, 2011, 2012).

The Monanthochloinae subtribe is monophyletic and is composed only of the *Distichlis* genus (Bell and Columbus, 2008). In this subtribe, inflorescences are non-homogenized and non-truncated, and they may vary among species from one panicle of spikelets to a raceme of spikelets or even one single spikelet. This diversity of inflorescences in *Distichlis* is due to reductive processes affecting the proximal portion of the primary branch zone or the entire zone of primary branches, with extreme cases where the inflorescence comprises only the terminal spikelet (Pilatti et al., under preparation). On the other hand, in *Bouteloua*, the distal portion of the inflorescence is reduced in a sequence that affects both the terminal spikelet and the short primary branches (Fig. 2). This reduction may also include some of the distal long primary branches. In Poaceae, reductive processes do not always affect equivalent areas (Perreta et al., 2009; Vegetti and Anton, 2000) as it occurs in inflorescences of *Distichlis* and *Bouteloua*.

In *Distichlis*, the spikelets that make up the UIF are multi-flowered and unisexual (they do not have rudimentary flowers); therefore, the reproductive system in species of this genus is diclinous-dioecious (Clayton and Renvoize, 1986; Nicora and Rúgolo de Agrasar, 1987; Negritto et al., 2003), unlike species of *Bouteloua*, which may be andromonoecious, gynodioecious, trimonoecious or dioecious.

Since the relationship between both subtribes is molecularly supported and there are marked differences between their inflorescences (UIF shape, homogenization and presence/absence of truncation), the following characteristics may be considered as synapomorphies of the Boutelouinae subtribe:

- Shape of the UIF in *Bouteloua*, which is a panicle of spiciform branches.
- Lack of development of the terminal spikelet on the main axis (main florescence) and of the subzone of short primary branches. The inflorescence main axis ends in a sterile prolongation above the most distal long primary branch. This prolongation is indicative of the truncation process of the abovementioned structures.

- Complete homogenization, since all long primary branches have the same degree of branching (second order).

Phylogenetic analyses based on chloroplast and nuclear DNA sequencing have revealed that the Boutelouinae subtribe is monophyletic and this has been the foundation for expanding circumscription of the *Bouteloua* genus to include species of *Buchloe, Buchlomimus, Cathestecum, Cyclostachya, Griffithsochloa, Opizia, Pentarrhaphis, Pringleochloa,* and *Soderstromia* (Columbus, 1999; Columbus et al., 1998, 2000). In our study, a typological analysis was carried out of inflorescences of *B. dimorpha* (*Opizia stolonifera*) and *B. diversispicula* (*Cathestecum brevifolium*) species, which have recently been included in the *Bouteloua* genus (Columbus et al., 1998). Both these species, like all other originally *Bouteloua* species, show a panicle of spiciform branches, complete homogenization, truncation of the main florescence and the short primary branches. Accordingly, the expansion of the *Bouteloua* genus proposed by Columbus et al. (1998) might be suggested not only in light of the findings from molecular analyses, but also because of the structure seen in inflorescences, since similarities have been observed among species native to the genus and other species that only later have been included in it. Nonetheless, typological research needs to be conducted on a larger number of newly included species in *Bouteloua* in order to reach a more definitive conclusion.

Furthermore, the phylogeny proposed by Columbus et al. (1998) shows well-supported internal clades, but the relationships among those clades are not completely clear; and not all the species belonging to the *Bouteloua* genus have been included in the cladistic analysis. However, this phylogeny suggests that the clade comprising the *B. gracilis, B. chasei, B. scorpioides* and *B. simplex* species has the most reduced inflorescences within the subtribe, since the number of long primary branches varies from 1 to 3. On the other hand, the clade composed of *B. curtipendula, B. triaena, B. media* and *B. uniflora* (*B. curtipendula* complex) is characterized by having the most developed inflorescences in terms of long primary branch numbers (13–74), as compared with the rest of the species. In conclusion, the number of long primary branches might be an interesting character to delimit internal clades and to establish their relationships within *Bouteloua.*

Various studies have shown that similar adult inflorescences may develop through different ontogenetic processes, and highly diverse mature inflorescence structures may share similar development patterns (Doust and Kellogg, 2002a; Kellogg et al., 2004; Reinheimer et al., 2009). In view of this, development studies are a useful tool that may help understand the mature structures of observed inflorescences, as well as provide new morphological traits to be used in future cladistic analyses (Stür, 1986; Reinheimer et al., 2005b; Reinheimer, 2007). Thus, the typological research presented in this work needs to be complemented with flower, spikelet and inflorescence development studies.

In turn, inflorescence development and structure characters of *Bouteloua* species should be mapped on a phylogeny incorporating more molecular data and a larger number of species in order to understand how the various processes that gave origin to inflorescence diversity in *Bouteloua* have evolved.

Acknowledgements

References

Allred, K.W., 1982. Describing the grass inflorescence. J. Range Manage. 35, 672–675.

Bell, H.L., Columbus, J.T., 2008. Proposal for an expanded *Distichlis* (Poaceae, Chloridoideae): support from molecular, morphological, and anatomical characters. Syst. Bot. 33, 536–551.

Bess, E.C., Doust, A.N., Kellogg, E.A., 2005. A naked grass in the "bristle clade": a phylogenetic and developmental study of *Panicum* section *Bulbosa* (Paniceae: Poaceae). Int. J. Plant Sci. 166, 371–381.

Cámara Hernández, J., 2001. Morfologáa de la inflorescencia de Digitaria sanguinalis (Poaceae). Bol. Soc. Argent. Bot. 36, 87–95.

Cámara Hernández, J., Miante-Alzogaray, A., 1994. Polytely: a general character in Poaceae. Beitr. Biol. Pflanz. 68, 249–261.

Cámara Hernández, J., Rua, G.H., 1991. The synflorescence of Poaceae. Beitr. Biol. Pflanz. 66, 297–311.

Columbus, J.T., 1996. *Bouteloua chihuahuana* (Gramineae) a new nomenclatural combination. Aliso 14, 227.

Columbus, J.T., 1999. An expanded circumscription of *Bouteloua* (Gramineae: Chloridoideae): new combinations and names. Aliso 18, 61–65.

Columbus, J.T., Kinney, M.S., Pant, R., Siqueiros-Delgado, M.E., 1998. Cladistic parsimony analysis of internal transcribed spacer region (nrDNA) sequences of *Bouteloua* and relatives (Gramineae: Chloridoideae). Aliso 17, 99–130.

Columbus, J.T., Kinney, M.S., Siqueiros-Delgado, M.E., Porter, J.M., 2000. Phylogenetics of *Bouteloua* and relatives (Gramineae: Chloridoideae): cladistic parsimony analysis of internal transcribed spacer (nrDNA) and trnL–F (cpDNA) sequences. In: Jacobs, S.W.L., Everett, J. (Eds.), Grasses: Systematics and Evolution. CSIRO Publishing, Melbourne, Australia, pp. 189–194.

Columbus, J.T., Cerros-Tlatilpa, R., Kinney, M.S., Siqueiros-Delgado, M.E., Bell, H.L., Griffith, M.P., Refulio-Rodriguez, N.F., 2007. Phylogenetics of Chloridoideae (Gramineae): a preliminary study based on nuclear ribosomal internal transcribed spacer and chloroplast trnL-F sequences. Aliso 23, 565–579.

Clayton, W., Renvoize, S.A., 1986. Genera Graminum. Grasses of the World. Kew Bulletin Additional Series, vol. 13. 1–389.

Doust, A.N., Drinnan, A.N., 2004. Floral development and molecular phylogeny support the generic status of *Tasmannia* (Winteraceae). Am. J. Bot. 91, 321–331.

Doust, A.N., Kellogg, E.A., 2002a. Inflorescence diversification in the panicoid "bristle grass" clade (Paniceae, Poaceae): evidence from molecular phylogenies and developmental morphology. Am. J. Bot. 89, 1203–1222.

Doust, A.N., Kellogg, E.A., 2002b. Integrating phylogeny, developmental morphology and genetics: a case study of inflorescence evolution in the "bristle grass" clade (Panicoideae: Poaceae). In: Cronk, Q.C.B., Bateman, R.M., Hawkins, J.A. (Eds.), Developmental Genetics and Plant Evolution. Taylor and Francis, London, UK, pp. 298–314.

Esparza Sandoval, S., Herrera Arrieta, Y., 1996. Revisión de *Bouteloua barbata* Lagasca (Poaceae: Eragrostideae). Phytologia 80 (2), 73–91.

Frank, L., 1998. Análisis del sistema de ramificación del complejo *Brachiaria–Urochloa* (Poaceae–Paniceae), Tesis. Universidad de Buenos Aires, Buenos Aires.

Gasser, M., Vegetti, A.C., 1997. Inflorescence typology in *Eleusine indica* and *Eleusine tristachya* (Poaceae). Flora 192, 17–20.

Gould, F.W., 1979. The genus *Bouteloua* (Poaceae). Ann. Missouri Bot. Gard. 66, 348–416.

Griffiths, D., 1912. The grama grasses: *Bouteloua* and related genera. Contr. U.S. Natl. Herb. 14, 343–428.

Grass Phylogeny Working Group (GPWG), 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C4 origins. New Phytol. 193, 304–312.

Herrera Arrieta, Y., De la Cerda-Lemus, M., 1997. Morfometría del Género *Bouteloua* Lag. (Poaceae) de México. Phytologia 83, 113–124.

Herrera Arrieta, Y., Cháirez Hernández, I., 2005. Flavonoids of the genus *Bouteloua* (Poaceae) from Mexico. Polibotánica 020, 17–29.

Herrera Arrieta, Y., Peterson, P.M., De la Cerda Lemus, M., 2004. Revisión de *Bouteloua* Lag. (Poaceae). Comisión Nacional para el Conocimiento y Uso de la Biodiversidad y Instituto Politecnico Nacional, Durango, México, pp. 1–187.

Herrera Arrieta, Y., Peterson, P.M., Reyna, J.V., 2008. *Bouteloua* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae) del noreste de México. J. Bot. Res. Inst. Texas 2, 917–981.

Hilu, K.W., Alice, L.A., 2001. A phylogeny of Chloridoideae (Poaceae) based on matK sequences. Syst. Bot. 26, 386–405.

Holmgren, P.K., Holmgren, N.H., 1998. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden, New York (continuously updated).

Kellogg, E.A., 2000. Molecular and morphological evolution in the Andropogoneae. In: Jacobs, S.W.L., Everett, J. (Eds.), Grasses: Systematics and Evolution. CSIRO, Collingwood, pp. 149–158.

Kellogg, E.A., Hiser, K.M., Doust, A.N., 2004. Taxonomy, phylogeny and inflorescence development of the genus *Ixophorus* (Panicoideae: Poaceae). Int. J. Plant Sci. 165, 1089–1105.

Kern, V., Guarise, N., Vegetti, A., 2008. Typology of the inflorescence in *Spartina* (Poaceae: Eragrostoideae). Plant Syst. Evol. 273, 51–61.

Kinney, M.S., Columbus, J.T., Friar, E.A., 2007. Dicliny in *Bouteloua* (Poaceae: Chloridoideae): implications for the evolution of dioecy. Aliso 23, 605–614.

Kunze, H., 1989. Probleme der Infloreszenztypologie vonW. Troll. Plant Syst. Evol. 163, 187–199.

Liu, Q., Zhao, N.X., Hao, G., 2005. Inflorescence structures and evolution in subfamily Chloridoideae (Gramineae). Plant Syst. Evol. 251, 183–198.

Maresquelle, H.J., 1970. Le teme évolutif des complexes d'inflorescence. Son aptitude à suscite des problèmes nouveaux. Bull. Soc. Bot. France 117, 1–4.

Morales Nieto, C.R., Quero Carrillo, A.R., Avendaño Arrazate, C.H., 2007. Caracterizaciñn de la diversidad nativa del zacate banderita [*Bouteloua curtipendula* (Michx.) Torr.], mediante su nivel de ploidóa. Rev. Mex. Cienc. Pecu. 45, 263–278.

Morrone, O., Zuloaga, F.O., 1992. Revisión de las especies Sudamericanas nativas e introducidas de los géneros *Brachiaria* y *Urochloa* (Poaceae: Panicoideae: Paniceae). Darwiniana 31, 43–109.

Morrone, O., Zuloaga, F.O., 1993. Sinopsis del género *Urochloa* (Poaceae: Panicoideae: Paniceae) para México y América Central. Darwiniana 32, 59–75.

Nicora, E.G., Rúgolo de Agrasar, Z.E., 1987. Los Géneros de Gramíneas de América Austral. Hemisferio Sur, Buenos Aires, Argentina.

Negritto, M.A., Scrivanti, L.R., Anton, A.M., 2003. 19. Poaceae, parte 5: tribu 16. Eragrostideae: subtribu a. Monanthochloinae. Flora Fanerogámica Argentina 86, 1–68.

Pensiero, J.F., Vegetti, A.C., 2001. Inflorescence typology in *Setaria* p.Beauv. (Poaceae, Paniceae). Feddes Repert. 112, 371–385.

Perreta, M., Vegetti, A.C., 1998. Tipología de la inflorescencia en *Leptochloa chloridiformis*, *Leptochloa virgata* y *Leptochloa mucronata* (Poaceae). Kurtziana 26, 135–144.

Perreta, M., Vegetti, A., 2004. Estructura de las inflorescencias en especies de *Melica* (Pooideae-Poaceae). Darwiniana 42, 37–49.

Perreta, M., Ramos, J., Vegetti, A.C., 2009. Development and structure of the grass inflorescence. Bot. Rev. 75, 377–396.

Peterson, P.M., Columbus, J.T., Pennington, S.J., 2007. Classification and biogeography of new world grasses: Chloridoideae. In: Columbus, J.T., Friar, E.A., Porter, J.M., Prince, L.M., Simpson, M.G. (Eds.), Monocots: Comparative Biology and Evolution – Poales, 23. Rancho Santa Ana Botanic Garden, Claremont, California, Aliso, pp. 580–594.

Peterson, P.M., Romaschenko, K., Johnson, G., 2010a. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. Mol. Phyl. Evol. 55, 580–598.

Peterson, P.M., Romaschenko, K., Johnson, G., 2010b. A phylogeny and classification of the Muhlenbergiinae (Poaceae: Cynodonteae: Cynodonteae) Chlori based on plastid and nuclear DNA sequences. Am. J. Bot. 97, 1532–1554.

Peterson, P.M., Romaschenko, K., Barker, N.P., Linder, H.P., 2011. Centropodieae and Ellisochloa a new tribe and genus in the Chloridoideae (Poaceae). Taxon 60, 1113–1122.

Peterson, P.M., Romaschenko, K., Snow, N., Johnson, G., 2012. A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chlorideae) *sensu lato* and related genera. Ann. Bot. 109, 1317–1329.

Reinheimer, R., 2007. Desarrollo y estructura de la inflorescencia de Brachiaria y Urochloa (Poaceae: Panicoideae: Paniceae) y sus implicancias sistemáticas. Tesis doctoral, Universidad Nacional del Litoral. Facultad de Bioquímica y Ciencias Biológicas, Santa Fe, Argentina.

Reinheimer, R., Vegetti, A.C., 2008. Inflorescence diversity and evolution in the PCK clade (Poaceae: Panicoideae: Paniceae). Plant Syst. Evol. 275, 133–167.

Reinheimer, R., Astegiano, M.E., Vegetti, A.C., 2005a. Tipología de la inflorescencia en especies de *Sporobolus* (Sporobolinae–Eragrostideae–Poaceae). Kurtziana 31, 7–19.

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

Reinheimer, R., Zuloaga, F.O., Vegetti, A.C., Pozner, R., 2009. Diversification of inflorescence development in the PCK Clade (Poaceae: Panicoideae: Paniceae). Am. J. Bot. 96, 549–564.

Richards, A.J., 1997. Plant Breeding Systems, second ed. Chapman and Hall, London, UK.

Rosales-Carrillo, O., Herrera-Arrieta, Y., 1996. Epidermis en láminas foliares del género *Bouteloua lagasca* (Poaceae: Chloridoideae) de México. Phytologia 81, 46–66.

Rua, G.H., 1993. The synflorescence of *Paspalidium rarum* (Poaceae) and an alternative hypothesis about the evolution of some Poaceous inflorescences. Aust. Syst. Bot. 6, 261–267.

Rua, G.H., 1996. The inflorescences of *Paspalum* (Poaceae, Paniceae): the Quadrifaria group and the evolutionary pathway towards the fully homogenized, truncated common type. Plant Syst. Evol. 201, 199–209.

Rua, G.H., 1999. Inflorescencias: Bases Teóricas Para Su Análisis. Sociedad Argentina de Botánica, Buenos Aires, Argentina.

Rua, G.H., Weberling, F., 1998. Growth form and inflorescence structure of *Paspalum* L. (Poaceae: Paniceae): a comparative morphological approach. Beitr. Biol. Pflanz. 69, 363–431.

Sell, Y., 1976. Tendances évolutives parmi les complexes inflorescentiels. Rev. Gen. Bot. 83, 247–267.

Siqueiros-Delgado, M.E., 2007. Culm anatomy of Bouteloua and relatives (Gramineae: Chloridoideae: Boutelouinae). Acta Bot. Mex. 78, 39–59.

Siqueiros-Delgado, M.E., Herrera Arrieta, Y., 1996. Taxonomic value of culm anatomical characters in the species of *Bouteloua* Lagasca (Poaceae: Eragrostideae). Phytologia 81, 124–141.

Siqueiros-Delgado, M.E., Ainouche, M., Columbus, J.T., Ainouche, A., 2013. Phylogeny of the *Bouteloua curtipendula* complex (Poaceae: Chloridoideae) based on nuclear ribosomal and plastid DNA sequences from diploid taxa. Syst. Bot. 38, 379–389.

Stür, W.W., 1986. Reproductive development of the apex of *Brachiaria decumbens* Stapf. Ann. Bot. 58, 569–575.

Tivano, J.C., Vegetti, A., 2004. Synflorescence typology in Pappophoreae (Eragrostoideae – Poaceae). Beitr. Biol. Pflanz. 71, 157–174.

Troll, W., 1964. Die Infloreszenzen, Typologie und Stellung im Aufbau des Vegetationskörpers, 1. G. Fischer, Jena.

Troll, W., 1966. Teil Botanischer. Kommission für Forschung Biologische, 110-131, Bericht. Jb. 1965. Akademie der Wissenschaften und der Literatur, Mainz.

Troll, W., 1969. Botanischer Teil. Kommission für Forschung biologische, 88-105, Bericht. Jb. 1968. Akademie der Wissenschaften und der Literatur, Mainz.

Troll, W., Weberling, F., 1989. Infloreszenzuntersuchungen an monotelen Familien: Materialien zur Infloreszenzmorphologie. G. Fischer, Stuttgart.

Vegetti, A.C., 1986. Contribución al conocimiento de las inflorescencias en *Chloris* y *Cynodon* (Poaceae). Kurtziana 18, 109–120.

Vegetti, A.C., 1991. Sobre politelia en las inflorescencias de Poaceae. Kurtziana 21, 267–274.

Vegetti, A.C., 1999. Typology of the synflorescence of Andropogoneae (Poaceae), additional comments. Feddes Repert. 110, 111–126.

Vegetti, A.C., 2000. Typology of synflorescence in *Oryzeae* (Poaceae). Phyton (Austria) 40, 71–88.

Vegetti, A.C., Anton, A.M., 1995. Some evolution trends in the inflorescence of Poaceae. Flora 190, 225–228.

Vegetti, A.C., Anton, A.M., 1996. The synflorescence concept in Poaceae. Flora 191, 231–234.

Vegetti, A.C., Anton, A.M., 2000. The grass inflorescence. In: Jacobs, S.W.L., Everett, J. (Eds.), Grasses: Systematics and Evolution. CSIRO, Melbourne, pp. 29–31.

Vegetti, A.C., Muller-Doblies, D., 2004. The inhibition areas within the synflorescence of Poaceae. Beitr. Biol. Pflanz. 73, 51–74.

Vegetti, A.C., Pensiero, J.F., 1990. Typology of the inflorescence in *Setaria poiretiana* (Poaceae). Beitr. Biol. Pflanz. 65, 313–318.

Vegetti, A.C., Pensiero, J.F., 1999. Tipología de la inflorescencia en Zizaniopsis (Poaceae, Oryzeae). Darwiniana 37, 345–349.

Vegetti, A.C., Weberling, F., 1996. The structure of the paracladial zone in Poaceae. Taxon 45, 453–460.

Watson, L., Dallwitz, M.J., 1992. The Grass Genera of the World. CAB international, Wallingford.

Weberling, F., 1965. Typology of inflorescences. Bot. J. Linn. Soc. 59, 15–221.

Weberling, F., 1983. Fundamental features of modern inflorescence morphology. Bothalia 14, 917–922.

Weberling, F., 1985. Aspectos modernos de la morfología de las inflorescencias. Bol. Soc. Argent. Bot. 24, 1–28.

Weberling, F., 1989. The architecture of inflorescences in the *Myrtal*es. Ann. Missouri Bot. Gard. 75, 226–310.

Weberling, F., Müller-Doblies, U., Müller-Doblies, D., 1993. Zur deskriptiven und vergleichend-morphologischen Terminologie komplexer Infloreszenzen. Beitr. Biol. Pflanz. 67, 453–473.

Weberling, F., Müller-Doblies, U., Müller-Doblies, D., Rua, G.H., 1997. Hacia una terminologüa descriptiva y morfológico-comparativa para inflorescencias complejas. Bol. Soc. Argent. Bot. 32, 171–184.

Yampolsky, C., Yampolsky, H., 1922. Distribution of sex forms in the phanerogamic flora. Bibl. Genet. 3, 1–62.