



Synflorescence morphology of grasses with reduced terminal inflorescences: a case study of *Jouvea* (Cynodonteae, Chloridoideae, Poaceae)

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Abstract

Jouvea is a dioecious genus of grasses with two species. Molecular phylogenetic analyses place it in tribe Cynodonteae, closely related to subtribes Hilariinae and Scleropogoninae, and the genera *Allolepis* and *Sohnsia*. The staminate inflorescence in *Jouvea* is an ordinary grass spike of spikelets, but the pistillate inflorescence is represented by a single spikelet which lacks glumes, has a thick and cylindrical rachilla, lemmas forming a tube that enclose the palea and pistil, stigmas protruding from an apical pore of this tube, and does not have lodicules. Within Cynodonteae, inflorescences reduced to a single spikelet also occur in subtribe Monanthochloinae, in which the small number of flowers of the terminal inflorescence is compensated by an increase in the number of lateral floriferous shoots. We here describe the floriferous shoot system (synflorescence) of *Jouvea* and compare it to other cynodonteae grasses with reduced inflorescences. *Jouvea* species display a high number of lateral shoots (trophotagma enrichment axes) growing from the medial and distal zones of the synflorescences. These shoots have prophyllar origins and form clusters of lateral inflorescences. The elevated number of trophotagma enrichment axes of *Jouvea* may be associated with the extreme reduction in the pistillate terminal inflorescence. In addition, the increase in number of spikelets by the development of prophyllar branches is a unique strategy within tribe Cynodonteae.

Keywords: Grasses, Prophyllar branches, Trophotagma enrichment axes

Introduction

Jouvea Fournier (1876: 475) is a perennial, dioecious genus with only two species: *J. straminea* Fournier (1876: 475) and *J. pilosa* (Presl 1830: 280) Scribner (1896: 143). These species are distributed from Mexico to Ecuador (Clayton *et al.* 2006), where they grow in sandy areas, coastal dunes and mud flats (Clayton & Renvoize 1986) of xerophytic, halophytic or glycolytic regions (Weatherwax 1939).

The taxonomic position of *Jouvea* within Poaceae remained unclear for many years (Pohl 1980). Reeder (1956) analyzed the embryo structure of *Jouvea* and suggested it could be related to the Panicoideae or Pooideae subfamilies. Pohl (1980) stated leaf anatomy and chromosome size and number indicated it belonged to the Chloridoideae subfamily. Within Chloridoideae, Clayton & Renvoize (1986) placed *Jouvea* in subtribe Monanthochloinae (tribe Cynodonteae). These authors suspected *Jouvea* to be a derivation of the genus *Monanthochloe* Engelman (1859: 436) due to morphological resemblances, such as inflorescences represented by a single terete spikelet embraced by a leaf sheath, absence of glumes, and coriaceous lemmas. Recent molecular phylogenetic studies contradict this hypothesized close relationship between *Jouvea* and *Monanthochloe*, as the two species of *Monanthochloe* [*M. acerosa* (Grisebach 1879: 285) Spegazzini (1902: 194) and *M. littoralis* Engelman (1859: 436), now *Distichlis acerosa* (Grisebach) Bell & Columbus (2008: 548) and *D. littoralis* Bell & Columbus (2008: 548)] are nested within the genus *Distichlis* Rafinesque (1819: 104) in the Monanthochloinae subtribe (Bell & Columbus 2008), while *Jouvea* is part of a clade composed of subtribes Hilariinae and Scleropogoninae, plus the genera *Allolepis* Soderstrom & Decker (1965: 34) and *Sohnsia* Airy Shaw (1965: 272) (Peterson *et al.* 2016). *Jouvea* is currently treated incertae sedis in Cynodonteae (Peterson *et al.* 2016).

Inflorescence morphology in Cynodonteae displays enormous variation, including panicles of spikelets, racemes of spikelets, spikes of spikelets and inflorescences reduced to a single spikelet (Pilatti 2016, Muchut *et al.* 2017). Inflorescences reduced to a single spikelet are homoplastic within Cynodonteae because they occur both in *Jouvea* and some species of *Distichlis*, including *D. acerosa*, *D. australis* and *D. littoralis* (Spegazzini 1902: 194) Villamil (1969: 388) (Peterson *et al.* 2016).

In both species of *Jouvea* the pistillate inflorescence is represented by a single spikelet with a unique morphology within the grass family. The spikelet lacks glumes and the lemmas are fused to the rachilla forming a tube that encloses a membranous palea, a fertile pistil and three rudimentary stamens (Weatherwax 1939). The lodicules are absent and the 2 to 5 florets of the spikelet are completely embedded in the spongy and cylindrical rachilla (Weatherwax 1939). On the other hand, the staminate inflorescence is a typical long-peduncled spike of spikelets with no significant differences from other grass genera. The spikelets, which are borne alternately in two rows on the rachis, have only one glume (first glume is rudimentary or absent), and 10 to 50 florets consisting of lemma, palea, two lodicules, three stamens and no visible rudiment of a pistil (Weatherwax 1939, Clayton *et al.* 2006).

Grasses with reduced terminal inflorescences may compensate for the small number of flowers by developing new floriferous shoots (Vegetti 1999, Rua & Weberling 1998, Perreta *et al.* 2009, Muchut *et al.* in press). These shoots are called trophotagma enrichment axes when they are present within the long internode zone below the terminal inflorescence (Vegetti & Weberling 1996). When the axes develop from the basal short internode zone, they are known as innovation shoots, basal branches or tillers (Rua & Weberling 1998). The location of these active meristems along the culm varies among species and might be genetically determined (Muchut *et al.* in press). Indeed, Doust *et al.* (2004) observed that the shoot development from the different zones is controlled by distinct loci.

In cynodonteae grasses, the correspondence between reduction of terminal inflorescence and increase of extra floriferous shoots has been registered in *Distichlis acerosa*, *D. littoralis*, and *D. australis* (Pilatti 2016), but has not been analyzed in the species of *Jouvea*. This kind of study requires not only an examination of the arrangement of flowers in terminal units (inflorescences), but also a structural analysis of the axis that bears them (=synflorescence) (Troll 1964, Weberling 1983, Vegetti & Anton 1996). A synflorescence is defined as a floriferous shoot system generated by the apical meristem of a seed embryo or by a bud located in the short internode zone of a plant (innovation) (Rua 1999). The aim of this work is to examine mature specimens of *Jouvea* to (1) characterize the ramification patterns of the staminate and pistillate synflorescences and (2) determine if these patterns are shared or not with the other cynodonteae species with reduced inflorescences.

Materials and Methods

Mature synflorescences of *Jouvea pilosa* and *J. straminea* were examined under a Nikon SMZ-10 stereoscopic microscope. A thorough examination of their reproductive morphology was carried out and described using the terminology proposed by Troll (1964), Weberling (1989), Vegetti & Weberling (1996), Vegetti & Anton (1995, 2000) and Rua & Weberling (1998). We studied the specimens loaned by KEW, NY, MO, and US herbaria listed in Table 1.

TABLE 1. Voucher information of the studied taxa. Abbreviations: (KEW) Royal Botanic Gardens; (NY) The New York Botanical Garden; (MO) Missouri Botanical Garden; (US) Smithsonian Institution.

Species	Herbarium	Voucher	Country of collection	State/Province of collection
<i>Jouvea pilosa</i>	KEW	<i>Pohl RW & Gabel M 13623</i>	El Salvador	La Unión
		<i>Pohl RW & Gabel M 13505</i>	Honduras	Choluteca
		<i>Reeder JR & Reeder CG 4427</i>	México	Colima
		<i>Wiggins IL 16152</i>	México	Baja California
	NY	<i>Johnston IM 3835</i>	México	Baja California Sur
		<i>Jones ME 24049</i>	México	Baja California Sur
		<i>Jones ME 27443</i>	México	Baja California Sur
		<i>Palmer E s.n. (NY-1730482)</i>	México	Baja California Sur
		<i>Palmer E. 124</i>	México	Baja California Sur
		<i>Palmer E s.n. (NY-1730485)</i>	México	Baja California Sur
		<i>Palmer E 1384</i>	México	Colima
		<i>Palmer E 235</i>	México	Guerrero
		<i>Rose JN 16365</i>	México	Baja California Sur
		MO	<i>Grayum MH 11540</i>	Costa Rica

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TABLE 1. (Continued)

Species	Herbarium	Voucher	Country of collection	State/Province of collection
		<i>Grayum MH 11843</i>	Costa Rica	Guanacaste
		<i>Grayum MH 12121</i>	Costa Rica	Guanacaste
		<i>Morales JF 11463</i>	Costa Rica	Guanacaste
		<i>Morales JF 11546</i>	Costa Rica	Guanacaste
	US	<i>Kock SD 89184</i>	México	Colima
		<i>Reina AL 2007-1095</i>	México	Sonora
		<i>Warren DS 22350</i>	Nicaragua	León
<i>Jouvea straminea</i>	NY	<i>Breedlove DE 54164</i>	México	Chiapas
		<i>McVaugh R 19729</i>	México	Jalisco
		<i>McVaugh R 19730</i>	México	Jalisco
		<i>McVaugh R 19731</i>	México	Jalisco
		<i>Palmer E 443a</i>	México	Guerrero
		<i>Palmer E 443b</i>	México	Guerrero
		<i>Palmer E 443c</i>	México	Guerrero
	MO	<i>Coronado González I 4953</i>	Nicaragua	León
		<i>Sidwell K 636</i>	El Salvador	San Vicente
		<i>Sidwell K 670</i>	El Salvador	La Unión
		<i>Rodríguez D 656</i>	El Salvador	La Unión
	US	<i>Grayum MH 5129</i>	Costa Rica	Guanacaste

Results

Synflorescence structure

The two species of *Jouvea* are dioecious with dissimilar staminate and pistillate inflorescences. The plants are composed of shoots of consecutive branching order. One of the shoots is the main axis of the plant and the others are axillary shoots. This main axis (synflorescence) (Fig. 1A–C, E–G; Fig. 2A–D) presents a vegetative part and a terminal inflorescence (Fig. 1D). The vegetative portion is formed by a short internode zone (SIZ) and a long internode zone (LIZ) (Fig. 1A). The short internode zone is an innovation zone producing orthotropic (tillers) and plagiotropic axes (stolons) (Fig. 1A), which are profusely branched in *J. pilosa*, and sparsely branched in *J. straminea*.

In both the pistillate and staminate synflorescences the medial and distal buds of the long internode zone of *J. pilosa* and *J. straminea* develop trophotagma enrichment axes (*tea*) (Figs. 1A–C, E–G; 2A, B, D). Immediately after the trophotagma enrichment axes, above the last distal leaf, the culm ends in a terminal inflorescence (Fig. 1D). This inflorescence may be a spike of staminate spikelets (in staminate synflorescences, Figs. 1E–G; 2C–D) or reduced to a single spikelet (in pistillate synflorescences, Fig. 1A–C; 2A, B). In both synflorescences, each trophotagma enrichment axis ends in a lateral inflorescence similar to the terminal one.

Jouvea pilosa

We propose a new specific classification for trophotagma enrichment axes identified in the pistillate synflorescence: type 1 trophotagma enrichment axes (*tea1*), located in the distal regions of the long internode zone (Fig. 1A–C); and type 2 trophotagma enrichment axes (*tea2*), located in the medial regions of the long internode zone (Fig. 1B, C). The *tea1* displays a reduced prophyll and a lateral inflorescence. Each *tea1* generates successive trophotagma enrichment axes from its prophyllar bud. Consequently, a typical prophyllar ramification system (cymose ramification) with extremely short internodes originates in distal leaves (even in the flag leaf). Each prophyllar branch carries its own prophyll and one lateral inflorescence, which is reduced to a single pistillate spikelet. For *tea1*, we registered a maximum branching degree of fifth order.

The *tea2* presents a prophyll and a variable number of leaves, and ends with an inflorescence (lateral inflorescence). The axillary buds present in the *tea2* may develop generating *tea1*, frequently in the distal leaves. The axillary bud of the prophyll of *tea2* rarely develops a new branch. This enrichment axis displays, beyond the prophyll, a variable number of leaves while the number of leaves in the *tea1* is limited to its unique prophyll.

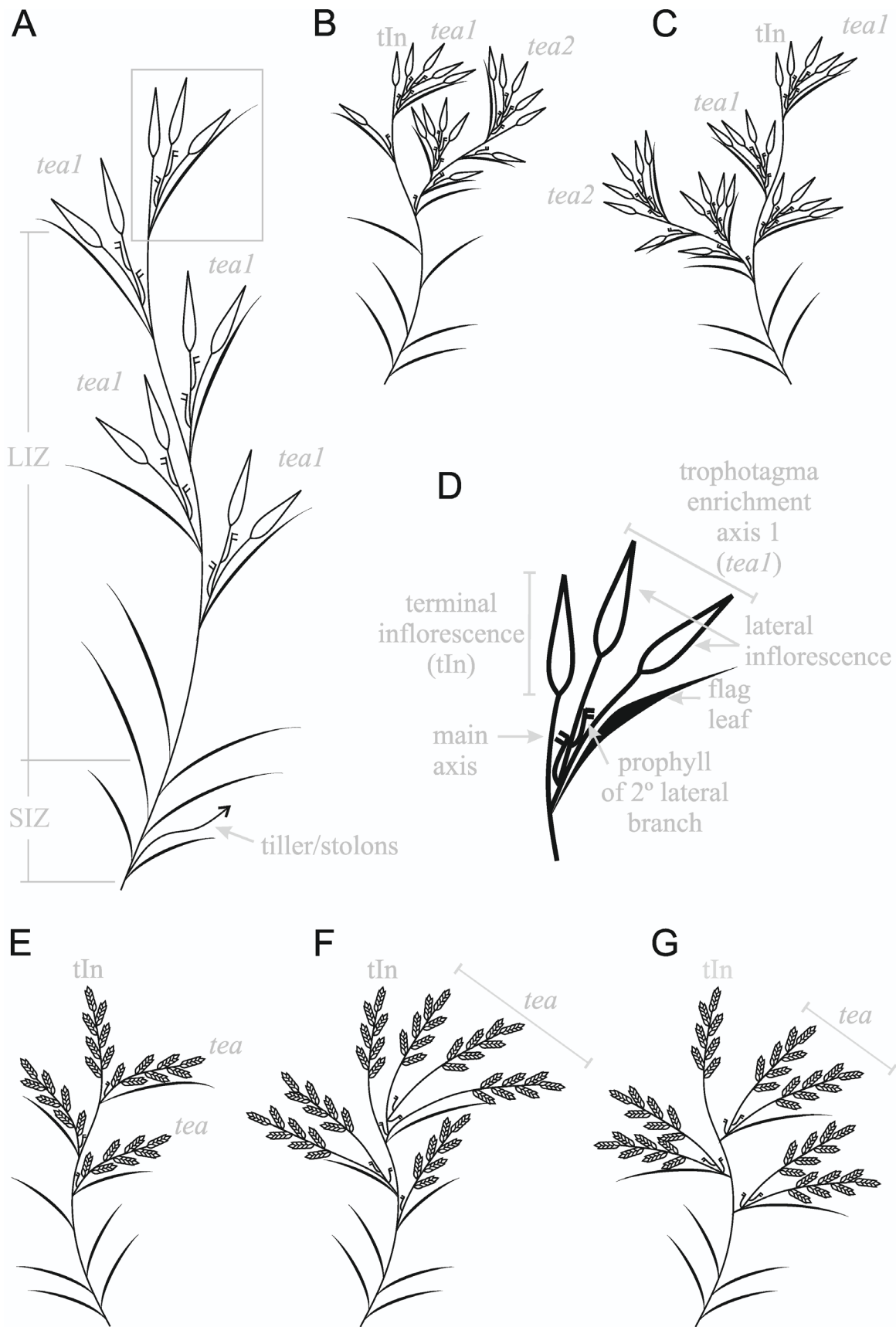


FIGURE 1. Synflorescence diagrams of *Jouvea pilosa*: A, Pistillate synflorescence showing the different internode zones. Dotted square indicates the terminal cluster. B, C, Other variations of pistillate synflorescences. D, Pistillate terminal cluster where the terminal inflorescence is associated with trophotagma enrichment axes. E, F, G, Variations of staminate synflorescences. References: LIZ, long internode zone; SIZ, short internode zone; *tea*, trophotagma enrichment axis of staminate synflorescences; *tea1*, trophotagma enrichment axis type 1; *tea2*, trophotagma enrichment axis type 2; tIn, terminal inflorescence.

The most conspicuous characteristic of the pistillate synflorescence is the combination of the reduced terminal inflorescence (=one pistillate spikelet) and the set of distal *teal* (Fig. 1A). Because of its prophyllar ramification and short internodes, each set of *teal* constitutes a dense, flabellate cluster of lateral pistillate inflorescences reduced to a single spikelet. Only one of these spikelets originates from an axillary bud of a leaf borne on the main axis (=primary branch). The rest of the lateral spikelets have a prophyllar origin.

The staminate synflorescence displays only one type of trophotagma enrichment axis, similar to the *teal* of the pistillate synflorescence (Fig. 1E–G). These trophotagma enrichment axes (*tea*) do not develop leaves beyond the prophyll. The staminate *tea* presents a prophyll and ends in a spike of staminate spikelets (=lateral inflorescence). The *tea* are generated in the distal leaves within the long internode zone, even in the flag leaf. In fact, some specimens exhibit trophotagma enrichment axes only in the flag leaf, while others in the two or three distal leaves. When these *tea* develop branches, they do it from the axillary bud of the prophyll (Fig. 1F, G). Some specimens show *tea* ramification of third order. Above the flag leaf, the internode of the main shoot elongates ending with a staminate terminal inflorescence (Fig. 1E–G).

Jouvea straminea

As in *J. pilosa*, the pistillate synflorescence exhibits two types of trophotagma enrichment axes. The *teal* originate in 2 to 4 distal leaves and the *tea2* in leaves of the medial portion of the long internode zone (Fig. 2A, B). The staminate synflorescence shows enrichment axes similar to those registered for *J. pilosa* and they are placed in the 1 to 2 distal leaves (Fig. 2C, D). These enrichment axes rarely produce more branches.

Discussion

The synflorescence of Jouvea species

The reduction in complexity of terminal inflorescences in grasses is commonly accompanied by an increase in the number of axillary shoots developing from vegetative leaves (Vegetti 1999, Rua & Weberling 1998, Muchut *et al.* in press). These axillary shoots may arise from the short internode zones, producing more innovations (tillers, stolons, or rhizomes), and/or from the axillary buds of the long internode zones, increasing the development of trophotagma enrichment axes (Vegetti 1999, Rua & Weberling 1998, Perreta *et al.* 2009, Muchut *et al.* in press). The innovations will eventually increase the number of synflorescences and, consequently, the number of inflorescences. The trophotagma enrichment axes, on the other hand, increase the number of lateral inflorescences of the main axis. Species with reduced inflorescences have these two mechanisms to increase the total number of inflorescences (terminal + lateral inflorescences) and consequently the number of spikelets, flowers and fruits (Muchut *et al.* in press). The high number of trophotagma enrichment axes in the long internode zone of *Jouvea*, along with its stoloniferous habit, may be associated with the extreme reduction in the pistillate terminal inflorescence.

According to Pohl (1980) the pistillate inflorescence structure of *Jouvea* and its aggregation into prophyllar clusters is extremely unusual and complicated compared to the rest of the grass family. Our work clarifies that (1) the prophyllar clusters are trophotagma enrichment axes generated in the medial and distal leaves of the long internode zone; and (2) the terminal cluster is a combination of the terminal inflorescence (a single spikelet) and a set of these enrichment axes. Pohl (1980) detailed that each of these fascicles is subtended by short, stiff leaf blades and interspersed with prominent prophylls. We expand upon this information by explaining that the stiff blades correspond to the leaves disposed in each node of the long internode zone and the prophylls belong to each trophotagma enrichment axis.

The presence of trophotagma enrichment axes in distal portions, forming floriferous units with the terminal inflorescence, is not exclusive to *Jouvea*. Similar arrangements are recorded in other grass species such as *Rhynchoryza subulata* Baillon (1894: 1063), *Coelorachis aurita* (Steudel 1854: 361) Camus (1922: 197), and *Andropogon bicornis* Linnaeus (1753: 1046) (Clayton 1972, Clayton & Renvoize 1986, Vegetti 1999). Grasses that do not display a remarkably reduced terminal inflorescence may or may not develop trophotagma enrichment axes. When present, these axes do not form intricate branching systems and it is easy to differentiate the terminal inflorescence (Muchut *et al.* in press). These trophotagma enrichment axes are recorded in Bambusoideae, a few Chloridoideae genera such as *Blepharidachne* Hackel (1887: 68), *Munroa* Torrey (1857: 158), *Schaffnerella* Nash (1912: 141), some species of *Bouteloua* Lagasca (1805: 134) and *Sporobolus* Brown (1810: 169) (Watson & Dallwitz 1992, Kellogg 2015, Pilatti 2016), and genera of the subfamily Panicoideae such as *Dichanthelium* Gould (1974: 59), *Dimorphochloa* Blake (1941: 1), *Xerochloa* Brown (1810: 196), *Zygochloa* Blake (1941: 7), and some species of *Stenotaphrum* Trinius (1822: 175) and *Streptostachys* Desvaux (1810: 190) (Watson & Dallwitz 1992, Vegetti 1999, Pilatti *et al.* 2014, Pilatti 2016).

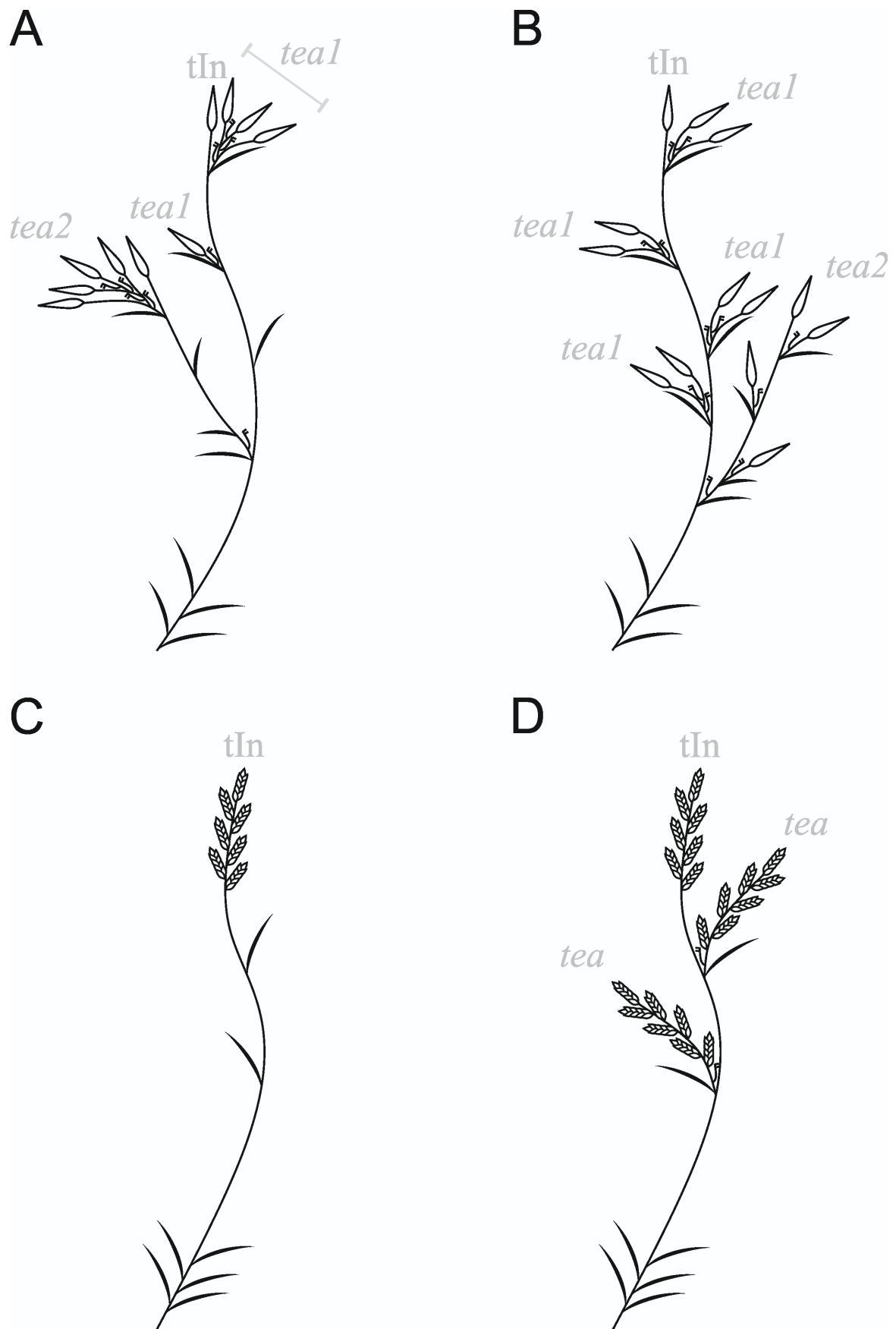


FIGURE 2. Synflorescence diagrams of *Jouvea straminea*. A, B, Variations of pistillate synflorescences. C, D, Variations of staminate synflorescences.

In many grasses, the promotion or repression of lateral meristems located in the long internode zones seems to be mainly affected by environmental factors (Rua & Weberling 1998, Perreta *et al.* 2009). This would explain the existence of variation within the same species. In the genus *Paspalum* Linnaeus (1759: 855), for example, the production of lateral shoots may vary between individuals (Rua & Grottola 1997, Rua & Weberling 1998). The species of *Jouvea* preserve the promotion of these axillary meristems, which may be genetically controlled as an evolutionary response to the decrease of inflorescence complexity. Genetic studies on maize identified *teosinte branched1* (*tb1*), a branching gene that inhibits axillary bud outgrowth (Doebley *et al.* 1993). When the expression of *tb1* decreases, the bud grows to form a tiller or an axillary shoot (Kebrom *et al.* 2013). Another maize gene (*grassy tillers1*) affects ear development by acting on the branching system of the trophotagma enrichment zone (Wills *et al.* 2013). The study of these genes in non-crop species would help understand the developmental background of the long internode zone in grasses.

***Jouvea* and subtribe Monanthochloinae**

Jouvea, along with the subtribes Monanthochloinae, Muhlenbergiinae, Hilariinae, Scleropogoninae, and Boutelouinae, plus the genera *Sohnsia*, *Allolepis*, and *Kalinia* Bell & Columbus (2012: 91), form a clade of species from the Western Hemisphere, and including a few Asian species of *Muhlenbergia* (Peterson *et al.* 2016). The only other species of Cynodonteae with inflorescences reduced to one spikelet belong to Monanthochloinae (*Distichlis acerosa*, *D. australis*, and *D. littoralis*) (Bell & Columbus 2008).

Subtribe Monanthochloinae, similar to *Jouvea*, includes dioecious species occurring in saline habitats (Bell *et al.* 2010, Peterson *et al.* 2016). In addition to having inflorescences reduced to one spikelet, the subtribe includes species with panicles of spikelets (*Distichlis laxiflora* Hackel (1911: 141), *D. palmeri* Fasset (1924: 984), *D. spicata* Greene (1887: 415), and some specimens of *D. bajaensis* Bell (2010: 59)), and racemes of spikelets (*D. bajaensis*, *D. eludens* (Soderstrom & Decker 1964: 335) Bell (2008: 548), *D. humilis* Philippi (1891: 86) and *D. scoparia* Arechavaleta & Balardo (1897: 457)) (Pilatti 2016). *Distichlis* comprises species that are stoloniferous (*D. acerosa* and *D. littoralis*) and rhizomatous (*D. australis*, *D. bajaensis*, *D. eludens*, *D. humilis*, *D. laxiflora*, *D. palmeri*, *D. scoparia*, and *D. spicata*) (Pilatti 2016). The trophotagma enrichment axes at the long internode zones may (*D. acerosa*, *D. australis*, *D. bajaensis*, *D. littoralis*, *D. scoparia*, and some specimens of *D. spicata*) or may not be present (*D. humilis*, *D. laxiflora*, *D. palmeri*, and some specimens of *D. spicata*) depending on the species and individual observed (Pilatti 2016). When present, these axes are generally unbranched and do not form prophyllar systems (Pilatti 2016). By contrast, *Jouvea* species have a constant and permanent presence of these axes, forming complex prophyllar branching systems.

Conclusions

The present study suggests a correlation between inflorescence reduction and increased shoot development from axillary buds of vegetative leaves in *Jouvea* species. Whether this morphological tradeoff is a result of genetic or ecological factors remains unclear and demands studies with different approaches. First, a detailed developmental and anatomical study of *Jouvea* is needed to reveal the true nature of its inflorescence structures. This would facilitate comparison with other species with reduced inflorescences. Second, due to the particular habitats and distributions of *Jouvea* species, studies with ecological and biogeographical focuses would be helpful.

Acknowledgments

We thank the curators of the herbaria KEW, NY, MO and US for providing plant material. We would also like to thank Dr. Vanesa Pilatti for helping in morphological interpretations. Funding was provided by the Agencia Nacional de Promoción Científica y Tecnológica Argentina (grant PICT-2015-0681).

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