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Floral reversion and first record of pseudovivipary in some species of Poaceae

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ABSTRACT

This contribution constitutes the first report of floral reversion and occurrence of pseudovivipary in *Paspalum ceresia* (Kuntze) Chase, *P. stellatum* Humb. & Bonpl. ex Flügge and *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda. Observations were made in material kept under cultivation in Buenos Aires (Argentina) since March 2001. Proliferating spikelets are described and illustrated, and some implications in the origin of spikelet organs are discussed. An up to date table including the genera of Poaceae where this phenomenon has been documented is also provided.

KEY WORDS

Poaceae,
flower reversion,
proliferation,
pseudovivipary.

RÉSUMÉ

Réversion florale et premier signalement de pseudo-viviparie dans certaines espèces de Poaceae.

Cette contribution constitue un premier rapport sur la réversion florale et l'apparition d'épillets pseudo-vivipares dans *Paspalum ceresia* (Kuntze) Chase, *P. stellatum* Humb & Bonpl. ex Flügge et *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda. Les observations ont été effectuées sur des plantes mises en culture depuis mars 2001 à Buenos Aires (Argentine). Les épillets prolifères sont décrits et illustrés, et quelques conclusions sur l'origine des organes des épillets sont proposées. Nous complétons un tableau mis à jour des genres de Poaceae dans lesquels ce phénomène a été documenté.

MOTS CLÉS

Poaceae,
proliferation,
pseudo-viviparie,
réversion florale.

INTRODUCTION

The term vivipary, in a strict sense, should be confined to the germination of seeds *in situ* without a resting period (Goebel 1905; Arber 1965; Font Quer 1993). The seeds germinate while still attached to the mother plant and the young seedling grows to a considerable length before falling. True vivipary appears to be relatively rare in Poaceae, restricted to maize and some species of woody bamboos (Kurz 1873, 1876; Stapf 1904; Troup 1921; Langer & Ryle 1958; Paulsen & Auld 2004).

The term vivipary has also been used to cover the development of plantlets from vegetative buds that have entirely replaced flower buds, as in *Agave* L. and *Phormium* J. R. Forst. & G. Forst. (Allan & Cranwell 1942), *Chlorophytum* Ker-Gawl. (Troll 1962) and, more rarely, in Dicots as *Kalanchoë* Adans. (Elmqvist & Cox 1996). This phenomenon is more appropriately referred to pseudovivipary to distinguish it from vivipary *sensu stricto*. In grasses, the most familiar situation is the conversion of the whole spikelet or part of the spikelet into a leafy shoot. Such a 'return' to the foliage-leaf condition is responsible for the vegetative aspect of proliferating spikelets. Pseudovivipary is an asexual reproductive mechanism exhibited by some arctic/alpine grasses in which leafy plantlets with conserved genomes constitute an advantage for stress tolerators in these nutrient-poor habitats (Pierce *et al.* 2003). Clones of *Poa bulbosa* L. showed inter-annual variation between normal and proliferated inflorescences attributed to differences in the onset of the rainy season resulting in different daylength and temperature conditions during the early stages of growth (Ofir & Kigel 2014).

Some grasses growing in temperate habitats occasionally show proliferated spikelets as a response to excessive soil humidity, shading, and other adverse conditions during a casual flowering that may occur several months after normal flowering time (Martínez Crovetto 1944, 1945, 1947). In *Poa alpina* var. *vivipara* L. parental plant and pseudoviviparous plantlets are physiologically connected in terms of contributing to photosynthesis and maintaining and driving the transpiration flow from senescent culms although water supply is not enough for the increasing transpirational demand of pseudoviviparous plantlets. During senescence, water content of culms determines the length of time that propagules remain attached, being of critical importance to grass reproduction (Pierce *et al.* 2000a)

These leafy shoots are not usually an effective method of reproduction in the wild but are somewhat easier to establish under controlled conditions (Beetle 1980). Both vegetative proliferation and "secondarily proliferated inflorescences" were also reported in *Ischaemum barbatum* Retz. during a wet and hot summer (Ma *et al.* 2006).

Pseudovivipary was always closely associated with various environmental factors and the molecular mechanism of this phenomenon is still unknown. Wang *et al.* (2010) found two MADS-box transcription factors that were essential for sexual reproduction and mutation of these factors lead to stable pseudovivipary in a naturally occurring mutant of rice.

Vega & Rúgolo de Agrasar (2006) reviewed the phenomena of vivipary and pseudovivipary in Poaceae, including the first record of pseudovivipary in the genus *Digitaria* Haller. The phenomenon of pseudovivipary was reported from 21 genera (Vega & Rúgolo de Agrasar 2006), although this list is extending with additional observations.

On this basis, subsequent studies about the phenomenon of pseudovivipary conducted us to report for the first time the occurrence of pseudovivipary in *Paspalum ceresia* (Kuntze) Chase, *P. stellatum* Humb. & Bonpl. ex Flüggé and *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda. *Paspalum ceresia* (Panicoideae: Paspaleae) is a South American species distributed in Argentina, Bolivia, Ecuador, and Peru (Zuloaga & Morrone 2003; Rua *et al.* 2008) while *P. stellatum* has a wider distribution, including Mexico, Central America, Caribbean, Colombia, Venezuela, Guyana, Bolivia, Brazil, Paraguay, Argentina and Uruguay (Denham *et al.* 2002). *Thysanolaena latifolia* (Panicoideae: Thysanolaeneae) is native from India and introduced as an ornamental in the Caribbean, El Salvador, and United States (Davidse 2003), and sporadically cultivated in South America (Argentina and Brazil) (Rúgolo de Agrasar & Puglia 2004). These species are representatives of two grass genera of tropical and subtropical distribution. Proliferating spikelets are described and illustrated, and some implications for the origin of spikelet organs are discussed. Also, a table is included that constitutes a review of those genera of Poaceae where this phenomenon has been elsewhere reported.

MATERIAL AND METHODS

Observations were made since March 2001 in plants kept under cultivation in the "Lucien Hauman" Botanical Garden, Universidad de Buenos Aires (Buenos Aires, Argentina), and voucher specimens are deposited at BAA (Thiers 2017).

MATERIAL EXAMINED

Paspalum ceresia (Kuntze) Chase. Argentina. Buenos Aires, cultivated in the 'Lucien Hauman' Botanical Garden, Faculty of Agronomy, University of Buenos Aires, origin Bolivia, Samaipata. *G. H. Rua s.n.*, 22.II.2001, BAA 24589.

Paspalum stellatum Humb. & Bonpl. ex Flüggé. Argentina. Buenos Aires, cultivated in the 'Lucien Hauman' Botanical Garden, Faculty of Agronomy, University of Buenos Aires, *M. Bonasora s.n.*, 15.VI.2017, BAA 28237. The non-proliferated specimen is under the voucher *M. Bonasora s.n.*, II.2017, BAA 28207.

Thysanolaena latifolia (Roxb. ex Hornem.) Honda. Argentina. Buenos Aires, cultivated in the 'Lucien Hauman' Botanical Garden, Faculty of Agronomy, University of Buenos Aires, from material grown in the Botanical Garden of Rio de Janeiro, Brazil, rhizome brought from India by Mrs D. Schulz, *J. J. Valla s.n.*, 31.X.1989, BAA 21576. — 10.III.2001, *J. J. Valla s.n.*, BAA 24607.

Spikelets of the three species were dissected and observed with a standard stereoscopic microscope.



FIG. 1. — *Paspalum ceresia* (Kuntze) Chase: **A**, specimen with proliferated spikelets (G. H. Rua s.n., BAA 24589); **B**, **C**, inflorescences and spikelets, detail. Scale bars: A, 5 cm; B, 2 cm; C, 1 cm.

RESULTS

In these three species, proliferating spikelets maintain the basic structure of normal spikelets.

Normal spikelets of *Paspalum ceresia* are 2.9-4 × 1.2-1.4 mm. Lower glume is absent; upper glume and lower lemma are

subequal, as long as the spikelets or scarcely shorter; upper glume 3-nerved and lower lemma 2-nerved, densely pilose toward the margins and on the lower back; lower floret absent; upper floret membranaceous with macro and microhairs in their apex, enclosing a perfect flower. Proliferated spikelets are composed of a glume and a sterile lower lemma, both



Fig. 2. — *Paspalum stellatum* Humb. & Bonpl. ex Flügge: **A**, specimen with proliferated and non-proliferated inflorescences (*Bonasora s.n.*, BAA 28207); **B**, normal spikelet, view from the upper glume; **C, D**, proliferated inflorescence; **C**, general view; **D**, detail; **E**, proliferated spikelet, lateral view. Abbreviations: **ll**, lower lemma; **ni**, non-proliferated inflorescence; **pi**, proliferated inflorescence; **ug**, upper glume; **ul**, upper lemma; **up**, upper palea. Scale bars: A, C, 1 cm; B, D, E, 1 mm.

bract-like although more developed than those of normal spikelets, and a fertile floret with lemma and palea strongly over-developed, green-colored (rather than whitish) and differentiated in sheath and blade (Fig. 1A). Later in the fall, the same plant produced completely normal spikelets.

Normal and proliferated spikelets were observed in the same specimen of *Paspalum stellatum* (Fig. 2A). The regular spikelets of *P. stellatum* are disposed in one or two racemes with winged rachises 4-10 mm width (Fig. 2A), whereas the proliferate inflorescence comprises a well-developed raceme with an anomalous rachis 0.5-0.6 mm wide (Fig. 2A) and a second, less-developed raceme with a rachis 0.8-0.9 mm wide and smaller bracts. The normal spikelets are 2.4-3.9 × 1.2-1.6 mm long, villous with long ciliated margins. Lower glume absent, upper glume 2.4-3.9 mm long, (2-)3 nerved, central nerve scarcely visible or absent and the remaining nerves

close to the margins (Fig. 2A, B). Lower lemma glume-like with 2 marginal nerves. Lower palea and lower floret lacking. In contrast, the proliferate inflorescence has a modified lower lemma, upper lemma, and upper palea, which exhibits reversion to the foliage-leaf condition with developed sheaths and blades (Fig. 2C, D). The upper glume is also enlarged (2.8-3.5 mm) and ends in an acute apex (Fig. 2E).

In *Thysanolaena latifolia* the normal spikelets are typically mesotonic, with lower glume 0.5-0.6 mm long and upper glume 0.7-1 mm long, both 1-nerved (Fig. 3A, B). The lower lemma is empty, 1.5-1.7 mm long, 3-nerved (Fig. 3B, C). Glumes and lower lemma membranaceous with purplish tints. Upper lemma *c.* 1.5 mm long, 3-nerved, membranaceous with long macrohairs on both margins (Fig. 3D). Upper palea 0.5-0.6 mm long, 2-nerved and membranaceous (Fig. 3E). Upper flower perfect. Rachilla internode prolonged beyond



FIG. 3. — *Thysanolaena latifolia* (Roxb. ex Hornem.) Honda: **A-E**, normal spikelets; **A**, spikelet, view from the lower glume and lemma; **B**, spikelet, view from the upper glume and fertile floret; **C**, sterile lemma and fertile floret, lateral view; **D**, fertile floret, lateral view; **E**, fertile palea and androecium; **F-H**, proliferated spikelets; **F**, **G**, spikelets in lateral view showing proliferated lower and upper lemmas; **H**, proliferated fertile palea, lodicules, androecium and gynoecium. Scale bars: A-D, H, 0.5 mm; E, 0.2 mm; F-G, 1 mm.

the upper floret, with a reduced empty lemma. Proliferating *T. latifolia* spikelets are similar, but fertile lemma and lower sterile lemma are green and differentiated in sheath and

blade; the fertile lemma is 3.8-4.5 mm long, being the most developed piece within the spikelet (Fig. 3F), with macrohairs *c.* 1 mm long, with a bulbous base above surface and distrib-

TABLE 1. — Extended list of pseudoviviparous spikelets occurrence in the Poaceae (based on Vega & Rúgolo de Agrasar 2006). The generic classification follows Judziewicz *et al.* (2000), and Soreng *et al.* (2003 and onwards).

Subfamily	Genera	References
Chloridoideae Kunth ex Beilschm.	<i>Bouteloua</i> Lag. <i>Eleusine</i> Gaertn. <i>Eragrostis</i> Wolf <i>Muhlenbergia</i> Schreb.	Hill (1982) Martínez Crovetto (1945) Martínez Crovetto (1944, 1945) Morden & Hatch (1986)
Panicoideae A. Braun	<i>Cenchrus</i> L. <i>Digitaria</i> Haller <i>Ichnanthus</i> P. Beauv. <i>Isachne</i> R. Br. <i>Ischaemum</i> L. <i>Panicum</i> L. <i>Paspalum</i> L. <i>Sacciolepis</i> Nash <i>Setaria</i> P. Beauv. <i>Sorghum</i> Moench <i>Thysanolaena</i> Nees	Schmelzer (1997, as <i>Pennisetum</i> Rich.), Milton <i>et al.</i> (2008), Bhowmik & Datta (2014), Penzig (1922), Martínez Crovetto (1945), Arber (1965) Rendle (1899), Vega & Rúgolo de Agrasar (2006) Martínez Crovetto (1945) Desai & Raole (2013) Ma <i>et al.</i> (2006) Martínez Crovetto (1944) Martínez Crovetto (1944), this paper De Gennaro (2011) Nygren 1954; this paper (Quarin pers. comm.) Arber (1965) this paper
Pooideae Benth.	<i>Agropyron</i> Gaertn. <i>Agrostis</i> L. <i>Alopecurus</i> L. <i>Arrhenatherum</i> P. Beauv. <i>Briza</i> L. <i>Bromus</i> L. <i>Cynosurus</i> L. <i>Dactylis</i> L. <i>Deschampsia</i> P. Beauv. <i>Festuca</i> L. <i>Koeleria</i> Pers. <i>Lolium</i> L. <i>Melica</i> L. <i>Phleum</i> L. <i>Poa</i> L. <i>Polypogon</i> Desf. <i>Sesleria</i> Scop. <i>Trisetum</i> Pers.	Wycherley (1954) Arber (1965), Moore & Doggett (1976) Wycherley (1954) Arber (1965) Martínez Crovetto (1944) Nielsen (1941), Martínez Crovetto (1945, 1947) Penzig (1922), Martínez Crovetto (1945), Arber (1965) Martínez Crovetto (1947), Arber (1965) Nygren (1949), Arber (1965), Chiapella (2000) Nielsen (1941), Martínez Crovetto (1945), Arber (1965), Moore & Doggett (1976) Martínez Crovetto (1947) Martínez Crovetto (1947) Arber (1965) Martínez Crovetto (1945) Arber (1965) Martínez Crovetto (1944), Wycherley (1953), Arber (1965), Moore & Doggett (1976), Aiken & Darbyshire (1984), Pierce <i>et al.</i> (2000b, 2003) Roalson & Allred (1997) Kuzmanović <i>et al.</i> (2012) Arber (1965)

uted in both marginal zones; upper palea 0.3-0.4 mm long, membranous (Fig. 3H). An upper perfect flower is developed. A rachilla extension is accompanied by a distal lemma totally transformed in a leaf with leaf sheaths *c.* 1 mm long, ligule, and blades *c.* 4.5 mm long. In the distal portion of the same panicle, anomalous spikelets occur which are provided with a fertile flower in the axil of the third lemma and one or two additional empty lemmas. Such anomalous spikelets bear normal, bract-like lemmas (Rua 2003).

Previous bibliographic search, as well as subsequent reports, provides an extending list of genera of Poaceae where the phenomena of pseudovivipary and vivipary have been documented (Table 1). The 33 genera belong to subfamilies Pooideae, Panicoideae, and Chloridoideae, according to representativeness.

DISCUSSION

Flower reversion involves a switch from floral development back to vegetative development. It can be considered as an unusual event, linked to environmental conditions that are

opposite to those that induce flowering, so flowering becomes a phase in an ongoing growth pattern rather than a terminal act of the meristem (Tooke *et al.* 2005).

Studies have shown that there are two ways in which pseudovivipary occurs, namely the proliferation of the spikelet axis or the modification of the lemmas (Tooke *et al.* 2005). Indeed, Wang *et al.* (2010) reported two different mutants in rice, showing these two mechanisms and the role of OsMADS1 as one of the lemma identity genes. Gene expression studies in rice revealed that leafy cotyledon gene (OsLEC1) interacts with several MADS proteins, affecting the development of leaves, panicles, and spikelets, being a key regulator of meristem identity determination in both vegetative and reproductive development (Zhang & Xue 2013). However, additional evidence is needed to clarify in which ways those genes interact with MADS and regulatory pathways, to get a better understanding of the factors that trigger pseudovivipary.

The new cases of pseudovivipary here reported correspond to the second case since they comprise modification of the lemmas which become similar to foliage leaves. In the case of *Thysanolaena*, the proliferation of the spikelet axis further occurs in the distal anomalous spikelets.

The three cases reported were observed in plants grown under cultivation in a location far away from the place where they naturally grow. It would be interesting to know whether cases of pseudo-vivipary occur in these species in their natural habitats. Reporting each case of pseudo-vivipary is important to gather more evidence meanwhile further research in gene expression is being undertaken to have a complete understanding of this phenomenon.

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