Development and Structure of the Grass Inflorescence

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Abstract This work presents the basics for interpreting the adult inflorescence structure in grasses. It provides an analysis of the variations in the grass inflorescence structure and their correlation with some of the developmental processes that give origin to it.

Keywords Poaceae · Grasses · Inflorescence · Structure · Development

Introduction

The grass family is one of the largest families of angiosperms. It includes approximately 10 000 species and 600–700 genera (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). Its taxa have been morphologically distinguished by differences in inflorescence and spikelet morphology, among other characters (Clayton & Renvoize, 1986). The grass inflorescence may be composed of one, a few or many spikelets arranged in different ways: panicles, racemes or spikes of spikelets. These types of inflorescences are not adequate for the characterization of the multiple variations of the grass inflorescences (Gould & Shaw, 1983; Clayton & Renvoize, 1986). The term "panicle" is too imprecise to describe the diversity of the branching system in these inflorescences (Kellogg, 2006). Many works have raised this problem (Vegetti, 1991, 2000; Cámara Hernández & Rua, 1992; Vegetti & Weberling, 1996; Rua & Weberling, 1998; Vegetti & Anton, 2000; Reinheimer & Vegetti, 2008) and have also highlighted the real complexity of the grass inflorescence (Kellogg, 2006). These works show that grasses exhibit an extensive variation in adult inflorescence forms; in addition, other works show that grasses have diverse inflorescence developmental patterns even when they have similar mature inflorescence morphologies (Doust & Kellogg, 2002; Kellogg, 2006; Reinheimer et al., 2009).

In view of this, this work aims at: a) stating the basics for interpreting inflorescence structures in Poaceae and their variations; and b) correlating such information with the various developmental processes that give origin to those structures. It must be noted that this work does not intend to comprise all of the variations occurring in the inflorescence structure in the Poaceae, but it includes the most relevant types.

The Structure of the Plant and its Floriferous Shoots

The grass plant is composed of shoots of consecutive branching order (Moore & Moser, 1995). One of the shoots is the main axis of the plant and the others are axillary shoots (innovations = basal branches = tillers) generated in the basal zone of short internodes (SIZ) or iterative innovation zone (Rua & Weberling, 1998). The axillary shoots may develop and flower within the same vegetative period as their parental axis, or their branch development may be substantially delayed relative to the development of the parental axis (Cámara Hernández & Rua, 1992). These are silleptic innovation shoots or catalyptic innovation shoots, respectively. In most grasses, basal axillary meristems grow out to produce a highly tillered plant, although the buds are still under hormonal and environmental control (Shimamoto and Kyozuka, 2002; McSteen, 2009). In maize (*Zea mays*), basal axillary buds remain suppressed during development, leading to a single axis of growth (Kiesselbach, 1949). However, in favourable environment and in absence of neighbouring plants, a modern elite maize variety displays a large amount of branching (Moulia et al., 1999).

During the vegetative phase, the apical meristem of each of these axes generates leaves and shoots and, following floral induction, the terminal inflorescence (tIn). In some species, branching in the zone of long internodes (LIZ) of this axis is restricted (Fig. 1A). However, in certain other species, the axillary meristems of vegetative leaves of this zone sprout facultatively (Fig. 1B, C); they form axillary shoots (enrichment shoots = paraclades of the trophotagma) (Vegetti & Weberling, 1996; Rua & Weberling, 1998; Vegetti & Müller-Doblies, 2004). Each of these axillary shoots bears a prophyll, a variable number of leaves, and ends in an inflorescence (axillary inflorescence). Accordingly, there are species with terminal inflorescences only (Fig. 1A) and others with both terminal and axillary inflorescences (Fig. 1B, C).

When the terminal inflorescence is highly reduced, increased development from the axillary buds of the vegetative leaves occurs, whether from the SIZ, producing more innovations, and/or from the axillary buds of the LIZ, increasing the development of floriferous shoots bearing axillary inflorescences (Vegetti, 1994, 1999; Rua & Weberling, 1998).

A special character is present in the SIZ and LIZ of some Poaceae species, such as *Cottea pappophoroides* Kunth, and species of *Enneapogon* N. A. Desv. ex P. Beauv. In the enrichment axes of these species, the axillary bud of the leaves develops cleistogamous spikelets that are enclosed in the leaf-sheath (Campbell et al., 1983; Tivano & Vegetti, 2004, 2009).

Some authors refer to the innovations as basal branches and to the enrichment shoots as axillary branches (Doust et al., 2004). As both types of shoots are generated
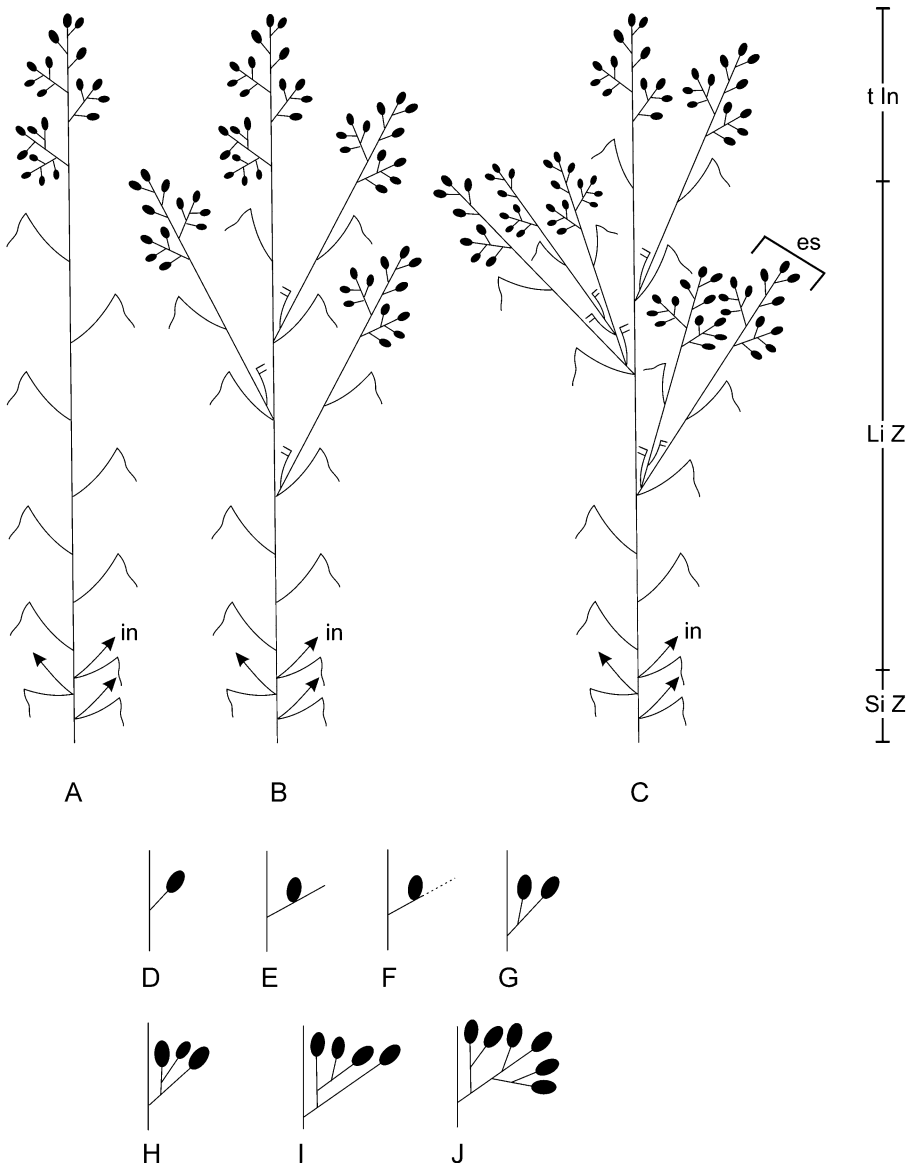
Fig. 1 Some variations in the structure of the grass inflorescences. References: es, enrichment shoot; in, innovation shoot; LIZ; long internode zone; SIZ; short internode zone;tIn, terminal inflorescence. Explications in the text

in the axillary bud of leaves located at different shoot levels, both types of axes are axillary branches, which makes it impossible to restrict the use of this term to only one of the types of shoots.

According to Rua and Weberling (1998), the occurrence of iterative innovation makes the differentiation between enrichment shoots and iterative innovation shoots somewhat artificial, since both types become in fact the ends of a variation continuum.

Doust et al. (2004) showed that tillering and enrichment shoots in *Setaria* P. Beauv. were controlled by distinct loci. Because of this, they argue that these results support their use as independent taxonomic characters.

Enrichment Shoots

Enrichment shoots are present in floriferous shoots of some grasses (Vegetti, 1999, 2000; Reinheimer & Vegetti, 2004; Reinheimer et al., 2005). Their development can be more o less repressed (Mühlberg, 1965, 1967; Rua & Gróttola, 1997) and their reaction norm shows great amplitude among different grass species (Fig. 1). The buds of the culm can be repressed thoroughly, so that the floriferous shoots are composed of a terminal inflorescence only. In many cases, however, the development of culm buds is strongly influenced by environmental variables. Sometimes, the branching behaviour of the culm is a valuable taxonomic trait (Vegetti, 1994, 1997a, b, 1998, 1999; Rua & Weberling, 1998).

Depending on whether axillary buds develop or not in the enrichment shoots, these can have different branching patterns. If the enrichment shoots do not branch, the floriferous shoots present a monophyad pattern (Fig. 1B, Souza-Chies et al., 2006). A monophyad pattern, as opposed to a pleiophyad pattern, means that only one branch is formed at a time (Troll, 1964). If the enrichment axes do branch, either a paniculate branching pattern (branches generated from the leaf axillary buds), or a cymose branching pattern (branches generated from the axillary buds of the prophyll) may occur. In Andropogoneae these shoots branch from the axillary buds of the prophylls and of their leaves (Fig. C), thus forming complex branching systems (Vegetti, 1997a, 1997b, 1999).

Grass Inflorescence Structure

During inflorescence development, the apical inflorescence meristem (IM) generates axillary meristems, called branch meristems (BM), which are indeterminate and produce the branches. After several branches are made, the IM switches and generates axillary meristems that produce one spikelet (spikelet meristem, SM), which are determinate (Wu et al., 2009). Finally, the IM generates the terminal spikelet. The identity and determinacy of these different meristem types are controlled by transcription factors (Bortiri & Hake, 2007; Thompson & Hake, 2009). Although hormones have been implicated in the regulation of inflorescence branching, the exact mechanism is unknown (Barazesh & McSteen, 2008; McSteen, 2009).

In a few grasses, the IM does not produce branches, which means the inflorescence has a single terminal spikelet (unispicate inflorescence) (Fig. 2A, Vegetti, 1991; Cámara Hernández & Rua, 1992; Kellogg, 2006). However, in most grasses, the IM produces lateral meristems that may behave either wholly as SMs and, consequently, do not produce branches and end immediately in a spikelet, e.g., *Triticum* L., *Lolium* L., *Brachyelytrum* P. Beauv. (Fig. 2B, C, Cámara Hernández & Rua, 1992; Kellogg, 2006), or partially as BMs and partially as SMs, and then the former go on to branch again (Fig. 2D–N, Cámara Hernández & Rua, 1992; Kellogg, 2006). As a consequence,
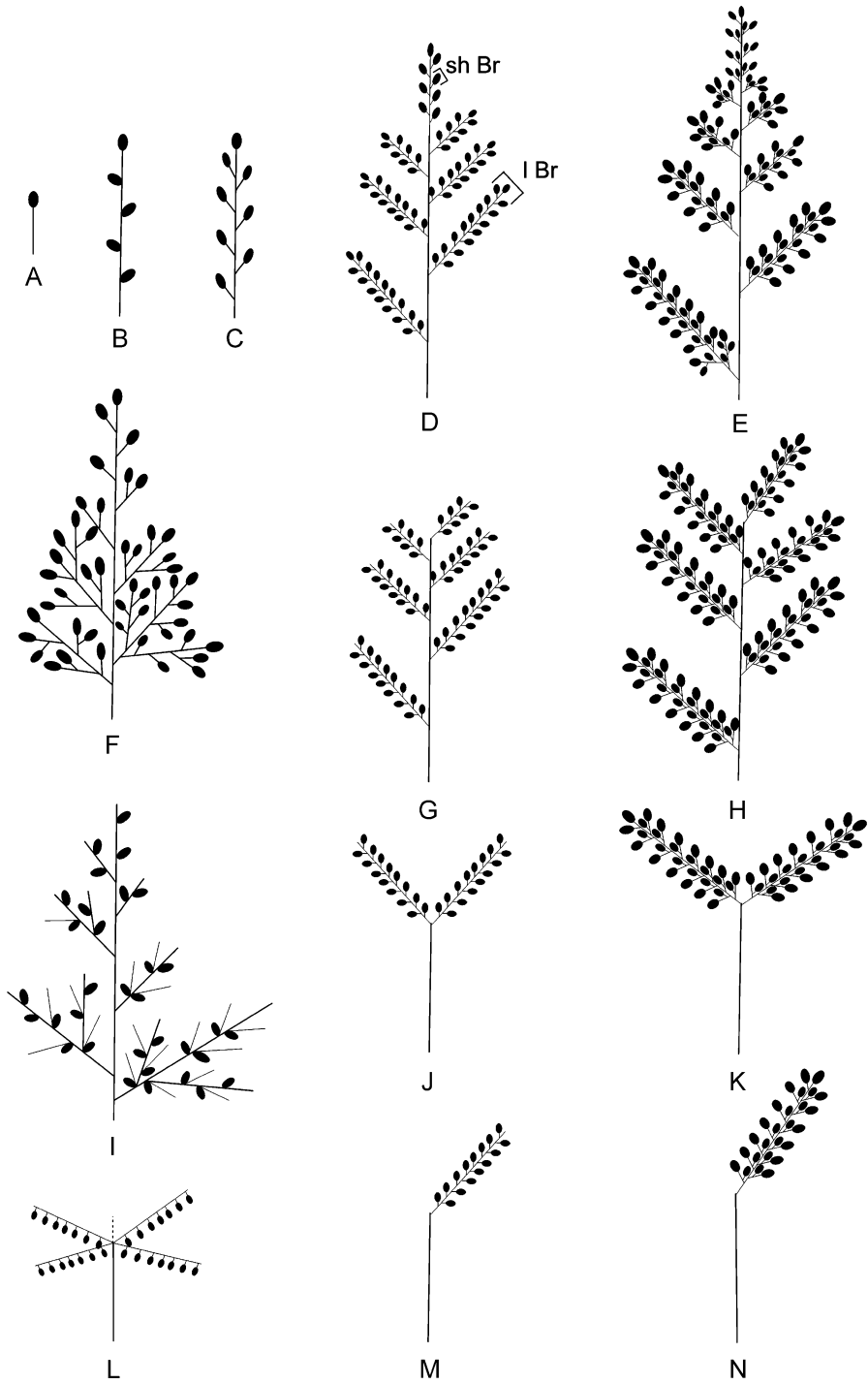
Fig. 2 Variations in the structures of the grass inflorescences and in the short branches. References: shBr, short branch; lBr, long branch. Explications in the text

based on the behaviour of the meristems, the inflorescence may comprise one or several spikelets arranged in a branching system with varying degrees of complexity (Fig. 2).

In unispicate inflorescence (Fig. 2A), the IM lacks axillary meristems. Branching in racemes or spikes of spikelets (Fig. 2B, C) is controlled by two types of axillary meristems: the SM and the floral meristem (FM). Branching in a panicle of spikelets (Fig. 2D–N) is controlled by three or four types of axillary meristems: BM, SM and FM and BM, SPM (spikelet pair meristem), SM and FM, respectively.

Inflorescence Branching

The architecture of the inflorescence depends on its branching pattern and the position of the flowers (Benlloch et al., 2007). The unispicate inflorescence (Fig. 2A) lacks branches and consists of the terminal spikelet only. However, in most species, the meristem forms lateral branches (primary branches). In some grasses (*Lolium, Triticum*), these primary branches are reduced to its terminal spikelet. The internode below the spikelet (pedicel = hipopodium?) may or may not elongate. Then the inflorescence is a raceme of spikelets (Fig. 2C) or a spike of spikelets (Fig. 2B), respectively. In other genera, the primary branches go on to branch again.

There is a gradual transition in the number of spikelets and in the branching order of the inflorescence branches. The branching degree becomes distally reduced and the branches become progressively shorter toward the apex (Fig. 2F)—a pattern established through apical dominance (Bortiri et al., 2006). Therefore, the basal and median branches are branched while the distal branches are not branched and reduced to their terminal spikelet (Vegetti, 2000; Liu et al., 2007; Reinheimer & Vegetti, 2008).

In other genera, most of the primary branches have a lower similar order of branching, except for the very distal ones, which are reduced either to the minimum branching degree or to the terminal spikelet (Fig. 2D, E, G, H, Vegetti, 1991, 1999; Cámara Hernández & Rua, 1992; Gasser & Vegetti, 1997; Rua & Weberling, 1998; Reinheimer & Vegetti, 2008). These inflorescences with many branches of the similar order of branching are homogenized inflorescences (see the following section).

Inflorescence Homogenization Degree

The homogenized inflorescences (Fig. 2D) show the following characteristics: (1) they have long primary branches with similar branching degree; (2) a variable number of these primary branches is seen on the main axis, after which the IM switches abruptly and short branches are observed on the main axis (reduced to one spikelet, a pair of spikelets, or a few spikelets); (3) the long branches have short branches similar to the short branches disposed on the main axis. Thus in homogenized inflorescences, we recognize two types of branches: long branches (lBr = long paraclade) and short branches (shBr, the distal one reduced to the terminal spikelet or with the lowest branching order = short paraclade). The shBrs may be composed of one, two or more axes (Fig. 1D–J) Cámara Hernández & Rúa, 1992; Vegetti & Tivano, 1991; Vegetti, 1991, 1992, 1993a, 1997a, b, 1999; Rúa, 1993; Rúa & Boccaloni, 1996; Rua & Weberling, 1998; Vegetti & Weberling, 1996).

The shBrs composed of one spikelet are considered first-level shBr or haplostachyous-monostachyous branches (Weberling et al., 1993).

Homogenization may be total or partial. When the inflorescence is fully homogenized, all the lBrs are equally homogenized and bear the shBrs. On the other hand, when the inflorescence is partially homogenized, only the distal and median parts of the inflorescence have been affected by the homogenization process, while the basal branches are more extensively branched with respect to the distal and median branches (Rua & Weberling, 1998; Reinheimer & Vegetti, 2008).

In fully homogenized inflorescences (Fig. 2D), the axillary meristems made up by the BMs only form SMs, which, in turn, generate branches reduced to one spikelet. After generating a certain number of primary branches with secondary branches reduced to one spikelet, the IM of the homogenized inflorescence switches abruptly to produce a certain number of branches reduced to their terminal spikelet. The homogenization process is related with the meristem determinancy. The BMs are indeterminate meristems and the SMs are determinate meristems. Indeterminate meristems make an indefinite number of organs, whereas determinate meristems are consumed after making a specific number of organs (Vollbrecht et al., 2005; Bortiri & Hake, 2007).

Homogenization processes have been described in many genera of Panicoideae (Vegetti & Tivano, 1991; Cámara Hernández & Rua, 1992; Rua, 1993, 1996; Vegetti, 1994, 1999; Vegetti & Anton, 1995, 2000; Rua & Weberling, 1998; Cámara Hernández, 2001; Pensiero & Vegetti, 2001; Reinheimer, 2007; Reinheimer & Vegetti, 2008) and Chloridoideae (Vegetti 1986; Cámara Hernández & Rua, 1992; Vegetti & Anton, 1995, 2000; Gasser & Vegetti, 1997; Perreta & Vegetti, 1998; Liu et al., 2005). In Maize, the tassel is a homogenized inflorescence with lBrs and shBrs; and the ear is a homogenized inflorescence without lBrs, fomed only by shBrs.

In Poaceae, the shBrs may be composed of one, two or more axes (Fig. 1D–J) Vegetti & Tivano, 1991; Vegetti, 1991, 1997a, 1997b, 1999; Cámara Hernández & Rúa, 1992; Rúa, 1993; Rua & Weberling, 1998; Rúa & Boccaloni, 1996; Vegetti & Weberling, 1996). The shBrs composed of one spikelet are considered first-level shBr or haplostachyous-monostachyous branches (Weberling et al., 1993).

Homogenized inflorescences have been most widely studied in the tribe Andropogoneae, where, in most genera, the shBrs are composed of two spikelets (spikelet pair = second-level shBrs = diplostachyous-distachyous branches) (Weberling et al., 1993). In these cases, during inflorescence development, the IM produces BMs which generate lBrs. After several lBrs are made, the IM switches abruptly to producing spikelet pair meristems (SPM), which are determinate (Wu et al., 2009).

In Andropogoneae, the shBr consists generally of a short hypopodium (virtual); a prophyll whose axillary bud forms a sessile spikelet; a long epipodium (pedicel); and a pedicellate, generally more reduced spikelet (Vegetti, 1994, 1999). In grasses, the pair of spikelets is a shBr that produces a single lateral meristem and then terminates in a spikelet. The sessile spikelet is lateral and the pedicellate one is terminal (Cámara Hernández & Gambino, 1990; Vegetti, 1994, 1999; Irish, 1997, 1998; Orr et al., 2001; Gallavotti et al., 2004; Vollbrecht et al., 2005; Bortiri et al., 2006; Wu and McSteen, 2007). In the Paniceae tribe, which is sister to Andropogoneae, most species have single spikelets, but a few species produce paired spikelets (Rua & Weberling, 1998; Kellogg, 2000; Kellogg et al 2004; Reinheimer, 2007; Reinheimer

& Vegetti, 2008). Therefore, the paired spikelet appears to be evolutionarily derived (Malcomber et al., 2006).

Sometimes, the shBr may also be composed of more than two axes, as it occurs with *Hordeum* L. (Cámara Hernández & Rua, 1992), *Paspalidium* Stapf (Rua, 1993), *Paspalum haumanii* Parodi (Rúa, 1996) and species of Andropogoneae (*Polytrias* Hack., *Thaumastochloa* C.E. Hubb. (Vegetti, 1999). In some genera of Andropogoneae (*Sorghastrum* Nash, *Asthenochloa* Büse, *Ratzeburgia* Kunth, *Thelepogon* Roth) the pedicellate spikelet is reduced and the shBr is formed either by the sessile spikelet and the pedicel (Vegetti, 1999) or by the sessile spikelet only (Cámara Hernández & Rua, 1992); these later branches are truncated second-degree shBrs (Weberling et al., 1993). Truncation of short branch primary axes is a common feature among several genera of Paniceae (*Setaria*, *Paspalidium*, *Ixophorus* Schltdl.*, Cenchrus* L., *Pennisetum* Rich., etc. (Butzin, 1977, 1979; Rua, 1993; Veldkamp, 1994) and Andropogoneae (Butzin, 1979; Sundberg, 1987; Cámara Hernández & Gambino, 1990; Sundberg & Orr, 1990; Cámara Hernández & Rua, 1992; Schneider & Vegetti, 1992; Vegetti, 1994).

The homogenization process is usually associated with the truncation process (see following section); however, Amsler et al. (2005) and Reinheimer and Vegetti (2008) have described species which undergo homogenization but do not undergo truncation; this usually occurs with partially homogenized inflorescences.

For non-homogenized inflorescences, Reinheimer (2007) and Reinheimer and Vegetti (2008) used the term "distal primary branch" (dBr) to describe those branches with the minimum expression structure, which are immediately below the inflorescence terminal spikelet. There are variations among the different species in the number of dBrs and their branching degree (Reinheimer & Vegetti, 2008).

Presence or Absence of the Distal Part of the Inflorescence

After producing a certain number of branches, the IM generally ends in a terminal spikelet (Fig. 2D–F). In some species, the IM forms a variable number of branches and then stops and does not form the distal floral structures (Fig. 2G–N). The process characterized by the lack of formation of the distal floral structures has been called "truncation" (Troll, 1964; Weberling, 1989). Often, truncation in grasses does not only affect the terminal spikelet, but also the primary shBrs (Fig. 2G, H) and some of the distal lBrs (Fig. 2J–L). Thus, in some cases, a single lBr develops, which, because of its position, appears to be terminal (Fig. 2M, N).

Truncated inflorescences have been described in many genera: *Chloris Sw., Cynodon* Rich., *Eleusine* Gaertn., *Eriochloa* Kunth, *Paspalidium*, *Paspalum* L.*, Setaria, Thuarea* Pers.*, Urochloa* P. Beauv. and genera of Andropogoneae (Bonnett, 1948; Vegetti & Tivano, 1991; Vegetti, 1991, 1994, 1997a,1997b, 1998, 1999; Cámara Hernández & Rua, 1992; Rua, 1993, 1996; Perreta & Vegetti, 1998; Rua & Weberling, 1998; Pensiero & Vegetti, 2001; Doust & Kellogg, 2002; Reinheimer et al., 2005; Liu et al., 2005, 2007; Reinheimer, 2007; Reinheimer & Vegetti, 2008). In grasses, the truncation process is always associated with the homogenization process. Both processes account for much of the diversity among grass inflorescences.

The truncation process may also affect the lBrs, which, as a consequence, do not have terminal spikelets. When this is the case, the lBrs may end in a pseudoterminal

spikelet or the axis may continue to grow to end in a microtip, a bristle (Fig...) or in a foliaceous rachis (Zuloaga et al., 2000; Liu et al., 2007; Reinheimer, 2007).

Branch Disposition and Inflorescence Symmetry

The inflorescence primary branches emerge in an alternate arrangement, one per node; however, some inflorescences show branches with a subopposite or pseudoverticillate arrangement (primary branches disposed in nodes very close around the main axis).

During the vegetative stage, the terminal meristem produces leaves in a distichous phyllotaxis; once the floral induction has taken place, the inflorescence primary branches generally have a spiral arrangement (Bonnett, 1948; Weir & Dale, 1960; Moncur, 1981; Sundberg & Orr, 1996; Doust & Kellogg, 2002; Kellogg et al., 2004; Bess et al., 2005; Ikeda et al., 2005; Itoh et al., 2005; Reinheimer et al., 2005). In other species, the inflorescence primary branches have a distichous disposition (Evans, 1940; Klaus, 1966; Moncur, 1981; Bossinger, 1990; Reinheimer et al., 2005; Kellogg, 2006; Reinheimer, 2007; Reinheimer & Vegetti, 2008). According to Malcomber et al. (2006), spiral inflorescence phyllotaxis is thus very probably ancestral in the grasses, and the distichous arrangement of the inflorescence primary branches appears to be a derived trait.

The verticillate disposition does not correspond with the basic distichy of vegetative structures and is the result of a polistichy in the inflorescence main rachis (Cámara Hernández, 2001). This hypothesis challenges that proposed by Gram (1961) and Vegetti and Anton (1995), who hold the view that such disposition is the result of the inflorescence main axis internodes shortening—a view that has been documented by development studies (Reinheimer et al., 2005; 2009).

As regards the distribution of the inflorescence branches on the main axis, three different types of inflorescence symmetry (Reinheimer et al., 2009) have been characterized for some grass species: (1) spiral symmetry (primary branches are initiated around the main axis); (2) unilateral symmetry (primary branches are formed in two rows on one side of the main axis); and (3) bilateral symmetry (primary branches are initiated on two sides of the main axis).

Inflorescence symmetry remains generally constant within a species. However, different individuals of the same species may have different inflorescence symmetries (Reinheimer & Vegetti, 2008).

Bracts and Leaves Subtending Branches

The axillary meristems (Bms, SPMs and SMs) emerge from axillary buds of a bract primordium. This bract primordium does not develop and generally disappears when spikelets begin to form (Reinheimer et al., 2009). Because of this, the subtending leaf in the mature inflorescence is often so reduced that it is cryptic or invisible (Bonnett, 1948; Long & Barton, 2000; McSteen et al., 2007). Sometimes, a rudimentary leaf primordium is observed at the base of basal branches (Malcomber et al., 2006; Reinheimer et al., 2009).

Thuarea involuta (G. Forst.) R. Br. ex Sm. has a spathaceous bract that encloses the inflorescence. This inflorescence is formed by a single primary branch and the bract is subtending the inflorescence branch (Reinheimer & Vegetti, 2008).

Malcomber et al. (2006) consider that some species, particularly in Bambuseae and in Andropogoneae, develop spathes subtending parts of the inflorescence. In the Andropogoneae inflorescences, the spathaceous bracts are not inflorescence branch subtending bracts, rather, each of them is the distal vegetative leaf located below each inflorescence. Some Andropogoneae show an inflorescence reduction and an increase in the number of enrichment shoots; as a result, numerous leaves appear in the floriferous shoots which do not form the numerous inflorescences (the terminal and axillary inflorescences) (Vegetti, 1994, 1999). These bracts show variations in form, size and colour (Clayton & Renvoize, 1986).

Elongation of Inflorescence Internodes

The internode elongation determines important variations in the external appearance of the inflorescence. The variation of this character can affect the main axis, the branches of consecutive orders and the basal internode between the flag leaf and the node of the most proximal primary branch.

The variations in the elongation of the inflorescence internodes and their consequences are: (1) shortening of the main axis and branch internodes determine dense inflorescences while lengthening of the internodes of both types of axes produce lax inflorescences (Reinheimer & Vegetti, 2008); (2) differential elongation of the basal internode (hipopodium?) of the primary shBrs determines a raceme of spikelets or a spike of spikelets depending on whether the internode has developed or not, respectively (Cámara Hernández & Rua, 1992; Vegetti & Anton, 2000); (3) different types of panicles: (a) with spicate or racemose branches (Vegetti & Anton, 2000); (b) with alternate, subopposite or pseudoverticillate branches (Vegetti & Anton, 2000; Reinheimer & Vegetti, 2008); (c) with branches along an axis with conspicuous intenodes, or with these internodes and two distal ones conjugated or with only two conjugated primary branches (*Paspalum*, Rua & Weberling, 1998; Souza-Chies et al., 2006); (4) panicles with bristles of similar or different lengths (Doust & Kellogg, 2002); (5) panicles with primary branches with short internodes, with the resulting appearance of a central axis surrounded by concentric rings of bristles (*Penisetum* and *Cenchrus*, Doust & Kellogg, 2002) (6) short or long inflorescence peduncle. Enlongation differential of this internode results in the inflorescence being partially covered by the flag leaf, as is the case with some species of Pappophoreae (Tivano & Vegetti, 2004).

Inflorescence with Rudimentary Spikelets or Sterile Branches

Sometimes, the main axis, or the primary axis, or the axis of following order have rudimentary spikelets (Reinheimer, 2007; Reinheimer & Vegetti, 2008). In certain genera, some inflorescence branch meristems become setae or bristles (Fig. 2I). This applies to the bristle clade (Doust & Kellogg, 2002).

Bristles have been interpreted as modified spikelets (Goebel, 1884; Schuman, 1890; Pensiero, 1995, 1999) or modified branches (Schuster, 1910; Arber, 1931, 1934; Sohns, 1954, 1955; Butzin, 1977; Vegetti & Pensiero, 1990; Pensiero & Vegetti, 2001; Doust & Kellogg, 2002). Butzin (1977) holds that the bristle is the sterile end of a partial inflorescence axis. However, not all bristles are the sterile ends

of an inflorescence branch, since it sometimes occurs that a whole branch or most of it become a bristle (Fig. 2I, Pensiero & Vegetti, 2001).

Hypothesized Evolutionary Processes

A comparative analysis of grass inflorescences shows that all grass inflorescences are variations of the same basic structure: the panicle of spikelets or paniculodium (Troll, 1969; Vegetti, 1991; Cámara Hernández & Rua, 1992; Vegetti & Anton, 1995, 2000).

Homogenization and truncation are reductive processes pointed out as the most important evolutionary processes of the inflorescences of Poaceae (Cámara Hernández & Rua, 1992). These processes, at varying levels, produce all types of grass inflorescences (Cámara Hernández & Rua, 1992; Rua & Weberling, 1998) as it was stated by Sell (1969, 1976), Maresquelle (1970) and Kunze (1989) for different Angiosperm groups. Nevertheless, other processes have also contributed to the grass inflorescence variations (Vegetti, 1991, 1994, 1999; Cámara Hernández & Rua, 1992; Rua & Weberling, 1998; Vegetti & Anton; 2000; Kern et al., 2008; Reinheimer & Vegetti, 2008). These processes seem to have taken place, independently or in combination, more than once and in different ways (Vegetti & Anton, 1995, 2000).

Furthemore, it is evident that the reductive processes do not always affect equivalent areas. Indeed, in some cases, it is the proximal part of the inflorescence that has reduced its extension (Fig..), in extreme cases resulting in the survival of the terminal spikelet only (Fig..). In other cases, it is the distal part of the inflorescence that is reduced in a sequence that can affect either the terminal spikelet alone (Fig...), or both the terminal spikelet and the short branches (Fig...). This reduction may also include some of the long branches (Fig.). Thus, in the last stage, a single long branch remains which, because of its position, appears to be terminal (Fig...) (Rua & Weberling, 1998; Vegetti & Anton, 1995, 2000; Reinheimer & Vegetti, 2008).

In Andropogoneae (Fig. 3), the inflorescence is truncated and can be formed either by a subzone of shBrs only (*Trachypogon montufari* (Kunth) Nees, Fig. 3D) or by both a subzone of shBrs and a subzone of lBrs (Fig. 3A–C, G, H). In turn, each floriferous shoot in this tribe may consist exclusively of the terminal inflorescence (Fig. 3A–D) or of the terminal inflorescence and enrichment shoots with axillary inflorescences (Fig. 3E–H). Vegetti (1994, 1999) proposes the following process to determine these variations: (1) reduction of the structure and the number of the inflorescence short branches (the maximum reduction of the subzone of short branches occurs in *Anadelphia trichaeta* Clayton, which consists of just one sessile spikelet and two reduced pedicels, and in some inflorescences of *Cleistachne* Benth., in which the subzone of short branches consists of just one sessile spikelet); (2) reduction of the inflorescence region of long branches, which may be well developed, with different degrees of branching, reduced to a few nodes and a few branches, reduced to just one branch or absent altogether; (3) development of enrichment axes from the axillary buds of the vegetative leaves; which occurs parallel to the reduction of the inflorescence branching system (Fig. 3E–H); (4) increasing branching degree of enrichment axes by development of branches of successive order from the axillary buds of the prophylls and bracts of these axes (Fig. 3F, H); (5) development of a larger number of bracts in the enrichment axis.
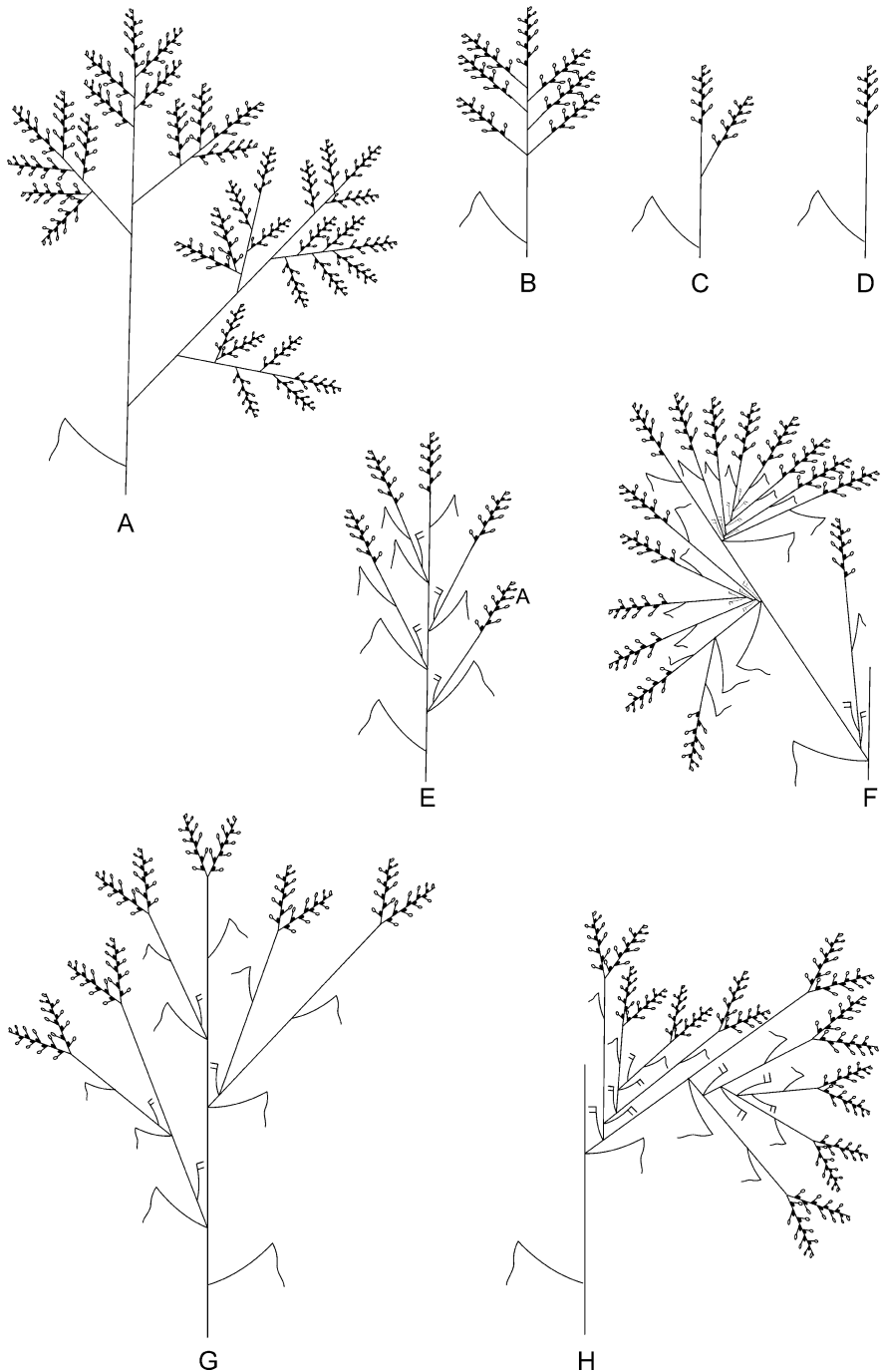
Fig. 3 The inflorescences of Andropogoneae: A, *Eriochrysis cayennensis* P. Beauv.; B, *Agenium villosum* (Nees) Pilger; C, *Ischaemum minus* Presl.; D, *Trachypogon montufari* (Kunth) Nees; E, *Elionurus muticus* (Spreng.) Kuntze; F, *Iseilema membranaceum* (Lindl.) Domin; G, *Andropogon selloanun* (Hack.) Hacker; H, *Andropogon lateralis* Nees

Adult Inflorescence Structure—Developmental Pattern Relation

The inflorescence architecture is determined by the branching process (Benlloch et al., 2007). Branching by axillary meristems is under hormonal, environmental, developmental, and genetic control (McSteen, 2009). Genetic and hormonal factors that regulate the initiation, arrest, and subsequent outgrowth of axillary meristems have been identified (McSteen et al., 2007). In particular, auxin, cytokinin and a new plant growth hormone (strigolactone) have been shown to play a critical role (McSteen & Leyser, 2005; Reinhardt, 2005; Schmitz & Theres, 2005; Beveridge, 2006; Bennett & Leyser, 2006; Shani et al., 2006; Gomez-Roldan et al., 2008; Kyozuka, 2007; Umehara et al., 2008; McSteen, 2009).

Undoubtedly, developmental studies constitute a powerful source of characters that are necessary toward understanding inflorescence morphology and diversification (Doust & Kellogg, 2002; Reinheimer, 2007; Reinheimer et al., 2009).

Initiation and Differentiation of Primary Branches and Relation to the Lack of Formation of the Distal Floral Structures

The initiation and differentiation of the primary branches may be acropetal or basipetal (Reinheimer et al., 2005, 2009; Liu et al., 2007). When the initiation and differentiation of primary branches is acropetal, the IM forms a variable number of branches and, finally, the terminal spikelet (non-truncated inflorescence) (Reinheimer et al., 2005, 2009). When the initiation of the primary branches is acropetal, the IM may stop after the initiation of a variable number of primary branches (Finger Millet clade, Chloridoideae, Liu et al., 2007). In the PCK clade (Panicoideae, Reinheimer et al., 2009), when primary branch initation is acropetal and differentiation is basipetal, the IM stops its activity after generating the most distal branch. In both cases the inflorescences are truncated. However, in some species of the PCK clade (Reinheimer et al., 2009), when primary branch initiation and differentiation is basipetal, the IM stops its activity after the initiation of the first primary branch. In these species, the inflorescence consists of 1-several basitonous lBrs. The terminal meristem does not form a terminal spikelet or short branches (truncated inflorescence) (Reinheimer et al., 2009).

Not much is known about lBr truncation. In the Finger Millet clade in *Microchloa* R. Br., the lBr spikelets are initiated basipetally and end in a microtip (truncated long branch); while in other cases, such as in species of *Cynodon*, the lBr spikelets are initiated amphipetally and end in a terminal spikelet (Liu et al., 2007).

Initiation and Differentiation of Secondary Branches

The initiation and differentiation of secondary branches may be acropetal, basipetal or amphipetal. In the PCK clade (Reinheimer et al., 2009), the primary branches that are acropetally initiated show, in turn, acropetal initiation of the secondary branches; while in the inflorescences with basipetal initiation of the primary branches, the initiation of the secondary branches may be acropetal, basipetal or amphipetal. In the Finger Millet clade (Liu et al., 2007), the secondary branches are initiated basipetally in *Cynodon* and amphipetally in the other genera of the clade.

Homogenization

In species of the PCK clade (Reinheimer et al., 2009) , the acropetal initiation and differentiation of primary branches produces homogenized and non- homogenized inflorescences; while species with basipetal differentiation of the primary branches (regardless of whether initiation is acropetal or basipetal) always show homogenized inflorescences.

Homogenization is related to the meristem determinancy. The sos1, ra1, ra2 and ra3 genes control meristem determinancy on the main axis of the inflorescences and on the lBrs (Vollbrecht et al., 2005; Bortiri et al., 2006; McSteen, 2006; Kellogg, 2007; Wu et al., 2009). Bortiri et al., (2006) argue that these genes reinforce apical dominance by abruptly imposing a determinate fate on lateral organs, causing the switch from lBrs to shBrs (spikelet pairs). As a consequence, they produce homogenized inflorescences.

The phylogenetic placement of spikelet pairs suggests that a novel genetic programme arose in the Andropogoneae to specify the fate of determinate axillary meristems (Bortiri & Hake, 2007). This genetic programme is possibly the key to understanding the formation of homogenized inflorescences in all the grasses.

The raceme of spikelets and the spike of spikelets are homogenized inflorescences without lBrs. The determinancy affects all of the axillary meristems generated in the IM.

Inflorescences with only Differentiation of Terminal Spikelet (No Branch Formation)

A very few species have inflorescences reduced to one spikelet. A mechanism similar to the one that determine whether the apical meristem of the inflorescence branch becomes a spikelet es responsible for the IM not developing axillary meristems (or BM, SPM, or SM) and acting only as SM generating the terminal spikelet. The unispicate inflorescences are one case of determinancy, too; the determinancy affects the IM.

Inflorescence Symmetry

Reinheimer et al. (2009) have correlated the acropetal initiation of primary branches with the presence of a determinate symmetry type; and the basipetal initiation of primary branches with an unstable simetry, that is, the existence of different types of symmetry among inflorescences within one species. Kellogg (2006) considers that the variations observed in the phyllotaxis of the primary inflorescence branches and in the inflorescence symmetry should be further looked into in future developmental studies.

Elongation of Internodes

The differential elongation of internodes occurs late in development, after all branching has occurred and spikelets are largely formed (Bess et al., 2005; Doust & Kellogg, 2002; Ikeda et al., 2004; Reinheimer, 2007; Reinheimer & Vegetti, 2008; Reinheimer et al., 2009). During the late stages of development, before the inflorescence emerges from the flag leaf, the internodes on the main axis and the branches lengthen on a proportional or differential basis (Reinheimer, 2007). The

elongation process of internodes bears no genetical relation to the branching process (Malcomber et al., 2006; Reinheimer et al., 2009).

Conclusions

The structure diversity of the grass inflorescences may be analized at the terminal spikelet and inflorescence branch level. The most significant variations affect the inflorescence branches and account for the fact that inflorescences be composed of numerous spikelets, arranged in a more or less complex branching system, or consist of a few spikelets or even one spikelet (Vegetti, 1991). Variations at the level of the inflorescence branches are related to:

- number of primary inflorescence branches;
- number of the primary branches in each node: alternate, subopposite or pseudoverticillate branches;
- development degree of the primary branches:

    * reduced to the terminal spikelet;
    * formed by the terminal spikelet and a variable number of branches of consecutive order (only secondary branches or from branches of orden n);
    * only formed by branches of consecutive order (without terminal spikelet);

- different elongation of the internodes
- disposition of the branches of consecutive order.

    Variations at the level of the entire floriferous shoots are:

- absence or presence of enrichment shoots and, accordingly, absence or presence of trophotagma (bracts an prophylls); variability in the development of bracts and in the number of bracts on each enrichment shoot;
- variations in the development degree of the buds of the bracts and prophylls in the enrichment shoot.

To establish a suite of characters to deal satisfactorily with general inflorescence form, we recommend to focus on determining the zones and regions of the grass floriferous shoots, paying special attention to the inflorescence and the existence of enrichment shoots of the trophotagma. The following traits must be looked for in the inflorescence: (1) presence or absence of the terminal spikelet of the main axis; (2) presence or absence of the terminal spikelet of the branches; (3) homogeneization degree; (4) characteristics of the subzone of short and long branches (in homogenized inflorescences) or of the distal and non-distal branches (in non-homogenized inflorescences); (5) number of primary branches; (7) branching degree; (8) arrangement of the branches of different order and inflorescence symmetry.

With respect to the structure of the enrichment shoots of the trophotagma, the following traits must be looked for: (1) presence or absence of the prophyll and bracts; (2) number of bracts; (3) development of the axillary buds of the prophylls and additional leaves.

In studying the evolution of morphological diversity of the grass inflorescences in large clades, the combination of developmental and mature structure studies is

essential—this will contribute to a more detailed interpretation of the family's different genera inflorescences as well as to a description of a larger morphological variability. Such studies will contribute to establishing new characters that may be useful in future taxonomic and philogenetic analyses.

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