

Trophotagma Enrichment Axes in Poaceae

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Abstract This review is intended: (1) to interpret and characterize morphological variations observed in the structure of the enrichment axes, located below the terminal inflorescence in Poaceae; and (2) to study the relationship between the intensity of development of such axes and the size of terminal inflorescence. An important reduction in the development of the terminal inflorescence is generally accompanied by a significant development of enrichment axes. It is necessary to adequately characterize these enrichment axes, differentiating them from the terminal inflorescence. Since the intensive development of enrichment axes in synflorescences of many grass genera has caused misinterpretations of the inflorescence structure, to include them as parts of the terminal inflorescence.

Keywords Synflorescence · Terminal inflorescence · Lateral inflorescence · Enrichment axes · Grasses

Introduction

It has been observed in some genera of the Poaceae the development of a variable number of floriferous axes below the terminal inflorescence. These shoots are enrichment axes that end in lateral inflorescences generally similar to the terminal inflorescence (Vegetti & Weberling, 1996). In studies of inflorescences it is necessary to characterize the structure of the entire shoot (=synflorescence) and its integration to the architectural pattern of the entire plant (Troll, 1964; Weberling, 1989; Vegetti, 1991). This allows the clear delimitation between the terminal inflorescence and the enrichment axis located below (Perreta et al., 2009).

In Poaceae, the species with reduced inflorescences often present an important development of floriferous shoots. These may appear just below the terminal

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inflorescence, and/or be produced by basal nodes which increase the number of axes bearing inflorescences (Vegetti, 1999; Perreta et al., 2009; Tivano et al., 2009).

This review is intended: (1) to interpret and characterize the morphological variations observed in the structure of enrichment axes, located below the terminal inflorescence in Poaceae; and (2) to study the relationship between the intensity of development of such axes and the complexity of the terminal inflorescence.

The Structure of the Grass Plant and its Floriferous Shoots

The grass plant is composed of shoots of consecutive branching order (Moore & Moser, 1995). In perennial species each of these shoots is a synflorescence (Vegetti, 1991; Perreta et al., 2009). One of these shoots is the main axis of the plant and the others are axillary shoots (innovations = basal branches) generated in the basal zone of short internodes or iterative innovation zone (Rua & Weberling, 1998). During the vegetative growth, the apical meristem of each of these axes produces leaves and internodes, then generates the terminal inflorescence (tIn) and finally the distal internodes begin to elongate. Only in a few species the elongation of internodes is prior to the formation of the inflorescence. After the emergence of the terminal inflorescence, three zones can be recognized in the axis: the short internodes zone (SIZ), the long internodes zone (LIZ), and tIn. The SIZ and the LIZ form the so-called trophotagma; and the tIn the antherotagma or inflorescence unit (Fig. 1) (Troll, 1964; Vegetti & Müller-Doblies, 2004).

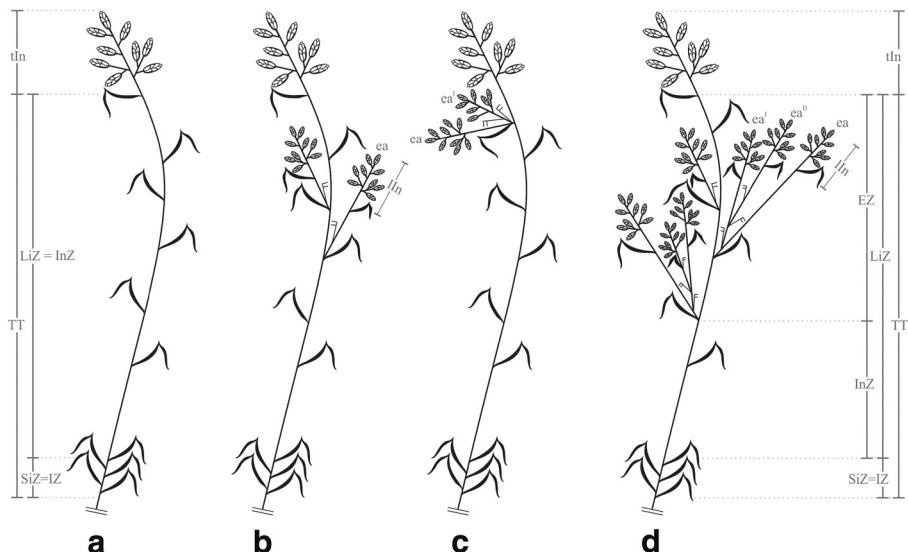


Fig. 1 Some variations in the structure of the grass synflorescences: **a**, Synflorescence without trophotagma enrichment axes; **b**, Synflorescence with unbranched trophotagma enrichment axes; **c**, Synflorescence with branched trophotagma enrichment axes in the more distal leaf (flag leaf); **d**, Synflorescence with branched trophotagma enrichment axes in the distal leaves (except on the flag leaf). References: ca-ca^{II}, enrichment axes of branch consecutive order; EZ, enrichment zone; InZ, inhibition zone; IZ, innovation zone; LIZ, long internode zone; In, lateral inflorescence; SIZ, short internode zone; tIn, terminal inflorescence; TT, trophotagma. **a**, **b** and **d**, modified from Perreta et al. (2009); **c**, modified from Amsler & Vegetti (1999)

In the Chloridoideae subfamily is common to found heteroblastic axes with alternance of LIZ with SIZ that form pseudovercils of leaves (Jacques-Felix, 1961).

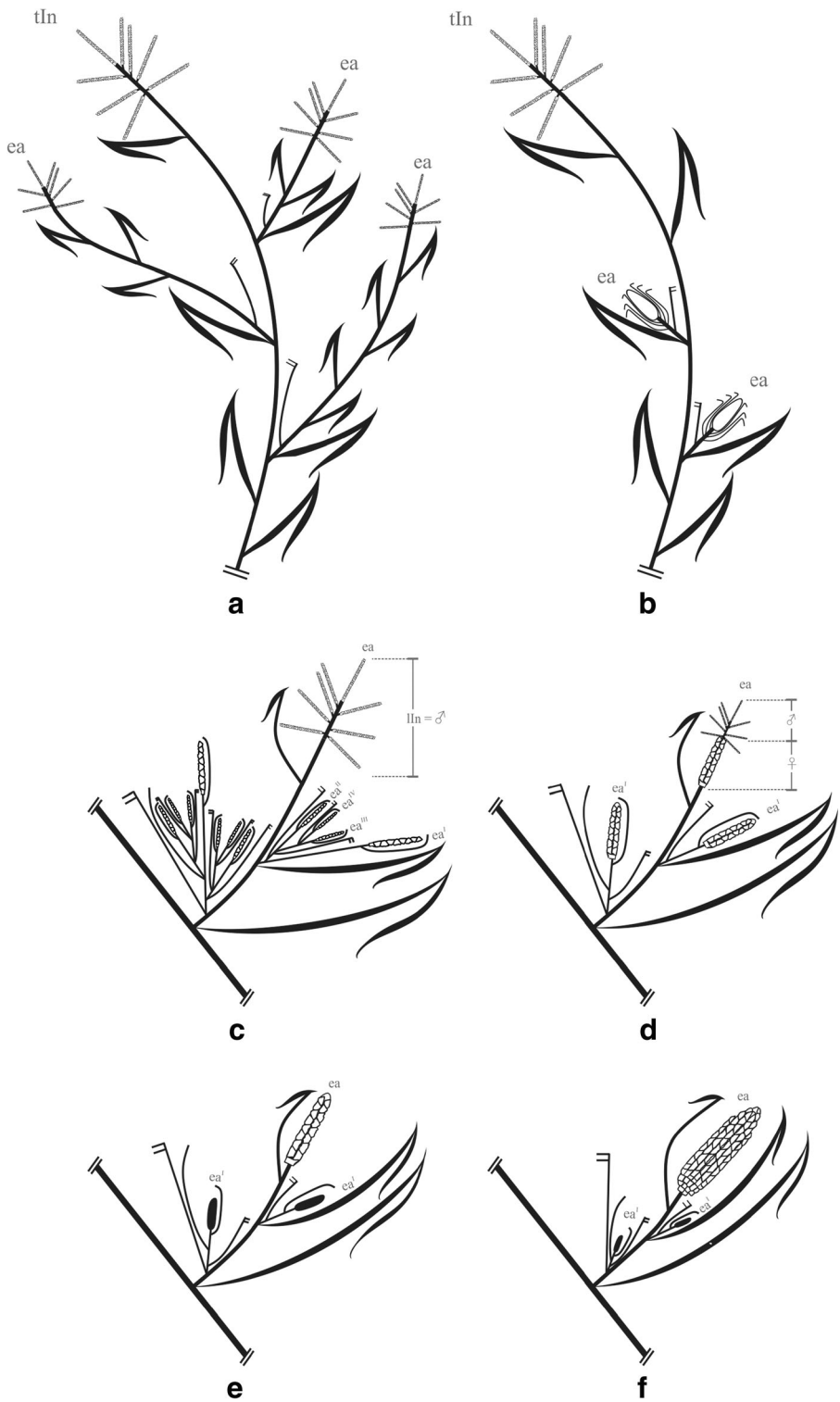
In most grasses, the inflorescence is easily identified as the product of the shoot apical meristem after the transition to flowering, and is a discrete structure that is terminal on the culm (Kellogg, 2015). In some species, the branching in the LIZ of this axis is restricted, thus acting as an inhibition zone (InZ, Fig. 1a), and the culm has only one terminal inflorescence. However, in other species, all or some of the axillary buds of vegetative leaves of the LIZ sprout facultatively (Fig. 1b-d); they generate axillary shoots (trophotagma enrichment shoots = paraclades of the trophotagma = trophotagma branches = axillary branches) (Vegetti & Weberling, 1996; Rua & Weberling, 1998; Doust et al., 2004; Vegetti & Müller-Doblies, 2004; Pilatti, 2016). If only occurs in some leaves, then the LIZ behaves as both an inhibition and enrichment zone (EZ, Fig. 1b-d). It acts only as an enrichment zone when all the leaves produce enrichment axes (Amsler et al., 2005; Perreta et al., 2011). When the LIZ produces axillary enrichment axes the synflorescence presents not only terminal but lateral inflorescences (Fig. 1b-d).

The Grass Trophotagma Enrichment Axes

The trophotagma enrichment axes bear a variable number and types of leaf structures, but always end in an inflorescence (lateral inflorescence, lIn). In most taxa they bear a prophyll and a variable number of leaves (Fig. 1b, d) (Vegetti, 1994; Vegetti & Weberling, 1996; Vegetti & Müller-Doblies, 2004); in some genera of Oryzaceae they bear only prophyll (Fig. 1c) (Vegetti, 1997c; Amsler & Vegetti, 1999; Weber & Vegetti, 2001). In most cases, these lateral inflorescences are similar to the terminal inflorescence. Nevertheless an important variation is presented in the synflorescence of species of *Zea* L. (Andropogoneae-Poaceae) (Fig. 2) in which some of the lateral inflorescences are morphologically different to the terminal one (Cámara Hernández & Gambino, 1990; Iltis, 2000; Wills et al., 2013).

Troll (1964) called enrichment axis or paraclade to each branch within an inflorescence. These enrichment axes must be differentiated from the trophotagma enrichment axes studied in this review. The enrichment axis or paraclade of an inflorescence is a branch of the inflorescence and does not possess leaf structures (except those that form the spikelets); meanwhile, trophotagma enrichment axis is a shoot with leaf structures and ends with an entire inflorescence. Studies in *Setaria* P. Beauv species showed that the branches of an inflorescence and the trophotagma enrichment axes are controlled by different genes (Doust et al., 2004). Based on these results, the authors support its use as an independent taxonomic character.

Doust et al. (2004) treated the trophotagma enrichments axes as axillary branches. But basal branches (formed in the SIZ) and the trophotagma enrichment axes (formed in the LIZ) are generated in the axillary bud of leaves located at different levels of the trophotagma of the main axis. This makes it impossible to restrict the use of “axillary” to only one type of branches (Perreta et al., 2011). Consequently, it is important to identify both types of branches clearly and unmistakably, because they play different roles within the plant and differ not only in their position in the axis but also in the time of emergence. During vegetative growth, tillers or innovation axes develop acropetally from the basal nodes and the buds that give origin to them develop early. By contrast,



◀ **Fig. 2** Synflorescence in species of *Zea* L.: **a**, Sinflorescence in *Zea diploperennis* Iltis, Doebley & R. Guzmán; **b**, Synflorescence in *Zea mays* L. ssp. *mays*; **c**, Diagram of one trophotagma enrichment axis in the synflorescence of *Zea diploperennis* Iltis, Doebley & R. Guzmán; **d-f**, Some proposed steps to explain the changes of the teosinte synflorescence into that of maize. References: ea-ca^{IV}, enrichment axes of branch consecutive order; tIn, terminal inflorescence. Explanations in the text. **a** and **c** modified from Cámara Hernández and Gambino (1990); **d** and **e**, modified from Iltis (2000)

trophotagma enrichment axes only grow when flowering occurs in the main axis that bears them (Doust et al., 2004). Besides, they develop basipetally and the meristems that give rise to them show a delayed development (McSteen & Leyser, 2005).

The trophotagma enrichment axes may or may not be produced. If they are present, they can arise of axillary buds located at different levels of the LIZ (Perreta et al., 2011): (1) in the distal leaves in some genera of Andropogoneae (Fig. 3e-g) (Vegetti, 1994, 1999); (2) in leaves located in the middle portions of the LIZ, as in *Melica sarmentosa* Nees (Perreta & Vegetti, 2006), *Bothriochloa pertusa* (L.) A. Camus (Vega & Vegetti, 2000) and many species with plagiotropic-growing axes (Rua & Weberling, 1998) (Fig. 3b); (3) in the basal leaves, with an inhibited zone in the medial and distal portions, as in the flowering shoots of *Melica macra* Nees (post-generative shoots: Perreta & Vegetti, 2004) and in many species of the genus *Paspalum* L. (Rua & Gróttola, 1997; Rua & Weberling, 1998); and (4) in every leaves of the LIZ, which occurs very rarely, e.g. in some species of *Panicum* L. sect. *Monticola* Stapf (Amsler et al., 2005) and in *Bothriochloa hybrida* (Gould) Gould (Vega & Vegetti, 2000). It should be noted that, in species where the trophotagma enrichment axes develop in the distal leaves, the axillary bud of the more distal leaf (flag leaf) generally does not develop (Vegetti, 1999; Vega and Vegetti, 2000; Vegetti & Müller-Doblies, 2004). Rarely though, in a few species of Poaceae, such axillary buds may also generate trophotagma enrichment axes (Fig. 1c) as in *Rhynchoryza subulata* (Nees) Baillon (Oryzoideae) (Amsler & Vegetti, 1999) and *Paspalum apiculatum* (Panicoideae, Rua & Weberling, 1998). In *R. subulata* (Fig. 1c) the axillary bud of the prophyll of the enrichment axis generated by the flag leaf, may set a secondary enrichment axis and so on, always with prophyllar origins (Amsler & Vegetti, 1999).

The promotion or repression of lateral meristems located in the LIZ, that seem to be coordinated by environmental variables, fluctuates sometimes within the same species giving us specimens with axillary production and specimens lacking it (Rua & Gróttola, 1997; Rua & Weberling, 1998). In other species a permanent inhibition or promotion of these meristems is registered (Rua & Gróttola, 1997; Vegetti, 1994). In these last cases the proliferation of trophotagma enrichment axes occurs at upper culm nodes. In some species, such as many Andropogoneae, the trophotagma enrichment axes always form in the distal region of the LIZ (Vegetti, 1999). These trophotagma enrichment axes next to the terminal inflorescence have often been confused with the inflorescence itself (Clayton, 1969, 1972; Mathews et al., 2002). In Andropogoneae, the set of terminal inflorescence and trophotagma enrichment axes next to it were considered often as the inflorescence and referred to as “false panicle” (Clayton, 1969, 1972; Clayton & Renvoize, 1986). Only the ultimate unit (terminal inflorescence) should be strictly considered the true inflorescence (Vegetti, 1999; Kellogg, 2000, 2015). In the so-called “false panicle” of Andropogoneae, the subtended leaves and prophylls have been described as “spathes” and “spatheolas” by grass taxonomist (Clayton, 1969, 1972).

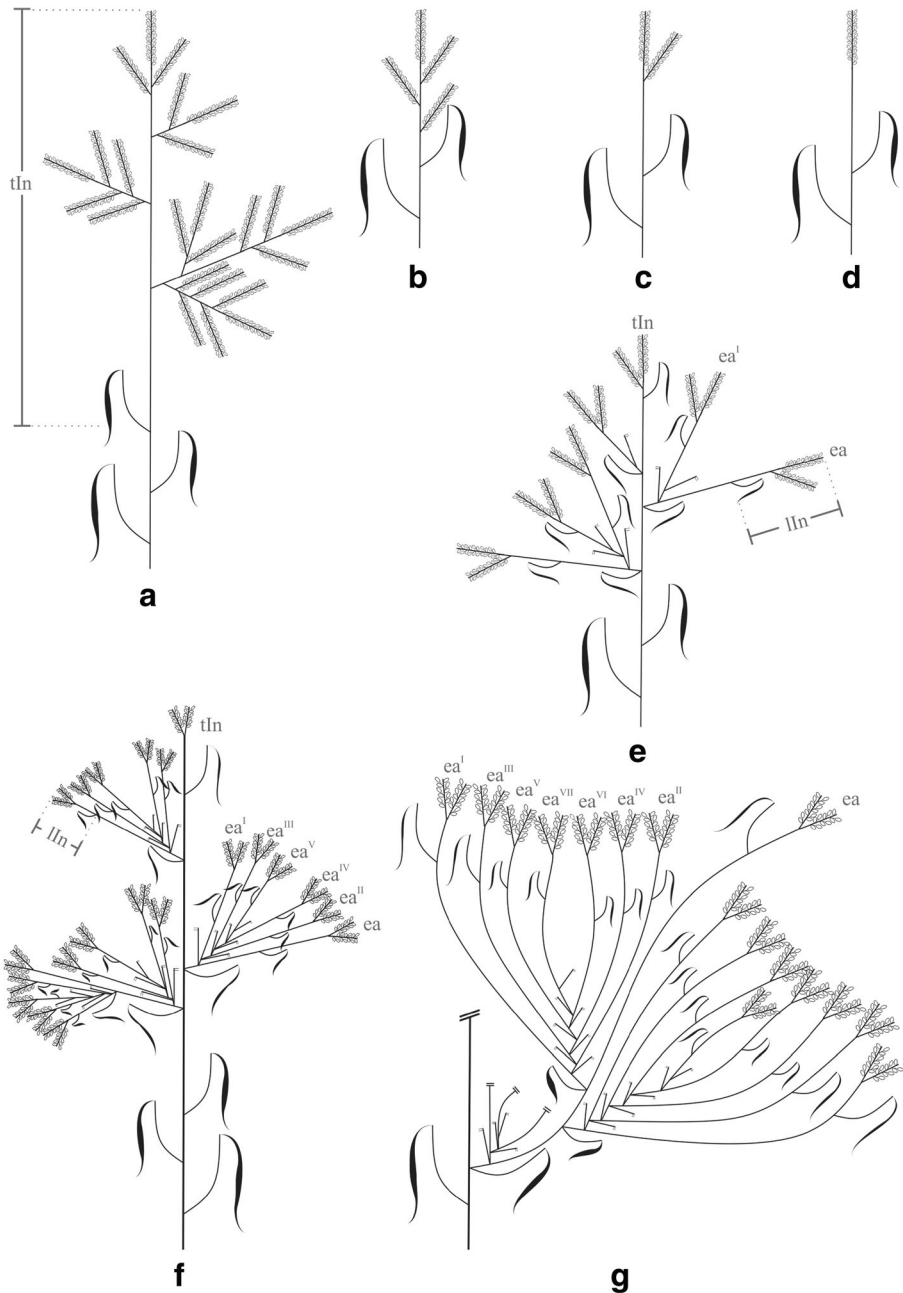


Fig. 3 Variations in Andropogoneae synflorescence: **a**, *Imperata brasiliensis* Trin.; **b**, *Agenium villosum* (Nees) Pilger; **c**, *Ischaemum minus* Presl.; **d**, *Trachypogon montufari* (Kunth) Nees; **e**, *Andropogon selleanus* (Hack.) Hack.; **f**, *Andropogon bicornis* L.; **g**, *Hyparrhenia rufa* (Nees) Stapf. References: ea-ea^{VII} enrichment axes of branch consecutive order; lIn, lateral inflorescence; tIn, terminal inflorescence. Modified from Vegetti (1999)

Each developing axillary bud of a prophyll can generate a complex branching system formed by enrichment axes of consecutive orders with their respective prophylls: a

“rhipidial cymose branch system” (Gram, 1961; Jacques-Felix, 1961; Cámara Hernández & Gambino, 1990; Vegetti, 1994).

The trophotagma enrichment axis is an open structure with potential for development of new enrichment axes from axillary buds of the bracts and prophylls (Vegetti, 1994, 1999). Regularly, the branches from the axillary buds of leaf structures carry enrichment axes in their own trophotagma, forming sometimes complex branching systems (Figs. 1d; 2c, d; 3e-g) (Cámara Hernández & Gambino, 1990; Vegetti, 1994, 1999; Iltis, 2000). As each of these branches ends in an inflorescence, the trophotagma enrichment axes increase the number of inflorescences on each culm. Depending on whether the axillary buds of the trophotagma enrichment axis leaf structures develop or not, these can have different branching patterns: (1) trophotagma enrichment axes without branches (Fig. 1b); (2) trophotagma enrichment axis with a paniculate branching pattern (branches generated from the leaf axillary buds); (3) enrichment axis with a cymose branching pattern (branches generated from the axillary buds of the prophyll, Fig. 1c, d) and (4) enrichment axis with a paniculate and a cymose branching pattern (Figs. 2c, d; 3f, g) (Vegetti, 1999; Perreta et al., 2009). In these last branching patterns, as occurs in Andropogoneae, the branches are generated from the axillary buds of the prophylls and leaves (Fig. 3f, g) thus forming extremely complex branching systems (Vegetti, 1994, 1997a, b, 1999). In these systems the prophylls, in particular, are highly relevant for the understanding of the branching pattern (Bugnon & Bonnard, 1966; Calderón & Soderstrom, 1973).

Distribution of the Trophotagma Enrichment Axes in Poaceae

Watson and Dallwitz (1992), describing the characteristics of inflorescences of Poaceae genera, indicate: “*comprising or not comprising partial inflorescences and foliar organs*”. This means that the terminal inflorescence is accompanied or not by trophotagma enrichment axes (with the corresponding subtending prophyll, leaves and the lateral inflorescences of these axes). These authors characterized, with the statement “*comprising partial inflorescences and foliar organs*”, those genera that have a permanent promotion of the trophotagma enrichment axes.

The presence of trophotagma enrichment axes forming floriferous units together with the terminal inflorescence varies in different grass subfamilies. In Pooideae, the LIZ behaves only as inhibition zone. Consequently, each culm has only one inflorescence (tIn) and no trophotagma enrichment axis (Kellogg, 2015). An exception in this subfamily is the species of *Cornucopiae* L. which has trophotagma enrichment axes (Watson & Dallwitz, 1992). In Bambusoideae and Andropogoneae (Panicoideae), the trophotagma enrichment axes are frequent (Vegetti, 1999; Kellogg, 2015). Permanent promotion of the trophotagma enrichment axes are also observed in a few genera of Chloridoideae: *Blepharidachne* Hack., *Calamagrostis* Adans, *Dasyochloa* Willd. Ex Rydb., *Jouvea* E. Fourn., *Munroa* Torr. and in some species of *Bouteloua* Lag., *Muhlenbergia* Schreb., *Buchlōe* Engelm. and *Crypsis* Aiton (Watson & Dallwitz, 1992; Pilatti & Vegetti, 2014; Pilatti, 2016), and in some few genera of Paniceae (Panicoideae): *Dichantherium* (Hitc. & Chase) Gould, *Dimorphochloa* S.T. Blake, *Xerochloa* R. Br., *Zygochloa* R. Br. and some species of *Stenotaphrum* Trin. and *Streptostachys* Desv. (Watson & Dallwitz, 1992).

Some species of Andropogoneae lack trophotagma enrichment axes (Fig. 3a-d), presenting only one terminal inflorescence that can display many long primary branches highly branched (*Saccharum* L., *Sorghum* Moench, *Vetiveria* Bory), moderately branched (*Bothriochloa* Kuntze, *Sorghastrum* Nash, *Imperata* Cirillo) (Fig. 3a), display a few primary branches as in *Ischaemum minus* J. Presl., *Agenium villosum* (Nees) Pilg., *Trachypogon spicatum* (L. f.) Kuntze and *Trachypogon canescens* Nees (Fig. 3b, c) or a very small inflorescence formed exclusively of short branches (*Trachypogon montufari* Nees) (Fig. 3d) (Vegetti, 1994, 1998, 1999). In others Andropogoneae, the trophotagma enrichment zone is formed in the distal portions of the main axis in the LIZ. In these species, parallel to the reduction of long branches at the terminal inflorescence level, there is a development of the trophotagma enrichment axes from the axillary buds of the leaves located in the LIZ (Fig. 3e-g). This zone can cover a few or numerous nodes of the main axis. The primary trophotagma enrichment axes have variable branching degree, from axes with only primary long branches (e.g. *Elionurus muticus* (Spreng.) Kuntze, *Rhytachne subgibbosa* (C. Winkl. Ex Hack.) and *Coelorhachis selloana* (Hack.) A. Camus, to others with tertiary, quaternary, fifth or higher order (e.g. *Coelorhachis aurita*, *Schizachyrium microstachyum* (Desv. Ex Ham.) Roseng. Arrill & Izag., *Andropogon bicornis*, *Andropogon lateralis* Nees, *Themeda quadrivalvis* (L.) Kuntze and *Hyparrhenia rufa* Fig. 3g) (Vegetti, 1994, 1997a, b, 1999).

Zea species (Andropogoneae) present extremely specialized trophotagma enrichment axes with some lateral inflorescences morphologically different to the terminal inflorescence (Fig. 2). In *Zea diploperennis* Iltis, Doebley & R. Guzmán, the terminal inflorescence is a pure staminate panicle (tassel). The primary trophotagma enrichment axes display a pure staminate inflorescence or mixed inflorescences with a variable form (a panicle or a spike-like raceme) and different relative number of staminate and pistillate spikelets. The secondary trophotagma enrichment axis has mixed panicles or mixed spike-like racemes. The tertiary and quaternary trophotagma enrichment axes end in a pure distichous pistillate spike (Fig. 2a, c) (Cámara Hernández & Gambino, 1990). Teosinte (*Z. mays* ssp. *parviglumis* Iltis & Doebley) present several long trophotagma enrichment axes that branch from their leaf structures. These lateral branches bear multiple small ears at their nodes and tassels at their tips (Wills et al., 2013). In maize (*Zea mays* L. ssp. *mays*) the terminal inflorescence is a panicle of staminate spikelets (tassel), and the lateral inflorescence (the inflorescence of each trophotagma enrichment axes) is a spike of pistillate spikelets (ear) (Fig. 2b). In Maize the ears number per plant will depend on the number of nodes of the culm that develop enrichment axes and on its branching degree. The morphological differences between Maize and Teosinte are the result of human selection under domestication (Wills et al., 2013). The domestication consisted in a reduction in the number of trophotagma enrichment axes (ears) and coincidentally a concentration of resources in a single large ear (the primary trophotagma enrichment axis, Fig. 2d-f) (Doebley & Stec, 1993; Iltis, 2000). As a result, the amount of branching and the number, size, sexuality and arrangement of the trophotagma enrichment axes changed drastically in comparison to Teosinte (Fig. 2c-f) (Iltis, 2000). Modern commercial varieties of Maize typically have only one or two ears per plant (Wills et al., 2013) and they are unbranched; therefore the culm presents a unique ear per node. Consequently, the number of ears per plant will depend on the number of axillary buds that are activated on the culm.

The Relationship Between the Intensity of Development of the Terminal Inflorescence and the Trophotagma Enrichment Axes

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 (specially stolons and rhizomes), and/or from the axillary buds of the LIZ, increasing the development of trophotagma enrichment axes (Vegetti, 1994, 1999; Rua & Weberling, 1998; Perreta et al., 2009). The basal branches of the SIZ multiply the number of orthotropic axes (synflorescences) and, consequently, the number of terminal inflorescences. The trophotagma enrichment axes increase the number of lateral inflorescences. Hence, species with reduced inflorescences have two possible mechanisms for increasing the number of inflorescences and consequently the number of spikelets, flowers and fruits of the plant.

In Andropogoneae (Fig. 3) the parallelism between reduction of the terminal inflorescence and the increase of highly branched enrichment axes of the trophotagma has been clearly characterized (Vegetti, 1994, 1997a, b, 1999; Kellogg, 2015). The development of the trophotagma enrichment zone is greater in the species having a very small region of long branches in the terminal inflorescence (*Andropogon bicornis* and *Hyparrhenia rufa*, Fig. 3e-g) or in species with inflorescences in which this region is not developed (*Iseilema*, *Schizachyrium* and *Themeda*). These last taxa present a trophotagma enrichment axes highly branched and a terminal inflorescence with only a region of short branches. This region of short branches can be well developed (*Schizachyrium*) or extremely reduced (*Themeda* e *Iseilema*) (Vegetti, 1994, 1999). In species of Andropogoneae with trophotagma enrichment axes are very difficult to determine which is the terminal inflorescence (Fig. 3e-g).

Parallelism between reduction of the terminal inflorescence and an increase of highly branched trophotagma enrichment axes can also be observed in the species of *Jouvea*, *Blepharidachne* and *Munroa* (Chloridoideae, Anton & Hunziker, 1978; Pilatti and Vegetti, 2016). Trophotagma enrichment axes were observed in all species of *Distichlis* (Chloridoideae) with inflorescences composed by one spikelet (Fig. 4a) (Pilatti, 2016). However, there are some cases where a very small terminal inflorescences (one or a few spikelets) is present but without a conspicuous development of trophotagma enrichment axes, such as in species of *Aciachne* (Vegetti & Tivano, 1991) (Fig. 4b). In these species the lack of trophotagma enrichment axes is compensated with an important development of the innovation zone, meaning new synflorescences for the plant.

In cases where the terminal inflorescence is not reduced the trophotagma enrichment axes may or may not be developed. If they develop they do not form complex distal branching systems and it is easy to infer which one is the terminal inflorescence. Trophotagma enrichment axes of this type were characterized in some genera of Paniceae (Rua & Grotola, 1997; Rua & Weberling, 1998; Reineimer, 2007; Reinheimer & Vegetti, 2008) and Chloridoideae (Pilatti, 2016).

Determining Processes of the Variations in Terminal Inflorescence and Trophotagma Enrichment Axes

In Andropogoneae, Vegetti (1994, 1999) characterized the following processes that determine the variations in the morphology of the terminal inflorescence and the

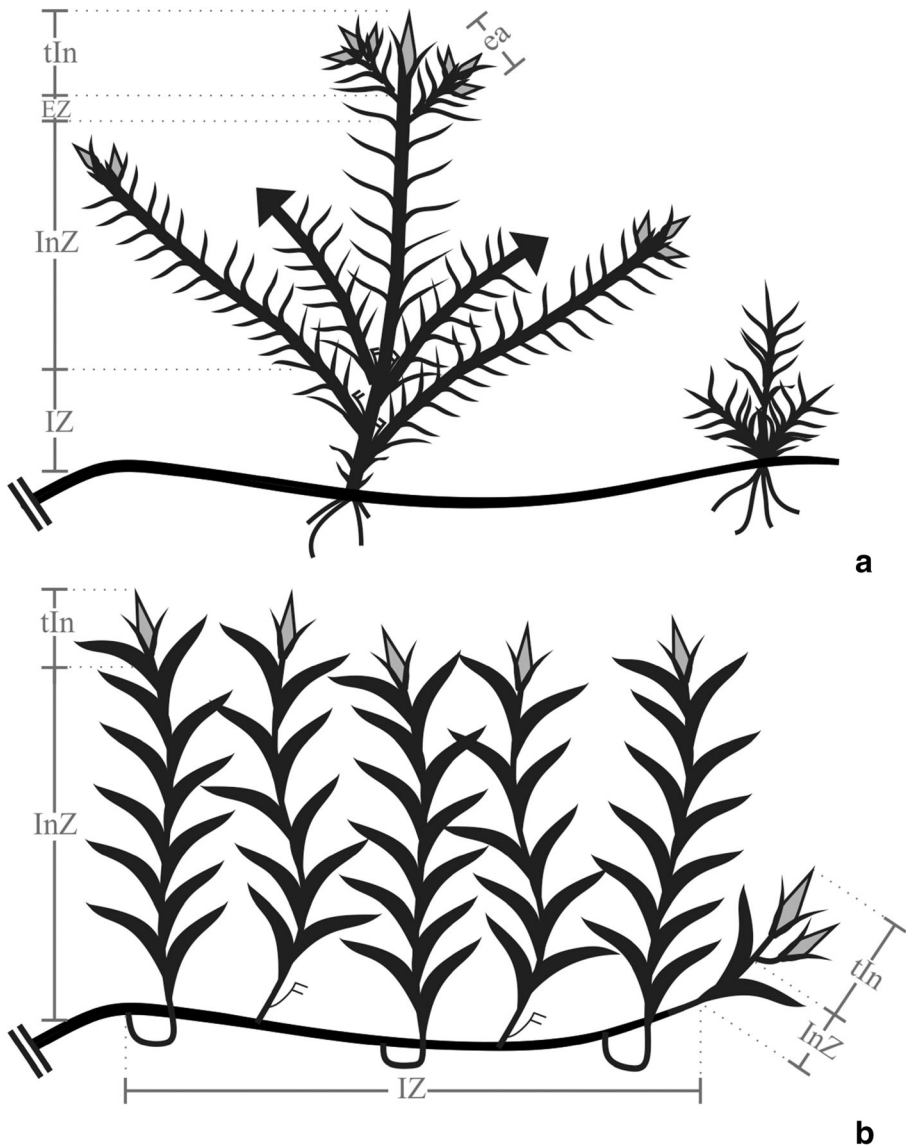


Fig. 4 Synflorescence in *Distichlis acerosa* (Griseb.) H. L. Bell & Columbus (a) and *Aciachne acicularis* Læggaard (b). References: ea, enrichment axis; EZ, enrichment zone; InZ, Inhibition zone; IZ, innovation zone; tIn, terminal inflorescence. a, modified from Pilatti, 2016; b, modified from Vegetti & Tivano (1991)

trophotagma enrichment zone: (1) reduction in the degree of development of the long branches zone of terminal inflorescences (Fig. 3a-d); (2) development of trophotagma enrichment axes from the axillary buds of the distal leaves of the main axis (Fig. 3e); (3) increase of degree of branching of the trophotagma enrichment axes by development from the axillary buds of the prophylls and leaves (Fig. 3e-g); (4) development of a great number of bracts in the trophotagma enrichment axes and the enrichment axes of consecutive branching order from the axillary buds of these bracts .

Many of the possible combinations of these characters determine significant variations in the floriferous shoots of Andropogoneae. This morphological diversity could be controlled by a small group of easily modified genes and/or polymorphs along the evolutionary history of the group (Kellogg, 2000, 2015). Kellogg (2000) states that the trophotagma enrichment axis is a morphological character that changes repeatedly in evolutionary time. Mathews et al. (2002) consider that the Andropogoneae inflorescence form must be fairly easy to modify in evolutionary time and is worth more detailed study. But these authors fail in considering inflorescence all distal floral axes (terminal inflorescence along with the trophotagma enrichment axes of the upper region of the culm). This is why the development of trophotagma enrichment axes is worth of more detailed studies, with many different approaches and techniques.

Genes Related to the Development of Trophotagma Enrichment Zone

Studies on the evolution of maize shoot architecture from its ancestor teosinte identified a branching gene (teosinte branched1, *tb1*) that inhibits axillary bud outgrowth (Doebley et al., 1997). The gene *tb1* encodes a protein belonging to the TCP family of transcription factors (Martin-Trillo & Cubas, 2010) conserved across monocots and eudicots, with orthologues identified in sorghum, rice, wheat, pea, tomato, and Arabidopsis. The *tb1* gene is expressed at a high level in axillary buds during early stages of development and remains high when the buds becomes dormant, whereas *tb1* expression decreases if the bud grows to forms a tiller or a branch (for a review, see Kebrom et al., 2013). Recently, a second transcription factor that regulates branch proliferation was identified in maize. Higher expression of Grassy tillers1 (*gt1*) reduces the number of proliferating branches, and so the ear development, in the trophotagma enrichment zone of maize (Wills et al., 2013). Expression of *gt1*, which encodes a Class I homeodomainleucine zipper (HD-Zip) transcription factor, is controlled by TB1 (Whipple et al., 2011) but it is not clear whether *gt1* is a direct or indirect target of TB1 activity.

While TB1 and GT1 play an important role in integrating light and hormonal signals, several lines of evidence indicate that there must be other factors that regulate bud outgrowth (Kebrom et al., 2013). The study of these and other factors regulating axillary branching in species different from crops will help to shed light in understanding the widely morphological variety observed in the development of the enrichment zone in Poaceae.

Conclusions

It is essential in inflorescences studies: (1) to analyze in detail the structure of the entire culm supporting the inflorescence (= synflorescence) in order to detect the presence or absence of trophotagma enrichment axes; and (2) to characterize the position, structure, quantity and probability of occurrence of these axes.

The presence of permanent promotion of trophotagma enrichment axes is associated with a very small structure of the terminal inflorescence. When this happens, the trophotagma enrichment axes are produced from the axillary buds of the distal leaves.

Maize is an exception to this rule, since its domestication led to a development of a small number of trophotagma enrichment axes emerging from the axillary buds of the leaves located in middle portion of the main axis.

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