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Homogenization and Truncation Processes in Inflorescences of Cyperaceae

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Abstract This work presents an analysis of the homogenization and truncation processes in Cyperaceae inflorescences. The truncation process is rare in Cyperaceae. There may be homogenized inflorescences but in general these inflorescences present a terminal spikelet. In the few studied cases of truncated inflorescences in Cyperaceae the truncation process may affect the terminal spikelet, only on the main axis and on the long primary branches (species of Cariceae, species of *Lipocarpha* and *Ascolepis*), or it may also affect the short branches on the main axis (some species of *Kobresia*; *Cyperus giganteus*, *C. papyrus* and *C. prolifer*) and on the primary long branches (*Cyperus giganteus*, *C. papyrus* and *C. prolifer*). The homogenized inflorescences can be disjunct or not disjunct. The disjunct homogenized inflorescences have a distal portion of short branches and a proximal portion of long branches, which lead in turn as short branches subunits. Meanwhile non-disjunct homogenized inflorescences have only short or long branches, all with the same branching degree.

Keywords Inflorescences · Truncation · Homogenization · Cyperaceae

Variations in the Structure of the Cyperaceae inflorescences

Cyperaceae show a significant variation in the structure of their inflorescences (Haines & Lye, 1983, Goetghebeur, 1998; Vegetti, 2003; Reutemann et al., 2012). The inflorescences in this family (Fig. 1) may consist of many spikelets arranged in a complex branching system, or a few spikelets or even a single spikelet (Haines & Lye, 1983, Vegetti & Tivano, 1991a; Vegetti, 1992, 1994, 2002, 2003; Heinzen & Vegetti, 1994; Goetghebeur, 1998; Browning & Gordon-Gray, 1999; Camelbeke, 2002; Guarise & Vegetti, 2007; Ahumada & Vegetti, 2009; Reutemann et al., 2009, 2012, 2014a, 2014b; Guarise et al., 2012; Lucero & Vegetti, 2012; Lucero et al., 2014; Dellaferrera & Vegetti, 2015).

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The inflorescence results from the activity of its own meristems, which defines the production or loss of iterative structures, and it is finally determined by the number, size and relative arrangement of their branches (Guarise & Vegetti, 2007). Angiosperm inflorescence can be described by a simple and dynamic model of development (Kellogg, 2000). In this model for Cyperaceae, any meristem may have one of these three fates: it may (1) produce indeterminate lateral branches, (2) terminate in a spikelet, or (3) stop the development without forming organs. Again, each of the indeterminate meristems could choose one of these three fates, and so on (Kellogg, 2000). Thus, different inflorescence architecture may be described by the combinatorial patterns of these meristems decisions (Reinheimer et al., 2013).

Early in development, the shoot apical meristem produces only leaves, each of which develops a meristem in its axil. After receiving an endogenous (hormonal) or exogenous (light, heat) signal the meristem acquires the capacity to produce an inflorescence (Colasanti & Coneva, 2009; Wellmer & Riechmann, 2010). As a general model, during inflorescence development, the apical inflorescence meristem (IM) generates bracts and their axillary meristems, called branch meristems (BM), which are generally indeterminate and produce the inflorescence branches. After several branches are produced, the IM switches and generates axillary meristems that produce one spikelet (spikelet meristem, SM), which is a determinate meristem. Next, the IM may generate or not a varying number of bracts whose axillary meristems do not develop and, finally, it generates fertile leaves (glumes) with floral meristems (FM) in their axils, which make up the terminal spikelet.

In Cyperaceae the inflorescence complexity is reduced distally (e.g., paniculodium, decomposed and composed anthelodium, Reutemann et al., 2012; Fig. 1 a). In some species the number of branches and their branching degree are reduced, appearing simple anthelodium, spike of spikelets and fascicle of spikelets (Fig. 1 b-e). In other species, due to lack of development of axillary buds, the inflorescence is reduced to a single spikelet (Fig. 1f).

In Cyperaceae the IM: (1) may produce only one terminal spikelet and the inflorescence lacks branches being formed only by one spikelet; (2) may produce spikelet meristems directly on their flanks, creating a “spike-like” structure or a fascicle of spikelets; (3) or it may produce branches. In this last case, these branches may only produce spikelet meristems (in species with inflorescences reduced to primary branches with secondary spikelets), or they may produce new branch meristems and the inflorescence producing second-, third-, or higher-order branches. Consequently, in the inflorescences of the cases 1 and 2 we recognize two only types of axillary meristems: the spikelet meristem (SM) and the floral meristem (FM). In the inflorescences of the case 3, we recognize three types of axillary meristems: the branch meristem (BM), the spikelet meristem (SM) and the flower meristem (FM). In the branched inflorescences, the fate of the inflorescence meristem is independent of that of the primary-, secondary-, and higher order branches, which may also terminate in spikelets or not (Kellogg, 2015).

As noted by Ikeda-Kawakatsu et al. (2009), the architecture of the branched inflorescence is determined by the precise developmental timing of the conversion of a branch meristem to a spikelet meristem. If the conversion happens early in development, then few higher-order meristems are produced, whereas if conversion from

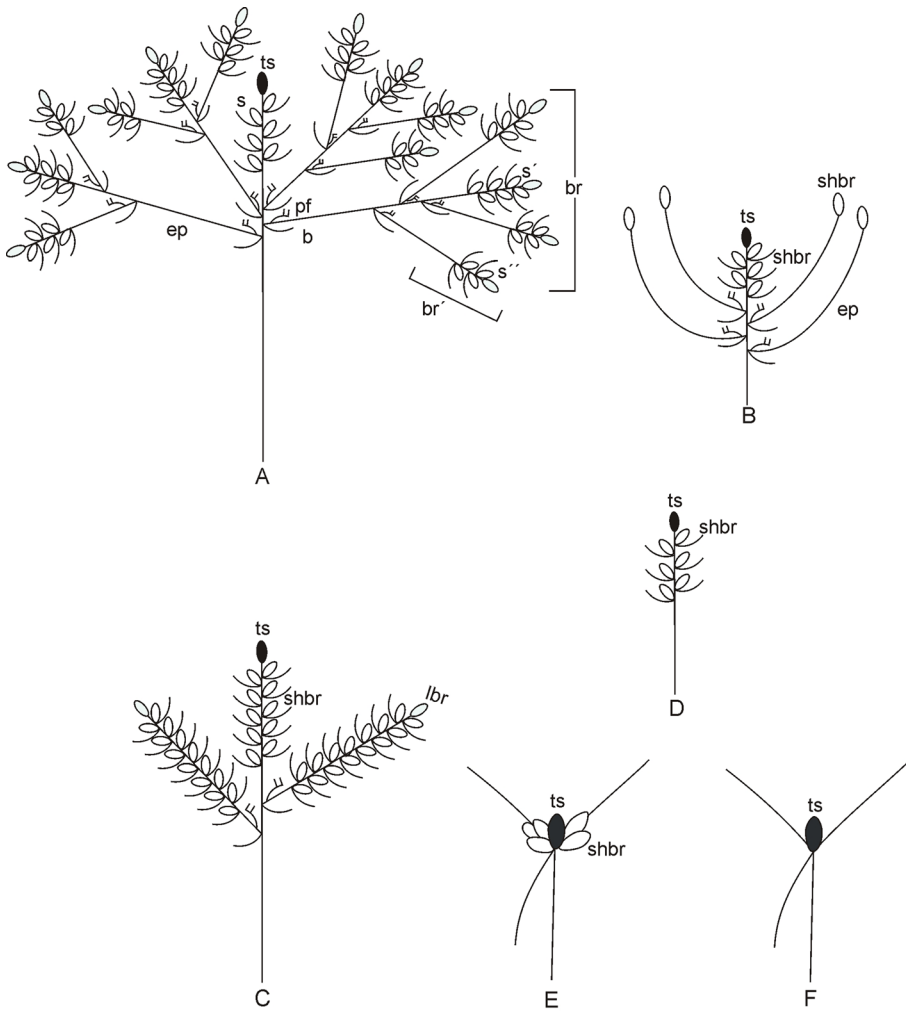


Fig. 1 Diversity of Cyperaceae inflorescences: **a**, Compound anthelodium; **b**, Simple anthelodium; **c**, Compound spike of spikelets; **d**, spike of spikelets; **e**, fascicle of spikelets; **f**, Inflorescence constituted by only one spikelet. References: b, bract; br, primary branch; br', secondary branch; ep, epipodium; lbr, long branch; pf, prophyll; s, primary spikelet; s', secondary spikelet; s'', tertiary spikelet; shbr, short branch; ts, terminal spikelet

branch meristem identity to spikelet meristem identity is delayed, then there is an opportunity for producing more branches (Kellogg, 2015).

Whether branches are produced or not is determined by the fate of the inflorescence meristem, which varies between species and genera (Kellogg 2000, 2006; Malcomber et al., 2006; Perreta et al., 2009). The complexity of the inflorescences is therefore related to the behavior of the IM that can produce branched inflorescences (Fig. 1a, c), simple anthelodium (Fig. 1b), fascicle of spikelets (Fig. 1e), spike of spikelets (Fig. 1d) or unispicate inflorescences (Fig. 1f). The complexity of inflorescences is related: (1) in the branched inflorescences, to the number and branching degree of the primary branches and to the number of primary spikelet meristems developed by the IM before

producing the terminal spikelet; and (2) in the spike of spikelets and fascicle of spikelets, to the number of primary spikelet meristems developed by the IM before producing the terminal spikelet.

This wide diversity shown by the Cyperaceae inflorescences can be explained by the analysis of some processes that operate in different way, combined or independently. These processes and the resulting structures are mainly reductives (Guarise & Vegetti, 2008). Among them, we can mention the homogenization and the truncation processes.

The Homogenization Process

In the Cyperaceae inflorescences the primary branches go on to branch again (Fig. 1a). And generally, there is a gradual transition in the number of spikelets in each inflorescence branch and in the branching order of the inflorescence branches. The branching degree becomes distally reduced and the branches become progressively shorter toward the apex. Therefore, the basal and median branches are branched, while the distal branches are not branched and reduced to their terminal spikelet. In these inflorescences, we recognize the terminal spikelet, a zone of primary branches reduced to the terminal spikelet and a zone of primary branched branches. These last branches generate secondary, tertiary and higher order branches.

Some inflorescences in Cyperaceae present middle and proximal primary branches with similar branching degree; all these branches bearing secondary spikelets (Fig. 1c). They are homogenized inflorescences. Above the homogenized primary branches appear a variable number of branches reduced to their terminal spikelet. This section of the main axis with primary spikelets is similar to the homogenized primary branches. In these homogenized inflorescences, a distal zone of short branches (all of the primary spikelet arranged on the main axis) and a middle and proximal zone of long branches (all of primary branches bearing secondary spikelets = homogenized primary branches) are differentiated.

In order to distinguish branches of various complexity, the terms long and short paracladia (=long and short branches) were applied by Vegetti & Tivano, 1991b as they had been previously used for Dicotyledonous families by Troll (1965) and Weberling (1989). The distinction between long and short branches should be associated with the presence of a discontinuity in the branch series along the main axis of the inflorescence (Weberling et al., 1993, 1997). These authors pointed out that the short branches must be homogeneous and must appear regularly as structural subunits of the long branches.

When short and long branches are distinguished, the inflorescence is disjunct and homogenized (Rua, 1999, Fig. 1c, Fig. 2a, b). If instead, on the main axis only primary spikelets are arranged (as in the spike of spikelets, Fig. 1d and simple anthelodium, Fig. 1b) or long branches are arranged (as in some truncated inflorescences, Fig. 2c), the homogenized inflorescence is non-disjunct. The homogenized inflorescences show disjunction (Fig. 1c, Fig. 2a, b) when an abrupt transition between the proximal portion of an inflorescence, which is provided with long branches and the distal portion, with short branches is presented (Weberling, 1989; Rua & Weberling, 1998).

The homogenization represents a reductive process because the homogenized inflorescence has only primary branches bearing secondary spikelets (i.e. it is primary branches with reduced branching degree Fig. 1c; Fig. 2 a, b). In these homogenized

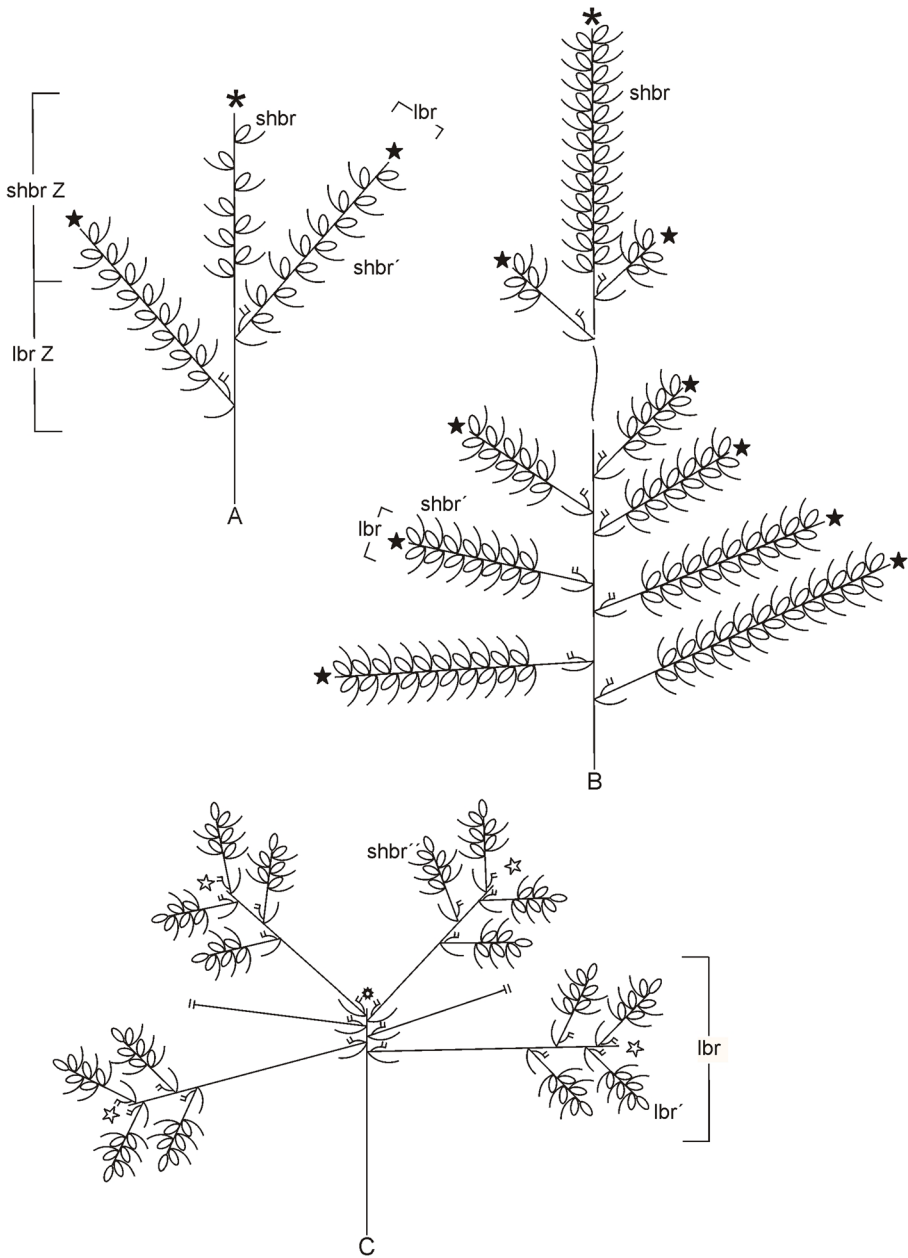


Fig. 2 Truncated Cyperaceae inflorescences: **a** and **b**, truncated spike of spikelet of *Ascolepis brasiliensis* (a) modified of Reutemann et al., 2014a) and *Carex disticha* (b) modified of Kukkonen, 1984); **c**, Truncated anthelodium of *Cyperus giganteus*. References: lbr, primary long branch; lbr', secondary long branch; lbrZ, Zone of long branches; shbr, primary short branch; shbr', secondary short branches; shbr'', terciary short branch; shbrZ, Zone of short branches; *, truncation of terminal spikelet of the main axis; ★, truncation of the terminal spikelet of the long branches; ✱, truncation of the terminal spikelet and zone of primary short branches of the main axis; ✱', truncation of the terminal spikelet and secondary short branch zone of the primary long branches

inflorescences the axillary meristems of 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 abruptly switches to produce a certain number of branches reduced to their terminal spikelet (Fig. 1c, Fig. 2a, b). 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; Kellogg, 2015). The homogenization process of the inflorescence is related to the meristem determinancy (Perreta et al., 2009; Kellogg, 2015). In this sense, the meristem determinancy would guide the degree of homogenization (Salariato et al., 2010).

Truncation Process

The inflorescence truncation process was characterized by Troll (1964) and Weberling (1989). It consists of the lack of formation of the distal floral structures. This process occurs when the IM stops growing: (1) not developed the terminal spikelet (truncation of the terminal spikelet, Fig. 2a, b); (2) before forming the subzone of short branches (= primary spikelets) and the terminal spikelet (truncation of the terminal spikelet and the subzone of short branches, Fig. 2c); or (3) when only a limited number of primary long branches were formed (truncation of the terminal spikelet + subzone of short branches + some long primary branches). In grasses, these truncated inflorescences may have not developed the terminal spikelet of the long branches (Liu et al., 2007; Perreta et al., 2009).

Consequently, the truncation process may affect only the development of the terminal spikelet (Fig. 2a, b), or it may also affect, on the main axis, the development of the subzone of short branches and some long branches (Fig. 2c); and the truncation of the terminal spikelet on the long branches (Fig. 2a, b).

In Cyperaceae inflorescences, after producing a certain number of branches, the IM generally ends in a terminal spikelet forming a non truncated inflorescence (Fig. 1). This non truncated inflorescence can be homogenized (Fig. 1c, d, e) or non homogenized (Fig. 1a). Although truncation is not frequent in this family, a few species show truncated inflorescences. There are reports of truncated inflorescences in two derived tribes of the subfamily Cyperoideae: in the Cariceae tribe (Vegetti, 2002; Reutemann et al., 2012) and in the Cypereae tribe (Reutemann et al., 2014a).

The inflorescence of the Cariceae (Fig. 2b) lacks a terminal spikelet. It is a truncated inflorescence consisting of a region of homogenized distal short branches (“pseudospikelet”) and a variable number of long branches. The latter have no terminal spikelet (truncated long branches) and are composed of a variable number of homogenized secondary short branches. In some species, the inflorescence present truncation of the terminal spikelet and truncation of the homogenized distal short branches. Consequently, it consists only of long branches, as described by *Kobresia macrolepis* Meinsh and *K. pygmaea* (C.B. Clarke) C.B. Clarke (Kukkonen, 1990; Vegetti, 2002).

The main characters of the inflorescences of Cariceae are related with the following reductive processes: (1) a reduction in the development of spikelets, resulting in a single flower or a few flowered spikelet; (2) a homogenization of short branches on the main axis and on long branches and 3) the truncation of the terminal spikelet on the

main axis and on the long branches and in some species the truncation of the homogenized short branches (Vegetti, 2002).

In the Cyperaceae tribe, the truncation has been described in some species of *Cyperus* L. (Perreta & Vegetti, 2002; Vegetti, 2003), *Lipocarpa* R.Br. and *Ascolepis* Nees ex Steud. (Reutemann et al., 2014a). In *Cyperus giganteus* Vahl the inflorescence is truncated (Fig. 2c). The truncation in this species affects the terminal spikelet and the subzone of short branches on the main axis and on the long primary branches (Perreta & Vegetti, 2002). Consequently, the inflorescence consist of one anthelodium with a variable number of long primary branches and long secondary branches with the epipodium developed (Fig. 2c). A similar situation occurs in *Cyperus papyrus* L. (Mora Osejo, 1960; Raynal, 1971; Haines & Lye, 1983) and *Cyperus prolifer* LAM. (Raynal, 1971; Haines & Lye, 1983). It is interesting to point out that even though in *C. giganteus*, *C. papyrus* and *C. prolifer* reduction of distal parts on the main axis and on long primary paracladia have occurred, the inflorescence is richly branched (Perreta & Vegetti, 2002). At the same time, in the inflorescence of *Cyperus papyrus*, the ramification is even more intense for the collateral buds development, generating a fascicle of long branches (Mora Osejo, 1960; Raynal, 1971). These collateral buds are not present in the other two species.

In *Lipocarpa humboldtiana* Nees and *Ascolepis brasiliensis* (Kunth) Benth. ex C.B. Clarke the truncation process affects only the terminal spikelet of the main axis and of the long branches (Fig. 2a). These species have inflorescences formed by one spike of spikelets or by a terminal spike and a reduced number of lateral spikes (Goetghebeur, 1998; Reutemann et al., 2014a). Both, the terminal spike and the lateral spikes, lacking the terminal spikelet, their are truncated (Fig. 2a).

In some families, such as grasses, truncation is a very common process which is frequently associated with homogenization (Vegetti, 1991; Vegetti & Anton, 2000; Reinheimer & Vegetti, 2008; Perreta et al., 2009), and both processes account for much of the diversity among grass inflorescences (Reinheimer & Vegetti, 2008; Perreta et al., 2009). However, while most inflorescences show varying degrees of homogenization in Cyperaceae, truncation is not common in this family. In those few species of Cyperaceae, where truncation does occurs, inflorescences are homogenized (Fig. 2). A similar situation has been reported for grasses in which all truncated inflorescences are homogenized. About this, Weberling et al. (1993) considers that the truncation of the terminal spikelet is generally synchronized with the homogenization of the distal portion of the main axis.

The developmental genetics has been extensively studied in grasses (Kellogg, 2000, 2006, 2007, 2015; Bommert et al., 2005; Vollbrecht et al., 2005; Malcomber et al., 2006; Bortiri & Hake, 2007; Skirpan et al., 2008; Huang et al., 2009; McSteen, 2009; Piao et al., 2009; Thompson and Hake, 2009; Terao et al., 2009; Gao et al., 2010; Kobayashi et al., 2010, 2012; Li et al., 2011). In Cyperaceae there is little research on developmental genetics (Prychid & Bruhl, 2013).

Conclusions

The truncation process is rare in Cyperaceae. There may be homogenized inflorescences, but in general these inflorescences present at terminal spikelet (Fig. 1 c-e). In the

few studied cases of truncated inflorescences in Cyperaceae, the truncation process may affect only the terminal spikelet on the main axis and on long primary branches (species of Cariceae, species of *Lipocarpa* and *Ascolepis*, Fig. 2a, b), or it may also affect the short branches on the main axis (some species of *Kobresia*; *Cyperus giganteus*, *C. papyrus* and *C. prolifer*, Fig. 2c) and on the primary long branches (*Cyperus giganteus*, *C. papyrus* and *C. prolifer*, Fig. 2c). Within Cyperaceae, homogenized inflorescences can be recognized disjunct (Fig. 1b, c, Fig. 2a, b) and non disjunct (Fig. 1d, Fig. 2c).

To establish a suite of characters to satisfactorily deal with general inflorescence form, we recommend to pay special attention in: (1) homogenization degree; (2) characteristics of the subzone of short and long branches (in homogenized inflorescences); (3) presence or absence of the terminal spikelet of the main axis; (2) presence or absence of the short branch subzone on the main axis; (3) presence or absence of the terminal spikelet on the primary long branches; (4) presence or absence of the short branch subzone on the primary long branches.

In studies of the evolution of morphological diversity of the Cyperaceae 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 establish new characters that may be useful in future taxonomic and phylogenetic analyses. In addition to the combination of morphological and developmental structural studies, the realization of development genetics studies would be important in Cyperaceae, by analyzing the genes that determine the homogenization and truncation processes in the family.

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