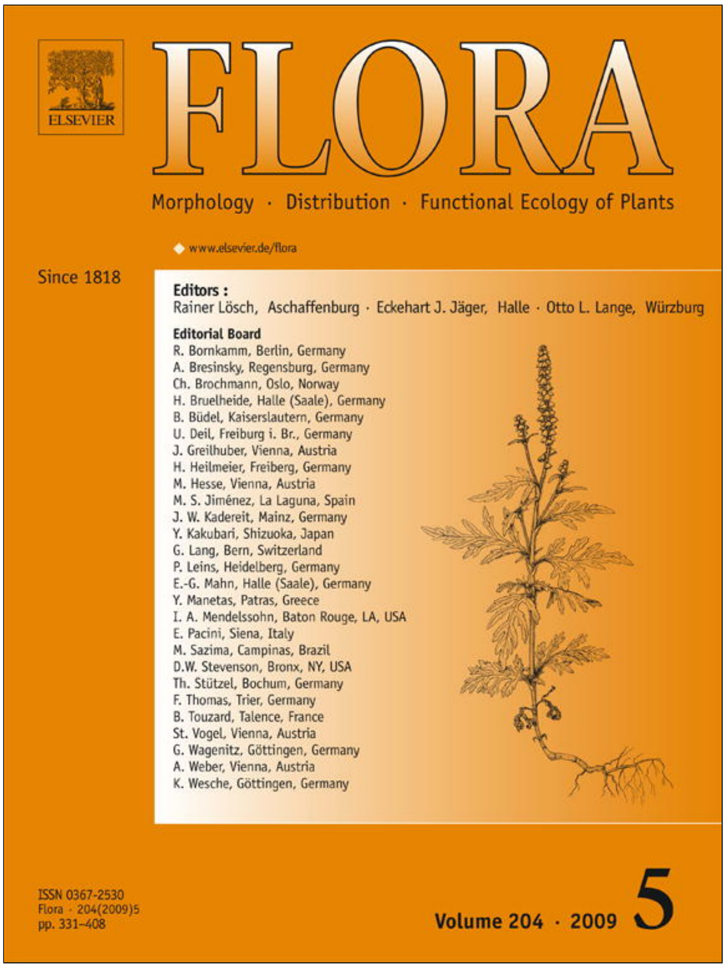
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Types of enrichment axes in Poaceae

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Abstract

The objective of this review work is to characterize the enrichment axes in Poaceae, especially integrating into that analysis of those species with basal or subterranean cleistogamous spikelets. We recognize five types of enrichment axes: paraclades of the unit of inflorescence (UIF), paraclades of the trophotagma (TT) with exposed UIF; paraclades of the trophotagma with not exposed UIF; subterranean paraclades on short rhizomes and subterranean paraclades upon plagiotropic axes of long internodes. According to the enrichment axes, we differentiate six types of synflorescences. The different types of enrichment axes and synflorescences types are characterized; their differences determine in some cases the existence of fruit heteromorphism.

Keywords: Poaceae; Synflorescence; Paraclades; Cleistogamous spikelets

Structure of the Poaceae synflorescence

In Poaceae, the plant is composed of shoots of consecutive order of ramification (Moore and Mooser, 1995). Each one of them is an innovation shoot that normally terminates in an inflorescence. According to the typological system of Troll, each one of these shoots constitutes a synflorescence.

In the synflorescence are recognized as two principal parts (Fig. 1): the unit of inflorescence (UIF) and the trophotagma (TT) (Vegetti and Müller-Doblies, 2004). The UIF can be composed, in polytelic inflorescences such as those of the Poaceae (Cámara Hernandez and Rua, 1991; Cámara Hernández and Miante Alzogaray, 1994; Troll, 1966; Vegetti, 1991) by the main florescence (MF) and paraclades (Pc_{UIF}) of various magnitude that constitute the enrichment zone (EZ) or paracladial zone.

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As long as the trophotagma (Fig. 1) bears proximally cataphylls and foliage leaves, it can be subdivided into a basal zone of short internodes (SIZ) and a distal zone of long internodes (LIZ) (Rua and Weberling, 1998). The LIZ can constitute an inhibition zone (HZ) (characterized by the absence of ramification), an extension of the enrichment zone (EZ) or a region that behaves in part as HZ and in part as EZ (Rua and Weberling, 1998).

In perennial Poaceae, the SIZ behaves principally as an innovation zone. Its buds develop axes of the synflorescence that can grow and flower during the same period as that of the mother axis or can grow and flower in the following period. Thus, these axes are innovation shoots that are sylleptic or cataleptic, respectively (Cámara Hernández and Rua, 1991).

The enrichment axes originating in the distal region of the LIZ normally present a prophyll and developed leaves (trophotagma) (Rua and Weberling, 1998; Vegetti and Weberling, 1996) and terminate in an UIF similar to that of the relative mother axis that supports them.

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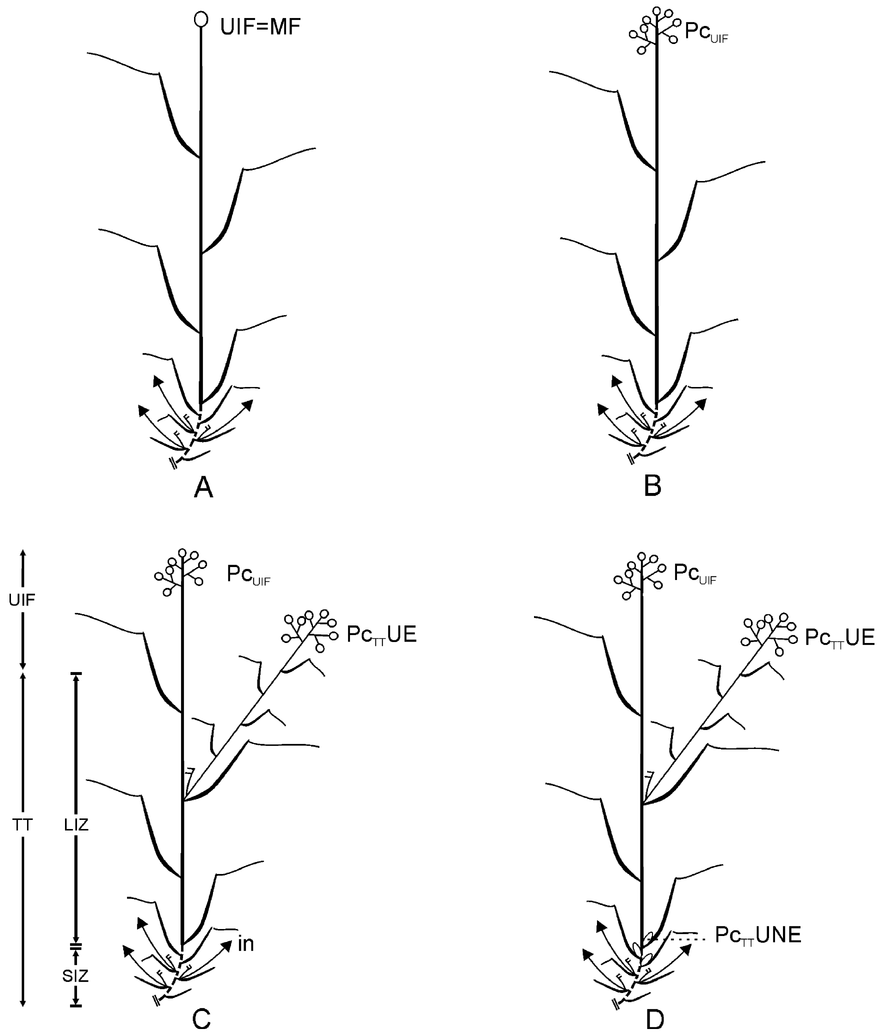

Fig. 1. Types of synflorescences according to the types of enrichment axes present: (A) type 0 synflorescence (S_0); (B) type I synflorescence (S_I); (C) type II synflorescence (S_{II}); (D) type III synflorescence (S_{III}). Abbreviations: in, innovation; LIZ, long internode zone; SIZ, short internode zone; TT, trophotagma; UIF, unit of inflorescence; MF, main florescence; Pc_{UIF}, paraclade of the unit of inflorescence; Pc_{TT}UE, paraclade of the trophotagma of the unit of inflorescence exposed; Pc_{TT}UNE, paraclade of the trophotagma of the unit of inflorescence not exposed. Explications in the text.

These axes have been denominated paraclades of the trophotagma (Vegetti and Müller-Doblies, 2004), long paraclades of second order (Weberling et al., 1993) or paraclades with trophotagma (Vegetti and Weberling, 1996). From the axillary buds of the trophotagma of these enrichment axes, new axes of similar structure can be originated. In this mode, the LIZ can contribute to increase the number of flowering branches of the plant (Rua and Weberling, 1998).

A case of particular interest is constituted by the enrichment axes (or paraclades) of species with cleistogamous spikelets. The presence of axes with cleistogamous spikelets on the aerial part of the shoot was reported for 22 species from 10 genera of Poaceae (Campbell et al., 1983), whereas eight species belonging to four genera of Poaceae (Barker, 2005; Campbell et al., 1983) present cleistogamous spikelets that are subterranean.

The cleistogamous spikelets are hidden in the foliar sheaths along the length of the culm (cleistogenes) or in specialized subterranean rhizomes (rhizantogenes). They are generated in areas that normally do not behave as enrichment zones. For this reason, it is necessary to analyze the total spectrum of the Poaceae branching systems and characterize the shoots that bear these cleistogamous structures (Connor, pers. com.) and specifying their integration into the structural plan of the entire plant.

For the above reasons, the objective of this work is to characterize the enrichment axes in Poaceae, especially integrating into that analysis those species with basal or subterranean cleistogamous spikelets.

Characterization of the types of enrichment axes present in Poaceae

Paraclades of the unit of inflorescence

Paraclades of the Unit of inflorescence (Fig. 1, Pc_{UIF}) are understood in the following in the sense of Vegetti and Müller-Doblies (2004). In a homogenous inflorescence are presented both short and long paraclades such as those described for species of *Paspalum*, *Panicum* s. l. and Andropogoneae (Amsler et al., 2005; Rua and Weberling, 1998; Vegetti, 1999) or only short paraclades such as occur in *Lolium*, *Triticum* and *Secale* (Cámara Hernández and Rua, 1991; Vegetti and Müller-Doblies, 2004) and in *Brachiaria dimorpha, B. epacridifolia* and *B. holosericea* (Reinheimer, 2007), or only long paraclades as they occur in homogenized inflorescences that show truncation of the main inflorescence and of the short paracladia subzone (Liu et al., 2005; Rua and Weberling, 1998; Vegetti and Anton, 1995, 2000).

Paraclades of the trophotagma

Paraclades of the trophotagma (Pc_{TT}) are generated in the trophotagma at the level of the SIZ as in that of the LIZ.

Pc_{TT} of the UIF exposed (Fig. 1C and D, Pc_{TT}UE) are enrichment axes ending in a UIF like the mother axis, with long internodes, a prophyll and a variable number of developed leaves. They usually develop from the axillary bud of some leaves of the LIZ, or less frequently from every axillary bud of the LIZ (as in some species of *Panicum* sect. *Monticola*, Amsler et al., 2005). Within this type, we discern the paraclades of the trophotagma with foliage leaves (present in species of Andropogoneae, $Pc_{TT}+L$, Vegetti and Müller-Doblies, 2004), from those without foliage leaves, only bearing a developed prophyll (present in Oryzeae, Pc_{TT}-L, Vegetti and Müller-Doblies, 2004).

Pc_{TT} of the UIF not exposed (Fig. 1D, Pc_{TT}UNE). Basal enrichment axes that are generally developed in the region proximal to the SIZ that present short internodes, few bracts and a reduced UIF consisting of one to various cleistogamous spikelets, hidden in the foliar sheath. Nonetheless, in some species they can also be present at nodes of the LIZ (species of *Amphibromus*, *Danthonia*, *Muhlenbergia, Stipa* and *Triplasis*, *Enneapogon desvauxi* and *Cottea pappophoroides*, (Campbell et al., 1983; Caro and Sanchez, 1971; Chase, 1918; Cheplick, 1995; Tivano and Vegetti, 2004). Connor (1979) reported several grass species that have Pc_{TT}UNE. This syndrome appears in taxa of the subfamily Pooideae and in the tribe Pappophoreae (Barker, 2005).

Pc subterranean (PcS)

These paraclades are formed on subterranean parts of the innovation shoots or over the creeping or subterranean plagiotropic axes (Fig. 2).

Pc subterranean on short rhizomes (Fig. 2A, PcSRc)

These enrichment axes are formed on a short rhizome (the subterranean region of the short internode zone of the innovation shoots). They are present on the basal part of the innovation zone and consist of a considerably reduced UIF, and are formed by one cleistogamous subterranean spikelet, as it was described for *C. pappophoroides* (Tivano and Vegetti, 2004).

Pc as subterranean plagiotropic axes with long internodes (Fig. 2B, PcSEP)

These enrichment axes are generated in the axillary bud of the cataphylls disposed over plagiotropic shoots with long internodes; they are creeping or subterranean. This type of Pc occurs in *Amphicarpum purshii* Kunth, *A. floridanum* Chapman, *A. muhlenbergianum* (Schult) Hitchc., *Chloris chloridea* (Presl.) Hitchc., *Paspalum amphicarpum* Ekman, and in species of *Eremitis* (Campbell et al., 1983; Kaul et al., 2000). In *P. amphicarpum* paracladia of the stoloniferous axes bear a cymous system of enrichment axes at their prophyllar node, each of them ending in a cleistogamous solitary spikelet. Therefore, these stolon-like shoots "must not be regarded as true "stolons"…, but as "delayed-flowering synflorescences" (Rua and Gróttola, 1997; Rua and Weberling, 1998).

Types of synflorescences referring to the types of enrichment axes

In the synflorescence of Poaceae, the development of the different types of enrichment axes is different, and one or more types of axes can be absent. According to the enrichment axes, it is possible to differentiate the following types of synflorescences (Table 1).

Synflorescence type 0 (S_0, Fig. 1A)

The UIF consists of the main florescence (terminal spikelet) only missing any paraclades within the UIF (Pc_{UIF}). It is uncommon in Poaceae and was characterized for some examples of *Aciachne* (Vegetti and Tivano, 1991).

Synflorescence type I (S_I, Fig. 1B)

This type presents only enrichment axes type Pc_{UIF}. In the LIZ, it behaves like the inhibition zone and in the SIZ like the innovation zone.

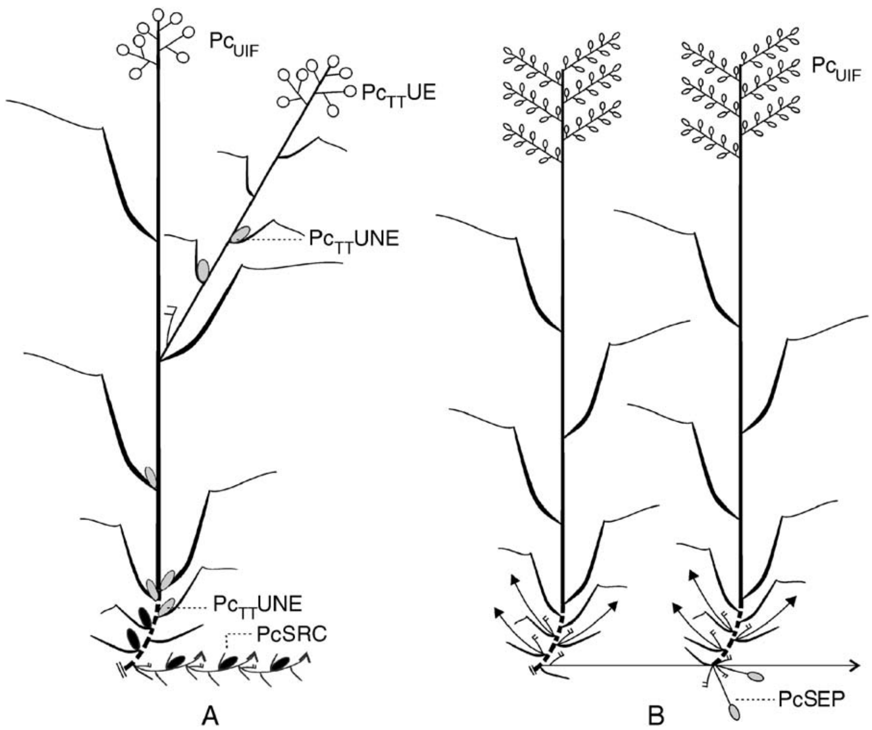

Fig. 2. Types of synflorescences with subterranean paraclades: (A) type IV synflorescence (S_{IV}); (B) type V synflorescence (S_{V}). Abbreviations: Pc_{UIF}, paraclade of the unit of inflorescence; $Pc_{TT}UE$, paraclade of the trophotagma of the unit of inflorescence, exposed; $Pc_{TT}UNE$, paraclade of the trophotagma of the unit of inflorescence, not exposed; PcSEP, subterranean paraclade over plagiotropic axes of long internodes; PcSRc, subterranean paraclade on short rhizomes. Explications in the text.

Table 1. Categories of synflorescences in Poaceae: types of axes of enrichment and behavior of the long internode zone (LIZ) and the short internode zone (SIZ); explications see text.

Type of synflorescence	Enrichment axes	Behavior of the LIZ	Behavior of the SIZ
S_0	–	HZ	IZ
S_I	Pc_{UIF}	HZ	IZ
S_{II}	Pc_{UIF} and $Pc_{II}UE$	EZ and HZ or only EZ[a]	IZ
S_{III}	$Pc_{UIF,}$, $Pc_{II}UE$ and $Pc_{II}UNE$	HZ and EZ	IZ and EZ
S_{IV}	Pc_{UIF}, $Pc_{II}UE$, $Pc_{II}UNE$ and PcSRc	HZ and EZ	IZ and EZ
S_V	Pc_{UIF}, and PcSEP	HZ	IZ and EZ

[a]In species of *Panicum* sect. *Monticola*.

Synflorescence type II (S_{II}, Fig. 1C)

This type presents enrichment axes of the types Pc_{UIF} and $Pc_{TT}UE$. In the SIZ, it behaves like an innovation zone, within the LIZ in part like an inhibition zone and in part as an enrichment zone or, in other cases, exclusively as an enrichment zone (species of *Panicum* sect. *Monticola*, Amsler et al., 2005).

Synflorescence type III (S_{III}, Fig. 1D)

This type presents enrichment axes of the types Pc_{UIF}, $Pc_{TT}UE$ and $Pc_{TT}UNE$. Here, the LIZ mostly behaves as an enrichment zone and partially as an innovation zone, the SIZ as an innovation zone and enrichment zone (*E. desvauxi*). Given that the development of the axes type $Pc_{TT}UE$ is strongly related to the environment (Rua and Weberling, 1998), there can be cases in which this type of axes does not develop, and, consequently, the synflorescence only bears axes of the types Pc_{UIF} and $Pc_{TT}UNE$.

Synflorescence type IV (S_{IV}, Fig. 2A)

This type presents enrichment axes as Pc_{UIF}, $Pc_{TT}UE$, $Pc_{TT}UNE$ and PcSRc. The LIZ mostly behaves as an enrichment zone and partially as an innovation zone; the SIZ as an innovation zone as well as an enrichment zone (*C. pappophoroides*). In this type of synflorescence, the enrichment zone presents the longest extension, comprising the paracladial zone of the UIF, part (or at times a great part) of the long internode zone and a short internode zone. This signifies that the entire axis of the synflorescence behaves as an enrichment zone.

Synflorescence type V (S_V, Fig. 2B)

This type presents enrichment axes of the types Pc_{UIF} and PcSEP. Consequently, the LIZ behaves as an inhibition zone and the SIZ acts as an innovation zone and enrichment zone. Synflorescences with this type of enrichment axes are characteristic for *A. purshii*, *A. floridanum*, *A. muhlenbergianum*, *C. chloridea*, *P. amphicarpum* and species of *Eremitis* (Campbell et al., 1983; Kaul et al., 2000).

In Poaceae, synflorescences of type S_I or S_{II} are the more frequent ones. Only few taxa present synflorescences S_0 and S_{III}. Less common are also species with synflorescences of the types S_{IV} and S_V. The development of enrichment axes with cleistogamous spikelets (Pc_{TT}UNE, PcSRc and PcSEP) present in the synflorescences of types S_{III}, S_{IV} and S_V, only occurs under certain environmental conditions, on unstable substrates and in an arid environment (Barker, 2005).

The different types of synflorescences described here possess enrichment axes at different positions of the shoot, in some cases leading to heteromorphism. Following the terminology of fruit heteromorphism proposed by Barker (2005), it is possible to affirm that the species with synflorescences types S_I and S_{II} produce one type of fruits only, which are aerial. If the species presents synflorescences of the type S_{III}, two types of fruits are developed: those generated in a chasmogamous way in flowers situated on an exposed UIF (Pc_{UIF} and Pc_{TT}UE) and those generated in cleistogamous flowers on enrichment axes of type Pc_{TT}UNE, hidden in the foliar sheaths. These latter ones can be situated at basal nodes (SIZ), the species then being amphi–basicarpic, or situated along the entire culm, then presenting aerial amphi–basicarpy.

Species with the synflorescence type S_{IV} are amphi–basigeocarpic, thus producing three types of fruits, two of them similar to those described in the preceding paragraph and a third type of fruit that is subterranean and generated in the cleistogamous flowers of the enrichment axes PcSRc.

Finally, it can be stated that if the synflorescence is of type S_V, the species is amphi–geocarpic and produces two types of fruits, the aerial fruits and subterranean ones, generated in the latter case from the cleistogamous flowers of enrichment axes of type PcSEP.

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