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An Analysis of the Inflorescences in Species of *Luziola* (Oryzeae – Poaceae)

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Summary

The inflorescences of *Luziola peruviana, L. bahiensis, L. pittieri, L. doelliana* and *L. gracillima* are analyzed typologically as a contribution to the knowledge of inflorescences within the tribe Oryzeae.

The inflorescence of *Luziola* is polytelic. In the paracladial zone, short and long paraclades can be distinguished. In the subzone of long paraclades two regions are present: one with and one without trophotagma.

The main florescence, the subzone of short paraclades, and the region of long paraclades without trophotagma form the "flowering unit". Additional long paraclades with trophotagma originate below these units. Each long paraclade with trophotagma repeats the structure observed on the main axis, and ends in a "flowering unit". Several features distinguish long paraclades with trophotagma from the flowering unit of the main floral axis: 1) they are generated by axillary buds developing from the axils of frondose leaves, 2) they bear a developed prophyll at the base, and 3) all spikelets have pistillate flowers.

Introduction

The Poaceae is one of the most interesting families within the Monocotyledons, particularly with respect to inflorescence morphology which shows an almost inexhaustible diversity (TROLL, 1969). Inflorescences present either complex branching systems with a high diversity of different forms and degrees of ramification, or extremely reduced systems, where only a few spikelets or even just one spikelet remain (BOR, 1960; VEGETTI and TIVANO, 1991).

There has not been any integrated research to explain this great variability in inflorescence structure of Poaceae. Descriptive terms referring to simple and complex racemose inflorescences have often been applied;

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even though in grass panicles branches terminate in spikelets and not in a flower. Furthermore, monopodial and sympodial branching systems can be combined in these inflorescences.

The need to revise inflorescence structure in grasses has been raised by several authors (ALLRED, 1982; GOULD and SHAW, 1983; CLAYTON and RENVOIZE, 1986). Among the characters often considered, the inflorescence – a structure quite characteristic at the tribal level – has been used to a lesser degree probably because it has not always been well understood. Its value, however, is relevant as a source of diagnostic characters and from the phylogenetic point of view (KELLOG, 2000a; VEGETTI and ANTON, 2000).

Typological analysis (TROLL, 1964; WEBERLING, 1965, 1989) can be a useful tool to describe the inflorescence in Poaceae in a more precise way and to establish relationships among taxa (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991; CÁMARA HERNÁNDEZ and MIANTE-ALZOGARAY, 1994; RUA and WEBERLING, 1995; VEGETTI, 1997a, 1997b; VEGETTI, 2000).

TROLL (1964) and WEBERLING (1965, 1989) considered that it is necessary to distinguish two types of inflorescences: monotelic and polytelic. In the first, the main axis ends in a flower; while in the second it ends in an aggregation of flowers, a florescence, without a terminal flower.

TROLL (1969) was the first to apply typological analysis to Poaceae. After that initial work, several studies have applied his concepts to various species or genera (VEGETTI and TIVANO, 1991; GASSER and VEGETTI, 1997), a tribe (VEGETTI, 1999), or the family Poaceae (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991; CÁMARA HERNÁNDEZ and MIANTE-ALZOGARAY, 1994; VEGETTI and WEBERLING, 1996).

Inflorescences in the Poaceae are polytelic (TROLL, 1966, 1969; CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991). In such inflorescences the main axis ends in an aggregation of flowers called the main florescence. Below the main florescence, branches may repeat the structure of the main axis by also producing florescences. These branches are termed paraclades, which means "repeating elements". Paracladial florescences are termed (co)florescences in order to distinguish them from the main florescence. Below their (co)florescences, paraclades can produce paraclades of second order, and so on (WEBERLING, 1989). Thus, the term "polytelic inflorescences" designates a "system of florescences": the main florescence and the lateral paraclades and their (co)florescences, up to the highest order. The florescences in grasses are the spikelets (TROLL, 1966, 1969). Those at the end of the main florescence axis constitute the main florescence, while other spikelets terminating the paraclades of successive orders are named (co)florescences (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991).

All inflorescence structures found in the Poaceae probably originated in various ways from a panicle of spikelets, during the evolutionary history of the family (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI and ANTON, 1995, 2000). In grasses, the great diversity of inflorescences is partly due to the process of truncation (WEBERLING, 1989) and homogenization (SELL, 1969, 1976) through progressive levels (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991; WEBERLING, MÜLLER-DOBLIES and MÜLLER-DOBLIES, 1993; VEGETTI and ANTON, 1995, 2000), leading to a secondary specialisation of the paraclades. Truncation (reduction or non development) of the apical flower led to the development of florescences; truncation of the florescence of the main axis and the long paraclades led to the development of the truncated polytelic inflorescences (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991). Homogenization (several successive paraclades become similar) occurs in the subzone of short paraclades on the main axis and on the long paraclades (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991; WEBERLING, MÜLLER-DOBLIES and MÜLLER-DOBLIES, 1993).

As a result of these modifications it is neccesary to carry out studies about inflorescence structure in the Poaceae in order to characterize the variability of the inflorescences in this family. These studies should provide the description of the types of variations that can occur within a closely related group of plants. The work presented here focuses in a study of the inflorescences in species of *Luziola* A. L. Juss. *Luziola* is an exclusively American genus of 11 species, distributed from the southern part of the United States to Uruguay (NÍCORA and RÚGOLO DE AGRASAR, 1987). The species are aquatic, rooting at the nodes and stoloniferous; the terminal panicle is male, conformed by single-flowered spikelets. Axillary panicles are female, also formed by single-flowered spikelets (NÍCORA and RÚGOLO DE AGRASAR, 1987).

The purpose of this study is to give a typological analysis of the inflorescences of *Luziola peruviana* Gmelin, *L. bahiensis* (Steudel) Hitchcock, *L. pittieri* Luces, *L. doelliana* Prod. and *L. gracillima* Prod. as a contribution to the knowledge of the variability in inflorescence structure in the Poaceae.

Materials and Methods

The compound inflorescence of *Luziola* species is interpreted according to the typology developed by TROLL (1964) and WEBERLING (1965, 1989). For the specific terminology used in this work see WEBERLING (1989), WEBERLING, MÜLLER-DOBLIES and MÜLLER-DOBLIES (1993) and VEGETTI and WEBERLING (1996).

Observations were made on living plants, alcohol-preserved material and herbarium specimens (see Material examined). Observations were organized according to the characteristics of the various zones in the synflorescence: the main in-

florescence, the paracladial zone (subzones of short and long paraclades) and each type of paraclade.

Dissections were performed under a stereoscopic microscope, and diagrams of the ramification systems were made. Drawings were scanned and corrected using graphic software.

Results

L. peruviana Gmelin (Fig. 1)

The following zones can be distinguished in the structural scheme of the whole plant of *Luziola peruviana*:

The innovation zone (J): this is the basal part of the plant, in which some shoots grow orthotropically and several grow plagiotropically. In the latter, axillary buds form new shoots, which can also grow either orthotropically or plagiotropically, amplifying the branching system.

The inhibition zone (Jh): in this region the internodes elongate and there are leaves without axillary buds. The length of this zone is variable; it can comprise 2–4 nodes, only a single node or even none. Internode length is also variable.

The paracladial zone (P): above the inhibition zone the axillary buds generate flowering shoots (paracladia) bearing a variable number of spikelets. These shoots are gradually reduced acropetally, until only one lateral spikelet appears on the main axis. This zone extends from the first proximal floral axis to the last distal lateral spikelet.

The main florescence (MF): the main axis terminates in a spikelet which represents the main florescence, located above the distal lateral spikelet. This florescence has staminate flowers.

In the paracladial zone two subzones can be distinguished: one with short paraclades (Ps) and another with long paraclades (Pl).

The subzone of short paraclades is composed of 2–3 Ps. Each Ps is reduced to its (co)florescence. Like those in the main florescence, spikelets of these short paraclades are staminated.

Long paraclades bear a coflorescence and a variable number of subsequent order paraclades. Some of these paraclades have a well developed prophyll and one bract (these are part of the trophotagma) whereas others lack the prophyll and the bract; thus, there are long paracladia with trophotagma (Pl+t) and long paracladia without trophotagma (Pl–t). Therefore, two regions can be distinguished within the subzone of long paraclades: one with (+t) and one without trophotagma (–t).

The –t region comprises 3–4 paraclades, bearing secondary paraclades reduced to their (co)florescence. Often two Pl–t per node are presented.

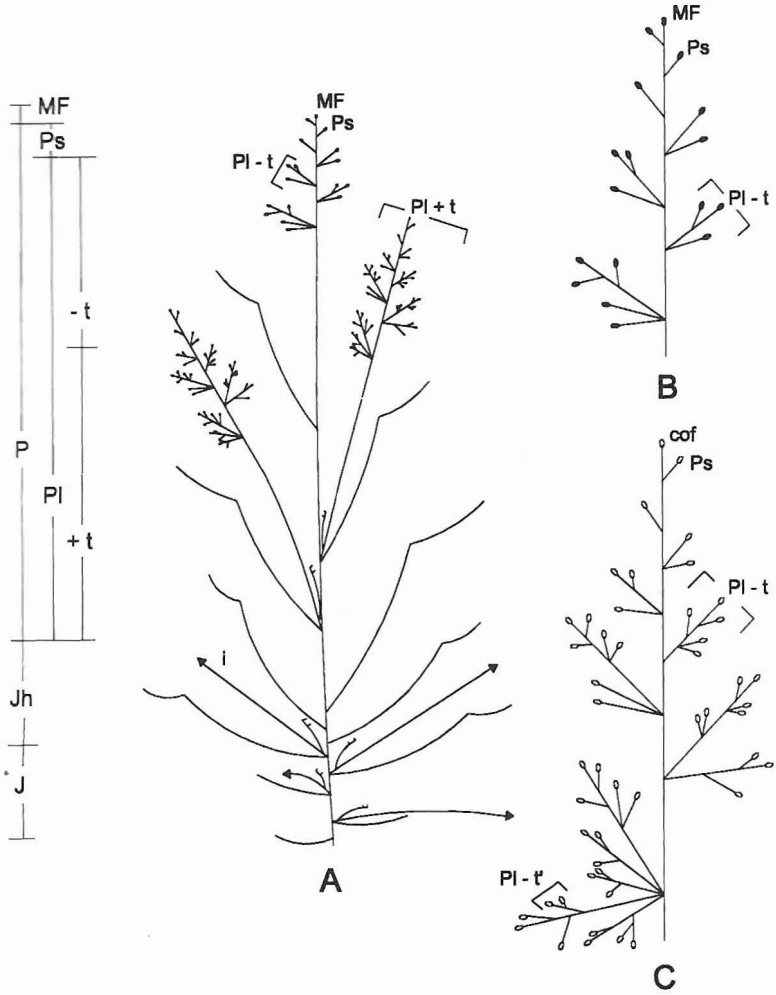

Fig. 1. *Luziola peruviana*. A, synflorescence structure; B, flowering unit along the main axis; C, flowering unit of a long paraclade with trophotagma. Figure abreviations: MF: main florescence; cof: coflorescence; P, paracladial zone; Jh, inhibition zone; J, innovation zone; Ps [subzone of] short paraclades; Pl, subzone of long paraclades; –t, region of long paraclades without trophotagma; +t, region of long paraclades with trophotagma; Pl–t, Pl–t′, consecutive order long paraclades without trophotagma; Pl+t, long paraclades with trophotagma; i, innovation; the main axis; C, flowering unit of a long paraclade with trophotagma. Figure abreviations: MF: main florescence; cof: coflorescence; P, paracladial zone; Jh, inhibition zone; J, innovation zone; Ps [subzone of] short paraclades; Pl, subzone of long paraclades; –t, region of long paraclades without trophotagma; +t, region of long paraclades with trophotagma; Pl–t, Pl–t′, consecutive order long paraclades without trophotagma; Pl+t, long paraclades with trophotagma; i, innovation; —○ pistillate spikelets; —● staminate spikelets.

Spikelets forming (co)florescences in this region present the same configuration as spikelets forming the (co)florescences of the short paraclades and the main florescence; thus these florescences have staminate flowers.

The +t region includes 3–4 very similar paraclades. Each one has a short hypopodium (first internode of a branch, preceding the prophyll), a prophyll, a long epipodium (the internode following the insertion of the prophyll), a bract, a region of Pl–t (5–8), a subzone of short paraclades (1–2 Ps), and the (co)florescence. In the Pl+t usually 2–4 Pl–t can be observed per node, having long secondary paraclades, which in turn can bear tertiary short paraclades. In very few specimens fourth order paraclades were observed.

All Pl+t have a typical intravaginal development, with a hyaline prophyll tightly bound around the paraclade, covered by the sheath of the corresponding bract. Spikelets comprising (co)florescences in these long paraclades bear only one female flower, and are smaller than the staminate spikelets.

The flowering unit (FU) comprises the main florescence, the subzone of Ps, and the region of Pl–t. Additional Pl+t originate below this flowering unit. Each Pl+t repeats the structure observed on the main axis, and ends in a flowering unit. The following features distinguish the flowering unit of the Pl+t from the flowering unit of the main axis: 1) they are generated by axillary buds in well developed leaves, with sheath and lamina; 2) they possess a well developed prophyll; and 3) all the spikelets have pistillate flowers.

It must be emphasized that the flowering unit on the main axis is initiated and unfolds before the region of Pl+t. This latter region then unfolds from the base to the distal area. Some specimens showed a basal Pl+t, various leaves and the distal end of the synflorescence with staminate spikelets, indicating that the latter region was formed early and that Pl+t grows acropetally, since only the basal ones were fully developed, and others would presumably develop from axillary buds in the distal leaves.

The synflorescences in the species described below follow the general pattern of *L. peruviana;* particular differences are noted for each one.

L. bahiensis (Steudel) Hitchcock (Fig. 2)

In this species, the synflorescence presents a short inhibition zone. The paracladial zone is formed by 2–4 Ps, 1–4 Pl–t and 1–4 Pl+t. Both types of Pl are disposed 1–2 per node. Each Pl+t are formed by 2–5 Ps and 2–6 Pl–t arranged 1 per node. This synflorescence exhibits very few and little ramified long paraclades, especially the long paraclades without trophotagma (staminate), and fewer long paraclades per node.

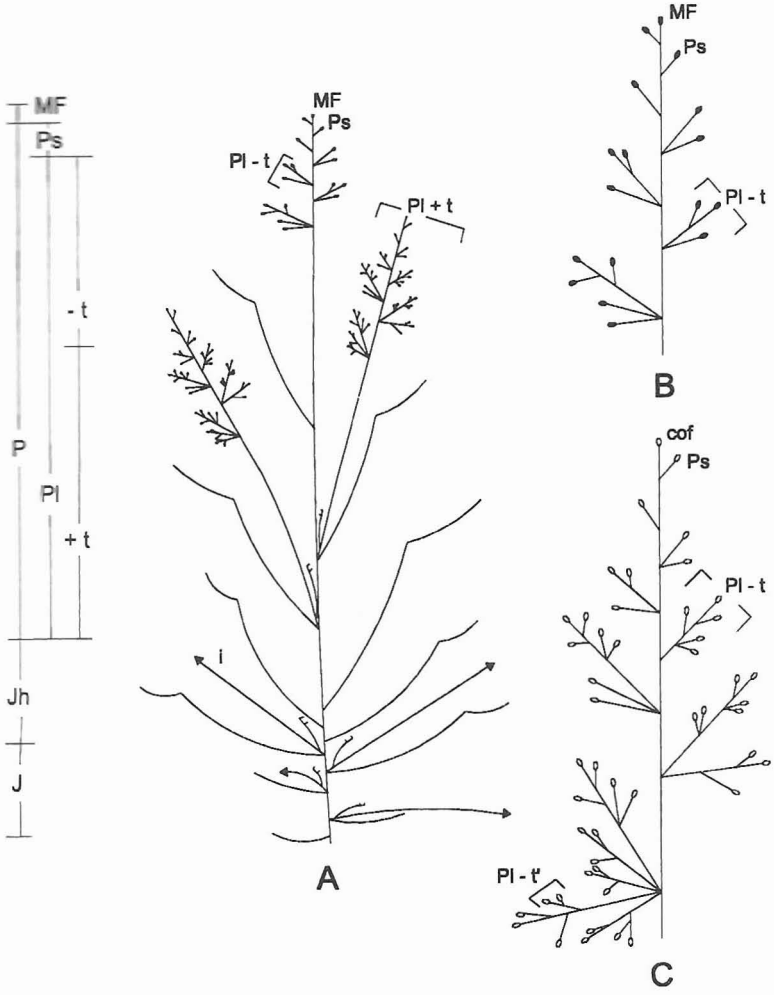

Fig. 2. Synflorescence structure in *Luziola bahiensis*.
Figure abreviations as in Fig. 1.

L. doelliana Prod. (Fig. 3)

In *L. doelliana* synflorescence internodes are longer than in *L. peruviana*, both in the main axis and in the long paraclades, resulting in a more open synflorescence with more distant spikelets. This synflorescence presents a paracladial zone formed by 1–2 Ps, 6–16 Pl–t and 2–3 Pl–t. Both types of Pl are disposed 1–2 per node. Each Pl+t is formed by 2–5 Ps and 2–6 Pl–t, arranged 1–2 per node.

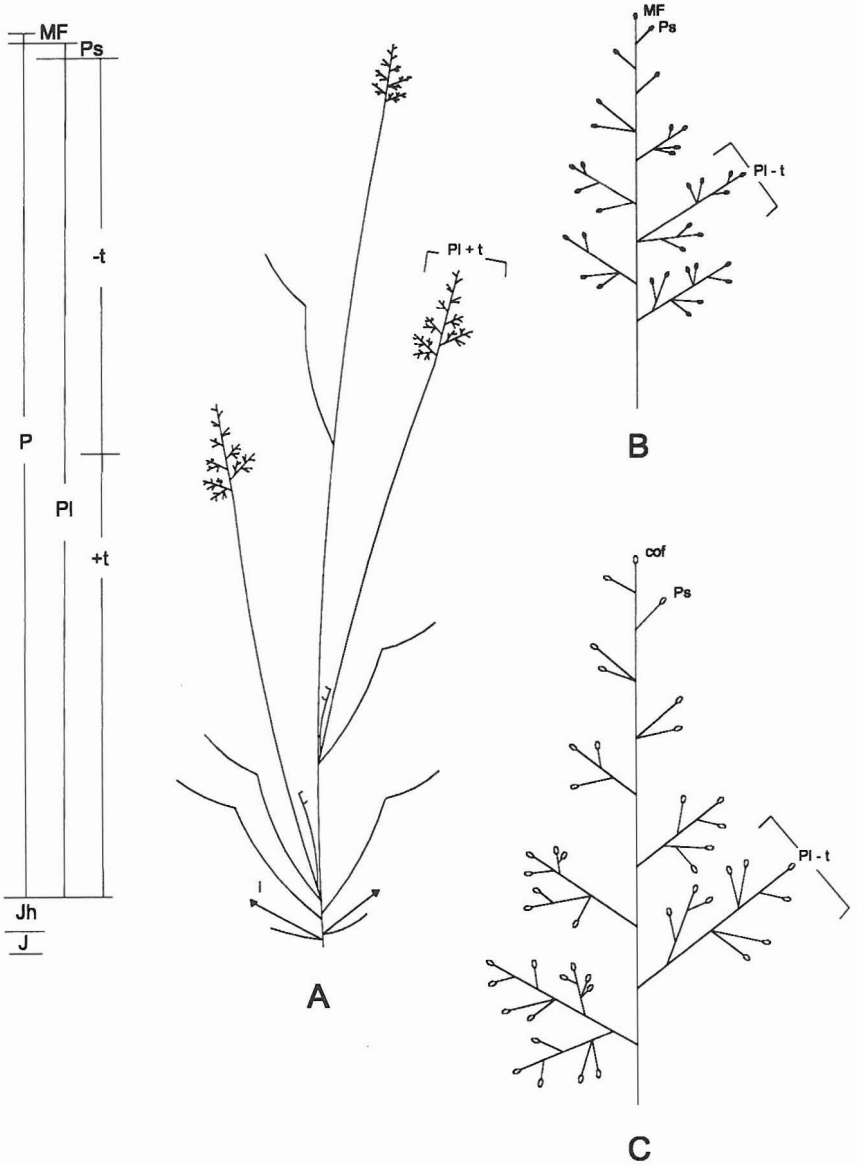

Fig. 3. *Luziola doelliana*. A, synflorescence structure; B, flowering unit on the main axis; C, Flowering unit of a long paraclade with trophotagma. Figure abreviations as in Fig. 1.

L. gracillima Prod. (Figs. 4, 5)

The synflorescence presents a paracladial zone formed by 2–4 Ps, 5–13 Pl–t and 1–2 Pl+t. The Pl–t are arranged 2–7 per node. Each Pl+t is formed by 1–2 Ps, 2–15 Pl–t disposed 4–5 per node. This synflorescence is basically similar to that of *L. peruviana*, but the flowering unit (Fig. 4 B) is more developed. Spikelets (staminate) in this zone are 6–8 mm long.

Long paraclades with trophotagma (Fig. 5) are more branched (with up to fifth order paraclades) and female spikelets are very small (0.9–1 mm long). There are more Pl–t in each Pl+t, as well as more Pl–t per node. Axes are generally very flexuous.

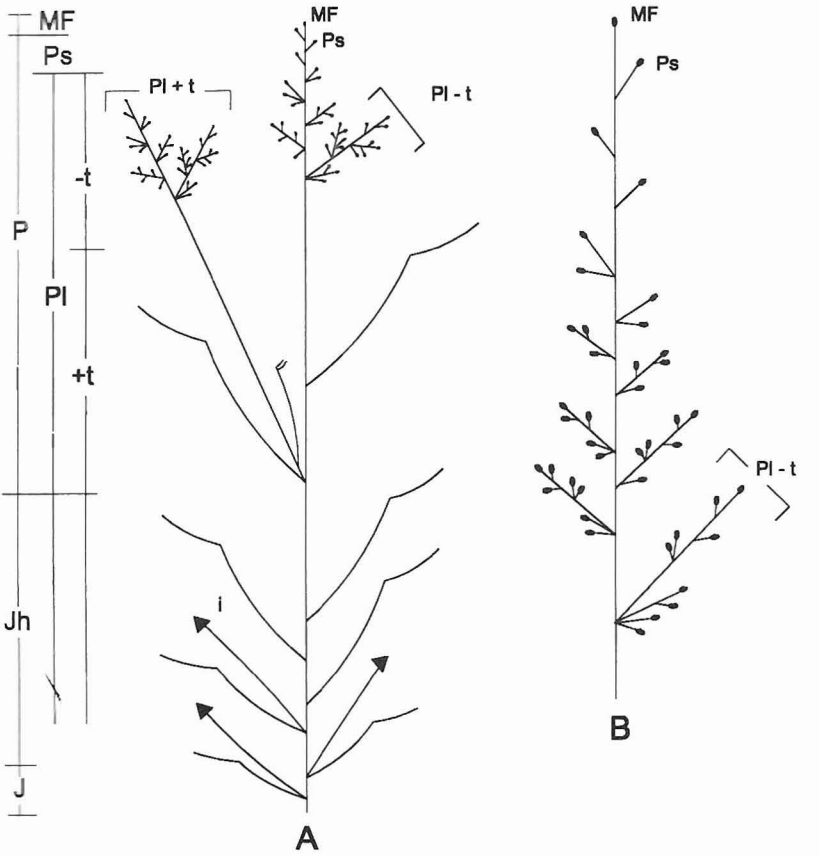

Fig. 4. *Luziola gracillima*. A. synflorescence structure; B, flowering unit on the main axis. Figure abreviations as in Fig. 1.

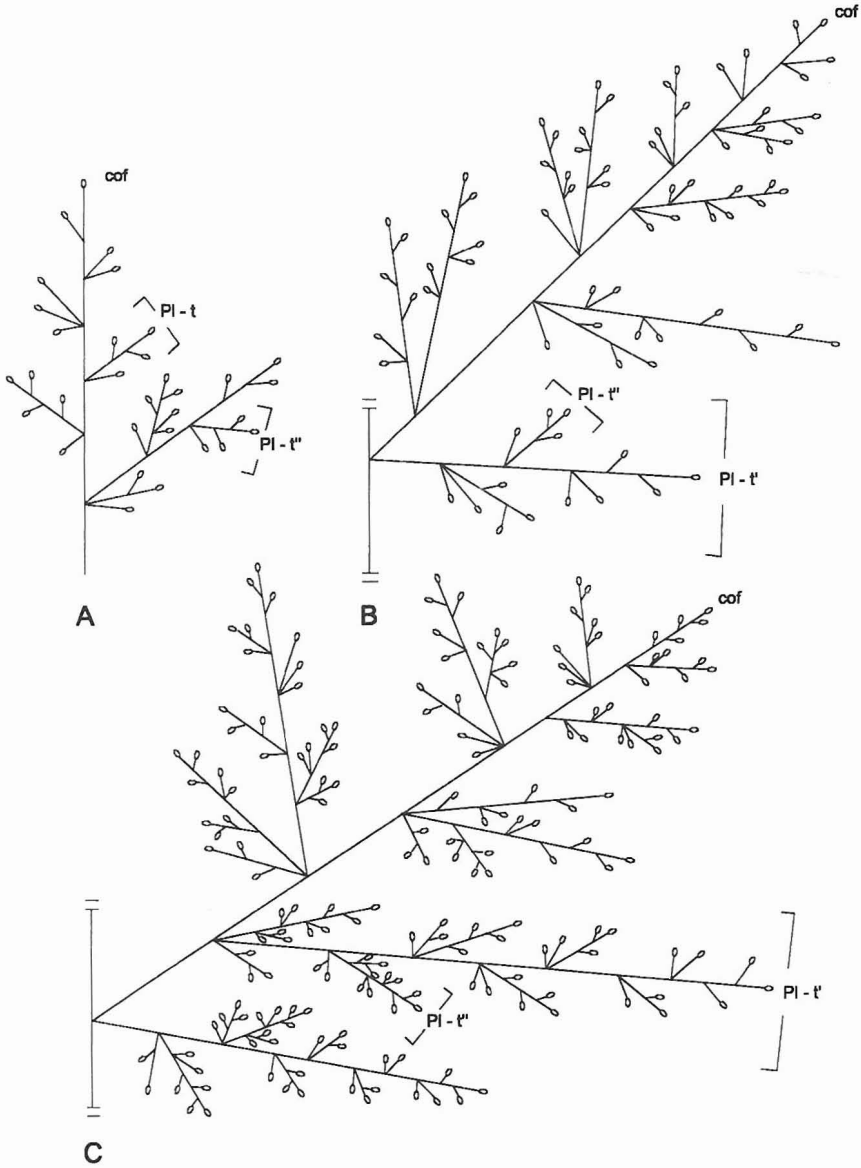

Fig. 5. Flowering unit of a long paraclade with trophotagma in *Luziola gracillima*. A, distal zone; B, intermediate zone; C, basal zone. Figure abreviations: as in Fig. 1.

L. pittieri Luces (Fig. 6)

The inhibition zone (Jh) in this species is shorter than in *L. peruviana*. The synflorescence presents a paracladial zone formed by 2–3 Ps, 4–8 Pl–t and 2–3 Pl+t. Both types of Pl are disposed 1 (–2) per node. Each Pl+t is formed by 2–5 Ps. and 2–6 Pl–t. The prophyllar ramification of Pl+t is more profuse. A secondary long paraclade with trophotagma (Pl+t′) ori-

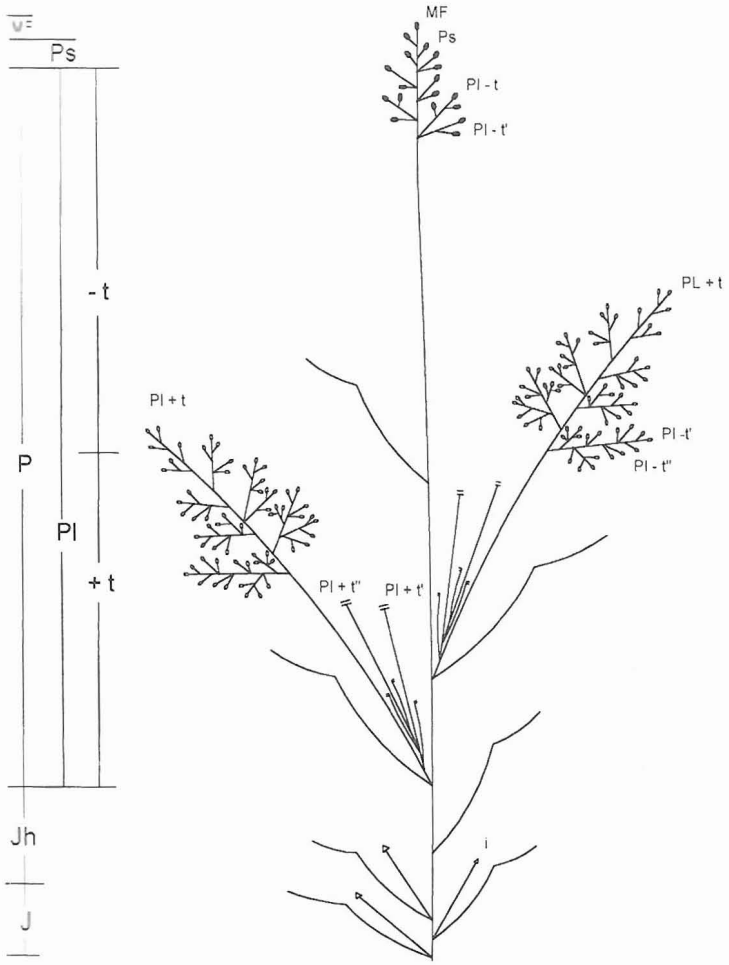

Fig. 6. Synflorescence structure in *Luziola pittieri*. Figure abreviations: Pl−t. Pl−t′, Pl+t″, consecutive order long paraclades with trophotagma: other abreviations as in Fig. 1. Only the hypopodium, prophyll and part of the epipodium of the Pl+t′. and Pl+t″ are shown.

ginates from the axillary bud of the prophyll of the primary (Pl+t), and a tertiary paraclade (Pl+t") originates from the axil of the former.

Inflorescence typology variations in *Luziola*

All the species studied exhibit a pattern similar to *L. peruviana*. The main variations are the number of short paraclades, the number and degree of ramification in long paraclades and the number of paraclades per node. The variations of theses characters are:

Along the main axis

There is little variation in the number of Ps within each species, the lower value is seen in *L. doelliana*.

The largest variability among species is in the number of Pl–t, from very few in *L. bahiensis* (1–4) and *L. peruviana* (3–4), to many in *L. doelliana* and *L. gracillima*. These last two species, in turn, show the greatest variation, with 6–16 Pl–t in *L. doelliana* and 5–13 Pl–t in *L. gracillima*.

Most of the studied species have few Pl per node (1–2), except *L. gracillima* with 2–7 Pl per node.

There is little inter- and intraspecific variability in the number of Pl+t: 1–2 in *L. gracillima*; 1–4 in *L. bahiensis*; 2–3 in *L. pittieri* and *L. doelliana*; and 3–4 in *L. peruviana*.

Along each long paraclade

There are few Ps, 1–2 in *L. peruviana* and *L. gracillima*, and 2–5 in *L. bahiensis, L. dolliana* and *L. pittieri*. The number of Pl–t is variable among species, and within each species. The largest variability in this character and in the number of Pl per node is observed in *L. gracillima*.

Branching degree on each flowering unit along the main axis is low. Only secondary paraclades reduced to a (co)florescence (formed by a single spikelet) are observed in *L. peruviana* and *L. bahiensis*, to third and fourth order paraclades reduced to a (co)florescence in the rest of the species. The degree of branching in the flowering units of the Pl+t shows little variability among species, and is comparatively lower in en *L. peruviana* and *L. bahiensis* (up to third order ramification); to third-fourth order in *L. doelliana* and *L. pittieri* and up to third-fifth order in *L. gracillima*.

Along the main axis and on each long paraclade

The number of short paraclades along the main axis and on each long paraclade is not very variable in *L. bahiensis* and *L. pittieri*; however, in *L. peruviana*, there is a larger number of Ps on long paraclades with trophotagma, and in *L. doelliana* it is higher on the main axis.

In regards to the main axis, the number of Pl–t is lower in long paraclades of *L. doelliana* and *L. pittieri*, higher in *L. peruviana* and *L. bahiensis*; in *L. gracillima* the number of Pl–t is large: 3–5 along the main axis, and 2–15 on each Pl+t, it can be higher or lower, according to the specimens.

The number of paraclades per node is higher in Pl+t than on the main axis in *L. peruviana*; in the other species such character does not vary very much (1 or 1–2 per node). *L. gracillima* is an exception; in this species the number of Pl per node is large: 2–7 Pl per node along the main axis and 4–5 Pl per node in each Pl+t.

In all the species, the branching degree of long paraclades with trophotagma is slightly higher than on the main axis.

Discussion

The synflorescence of *Luziola* presents terminal single-flowered spikelets on the main axis and on the long paraclades. Because the flowers in Poaceae are lateral (BUTZIN, 1979; CÁMARA HERNÁNDEZ and MIANTE-ALZUGARAY, 1994) the inflorescence in *Luziola* is polytelic, as has been described for other grasses (TROLL, 1966, 1969; CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991).

The wide diversification exhibited by these polytelic inflorescence in grasses can be explained by analyzing the different processes that, departing from a very simple panicle have taken place throughout the evolutionary history of the family (VEGETTI and ANTON, 2000). These processes seem to have operated independently or to have been combined more than once, and in different ways. They have mostly affected the main florescence and the paracladial zone (VEGETTI and ANTON, 2000).

In the *Luziola* inflorescences the main axis as well as long paraclades bear main florescence and (co)florescences; consequently, truncation has not taken place in this taxon (CÁMARA HERNÁNDEZ and RUA, 1991; VEGETTI, 1991; VEGETTI and ANTON, 1995, 2000). The paraclades have not been homogeneized either, a character usually associated to the truncation of the main florescence (VEGETTI and ANTON, 1995, 2000).

In order to differentiate paraclades of various complexity, the terms long and short paraclades were applied by VEGETTI and TIVANO (1991), as had been previously used for Dicot families by TROLL (1965) and WEBERLING (1989). The distinction between long and short paraclades should be associated to the presence of a discontinuity in the paracladial series along the main axis of the synflorescence (WEBERLING, MÜLLER-DOBLIES, MÜLLER-DOBLIES, 1993). Those authors point out that short paraclades must be homogeneous and must appear regularly as structural subunits of long paraclades. In the *Luziola* species studied, paraclades gradually reduce acropetally, and consequently, there is no evident paracladial discontinuity along the main synflorescence axis. Yet in this work the term short paraclades is used to describe paraclades reduced to a (co)florescence, and to distinguish them from long branched paraclades that bear both a (co)florescence and higher order paraclades. In all the inflorescences of *Luziola* it is possible to distinguish the subzone of short paraclades from the region where long, branched paraclades are found (subzone of long paraclades).

In this subzone, regions of long paraclades without trophotagma and regions of long paraclades with trophotagma can be characterized. This condition has been described for *Rhynchoryza subulata* (Nees) Baillon (AMSLER and VEGETTI, 1999; VEGETTI, 2000), for *Paspalum* L. (RUA and WEBERLING, 1995) and for some taxa of Andropogoneae (VEGETTI and WEBERLING, 1996; VEGETTI, 1997a, 1997b, 1998, 1999).

The term trophotagma was introduced by HAGEMANN (1990) to designate the basal vegetative region of shoots: it means the feeding (trophe) part (tagma) of a shoot. In each long paraclade the trophotagma can be formed by the prophyll and bracts (VEGETTI and WEBERLING, 1996; VEGETTI, 1997a, 1997b, 1998, 1999); in the studied species of *Luziola* and in *Rhynchoryza subulata* the trophotagma of each paraclade is formed by the prophyll and one bract (VEGETTI, 2000). They lack other bracts.

In the area of long paraclades with trophotagma, ramification can be increased by the development of the axillary bud of prophylls and bracts, except those of the distal bract (VEGETTI and WEBERLING, 1996; VEGETTI, 1999). The development of the prophyllar bud of the long paraclades with trophotagma generates large branch complexes in some grasses. These complexes constitute a series of branches and their prophylls (JACQUES-FELIX, 1961; VEGETTI, 1997a, 1997b, 1998, 1999). This character changes repeatedly in evolutionary time, as seen when it is mapped on a molecular phylogeny (KELLOG, 2000a). In *Luziola* this increase of ramification only occurs in *L. pittieri* in which the prophyllar buds of the long paraclades with trophotagma develop a Pl+t′ and a Pl+t″.

The branching pattern of the long paraclades with trophotagma is generally more or less paniculate, although in some cases it shows a remarkable tendency to cymose branching and seems to be independent of the structure of the flowering unit (RUA and WEBERLING, 1995). In the studied species of *Luziola* only *L. pittieri* has a cymose branching pattern. All the other species present a paniculate branching pattern.

More than one paraclade per node is observed in both the Pl+t and the Pl-t zones as has been described in other grasses (GRAM, 1961; RUA and WEBERLING, 1995; VEGETTI and ANTON, 1995). According to GRAM (1961) these could originate by either a) lack of development of the basal internode in the long paraclade, and thus the following order paraclades appear to be inserted in the same node, or, b) alternatively, by a reduction in internode length along the main axis, where two or more primary paraclades seem to be inserted in the same node, forming pseudoverticils. The first of these processes seems to explain the presence of more than one paraclade per node in the species of *Luziola* that we have studied, where only one would be primary and the others of higher order.

The florescences in grasses can be hermaphrodite, staminate or pistilate. In *Luziola* the florescences of the flowering unit on the main axis are staminate and the (co)florescences of the flowering unit of the Pl+t are pistilate. In Andropogoneae LEROUX and KELLOG (1999) had shown that in all staminate flowers the gynoecium is aborted following a pattern of controlled cell death in the subepidermal layers. The oryzoid grass, *Zizania aquatica*, has staminate flowers, but these appear to be derived independently from those in the Panicoideae (KELLOG, 2000a). This author considers that either the mechanism of gynoecial abortion is entirely different in oryzoids and panicoids, or that a common mechanism is deployed at different developmental times and in different ways.

In some grasses the inflorescence branches initiate early in development and all differentiate and elongate simultaneously, or, alternatively, branch production can be delayed substantially, until after spikelet pairs are formed on the main axis (KELLOG, 2000a). These authors consider that when these characters are mapped onto a phylogeny it is clear that they change repeatedly in evolutionary time. Thus, some distinction between different types of inflorescences, among other features, may be a heterochronic shift in the timing of development of lower branches. Inflorescences that look similar at maturity may develop in quite different ways, and conversely, inflorescences that look different may be developmentally similar (KELLOG, 1998). For this reason this latter author considers that developmental studies are critical for interpreting the evolution of inflorescence form.

KELLOG (2000b) presents a model of inflorescence development. She proposes a dynamic developmental approach to describe inflorescences, which is compatible with both genetic and cladistic approaches and she uses the model to describe some inflorescences in the grass family. This model relates structures by known genetic mechanisms and by developmental transformations, rather than by typology of adult form. Nevertheless we think that it is neccesary to have more precise knowledge on the morphology of adult inflorescences and that typological analysis is useful and can provide suitable characters for phylogenetic studies.

On account of the above issues, studies on inflorescence typology should be complemented with research on floral and inflorescence development.

Material examined

Luziola bahiensis (Steud.) Hitchc.

ARGENTINA: Burkart 1104 (BAA), Cusato 3690 (BAA), Hatschbach 1884 (BAA), Krapovickas et al. 25380 (CTES), Parodi 5470, 5610, 5649 (BAA), Pedersen 6418 (BAA), Quarin 459 (CTES).

BRAZIL: Davidse et al. 11063, 11505 (BAA).

PARAGUAY: Pedersen 7659 (BAA).

Luziola doelliana Prod.

BRAZIL: Manet 670 (BAA), Swallen 4407 (BAA).

Luziola gracillima Prod.

ARGENTINA: Del Aguila et al. 24 (BAA), Saravia Toledo 1563 (CORD; CTES), 1035 (CTES).

Luziola peruviana Gmelin

ARGENTINA: Ahumada 419 (BAA; CTES), Arbo 472 (BAA; CTES), Benitez et al. 119, (BAA; CTES), Burkart s/n (BAA), Cusato 3427 (BAA), Hunziker 941 (BAA; CORD), 9906 (BAA), Ibarrola 166 (BAA), Krapovickas et al. 18243, 23840, 24575 (BAA), Krapovickas e Irigoyen 17847, (BAA), Legrand 1353 (BAA), Lewis y Collantes 235 (BAA), Martinez 11, (BAA), Meyer 76 (BAA; CTES), Meyer et al. 20563 (BAA), Millan 283 (BAA), Morgan 14 (BAA), Nicora 3030, 5093 (BAA), Nicora et al. 170, (BAA), Parodi 682, 1018, 1917, 2652, 3275, 6210, 6310, 6357, 6363, 6949, 6981, 7720, 9094, 13485, 15088, 15281, s/n (BAA), 6729 (BAA; CTES), Quarin 774 (BAA; CTES), Quarin et al. 525 (BAA; CTES), Ragonese 106 (BAA), Rojas 8973 (BAA), Schinini 7799 (BAA; CTES), Schulz 1057 (BAA), Spegazzini 2437 (BAA), Claren 12247 (CORD), Hackel 18746

(CORD), Hunziker 5880 (CORD), Stuckert 2432, 2451, 12666, 15819, 22404 (CORD), Ahumada 2627, 2811, 2978, 3210 (CTES), Arbo et al. 6319, 6904 (CTES), Krapovickas et al. 20323 (CTES), Neiff 852 (CTES), Pedersen 12757 (CTES), Piccinini y Hilfer 4291 (CTES), Quarin 59, 624, 686, 2153 (CTES), Quarin et al. 2153 (CTES), Quarin y Schinini 1024 (CTES), Schinini et al. 19075 (CTES), Schulz 10302, 10904 (CTES), Tressens et al. 2774, 4179, 4230, 4279 (CTES), Ragonese 2106, (LP), Zuloaga et al. 557 (LP), LP 018733.

BRAZIL: Araujo N282 (BAA), Capparelli 195 (BAA), Leopoldo 1051, (BAA), Rambo 54926 (BAA), Sacco 810, 811 (BAA).

UNITES STATES: Langlais 1888 (BAA).

PARAGUAY: Hassler 5534, 12473 (BAA), Jimenez 106 (BAA), Ramirez 138 (BAA), Rojas 12466, 13144 (BAA), Woolston 98 (BAA), 4084 (BAA), Jörgensen 4084 (LP).

URUGUAY: Boelcke 8245 (BAA), Leon 289 (BAA), Montoro Guarch 3240 (BAA), Rosengurtt B208 (BAA).

Luziola pittieri Luces

VENEZUELA: Davidse 2987, 4395 (BAA).

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