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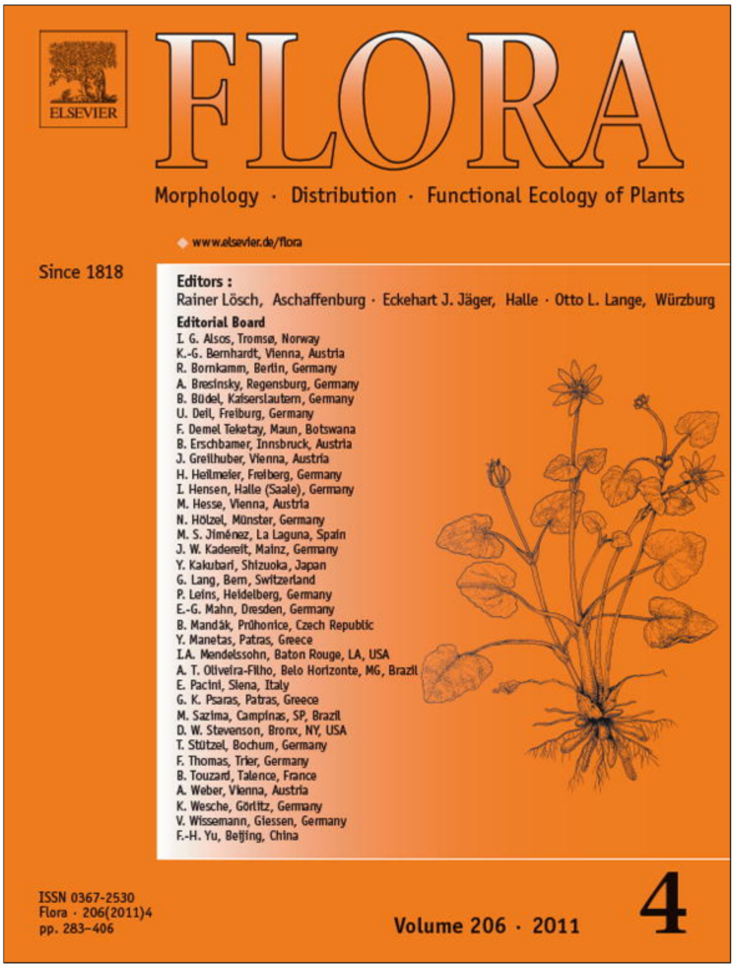

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Review

Descriptive characters of growth form in Poaceae—An overview

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ABSTRACT

The architecture of the shoot branching system in Poaceae defines the growth forms within this family. The specific characteristics of the main axis as well as the disposition and characteristics of the lateral shoots determine the main structural variations found among species. In this work, we discuss the set of parameters to be taken into account in describing the vegetative structure of Poaceae in order to achieve a full diagnosis of the system and to thoroughly assess and interpret its variations.

Contents

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Introduction

Each grass plant is composed of morphologically equivalent shoots of consecutive branching order (Moore and Mooser, 1995). The spatio-temporal disposition of these shoots is one of the major determining factors in the variation of the branching system structure and, consequently, of the growth form in Poaceae (Moore and Mooser, 1995; Mühlberg, 1967, 1970; Serebriakova, 1969; Vegetti, 1997a). This determines how the plant explores and utilizes resources and how it interacts with its neighbors (Grime et al., 1986; Kull, 1995). The plant enlarges and colonizes the surrounding environment, constantly increasing and changing its structure (Bell, 1993), gradually becoming more complex (Bell, 1986).

The growth form is a useful tool to understand the dynamics of the structure, since it covers the successive stages that lead to the construction of the whole plant, from its germination (Meusel, 1952) through the distinct phenological phases it undergoes throughout the year (Meusel et al., 1977). The growth form is the complex of genetically constant vegetative and reproductive characters, which vary within one specific range of phenotypic plasticity (Meusel, 1952, 1970). It involves a comprehensive, dynamic analysis of the shoot branching system that can be applied to plants growing in natural or man-altered conditions as well as to agronomic studies (Meusel et al., 1977) or studies on the productive management of native species (Montenegro and Ginocchio, 1992). Research on growth form is the foundation of many phytosociological, population and community ecology, and biogeographical studies (Krumbiegel, 1998), which make it possible to understand and interpret ecological relationships (Hagemann, 1981) and their correlation, for instance, with dispersion (Bernard, 1990).

In this work, we discuss the set of parameters required to describe the vegetative structure in Poaceae, given that a thorough understanding of these species requires knowing their structure and the growth form of their branching system. This will enable us to establish how the plant uses space, how its structure develops and what the reason is for the plant to persist or not within systems subject to disturbances.

Complexity levels

Poaceae, both juvenile and adult, are easily recognizable because of their characteristic growth pattern (Bell, 1994; Mühlberg, 1967). Each plant is composed of shoots of consecutive branching order (Moore and Mooser, 1995) (Fig. 1A). Each shoot is considered a module, tiller or innovation usually terminating in an inflorescence. These tillers or modules are in turn composed (Fig. 1B) of a group of smaller sub-units called phytomers (Moore and Mooser, 1995).

The phytomer, considered the essential unit of shoot construction in Poaceae (Briske, 1991; Hyder, 1972; Wilhelm and McMaster, 1995) is specific to Poaceae, but it is closely related to the concept of metamer (White, 1984). The term "phytomer" provides a useful framework in the analysis of the shoot structure in different species and in the characterization of mutant phenotypes (McSteen and Leyser, 2005). A phytomer basically consists of a leaf, an axillary bud, the insertion node, the related internode and, in some cases, adventitious roots. The main variation of its definition lies in the internode that is part of the metamer, which (Bell, 1991; Clark and Fisher, 1986) may belong to the precedent one, to the next, or be a portion of the actual one (Fig. 1B). There are also differences (Clark and Fisher, 1986) in the position of the axillary bud and of the subtending leaf (Fig. 1B). However, in spite of these variations, the essential characteristic of the phytomer is its repetitive condition rather than the details in its structure (White, 1979) and the fact that it has a site (the axillary bud) with the potential to generate a new phytomer (Barlow, 1989, 1994). The destiny of this axillary meristem is one of the major sources of evolutionary and environmental diversity in the architecture of the shoot branching systems (McSteen and Leyser, 2005). Each component may be modified (longer or shorter internode, development of the axillary buds and roots or lack of it, shape and development of the leaf), affecting the final appearance of the phytomer. The development sequence of phytomers and their interrelations provide an appropriate way of delimiting and quantifying growth events (Moore and Mooser, 1995).

Phytomers connect sequentially to give origin to a higher hierarchy structure: the module or tiller (Moore and Mooser, 1995). The tiller (a set of phytomers formed from an apical meristem) (Briske, 1991; Hyder, 1972; Moore and Mooser, 1995) is considered the morphological and structural unit (Cámara Hernández and Rúa, 1992; Rúa and Weberling, 1998) and the basic element of the growth form. It comprises an axis generally ending in an inflorescence, which emerges from the axillary meristem of a higher order unit by iterative innovation (Cámara Hernández and Rúa, 1992). Typologically, each tiller is considered a synflorescence (Cámara Hernández and Rúa, 1992; Rúa and Weberling, 1998; Weberling, 1985). Tiller life is limited; however, their continuous production and potential to survive are key aspects of perenniality and vegetative reproduction of many grasses (Gould and Shaw, 1983). The wide variety of tillers observed among and within species results from variations in the structure and distribution of the phytomers that make them up.

Structure and variations at the tiller level

Zones

Two regions may be recognized within the structural unit (the tiller or module): the anthotagma and the trophotagma (Hagemann, 1990). The anthotagma involves the inflorescence and comprises the distal region of the shoot, also referred to as flowering unit (Sell, 1969, 1976) or inflorescence unit (Vegetti and Müller-Doblies, 2004). On the other hand, the trophotagma involves the axis portion bearing foliar structures (foliage leaves and cataphylls). Consequently, the trophotagma comprises the medial and proximal region of each tiller or structural unit.

In Poaceae, the trophotagma zones may be delimited according to two criteria: the length of the phytomer internodes and the activity of the axillary meristems. An unequal elongation of the internodes determines two different zones (Serebriakova, 1969; Mühlberg, 1970): (1) the short internode zone and (2) the long internode zone (Fig. 1C). Based on the role that each region plays in the axis (Troll, 1964; Weberling, 1965, 1985), the following regions may be recognized in the trophotagma: (a) innovation zone, (b) inhibition zone, and (c) paracladial or enrichment zone (Vegetti and Müller-Doblies, 2004) (Fig. 1C). Both criteria may be combined for a better description of variations that occur in the vegetative structure of Poaceae. The final name given to the different zones will depend on what is considered the main criterion.

Zones of the trophotagma based on internode length

Short internode zone (SIZ)

In this zone, the buds develop axes that may grow and flower in the same period as the parent axis or in the next period (Cámara Hernández and Rúa, 1992). The main variations in this zone are related to the number of internodes, the internode position with respect to the ground level – depth – (Mühlberg, 1967; Rechentin, 1956; Vegetti, 1997a), their location within the structural unit and the number of buds they develop. For example, in *Melica macra* Nees and *Melica sarmentosa* Nees, the SIZ is composed of the first four

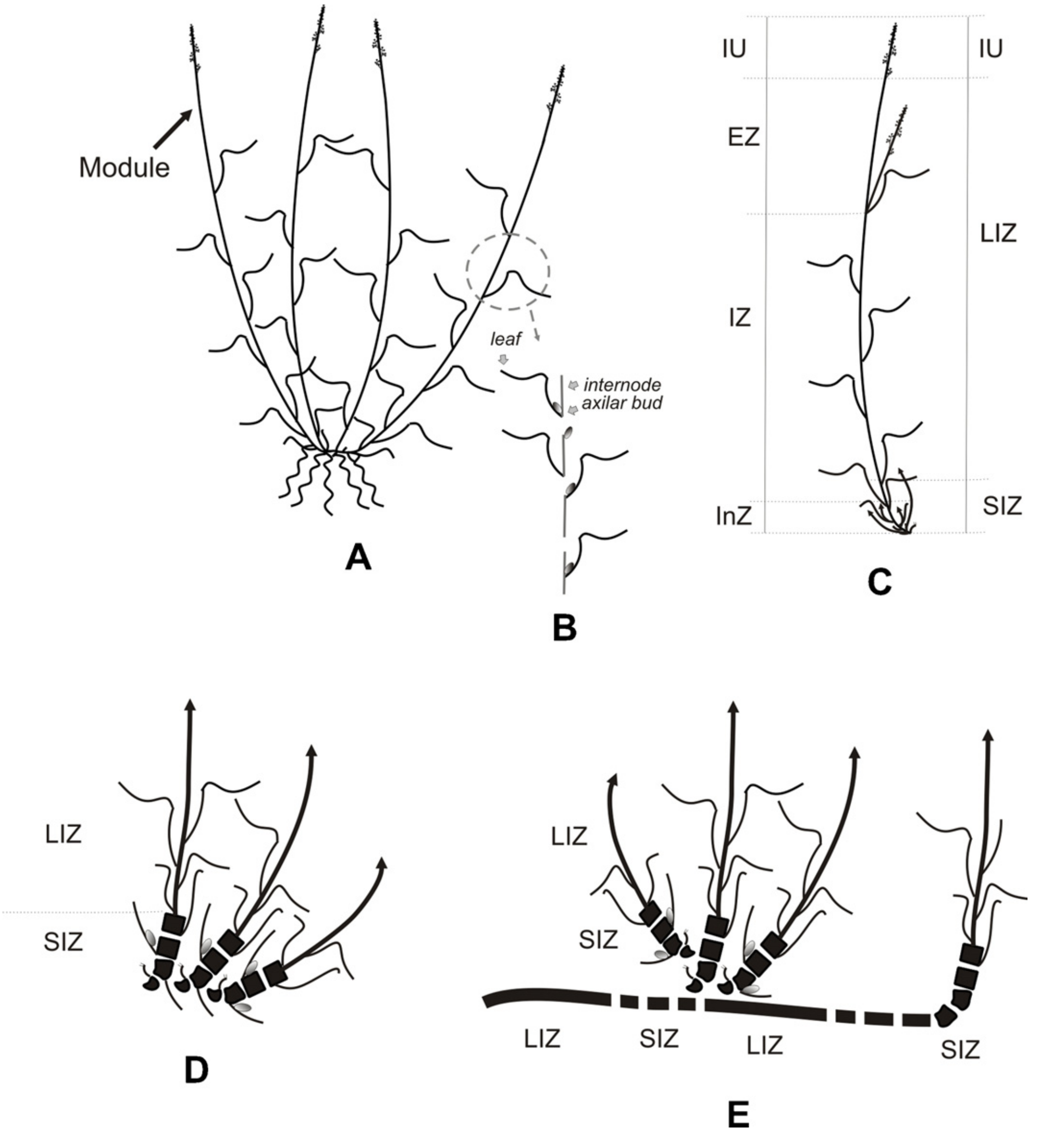

Fig. 1. (A) Poaceae plant; (B) variations in the term "phytomer"; (C) criteria in the characterization of module or tiller zones; (D) axes with basal zone of short internodes that form a small rhizome by substitution; (E) axes with alternation of long and short internodes. *Abbreviations*: EZ, enrichment zone; InZ, innovation zone; IZ, inhibition zone; LIZ, long internode zone; SIZ, short internode zone; IU, inflorescence unit.

(including a reduced hypopodium) basal internodes. In adult tufts the axillary buds which are located in the axils of the first and second cataphylls (excluding the prophyll) usually develop (Fig. 1D). Except for the first internode, the remaining internodes are generally above the ground (Perreta and Vegetti, 2004, 2006). However, the number of internodes may be higher in other species, such as in *Leptochloa chloridiformis* (Hack.) Parodi (Perreta et al., 2000) and *Rhynchoryza subulata* (Nees) Baill. (Vegetti, 2002), which show more than five internodes. Other examples are *Andropogon scoparium* Michx. and *Bouteloua curtipendula* (Michx.) Torr. which show 12–15 very short internodes reaching no more than 3.5 cm long. Most of these internodes are below the ground level and not all buds are developed (Rechentin, 1956).

While this zone is generally basal in most species, in other species and depending on the environment, it may also be basal and alternate with long internode zones (Mühlberg, 1967). This can be found (Vegetti, 2002) in *Leersia hexandra* Sw. and *Luziola peruviana* G. Mey. ex Benth. (Fig. 1 E), and in *Eleusine indica* (L.) Gaertn. (Jaques-Felix, 1962), all species with plagiotropic-growing axes. There are also species with a basal subterranean zone of more or less long internodes, followed by a short internode zone where the meristem approaches the ground surface. This can be found, e.g. in *Bromus auleticus* Trin. ex Nees (Vegetti, 1997a), *Zizaniopsis bonariensis* (Balansa & Poitr.) Speg. (Vegetti, 2002), *Paspalum monostachyum* Vasey, *P. hyalinum* Nees ex Trin., *P. jürgensii* Hack., and *P. nicorae* Parodi (Rúa and Gróttola, 1997; Rúa and Weberling, 1998). This leads to a rhizome-like specialization of the short internode zone (Rúa and Gróttola, 1997).

Long internode zone (LIZ)

In this zone, internodes are more or less elongated. Axillary buds may not develop throughout the zone, or they may develop only in specific regions of this zone. The following variations can be observed:

- inhibited axillary development of the whole zone, as is the case with shoots that develop early in the growing season in *Melica macra* (pre-generative shoots) (Perreta and Vegetti, 2004; Fig. 2A);
- inhibited bud development in the basal region with branch development in the distal region (Fig. 2B), as in some species of *Brachypodium* P. Beauv. (Mühlberg, 1970) and in Andropogoneae

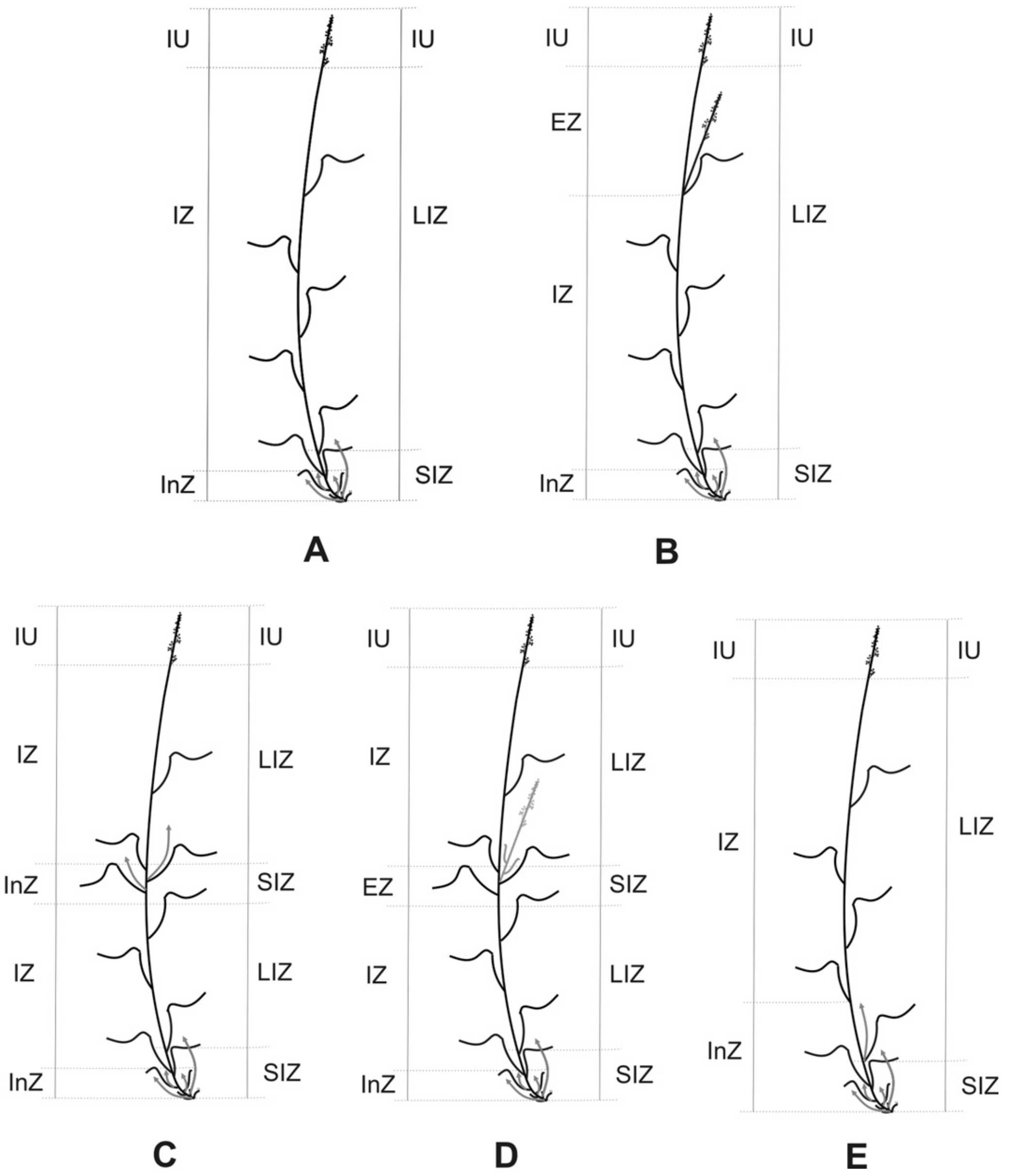

Fig. 2. (A) Axis with innovations in the basal zone of short internodes; (B) axis with innovations in the basal and distal region of the short internode zone and with development of enrichment axes; (C and D) axis with alternation of long and short internodes; (E) axis with innovations in the basal region of the short internode zone and in the distal part of the long internode zone. *Abbreviations*: EZ, enrichment zone; InZ, innovation zone; IZ, inhibition zone; LIZ, long internode zone; SIZ, short internode zone; IU, inflorescence unit.

(Schultka, 1984; Vegetti, 1999), *Luziola peruviana*, *L. bahiensis* (Steud.) Hitchc., *L. pittieri* Luces, *L. doelliana* Prod. and *L. gracillima* Prod. (Weber and Vegetti, 2001). Normally, the axes that develop in this region have a prophyll and a variable number of leaves (Rúa and Weberling, 1998; Vegetti and Weberling, 1996) and end in a flowering unit similar to that of the supporting axis. They have been called paraclades of the trophotagma (Vegetti and Müller-Doblies, 2004), long paraclades of second order (Weberling et al., 1993) or paraclades with a trophotagma (Vegetti and Weberling, 1996). From the axillary buds of the trophotagma of these axes, new axes with a similar structure may originate; thus, the long internode zone contributes to increasing the number of floral branches of the plant (Rúa and Weberling, 1998);

- a basal zone with inhibited bud development and non-inhibition regions alternating along the axis with inhibition zones (Fig. 2C and D), as in *Melica sarmentosa* (Perreta and Vegetti, 2006) and many species with plagiotropic-growing axes (Rúa and Weberling, 1998);
- axillary bud development in the basal portion and an inhibited development zone in the medial and distal portions (Fig. 2E), as in shoots occurring late in the growing season (after flowering) in *Melica macra* (post-generative shoots: Perreta and Vegetti, 2004) and in many species of the genus *Paspalum* L. (Rúa and Gróttola, 1997; Rúa and Weberling, 1998);
- axillary bud development in the whole zone, which occurs very rarely. It has been found in some species of *Panicum* L. sect. *Monticola* Stapf (Amsler et al., 2005).

In some species, there are some rare cases of a gradual short-to-long internode transition; in such cases, the decision to allocate this region to either zone is relatively arbitrary (Rúa and Gróttola, 1997).

Zones of the trophotagma based on activity of the axillary meristems

Innovation zone

Innovations are axes that ensure the tuft's perenniality and vegetative growth. These axes which are typical of perennial plants, arise from undeveloped buds that are growing during the following season (Weberling, 1985). Since they increase vegetative propagation and perennation, tillers are considered innovations in Poaceae, regardless of the time when they develop (Cámara Hernández and Rúa, 1992), i.e., innovation shoots and tillers are equivalent concepts, as regards the Poaceae family (Troll, 1964).

This zone may comprise only the short internode zone, as it occurs in caespitose species and in the pre-generative shoots in *Melica macra* (Figs. 1D, 2A and B); the short internode zone and the basal portion of the long internode zone, as it is shown in the post-generative shoots in *Melica macra* (Fig. 2E) (Perreta and Vegetti, 2004); or the short internode zone and the alternate areas of the long internode zone, as in species with rhizomatous or stoloniferous plagiotropic-growing axes (Rúa and Weberling, 1998). Examples are *Bromus auleticus* (Vegetti, 1997a) and *Zizaniopsis bonariensis* (Fig. 2C and D) (Vegetti, 2002).

For purposes of delimiting this zone, the most important characteristic is that axes (or at least their basal parts) produced here should stay in the structure longer than a growth season, contributing axillary buds for the next growth period, i.e., taking part in the tuft construction.

Inhibition zone

The inhibition zone is so called because axillary buds do not develop. It may comprise the whole long internode zone, as it occurs in pre-generative shoots in *Melica macra* (Fig. 2A); the distal portion of the long internode zone, with the basal portion functioning as an innovation zone (post-generative shoots in *Melica macra*) (Fig. 2E) (Perreta and Vegetti, 2004); the proximal portion of the long internode zone (Fig. 2B), as in species of Andropogoneae (Vegetti, 1999); or it may alternate with non-inhibition regions (Fig. 2C and D), as in climbing axes of *Melica sarmentosa* (Perreta and Vegetti, 2006) or the distal internodes of the short internode zone (Fig. 1D), as it occurs in *Melica macra* and *Melica sarmentosa* (Perreta and Vegetti, 2004, 2006).

Enrichment zone

Enrichment axes increase the number of inflorescences. There are two types of enrichment axes: those without trophotagma, which make up the basal portion of the inflorescence unit, as it may be observed in all species with panicles of spikelets (Cámara Hernández and Rúa, 1992; Perreta and Vegetti, 2004; Vegetti, 1991), and those with trophotagma. Enrichment axes with trophotagma are usually located (Fig. 2B) in the distal portion of the long internode region (Vegetti and Müller-Doblies, 2004), as in some species of Andropogoneae (Vegetti, 1999), or they may be found in enrichment zones alternating with inhibition zones (Fig. 2D), as in *Melica sarmentosa* (Perreta and Vegetti, 2006). These enrichment axes may show different branching patterns which specifically depend on the destiny of their axillary buds (Souza-Chies et al., 2006) and they may even generate complicated reproductive branching systems, as it happens in Andropogoneae (Vegetti, 1997b,c,d, 1999).

A special case of enrichment axes is found in the short internode zone in which cleistogamous, often underground, spikelet-bearing axes may be observed (Tivano et al., 2009). This syndrome is present in several taxa of subfamily Pooideae (Barker, 2005) and in tribe Pappophoreae (Tivano and Vegetti, 2004, 2010; Tivano et al., 2009).

Some authors refer to basal branches as innovations and they class axillary branches with the enrichment axes (Doust et al., 2004). However, to refer the term "axillary" just to one type of branches is not appropriate because both axes are the result of axillary bud development. Then, it is important to identify both types of branches clearly and unmistakably, given that 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 they are usually associated with short phytomers, *see above*) and the buds that give origin to them develop early. By contrast, enrichment axes only grow when flowering occurs in the axis that bears them (Doust et al., 2004). They are found in the long internode zone, they develop basipetally and the meristems that give rise to them show a delayed development (McSteen and Leyser, 2005). Rúa and Weberling (1998) argue that the occurrence of iterative innovation establishes an artificial difference between innovation axes and enrichment axes, since both types of axes are indeed ends within a variation continuum. Nevertheless, in species of *Setaria* P. Beauv., both types of axes are partially controlled by separate *loci* (Doust et al., 2004), in view of which these authors state that these results support their use as independent taxonomic characters.

Variations

Other specific characteristics of modules to be taken into account for a complete depiction of variations in Poaceae include: growth direction (orthotropism or plagiotropism); types of shoots that develop from axillary buds (identical tillers, differential tillers, rhizomes, stolons); branching (intravaginal or extravaginal shoots), timing of bud development (immediate or deferred branching, pre- or post-generative shoots); timing of flowering or axis senescence; and foliar sequence. All these characteristics make it possible to clearly identify the plant form at each ontogenetic stage (Barlow, 1994), as well as to analyze how the environment may limit the plant structure on the basis of certain conditions or factors chosen for the analysis (Meusel et al., 1977).

Growth direction

Axes may be completely orthotropic, or they may be mostly orthotropic with a plagiotropic basal portion functioning as a short rhizome (Rúa and Gróttola, 1997; Fig. 3A), or they may even be completely or largely plagiotropic. In the latter case, only the inflorescence is often orthotropic, as it happens in post-generative axes of *Melica macra* (Perreta and Vegetti, 2004).

Types of shoots

Grasses may be strictly caespitose (composed only of orthotropic axes), caespitose by short rhizomes (made up by axes with an underground plagiotropic basal portion), rhizomatous, stoloniferous, and, more rarely, climbers, as in *Melica sarmentosa* (Perreta and Vegetti, 2006). Nonetheless, many taxa combine rhizomes and stolons and, sometimes, the distinction between both types is artificial, as in *Cynodon* Rich. (Gould and Shaw, 1983). Rhizomes are subterranean, with scaly leaves, and their growth may be determinate or indeterminate. Stolons are plagiotropic stems growing above the soil (Bor, 1960); they may either be similar to erect tillers or they may be highly modified, and their growth pattern is usually indeterminate (Hyder, 1974). Other structures specialized as bulbs occur in relatively few species, such as *Poa bulbosa* L. and two species of *Festuca* L. (Arber, 1934). Corms (or corm-like thickenings) occur more commonly in several genera, viz. *Poa* L., *Melica* L., *Molinia* Schrank, *Colpodium* Trin., *Arrhenatherum* P. Beauv., *Beckmannia* Host, *Hordeum* L., *Phleum* L., *Ehrartha* P. Beauv., and *Panicum* (Arber, 1934; Gould and Shaw, 1983; Tsvelev, 1983).

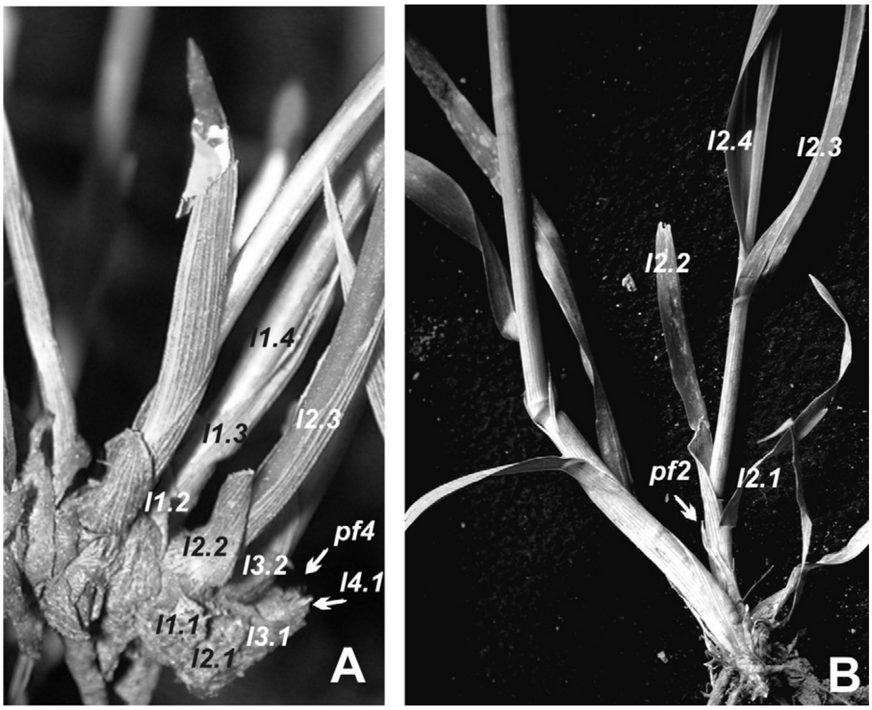

Fig. 3. (A) Extravaginal tillers in *Melica macra* Nees; (B) intravaginal tiller in *Bromus catharticus* Vahl. *Abbreviations*: In, leaf of tillers of the successive order; In.n, leaves in each tiller; pf, prophyll.

Branching

Branching may be intra- or extravaginal (Fig. 3; Clark and Fisher, 1986). In some species, shoots are only extravaginal (*Phragmites communis* Trin.) or only intravaginal (*Deschampsia cespitosa* (L.) P. Beauv.), or both types may be present (Perreta and Vegetti, 2004; Serebriakova, 1969; Tsvelev, 1983). In most Festucoideae, a combination of both types of branching is observed, although one type usually predominates over the other (Serebriakova, 1969). Depending on whether the shoots are intra- or extravaginal, a constant and significant variation takes place in the foliar sequence in a tiller and in the type of axis it originates. Extravaginal origin correlates with subterranean initial growth, while intravaginal origin correlates with aerial initial growth (Serebriakova, 1969; Tsvelev, 1983). The development of intravaginal tillers always results in the formation of compact structures. By contrast, extravaginal tillering is a prerequisite for the formation of plagiotropic growth forms (Briske, 1991).

Timing of branch emergence

Once a phytomer's axillary meristem has been formed, it may develop a lateral axis or remain latent. If the new axis develops immediately, the branching pattern is sylleptic (Halle et al., 1978; Müller-Doblies and Weberling, 1984). However, if it goes through a dormancy period, it branches in a cataleptic pattern according to Müller-Doblies and Weberling (1984) or a proleptic one according to Halle et al. (1978) and Bell (1991). Müller-Doblies and Weberling (1984) restrict the term proleptic to the early development of an organ in a species compared to the time considered normal for similar species (Rúa, 1999). In view of the terminological ambiguity, Barthélémy and Caraglio (2007) suggest using the terms immediate and deferred branching, respectively.

Another classification criterion takes into account whether lateral shoot formation occurs during the vegetative stage of the main shoot or after it makes the transition to the reproductive stage, making a distinction between early, primary or pre-generative tillering in the former case, and late, secondary or post-generative tillering in the latter case (Serebriakova, 1969). Grass species may have shoots of one type or a combination of both types (Perreta and Vegetti, 2004; Serebriakova, 1969; Tsvelev, 1983; Vegetti, 1997a).

Timing of axis flowering or senescence

In most species, axes flourish in the growing season in which they have been formed. However, in some species they may stay in the vegetative phase longer or die without flowering, as is the case with the main axis and the first order axes in *Melica macra* (Perreta and Vegetti, 2004) and *Melica sarmentosa* (Perreta and Vegetti, 2006), or they may show indefinite growth, as in *Paspalum distichum* L. (Castro-Dos Santos, 1981). After flowering, the distal portion of the axes becomes senescent while the basal portion stays alive. The basal portion generally coincides with the short internode zone, which will give origin to new innovations.

Foliar sequence

The foliar sequence is closely related to the extra- or intravaginal character of the axes and their position, i.e., whether they are aerial or subterranean. Extravaginal shoots show a short, compact prophyll, followed by scaly leaves or cataphylls and then by the fully developed leaves or, before these, by reduced-blade to normal leaves (Fig. 3A); intravaginal shoots show a long, transparent prophyll immediately followed by the first green leaf. However, there also exist transitional forms (Serebriakova, 1969; Fig. 3B). It has also been found that shoots with an intravaginal morphology, with large prophylls and no scales, always grow only intravaginally, at least initially. By contrast, shoots with an extravaginal structure may break out of the sheath, growing extravaginally, or they may remain within the sheath, growing intravaginally (Mühlberg, 1967; Serebriakova, 1969). In some species, such as *Leptochloa chloridiformis*, and others with enrichment axes in the long internode zone, both types of prophylls are present: there is a short prophyll and several cataphylls in the basal shoots and a long prophyll and true leaves in the upper shoots (Perreta et al., 2000). The smaller the prophyll is, the higher the number of cataphylls (Mühlberg, 1967).

Structure of the shoot system

The shoot system enlarges depending on the successive structural units produced. Each new structural unit or tiller is generated at a specific time and site on a higher order module. For a thorough structural analysis, the specific characteristics of the main axis and the morphological variation of the lateral shoots, as well as their spatio-temporal disposition, should be considered in combination (Serebriakova, 1969).

In annual species, the whole branching system constitutes a synflorescence and is usually characterized by a large number of branches (Rúa and Gróttola, 1997). In such species, the innovation zone is useless and should be called just a tillering zone.

Perennial species show a number of axes that flower while the remaining axes continue their vegetative growth, at least until the following year. They also have some storage or propagation organ at the base. Meristem repression along somewhat extended zones is frequently associated with perennial habits (Rúa and Gróttola, 1997). The innovation zone is typical of perennial plants and comprises a determinate number of internodes, where not all axillary buds develop. Those buds that do not develop during the growth season will develop during the next growing period (Weberling, 1985).

Spatial disposition of the shoots

In Poaceae, the spatial distribution of shoots varies significantly. On the one hand, this family shows two types of growth: one, occurring in most species, which results from the successive chain of sympodial axes, and the other, seen in species with a plagiotropic monopodial axis branching laterally, as in *Paspalum distichum* (Castro-Dos Santos, 1981). In the former case, branch distribution may be the same between the main axis and successive tillers, or it may be different. In the latter case, the plant may be formed by the combination of different types of axes, as in *Imperata cylindrica* (L.) Raeusch., where underground plagiotropic axes, eventually becoming orthotropic and flowering, combine with axes that do not grow underground and quickly become orthotropic (Castro-Dos Santos, 1981).

Axis distribution is closely related to the delimitation of different axis zones, which makes it possible to find densely or sparsely branched plants, or with a combination of both types of branching (Serebriakova, 1969). The plant branches may be limited to the basal short internode zone (with or without a rhizome-like specialization) while the meristems present at the long internode zone are completely inhibited (Rúa and Gróttola, 1997; (Figs. 1D and 4A). This type of branching pattern is common in Pooideae and Ehrartoideae (Doust, 2007a,b). In these cases, the tuft is densely branched, as it occurs in *Melica macra* (Perreta and Vegetti, 2004), *Botriochloa edwardsiana* (Gould) Parodi and *B. springfieldii* (Gould) Parodi (Vegetti and Vega, 2000), *Bromus catharticus* Vahl, *Eleusine tristachya* (Lam.) Lam., *Festuca pratensis* Huds., and *Paspalum dilatatum* Poir. (Jacques-Felix, 1961; Rúa and Weberling, 1998; Serebriakova, 1969; Vegetti, 1997a). In other species, the plant is sparsely branched along the rhizome and the culm, as in *Phragmites communis* and *Arundo donax* L. (Fig. 4B); along the stolons and the culm, as in *Themeda quadrivalvis* (L.) Kuntze and *Themeda triandra* Forssk., *Bothriochloa insculpta* (Hochst. ex A. Rich.) A. Camus, *Holcus lanatus* L. (Fig. 4C); only along the rhizome as in *Melica uniflora* Retz. (Fig. 4D); or only along the plagiotropic axis as in *Catabrosa aquatica* (L.) P. Beauv. and *Gyceria fluitans* (L.) R. Br. (Serebriakova, 1969) (Fig. 4E). However, the most frequent model is a combination of dense and sparse branching: sparse branching on the stolon and dense branching on the erect shoots (Fig. 5A), e.g. in *Agrostis stolonifera* L., *Digitaria sanguinalis* (L.) Scop., and *Stenotaphrum secundatum* (Walter) Kuntze); sparse branching on sympodial rhizomes and dense branching on aerial shoots (*Bromus auleticus*, *Briza media* L.; Fig. 5B); sparse branching on monopodial rhizomes and dense branching on aerial shoots (*Sorghum halepense* (L.) Pers.; Fig. 5C); sparse branching on stolons and rhizomes and dense branching on aerial shoots (*Pennisetum clandestinum* Hochst. ex Chiov.); sparse branching on culms and dense, rhizome-producing branching on short internodes (Fig. 5D), e.g. in *Glyceria maxima* (Hartm.) Holmb. (Mühlberg, 1967; Serebriakova, 1969). Species with a combination of short and long internodes along the axis may be densely branched, since branching is only observed on short internodes (Fig. 1E), for example, in *Eleusine indica* (Jacques-Felix, 1961).

Time-related emergence patterns of lateral shoots on the main shoot

This description encompasses the different and successive stages of a species ontogeny starting with the development of the plumular axis following germination. The sequence of these stages has significant implications for the capacity of establishment and exploration. However, the sequence of the different ontogenic stages (plantule, juvenile, virginal, first flowering, adult tuft, senescence), even though genetically determined, is highly influenced by environmental variables. As a consequence, different individuals may reach different stages at different times (Gatzuk et al., 1980; Huber, 1997).

Plantule – young plant stage (prior to first flowering)

Plantules have an axis with no branches and 2–3 fully developed leaves (Gatzuk et al., 1980). A complete description of the plantule includes determining the location and time of development of adventitious roots, the elongation (or lack of elongation) of the mesocotyl or of subsequent internodes, and the characteristics of the first leaf. A detailed analysis of these parameters and their variations is found in Hoshikawa's work (1969).

Gatzuk et al. (1980) suggest the existence of two more stages prior to flowering in *Deschampsia cespitosa*, which they call juvenile and virginal stages. Juvenile individuals also have a simple structure. They generally show small leaves and a shoot and root system that are different from those of mature plants, while virginal plants are transitions between the juvenile and the adult periods, when the typical adult tuft form becomes evident.

Senescence

Senescence is considered to start in a Poaceae tuft when about half of its surface is covered by senescent or dead axes. There are few reproductive axes and branch and root biomass production decreases; shoot death usually starts at the center of the tuft and progresses centrifugally (Gatzuk et al., 1980). However, this does not necessarily mean the individual's death, since some species may experience rejuvenation in the peripheral region of the tuft (Gatzuk et al., 1980), due to the fact that the genet becomes fragmented because of the death of the inner part. Thus, independent clones are generated, which recover the ability to grow and form new tufts.

Branching control: genes, hormones and the environment

The branching ability is the main reason for the architectural variations described (McSteen, 2009; Wang and Li, 2006). Branching from axillary meristems is under the control of hormones, genes and the environment (Doust, 2007a; McSteen, 2009; Shimamoto and Kyozuka, 2002). If plants grow under unrestricting conditions, it is possible to identify, by means of systematic observation, the endogenous sequence of development, and also to differentiate

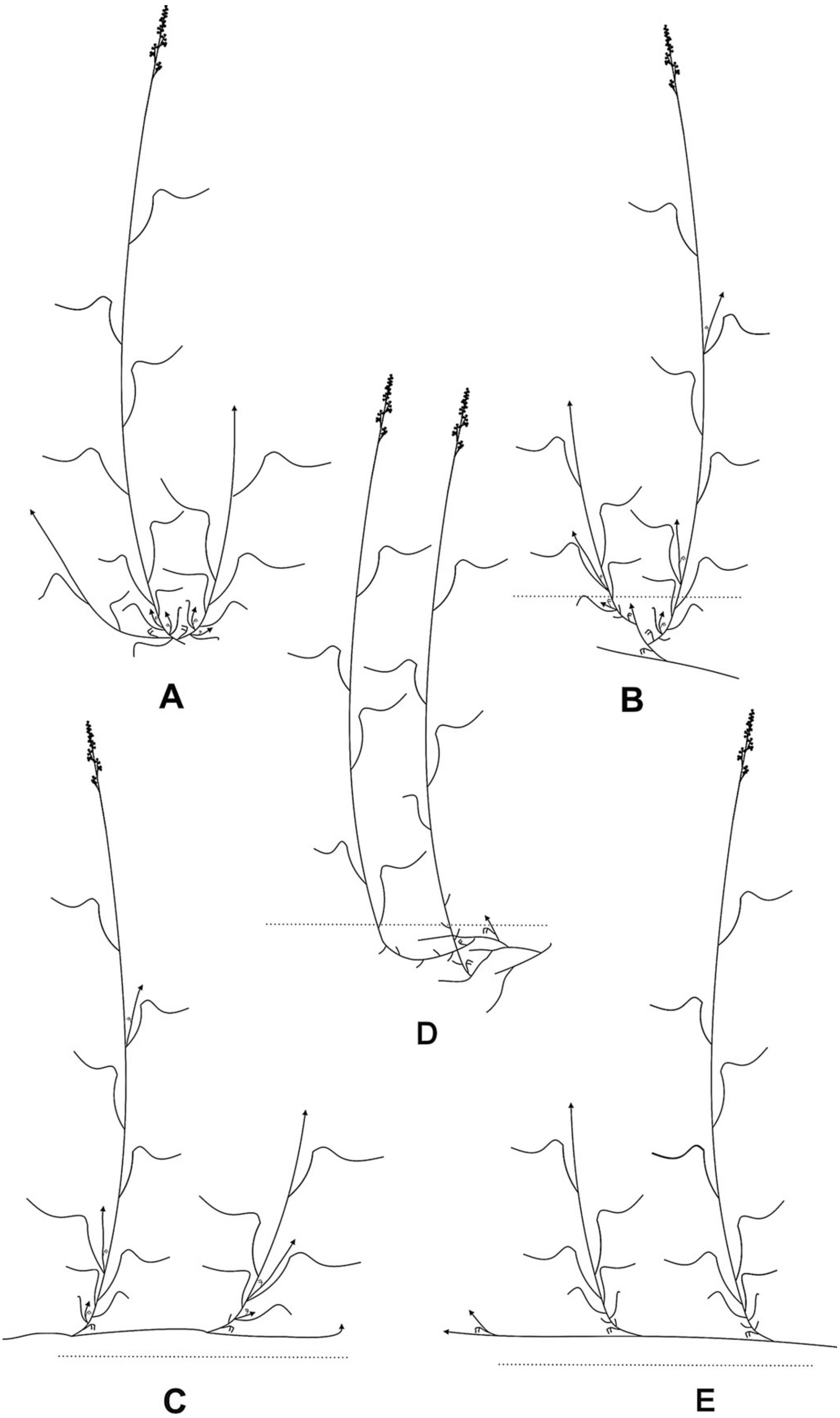

Fig. 4. Distribution of lateral shoots along the parental axis: dense and sparsely branching. (A) Branches limited to the basal short internode zone (dense branching); (B) sparse branching along the rhizome and the culm; (C) sparse branching along the stolons and the culm; (D) sparse branching only along the rhizome; (E) sparse branching along the plagiotropic axis.

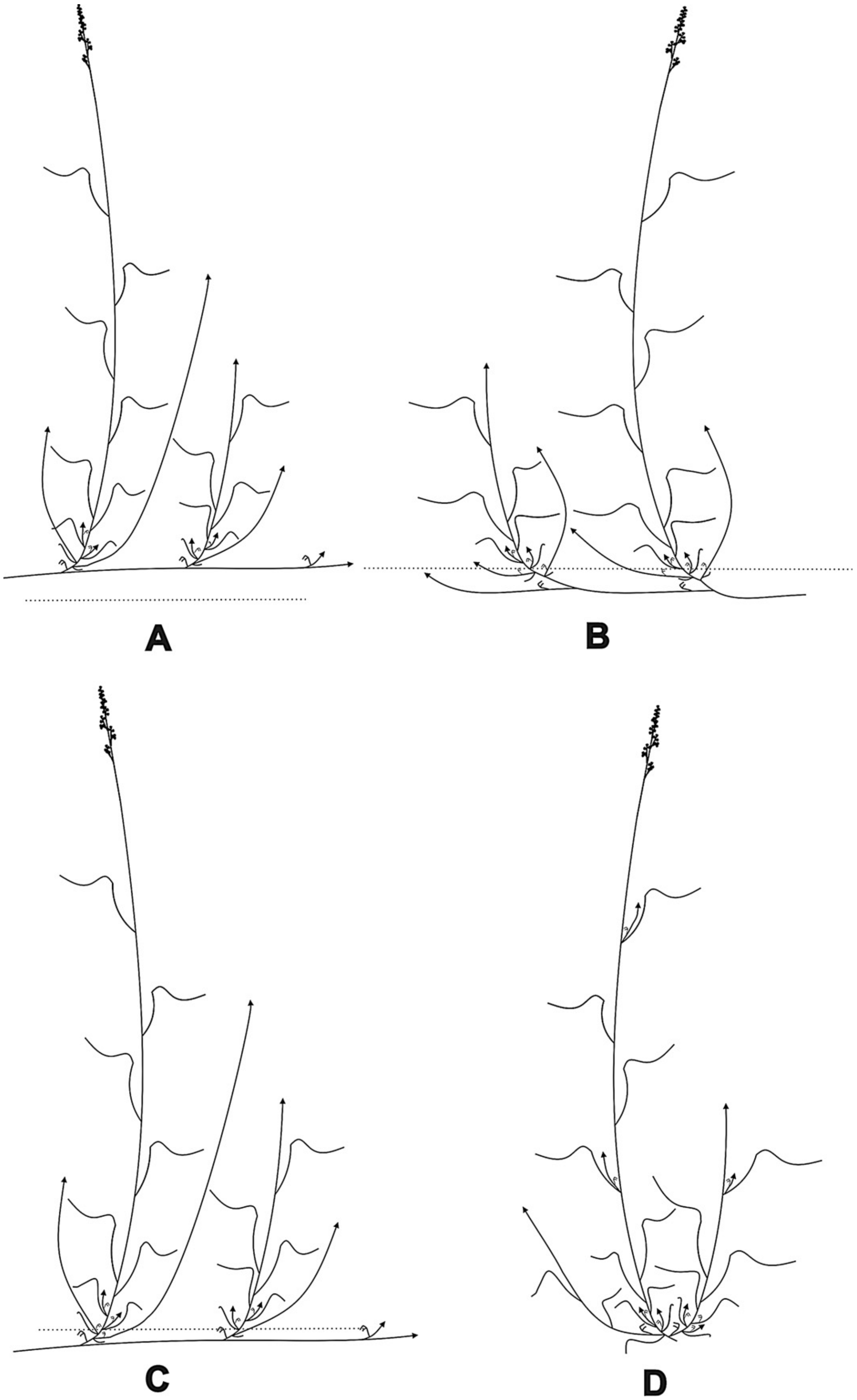

Fig. 5. Distribution of lateral shoots along the parental axis: combination of dense and sparse branching. (A) Sparse branching on the stolon and dense branching on the erect shoots; (B) sparse branching on sympodial rhizomes and dense branching on the erect shoots; (C) sparse branching on monopodial rhizomes and dense branching on aerial shoots; (D) sparse branching on culms and dense, rhizome-producing branching on short internodes.

it from environmental effects (Puntieri et al., 1995). For example, *Zea mays* L. is considered a non-tillering plant (Kiesselbach, 1949); however, even in modern varieties of corn, if provided with unrestricting growing conditions (basically adequate distance from neighboring plants) a large development of basal buds takes place (Doust, 2007a; Moulia et al., 1999).

Although the pattern of lateral organs is, to some extent, flexible in response to environmental conditions, it is essentially determined by the genetic background (Wang and Li, 2008). It has been detected through systematic observation that the behavior of axillary buds present in the basal short internode zone or in the innovation zone shows a strong genetic component that determines the presence of a well-defined pattern for each species (Rúa and Gróttola, 1997). By contrast, the promotion or repression of the development of lateral meristems located in the long internode zone, seems to be more affected by environmental variables in many species, with a fluctuation within the same species showing specimens with axillary production and specimens lacking it (Rúa and Gróttola, 1997; Rúa and Weberling, 1998). In other species, on the other hand, a permanent inhibition of these meristems exists (Rúa and Gróttola, 1997). It has been found that when the terminal inflorescence is reduced in size, axis development from axillary buds in both zones tends to be higher (Rúa and Weberling, 1998; Vegetti, 1994, 1999).

Not all axillary meristems present at different parts of the plant will produce branches – the ability to selectively suppress meristem growth in response to internal or external signals is a strategy that allows the plant to control its form (McSteen, 2009). These formed, but unused meristems remain available for a quick re-growth following damage (Doust, 2007a). The dormant buds will release their outgrowth upon sensing permissible environmental or developmental signals, through which the plant sustains its species-specific shoot system development (Wang and Li, 2008).

The development of shoot branches undergoes two distinct stages: the initiation of a new axillary meristem and the outgrowth of axillary buds with or without dormancy (Doust, 2007a; Wang and Li, 2006). Many genes have been identified in different species of Poaceae regulating these stages (Doust, 2007b; McSteen and Leyser, 2005; McSteen, 2009; Wang and Li, 2006, 2008). Hormones appear to play a key role in the initiation and subsequent growth of axillary meristems. Some of the genes related to branching encode integral components of hormone biosynthesis, perception, or signaling pathways (McSteen, 2009).

As regards the environment, many factors affect branching, such as planting density – respective site competition with other plants in natural habitats –, shading and fertility levels (Doust, 2007b). These responses involve numerous gene–environment relationships that are associated with various effects on plant morphology (Doust, 2007a). Much work has been done in major cereal crops to elucidate the environmental conditions that contribute to variation in branching, and to identify genome regions and genes that control branching (Doust and Kellogg, 2006; Lafarge et al., 2002). But a comprehensive understanding of how axillary meristems at different stages of development respond to genetic, environmental, and hormonal factors is still lacking (McSteen, 2009). Future work promises to integrate knowledge of phenotypic responses to environment with the understanding of the genetic and hormonal changes that underlie the phenotypic changes (Wang and Li, 2006).

Conclusion

The broad spatio-temporal characterization of the branching system of Poaceae makes possible a complete description of plant structures in this family. Thus, key times during development may be identified, the branching process may be understood, and knowledge and interpretation of the invading capacity, as well as of the productive uses of different species may be advanced. Information on growth models, the forms of exploring the space, and patterns of species dispersion will allow recognizing different patterns of growth and structures. Within the family, a detailed characterization of the branching system in the different genera, tribes and subfamilies, based on this unified system of morphological patterns, will contribute to using the growth form typology in taxonomic and phylogenetic studies.

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