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Growth forms in Pappophoreae (Poaceae)

Juan Carlos Tivano, Abelardo Carlos Vegetti*

Morfología Vegetal, Facultad de Ciencias Agrarias, Instituto de Agrobiotecnología (CONICET-Universidad Nacional del Litoral), Kreder 2805, S3080HOF Esperanza, Santa Fe, Argentina

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ABSTRACT

The architecture of the branching system in species of Pappophoreae (Poaceae) has not been studied in detail. This work covers the spatial and temporal variation of the shoot system in species of *Cottea*, *Enneapogon*, *Kaokochloa*, *Pappophorum* and *Schmidtia* (Pappophoreae). Growth form variation of the species of Pappophoreae is related to the different functions of the axillary buds. We identify six growth form models within Pappophoreae. These models represent reference points along a *continuum* of variations that are characteristic of certain genera or species within a genus.

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1. Introduction

Gramineae have been considered to have a great diversity at the level of inflorescences above an architecture of the vegetative parts that is essentially homogenous (Cremers and Sell, 1986). However, such homogeneity is not so evident when the structure of the entire plant is analyzed to study its growth form (Mühlberg, 1966). The growth form has been defined as a complex of genetically constant vegetative and reproductive characters, which vary within a range of phenotypic plasticity (Meusel, 1952, 1970). It determines the habit of the plant and the spatial and temporal adaptation to its environment (Meusel, 1970). The study of growth forms takes into account the successive stages that govern the construction of the plant body from its germination (Meusel, 1952) through its distinct phenological phases (Meusel et al., 1977).

A comprehensive, dynamic analysis of the shoot branching system in Poaceae makes it possible to establish taxonomic and phylogenetic relationships (Meusel, 1970) and, consequently, it has important ecological and agronomic management implications (Fournier, 1982; Bernard, 1990; Perreta et al., 2000).

Mühlberg (1966, 1970), Serebriakova (1969), Rúa and Gróttola (1997), Vegetti (1997, 2002), Rúa and Weberling (1998), Perreta et al. (2000) and Perreta and Vegetti (2004, 2006) provide information about growth forms in Gramineae species; however, studies in this matter are not common.

Pappophoreae s. l. includes five genera, namely *Cottea* Kunth, *Enneapogon* N. A. Desv. ex P. Beauv., *Kaokochloa* Winter,

Pappophorum Schreber and *Schmidtia* Steud. *Pappophorum* and *Cottea* are exclusively American, *Enneapogon* grows in warm regions of America, Africa, Asia and Australia, *Schmidtia* and *Kaokochloa* are African genera. These are aestival species, typical of semiarid areas and open habitats (Nicora and Rugolo de Agrasar, 1987). Some of these species are important forage for the marginal areas (Dalmasso et al., 1983; Dalmasso, 1994; Guevara et al., 1996).

The architecture of the branching system of the shoot in Pappophoreae has not been studied in detail. This work covers the spatial and temporal variation of the shoot system in species of *Cottea*, *Enneapogon*, *Kaokochloa*, *Pappophorum* and *Schmidtia*.

2. Materials and methods

Field-collected and greenhouse-grown live plants (Agronomy School at the Universidad del Litoral, Argentina) as well as herbarium specimens from seven different herbaria (CTES, LIL, BAA, SI, LP, CANB, PRE) were studied under a stereoscopic microscope (Table 1).

The following characters relating to the growth form were studied: internode length, growth direction, position of adventitious roots, branch disposition, leaf types and spikelet disposition. These characters were analyzed in their spatial and temporal variations.

The inflorescence was considered as a unit of inflorescence in the sense of Vegetti and Müller-Doblies (2004). Description of inflorescences for species of the Pappophoreae is the object of another work (Tivano and Vegetti, 2004).

Terminology and abbreviations used follow those of Rúa and Weberling (1998) and Vegetti and Müller-Doblies (2004).

* Corresponding author.

E-mail address: avegetti@fca.unl.edu.ar (A.C. Vegetti).

Table 1
Material studied.

Species	Voucher
<i>Cottea pappophoroides</i> Kunth	20748 1/2 (BAA); Cabrera et al. 14998 (BAA); Cámara Hernandez 154 (BAA); Marchessi et al. (BAA); Kunst et Perez 2 (CTES); Saravia Toledo et al. 12680 (CTES); Ballespin s/n. (LP); Biraben et Biraben 1152 (LP); Cabrera et al. 13354 (LP); Cabrera et al. 19763 (LP); Cabrera et al. 24552 (LP); Covas 1166 (LP); Kurtz 13378 (LP); Morello et Cuevo 210 (LP); Reales 1798 (LP); Ahumada 4474 (SI); Cabrera et al. 30712 (SI); Hunziker 5018 (SI); Kiesling 4696 (SI); Kiesling et Saenz 4044 (SI); Nicora et al. 9160 (SI); Nicora et al. 9103 (SI); Nicora 17540 (SI); Nicora 18525 (SI); Priotti 98938 (SI); Semper s/n (SI); Venturi 1124 (SI). Biurrun 6473; Renolfi 210.
<i>Enneapogon asperatus</i> C.E. Hubb	Lazarides 4049 (CANB); Blake 11518 (CANB); Lazarides 3991 (CANB); Lazarides 4801 (CANB).
<i>Enneapogon avenaceus</i> (Lindl.) C. E. Hubbard	Chippendale 579 (CANB); Christian 931 (CANB); Gardner 3281 (CANB); Latz 2302 (CANB); Moore 5069, 5813 (CANB); Perry 985 (CANB); Winkworth 265 (CANB).
<i>Enneapogon brachystachyus</i> (Jaub. & Spach) Staff	Werger 143 (PRE).
<i>Enneapogon caerulescens</i> (Gaud.) N. T. Burbidge	Payne 1392 (CANB); Perry 5564 (CANB); Speck 643 (CANB); Strid 20143 (CANB).
<i>Enneapogon cenchroides</i> (Licht.) C.E. Hubbar	Camerik 1023 (CANB); Hubbard 1805 (CANB); Robinson 362 (CANB); Smook 10089 (CANB); N Van Rooyen 3220 (PRE); Owens 92 (PRE); Smook 9132 (PRE); Leipert 6363 (SI); SI 28305; SI 28306; Wilman (SI).
<i>Enneapogon cylindricus</i> N. T. Burbidge	Blake 11645 (CANB); Blake 17885 (CANB); Forde 394 (CANB); Perry 3265 (CANB); Mitchell S/N (CANB); Huerto 637 (SI).
<i>Enneapogon decipiens</i> Kakudidi	Blake 17728 (CANB); Blake 17587 (CANB); Winkworth 1072 (CANB); Wolfe et Martin 57 (CANB).
<i>Enneapogon desvauxii</i> P. Beauv.	Dawson 21 (BAA); Brzostowski 1029 (CANB). Neie 5 (CANB); Lobely 37 (CANB); Smook 5258 (CANB); Reales 1796 (CTES); Bridarolli 1631 (LP); Cabrera et al. 23557 (LP); Fabris et Crisci 6826 (LP); Fabris et Crisci 7445 (LP); Germishuizen 8254 (PRE); Jürgens 28878 (PRE); Smook 3524 (PRE); Smook 7996 (PRE); Gomez-Kapla 064 (SI); Kiesling 7871 (SI); Morello 1052 (SI); Pedersen 15250 (SI); SI 28037;
<i>Enneapogon elegans</i> (Nees) Stapf	Verdcourt 2575 (CANB).
<i>Enneapogon eremophilus</i> N. Burt.	Cumming 17503 (CANB); Perry 986 (CANB); Story 7136 (CANB).
<i>Enneapogon gracilis</i> (R. Br.) Beauv.	Burbidge 5411 (CANB); Prober S/N (CANB); Rubbard 7980 (CANB).
<i>Enneapogon intermedius</i> N. T. Burbidge	Blake 13978a (CANB); Lazarides 4395 (CANB); Moore 7358 (CANB); Roe 142 (CANB).
<i>Enneapogon lindleyanus</i> (Domin.) C. E. Hubbard	Beaumont 7058 (CANB); Blake 6188 (CANB); Blake 6276 (CANB); Blake 6974 (CANB); Blake 8655 (CANB); Blake 13978a (CANB); Pullen 10917 (CANB); Thomas 165 (CANB).
<i>Enneapogon nigricans</i> (R. Br.) Beauv.	Burbidge et Gray 4069 (CANB); Hubbard 5643 (CANB); Pullen 1284 (CANB); Taws 1118 (CANB).
<i>Enneapogon pallidus</i> (R. Br.) Beauv.	Beaglehole 39249/Errey 2989 (CANB); Blake 17224 (CANB); Symon 5048 (CANB); Waddy 779 (CANB).
<i>Enneapogon polyphyllus</i> (Domin) Burbidge	Aplin 4660 (CANB); Aplin 4819 (CANB); Blake 6189 (CANB); Blake 17588 (CANB); Blake 17904 (CANB); Martensz 2206 (CANB); Martensz 4538 (CANB); Rust 33 (CANB); Symon 1416ob (CANB).
<i>Enneapogon pretoriensis</i> Stent.	Archer 124 (PRE); Du Toit 619 (PRE); Theron 2106 (PRE).
<i>Enneapogon purpurascens</i> (R. Br.) Beauv.	Black 6 (CANB); Blake 17884 (CANB); Pajmans 2248 (CANB); Pullen 10810 (CANB).
<i>Enneapogon robustissimus</i> (Domin) N. T. Burbidge	Cumming 17352 (CANB); M _c Kee 8609 (CANB); George 10653 (CANB).
<i>Enneapogon scaber</i> Lehm.	Jurgens 22693 (CANB); Oliver et al. 263 (CANB); Smook 6816 (PRE); Smook 8028 (PRE) (CANB); Stirton 6013 (PRE); 22-II-89 (PRE).
<i>Enneapogon scoparius</i> Stapf	S/Col. 6534 (CANB); Davidse 5881 (PRE) (CANB); Gubb 268-R (PRE); Leistner et al. 86 (PRE); Smook 2057 (PRE); Smook et Gibbs 2156 (PRE); Smook 7659 (CANB).
<i>Enneapogon spathaceus</i> Goznes	Fischer et Schweickerdt 543 (PRE).
<i>Enneapogon truncatus</i> Kakudidi	Blake 5725 (CANB); Blake 8024 (CANB); Blake 10723 (CANB); Burbidge 5111 (CANB).
<i>Enneapogon virens</i> Kakudidi	Adams 1159 (CANB); Adams 1176 (CANB); Everist 2814 (CANB); Moore 7631 (CANB);
<i>Kaokochloa nigrirostris</i> de Winter	Nordenstam 3718 (PRE); Smook 7765 (PRE).
<i>Pappophorum alopecuroides</i> Vahl.	Nicora 7107 (BAA).
<i>Pappophorum caespitosum</i> Fries	Boelcke et al. 9907 1/2 (BAA); Gomez 7316 (BAA); Parodi 7848 (BAA); M. Crovetto Ap99 (CTES); Schulz 5822 (CTES); Arias 47 (LIL); Cuezco 2061 (LIL); Isasmendi et al. 93 (LIL); Baez 32 (LP); Cabrera 12393 (LP); Contardi 7 (LP); Guiñazu 43, (LP); Guiñazu 23 (LP); Cabezas 23170 (SI); Cabrera 30101 (SI); Cabrera et al. 31608 (SI); Burkart 12236 (SI); Guaglianone et al. 1348 (SI); Hunziker 4726 (SI); Kiesling et Saenz 4035 (SI); Kiesling et al. 5968 (SI); Nicora et al. 8785 (SI); Pedersen 15249 (SI); Spegazzini 13353 (SI).
<i>Pappophorum hassleri</i> Hackel	Soria 6805 (CTES);
<i>Pappophorum krapovickasii</i> Roseng.	Adamoli Baa 16189 (BAA); Morello 1229 (BAA); Parodi 14027 (BAA); Krapovickas et Cristobal 24530 (CTES) (BAA); Schinini et Borda 16490 (CTES); Schinini 30424 (CTES); Krapovickas et Legname 10916 (LIL); Arenas 1744 (SI); Krapovickas et Schinini 31340 (SI); Musch. 113 (SI).
<i>Pappophorum macrospermum</i> Roseng.	Schinini et al. 17363 (CTES).
<i>Pappophorum mucronulatum</i> Nees	Bridarolli 1220 (BAA); Cano et Camara 278 (BAA); Ruiz Leal 17188 (BAA).
<i>Pappophorum pappiferum</i> (Lam.) OK.	Spegazzini S/N (LP); Schulz 3303 (SI); Schulz 3885 (CTES); Boffa 1115 (LP); Cámara Hernandez 75 (BAA); Nicora 1759 (SI); Bruch S/N (LP); Parodi 6477 (BAA); Asp 22 (SI); Boelcke 1583 (SI); Pedersen 10055 (CTES); Burkart 6578 (SI); Burkart 20250 (SI); Parodi 14585, (BAA); Abbiatti et Claps 622 (LP); Abbiatti et Claps S/N (LP); Legname et al. 5246 (LIL); Piccinini et Petetin 2868 (CTES); Venturi 2546 (LP); Villa Carenzo 413 (LIL); Schinini et Palacios 25752 (CTES).
<i>Pappophorum philippianum</i> Parodi	Joergensen 1355 (SI); Cabrera 1147 (LP); Ponessa S/N (LIL); LP 007716 (LP); Sanchez et Arriaga 1342 (SI); Fernandez 503 (CTES); Hicken 38/10680 (SI); Burkart 12214 (SI); Parodi 7764 (BAA); Burkart 12207 (SI); Maccola P.113 (BAA); Covas 3589 (SI); Covas 1521 (SI); Melis et Paci 288 (CTES); Ruiz Leal 9256 (BAA); Schulz 6182 (CTES); Nicora et al. 8349 (SI); Kiesling et Saenz 4052 (SI); Gez 24 (SI); Bruch - Carette 123 (SI); -LI-14 ; S/N (LP); S/N (LP); Job 850 (LP); Villa Carenzo 412 (LIL); Venturi 2439 (SI); Legname et Cuezco 9426 (LIL); Venturi 1068 (SI); Venturi 2328 (LP); Rodriguez 248 (BAA); Morello 1229 (SI).
<i>Pappophorum saccharoides</i> Griseb.	Böcher et al. 2211 (BAA); Spegazzini 57954 (BAA).
<i>Pappophorum subbulbosum</i> Arech.	Castellanos Ba28/1054 (BAA); Martilliti S/N (BAA); Nicora 5514 (BAA); Valla 10 (BAA); Burkart 15802 (SI); Burkart 15841 (SI); Burkart 17775 (SI); Burkart 25606 (SI); Burkart 28163. SI 13354 ; Cabrera 8046 (SI); Nicora 3042 (SI); Saravia Toledo 1280 (SI).
<i>Pappophorum vaginatum</i> Buckley	Parodi 4826 (BAA); Krapovickas 1953 (LIL).
<i>Schmidtia kalihariensis</i> Stent	Smook 5148 (CANB); Gibbs et Smook 5577 (PRE); Leistner et al. 1712 Bb (PRE); Moss et Jacobsen K270 (PRE); Van Rooyen 3701 (PRE).
<i>Schmidtia pappophoroides</i> Steud.	Gonde 33/73 (CANB); Shantz 243 (CANB); Smith 11 (CANB); Smook 10082 (CANB); Camerik 44 (PRE); Coetzee 1189 (PRE); Du Toit 46 (PRE); Smook 9056 (PRE).

Abbreviations: BAA, Herbario "Gaspar Xuaez"; CANB, Australian National Herbarium; CTES, Herbario del Instituto de Botánica del Nordeste; LIL, Herbario Fanerogámico de la Fundación Miguel Lillo; LP, Herbario del Museo de La Plata; PRE, Pretoria, National Herbarium; SI, Herbario del Instituto de Botánica "Darwinion".

3. Observations

3.1. Common structural pattern

3.1.1. Description of the structural unit

In all investigated species the plant is composed of a group of shoots of consecutive branching order (Figs. 1 and 2). Each shoot is an innovation axis representing the growth form unit of the plant. In these shoots (Fig. 1B) we can recognize the unit of inflorescence (UIF) and the trophotagma (TT). The trophotagma bears proximal cataphylls and foliage leaves; it usually comprises a proximal zone with short internodes (SIZ) and a distal one with elongated internodes (LIZ).

The buds of the SIZ form axes that can flower in the same season as the mother axis, or in the following year—these are sylleptic or cataleptic shoots, respectively. These shoots represent innovation axes and, consequently, the SIZ represents an innovation zone. Cleistogamous spikelets develop in this innovation zone in a few species. When this happens, the SIZ also becomes an enrichment zone. The SIZ can show variations in the number and

length of its internodes, and in the depth at which they are disposed, consisting of a subterranean part and an aerial region. The proportion between both regions depends on the species, and within the same species, on the depth at which the axillary shoot is formed. The adventitious radical system develops in the proximal part of the SIZ.

The LIZ may represent either an enrichment zone or an inhibition zone. If the buds in this zone do not develop, then the LIZ represents an inhibition zone (Fig. 1A). However, some buds can generate floriferous shoots, and then the LIZ behaves partially as an inhibition zone and partially as an enrichment zone (Figs. 1B and C; Fig. 2). The axillary buds of the LIZ in Pappophoreae (Figs. 1 and 2) can generate two types of enrichment axes: (1) an axis with a prophyll, developed leaves and an exposed UIF; (2) an axis with a reduced UIF with one to a few spikelets, hidden in the leaf sheath.

3.1.2. The structure of the whole plant

The plant (Figs. 1 and 2) is formed by basal axillary shoots of consecutive branching order. These shoots are morphologically

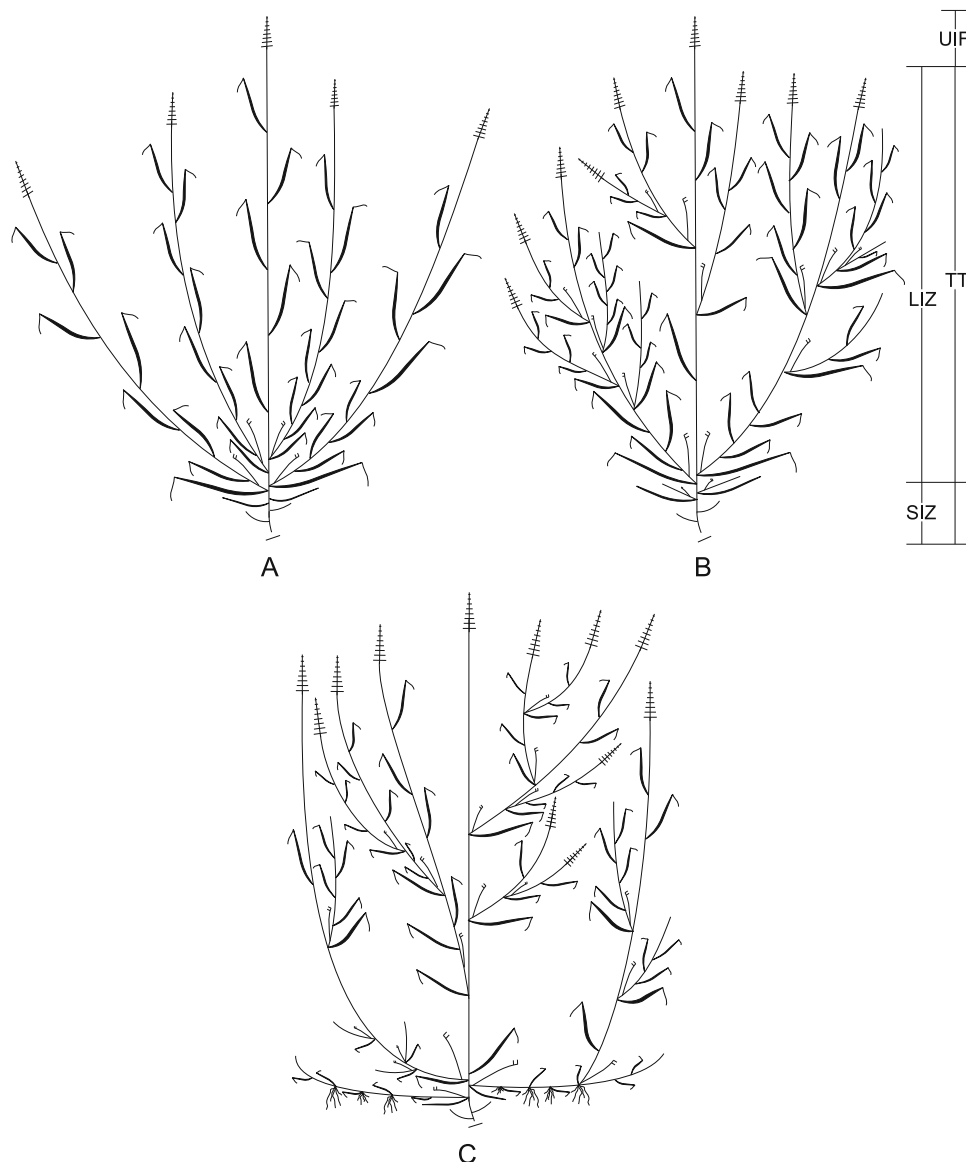


Fig. 1. Growth forms in Pappophoreae: (A) *P. pappiferum*; (B) other species of *Pappophorum*, species of *Schmidtia* and species of *Enneapogon* without cleistogamous spikelets; (C) *Kaokochloa nigrirostris*. Abbreviations: LIZ, long internode zone; SIZ, short internode zone; TT, trophotagma; UIF, inflorescence unit.

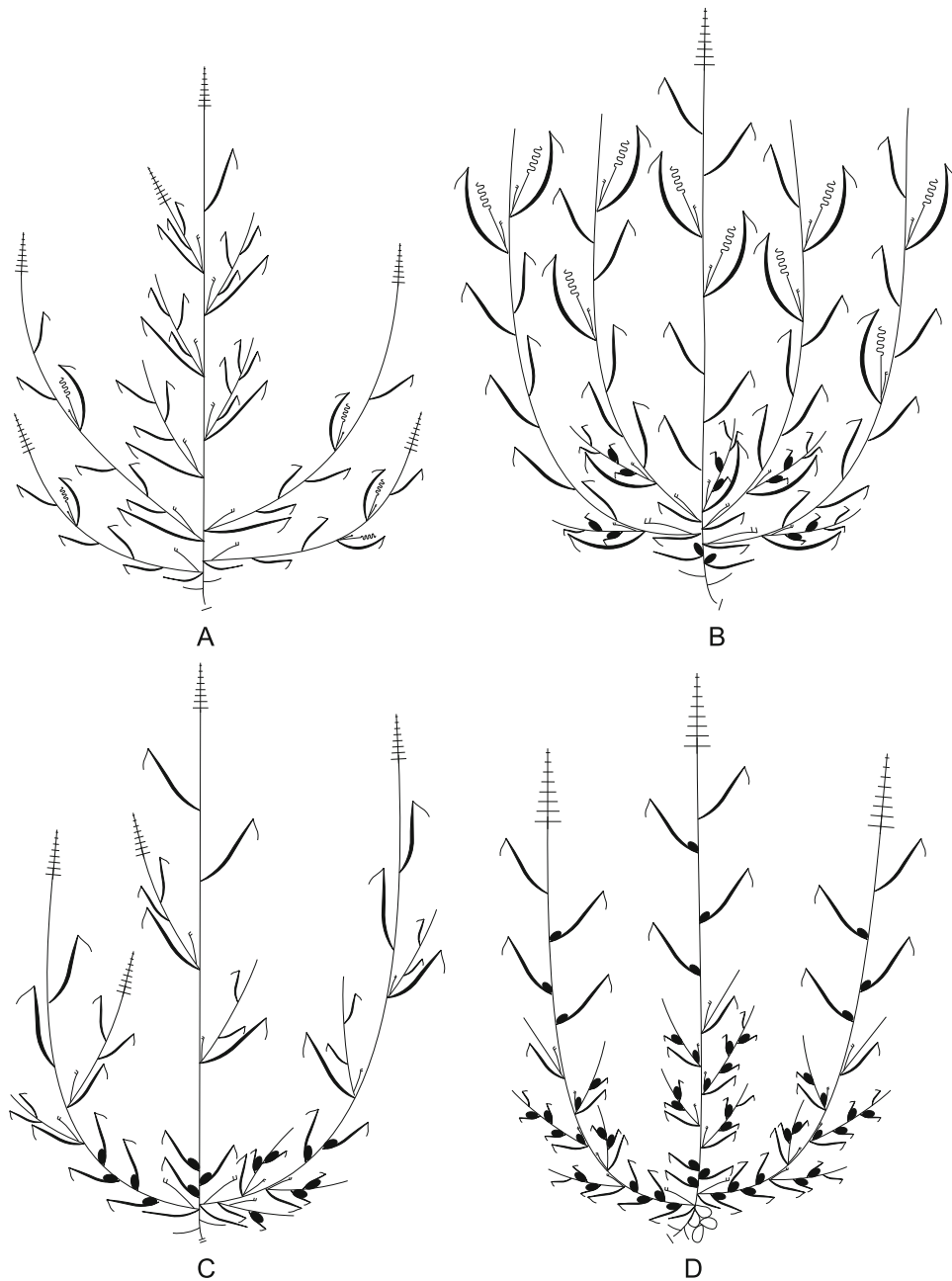


Fig. 2. Growth forms in Pappophoreae: (A) *Enneapogon asperatus*; (B) *E. cylindricus*; (C) *E. caerulescens* and *Enneapogon desvauxii*; (D) *Cottea pappophoroides*.

equivalent and they diversify in the branching hierarchy. They are linked sympodially and form the tussock by iterative innovation. In the plant already established, the innovation axes maintain their interrelation through short rhizomes (Figs. 1 and 2). These short rhizomes correspond to the thickened, cataphyll-covered proximal plagiotrope part of the SIZ of old shoots. The buds of these short rhizomes vary in size and degree of differentiation. All of the species covered in this study are caespitose with short rhizomes except for *Kaokochloa* (Fig. 1C), which has plants with prostrate branches.

Due to the slight development of the cataphylls, the axillary shoots of the SIZ, which grow plagiotropically for a short time, develop intravaginally, and so do the enrichment shoots of the LIZ (Figs. 3 and 4).

3.1.3. *Cottea pappophoroides*

Cottea pappophoroides is a perennial species. Its SIZ is reduced in length (5–6 mm), it has numerous very short internodes, numerous cataphylls and, to a great extent, it grows under ground. The characteristics of the cataphylls depend upon the soil depth at which each shoot originates. The LIZ, which is 150–515 mm long, consists of 6–8 internodes (Table 2).

Each axillary shoot (sympodium) of the SIZ consists of a prophyll, four cataphylls and a vegetative apex, which, in the course of the following year, can generate an aerial orthotropic shoot with a terminal UIF. The axillary buds of the third and fourth cataphyll of the sympodium form a cleistogamous spikelet, covered by the prophyll and one cataphyll (Fig. 5D). From the axillary bud of the second cataphyll originates a new sympodium of similar characteristics (Fig. 5D). As a consequence of this

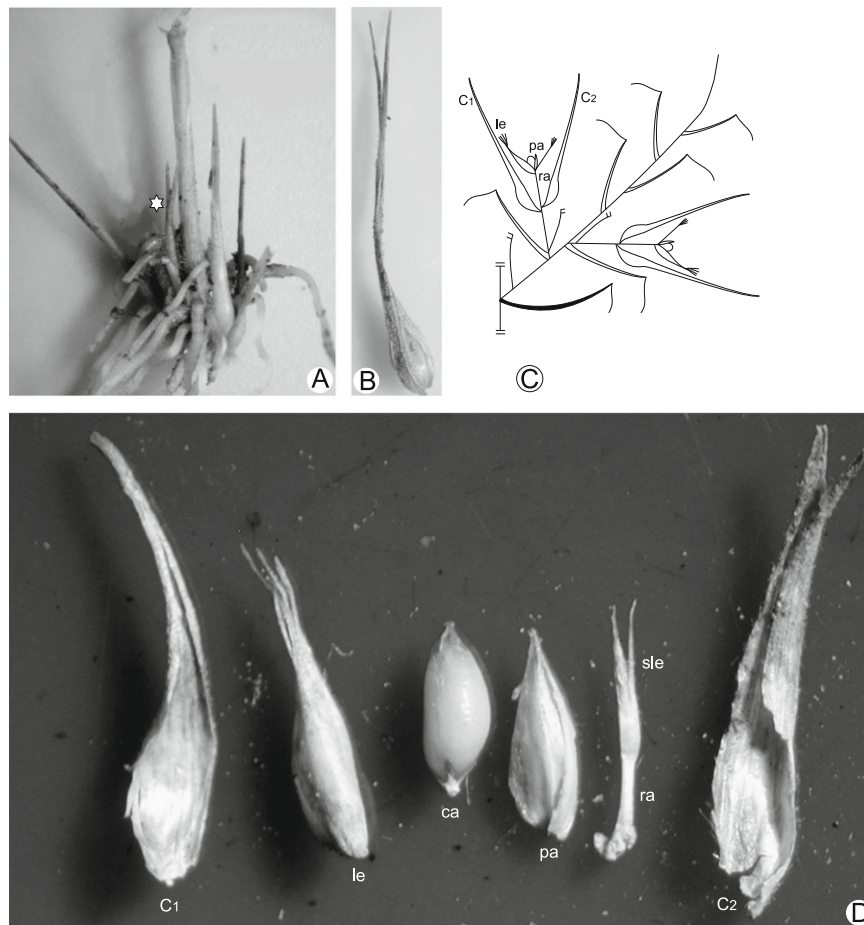


Fig. 3. *Enneapogon desvauxii*: (A) Basal cleistogamous spikelets; (B) one cleistogamous spikelet (white asterisk in A); (C) diagram of an innovation axis with two cleistogamous spikelets; (D) longitudinal section of the cleistogamous spikelets shown in B. Abbreviations: c_1, c_2 , cataphylls; ca, caryopsis; le, lemma; pa, palea; ra, rachilla; sle, sterile lemma.

iteration, the first five internodes (including a very reduced hypopodium) of each innovation form by substitution a short plagiotrope rhizome. Thus, they form chains of linked sympodia (Figs. 5C and 6). Formation of various series of sympodial shoots, which surround the base of the plant may be observed at the level of the SIZ. The large number of such sympodial innovations, the short distance separating them, the abundant radical system associated with them and the development of large fruits at the cataphylls 3 and 4 of each sympodium make both the plant base and the subterranean part very complex in structure (Fig. 5A). The subterraneously located caryopses germinate linked to the mother plant (Fig. 7). In the seedling we observe the formation of the first subterranean sympodium with caryopsis (Figs. 7E and F).

Two types of axes of enrichment develop in the LIZ (Fig. 2D): (1) those consisting of one very reduced UIF formed by one or a few cleistogamous spikelets, and (2) those bearing a prophyll, leaves and an exposed UIF. In the latter, the axillary buds of their prophylls and their leaves generate cleistogamous spikelets hidden in the leaf sheaths. These cleistogamous aerial UIF can be formed by 1–3 spikelets (Fig. 4). The UIF formed by one spikelet (Fig. 4A, B and F) consists of one prophyll and one cataphyll (which functions as glumes), a basal fertile antherium formed by the lemma, palea, the caryopsis and a rachilla that bears a rudimentary sterile upper lemma. The UIF formed by three spikelets (Figs. 4C–E, G and H) consists of one prophyll and three cataphylls. The basal spikelet develops from the axillary bud of the prophyll; the following one develops from the axillary bud of

the first cataphyll, and the third spikelet can originate from the terminal bud of this branch.

Both in the SIZ and in the LIZ the axillary buds can generate enrichment axes that bear very reduced UIF, with cleistogamous spikelets, and remain hidden by the leaf sheaths (Fig. 2D). In the distal part of the SIZ and in the LIZ, these UIF are basal aerial ones while in the proximal part of the SIZ they are subterranean. In this species, the entire synflorescence axis behaves as a zone of enrichment (Fig. 2D).

Another peculiarity is the intensive proliferation of adventitious roots associated to the proliferated subterranean cauline system. These roots develop above the axillary bud on a one per node basis.

3.1.4. *Enneapogon*

The species of *Enneapogon* are perennial, rarely annual. They have a SIZ with few internodes (3–8, *E. asperatus*, *E. avenaceus*, *E. cenchroides*, *E. decipiens*, *E. desvauxii*, *E. elegans*, *E. eremophilus*, *E. gracilis*, *E. intermedius*, *E. lindleyanus*, *E. nigricans*, *E. pallidus*, *E. polyphyllus*, *E. purpurascens*, *E. robustissimus* and *E. virens*) or with many internodes (more than 8, *E. caerulescens*, *E. cylindricus*, *E. pretoriensis*, *E. scaber*, *E. spataceus*, and *E. truncatus*); and a LIZ that may comprise 3–12 internodes (Table 2). The adventitious roots develop in the SIZ, usually one root per node.

In *E. desvauxii*, *E. caerulescens* and *E. cylindricus* the axillary buds of the basal 2–3 cataphylls of each innovation shoot bear an enrichment axis with cleistogamous spikelets (Figs. 2B and C). In

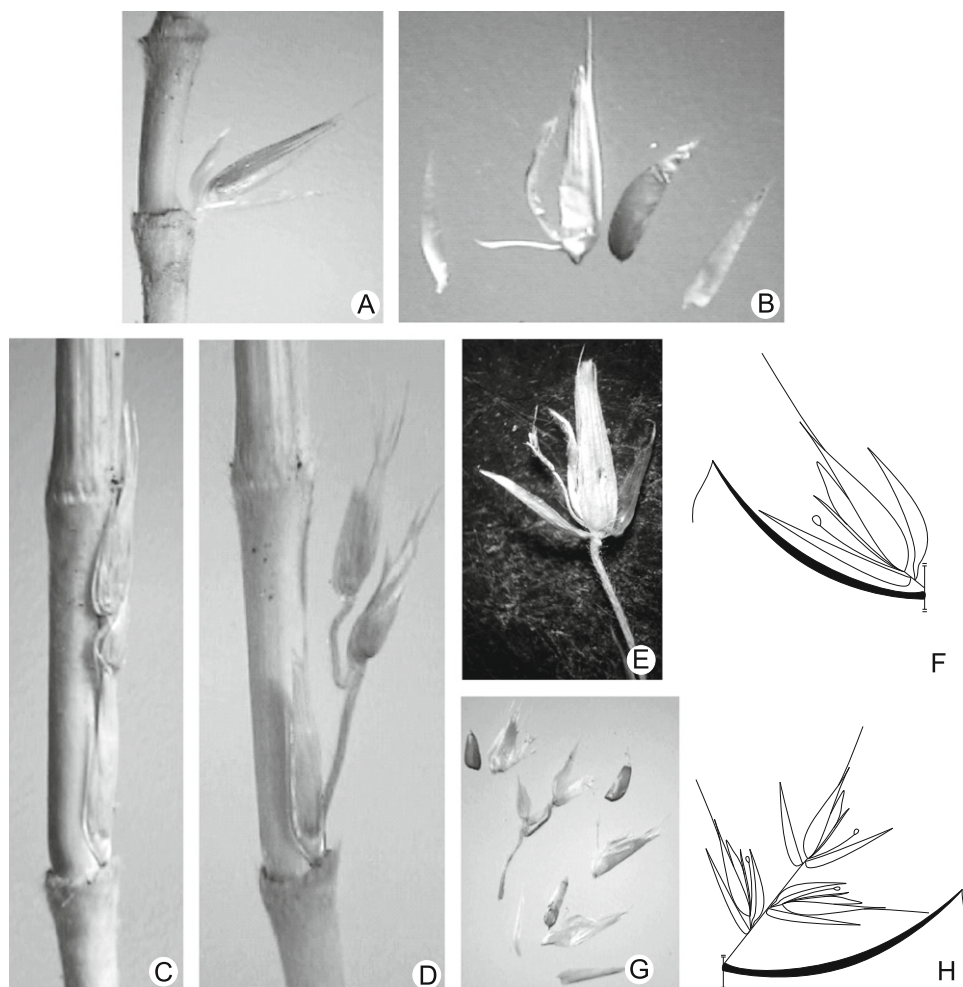


Fig. 4. Branching in the zone of long internodes in *Cottea pappophoroides*: (A), (B), (F) branch with one cleistogamous spikelet; (C), (D) branch with three cleistogamous spikelets; (E) detail of the distal spikelet in D; (G) isolated parts of the disassembled branch shown in D; (H) diagram of the branch with three cleistogamous spikelets.

E. desvauxii, this shoot (Fig. 3C) consists of a prophyll, two cataphylls, and a certain number of foliar primordia together with the terminal bud of the axis. This bud will finally form one exposed UIF. From the axil of the basal cataphyll (and, in most samples, also from the second cataphyll), a highly reduced enrichment axis is formed (Figs. 3B and D). This axis consists of the prophyll and 2 (-3) cataphylls, a coriaceous lemma with 5–6 awns, a membranaceous palea, 1 caryopsis, the rachilla and a rudimentary sterile lemma (a unifloral cleistogamous spikelet) in its distal end. When only the axillary bud of the basal cataphyll develops, the innovation axis appears as pseudolateral due to the intensive growth of its caryopsis.

The variations in the growth form of the studied species result from the function of the buds of the SIZ and the LIZ (Table 2). *E. cylindricus* (Fig. 2B) has a SIZ that functions as an innovation zone and partly as an enrichment zone. In the LIZ, it shows three types of shoots: those ending in an exposed UIF, those that bear cleistogamous inflorescences hidden in the upper and middle foliar sheaths, and those which are reduced to a cleistogamous spikelet hidden in the foliar sheath. *E. asperatus* (Fig. 2A) has a SIZ that functions as an innovation zone and a LIZ, which shows two types of enrichment axes: those terminating in an exposed UIF and others bearing a cleistogamous inflorescence hidden in the upper leaf sheaths. *E. caerulescens* and *E. desvauxii* (Fig. 2C) have a SIZ that functions partly as a zone of innovation and partly as a zone of enrichment and a LIZ that has two types of enrichment axes: those ending in an exposed UIF, and those that

bear shoots reduced to cleistogamous spikelets hidden in the basal sheaths.

In the rest of the studied species (Fig. 1B), the SIZ functions as a zone of innovation and the LIZ bears only axes of enrichment terminating in an exposed UIF. Within this group, variations are related to the number and length of the internodes of the LIZ (Table 2).

The LIZ is observed to be ramified throughout its extension in *E. caerulescens*, *E. decipiens*, *E. gracilis*, *E. intermedius*, *E. lindleyanus*, *E. pallidus*, *E. polyphyllus*, *E. scaber* and *E. scoparius*; or intensively ramified only at the base in *E. gracilis*, *E. pallidus* and *E. polyphyllus*. The LIZ is less ramified in *E. asperatus*, *E. avenaceus*, *E. cenchroides*, *E. desvauxii*, *E. eremophilus*, *E. purpurascens*, *E. robustissimus* and *E. spataceus*; slightly ramified in *E. nigricans*, *E. truncatus* and *E. virens*; and unbranched in *E. elegans* and *E. pretoriensis*. The maximum degree of ramification observed in the LIZ is tertiary (*E. caerulescens*).

The disarticulation of the internodes of the LIZ can be observed in all the studied species. The cleistogamous UIF falls together with the internode and the leaf sheath.

3.2. *Kaokochloa nigrirostris*

In this annual species, the SIZ is 3–5 mm long and consists of 5–9 internodes. The LIZ is 175–257 mm long and consists of 7–8 internodes (Table 2). Most of the shoots show an abrupt transition between the SIZ and the LIZ.

Table 2

: Growth form characters in species of Pappophoreae.

Species	SIZ			LIZ			Synflorescence		Growth form models**
	Length (mm)	Internode number	Represents	Length (mm)	Internode number	Represents	Pc type*	Synf Type*	
<i>Cottea pappophoroides</i>	5–6	?	ZI and ZE	150–515	6–8	ZH and ZE	PC _{UIF} , PC _{II UE} , PC _{II UNE} , PC _{SRC}	S _{IV}	PB+csa
<i>Enneapogon asperatus</i>	2–5	4–5	ZI	235–370	4–9	ZH and ZE	PC _{UIF} , PC _{II UNE}	S _{III}	PB+ci
<i>Enneapogon avenaceus</i>	3–5	4–5	ZI	215–327	2–5	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{IV}	PB–c
<i>Enneapogon caeruleus</i>	7–8	9–10	ZI and ZE	250–260	4–5	ZH and ZE	PC _{UIF} , PC _{II UE} , PC _{II UNE}	S _{III}	PB+cb
<i>Enneapogon cenchroides</i>	3–5	4–6(-10)	ZI	430–650	5–8	ZH	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon cylindricus</i>	4–5	9–10	ZI y ZE	120–245	4–6	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{III}	PB+cbi
<i>Enneapogon decipiens</i>	3–4	2–5	ZI	280–370	2–8	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon desvauxii</i>	3–4	3–5	ZI and ZE	90–240	4–5	ZH and ZE	PC _{UIF} , PC _{II UE} , PC _{II UNE}	S _{III}	PB+cb
<i>Enneapogon elegans</i>	5–6	4–5	ZI	350–375	4–5	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon eremophilus</i>	2–3	4–5	ZI	200–275	10–12	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon gracilis</i>	4–5	4–5	ZI	250–283	5–6	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon intermedius</i>	4–5	5–6	ZI	300–432	4–5	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon lindleyanus</i>	5–6	4–5	ZI	380–406	4–5	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon nigricans</i>	5–6	6–8	ZI	235–470	3–4	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon pallidus</i>	6–8	5–8	ZI	440–580	6–7	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon polyphyllus</i>	3–4	5–6	ZI	160–225	6–7	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon pretoriensis</i>	6–8	8–10	ZI	380–450	4–5	ZH	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon purpurascens</i>	0,5–1	4–5	ZI	350–390	5–6	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon robustissimus</i>	0,5–1	6–8	ZI	550–600	6–8	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon scaber</i>	10–15	10–11	ZI	115–127	4–5	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon scoparius</i>	14–15	10–11	ZI	560–690	10–12	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon spathaceus</i>	10–11	10–12	ZI	780–835	12–13	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon truncatus</i>	5–6	7–17	ZI	275–355	3–4	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Enneapogon virens</i>	5–6	5–8	ZI	220–282	5–7	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Kaokochloa nigrirostris</i>	3–5	5–9	ZI	175–257	7–8	ZH	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Pappophorum pappiferum</i>	10–12	8–10	ZI	300–950	7–8	ZH	PC _{UIF}	S _I	PU
<i>Pappophorum philippianum</i>	10–12	7–10	ZI	150–600	5–7	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Pappophorum saccharoides</i>			ZI			ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Schmidtia kalihariensis</i>	5–10	5–8	ZI	297–302	6–9	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c
<i>Schmidtia pappophoroides</i>	5–10	5–8	ZI	390–710	6–9	ZH and ZE	PC _{UIF} , PC _{II UE}	S _{II}	PB–c

Abbreviations: ZI, innovation zone; ZE, enrichment zone; ZH, inhibition zone; Synf, synflorescence; ?, missing data; *see Tivano et al. (2009); **explication in the text.

Each axillary shoot generated in the SIZ grows prostrate and develops adventitious roots at the basal nodes. The intercalary growth of the internodes of the plagiotropic part of the innovation shoots is responsible for the lax constitution of the plant that characterizes *Kaokochloa*. The axes of enrichment of the LIZ (Fig. 1C) consist of the prophyll, a certain number of leaves and an exposed terminal UIF. The axes of enrichment may or may not ramify; with some of them showing fourth order ramifications.

3.3. *Pappophorum*

The variations in the growth form of the studied species of *Pappophorum* appear as a continuum between the two ends represented by *P. philippianum* (Fig. 1B) and *P. pappiferum* (Fig. 1A).

In *Pappophorum philippianum*, the SIZ is 10–12 mm long and comprises 7–10 internodes. The LIZ is 150–600 mm long and consists of 5–7 internodes (Table 2). The transition between the SIZ and the LIZ is gradual and generally consists of two internodes, which are 5–10 mm long. Axillary shoots of varying degrees of development and branching are observed in the SIZ (Fig. 1B). The unfolding of enrichment axes occurs when the terminal UIF is developed and it takes place in basipetal form. In the very short SIZ the totality of the roots are emerging on a one per node basis.

In *P. pappiferum* the SIZ is 9–10 mm long and may reach 8–10 internodes. The LIZ is 300–950 mm long and consists of 7–8 internodes (Table 2). Ramifications are not observed in the LIZ, as this zone behaves as a zone of inhibition (Fig. 1A). All of the roots converge in the SIZ and they emerge as two in the proximity of each

axillary bud, one at the level of the node in which the bud is disposed and the other in the distal part of the internode immediately below.

3.4. *Schmidtia kalihariensis* and *S. pappophoroides*

In these species (Fig. 1B), the SIZ measures 5–10 mm long and consists of 5–8 internodes, most of which are not subterranean. The LIZ consists of 6–9 internodes in both species with a variable length of 297–302 mm in *S. kalihariensis*, and 390–710 mm in *S. pappophoroides* (Table 2). In most shoots, the transition between the SIZ and the LIZ is abrupt.

Axillary shoots of varying degrees of development and ramification are observed in the SIZ. The enrichment axes consist of a prophyll, a certain number of leaves and an exposed UIF. These axes may or may not ramify – in some of them, ramifications of up to the third order have been observed. The plants have adventitious roots at the level of the short internodes. On very few occasions, adventitious roots may be observed on the basal nodes of the LIZ.

3.5. Comparative study of the growth forms in Pappophoreae

In Pappophoreae (Figs. 1 and 2), we can recognize (1) caespitose plants connected by short rhizomes (*Cottea*, *Enneapogon*, *Pappophorum* and *Schmidtia*), and (2) plants with prostrate branches (*Kaokochloa*). The main differences in their growth forms are given by: (1) the number and length of the internodes, (2) the foliar succession, (3) the development of the axillary buds in the SIZ and the LIZ, and the nature of their production. Based on

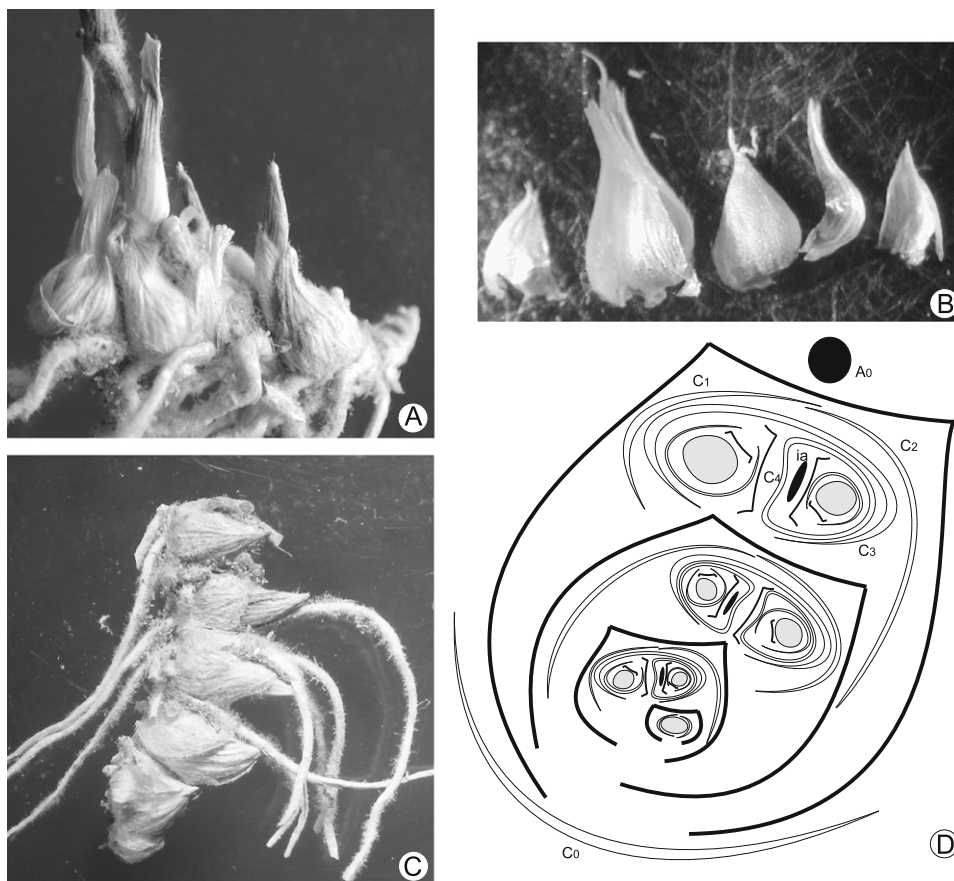


Fig. 5. Subterranean sympodia in *Cottea pappophoroides*: (A) base of one shoot with subterranean sympodia; (B) one cleistogamous spikelet with its cataphylls; (C) connected series of subterranean sympodia; (D) diagram of the branching system in the subterranean sympodia connected in series. Abbreviations: A_0 , parent axis; C_0 , cataphyll in axis A_0 ; C_1 , C_2 , C_3 , C_4 , cataphylls in the innovation axis; ia, innovation axis.

this, we characterize the following growth form models in Pappophoreae:

1. Plants with unbranched culms (PU-model)

This model corresponds to the structural pattern of *Pappophorum pappiferum*. The plant is caespitose, connected by short rhizomes, and it bears a partially plagiotropic and subterranean SIZ, and a LIZ without enrichment axes. This model has a terminal UIF of chasmogamous spikelets (Fig. 1A).

2. Plants with branched culms (PB-model)

2.1. *PB-model without cleistogamous spikelets or cleistogamous inflorescences (PB-c)*: This model corresponds to the structural pattern of *Kaokochloa*, *Schmidtia*, the species of *Enneapogon* without cleistogamous UIF, and the rest of the studied species of *Pappophorum*. The plant is caespitose, with short rhizomes (*Pappophorum*, *Schmidtia* and *Enneapogon*) or with prostrate axes (*Kaokochloa*). The shoots bear a vegetative, partially plagiotropic and subterranean SIZ. This model has a terminal UIF and multiple lateral UIF of chasmogamous spikelets (Figs. 1B and C).

2.2. *PB-model with cleistogamous spikelets and/or cleistogamous inflorescences (PB+c)*

2.2.1. *PB-model with basal cleistogamous spikelets (PB+cb)*: This model corresponds to the structural pattern of *E. caerulea* and *E. desvauxii*. The plant is caespitose, with short rhizomes. The ramification pattern of the shoots is similar to that of the previously mentioned model; however, in the SIZ, the axillary buds of the aerial nodes may develop

enrichment axes with UIF reduced to one cleistogamous spikelet, hidden in the basal foliar sheaths. This model bears terminal and lateral UIF of chasmogamous spikelets, and very reduced aerial lateral UIF, of one cleistogamous spikelet (Fig. 2C).

2.2.2. *PB-model with subterranean and aerial cleistogamous spikelets (PB+csa)*: This model corresponds to the structural pattern of *C. pappophoroides*. The plant is caespitose, with short rhizomes. From the axillary buds of the subterranean and aerial nodes of the SIZ and the basal, medial and distal nodes of the LIZ develop axes of enrichment that bear UIF reduced to one or a few cleistogamous spikelets. This model has terminal and lateral UIF of chasmogamous spikelets, and highly reduced lateral aerial and subterranean UIF of cleistogamous spikelets (Fig. 2D).

2.2.3. *PB-model with basal cleistogamous spikelets and cleistogamous inflorescences (PB+cbi)*: This pattern is characteristic of *E. cylindricus*. The plant is caespitose, with short rhizomes. In the SIZ, the axillary buds generate innovations and reduced UIF of cleistogamous spikelets; some of the axillary buds of the LIZ form cleistogamous inflorescences hidden in the medial and distal sheaths. This model has both terminal and lateral UIF of chasmogamous spikelets, as well as lateral UIF with cleistogamous inflorescences and others reduced to a few cleistogamous spikelets (Fig. 2B).

2.2.4. *PB-model with cleistogamous inflorescences (PB+ci)*: This pattern is characteristic of *E. asperatus*. The plant is caespitose, with short rhizomes and vegetative SIZ. The axillary buds of the LIZ form enrichment axes that end in inflorescences with chasmogamous spikelets. They also

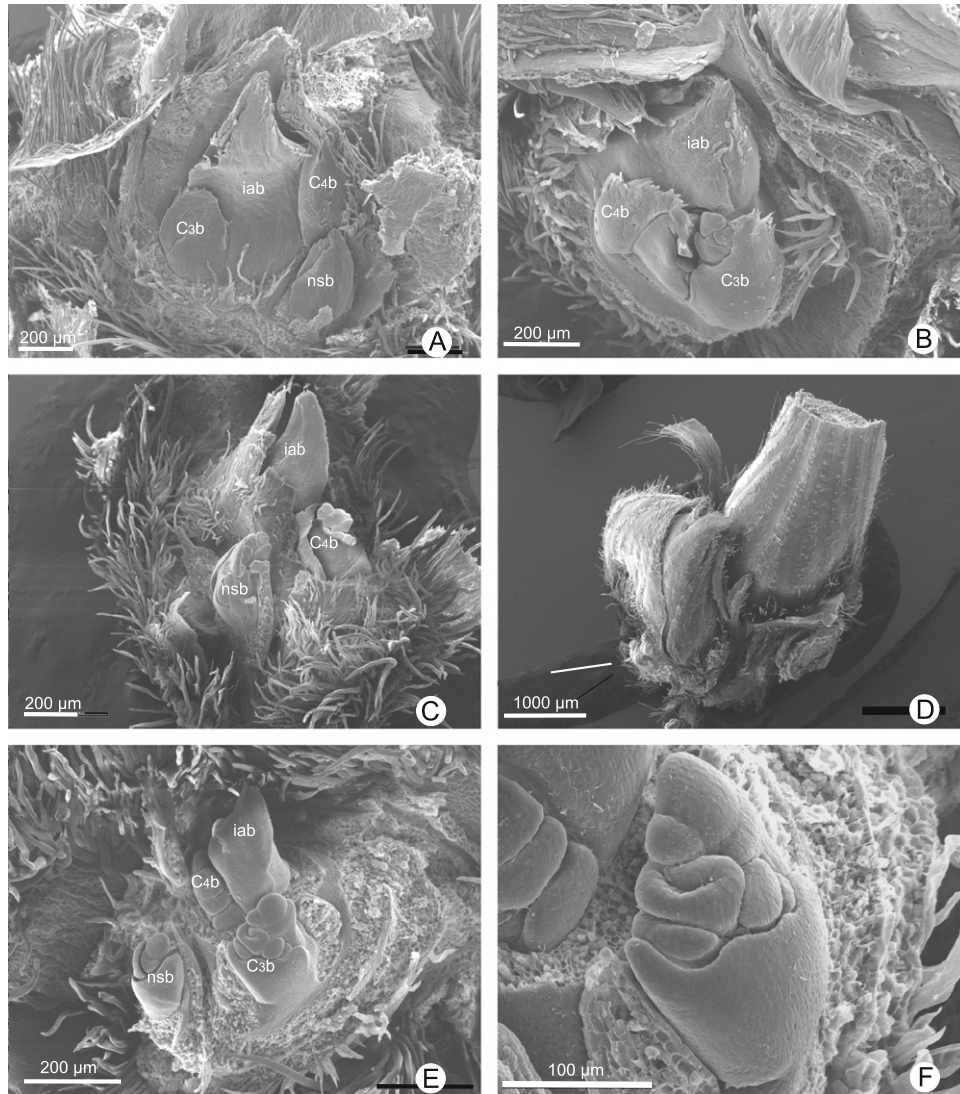


Fig. 6. Buds of the subterranean sympodia in *Cottea pappophoroides*: (A)–(C) different view of one sympodium and the bud of a new sympodium; (D) basal part of one shoot with subterranean sympodia; (E) detail of one sympodium and of a bud of the new sympodium; (F) detail of one cleistogamous spikelet. Abbreviations: c_3b, c_4b , axillary bud of the cataphyll number three and the cataphyll number four; iab, innovation axis bud; nsb, new sympodium bud.

bear cleistogamous inflorescences hidden in their medial and distal foliar sheaths (Fig. 2A).

4. Discussion

The growth form of the species of Pappophoreae fits the common pattern among grasses (Mühlberg, 1966; Bell, 1994). Along each growth form unit (i.e., innovation shoot), we recognize the SIZ and the LIZ (Fig. 1B). Species of grasses vary in the number of short basal internodes and the position of the SIZ in relation to the ground level (Rechentín, 1956). Rechentín considers that the number and the position of the SIZ in relation to the ground level influences how soon the growing part slides up above the ground, coming into the reach of a grazing animal. The studied species of *Enneapogon*, *Kaokochloa*, *Pappophorum* and *Schmidtia* bear one very short SIZ, which is barely subterranean, whereas *Cottea* bears a largely subterranean SIZ with many very short internodes.

In Poaceae, the axillary buds of the SIZ generate innovations and the axillary buds of the LIZ form enrichment axes or do not

develop (Rúa and Weberling, 1998). The LIZ in Poaceae represents an extension of the enrichment zone and/or an inhibition zone (Rúa and Weberling, 1998; Amsler et al., 2005). In the post-generative shoots of *Melica macra* Nees the proximal region of the LIZ also behaves as a zone of innovation (Perreta and Vegetti, 2004). This also occurs in *Kaokochloa*.

Pappophorum philippianum lacks enrichment axes (Fig. 1A) and the LIZ represents an inhibition zone (Table 2). The other species of Pappophoreae show this type of axes and the LIZ represents partially an enrichment zone and partially an inhibition zone (Figs. 1B and C and 2). These axes of enrichment in Poaceae generally bear a basal trophotagma and end in a terminal UIF (Vegetti and Müller-Doblies, 2004).

In *C. pappophoroides* (PB+csa model, Fig. 2D), *Enneapogon caerulescens* and *E. desvauxii* (PB+cb model, Fig. 2C), *E. asperatus* (PB+ci model, Fig. 2A), and *E. cylindricus* (PB+cbi model, Fig. 2B), the axillary buds of the trophotagma (in the SIZ and/or in the LIZ) can originate enrichment axes bearing 1-various cleistogamous spikelets. In the SIZ they can be present in the distal part corresponding to the distal aerial nodes (*C. pappophoroides*, *E. asperatus*, *E. caerulescens*, *E. cylindricus* and *E. desvauxii*) as well as

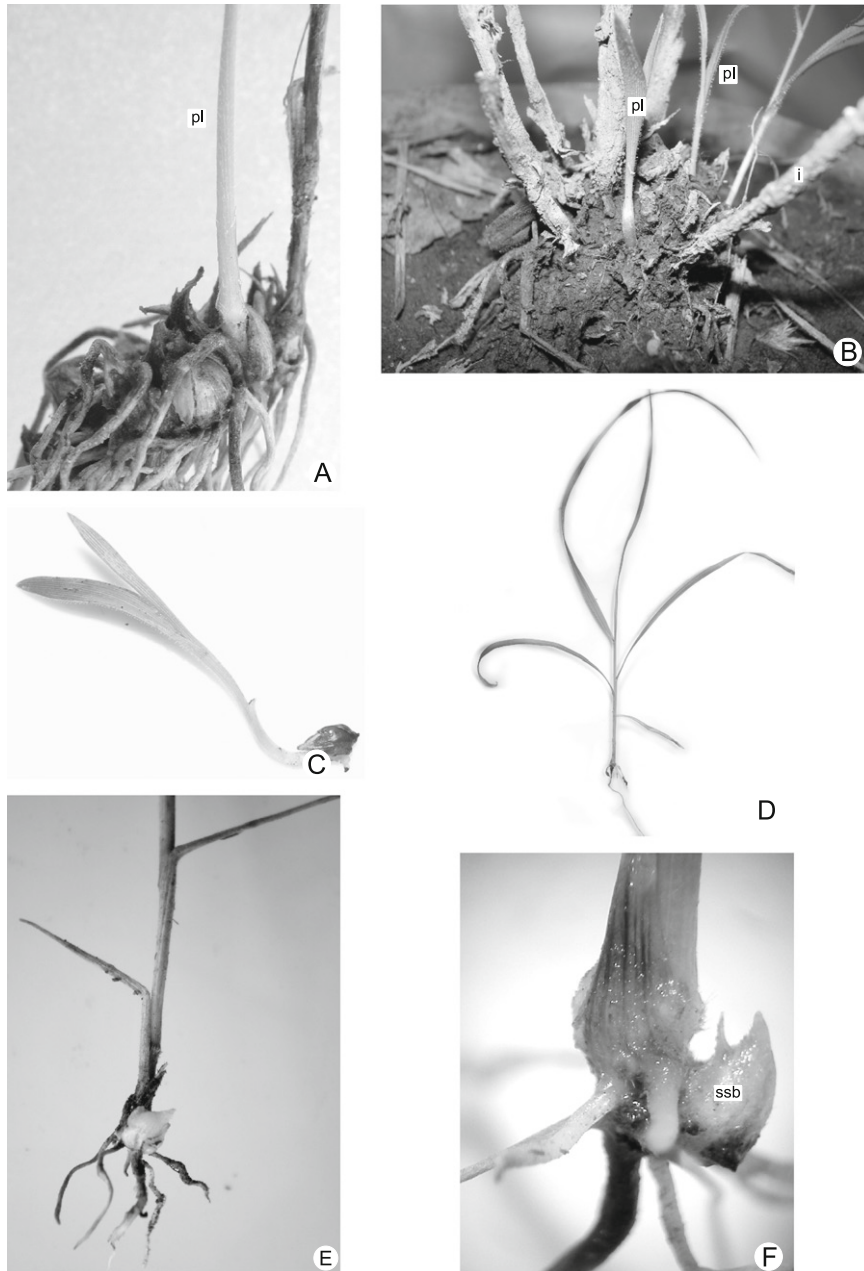


Fig. 7. Germination of the subterranean caryopsis: (A), (B) germinated subterranean caryopsis linked to the mother plant; (C) germinated subterranean caryopsis; (D) plantlet produced by the germination of a subterranean caryopsis; (E), (F) early development of the first subterranean sympodium in the plantlet. Abbreviations: i, innovation; pl, Plantlet; ssb, Subterranean sympodium bud.

in the subterranean nodes (*C. pappophoroides*, Fig. 2D). Consequently, in these species, the SIz behaves as a zone of innovation as well as as a zone of enrichment – a rare character in the Poaceae (Tivano et al., 2009) and only present in very few genera within the Chloridoideae (Campbell et al., 1983).

Two types of caespitose plants can be characterized: those constituted exclusively by orthotropic shoots and those with short rhizomes (Perreta et al., 2000) formed by plagiotropic substitution (Bell, 1991). Caespitose plants with short rhizomes correspond to some of the growth forms described by Rúa and Gróttola (1997), Rúa and Weberling (1998), Perreta et al. (2000), Vegetti (2002), and Perreta and Vegetti (2004, 2006). This is the growth pattern present in Pappophoreae, with the exception of *Koakochloa*.

In caespitose grasses, like Pappophoreae, the innovations develop at several basal nodes (Tsvelev, 1983). In *C. pappophoroides*,

the innovations are generated in the bud of the second cataphyll of each sympodium. The fact that axillary shoots are produced recurrently at the same node in each branching event determines a phalanx-like growth (Schmidt and Harper, 1985; Herben and Toshihiko, 1997; Perreta and Vegetti, 2004), with all the implications derived from such a horizontal exploration type (Perreta and Vegetti, 2004).

Cleistogamy in the species of Pappophoreae has been known for some time (Chase, 1918), but the system of ramification that supports these cleistogamous inflorescences is described for the first time in this work.

The cleistogamous spikelets present in the studied species of Pappophoreae afford a greater quantity of seeds to the system, and in the case of the subterranean ones, secure a seed bank protected from fire and overgrazing, assuring the growth of new plants in their environment (Fig. 7).

As regards the number and distribution of adventitious roots per node in Poaceae, the most frequent condition is the production of 3–4 roots per basal node (Mühlberg, 1970). In the studied species of Pappophoreae only one root is produced at each node, as has been also described in species of *Brachypodium* Beauv. (Mühlberg, 1970), *Leptochloa chloridiformis* (Hack.) Parodi (Perreta et al., 2000) and *Melica macra* (Perreta and Vegetti, 2004). In *P. pappiferum* two roots are produced at each node.

We characterize a series of growth form models in Pappophoreae (Figs. 1 and 2). These models correspond to the following synflorescence types (Table 2) characterized by Tivano et al. (2009): synflorescence type S_I (*P. pappiferum*), synflorescence type S_{II} (the rest of the studied species of *Pappophorum*, *Schmidtia*, *Kaokochloa* and the species of *Enneapogon* without cleistogamous UIF), synflorescence type S_{III} (*Enneapogon desvauxii*, *E. asperatus*, *E. caeruleus*, *E. cylindricus*) and synflorescence type S_{IV} (*C. pappophoroides*).

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