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## Structure and development of the branching system in *Melica sarmentosa* NEES (Poaceae)

With 2 Figures and one Table

### Summary

The branching system of cultivated and wild populations of the climbing grass *Melica sarmentosa* NEES is described on the basis of cultivated and field plant observation. Two types of axes are recognized, namely, 'basal climbing axes' and 'distal climbing axes'. These axes differ in position and morphology and show a particular distribution of branching and branch repression zones associated with their climbing habit. The branching system of the plant can be summarized by the following traits: (1) limited production of innovation axes (basal climbing axes); (2) vigorous development of such axes, which produce a large number of internodes as well as profuse distal branching (distal climbing axes, enrichment shoots), and consequently, (3) remarkable ability of the distal region of the plant for environmental exploration.

### Zusammenfassung

Struktur und Entwicklung des Verzweigungssystems von *Melica sarmentosa* NEES (Poaceae)

Das Verzweigungssystem kultivierter und wilder Populationen des Klettergrases *Melica sarmentosa* NEES wird auf der Basis der Beobachtung kultivierter und wilder Pflanzen beschrieben. Zwei Achsentyphen wurden nachgewiesen: Basal kletternde Achsen und distal kletternde Achsen. Diese Achsen differieren in Position und Morphologie und zeigen eine partikuläre Verteilung der Verzweigung und zwei Repressionszonen im Zusammenhang mit ihrem Kletterverhalten. Das Verzweigungssystem der Pflanzen kann durch folgende Erscheinungen charakterisiert werden: 1. begrenzte Bildung von Innovationsachsen (basal kletternde Achsen); 2. kräftige Entwicklung derartiger Achsen, die sowohl eine große Anzahl von Internodien als auch eine üppige Verzweigung ausbilden (distal kletternde Achsen, Bereicherungstriebe) und folglich, 3. bemerkenswerte Fähigkeit der distalen Region der Pflanze zur Umweltexploration.

### Introduction

*Melica sarmentosa* NEES is one of the few climbing grasses. The climbing is possible because of the tendril-like filiform tip of the leaf blades (TORRES 1980). It is a sciophilous species native to Argentina, Bolivia, Brazil, Uruguay, and Paraguay (TORRES 1980; SORENG et al. 2005). Three varieties are currently recognized: var. *sarmentosa*, var. *pilosula* DÖLL and var. *monticola* TORRES. In Argentina, the two former varieties inhabit woodlands in the

La Plata basin (TORRES 1980), whereas *M. sarmentosa* var. *monticola* is endemic of the Yungas, between 800 and 2000 m altitude (TORRES 1980; ZULOAGA et al. 1994).

The detailed study of the morphological features of the given species caused us to infer in the local and temporal adaptation of the plant to be the environmental conditions in which it grow, and make it possible to infer taxonomic as well as phylogenetic relationships (MEUSEL 1970). On one hand, the study of plant development on the basis of structural criteria (BAR-

THÉLEMY 1988) permits to understand the integration of structure and its perpetuation, and on the other hand it is the basis for its quantification (DE REFFYE et al. 1989). Studies of *M. sarmentosa* are scarce and related to systematics and leaf anatomy (TORRES 1980). Since such studies are based on a few morphological characters, they are insufficient to explain the dynamic development of the branching system. For this reason, the aim of this paper is to describe in a detailed way the branching development in *M. sarmentosa*, and the resulting structure of old individuals of this species.

### Materials and methods

Observations were made on living plants collected in Department Manuel Belgrano, Jujuy province (Argentina), and in bank woodlands of the Entre Rios province, near Paraná town (Argentina), belonging to var. *monticola* and *sarmentosa* respectively. Morphological characters were scored on about 100 climbing axes arising from the basal region of the plant.

Studies on branch development in earlier stages from germination were carried out. Seeds of *M. sarmentosa* var. *sarmentosa* were collected near Oro Verde (Dept. Paraná, Entre Rios province) and sown in Petri plated covered with filter-paper. After seedling, 100 seedlings were transplanted into pots previously filled with fertile soil. Plants were periodically dissected during six months every 15 days and observed with a stereoscopic microscope, diagrams of the branching system were drawn each time.

Observations on living plants were complemented using herbarium material of the three varieties.

The inflorescence was treated as a unit ('flowering unit', sensu SELL 1969, 1976) and not further described (for a detailed description of the flowering unit see PERRETA & VEGETTI 2004a). The description of the seedling stages follows the terminology proposed by HOSHIKAWA (1969).

Leaf forms of the tillers referred follows an acropetal sequence: prophyll, 2 or 3 cataphylls, and the foliage leaves being reduced to well developed blades, according to the axis type described.

### Results

#### Plant structure

Clumps of *M. sarmentosa* are built as a result of the successive development of basal climbing axes which originate from the main axis by

iterative innovation (TROLL 1964: 325ff). Since basal climbing axes represent tillers, the ultimate plant structure depends on the repetition of these axes.

Each climbing axis is composed of a short internode-zone, a long internode-zone, and flowering unit (Fig. 1A). The short internode zone comprises a few internodes at the basal portion of the axes, and behaves as an innovation zone (TROLL 1964: 282ff.). About three adventitious roots develop at each node along this portion.

The long internode-zone develops profusely, comprising in vigorous culms more than 60 internodes. Two portions can be distinguished along this zone. In the proximal one, comprising about the half of the internodes, the axillary buds do not develop at all. The distal one can be further subdivided into two halves. Axillary buds can develop either in the proximal half only or in the distal half, or in both. In the latter case they are separated by a variable number of internodes, in which the axillary buds remain repressed (Fig. 1A).

Climbing axes arise from the long internode zone buds, which we call distal climbing axes (Fig. 1B) in order to distinguish them from the basal ones. Both always grow extravaginally, and differ not only in position but also in structural traits (Table 1)

Basal and distal climbing axes present a similar structure, however, the distal ones lack roots and thus do not contribute to the renewal of the clump. In return, distal climbing axes are capable of further branching from the basal and middle nodes of the long internode-zone, reaching up to five consecutive orders of branches. The distal climbing axes contribute to a major extent to build up the the growth form, and provide most inflorescences.

#### Plant development

First phase: cespitose growth (basal branching and clump formation)

The seedling bears as well developed mesocotyl. About 20 days after germination, the root system is composed of the embryonic root and an additional root arising from the coleoptylous node. No further roots were observed, neither on the mesocotyl nor in the so-called transitional node.

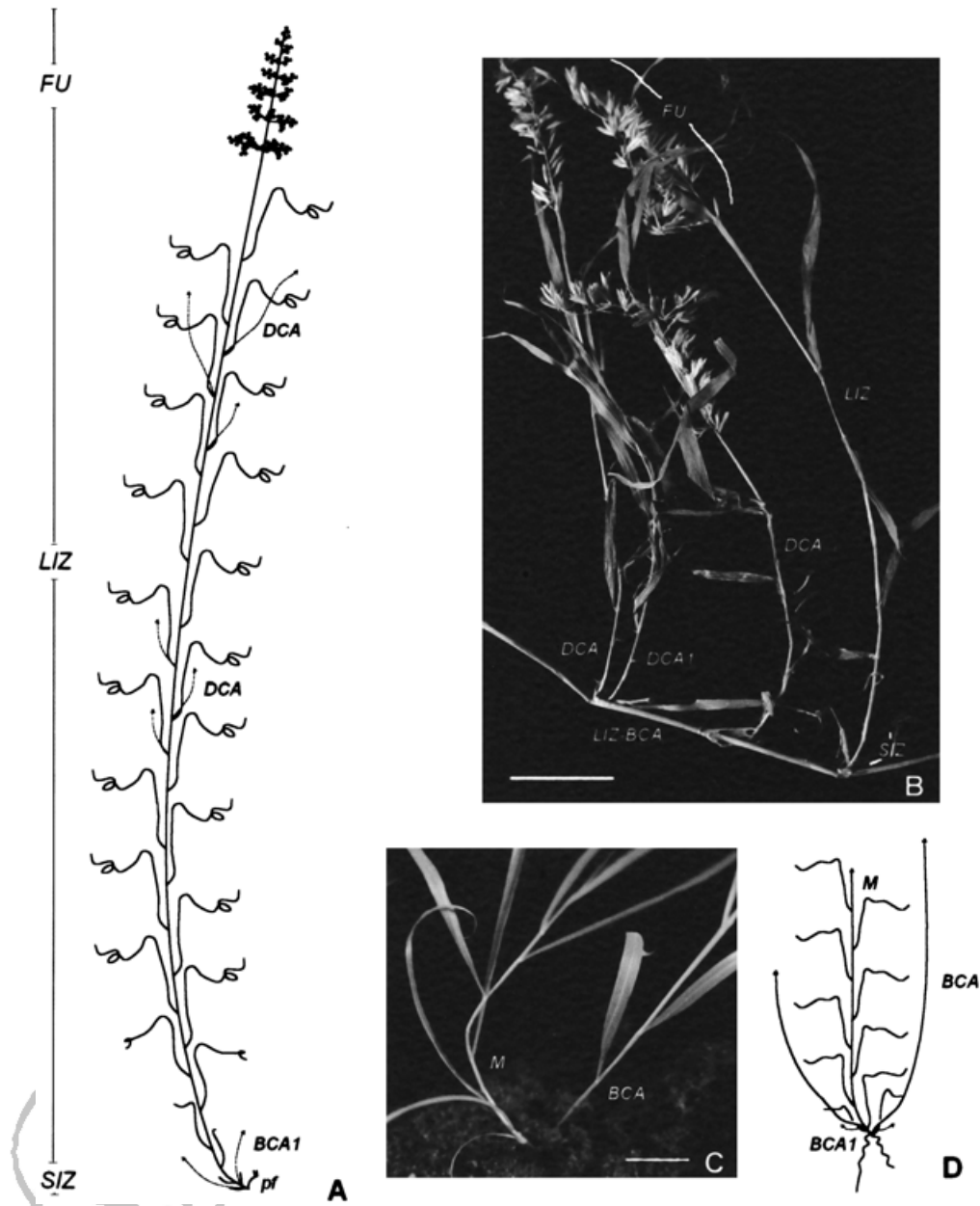


Fig. 1  
*Melica sarmentosa* NEES

A — structure of Basal Climbing Axes; B — Basal Climbing Axes bearing Distal Climbing Axes; C — seedling with one branch; D — basal branching of clump (cespitose growth)

BCA-1 – Basal Climbing Axes of successive order; DCA-1 – Distal Climbing Axes of successive order; FU – flowering unit; LIZ – long internode-zone; M – main axis; pf – prophyll; SIZ – short internode-zone  
Scale bar: B = 4 cm; C = 2.5 cm

Once the seedling has three unfolded leaves, the internode following the third leaf elongates. From this point on, each of the successive internodes elongates immediately after leaf unfolding. Such internode elongation is not associated with floral differentiation of its apical meristem, which remains vegetative. When the main axis bears (4–) 5 (–8) unfolded leaves an axillary shoot develops from the axil of the first leaf (Fig. 1C), followed by another one from the axil of the second leaf. Then, no axillary shoots were formed on the subsequent basal nodes of the main axis. Only in particular circumstances caused by damage of the two first axillary buds, lateral shoots can develop from the axil of leaves 3 and 4.

Further increase of branch number occurs as a consequence of the development of new shoots from the axis of the two proximal cataphylls of the first order lateral axes (Fig. 1D), then from the axils of the two proximal cataphylls of the second order lateral axes, and so on. Thus, the innovation zone only comprises the two proximal nodes of each axis. Such innovation buds produce basal climbing axes only. Thus the branching system determines the formation of a loose clump with few structural units (Fig. 2A).

The laxity of such clumps is due to the shortness of the innovation zone of both the main axis and the basal climbing axes, as well as the relatively low degree of basal branching of the late ones.

After six months of growth, the main axis bears 10–11 leaves and begins to slow down its growth with respect to the remaining axes. Finally, the main axis becomes senescent in most plants studies. During the first year no flowering axis was observed.

#### Second phase: climbing growth (distal branching of basal axes)

The basal climbing axes are long, bending shoots capable of climbing because of the tendril-like apices of their leaf blades, by which they climbing on the surrounding vegetation. Vegetative growth of basal axes developed during the first year continues until flowering in the next season.

As described above, the basal axillary buds of these shoots give rise to new basal climbing

axes and so increase the number of structural units composing the clump. On the other hand, axillary buds located in the distal portion of basal climbing axes originate of different type of climbing axes, the distal ones. Distal climbing axes producing buds start to develop from the middle portion of the basal axes. Nevertheless, they can appear at different relative positions depending of the shoot condition (vegetative, dead apex, or trimmed).

Most axes developed are pre-generative (cf. SEREBRYAKOVA 1969). Nevertheless, in basal climbing axes that flowered or withered distally during the preceding season, axillary buds immediately below the withered portion remain active and give rise to post-generative distal climbing axes. In some cases, the distal axis originated from the more distal axillary bud continues the growth direction of the main axis, giving the appearance of an indefinite growth of the basal climbing axes. The remaining axillary branches grow more or less perpendicular to their mother axis depending on the surrounding vegetation.

Flowering occurs in spring, principally during October and November. Basal and distal climbing axes come to flower in the same period (Fig. 2B). Both, the extent of the developmental period and the different position on the relative mother axes account for the variable number of internodes at flowering stage (Table 1). Of course, for the distal axes developed at the beginning of the growth season the time of disposal for vegetative growth is longer, therefore they produce longer axes capable of a more extensive exploration of the environment by themselves and by producing more numerous axes of higher branching order. Distal climbing axes developed later in the growth season are shorter, produce fewer additional axilar axes, do not contribute substantially to environment exploration, and behave purely as enrichment axes.

#### Variations associated to environmental conditions and/or taxonomic varieties

As mentioned above, usually no adventitious roots develop on the distal climbing axes. Nevertheless, adventitious roots were observed at the base of these axes when their mother basal climbing axes were far away from a clasping

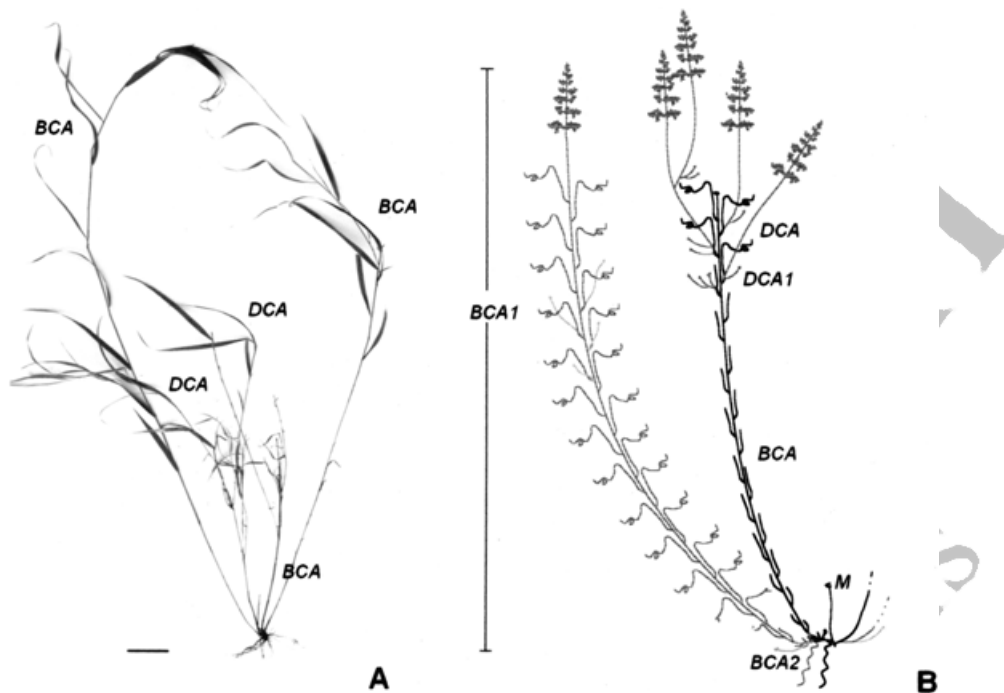


Fig. 2

A — plant of *Melica sarmentosa* var. *sarmentosa*; B — schematic representation of a flowering plant

BCA-2 – Basal Climbing Axes of successive order; DCA-1 – Distal Climbing Axes of successive order; M – main axis  
Scale bar = 5 cm

Table 1  
Structural traits of different types of axes

Trait	BCA	DCA
Extension of the SIZ	3 internodes + hypopodium	2 internodes + hypopodium
Extension of the LIZ	(13–)29–42(–67) internodes	more than 22 internodes in axes developed at the beginning of the growth season, 6–21 in later axes
Leaf succession	prophyll minute, 3 cataphylls, 2 transitional leaves with reduced blade, following leaves with well developed sheath and blade	prophyll minute, 2 cataphylls, transitional leaf with reduced blade, following leaves with well developed sheath and blade
Position of basal branches	axillary of cataphylls 1 and 2	axillary of cataphylls 1 and 2, and sometimes of the prophyll as well
Position of distal branches	axillary of middle to distal leaves of the LIZ	axillary of middle to distal leaves of the LIZ

BCA – basal climbing axes; DCA – distal climbing axes; SIZ – short internode-zone, LIZ – long internode-zone

support. In such cases, the distal climbing axes behave as innovation shoots.

The clump size does not vary substantially since the production of basal axes is scarce, and the distal production is promoted in order to

favour the exploitation of light patches. The great length growth ability of the basal climbing axes allows the plant to grow in very shaded habitats to overtop the canopy and to flower above it. This was observed in the field

in plants of *M. sarmentosa* var. *monticola* (Los Nogales, Dept. Manuel Belgrano, province Jujuy). As a consequence of such a behaviour, both kinds of axes of the thick forest-inhabiting *M. sarmentosa* var. *monticola* are longer than those of *M. sarmentosa* var. *sarmentosa*, growing on more open habitats.

### Discussion

The growth habit of Poaceae has been characterized as caespitose, rhizomatous or stoloniferous (NICORA & RÚGOLO DE AGRASAR 1987). *Melica sarmentosa* has been described as rhizomatous but has a climbing habit because of its branching bending culms, which can grow more than 350 cm tall (TORRES 1980).

This species can be described as a hierarchic arrangement or structural subunits or modules (BRISQUET 1991; MOORE & MOSER 1995), with developmental particularities according to their growth habit. As usual among grasses, iterative innovation is the process responsible for such as modular structure (RUA & WEBERLING 1998).

Along a structural unit (= tiller) of *M. sarmentosa* two different zones can be recognized: a proximal zone composed of short internodes and a distal one composed of long internodes. In the structural units of some Poaceae two branching regions can be distinguished, one of them basal and restricted to the short internode-zone, and the other one subfloral. This is accordance with the results of MÜHLBERG (1970) who found that in thus comprising a portion of the long internode-zone. The basal branching region produces innovation axes, whereas the subfloral region in certain species behaves as an enrichment zone in which buds sprout facultatively as a response to variable environmental conditions (RUA & WEBERLING 1998). A considerable variation in the number of internodes comprising the short internode-zone occurs among grasses and in many cases all buds located in the region develop to produce innovation shoots. In the case of *M. sarmentosa* the short internode-zone comprises few internodes (Table 1). Only the buds in the axils of to the two first cataphylls (following the prophyll) develop. Thus, the species combines a very brief short internode-zone with an even more limited innovation-zone (i.e. the zone produc-

ing basal climbing axes. On the other hand, the long internode-zone of *M. sarmentosa* shows a variable degree of the development, and can reach a considerable length. The location of distal climbing axes producing axillary buds determines this species to have a discontinuous zone in which enrichment axes are produced. Thus, when compared with other grasses, an additional differentiation of zones occurs within the long internode-zone, namely two enrichment zones alternating with inhibition zones.

In *M. macra* shoots mostly originate from basal buds (PERRETA & VEGETTI 2004b). Therefore, regarding the position of innovation buds, the clump is formed by the iteration of unique type of shoots, although two types of morphologically differentiated axes (pre- and post-generative) can be recognized if developmental timing is taken into account. In *M. macra*, branch production at the long internode-level only occurs at the most proximal nodes of post-generative shoots, otherwise it is rare. Thus axillary branches do not contribute substantially to plant propagation, nor to environment exploration, nor to the production of floral structures. In *M. sarmentosa*, on the contrary, axillary buds located within the long internode-zone produce numerous axes which are essential for environment exploration and contribute substantially to inflorescence production. In spite of the fact that the shoots of both species bear a basal innovation zone composed of the same number of internodes (four internodes including the hypopodium), the different strategies of space colonization lead to the formation of either dense tussocks (*M. macra*) or loose clump (*M. sarmentosa*). Such contrasting growth strategies become already evident at early developmental stages of the branching system, since the seedling axis can produce branches up to the sixth node in *M. macra*, but only on the second node in *M. sarmentosa* (in later stages branches develop regularly only from the first and/or second node on both species). In periods of active growth, *M. macra* is also capable of producing new tillers from the four proximal axillary buds of each structural unit, whereas in *M. sarmentosa* thus only occurs when the two proximal buds are damaged.

Transition from dispersed branching in a mixed mode to concentrated tillering was illus-

trated by SEREBRYAKOVA (1969) using three Old World species of *Melica*. Branching of *M. macra* corresponds to the concentrated mode, whereas that of *M. sarmentosa* belongs to the intermediate or combined type in which branching is concentrated in the basal region of basal climbing axes but more or less disperse in their distal portion.

A grass species producing two different axis types and displaying a growth form analogous to that of *M. sarmentosa* is *Brachypodium arbuscula* GAY ex KNOCH (MÜHLBERG 1970). Basal shoots of this species grow at first erect to ascending, but soon bend down because of their own weight, only the distal portion remaining erect to form many long internodes and finally to produce a flowering unit. Tillers of *B. arbuscula* bear two branching zones: the proximal one, located at the short internode-zone, produces innovation shoots; the other one, sub-floral originates enrichment axes. Such acrotonic enrichments shoots become exhausted after flowering, whereas clump growth continues from basal innovation buds. Plants of *B. arbuscula* can become climbing in shaded habitats. As occurs with the basal climbing axes of *M. sarmentosa*, the more or less erect shoots of *B. arbuscula* can survive an unfavorable season (MÜHLBERG 1970). Nevertheless, basal climbing axes of *M. sarmentosa* remain alive for a long time and branch profusely. In this fact they differ from *B. arbuscula*, the enrichment shoots of which are ephemeral and rarely undergo further branching (MÜHLBERG 1970).

On the other hand, species of Poaceae regarded as stoloniferous or rhizomatous usually combine plagiotropic axes of continued vegetative growth, generally having elongated internodes, with orthotropic axes originated from axillary buds of the plagiotropic ones (RUA & WEBERLING 1998; RUA 1999). Plagiotropic and orthotropic axes of such species should be comparable to basal and distal climbing axes of *M. sarmentosa* respectively. The distal climbing axes in being enrichment, flowering shoots, although, because of their climbing habit, they do not necessarily grow orthotropically but assume variable growth directions. On the other hand, the distal axes differ the orthotropic axes of stoloniferous and rhizomatous grasses in that: (1) they bear numerous long internodes as required for environment exploration (in

stoloniferous and rhizomatous species this function is usually undertaken by the plagiotropic axes); and (2) they generally do not root, thus they cannot become free ramets. Nevertheless, the rooting ability becomes evident in basal climbing axes growing plagiotropically on the soil surface because of the lack of a clasping support. In such cases the axillary buds originate rooting distal climbing axes which form innovation buds basally and behave as new ramets in a way entirely similar to that of the orthotropic axes of stoloniferous and rhizomatous species. A well known grass species producing both rhizomes and stolons bearing axillary orthotropic axes is *Cynodon dactylon* (L.) PERS. (NICORA & RÚGOLO DE AGRASAR 1997). When growing in flooding areas with a low canopy it produces axes that lean over the surrounding vegetation as a result of their exuberant growth, thus the plant becomes climbing (J. Pensiero, pers. comm.).

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*Melica sarmentosa* var. *sarmentosa*: PERRETA & VEGETTI 14 (SF)

*Melica sarmentosa* var. *pilosula*: BURKART 1051 (SI)

*Melica sarmentosa* var. *monticola* PERRETA 1 (SF)

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