ISSN 0373-580 X
Bol. Soc. Argent. Bot. 49 (3): 361-372. 2014

GROWTH FORMS OF *PARIETARIA DEBILIS* (URTICACEAE) AND *VERONICA PERSICA* (PLANTAGINACEAE)

IGNACIO M. DELLAFERRERA[1], ELISA S. PANIGO[2], ABELARDO C. VEGETTI[2] and MARIEL G. PERRETA[2]

Summary: This work analyzes growth forms in *V. persica* and *P. debilis*, in order to identify their structural development under undisturbed conditions. Branching systems of shoots and their temporal and spatial variation, several structural and developmental features as well as growth direction and foliar sequence were studied in plants grown from seed in growth rooms and plants collected in the field.In both species studied, the main axis and the basal branches behave similarly, so they may be considered equivalent structures. In these axes, the zone that produces long branches has an opposite phyllotaxis, while the zone that bears reproductive structures has an alternate phyllotaxis. Along the main axis and the basal paracladia of *V. persica*, an inhibition zone is observed. *Parietaria debilis* lacks such a region and shows, instead, a continuous type of branching. As annual species, the whole branching systems forms a synflorescence. As regards the relationship between the growth form of these two species and their behavior as crop weeds, it may be stated that, being annual species, their high capability to produce flowering structures determines a significant rate of seed production.

Key words: growth forms, sinflorescences, profileration, phyllotaxis, paraclades, branching system

Resumen: Formas de crecimiento de *Parietaria debilis* (Urticaceae) y *Veronica persica* (Plantaginaceae).

Este trabajo analiza las formas de crecimiento en *V. persica* y *P. debilis*, para identificar su desarrollo estructural. El sistema de ramificación, su variación temporal y espacial, características estructurales y de desarrollo, así como la dirección de crecimiento y secuencia foliar fueron estudiados en plantas cultivadas a partir de semillas, en cámaras de crecimiento y en plantas coleccionadas a campo. En ambas especies tanto el eje principal como las ramas basales se comportan de manera similar, constituyendo estructuras equivalentes. A lo largo del eje principal y de los paracladios basales de *V. persica*, se observó una zona de producción de ramas largas, una zona de inhibición, con hojas en filotaxis opuesta, y una zona terminal que porta las flores de filotaxis alterna. *Parietaria debilis* no presentó de zona de inhibición y muestró un tipo continuo de ramificación. Presentó un eje principal y ramas largas de hasta sexto orden, sobre estos ejes se desarrollan ramas cortas que portan a su vez las ramas florales. Al ser anuales todas las estructuras producidas durante el ciclo crecimiento constituyen una sinflorescencia. La forma de crecimiento de estas dos especies, tiene implicancias importantes en su comportamiento como malezas de cultivos, debido a su alta capacidad de producir estructuras florales en forma rápida y continua asegurando ampliamente su producción de semillas.

Palabras clave: formas de crecimiento, sinflorescencias, profileración, filotaxis, paracladios, sistema de ramificación.

INTRODUCCIÓN

Traditionally, plant morphology approaches have been based on isolated organs, ignoring dynamic aspects of the branching systems. Thistendency has been changed during the last years with studies on growth forms and a more thorough insight into the plant structure which allowed a better understanding of the growth strategy of each plant species has been gained (Perreta&Vegetti, 2005). This dynamical morphological approach is a comprehensive tool to clarify the various adaptations that occur in species concerning space occupation, competition and resistance to disturbing factors (Fournier, 1982; Barthélémy and Caraglio, 2007).

A species growth form may be defined as the set of

---

[1] Cultivos Extensivos, Facultad de Ciencias Agrarias (UNL), Instituto de Agrobiotecnología del Litoral (CONICET-UNL).

[2] Morfología Vegetal, Facultad de Ciencias Agrarias (UNL), Instituto de Agrobiotecnología del Litoral (CONICET-UNL).

genetically consistent vegetative characters that vary only within a specific range of phenotypic plasticity (Dengler, 1994; Grosso, 2001). Such variation reflects the species adaptation to the environment in terms of growth time and space occupation (Meusel, 1970). The last author emphasizes also the importance of exploring not only vegetative parts, but also inflorescence development in the sense of Troll (Troll, 1964). Growth form defines a plant habit (Meusel, 1970). This growth form is the result from the equation between endogenous growth processes and external environmentally-driven actions, and it becomes evident in the relative disposition of the aerial and subterranean vegetative shoots (Edelin, 1984). The analysis of growth forms does not only encompass the characteristics of an adult specimen, but also integrates the developmental stages from germination and involves an ordered and organized description of morphogenetic events (Bell, 1986).

Research on growth forms are the basis for many studies on phytosociology, population and community ecology, and biogeography (Krumbiegel, 1998), and in understanding and interpreting ecological relationships (Hagemann, 1981) and their correlation, for instance, with dispersion (Bernard, 1990). Also, they may be applied to plants growing in natural or anthropic environments, to agronomical studies (Meusel *et al.*, 1977, Panigo *et al.*, 2012) or to productive management of native species (Montenegro & Ginocchio, 1992). Several growth form models of perennial species have been established; however, variations in growth forms have not been thoroughly studied for annual species (Malpassi, 2004). These studies are relevant considering the economic and ecologic significance of these plants, many of which are crops, weeds or ornamental plants (Krumbiegel, 1998; Perreta & Vegetti, 2006).

Parietaria debilis G. Forst. (Urticaceae) and *Veronica persica* Poir. (Plantaginaceae) are two annual species that spreads by seeds (Burkart, 1979; Cabrera, 1967) and both are described with ascending or decumbent stems (Burkart, 1979; Sorarú, 1972). In *Veronica persica* fruit production was positively correlated with the number, length and amount dry matter of the stem (Huai *et al.*, 2004). *Parietaria debilis* produces considerable numbers of seeds (Puricelli & Papa, 2006). These species grow better in undisturbed environment and they produce a high amount of seed during the growing season (Puricelli *et al.*, 2005; Puricelli & Papa, 2006). Both are considered important weeds in crops under no tillage (Faccini, 2000; Dellaferrera *et al.*, 2007, 2009; Leguizamón & Ferrari, 2005; Papa & Carrancio, 2005; Puricelli *et al.*, 2005; Puricelli & Papa, 2006).

Parietaria debilis and *V. persica* have not been studied regarding the architectural and growth characteristics that may lead to establishing their strategies for space occupation. In view of this, the aim of this paper is to analyze the growth form of these two weeds species. This may allow the identification of the structural development of these species under undisturbed conditions.

MATERIAL AND METHODS

Twenty plants of each species were grown in a growth room from seeds harvested in the Experimental field of Universidad Nacional del Litoral in Esperanza (Santa Fe) (31° 26'S- 60° 55'W). Seeds were germinated in trays with fertile soil and were transplanted after the cotyledons completed their expansion, first to 0.5 l pots and 36 days later, to 3 l pots. Field-grown plants were collected at several developmental stages, herborized and later analyzed under a stereoscopic microscope for structure characterization.

Organ emergence, as well as organ development over time, were recorded once every day until flowering. After flowering, measurements were taken on a weekly basis. Organ size was recorded once they have stopped growing. Data were collected over a 102-day period (maximum branching order on studied conditions), with day zero occurring on the first transplantation (emerged cotyledons). The growth conditions throughout the experiment were 27ºC during the day and 19ºC at night with a 14 h photoperiod.

Nodes were numbered in the following way: node zero corresponds to the cotyledonary node on the main axis and the prophyllar node on the branches; nodes counted from node zero towards the axis' distal end.

RESULTS

Veronica persica

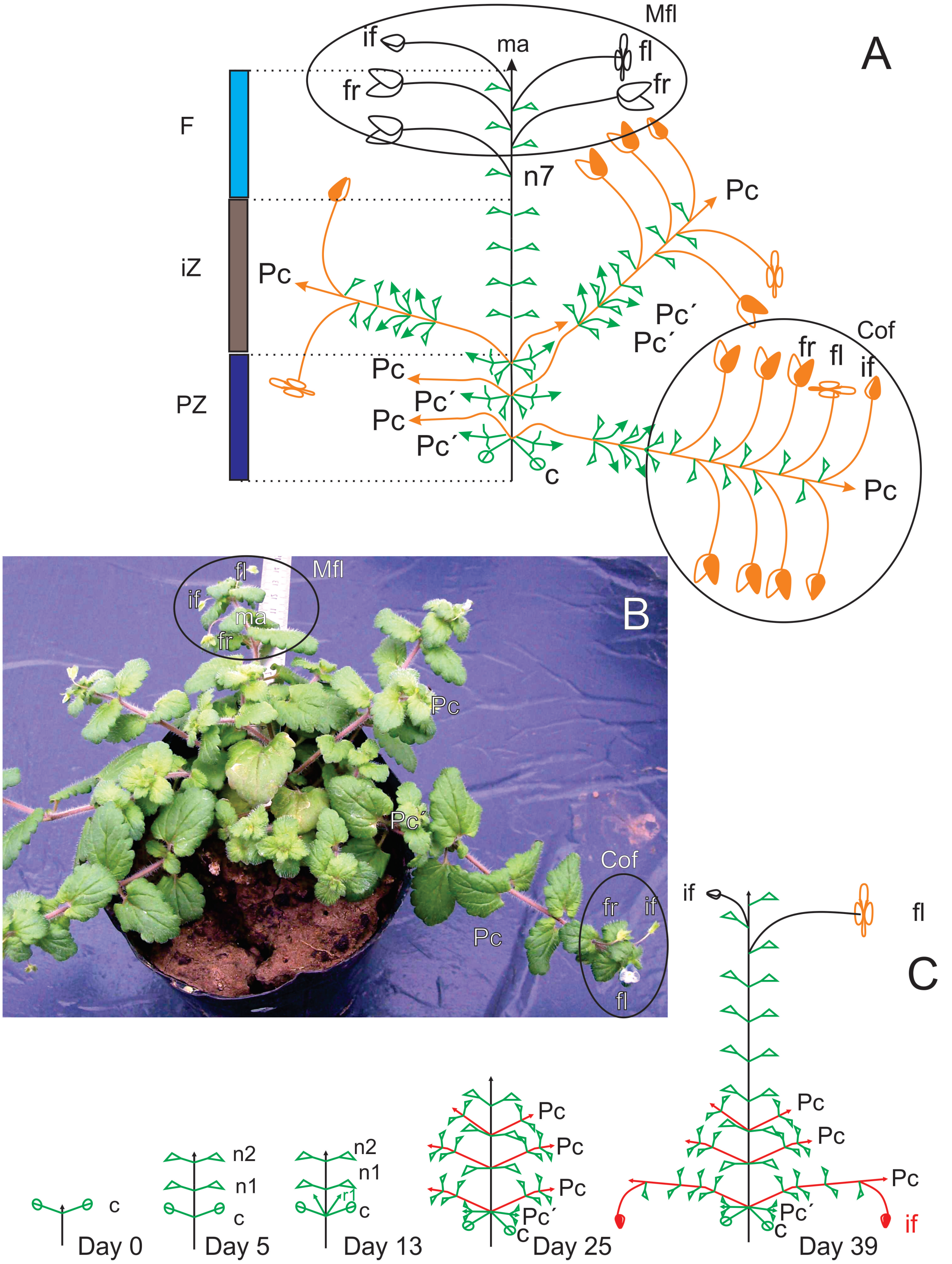


Fig. 1: *Veronica persica*. A: scheme of the plant that represents in detail only one of the two paraclades produced from each basal node. B: 102 day full individual. C: plant structure evolution from emergence. References: c, cotyledon; Cof, Co-florescence; F, florescence; *fl,* flower anthesis; *fr*,fruit; *if,* pre-anthesis flower; ma, main axis; Mfl, Main florescence; n1-n2-n7, nodes 1, 2 and 7; Pc, Pc', successive order paraclades; iZ, inhibition zone; PZ, paracladial zone.

It is an annual species with a basitonic branching system. The main axis shows: (1) a branched zone where branches develop from the axillary buds of cotyledons and nodes one and two; (2) an inhibition zone, which encompasses nodes 3-6, where neither branches nor reproductive structures develop; and (3) a distal zone where only single flowers grow from axillary buds located in node 7 onwards (Fig. 1A). No terminal flower was formed, so the apex of the main axis continued growing up to node 30 during the study period.

The flower-bearing terminal zone of the main axis forms a foliose raceme corresponding to the species flowering unit (inflorescence), which is polytelic because there is no terminal flower (Fig. 1A, B). In terms of structure, this flowering unit is reduced to the main florescence (florescence of the main axis).

The first-order basal branches (primary paraclade) show a growth pattern similar to that of the main axis (Fig. 1A). They develop second-order axes from the axillary buds of the prophylls and nodes one and two, no axillary production is observed in node three and, from node four onwards, only single flowers may be observed; this flowering terminal region represents the coflorescence (florescence of the primary paraclade) (Fig. 1A, B). Second-order branching is the maximum order achieved under growth room conditions; these branches share the same characteristics as those of the first order, but they have a lower number of internodes.

The foliar structures present in the first six nodes of the main axis and in the proximal three nodes of branches show an opposite decussate arrangement, while the florescences show an alternate distichous phyllotaxis (Fig. 1A).

This structure observed in plants cultivated in growth rooms, is similar to that of field-collected plants; however, in the latter the branching basal zone extends up to node five, reducing the inhibition zone to one node (the sixth). Branches may develop as much as to the fourth order.

Development of the branching system from germination (Fig. 1C)

Germination was epigeal in this species; seedlings emerged and expanded their cotyledons six to ten days after the seeds have been placed to germinate.

Five days after emerging, the seedling developed the first pair of leaves and ten days later, the second pair, in opposite decussate phyllotaxis. Around day 13, branch development started from the axillary buds of the cotyledons, before the emergence of the third pair of leaves, which took place around day 15 under the environmental conditions used in this work. From that moment, branch production continued acropetally up to node 2, always synchronized with the emergence of new foliar structures. Branches developed from the axils of leaves located beneath the two lately differentiated leaves, that is, cotyledonary branches developed when two pairs of expanded leaves may already be observed on the main axis. Branches located in the axil of the first pair of leaves developed when the third pair of leaves may already be observed on the main axis, and branches produced in the axil of the second node leaves developed once the fourth node leaves have expanded. The same behavior is observed in the production of second-order branches. Following the expansion of the second pair of leaves, first-order cotyledonary branches started producing second-order branches from the prophyllar buds.

On day 39 the anthesis of the first flower occurred. It is located in the axil of the seventh leaf, which is the latest expanded leaf. From that moment, flowers started to form in the axil of each alternate leaf on the main axis and the first-order axes (in these branches, starting from the axil of the fourth node leaf), with only one flower in anthesis existing on each axis at a given time.

The main axis and the branches grew upright to the eighth node and then became decumbent 45 days after the emergence of the cotyledons. On day 102 (Fig. 1A), the plant had three pairs of primary branches, which were developed from the cotyledonary node to the second node, and as many as 28 second-order branches, which had been formed from some of the axillary buds of the prophyll and the region of opposite leaves from the 6 primary branches. Each first-order axis had 6-22 flowers and each second-order axis had 1-4 flowers; therefore, it is estimated that the species has produced between 110 and 150 flowers under the test conditions.

Parietaria debilis

It is an annual species with a basitonic branching system (Fig. 2A and B). Long branches develop early from the axillary buds of the lowermost three nodes of the main axis and the prophyllar nodes of all the long branches (Fig. 2A). First-order long branches develop basal secondary branches from the

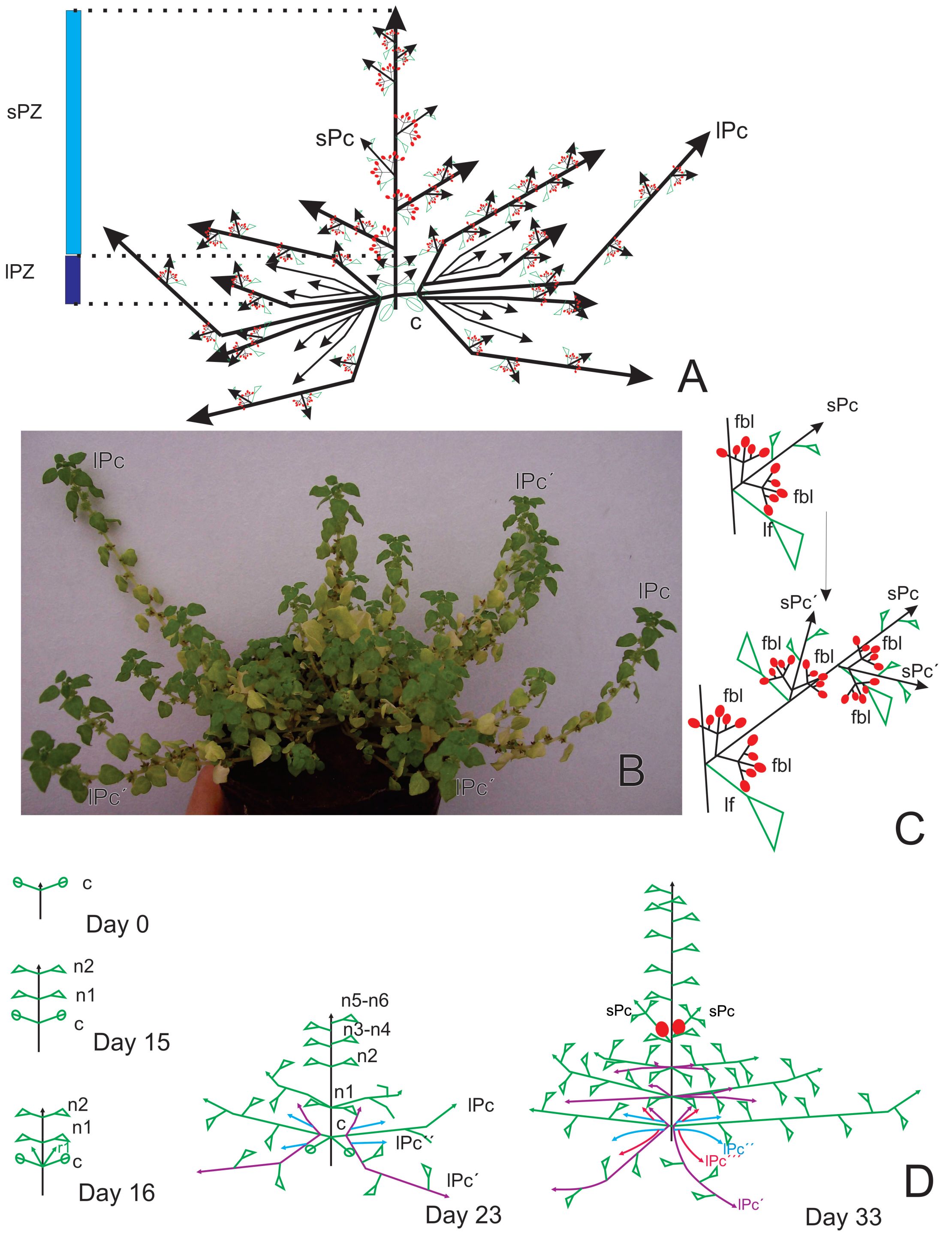


Fig. 2: *Parietaria debilis*. A: scheme of the plant where only represents successive order branches arising in the axils of the cotyledons. B: 102 day full individual. C: developement stages of a short paraclades. D: plant structure evolution from emergence. References: c, cotyledon; fbl, flowering branchlets; lf, leaf; lPc- lPc´´´, suscessive order long paraclades; lPZ, long paracladial zone; n1-n6, nodes 1-6; sPc, sPc´, successive order short paraclades; sPZ, short paracladial zone.

axillary buds of their two prophylls, while higher-order branches develop new branches only from one prophyll (the located in internal position) (Fig. 3A).

The main axis shows an opposite decussate phyllotaxis up to the second node and shifts to an alternate distichous arrangement from the third node onwards. This variation may not be seen initially due to the fact that internodes lengthen late. Long basal branches (long paraclades) show an alternate phyllotaxis throughout their length.

This species shows three types of branches that are distinguished on the basis of their position, structure and axillary productions. The first type (long branches or long paraclades) is located in the basal region of the axes (on the main axis, up to node two, and on the branches, only in the prophyllar node) and develops new basal long branches from its prophyllar axillary buds, and short branches from the axillary buds of the remaining leaves (Fig. 2A). This type of basal long branches produces numerous leaves (Table 1). The zone where the short branches are located has an alternate phyllotaxis. Basal long paraclades develop first plagiotropically, exploring the soil surface, and the apical portion becomes then orthotropic (Fig. 2B and 3A). The maximum branching order reached from these basal long branches is the sixth order for the essay conditions; the apical meristem of these branches remains in the vegetative state, as well as that of the main axis. The second type of branches (short branches or short paraclades), whose growth is more limited, develops flowering branchlets from the prophyllar axillary buds, and new short branches from the rest of the axillary buds (Fig. 2C, 3 B and C) (Table 1). Each of these short paraclades developed acropetally and has two prophylls, a varying number of leaves according to the stage of development (around two or three at 102 days of growth) and an apex in the vegetative state. The third type of branches is flowering branchlets, which comprise one terminal flower and two prophylls (monotelic structure). Flowering branchlets develop from the axillary buds of the prophylls of the short branches. In turn, these flowering branchlets produce new flowering branchlets from their prophyllar buds, reaching up to the sixth order; however, starting from the second order, only the axillary bud of the inner prophyll develops (Fig. 3 B and C). In turn, they develop new flowering branchlets, giving origin to a cymose reproductive structure that may be made up by as many as 11 flowers.

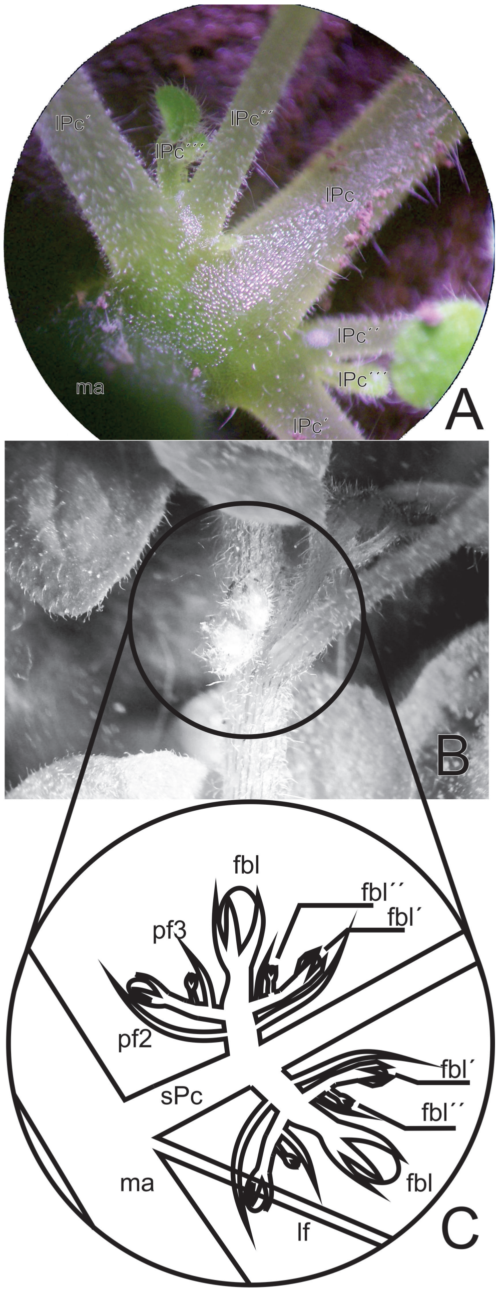
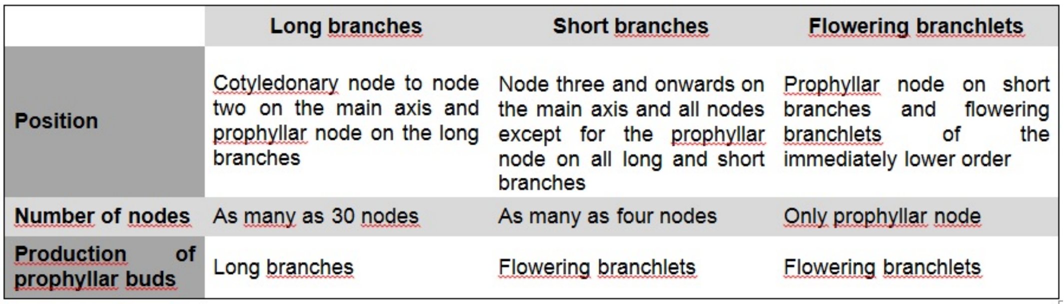


Fig. 3:*Parietaria debilis.* A: Disposal of long branches of prophyllar origin developed from one of the cotyledons. B: image of a sort branch. C: Structure of short branches and flowering branchlets. References: fbl – fbl´´, flowering branchlets of successive order; ma, main axis; sPc, short paraclades; lf, leaf; lPc-lPc´´´, suscessive order long paraclades pf2 and 3, prophyllar structure belongs to 2nd and 3rd order of flowering branchlets. Scale: 4X.

Table 1. Characterization of the different types of branches observed in *Parietaria debilis*.



	Long branches	Short branches	Flowering branchlets
Position	Cotyledonary node to node two on the main axis and prophyllar node on the long branches	Node three and onwards on the main axis and all nodes except for the prophyllar node on all long and short branches	Prophyllar node on short branches and flowering branchlets of the immediately lower order
Number of nodes	As many as 30 nodes	As many as four nodes	Only prophyllar node
Production of prophyllar buds	Long branches	Flowering branchlets	Flowering branchlets

As far as axis zonation is concerned, it may be highlighted that *P. debilis* lacks an inhibition zone, since all nodes have axillary productions (Fig. 2A). The main axis showed no terminal flower and since the apical meristem continued its vegetative growth until the end of growing season, it may be described as a truncate proliferating monotelicsynflorescence. All branches arranged along the main axis show paraclades. Long paraclades behaved similarly to the main axis. Short paraclades (i.e., short branches) were very peculiar structures, and at the base showed flowering branchlets in the prophyllar axil. This unique structure of the floriferous shoots was due to the high degree of proliferation affecting the terminal bud and the distal axillary buds of the main axis, the long branches and the short branches.

Under field conditions, the number of internodes and the branching degree was lower for all types of branches. In older herbarium specimens, another characteristic was observed in several cases, namely, the loss of the distal portion of the short branches, with only the reproductive structure remaining on the long branches and the main axis, giving the plant a different appearance. The most extreme cases were found in frost-sheltered specimens that continued their growth cycle for over a season, showing a similar behavior, albeit, with a much higher number of internodes on the main axis, long branches and short branches.

Development of the branching system from germination (Fig. 2D)

Germination was epigeal in this species. Under the conditions of this study, a high proportion of seedlings had expanded their cotyledons eight days after seeds had been placed to germinate. The first pair of nomophyllswere developed in opposite phyllotaxis ten days after emergence, followed by the second pair, which developed after fifteen days, in decussate opposite phyllotaxis. Before the emergence of the third pair of leaves, the first branches were developed from the axillary buds of the cotyledons. Basal branches produced in nodes one and two on the main axis developed when there are three and four pairs of expanded leaves on the axis, respectively, that is, when the axis had two expanded leaves above their node of insertion. As from day 25, short branch production on the main axis started in the third leaf node. Short branches began to develop when the axis has two expanded leaves above their node of insertion. Approximately on day 33, the cotyledonary node branches had branched up to the fourth order, and the basal long branches of nodes one and two had branched up to the third and second order, respectively. The number of leaves on the cotyledonary long branches was similar to that of the main axis and all branches elongated their internodes occupying the space horizontally. On the other hand, over the main axis scarcely were lengthened its internodes and kept its vertical position. At this stage also taked place the anthesis of the terminal flower of the first flowering branchlet, which had developed from the prophyllar axillary bud of the short branch located in node three (which, by now, has two leaves).

On day 42, the cotyledonary branches showed as high as sixth-order prophyllar basal branches, the first node branches showed up to fourth-order branches, and the second node branch showed up to third-order branches. Exceptionally, long branches also developed in node three, following an opposite phyllotactic arrangement. On day 102 (Fig. 2A), the plants had 4 first-order long branches with 30 nodes, 8 second-order branches, each with an average of 15 nodes; with third- and higher order long branches developing to a lesser extent and some even senescing. Cotyledonary branches had, on average, an equal or higher number of nodes than the main axis and they were longer because their internodes are longer. As from node 15, the distal end of the first-order long branches became orthotropic. The same, though with a lower number of internodes, occurred with all second- and higher order long branches, which elongated their internodes and whose distal end became orthotropic.

Once they have produced 3-5 fruits in the prophyll axils, short branches elongated their 2-3 internodes and, from the axillary buds of their leaves, developed new short branches (Fig. 2C).

Based on the number and development of long and short branches and considering that each branchlet develops 9-11 flowers, it may be estimated that flower production at day 102 ranged between 2800-3500 per plant.

DISCUSSION

The plant builds its structure as it develops and branching takes place. The typical growth pattern of a species may be defined as a hierarchical arrangement of structural sub-units or modules (Brisque, 1991; Moore & Moser, 1995). In the morphological description of plant structures, it is important to bear in mind their homology; otherwise, similar structures might be differently named, and vice versa, resulting in a confusing interpretation of the branching systems (Mora-Osejo, 1987). In order to compare branching systems, it is essential to determine what parts of the branching system resolve into flowers and what parts of branching system are equivalent (Weberling, 1985). In the species studied, both the main axis and the basal branches behave similarly, so they may be considered equivalent structures. In these axes, the zone that produces long branches has an opposite phyllotaxis, while the zone that bears reproductive structures has an alternate phyllotaxis. However, in descriptions of these species (Burkart, 1979), this fact is rarely mentioned; reference to the phyllotaxis shift has only been found in connection with the genus *Veronica* L. (Weberling, 1998).

The flowering unit represents the minimum expression of the system of reproductive axes usually called inflorescence (Sell, 1976). The term inflorescence has been mostly used to designate the group of flower-bearing branches, regardless of their position relative to the plant structure. This has led to data presented for different species not being comparable, since they referred to structures that were not homologous (Weberling, 1985). The concept of synflorescence, on the other hand, refers to the system of floriferous shoots produced from the apical bud of the embryonal axis or from an innovation bud during a growth period, that is to say that an annual plant would represent a synflorescence and a perennial plant would have several synflorescences, according to its growth form (Rúa, 1999). Based on this, and since both species studied have an annual growth cycle, the whole branching development observed is that of a synflorescence. Also, as a consequence of their growth cycle, development of all axillary buds takes place as the main axis develops, thus being considered sylleptic branches (Rúa, 1999: 84).

Initially, both *Veronica persica* and *Parietariadebilis* develop in a similar fashion, with cotyledonary branches developing when there are two pairs of expanded leaves on the main axis. Also, both species behave similarly in the basal zone, which coincides with an opposite phyllotaxis zone that produces branches equivalent to the main axis (i.e., which replicate its structure). In *V. persica*, both types of axes have a similar structure, although there is still a variation in the number of nodes involved. This variation has already been observed by Weberling (1998), who also noted that the branching are located until nodes 3-4. This behavior is similar to that observed in this study with field plants. In *P. debilis*, the main axis and the basal branches may be considered equivalent structures, since they have a zone that produces basal branches for exploration and another zone that produces short branches bearing reproductive structures, although these zones differ in terms of length in both types of axes (the prophylls are reduced in the basal branches). In other words, basal axes present the typical structure of the main axis, except because that the zone producing basal branches is significantly reduced. Such quantitative variations between the main axis and the basal axes have been observed in many species (Perreta&Vegetti, 2005; Perreta&Vegetti, 2006; Panigo, 2007). These basal axes, which are morphologically equivalent in both species, are called paraclades. Both the basal paraclades of *V. persica* and the long basal paraclades of *P. debilis* are enrichment axes, which increase the number of flowering structures and replicate the main axis structure (Rúa, 1999). They have a somewhat developed vegetative proximal portion, and generally show more plasticity than the main axis, because both the number of such axes and their degree of development are often strongly influenced by environmental conditions (Rúa, 1999).

Along the main axis and the basal paraclades of *V. persica*, an inhibition zone is observed, with leaves in opposite phyllotaxis, continuing from the zone of basal branch production and prior to the beginning of the zone of flower production, where the development of axillary productions may again be observed. Troll (1964) and Weberling (1998) did not mention the presence of an inhibition zone in *V. persica*, however even in the field plants with greater development of basal branches, it is possible to observe at least one internode does not develop branches. *P. debilis* lacks such a region and shows, instead, a c ontinuous type of branching (all nodes develop axillary productions).

In *V. persica*, the inflorescence (or flowering unit) is reduced to the main florescence (Fig. 1A and B). The establishment of the last foliage leaf as a lower limit of an inflorescence has brought about much confusion in recognizing homologous structures (Troll, 1964; Weberling, 1965, 1985, 1989). Confusion has also arisen regarding the interpretation of inflorescences in the genus *Veronica*. While *V. persica* and *V. didyma*Ten. have been described as having single axillary flowers, other species, such as *V. longifolia*L. and *V. peregrina*L., have terminal racemes, with the only difference being that in the former group flowers are located in the axils of foliage leaves whereas in the latter group, they are located in the axils of bracts, i.e., they only differ in the type of foliation (Weberling, 1998). In this work, the flowering cluster in which axes end is considered a florescence, a single structure that makes up the inflorescence or flowering unit in *V. persica*, a situation that may also apply to the other above mentioned species of *Veronica*. Given the fact that there is no terminal flower as a consequence of the continuous development of the apical meristem, the whole flowering system is recognized as a polytelicsynflorescence (Troll, 1964; Weberling, 1985), where the apical meristems continuously elongate the florescence zone.

A more complex synflorescence structure is seen in *Parietariadebilis*. This species has two types of paraclades differing in their position and length and in the production of their prophyllar buds: long paraclades (or long branches) and short paraclades (or short branches). Long paraclades develop new long branches from their prophyllar buds, and short paraclades from the axillary buds of the remaining leaves. Short paraclades develop cymes (monotelic structures) from their prophyllar buds, and new short paraclades from the rest of their axillary buds. Cymose branching may repeat from the prophyll axil of each new flowering axis in increasing order (Fig. 3C), so that some cymes may achieve a fairly complex structure (Rúa, 1999). Such axillary bud development may be delayed, as it happens with the production of new short branches, which only form when the short branch bearing them has already developed prophyllar flowering branchlets.

A distinctive feature of *P. debilis* is that the main axis, the basally-produced long branches and the short branches keep their apical meristems in the vegetative state: neither the apical meristems nor the axillary meristems existing in the axil of their leaves develop reproductive structures. Keeping apical meristems in the vegetative state in parallel with flower development is a characteristic that has been named early proliferation (Weberling, 1989). Early proliferation occurs when the main axis does not stop growing during flowering, originating a somewhat continuous production of paraclades from the lateral meristems, while the apical meristem continues extending the main axis in length (Rúa, 1999). This phenomenon originates the so-called proliferating structures. Early proliferation may take place in monotelic and polytelic inflorescences; in the latter, the passage to proliferating growth occurs before the main florescence has been formed, which results in the synflorescence truncation. In monotelic inflorescences, the passage to proliferating growthhappens before the meristem forms the terminal flower. In both cases, the apical meristem resumes and continues vegetative growth (Mora-Osejo, 1987).

Parietaria debilis present a truncate, proliferating monotelicsynflorecence. In this synflorescence are observed short branches bearing flowering structures only in prophyllar position. These flowering structures present a terminal flower and prophyllar flowering branchlets accordingly, both cymose branching system developed from the two prophylls of the short branch determines that the short branch or short paraclades would be the proliferating flowering unit. Short paraclades also show early proliferation but, unlike the main axis, which bears no flowers, they have monotelic structures in their prophyll axils.

The typological system of description makes it possible to compare shoot structures (Mora-Osejo, 1987) and avoid any common confusion in the interpretation of branching systems, especially of those bearing flowers (inflorescences) (Rúa, 1999). This system has proved to be repeatedly useful when it comes to establishing homology hypotheses between inflorescences in systematic and phylogenetic studies (Rúa, 1999), making it possible to accurately describe different species and establish hypotheses of homologies (Vegetti&Antón, 1995; Perreta&Vegetti, 1998, 2004; Reinheimer, 2007). At present, synflorescence analysis incorporates studies on the dynamics of development in order to generate inflorescence description models by relating adult structures, genetic mechanisms and transformations taking place during ontogeny (Kellog, 2000).

As regards the relationship between the growth form of these two species and their behavior as crop weeds (Dellaferrera, 2007), it may be stated that, being annual species, they lack buds persisting for regrowth the following year; that is, both species lack innovations (Troll, 1964). Nonetheless, their high capability to produce flowering structures determines a significant rate of seed production. Highlights of the invasion and persistence behavior of *V. persica* are the wide period of germination, which takes place at various times in autumn, spring and summer, and high seed viability, which is over 5 years in undisturbed soils (Boutin and Harper, 1991). This determines the species ability to survive and germinate after herbicide application. There is no available information for *P. debilis* regarding its germination behavior. Proliferation in *P. debilis*, which affects apical and axillary buds, keeps them active when faced with certain disturbance. This proliferation enables the development of new short branches and, from these, the generation of new flowering branchlets (Dellaferrera, 2007).

The morphological plasticity of *P. debilis* could probably contribute to its adaptability to the actual crop system and partly explain its ability of surviving glyphosate applications (Dellaferrera, 2007). Furthermore, *V. persica* also showed great plasticity to produce more basal branching in field conditions.The capacity of annual species of modifying the amount of branches and the timing of production of flowers in response to different environments, enabling them to react fast ensuring their seed production. Although the prolonged emergence pattern of this two species is known (Popay *et al.*, 2006; Puricelli& Papa, 2006), its effect on flowering phenology and success is less well understood. Later cohorts have more or less seed production potential? Ecological and morphological knowledge of annual and perennial weeds, such as reproductive phenology and capacity of develop flowers and branches, would help us better understand the invasiveness of these weeds and thus facilitate the development of more targeted control methods.

BIBLIOGRAFÍA

BARTHÉLEMY, D. & CARAGLIO, Y., 2007.Plant Architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny.*Ann. Bot.* 99: 375-407.

BELL, A. D., 1986. The simulation of branching patterns in modular organisms. *Phil. Trans. R. Soc. Lond. B.* 313: 143-159.

BERNARD, J.H., 1990. Life history and vegetative reproduction in *Carex.Canad. J. Bot.* 68: 1441-1448.

BOUTIN, C. & HARPER, J. L., 1991. A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *J. Ecol.* 79: 199-221.

BRISKE, N., 1991. Developmental morphology and physiology of grasses. In: HEITSCHMIDT, R.K., STUTH, J.W., (Eds.). *Grazing management: An ecological perspective*. pp. 85-108. TimberPress, Portland, Ore.

BURKART, A., 1979. Flora *Ilustrada de Entre Ríos (Argentina)*. Colección Cientifica del INTA 6, Buenos Aires.

CABRERA, A., 1967. *Flora de la provincia de Buenos Aires*. Coleccion científica del INTA (III), Buenos Aires.

DELLAFERRERA, I., 2007. *Variación en la forma de crecimiento de VeronicapersicaPoir. y Parietaria debilis G. Forst. producida por glifosato.* Tesis de grado. Universidad Nacional del litoral, Santa Fe.

DELLAFERRERA, I., GUARISE, N. AND AMSLER, A., 2007. Relevamiento de malezas en cultivos de soja en sistema de siembra directa con glifosato del departamento san justo (provincia de santa fe). *Revista FAVE* 5: 15-25.

DELLAFERRERA, I., ACOSTA, J. M., CAPELLINO, P. AND AMSLER, A., 2009.

Relevamiento de malezas en cultivos de soja en sistema de siembra directa con glifosato del departamento las colonias (provincia de Santa Fe). *Revista FAVE* 8: 7-12.

DENGLER, N.G., 1994. The influence of light on Leaf Development. In: IQBAL, M. (Ed). *Growth Patterns in Vascular Plants*, pp.100-136.Dioscorides Press, Oregon.

EDELIN, C., 1984. *L'architecture monopodiale: l'exemple de quelques arbres d'Asie tropicale.*ThéseDoctorat. Universite de Montpellier II.

FACCINI, D. E., 2000. Los Cambios Tecnologicos y Las Nuevas Especies de Malezas en Soja. *Agromensajes* 4: 5-8.

FOURNIER, A., 1982. *Cyclesaisonnier de la biomasse et démographie des feuilles de quelques graminées dans les savanes guinéennes de Ouango-Fitini (Côte d'Ivoire).*These Doctorat. Universite des Sciencies et Techniques du Languendoc, Montpellier.

GROSSO, M. A., 2001. *Formas de crecimiento de especies herbáceas y arbustivas a lo largo de un gradiente altitudinal en el área serrana de la provincia de Córdoba.* Tesis de Doctorado. Universidad Nacional de Río Cuarto.

HAGEMANN, W., 1981.WuchsformenuntersuchungenanBalkanischenHypericum – sippen. *Bot. Jahrb. Syst*. 102: 239-254.

HUAI, H. Y., ZHANG, B., ZHANG, G.Y.,JIANG, L. 2004. Characteristics of vegetative growth of *Veronica persica* and their contribution to its sexual reproduction. Journal of Yangzhou University –Agricultural and Life Sciences Edition 25(3): 70-73.

KÄSTNER, A.,1989. BeiträgezurWuchsformanalyse und systematischenGliederung von Teucrium L.*Flora* 183: 189-224.

KELLOG, E., 2000. A model of inflorescence development. - In: JACOBS, W.L., EVERETT, J. (Eds*.). Monocots, Systematics and Evolution,* Vol. 1 of Proceeding 2nd International Conference on the Comparative Biology of Monocotyledons, pp. 84.88.Csiro Publishing, Melbourne.

KRUMBIEGEL, A., 1998. Growth forms of annual vascular plants in central Europe. *Nord. J. Bot.* 18 : 563-575.

LEGUIZAMÓN, E. S., FERRARI, G., 2005. Relevamiento de las comunidades de malezas en sistemas de producción de soja bajo siembra directa. Soja en siembra directa. *Rev. Técnica AAPRESID*, septiembre, 124-127.

MALPASSI, R., 2004. *Efecto de la aplicación de herbicidas sobre la morfología y anatomía de Eleusine indica (L.) Gaertner y Portulacaoleracea L.* Tesis Doctoral, Universidad Nacional de Río Cuarto.

MEUSEL, H., 1960. Bewurzelung und WuchsformeinigerAsteriscus-Arten.*Flora* 150: 441-453.

MEUSEL, H. 1970. Wuchsformenriehen Mediterranean-mitteleuropäischer Angiosperm-Taxa.*FeddesRepert.* 81: 41-59.

MEUSEL, M., JÄGER, E., MÖRCHEN, G., 1977. The study of growth-forms of higher plants in relation to application of biocide.*Veget. Sci. Environ. Protect.*71-76.

MONTENEGRO, G., GINOCCHIO, R., 1992. Modular interpretation of architecture in shrub species.*An. Acad. Bras. Ci.* 65: 189-202.

MOORE, K. J., MOOSER, L. E., 1995. Quantifying developmental morphology of perennial grasses.*CropSci.* 35: 37-43.

MORA OSEJO, J. E., 1987. *Estudios Morfológicos, Autoecológicos y Sistemáticos en Angiospermas.* Academia Colombiana de Ciencias Exactas, Físicas y Naturales, Bogotá.

PANIGO, E., 2007. *Variaciones de los Patrones Estructurales de Commelina erecta por acción del Glifosato.* Tesis de grado, Universidad Nacional del litoral, Santa Fe.

PANIGO, E.; DELLAFERRARA, I., ACOSTA, J.M., BENDER, A., GARETTO, J.M., PERRETA, M. 2012. Glyphosate-Induced Structural Variations in *Commelinaerecta* L. (Commelinaceae).*Ecotoxicol.Environ. Safety* 76: 135-142.

PAPA, J.C., CARRANCIO, L., 2005. Experiencias de control de ocucha (*Parietaria debilis*). INTA EEA Oliveros. *Para mejorar la producción* 30: 153 -154.

PERRETA, M., VEGETTI, A., 1998. Tipología de la inflorescencia en *Leptochloa* (Poaceae). *Kurtziana* 26: 135-144.

PERRETA, M., VEGETTI, A., 2004.Structure development of the branching system in *Melicamacra* (Poaceae).*Flora* 199: 36-41.

PERRETA, M., VE GETTI, A., 2005. Patrones estructurales en plantas superiores. *Gayana Bot.* 62: 9-19.

PERRETA, M., VEGETTI, A., 2006.Structure and development of the branching system in *Melicasarmentosa.FeddesRepert.* 117: 264-271.

POPAY, A. I., COX, T. I., INGLE, A., KERR. R., 2006.Seasonal emergence of weeds in cultivated soil in New Zealand.*Weed Res.* 35: 429 - 436.

PURICELLI, E., PAPA, J.C., 2006. Growth of *Parietariadebilis* in fallow and in undisturbed areas.*Weed Res.* 46: 129–137.

PURICELLI, E., TUESCA, D., FACCINI, D., NISENSOHN, L., VI TTA, J. I., 2005. *Análisis en los cambios de la densidad y diversidad de malezas en rotaciones con cultivos resistentes a glifosato en Argentina.* Seminario - la densidad y diversidad de malezas en rotaciones con cultivos resistentes a glifosato en Argentina. Seminario-Taller Iberoamericano, Colonia del Sacramento.

RAUH, W., 1938. Über die VerzweingungausläuferbildenderStrauchemit besondererBerücksichtigungihrerBeziehungenzu den Stauden. *Hercynia* 1: 187-231.

REINHEIMER, R., 2007. *Desarrollo y estructura de la inflorescencia deBrachiaria y Uruchloa(Poaceae: Panicoideae: Paniceae) y sus implicancias sistemáticas*. Tesis doctoral. Universidad Nacional del Litoral, Santa Fe.

RUA, G. H., 1999. *Inflorescencias. Bases teóricas para su análisis*. Soc. Argent. Botánica, Buenos Aires.

SELL, Y., 1976. Tendancesévolutivesparmi les complexesinflorescentiels. *Rev. Gén. Bot.* 83: 247-267.

SORARÚ, S.B., 1972. Revisión de las “Urticaceae” argentinas. *Darwiniana* 17: 246-325.

TROLL, W., 1964. Die Infloreszenzen, Typologie und StellungimAufbau des Vegetationskörpers 1, Gustav Fischer, Jena.

VEGETTI, A.,C., ANT ON, A. M., 1995. Some evolution trends in the inflorescence of Poaceae. *Flora* 190: 225-228.

WEBERLING, F., 1965.Typology of inflorescences.*Bot. J. Linn. Soc*. 59: 15-221.

WEBERLING, F., 1985.Aspectos modernos de la morfología de las inflorescencias. *Bol. Soc. Argent. Bot.* 24: 1-28.

WEBERLING, F., 1989.*Morphology of flowers and inflorescences*.Trans. by J. Pankhurst, - Cambridge University Press, Cambridge.

WEBERLING, F., 1998.Monotele und polyteleSynfloreszenzen. In: TROLL, W. *Die Infloreszenzen, Typologie und Stellung in Aufbau des Vegetationskörpers* II/2. - G. Fischer, Jena.

Recibido el 10 de diciembre de 2013, aceptado el 19 de agosto de 2014.