

---

## THE DEVELOPMENT OF THE TUSSOCK OF A CLONAL GRASS

---

Susana Raquel Feldman, Susana Julio Gattuso and Juan Pablo Lewis

### SUMMARY

The development of the tussock architecture in *Spartina argentinensis* Parodi (Poaceae: Chlorideae) is analyzed. The anatomy of the rhizomes and the position of the buds that continue growth after disturbances such as fire are described, using pot grown plants and field collected adult plants. The plant exhibits a phalanx type of growth and begins to differentiate sympodial rhizomes after

bearing more than five shoots. All buds are protected from fire by strips of lignified tissues. Monk tonsure-like gaps are regularly produced in the life cycle of the plant; their development begins when the plant has at least ten shoots and the growth of the rhizomes determines the future rays of the tussock. Environmental factors only allow the central gap to be seen.

### RESUMEN

Se analiza el desarrollo de la arquitectura de las macollas de *Spartina argentinensis* Parodi (Poaceae: Chlorideae). Utilizando plantas crecidas en potes y plantas recogidas en campo, se describió la anatomía de los rizomas y la posición de las yemas, que continúan el crecimiento después de disturbios tales como el fuego. La planta presenta un crecimiento tipo falange y comienza a diferenciar rizomas simpodiales después de emitir cinco o

más vástagos aéreos. Todas las yemas están protegidas contra el fuego por bandas de tejidos lignificados. Las tonsuras de monje se producen regularmente a lo largo del ciclo de vida de la planta, su desarrollo comienza cuando la planta tiene al menos diez vástagos aéreos y el crecimiento de los rizomas determina los futuros rayos de las macollas. Los factores ambientales solo permiten que se visualice ese claro o tonsura de monje.

---

### Introduction

Clonal plants are characterized by bearing modules that can achieve independent life, giving rise to a new individual or ramet according to different growth patterns. Therefore, grasses can be considered as modular organisms where the shoots are the structural units (Harper, 1977) and their shape or architecture is determined mainly by the angles formed by the shoots that appear successively (Godin *et al.*, 1999; Godin, 2000).

In some cases, as the plant grows radially the central part of the plant dies out. This phenomenon

has been described in many species by several authors (Ruiz Leal, 1959; Lewis *et al.*, 1990, 2001; Danin and Orshan 1995; Wikberg and Mucina, 2002) but it has not been established if it is due to environmental factors or if it is inherent to the growth pattern of the plant, as thought by Adachi *et al.* (1996), who claimed that at least the forb of *Reynoutria japonica* it was brought about by the growth pattern of the rhizome system.

Strickland (1983) described this phenomenon in grasses from North America (*Oryzopsis hymenoides*, *Festuca idahoensis*, *Stipa* spp., *Muhlenbergia torreyii*,

*Agropyron spicatum* and *A. desertorum*) and postulated that it can be the result of three mechanisms: overgrazing, undergrazing or senescence. There is no solid evidence of any of these hypotheses.

*Spartina argentinensis* Parodi (Poaceae) is the dominant species of the tall grasslands of depressed areas of the Chaco-Pampean plain of north-central Argentina (Cabrera and Willink, 1973; Lewis *et al.*, 1990). The communities of *S. argentinensis* thrive on hydro-halomorphic soils with high Na concentration, and pH ~8, and have an almost unspecific matrix with *S.*

*argentinensis* and interstitial species such as *Chloris halophylla*, *C. ciliata*, *Distichlis spicata*, *Sesuvium portulacastrum*, *Heliotropium curassavicum*, *Pluchea sagittalis*, *Salicornia ambigua*, *Verbena litoralis*, etc.

The tussocks of *S. argentinensis* can be >1m in diameter, and very often large central gaps can be seen. They have been called monk's tonsure-like gaps (MTLG) and it has been proposed that they could be the result of tussock development, or disturbance such as fire (Lewis *et al.*, 2001). The MTLG increase in size with time and the ring of shoots around them

---

### KEYWORDS / Disturbance / Fire / Grasslands / Ontogeny / *Spartina argentinensis* /

Received: 11/09/2006. Modified: 03/05/2007. Accepted: 03/20/2007.

Susana Raquel Feldman. Agromonic Engineer, Universidad Nacional de Rosario (UNR), Argentina. Doctor Biological Sciences, Universidad Nacional de Córdoba, Argentina. Professor, UNR, Researcher Consejo

de Investigaciones of the UNR (CIURN). Address: Universidad Nacional de Rosario, CC 14, S2125ZAA Zavalla, Argentina. e-mail: sfeldman@unr.edu.ar

Susana Julio Gattuso. Pharmacist and Doctor, UNR, Argentina. Professor, UNR, Argentina. Juan Pablo Lewis. Agromonic Engineer, Universidad de Buenos Aires, Argentina. Ph.D. en

Botanics. University of Cambridge. UK. Professor, UNR Researcher, CONICET, Argentina.

*Analisa-se o desenvolvimento da arquitetura dos maços de Spartina argentinensis Parodi (Poaceae: Chlorideae). Utilizando plantas crescidas em potes e plantas recolhidas em campo, se descreveu a anatomia dos rizomas e a posição das gemas, que continuam o crescimento depois de distúrbios tais como o fogo. A planta apresenta um crescimento tipo falange e começa a diferenciar rizomas simpodiais depois de emitir cinco ou*

*mais caules aéreos. Todas as gemas estão protegidas contra o fogo por bandas de tecidos lignificados. As tonsuras de monge se produzem regularmente ao longo do ciclo da vida da planta, seu desenvolvimento começa quando a planta tem pelo menos dez caules aéreos e o crescimento dos rizomas determina os futuros diâmetros dos maços. Os fatores ambientais somente permitem que se visualize esse claro ou tonsura de monge.*

eventually breaks down in several segments, some of which may give rise to new tussocks. Therefore, their development may be very significant for the vegetative regeneration of the grassland matrix, in a similar way as the directional growth of a clonal bromeliad species in the Brazilian *restinga* community (Sampaio *et al.*, 2004).

Fire is a common disturbance in American grasslands, even before European colonization (Uresk *et al.*, 1980; Knapp, 1985; Eskuche, 1992). Large biomass accumulation is a common feature in *S. argentinensis* grasslands (Feldman and Lewis, 2005), so fires are frequent at the end of winter or during dry summers.

Although there are several studies on the morphology of different species of *Spartina* (Sutherland, 1916; Caldwell, 1957; Metcalfe, 1960; Levering and Thomson, 1972; Anderson, 1974; Walsh, 1990; Perazzolo and Pinheiro, 1991), there are neither morphological nor anatomical descriptions corresponding to *S. argentinensis*. After fire or clipping, gaps in large tussocks of *S. argentinensis* were visible (Feldman *et al.*, 2004) but there is no evidence if the MTLG were the result of disturbance or otherwise; it is a characteristic of the plant ontogeny. The objectives of this paper are 1) to analyze the plant architecture (*sensu* Godin *et al.*, 1999; Perreta and Vegetti, 2005) of *S. argentinensis*, 2) to describe the anatomy of the rhizomes and the position of the buds that restart

growth after fire, and 3) to determine what mechanisms trigger MTLG (Lewis *et al.*, 1990, 2001) development.

### Material and Methods

Morphological and anatomical observations and studies were made on seedlings obtained from seeds (caryopses) or from adult plants of the Federico Wildermuth Reserve, Argentina (31°57'S, 61°23'W). The Reserve is representative of the halophylous grasslands of the area and was established in 1988, cattle being excluded from the area since 1991. Adult plants randomly collected from the Reserve were from an area free of fire at least for the last 15 years. Seedlings were grown in 20cm diameter pots filled with Reserve soil and maintained outdoors from March (autumn) onwards at the *Facultad de Ciencias Agrarias* gardens, 150km SE from the Reserve. Botanical terms are according to Hickey and Clive (2000).

### Rhizome ontogeny

Seedlings with 3, 4 and 6 shoots were collected in order to determine from what stage they begin to develop rhizomes, when lignified cell strata are differentiated and the characteristic architecture of the plant set up. The 10 basal mm were cut off, removing the roots, and the remaining portions were put in a 30% hydrofluoric acid solution during six days (Ruzin, 1999). Then, they were rinsed under running water, dehydrated in alcohols and included in paraffin

wax. Cross and longitudinal sections (18-20µm thick) were obtained and colored with safranin-fast green (Dizeo de Strittmater, 1979). Drawings were made using a Wild TYP 308700 stereomicroscope equipped with a drawing device. The presence of lignin in the sheath of non-elongated shoots of seedlings with no more than three aerial shoots was determined with the fluoroglucine test (Ruzin, 1999).

### Tussock ontogeny

The architecture analysis was made by measuring the angles determined by the first and successive shoots corresponding to eight seedlings. Seedlings grown in pots and with 3 to 13 emerged shoots were cut at 5cm from the base and kept vertically below a glass panel mounted on a 10cm high wooden frame, so that the points corresponding to each shoot could be marked on a transparent sheet. The angles were measured according to a Cartesian coordinate system, with the origin passing through the first shoot, in such a way that the angles determined by the abscissa axis and the segments of shoots 1-2 and 1-3, clockwise and counter clockwise respectively, were equal. Angles of each shoot in relation to the abscissa were determined relating points corresponding to each shoot to the first shoot. The cross section of a plant with six primary shoots was outlined showing the position of the primary and secondary shoots at 5cm from the base.

### Rhizome anatomy

Portions of the rhizome from tussocks >20cm in diameter were taken from the field and placed during 48h in 10% ethilendiamine (Carlquist, 1982). Then they were rinsed under running water, dehydrated and colored in the same way as indicated above. Starch presence was determined by iodine-iodide test using plants with seven emerged shoots. In all schematic anatomical representations Metcalfe (1960) symbols were used.

### Structure analysis of adult plants and their response to disturbance

Plants corresponding to different ranges of basal diameters (7-15cm, n=10; 25-30cm, n= 6; and 40-45cm, n= 3) were randomly selected from the population, and leaves and roots were removed leaving the rhizomes exposed. Diameters of tussocks and the central area of each plant were measured. The sector bearing shoots with all its senescent leaves was considered the central area. The ratio between the central area and tussock diameters was calculated, and differences among groups were assessed using ANOVA and Duncan test. Bud viability of the nearest live shoot to the removed central area (n=6 per plant) was determined by incubating them during 6h in the dark at 28°C in 1% phenyl-tetrazolium chlorine (Busso *et al.*, 1993). Similar plant series as stated above (n=5 in the first two categories and n=3

in the third one) were placed on trays with humid sand and the aerial part up to 3-5cm from the base was removed, in order to analyze the resprout pattern after clipping.

## Results

### Rhizome ontogeny

When the first two leaves start to age, two new shoots emerge in an alternate way, very near to each other and usually enveloped by the sheath. Adventitious roots originate at the basis of these shoots, as in the main shoot, when seedlings are 2-3 months-old; the first leaf is 4-5cm long and may have started to age.

The cross section at the base of a 25.8cm high, 4.5 month-old plant with four shoots is presented in Figure 1. The principal shoot is surrounded by a sheath of several layers of sclerenchyma cells. Lateral stems are protected by the sheath blade. A rhizome, which would be evident as a longitudinal stem structure, is not seen.

The rhizome was observed in a 35.1cm high plant with six emerged shoots, six months after germination (Figure 2). A stem structure in the longitudinal section is observed at the base of the plant, as well as stems in the transversal section, roots and an emerging bud protected by the blades sheath

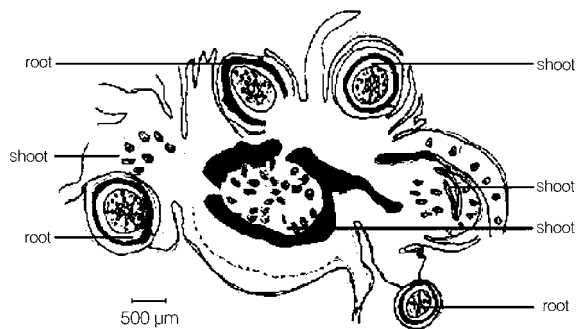


Figure 1. Cross section of the base of a 4.5 month-old seedling of *S. argentinensis* with roots in transverse section. No rhizome is present.

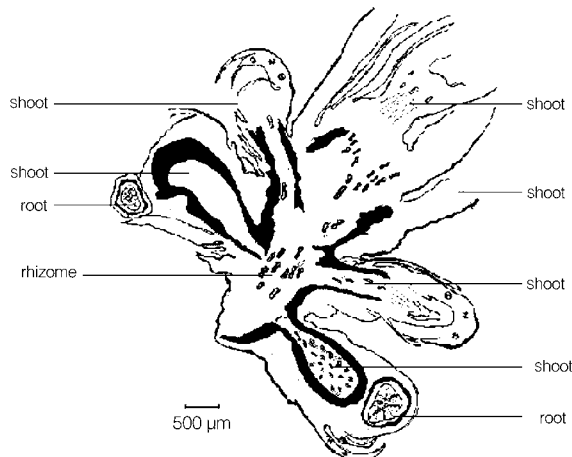


Figure 2. Cross section of the base of a 6 month-old seedling of *S. argentinensis* with six shoots and two roots in transverse sections, showing the rhizome in longitudinal section.

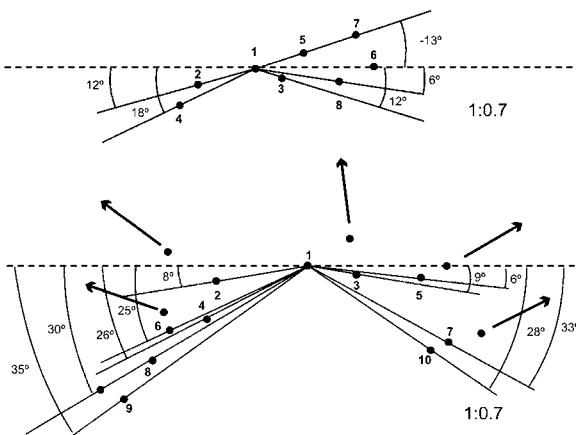


Figure 3. Diagram of the angles between the first and subsequent shoots. A: 6.5 month-old plant with 8 shoots, b: 7 month-old plant with 10 shoots. Arrows show growth direction.

that have sclerenchyma cells. There are also several layers of sclerenchyma and parenchyma cells with thickened walls in the blades of sheaths that protect the apex

of aerial shoots. All transversal sections of the sheaths bases tinted with fluoroglucine were wine-red; therefore, their cell walls were already lignified, although seedlings were only 2-3 months old.

### Tussock ontogeny

The second and third shoots grew at a  $29 \pm 14^\circ$  angle in relation to the vertical plane of the first one, projecting them clockwise and counter clockwise, respectively, on the horizontal plane of the developing tussock. Successive shoots emerged in an alternate way, at each side of the first shoot, turning away from it and forming a circumference on the tussock horizontal plane. The measured angles were progressively larger. Usually, shoots originate at the distal side of the first one (positive angle, *sensu* Routledge, 1987), although in some of the cases there was a reversion forming a negative angle in relation to the previous ones. A 6.5 month-old plant had eight primary shoots, two of them forming angles which reverse the circumference (shoots 5 and 7; Figure 3a). In the 7 month-old plant the position of 10 primary shoots can be observed and, according to the thickness of the bases of the shoots, it was evident that rhizomes differentiated in some of them and they were very near to

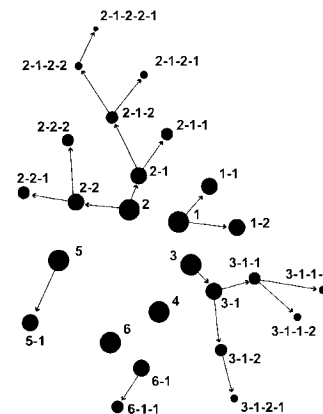


Figure 4. Cross section of a tussock of *S. argentinensis* with primary (1-6) and higher order shoots (section at 5cm from the ground). Bigger circles mark the position of the primary shoots, the numbers indicate the order of emergence, and secondary shoots have as first digit the number of the primary shoot where they grew. Arrows show growth direction.

start growth in the arrows direction (Figure 3b).

The diagram of the growing tussock's base and the circumference formed by all the shoots (6 primary and 20 of higher order) is presented in Figure 4. Each emerged shoot produced new aerial tillers from the axillary buds of the leaves, and simultaneously started to differentiate a rhizome that determined the plant's radial centrifugal growth.

The rhizomes had very short internodes and sympodial ramification, because the apex differentiated an orthotropic shoot and a sub-apical bud that continued plagiothropic growth. All rhizome nodes differentiated shoots, which could differentiate one or several "daughter" tillers from the basal nodes, resulting in a very tight and compact tussock. The rhizomes grew in a centrifugal way; however, sometimes they branched, *i.e.* the bud did not produce an aerial shoot but originated rhizomes of higher order that continued to grow. A branching pattern, such as a number of nodes between

two successive ramifications, was not observed, and usually the angle between a rhizome and another of higher order was  $\sim 30^\circ$ . Initial growth stages are slow, and only after six months the tussock is formed with an aerial shoot system, with shoots concentrated at the base and a system of half-buried rhizomes. The inflorescences differentiated around midsummer (January), in two-year old plants and, as in other grasses, all internodes elongated during this pre-flowering period. The inflorescence emerged wrapped in the flag leaf of the shoot. After flowering, the shoot aged and died.

#### Rhizome anatomy

Rhizomes had lignified tissues of several cell layers, cells thick sclerenchyma strip, all with thickened and lignified walls (Figure 5). The vascular bundles are arranged in the characteristic atactostelae of grasses, surrounded by lignified tissue. A central cavity that occupies part of the pith is evident together

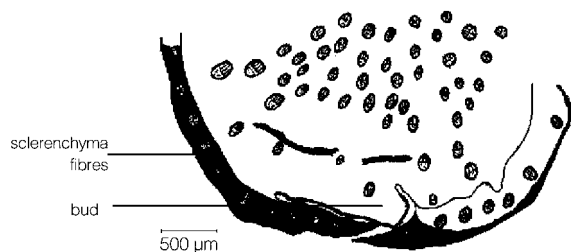


Figure 5. Cross section of a rhizome of *S. argentinensis*. Sclerenchyma and parenchyma tissues are visible. A bud is emerging protected by lignified tissue.

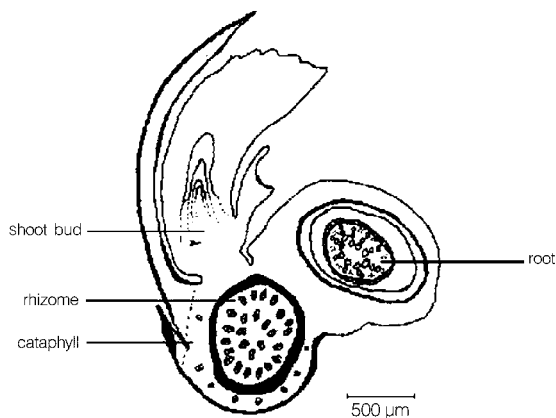


Figure 6. Cross section of a rhizome and longitudinal section of an emerging shoot bud of *S. argentinensis*, protected by the sheath bases.

with the vascular bundles surrounded by a sheath of thick layers of sclerenchyma cells. Emerging buds are protected by the sheath bases that wrap rhizomes and shoots, which have highly lignified subepidermic tissue layers (Figure 6). The iodine-iodite dye indicated that rhizomes had a high density of round and simple starch grains that occupy most of the parenchyma cells volume. There were

also starch grains at the base of the sheath that emerges from rhizomes, more densely at the abaxial side.

#### Structure analysis of adult plants and their response to disturbance

The central area of the three plant size groups was observed dead and undergoing different degrees of decomposition. In the larger plants the ratio between the central area and the tussock diameters was approximately three times larger than in two smaller groups of plants, which means that as plants aged, the central area, already senescent, increased faster than the plant diameter

(Table I). In the three kinds of plants used, the first and sometimes the first and second nearest shoot to the central senescent part of the plant and still bearing at least one green leaf, were not dyed with tetrazolium, indicating that they did not have living meristematic tissue. All other buds were metabolically active.

When incubated in humid sand, central shoots did not restart growth after they were cut. Only those shoots that were in the outer circle restarted growth, forming the quasi circular monk's tonsure-like gaps (MTLG). In plants with diameters  $>25\text{cm}$  (classes II and III), the periphery circle did not always restart growth homogeneously and in several cases it was evident that 2-4 groups of shoots were not parts of the same tussock any more, but they had formed new individuals instead.

#### Discussion

The growth pattern of the whole tussock of *S. argentinensis*, which allows it to occupy space in all its rays simultaneously without leaving gaps and preventing the establishment of other species, resembles what Lovett-Doust (1981) and Schmid and Harper (1985) termed "phalanx" growth (centrifugal and multidirectional). As a result of this centrifugal and multidirectional growth, *S. argentinensis* plant structure is compact and formed by a high number of aerial shoots with internodes that have not elongated, and therefore their meristems are protected by the sheaths of all the emerged leaves, which have layers of sclerenchyma cells. This growth pattern results in an adaptive feature in face of the most common disturbance factor, which is fire, and together with its high photosynthetic rate even under drought conditions (Feldman *et al.*, 2004) are characteristics that enable *S. argentinensis* to form almost monospecific stands (Feldman and Lewis, 2005).

Sarmiento (1992) pointed out that in grasses where there is no elongation of vegetative shoots, such as *Leptocoryphium lanatum*, *Sporobolus cubensis* and *Elyonurus adustus*, meristems are buried in the soil, thus ensuring re-sprout after defoliation. In the case of *S. argentinensis*, the meristems of the rhizomes are half-buried in the soil and the aerial shoots are protected by strongly lignified cataphyll-like leaf sheaths. Starch grains in the rhizome as well as in the sheath would provide a source of energy to allow tiller regeneration after fire until the plant shoot is again photosynthetically independent.

The results show that the basic structure of the tussock is already developed

TABLE I  
DIAMETERS OF SPARTINA ARGENTINENSIS TUSSOCKS (CM) CORRESPONDING TO THREE GROUPS OF PLANTS OF INCREASING DIAMETERS \*

Group	MD	SCA	SCA /MD (*)
I	10.34 $\pm$ 0.59	1.24 $\pm$ 0.17	0.121 a
II	27.60 $\pm$ 1.15	5.78 $\pm$ 0.52	0.149 ab
III	43.27 $\pm$ 1.62	16.2 $\pm$ 1.12	0.377 c

\* I: 7-15cm, II: 25-30cm, III: 40-45cm (n=10, 6 and 3, respectively). Average  $\pm$ SEM.

MD: maximum diameter, SCA: senescent central areas. Values followed by the same letter are not statistically different,  $p < 0.05$ .

before the plant is one year old. Only in the summer of the second year some shoots will flower and produce seeds, ageing later, while the rhizomes continue growing and new tillers emerge from the bases of the already grown shoots. Parallel to the tussock growth, dead organic matter accumulation starts as a result of i) shoots which have flowered, ii) shoots which die before flowering, and iii) senescence of basal leaves of shoots that are still alive. This accumulation of dead matter will favor initiation and propagation of fire.

No regrowth was resumed in any of the disturbed plants of their geometrical center, not as consequence of cutting or burning but due to the fact that there was no living tissue before the disturbance, though the gaps were not evident because long leaves completely covered it. The data indicate that in *S. argentinensis*, "hollow crowns" (Strickland, 1983) or "monk's tonsure-like gaps" (Lewis *et al.*, 2001) are the result of the ontogeny and senescence of the tussock, as it was already suggested for *Festuca ovina*. Working with plants obtained from seeds and adult plants not subjected to grazing or fire, it was shown that in *S. argentinensis* tussocks the formation of a central gap is a consequence of its tillering pattern and rhizome growth, which constitute its normal architecture. Although the phenomenon begins when the plant is younger than a year, it will become evident only after the second or third year. Different environmental factors such as grazing and fire, do not trigger the formation of the central gap; they only allow it to be seen.

#### ACKNOWLEDGEMENTS

We authors thank JM Vázquez for his help with

the figures of the final draft, the Federico Wildermuth Foundation for permission to work with plants from their Reserve, and the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET) for financial aid.

#### REFERENCES

Adachi N, Ichiro T, Takahashi M (1996) Central die-back of monoclonal stands of *Reynoutria japonica* in an early stage of primary succession on Mount Fuji. *Ann. Bot.* 77: 477-486.

Anderson CE (1974) A review of structure in several North Carolina salt marsh plants. In Rendt RJ, Queen WH (Eds.) *Ecology of halophytes*. Academic Press. London, UK. 605 pp.

Busso CA, Boo RM, Pelaez DV (1993) Fire effects on bud viability and growth of *Stipa tenuis* in semiarid Argentina. *Ann. Bot.* 71: 377-381.

Cabrera AL, Willink A (1973) *Biogeografía de América Latina*. Serie de Biología, Monografía N° 13. OEA. Washington, USA.

Caldwell PA (1957) The spatial development of *Spartina* colonies growing without competition. *Ann. Bot.* 21: 203-216.

Carlquist S (1982) The use of ethylenediamine in softening hard plant structures for paraffin sectioning. *Stain Technol.* 57: 311-317.

Danin A, Orshan G (1995) Circular arrangement of *Stipagrostis ciliata* clumps in the Negev, Israel and near Gokhaeb, Namibia. *J. Arid Environ.* 30: 307-313.

Dizeo de Strittmater C (1979) Modificación de una técnica de coloración safranina-fast green. *Bol. Soc. Arg. Bot.* 18: 121-122.

Eskuche U (1992) *Los espartillares, un monumento histórico pre-colombino en el tapiz vegetal del NE argentino*. Herbarium Humboldtianum. Universidad. Nacional del Nordeste. Argentina. 37 pp.

Feldman SR, Bisaro V, Lewis JP (2004) Photosynthetic and growth responses to fire of the subtropical-temperate

grass, *Spartina argentinensis* Parodi. *Flora* 199: 491-499.

Feldman SR, Lewis JP (2005) Effect of fire on the structure and diversity of a *Spartina argentinensis* tall grassland. *Appl. Veget. Sci.* 8: 77-84.

Godin C (2000) Representing and encoding plant architecture. A review. *Ann. Forest Sci.* 57: 413-438.

Godin C, Costes E, Sinoquet H (1999) A method for describing plant architecture which integrates topology and geometry. *Ann. Bot.* 84: 343-357.

Harper JL (1977) *Population Biology of Plants*. Academic Press. London, UK. 892 pp.

Hickey M, Clive K (2000) *Illustrated Glossary of Botanical Terms*. Cambridge University Press. Cambridge, UK. 208 pp.

Knapp AK (1985) Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. *Ecology* 66: 1309-1320.

Levering CA, Thomson WW (1972) Studies of the ultrastructure and mechanism of secretion of the salt gland of the grass *Spartina*. *Proc. 30th Electron Microscope Soc. of America*. pp. 222-223.

Lewis JP, Stofella SL, Prado DE, Pire EF, Franceschi EA, Carnevale NJ (1990) Dynamics and development of floristic richness in the vegetation of a large depressed area of the Great Chaco. *Flora* 184: 63-77.

Lewis JP, Stofella SL, Feldman SR (2001) The origin of tonsure like gaps in *Spartina argentinensis* Parodi. *Rev. Biol. Trop.* 49: 313-316.

Lovett-Doust L (1981) Population dynamics and local specializations in a clonal plant *Ranunculus repens* L. The dynamics of ramets in contrasting habitats. *J. Ecol.* 69: 743-755.

Metcalfe CR (1960) *Anatomy of the Monocotyledons*. Vol I. Gramineae. Clarendon Press. Oxford, UK. 731 pp.

Perazzolo M, Pinheiro F (1991) Aspectos anatómicos e ad-

aptativos das partes vegetativas de *Spartina densiflora* Brong. (Gramineae) da marisma do estuário da lagoa dos Patos-RS. *Acta Bot. Bras.* 5: 3-16.

Perreta MG, Vegetti AC (2005) Patrones estructurales en las plantas vasculares: una revisión. *Gayana Botanica*. 62: 9-19

Routledge RD (1987) Rhizome architecture for dispersal in *Eleocharis palustris*. *Can. J. Bot.* 65: 1218-1223.

Ruiz Leal A (1959) El desarrollo de estructuras subcirculares en algunas plantas. *Rev. Agron. Nordeste Arg.* 3: 83-138.

Ruzin S (1999) Plant Microtechnique and Microscopy. Oxford University Press. Oxford, UK. 534 pp.

Sampaio MC, Araújo TF, Scarano FR, Stefer JF (2004) Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity. *Evol. Ecol.* 18: 409-428.

Sarmiento G (1992) Adaptive strategies of perennial grasses in South American savannas. *J. Veget. Sci.* 3: 325-336.

Schmid B, Harper JL (1985) Clonal growth in grassland perennials. I. Density and pattern-dependent competition between plants with different growth forms. *J. Ecol.* 73: 793-808.

Strickland R (1983) Hollow crowns: overgrazing, undergrazing, or old age?. *Rangelands* 5: 13-14.

Sutherland GK (1916) The physiological anatomy of *Spartina townsendii*. *Ann. Bot.* 30: 333-351.

Uresk DW, Rickard WD, Cline JF (1980) Perennial grasses and their response to a wild-fire in south-central Washington. *J. Range Manag.* 33: 111-114.

Walsh GE (1990) Anatomy of the seed and seedling of *Spartina alterniflora* Loes. (Poaceae). *Aquatic Bot.* 38: 177-193.

Wikberg S, Mucina L (2002) Spatial variation in vegetation and abiotic factors relative to a ring-forming sedge. *J. Veget. Sci.* 3: 677-684.