Spatial structure and development of *Paspalum vaginatum* (Poaceae): an architectural approach

Liliana T. Fabbri[A,D], *Mariel Perreta*[B,C] *and Gabriel H. Rua*[A,C]

[A]Universidad de Buenos Aires, Facultad de Agronomía, Av. San Martín 4453, C1417DSE, CABA, Argentina.
[B]Universidad Nacional del Litoral, Facultad de Ciencias Agrarias, Kreder 2805, S3080HOF, Esperanza, Santa Fe, Argentina.
[C]Member of 'Carrera del Investigador', Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.
[D]Corresponding author. Email: fabbri@agro.uba.ar

Abstract. *Paspalum vaginatum* Sw. is a perennial grass originating from tropical and subtropical regions worldwide that plays important ecological and utilitarian roles such as dune stabilisation and erosion control, and is used as a lawn and forage plant. The vegetative morphology of shoots was studied using an architectural approach with the aim of identifying constant features that characterise the architectural unit of this species, describing its developmental dynamics, and exploring the morphological basis of its extraordinary plasticity and adaptability to multiple ecological conditions. Plants of two ecotypes were cultivated in pots outdoors during two consecutive summers, and axes of different branching order were marked for periodical observations. Leaf typology, orientation and position of branches and occurrence and position of reproductive axes were considered. The basic growth pattern arises as a result of extensive plagiotropic growth of axes up to fourth branching order, which initially behave as stolons but can become rhizomes insofar the soil cover increases. Orthotropic floriferous axes up to fifth order develop at the axils of stolons, which can form 'daughter' clumps by basal tillering. Despite quantitative differences, both ecotypes share similar architectural features. Architectural analysis provides the basis to predict space occupation dynamics under different environmental conditions of growth.

Additional keywords: branching system, morphology, seashore paspalum.

Received 7 July 2015, accepted 25 February 2016, published online 1 April 2016

Introduction

Architectural analysis provides a methodological protocol to describe the growth and branching pattern of plants and predict their space occupation dynamics (Barthélémy and Caraglio 2007). The plant body is composed of sequences of modular units called metamers or phytomers (Fig. 1*a*; White 1979; Marfenin 1999; Perreta and Vegetti 2005). Each sequence of phytomers produced by a shoot apical meristem forms an axis (A), and axes of different order are sequentially linked to make up the architectural unit typical of each species (Barthélémy *et al*. 1991). Modules of the same hierarchical level (phytomers, axis, architectural units) are structurally equivalent but not necessarily identical to each other, and they may play different roles in the dynamics of plant development (Bonser and Aarssen 2003; Barthélémy and Caraglio 2007).

The architectural behaviour of most Poaceae can be summarily described by the Tomlinson's model, i.e. one of the architectural models originally proposed by Hallé *et al*. (1978) for describing trees. It characterises most Monocots and is defined by sympodial sequences of similar axes that are generally composed by a proximal plagiotropic zone and a distal orthotropic one (Jeannoda-Robinson 1977). In Poaceae, each axis (Fig. 1*b*) is usually composed of a short-internode zone (SIZ) followed by a long internode zone (LIZ). Orientation of successive branches in relation to their respective mother axes determines different branching types (Rua and Gróttola 1997), and seems to be correlated with the ecological behaviour of the species (Serebriakova 1969). However, none of the models described by Hallé *et al*. (1978) is suitable for describing stoloniferous/rhizomatous herbaceous species that combine both monopodial plagiotropic vegetative axes and orthotropic floriferous axes (Fig. 1*c*). Hence, a new architectural model has been proposed to take account of such cases ('Bell's model', Hallé 2004).

Paspalum vaginatum Sw. is a perennial warm-season grass with large stolons and rhizomes, native to tropical and subtropical regions worldwide, between 30 and 35° N–S latitudes (Burkart *et al*. 1990; Zuloaga and Morrone 2001). Commonly known as 'seashore paspalum', it is considered to be one of the most important C4 grasses since it plays different ecological and utilitarian roles. In fact, it occupies coastal salt and brackish water marshes and other wet habitats worldwide that are subject
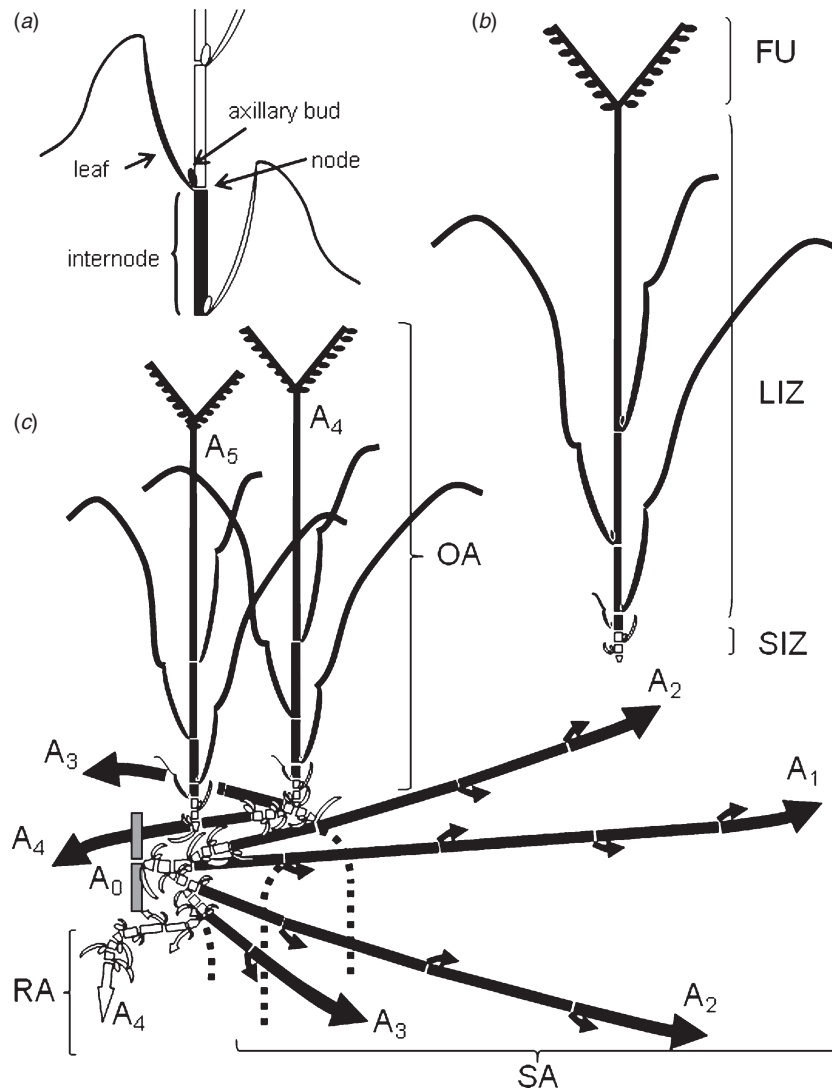
Fig. 1. Architectural features of *Paspalum vaginatum*. (*a*) Phytomer (in black). (*b*) Flowering shoot (tiller). (*c*) Branching system with axes of consecutive order (A_1, A_2, A_3, A_4, A_5). All axes are plagiotropic except the flowering shoots (black axes: aerial, white axes: underground, dotted lines: adventitious roots). Abbreviations: OA, orthotropic axes; SA, stoloniferous axes; RA, rhizomatous axes; SIZ, short-internode zone; LIZ, long-internode zone; FU, flowering unit; A_0, initial axis (in grey).

to different environmental disturbances (Insausti *et al*. 1999). Because of its easy and rapid expansion, it behaves as a weed that competes with native species in natural areas (Campos *et al*. 2004; Riefner and Columbus 2008; Riefner *et al*. 2010). Nevertheless, it is a useful species for dune stabilisation and erosion control, and has been used in rehabilitation programs of salt-affected lands in Australia (Shaw and Allen 2003). *P. vaginatum* is used as forage for cattle and horses (Gates 2003) and is eaten by wild geese and manatees in Florida (Graeme and Kendal 2001) and green turtles in Hawaii (McDermid *et al*. 2015). Moreover, it is a well-known turfgrass primarily recommended for coastal golf courses because of its tolerance to multiple stress factors such as salinity, drought and waterlogging, its ability to tolerate ranges of water sources and soil pH, and its efficiency for nutrient uptake (Duncan and Carrow 2000).

In this paper, *P. vaginatum* is taken as a model plant to study the possibilities of expression of a complex architectural pattern involving different axis categories (Rua and Gróttola 1997). Thus, the aims of our study are to identify the permanent morphological features that characterise the architectural unit (the 'structural blue-print' *sensu* Huber *et al*. 1999) of this species, to describe its developmental dynamics, and to explore the morphological basis of its extraordinary plasticity and adaptability to multiple ecological conditions.

Materials and methods

Observations were made during two consecutive growing seasons in 2007 and 2008 in the Botanical Garden of the Facultad de Agronomía, Universidad de Buenos Aires, Argentina (34°35'S, 58°29'W). Plant material was obtained by

vegetative division of one individual (*genet*) of each of two ecotypes: (1) a wild ecotype from the Flooding Pampa grassland (Argentina: Prov. Buenos Aires, Pila; BAA: 26686, 26689); and (2) a commercial cultivar, Sea Isle 2000 (USA: Florida; BAA: 26687, 26690), obtained from a commercial supplier. Because Sea Isle 2000 originates from one individual and is propagated vegetatively, no genetic variation would be expected. Conversely, the wild ecotype probably reproduces sexually, as is the rule among diploid cytotypes of *Paspalum* (Quarín 1992; Echarte and Clausen 1993). In order to standardise the methodological criteria and make a genotype-to-genotype comparison, we decided to propagate each ecotype from one single individual. Voucher specimens are deposited at BAA.

Several cuttings of similar diameter (A_0 axes), comprising each a node with its corresponding axillary bud, were obtained from each source plant and placed in volcanic gravel to induce rooting and sprouting (Fig. 2*a*). Then, 25 plants from each ecotype were transferred to plastic pots (12 cm diameter × 12 cm depth) containing a mixture of organic soil and sand (9 : 1 v/v). After seven days of establishment in a glasshouse (natural sunlight and 20/17°C day/night mean temperature), the plants were exposed outdoors.

The initial development of axillary meristems was studied by dissection of five of the growing plants. The remaining plants were transferred to 10 containers (58 cm long × 38.5 cm wide × 30 cm deep) per ecotype, filled with the same substrate used in the small pots and watered to field capacity. Two plants were placed in each container to obtain a quick covering (Fig. 2*b*). Axes from similar positions were selected sequentially as they arose from an axillary meristem of a higher order unit. Axes of different branching order (A_1, A_2, A_3, A_4 and A_5 axes) were marked with plastic cords of different colours. Internode and branch production was periodically recorded in at least two axes of different branching orders per plant starting from the initial stage of plant cultivation in the small pots to full cover in the containers. At the end of the growing period, all plants were removed from their containers and their axes were separated by water pressure and carefully washed to allow observation. The whole procedure was repeated the following year. For the architectural study the following traits were analysed: leaf typology (cataphylls versus foliage leaves), orientation and position of branches, occurrence and position of reproductive axes. Quantitative results will be published in an upcoming paper.

Rhizome observation was possible only at the end of each growing period, when plants were removed from the containers.

Results

Paspalum vaginatum showed three types of axes which differed by their growth direction and foliation: (1) orthotropic, (2) plagiotropic stoloniferous with foliage leaves, and (3) plagiotropic rhizomatous with cataphylls. In every case, axes showed distichous phyllotaxis of leaves and cataphylls. The orthotropic axes could or could not produce a terminal inflorescence (Figs 1*b*, *c*, 2*c*).

The proximal portions of the axes behaved differently depending on their proximal or distal position in relation to their mother axes. Indeed, the SIZ of proximal axes comprised a hypopodium (the internode below the prophyll, cf. Weberling

1981), a short prophyll (~3.6 mm) and one or two short cataphyll-bearing phytomers. In contrast, more distal axes bore no cataphylls in their SIZ but rather a larger prophyll (10–20 mm) and a few leaves of increasing size. The LIZ also showed a gradual increase in leaf length and development from the proximal to the distal nodes. The flowering unit (FU) consisted of two conjugated racemes with solitary glabrous spikelets, distributed in two series along the rachis. Both ecotypes had the same foliage sequence along shoots, i.e. a prophyll, occasionally some cataphylls, then leaves with fully-developed sheaths and reduced blades, and finally typical foliage leaves in the distal portion of the LIZ (Fig. 1*b*). Leaf blades of foliage leaves varied in length along the LIZ depending on the axis orientation. They could exceed 100 mm in orthotropic shoots but were significantly shorter (3 mm) in plagiotropic axes, and could undergo total reduction as stolons became rhizomes.

Along each A_1 a SIZ composed of a hypopodium and one or two short internodes could be recognised, followed by a LIZ that would then become a stolon (Fig. 2*c*). The following axis order (A_2) emerged immediately from proximal axillary meristems, i.e. those of the SIZ. Their development was usually acrotonic and extravaginal. Each A_2 repeated the same structure as the A_1, forming units up to fifth order.

Along the LIZ, basitonic intravaginal branches developed immediately. Such branches bore a hypopodium and a short internode. Regardless of the axis order, the nodes of the SIZ and LIZ initially produced 2–4 adventitious root primordia which developed into a profuse root system when they came in contact with the ground. The A_1 axes showed relatively reduced activity throughout the growing season. In fact, they became plagiotropic early on, producing a small number of internodes and lacking a terminal FU. In turn, A_2 and A_3 axes also showed an early shifting from orthotropic to plagiotropic growth, with the exception of the most proximal ones, which usually remained orthotropic and produced a terminal FU (Fig. 2*c*). Distal A_2 and A_3 axes usually became long and vigorous stolons that were able to temporarily behave as underground rhizomes, as long as the soil surface was covered by other stolons (Fig. 1*c*).

Axes developing from the SIZ of A_2, A_3 and, occasionally, A_4 shoots could become cataphyll-bearing rhizomes, which either remained short until their distal internodes elongated to rise above the soil surface, or grew to form an extensive underground LIZ that eventually emerged above the ground, produced foliage leaves and repeated the initial branching pattern.

Flowering axes bore ~10 foliage leaves and showed a gradual transition from SIZ to LIZ with a progressive increase of internode length towards the apex. Orthotropic axes with apical FU did not usually branch, but non-flowering orthotropic axes could produce axillary innovation branches, which would give rise to 'daughter clumps' in the following growing season (see below). Flowering orthotropic axes develop from the proximal nodes of the LIZ on A_4 and A_3, and occasionally on A_2. Although the spatial distribution of flowering shoots was similar in both ecotypes, the number of them was not, since flowering of the LIZ on A_3 was almost double in the wild ecotype than in commercial cultivar plants.
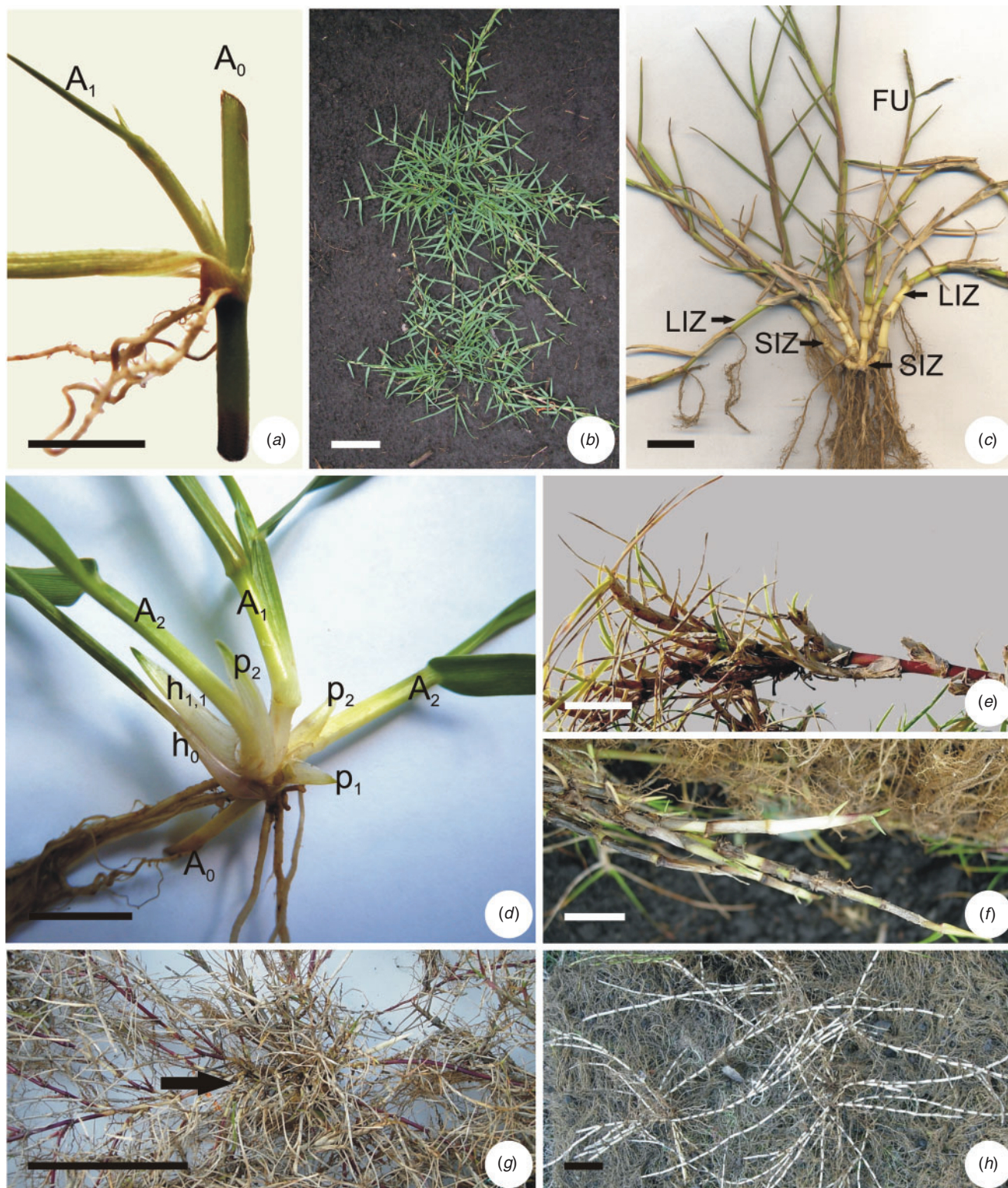
Fig. 2. *Paspalum vaginatum.* (*a*) One-node cutting (A₀) with a first order axillary branch (A₁). (*b*) Two 6-week-old plants growing in a pot. (*c*) Branching complex with stoloniferous and orthotropic axes with a flowering unit (FU). Short-internode zones (SIZ) and long-internode zones (LIZ) are indicated by arrows. (*d*) Axillary branching complex at a node of a cutting (A₀), composed of a first-order axis (A₁) with its respective leaf (h₀) and two axillary branches of second order (A₂). The A₂ axis on the right arises from the prophyllar (p₁) node and the A₂ axis on the left arises from a cataphyll (h₁,₁) node. Both A₂ axes bear prophylls (p₂). (*e*) Stolon at the end of the growing season. Axillary branches retain their living apex and some green leaves. (*f*) Detail of rhizomatous axes with cataphylls and some distal foliage leaves. (*g*) The arrow points a daughter clump at the end of a growing period. (*h*) Overview of the rhizome complex after removing the substrate at the end of the growing period. Scale bars = 0,5 cm (*a*), 5 cm (*b*, *g*, *h*), 1,5 cm (*c*), 1 cm (*d*, *e*, *f*).

Dynamics of plant growth

The branching system began to develop in a similar way in both ecotypes, five to seven days after each one-node cutting (A_0, Fig. 3*a*) had produced its first adventitious roots and the initial A_1 had borne four or five expanded leaves (Figs 2*d*, 3*b*). As new phytomers were formed, axillary branches developed successively below the five last top nodes, as the apical dominance became weaker (Fig. 3*c*). This pattern was repeated in all stolons.

A_3 axes emerged very fast, 2 weeks after rooting (Fig. 3*d*). As new A_2, A_3, and A_4 stolons were produced, foliage biomass increased and their LIZ became more lignified, reaching lengths to over 80 internodes (Fig. 3*e*). Their apical meristems continuously produced new phytomers throughout the summer and remained vegetative until the winter, when growth inhibition occurred (Fig. 2*e*).

Stolons could produce axillary rhizomes from their second nodes. Rhizomes appeared only at advanced stages of development, when the aerial surface was completely covered with stolons. Then, some stolons became rhizomes in their distal portion by turning underground and shifting to cataphyll production (Fig. 2*f*).

Axillary shoots developing from the peripheral regions of A_3 and A_4 stoloniferous axes sometimes formed 'daughter clumps' (Fig. 2*g*) through successive tillering, starting from their second phytomers. Such new tillers arose by extravaginal branching and were initially plagiotropic, but they quickly
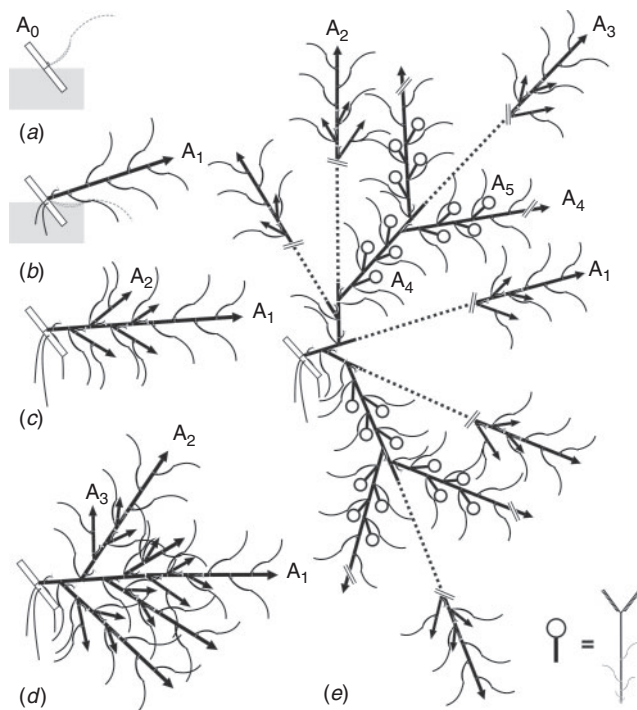
became orthotropic and produced proximal branches of successive branching orders to form bunch-like structures. Such tillering events typically occurred away from the plant crown, apparently as a response to apical damage by herbivory or breakage, and immediately below the damaged zone. The new clumps remained vegetative during the corresponding growing season and, if they were not damaged during winter, they gave rise to reiterated complexes in the following growing season, and eventually became independent from the mother plant. Stolons in which such a tillering process occurred were usually thicker than the others, altering the regular basitonic pattern.

Orthotropic shoots of any branching order remained unbranched along their LIZ but sometimes branched in their SIZ (Fig. 1*c*). Orthotropic A_4 and A_5 axes flowered from mid-January to February. At the end of the growing season, clumps and stolons remained vegetative.

Discussion

Paspalum vaginatum is a clonal species, i.e. individuals ('genets') are composed of several 'ramets' that are integrated by connecting structures or spacers (Harper and White 1974). Namely, stolons and rhizomes act as spacers placing young ramets in new locations and allowing a greater use of horizontal and vertical space. By acquiring independence from the mother plant, ramets may generate clones, i.e. daughter plants or clumps, derived from genets by vegetative propagation (White 1979). Depending on the length of the spacers and the resulting distance between tillers, plants may take different exploring strategies (Klimeš *et al.* 1997). *P. vaginatum* follows a guerilla-like growth pattern with new tillers that cross their subtending leaf sheaths and develop rhizomes or stolons. This type of tillering is typical of sod-forming grasses (Pottier and Evette 2010).

Both ecotypes share similar architectural features: they have the same number of axis types and orders, stable qualitative characters and stems of each type arranged in equivalent positions. From the architectural point of view, the three types of axes and their hierarchical relationships build up the architectural unit characteristic of this species. The plagiotropic axes of first to fourth orders form stolons and rhizomes that develop aboveground and underground respectively. Stolons produce large innovation areas from which orthotropic axes up to fifth order develop. The aggregation of axes of different growth direction provides an abundant foliar coverage and the profuse development of adventitious roots allows for exploration of a vast area. These features increase resource uptake and favour both vegetative propagation and sexual reproduction.

In both ecotypes the leaf sequence is consistent with that observed in other Poaceae (Mühlberg 1967), i.e. the smaller the prophyll, as in the axillary branches from the SIZ, the greater the number of cataphylls and transitional leaves. Conversely, if the prophyll is large, as in the axillary branches from the LIZ, no cataphylls are present. This seems to be a general trend among Angiosperms, where the presence or absence of cataphylls and intermediate leaves on the proximal stem region are related, respectively, to the delayed or immediate development of the shoots (Hallé *et al.* 1978; Barthélémy and

Fig. 3. Architectural construction over time of the aerial shoot system of *Paspalum vaginatum*. (*a*) Initial one-node cutting (A_0). (*b*) The first order axis (A_1) developing after seven days of growth. (*c*) Two-week-old plant with A_1 and A_2 axes. (*d*) Three-week-old plant with initial A_3 axes. (*e*) Two-month-old plant with axes up to the fifth branching order showing the placement of flowering units (FU).

Caraglio 2007). Delayed branches grow after a rest period and initially produce scaly leaves, to gradually shift to foliage leaf production. Sylleptic branches, on the contrary, grow simultaneously with their mother axes and lack transitional leaves.

Monopodial branching, a rare feature among monocots (Holttum 1955), occurs in *P. vaginatum.* Plagiotropic stems keep their original directions indefinitely, and ramets are formed from lateral buds. Flowering occurs mainly at the apex of the proximal orthotropic axes of third, fourth and fifth order, confirming the pattern described by Rua and Gróttola (1997). Stolons of both ecotypes studied here remained vegetative at their apex and appeared to maintain apical dominance until the end of the growing season. Stolon survival with axillary sprouting at the next growing season may be possible if winter frosts are rare (Fabbri *et al*. 2016). The perennial nature of this species is principally ensured by the monopodial rhizomes (Fig. 2*h*), whereby underground meristems remain alive until the next growing season and can produce new aerial shoots or rhizomes. The formation of clumps that produce adventitious roots and behave as 'daughter plants' also contributes to the vegetative propagation of this species (Fig. 2*g*). Their occurrence on broken axes appears to be a response to the loss of apical dominance. Thus, it would be expected that a greater number of daughter plants would occur with frequent mowing. These 'daughter plants' are repetitions of the 'mother plant'; and can be considered cases of 'traumatic' or 'adaptive' reiteration (Barthélémy and Caraglio 2007), depending on whether they occur as an outcome of meristem damage or as an extraordinarily vigorous growth of axes respectively.

There are several pieces of evidence of the high efficiency of *P. vaginatum* to colonise open spaces and to form dense populations in areas where other species may not grow (Anderson and Ehringer 2000). Its rapid root production rate, the continuous axillary bud development, the profuse tiller production along their spacers, and the monopodial growth of their stolons and rhizomes are qualities that favour its rapid space occupation. Moreover, the production of axes with different spatial orientations and the formation of clumps at the end of the growing season are adaptive traits that allow plastic responses to environmental changes with a better chance of survival. These vegetative features are strongly responsible for the invasive nature of *P. vaginatum* when it is introduced into natural ecosystems, where it affects biodiversity by reducing the establishment of other species (Campos *et al*. 2004; Riefner and Columbus 2008; Riefner *et al*. 2010). However, they also lend to this species its desirable characteristics as a turfgrass in sport fields or as a pioneer species for restoration and control of erosion in natural environments.

Acknowledgements

References

Anderson J, Ehringer NJ (2000) Ecological uses for *Paspalum vaginatum* (Swartz) seashore paspalum. In 'Proceedings of the 27th annual conference of ecosystem restoration and creation'. (Ed. PJ Cannizzaro). pp. 10–13. (Hillsborough Community College: Tampa, FL, USA)

Barthélémy D, Caraglio Y (2007) Plant architecture: a dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Annals of Botany* 99, 375–407. doi:10.1093/aob/mcl260

Barthélémy D, Edelin C, Hallé F (1991) Canopy architecture. In 'Physiology of trees'. (Ed. AS Raghavendra) pp. 1–20. (John Wiley & Sons Inc: New York, USA.)

Bonser SP, Aarssen LW (2003) Allometry and development in herbaceous plants: functional responses of meristem allocation to light and nutrient availability. *American Journal of Botany* 90, 404–412. doi:10.3732/ajb.90.3.404

Burkart SE, León RJC, Movia CP (1990) Inventario fitosociológico del pastizal de la Depresión del Salado (Prov. Bs. As.) en un área representativa de sus principales ambientes. *Darwiniana* 30, 27–69.

Campos JA, Herrera M, Biurrun I, Loidi J (2004) The role of alien plants in the natural coastal vegetation in central-northern Spain. *Biodiversity and Conservation* 13, 2275–2293. doi:10.1023/B:BIOC.0000047902.27442.92

Duncan RR, Carrow RN (2000) 'Seashore paspalum. The environmental turfgrass.' (Ann Arbor Press: Chelsea, MI, USA)

Echarte AM, Clausen AM (1993) Afinidades morfológicas entre *Paspalum distichum sensu lato y Paspalum vaginatum* (Poaceae). *Boletín de la Sociedad Argentina de Botánica* 29, 143–152.

Fabbri LT, Ploschuk EL, López MV, Insausti P, Rua GH (2016) Freezing tolerance differs between two ecotypes of *Paspalum vaginatum* (Poaceae). *Acta Botanica Brasilica* 30(1), 152–156. doi:10.1590/0102-33062015abb0233

Gates M (2003) Seashore paspalum. USDA Natural Resources Conservation Service Plant Guide 5–8. Available at http://plants.usda.gov/plantguide/pdf/pg_pava.pdf [Verified 14 January 2016].

Graeme M, Kendal H (2001) Saltwater paspalum (*Paspalum vaginatum*): a weed review. Available at http://www.ew.govt.nz/PageFiles/15227/TR 2001–18.pdf [Verified June 2015].

Hallé F (2004) 'Architecture de plantes.' (JPC Edition: Montpellier, France)

Hallé F, Oldemann RA, Tomlinson PB (1978) 'Tropical trees and forests: an architectural analysis.' (Springer-Verlag: New York)

Harper JL, White J (1974) The demography of plants. *Annual Review of Ecology and Systematics* 5, 419–463. doi:10.1146/annurev.es.05.110174.002223

Holttum RE (1955) Growth-habits of monocotyledons. Variations on a theme. *Phytomorphology* 399–413.

Huber H, Lukác S, Watson M (1999) Spatial structure of stoloniferous herbs: an interplay between architectural blue-print, ontogeny and phenotypic plasticity. *Plant Ecology* 141, 107–115. doi:10.1023/A:1009861521047

Insausti P, Chaneton E, Soriano A (1999) Flooding reverted grazing effects on plant community structure in mesocosms of lowland grassland. *Oikos* 84, 266–276. doi:10.2307/3546721

Jeannoda-Robinson V (1977) Contribution a l'étude de l'architecture des herbes. PhD Thesis. Université des Sciences et Techniques du Languedoc-Montpellier, France.

Klimeš L, Klimešova J, Hendriks R, van Groenendael JM (1997) Clonal plant architecture: a comparative analysis of form and function. In 'The ecology and evolution of clonal plants'. (Eds H de Kroon, V Groenendael) pp. 1–29. (Backbuys Publishers: Leiden, The Nederlands)

Marfenin NN (1999) The development of modular organization concept. *Journal of General Biology* 60, 6–17.

McDermid KJ, Lefebvre JA, Balazs GH (2015) Nonnative seashore paspalum, *Paspalum vaginatum* (Poaceae), consumed by Hawaiian green sea turtles (*Chelonia mydas*): evidence for nutritional benefits. *Pacific Science* **69**, 48–57. doi:10.2984/69.1.3

Mühlberg H (1967) Die Wuchstypen der mitteldeutschen Poaceen. *Hercynia* **4**, 11–50.

Perreta M, Vegetti A (2005) Patrones estructurales en las plantas vasculares: una revisión. *Gayana Botanica* **62**, 9–19. doi:10.4067/S0717-66432005000100003

Pottier J, Evette A (2010) On the relationship between clonal traits and small-scale spatial patterns of three dominant grasses and its consequences on community diversity. *Folia Geobotanica* **45**, 59–75. doi:10.1007/s12224-009-9053-x

Quarín CL (1992) The nature of apomixis and its origin in Panicoid grasses. *Apomixis Newsletter* **5**, 8–15.

Riefner RE, Columbus JT (2008) *Paspalum vaginatum* (Poaceae), a new threat to wetland diversity in southern California. *Journal of the Botanical Research Institute of Texas* **2**, 743–759. http://www.scopus.com/inward/record.url?eid=2-s2.0-74049134645&partnerID=tZOtx3y1

Riefner RE, Denham SS, Columbus JT (2010) *Paspalum pubiflorum* and *P. quadrifarium* (Poaceae) new to California, with a key and notes on invasive species. *Journal of the Botanical Research Institute of Texas* **4**, 761–770. http://www.scopus.com/inward/record.url?eid=2-s2.0-78650658209&partnerID=tZOtx3y1

Rua GH, Gróttola MC (1997) Growth form models within the genus *Paspalum* L. (Poaceae, Paniceae). *Flora* **192**, 65–80.

Serebriakova TI (1969) Vetvlenie i Kutsenie v Semeistve Poaceae. *Botanicheskii Zhurnal* **54**, 858–871.

Shaw WB, Allen RB (2003) Ecological impacts of sea couch and saltwater paspalum in Bay of Plenty estuaries. DOC Science Internal Series, Department of Conservation, Wellington, New Zealand 113. Available at http://www.doc.govt.nz/documents/science-and-technical/dsis113.pdf [Verified 14 January 2016].

Weberling F (1981) 'Morphologie der Blüten und der Blütenstände.' (Eugen Ulmer: Stuttgart, Germany)

White J (1979) The plant as a metapopulation. *Annual Review of Ecology and Systematics* **10**, 109–145. doi:10.1146/annurev.es.10.110179.000545

Zuloaga F, Morrone O (2001) *Paspalum*. In 'Flora Fanerogámica Argentina 71'. pp. 48–49. (Proflora CONICET: Córdoba, Argentina)