



Population rules can apply to individual plants and affect their architecture: an evaluation on the cushion plant *Mulinum spinosum* (Apiaceae)

Javier G. Puntieri^{1,2*}, María A. Damascos³, Yanina Llancaqueo³ and Maya Svriz¹

¹ Instituto de Investigación en Biodiversidad y Medioambiente (INIBIOMA), Quintral 1250, (8400) Bariloche, Argentina

² Universidad Nacional de Río Negro, Sede Andina, (8400) Bariloche, Argentina

³ Departamento de Botánica, Universidad Nacional del Comahue, Quintral 1250, (8400) Bariloche, Argentina

Received: 14 July 2010; **Returned for revision:** 5 September 2010; **Accepted:** 14 October 2010; **Published:** 25 October 2010

Citation details: Puntieri JG, Damascos MA, Llancaqueo Y, Svriz M. 2010. Population rules can apply to individual plants and affect their architecture: an evaluation on the cushion plant *Mulinum spinosum* (Apiaceae). *AoB PLANTS* 2010: plq019, doi:10.1093/aobpla/plq019

Abstract

Background and aims

Plants are regarded as populations of modules such as axes and growth units (GUs, i.e. seasonally produced axis segments). Due to their dense arrays of GUs, cushion plants may resemble crowded plant populations in the way the number of components (GUs in plants, individuals in populations) relates to their individual sizes.

Methodology

The morphological differentiation of GUs and its relationship with biomass accumulation and plant size were studied for the cushion subshrub *Mulinum spinosum* (Apiaceae), a widespread species in dry areas of Patagonia. In 2009, GUs were sampled from one-quarter of each of 24 adult plants. Within- and between-plant variations in GU length, diameter, number of nodes and biomass were analysed and related to whole-plant size.

Principal results

Each year, an *M. spinosum* cushion develops flowering GUs and vegetative GUs. Flowering GUs are larger, twice as numerous and contain two to four times more dry mass (excluding reproductive structures) than vegetative GUs. The hemispherical area of the cushions was positively correlated with the biomass of last-year GUs. The biomass of flowering GUs was negatively correlated with the density of GUs. *Mulinum spinosum* plants exhibited a notable differentiation between flowering and vegetative GUs, but their axes, i.e. the sequences of GUs, were not differentiated throughout the plants. Flowering GUs comprised a major proportion of each plant's photosynthetic tissues.

Conclusions

A decrease in the size of flowering GUs and in their number relative to the total number of GUs per plant, parallel to an increase in GU density, is predicted as *M. spinosum* plants age over years. The assimilative role of vegetative GUs is expected to increase in summer because of their less exposed position in the cushion. These GUs would therefore gain more from warm and dry conditions than flowering GUs.

* Corresponding author's e-mail address: jgpuntieri@gmail.com

AoB PLANTS Vol. 2010, plq019, doi:10.1093/aobpla/plq019, available online at www.aobplants.oxfordjournals.org

© The Authors 2010. Published by Oxford University Press. This is an Open Access article distributed under the terms of the Creative Commons Attribution Non-Commercial License (<http://creativecommons.org/licenses/by-nc/2.5/uk/>) which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original work is properly cited.

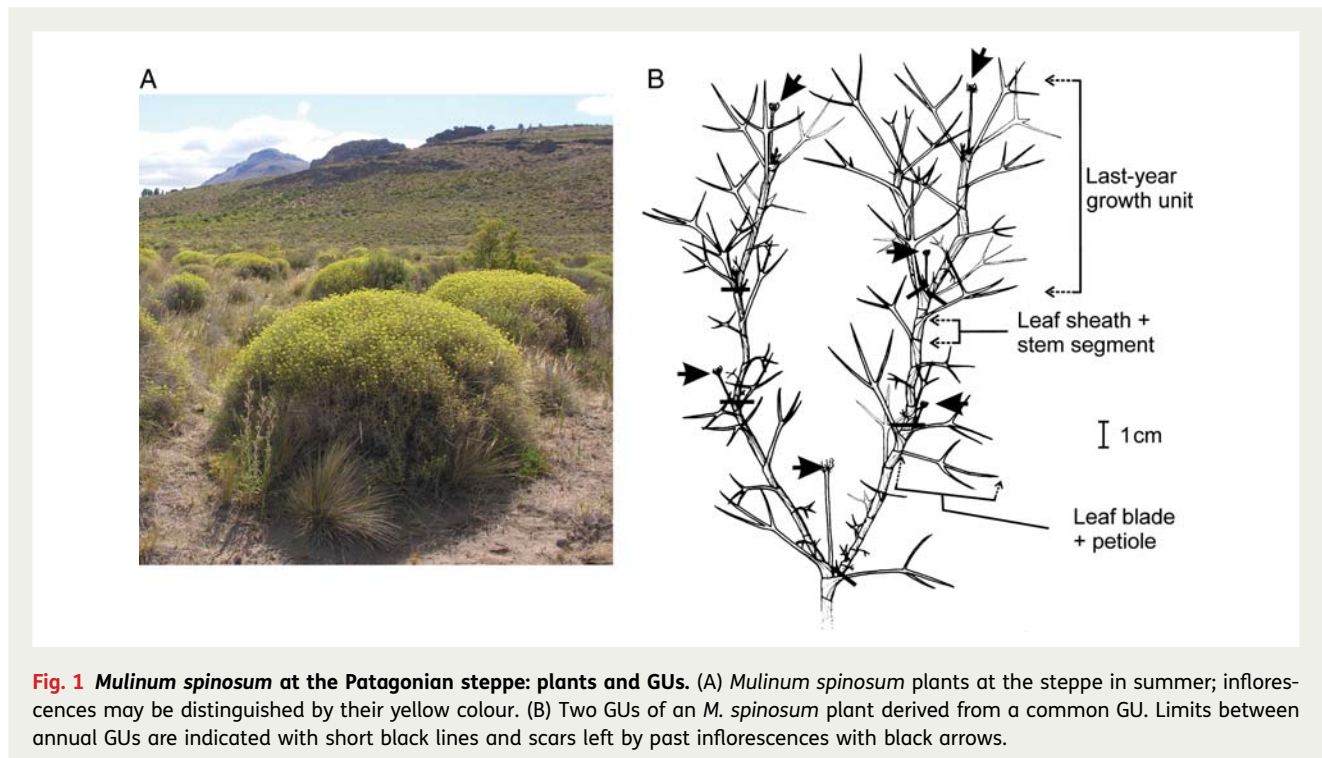
Introduction

In plants with rhythmic growth, their constituting axes increase in length at their distal ends through the production of structural units known as growth units (GUs; Barthélémy and Caraglio 2007). Within each plant, and depending on the species, GUs of several forms and functions may coexist (Reffye et al. 1991; Costes 1993; Puntieri et al. 2003). For instance, the coexistence of short GUs, long GUs and flowering GUs is common in adult individuals of woody plants and parallels a hierarchical axis organization (Edelin 1991; Kozłowski and Pallardy 1996; Yagi 2000; Ishihara and Kikuzawa 2009). In other species, all coexisting GUs are alike and each plant consists of a non-hierarchical system of axes (Prévost 1978). This seems to be the case in many plant species with dome-like aerial growth, such as cushion-forming plants (Rauh 1939; see Leeuwenberg model in Hallé et al. 1978).

Under the interpretation of plants as meta-populations of modules (e.g. White 1979; Enquist et al. 1998; Kikuzawa 1999), interactions between GUs in plants with dense arrangements of GUs, such as cushion plants, may resemble those between plants in a crowded population. Competition among plants in a crowded population leads to a negative relationship between the number of plants per unit of area occupied by the population (plant density) and mean plant size

(Kira et al. 1953); the dispersion around the mean of individual plant size is also affected by competition (Weiner 1990, 1995; Puntieri and Pyšek 1993; Kikuzawa 1999; Damgaard et al. 2002). At plant level, an increase in the number of GUs per unit of surface of a cushion plant (GU density) may be expected to affect both the mean and the dispersion of GU size.

Mulinum spinosum (Apiaceae) has been described as a hemispherical cushion subshrub with densely arranged peripheral GUs on a relatively loose and dry core (Rauh 1939; Fig. 1A). Each *M. spinosum* plant develops vertical or slanted GUs (Fig. 1B). In adult plants of this species, each GU extended in a particular growing season develops between one and three lateral and/or terminal GUs in the following growing season (Damascos et al. 2008), so that the total number of GUs at the surface of a plant tends to increase exponentially from one year to the next. Meanwhile, the yearly increase in the outer surface of a 30- to 80-cm-high *M. spinosum* cushion is much slower, since new GUs add a layer <12 cm thick to the plant each year (Damascos and Ghermandi 2007). This means an increase in GU density over the years. Under these assumptions, older plants would have a higher number and density of GUs and total mass, but a lower mean GU size than younger cushions. The present study evaluates the extent to which individual *M. spinosum* plants may be



equated to populations of competing GUs regarding size–density relationships and variations in GU size.

Materials and methods

Study species

Mulinum spinosum is one of the most characteristic species in dry and disturbed areas of Patagonia (Cabrera and Willink 1980; Anchorena and Cingolani 2002). It is frequently dominant, replacing palatable tussock grasses in regions under intense grazing pressure (Sala et al. 1989; Aguiar and Sala 1998), and invading disturbed areas in nearby temperate forests (Cabrera and Willink 1980). An adult *M. spinosum* cushion reaches ~50–100 cm in height, and regenerates its aerial plant biomass in a few years after fire (Damascos and Ghermandi 2007). Each leaf base consists of a close sheath that embraces the stem tightly; the stem is hidden under the leaf bases until the leaves decay, which occurs several years after their growth (Soriano 1983). Leaf blades are trisect and spiny, and dry out completely in the autumn following the growing season of their extension, although they remain standing for years (Damascos and Ghermandi 2007; Damascos et al. 2008; Fig. 1). Plants have a 35- to 45-cm-long taproot with dense horizontal ramifications (Soriano 1983).

The annual growth of adult *M. spinosum* cushions consists of the development, in spring, of long GUs derived from short GUs initiated at the end of the previous summer period (the latter are described as temporary short shoots in Damascos et al. 2008). Most of the GUs extended in spring develop a terminal inflorescence. Both flowering and vegetative (i.e. non-flowering) GUs may develop short GUs from axillary buds in late summer; the number of these branches is higher in flowering than in vegetative GUs (Damascos et al. 2008). The biomass produced by an *M. spinosum* plant in 1 year is circumscribed to the peripheral layer, including all GUs extended in that year.

Study area

This study was performed in a temperate semi-arid area of northwestern Patagonia, Argentina. Annual precipitation in this area is ~900 mm, but the dry season coincides with the growing period, so that water deficit is frequent in many plants (Damascos et al. 2008). Soils have been described as aridisols (Del Valle 1998), and water availability in them fluctuates from high levels in winter to low levels in late summer (Sala et al. 1989; Adler et al. 2006). The vegetation of the area has been described as a semi-arid grass steppe. The dominant life forms are tussock grasses, low shrubs and cushion plants. During the last two centuries, this

region has been affected by cattle grazing (and especially grazing by sheep and horses).

Two natural populations of *M. spinosum* ~3 km apart were selected, one at Paraje Ñirihuau (Río Negro province; 41°03'58"S, 71°08'54"W) and the other at Paraje Nahuel Huapi (Neuquén province; 41°02'20"S, 71°09'33"W). Large herbivores have been excluded from these two areas for the last decade, although horses may sometimes be found.

Sampling

The sampling was performed in February 2007, when the GUs of *M. spinosum* had completed their extension and flower production, and before the beginning of the development of their fruits and summer short GUs (see Damascos et al. 2008). At each site, a 50 × 50 m plot was delimited and 12 adult *M. spinosum* plants were randomly selected and labelled. The height and two perpendicular diameters of each plant were measured. Each plant was divided into quarters by means of two perpendicular vertical planes crossing at the centre of a cushion's outer surface. One-quarter of each plant was selected and its last-year GUs, i.e. those extended in the 2006 spring (referred to, for simplicity, as GUs in the following text), were identified using the criteria established in a previous study (Damascos and Ghermandi 2007). All GUs were separated from the selected quarter portion of each plant and two random sub-samples were taken: one of them consisted of 10 GUs with an inflorescence (henceforth flowering GUs) and the other one consisted of 10 GUs without an inflorescence (vegetative GUs). For each of these GUs, stem length (from its proximal end up to the base of the inflorescence or the apical meristem), basal diameter (both measures taken with digital callipers) and number of leaves were obtained. We considered two vegetative fractions of each GU: one fraction constituted by the stem and the leaf sheaths attached to it, and the other fraction constituted by the leaf petioles and blades. For the sake of simplicity, these fractions will be termed, respectively, 'stem' and 'leaf blades'. The leaf blades of each GU of the sub-samples were cut at their point of union to the stem. Leaf blades, inflorescences and stems were dried at 70 °C to constant weight and the dry mass for each of these GU fractions was measured to the nearest 0.01 g after pooling all 10 sub-sample GUs (either vegetative or flowering) of each plant. The remaining GUs of each quarter plant were counted, dried and weighed, discriminating vegetative and flowering GUs.

Data analysis

The area of the hemispherical dome of each plant, hereafter termed 'hemispherical area' for simplicity, was

calculated as:

$$\text{hemispherical area} = \pi h \sqrt{d_1 d_2},$$

where h is plant height, and d_1 and d_2 are the perpendicular plant diameters.

The number and dry mass of flowering and vegetative last-year GUs were calculated for each plant and per unit of plant hemispherical area (GU density). For each plant, the dry mass of leaf blades, stems and inflorescences was estimated from the sub-samples of flowering and vegetative GUs. For flowering and vegetative GUs independently, as well as for all GUs, the correlations (Pearson's coefficient) were analysed between each pair of the following variables: mean GU dry mass, dry mass of GUs per plant, number of GUs, hemispherical area and GU density.

The following ratios were computed for each sub-sample GU: number of leaves · stem length⁻¹, stem length · basal diameter⁻¹ and basal diameter · number of leaves⁻¹. The number of leaves · stem length⁻¹ ratio, sometimes referred to as 'leafing intensity', measures the degree of clumping of leaves along the stem in GUs with similar mean leaf size (Kleiman and Aarssen 2007; Valladares and Niinemets 2008). The ratio between stem length and GU diameter is often termed 'slenderness' and gives an idea of the extension and mechanical properties of a GU (Puntieri et al. 2003; Osunkoya et al. 2007). The GU diameter · number of leaves⁻¹ ratio relates to the amount of conducting tissue available per leaf and is also an indication of the proportional investments in support and photosynthetic tissues (Puntieri and Ghirardi 2010). For each of these variables as well as for the stem length, basal diameter and number of leaves of the GUs of each plant, the coefficient of variation (CV = standard deviation · mean⁻¹ × 100) was calculated, including both vegetative and flowering GUs (i.e. $n = 20$ for each plant). The CV is a scale-independent measure of the dispersion of a set of numerical data frequently used to evaluate size inequality among individuals in plant populations (Weiner 1995). The CVs obtained were correlated with the dry mass of GUs per plant and with the density of GUs per unit of hemispherical area. Descriptor variables were compared between sub-sample vegetative and flowering GUs (main factor) by means of analysis of variance (ANOVA) including sampling site as a random variable and the plant as a nested factor within each sampling site (Zar 1999).

Using the data obtained for all sub-sample GUs per plant, vegetative and flowering GUs were compared regarding: dry mass of stem, dry mass of leaf blades, dry mass of stem and leaf blades, dry mass in leaf blades relative to the dry mass in stem and leaves of

the GU, and dry mass per leaf blade. These comparisons were carried out by means of two-way ANOVAs whenever data distribution was normal after log_e transformation (graphically and with Kolmogorov–Smirnov tests), including the type of GU (vegetative or flowering) as main factor and sampling site as random factor. Kruskal–Wallis tests were applied when the data distribution deviated significantly from normality. In the case of dry mass per leaf blade, the dry mass of all leaf blades per GU was included as a covariable due to its possible relationship with the size of individual leaves. In all comparisons, a 0.05 significance level was adopted.

Results

Whole-plant features

The morphological characteristics of the *M. spinosum* plants selected for this study are summarized in Table 1. The contributions to each plant of vegetative and flowering GUs differed clearly both in number and in dry mass. On average, there were about twice as many flowering GUs as vegetative GUs per plant, although large variations were found. The dry mass of flowering GUs per plant was between two and four times higher than that of vegetative GUs (Table 1).

The hemispherical area of plants correlated positively with the dry mass and number of flowering GUs per plant, but not with those of vegetative GUs (Table 2A).

Table 1 Cushion size and dry mass of GUs of *M. spinosum* in two populations.

Plant traits	Ñirihuau		Nahuel Huapi	
	μ	SE	μ	SE
Height (cm)	0.55	0.030	0.72	0.032
Hemispherical area (m ²)	1.87	0.205	2.72	0.293
Volume (m ³)	0.34	0.056	0.57	0.098
No. of flowering GUs	830	143.7	1484	226.3
No. of vegetative GUs	450	60.3	616	112.8
Dry mass of flowering GUs (g) ^a	215	38.6	409	71.7
Dry mass of vegetative GUs (g) ^b	85	23.1	93	40.2

Mean (μ) and standard error (SE) of the height, hemispherical area and volume of *M. spinosum* plants, and number and dry mass of flowering and vegetative GUs of *M. spinosum* plants sampled at Ñirihuau and Nahuel Huapi. $n = 12$ plants for each site.

^aStems + leaves + flowers.

^bStems + leaves.

The correlation between the hemispherical area of the plants and the mean mass per GU was significant and positive for flowering GUs, but not for vegetative GUs (Table 2A). The dry mass of flowering GUs per plant correlated positively with their number. The dry mass per flowering GU correlated negatively with the density of flowering GUs (Table 2A, Fig. 2). For both flowering and

vegetative GUs, the number of GUs per plant correlated positively with GU density.

When considering both vegetative and flowering GUs of each plant, the mean dry mass per GU correlated positively with the dry mass of GUs and the hemispherical area per plant (Table 2B). The dry mass of GUs per plant was positively correlated with the number of GUs and with the hemispherical area of the plant. The number of GUs per plant correlated positively both with the plant's hemispherical area and with GU density. The GU density did not correlate significantly with either the dry mass per plant or the mean dry mass of the GUs.

Negative correlations were found between the dry mass per plant and the CVs of: GU length · diameter⁻¹, length and number of leaves (Table 3). The dry mass per plant did not correlate significantly with the CVs of the GU basal diameter, number of leaves · length⁻¹ and diameter · number of leaves⁻¹. The GU density did not correlate significantly with any of the descriptor variables of the GUs (Table 3).

Comparisons between flowering and vegetative GUs

Flowering GUs were longer and thicker and had more leaves and a higher length · diameter⁻¹ ratio than vegetative GUs. The number of leaves · length⁻¹ and the diameter · number of leaves⁻¹ of vegetative GUs were higher than those of flowering GUs. All of these variables were affected by the individual plant; none of them was affected by sampling site (Table 4).

Table 2 Relationships between measures of GU size and measures of cushion size and GU density.

	dmGU	dmP	nGU	haP	nGU/ha
A					
dmGU	–	0.55	0.35	0.36	0.09
dmP	0.52	–	0.73	0.22	0.48
nGU	–0.04	0.80	–	0.24	0.78
haP	0.51	0.68	0.50	–	–0.31
nGU/ha	–0.48	0.32	0.73	–0.20	–
B					
dmGU	–	0.75	0.13	0.45	–0.37
dmP		–	0.72	0.70	0.10
nGU			–	0.55	0.60
haP				–	–0.32

Correlations between mean dry mass per GU (dmGU), dry mass per plant (dmP), number of GUs per plant (nGU), hemispherical area per plant (haP) and number of GUs per unit of hemispherical area (nGU/ha), for (A) vegetative GUs (upper side) and flowering GUs (lower side), and (B) for all last-year GUs of *M. spinosum* plants. Significant correlations ($P < 0.05$) are indicated in bold.

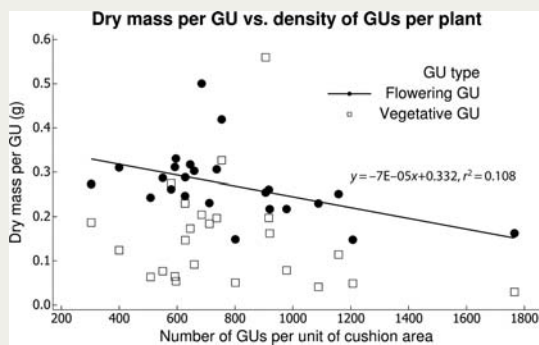


Fig. 2 Size-density relationship for GUs of individual *M. spinosum* plants. Relationships between the mean dry mass of flowering and vegetative GUs and the number of each GU type per unit of hemispherical area of the *M. spinosum* plant. The least-squares regression line for flowering GUs is drawn and its equation and coefficient of determination (r^2) are indicated.

Table 3 Relationships between plant attributes and the CVs of GU traits.

GU trait	Dry mass per plant	Number of GUs per plant hemispherical area	
Length	–0.58 ***	0.30	ns
Diameter	–0.08 ns	0.16	ns
Number of leaves	–0.53 ***	0.39	ns
Length · diameter ⁻¹	–0.64 ***	0.39	ns
Number of leaves · length ⁻¹	–0.14 ns	–0.05	ns
Diameter · number of leaves ⁻¹	–0.30 ns	0.26	ns

Correlation coefficients between the dry mass per plant and the number of GUs per plant hemispherical area and the CVs of the GU traits: length, diameter, number of leaves, length · diameter⁻¹, number of leaves · length⁻¹ and diameter · number of leaves⁻¹. *** $P < 0.001$; ns, $P > 0.05$.

Table 4 Statistical comparisons of morphological attributes between vegetative and flowering GUs of *M. spinosum*.

GU trait	GU type				ANOVA					
	Vegetative		Flowering		GU type		Site		Plant	
	μ	SE	μ	SE	F	P	F	P	F	P
Length (mm)	40.7	1.88	61.9	1.08	216.0	***	0.0	ns	8.6	***
Number of leaves	7.7	0.16	9.3	0.07	95.2	***	0.0	ns	5.7	***
Diameter (mm)	1.6	0.02	1.7	0.02	40.7	***	0.8	ns	3.4	***
Number of leaves · length ⁻¹	2.5	0.07	1.6	0.03	202.4	***	0.0	ns	9.9	***
Length · diameter ⁻¹	25.0	1.00	36.3	0.61	136.5	***	1.6	ns	9.2	***
Diameter · number of leaves ⁻¹	0.23	0.006	0.19	0.002	42.8	***	3.6	ns	4.4	***

Mean (μ) and SE of the length, number of leaves, basal diameter, number of leaves · length⁻¹, length · diameter⁻¹ and diameter · number of leaves⁻¹ for flowering GUs ($n = 252$) and vegetative GUs ($n = 240$). For each variable (\log_e transformed), the significance levels of the differences detected with ANOVA (Fisher's F statistic, GLM for unbalanced designs) between GU types (fixed factor), site (random factor) and plant (nested factor within each site) are indicated.

*** $P < 0.001$; ns, $P > 0.05$.

Table 5 Comparison of the dry mass of vegetative and flowering GUs and their morphological components for *M. spinosum*.

GU trait	GU type				ANOVA/Kruskal–Wallis					
	Vegetative		Flowering		GU type		Site		Covariable	
	μ	SE	μ	SE	F	P	F	P	F	P
Dry mass of stems and leaf bases (g)	0.62	0.075	1.19	0.093	23.2	***	1.1	ns	–	–
Dry mass of leaf blades (g)	0.85	0.085	1.43	0.098	20.4	***	1.6	ns	–	–
<i>Dry mass of stems + leaves (g)</i>	1.46	0.157	2.62	0.184	23.1	***	1.5	ns	–	–
Dry mass per leaf blade (g) × 100	1.06	0.086	1.55	0.110	6.4	*	0.5	ns	532.8	***
Proportion of dry mass in leaf blades	0.59	0.011	0.54	0.011	7.1	*	0.1	ns	–	–

Mean (μ) and standard error (SE) of the dry masses of stems and leaf bases, leaf blades, stems and leaves and individual leaf blades, and the ratio between the dry mass in the leaf blades and the dry mass of stems + leaves (proportion of dry mass in leaf blades) for 10 flowering GUs and 10 vegetative GUs per plant of *M. spinosum* ($n = 24$ plants). For each variable (\log_e transformed), the results of the statistical comparisons with ANOVA (GLM for unbalanced designs) or with Kruskal–Wallis tests (for dry mass of stems + leaves, in italics) between GU types (fixed factor) and between sampling sites (random factor) are indicated. In the case of the dry mass per leaf blade, the total biomass of all leaf blades was incorporated as a covariable in the analysis.

*** $P < 0.001$; * $P < 0.05$; ns, $P > 0.05$.

Flowering GUs had higher leaf blade mass and stem mass, and a lower proportion of their dry mass in leaf blades than vegetative GUs (Table 5). The dry mass per leaf blade was significantly higher for flowering than for vegetative GUs. The dry mass of all GU leaf blades had a very significant effect on the dry mass per leaf blade (Table 5).

Discussion

GU size in relation to cushion size

The analyses presented here indicate that the sampled *M. spinosum* plants with a higher hemispherical area

tended to have more and larger GUs. Studies on the ontogenetic gradients of plants and the physiological age of meristems indicate that, on average, the size of GUs in plants tends to increase from the establishment phase to the juvenile stage and to decrease during the adult stage of development (Sabatier et al. 1998; Barthélémy and Caraglio 2007). Therefore, the plants sampled for the present study could be described as plants at a relatively early adult developmental stage.

Under the conservative assumption that each year an *M. spinosum* plant produces, on average, two GUs for each pre-existing GU (Damascos et al. 2008), an exponential increase over time in the number of GUs per

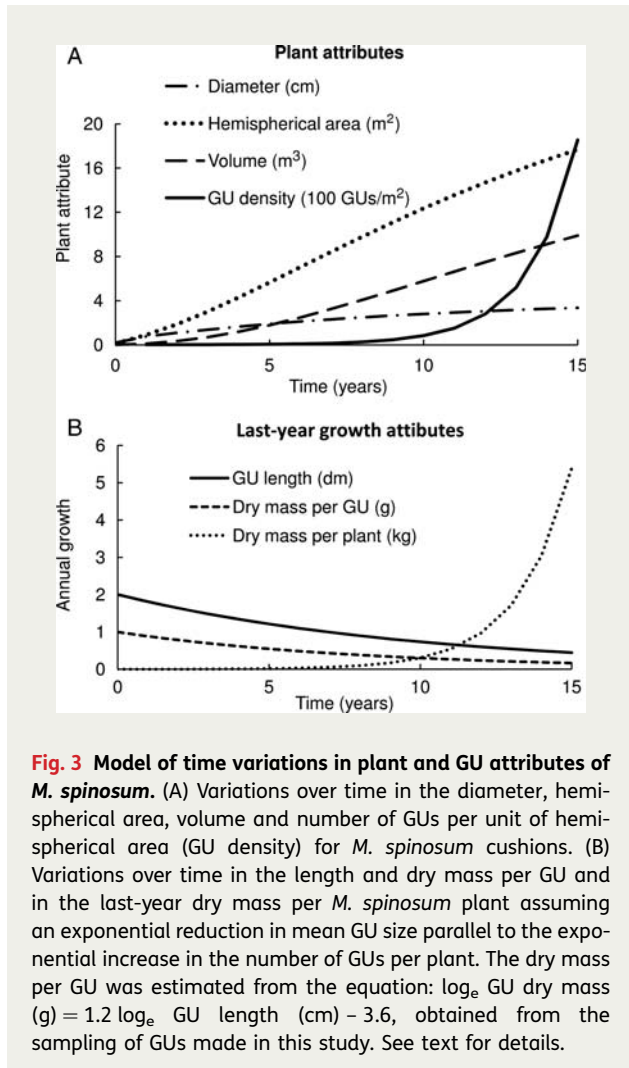


Fig. 3 Model of time variations in plant and GU attributes of *M. spinosum*. (A) Variations over time in the diameter, hemispherical area, volume and number of GUs per unit of hemispherical area (GU density) for *M. spinosum* cushions. (B) Variations over time in the length and dry mass per GU and in the last-year dry mass per *M. spinosum* plant assuming an exponential reduction in mean GU size parallel to the exponential increase in the number of GUs per plant. The dry mass per GU was estimated from the equation: $\log_e \text{GU dry mass (g)} = 1.2 \log_e \text{GU length (cm)} - 3.6$, obtained from the sampling of GUs made in this study. See text for details.

plant would be expected (Fig. 3A). If GUs of different sizes are assumed to be evenly distributed in each plant (see the following section), the surface on which new GUs could be deployed would increase notably less than the number of GUs. In *M. spinosum* plants, the provision of water and minerals to all GUs depends on a single conducting system at the cushion's base, connected to its taproot (Soriano and Sala 1983). According to the long-standing 'pipe-model', the increment in the sum of all section areas of new GUs would be determined by the section area of the stem supporting these new GUs (Kira et al. 1953; Yoda et al. 1963). One of the implications of this hypothesis is that mean GU size must decrease proportionally to the increase in GU density. The mathematical resemblance between this relationship at the plant level and the negative relationship repeatedly observed in crowded plant populations has been highlighted several times (e.g. Yoda et al. 1963;

Guo and Rundel 1998). The negative correlation between mean GU size and GU density found here for flowering GUs is consistent with this idea, although other explanations cannot be ruled out at this point. A simple model could help visualize some consequences of the developmental pattern of *M. spinosum*.

Let us consider *M. spinosum* plants with initial GU sizes similar to those reported so far (Damascos and Ghermandi 2007; present study). Under the assumption of a sustained exponential decrease in the mean mass of GUs (compensating for the exponential increase in GU density), these plants would be developing, after a few years of growth, GUs notably smaller than those observed here (Fig. 3B). It has been shown in this study that the vegetative GUs of this species are smaller, on average, than flowering GUs. In addition, previous results and unpublished observations indicate that vegetative GUs of this species tend to produce fewer branches and be shorter lasting than flowering GUs (Damascos et al. 2008). For these reasons, the development of an increasing proportion of vegetative GUs over time would lower the rate of increase in GU density over time.

The regulation of GU size and type according to GU density could be frequent in cushion-forming plants. Cushion plants are common in sunny, arid and windy areas, where the combination of low water availability and high levels of incident radiation limits plant growth (Bliss 1971; Gibson 1990). Under these conditions, water loss due to transpiration could be reduced by means of achieving a low stature (Kytparissis and Manetas 1993; Freitas 1997; Valladares and Pugnaire 1999; Lambrinos et al. 2006). Furthermore, a high level of GU packing would generate a metabolically more favourable environment as each GU would exert a moderating effect on its neighbour GUs, e.g. reducing wind speed and direct sun exposure, and providing physical support. In *M. spinosum*, the spiny leaf blades would have a low level of transpiration due to their thick cuticle, and would cast a moderate degree of shade over the lower leaves. Hard leaf blades could also play a role in the mutual support of neighbour GUs and of the cushion as a whole. Both living and standing dead leaves of *M. spinosum* cushions constitute a three-dimensional locking system which concerns the whole plant and determines that the energy of wind or snow loads on each GU be transferred to the soil surface below the cushion. For this system of positive interactions to work properly, GUs constituting each plant must be similar to one another despite the increase in the number of GUs over time. Once the hemispherical structure of an *M. spinosum* plant has developed, a negative relationship between GU density and GU size

would be predicted. In the present study, such a relationship was observed for the larger, more numerous and more even-sized flowering GUs, but not for the total-ity of GUs per plant (Fig. 2). The notable variations in the size of vegetative GUs in plants of different sizes could explain this contrast.

In crowded plant populations, size inequality among neighbour plants increases over time more notably in denser populations whenever light is the limiting factor (Weiner 1985; Weiner et al. 1990). In such cases, taller plants are at an advantage over smaller plants, so that the former get a disproportionately higher share of the limiting resource (Weiner 1985). This hierarchical relationship eventually leads to the death of the smallest individuals (self-thinning; Weiner 1985, 1995). Crowding in plant populations does not lead to higher size inequalities in cases where soil resources become limiting sooner than light (Weiner 1990; Bagchi 2007), and when crowding benefits neighbour plants through physical support (Puntieri and Pyšek 1993). In the present study, GU density in *M. spinosum* cushions was not correlated with size inequality among GUs (measured by the CV). On the other hand, the negative correlations found here between the biomass produced by each plant in its last growing season and the CVs of GU length, number of leaves and length · diameter⁻¹ indicate that those individuals producing more biomass develop morphologically more similar GUs. In view of these results, it could be suggested that the low degree of inequality among GUs of *M. spinosum* at the individual level would be a consequence of GUs being limited in their growth by the influx of resources from further down on the plant rather than by light availability. The distribution of soil resources among GUs of a plant would be determined by the physiological age of the meristems, a key factor in axis differentiation (Barthélémy and Caraglio 2007). It could be argued, in the present case, whether the terminal flowering of the most vigorous GUs would affect apical control and differentiation among neighbour GUs (Wilson 2000). The development of a hierarchical architecture, with some GUs distinctively taller than their neighbour GUs, may represent a disadvantage in some habitats, and selective forces would have favoured GU evenness at the whole-plant level. This would explain the low level of specialization among GUs at the plant level and the mixed roles played by flowering GUs in *M. spinosum*.

GU differentiation in *M. spinosum*

Despite their external homogeneity, adult *M. spinosum* plants exhibit a clear distinction between flowering and vegetative GUs. Flowering GUs constitute about two-thirds of all GUs produced and three-quarters of

the nearly 400 g of dry mass produced yearly, on average, by an adult *M. spinosum* plant. The majority of vegetative GUs are shorter and have fewer leaves than the flowering GUs, although there is a higher degree of variation in size (especially length) among vegetative GUs than among flowering GUs. The average vegetative GU has shorter internodes (indicated by the ratio between number of leaves and stem length) and a higher allocation to leaves than a flowering GU. Another difference between vegetative and flowering GUs in *M. spinosum* is their persistence over time: whereas flowering GUs ramify after producing inflorescences at their apex, vegetative GUs either dry up completely (most of them) or persist after extension and develop a terminal bud (the longest ones; M.A. Damascos, pers. obs.).

The present results suggest that flowering GUs of *M. spinosum* play a more relevant role in photosynthesis and in the exploration of the surrounding space than vegetative GUs. This is supported by the differences in length, number of leaves and dry mass between both GU types. The higher stem slenderness and lower number of leaves · length⁻¹ ratio of flowering GUs as compared with those of vegetative GUs are also indicative of the exploratory role of flowering GUs (Puntieri et al. 2003). These results are at odds with those of studies on tree species showing that flowering GUs have a lower allocation to stems (or axialization) than vegetative GUs (Lauri and Kelner 2001; Normand et al. 2009). It may be argued whether the relationship between axialization and allocation to reproductive structures could depend on the species' architecture. Environmental conditions determining sub-optimal conditions for photosynthesis, but optimal conditions for pollination at the plant's periphery, could favour the development of plants whose peripheral GUs have a high allocation to flowers and a low allocation to leaves. In the case of adult *M. spinosum* plants, most vegetative GUs do not reach the plant's periphery and, as a result, are less exposed to direct radiation than flowering GUs. The partial shade cast by flowering GUs would allow vegetative GUs to increase their photosynthetic activity in the summer period. At that time, flowering GUs would exhibit a lower photosynthetic efficiency due to the low levels of water availability and the high levels of incident radiation to which they are subject, as shown for other species (Thiébaud and Comps 1991; Valladares and Pugnaire 1999; Valladares and Percy 2000). Therefore, vegetative GUs would play a short-term exploitative role. The development of short GUs from axillary buds in late summer would further increase the profit each *M. spinosum* plant would be able to make under the dry and warm summer conditions.

Thus, adult *M. spinosum* cushions have a clear differentiation between vegetative and flowering GUs. Considering that each plant has a relatively even external structure (Fig. 1A), it may be concluded that each of these GU types must be distributed homogeneously on each cushion. On the other hand, the fact that all variables used here to describe GUs depended, to some extent, on the individual plant concerned indicates that each *M. spinosum* plant exhibits some degree of homogeneity in GU structure. In this respect, the differences between the individual plants studied here concerning these variables could be related to the fact that each plant would have been expressing a different ontogenetic developmental stage at the time of sampling (see Yagi 2009), despite the size evenness among the plants sampled for this study.

Conclusions and forward look

Plants with dense arrangements of GUs may resemble populations in the way GU size and density interact after threshold values are reached. The relative influences of positive and negative interactions between neighbour GUs may affect the relationship between GU density and GU size. In the case of *M. spinosum*, cushion growth means a dense crowding of GUs, which is compensated, after some years, by the production of smaller GUs and an increase in the production of non-flowering GUs. A decrease in the size of flowering GUs and in their number relative to the total number of GUs per plant, parallel to an increase in GU density, is predicted over time. The assimilative role of vegetative GUs is expected to increase in summer because of their less-exposed position in the cushion compared with flowering GUs. Further studies could test these findings for other cushion plants with different architectural models and/or with contrasting morphological traits.

Sources of funding

This study was supported by the Secretaría de Investigación of Universidad Nacional del Comahue, Argentina (Project B-138).

Contributions by the authors

J.P. and M.D. conceived the main idea, planning, sampling, data analysis and writing. Y.L. and M.S. were involved in sampling, measuring, data analysis and text editing.

Acknowledgement

We thank the Administración de Parques Nacionales for providing permits for the sampling of *Mulinum* populations within the Nahuel Huapi National Park.

Conflict of interest statement

None declared.

References

- Adler PB, Garbulskyi MF, Paruelo JM, Lauenroth WK. 2006. Do abiotic differences explain contrasting graminoid functional traits in sagebrush steppe, USA and Patagonian steppe, Argentina?. *Journal of Arid Environments* **65**: 62–82.
- Aguiar MR, Sala OE. 1998. Interactions among grasses, shrubs, and herbivores in Patagonian grass–shrub steppes. *Ecología Austral* **8**: 201–210.
- Anchorena J, Cingolani A. 2002. Identifying habitat types in a disturbed area of the forest–steppe ecotone of Patagonia. *Plant Ecology* **158**: 97–112.
- Bagchi S. 2007. Relationship between size hierarchy and density of trees in a tropical dry deciduous forest of western India. *Journal of Vegetation Science* **18**: 389–394.
- 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.
- Bliss LC. 1971. Arctic and alpine plant life cycles. *Annual Review of Ecology and Systematics* **2**: 405–438.
- Cabrera A, Willink A. 1980. *Biogeografía de América Latina*. Washington, DC: General Secretariat of the Organization of American States, Serie de Biología 13.
- Costes E. 1993. Architecture aérienne de l'abricotier en développement libre. *Acta Botanica Gallica* **140**: 249–261.
- Damascos MA, Ghermandi L. 2007. Morfología del arbusto nativo *Mulinum spinosum* en sectores quemados de pastizales del NO de la Patagonia. *Ecología Austral* **17**: 143–150.
- Damascos MA, Barthélémy D, Ezcurra C, Martinez P, Brion C. 2008. Plant phenology, shoot growth, and branching pattern in *Mulinum spinosum* (Apiaceae), a cushion shrub of the arid Patagonian steppe of Argentina. *Journal of Arid Environments* **72**: 1977–1988.
- Damgaard C, Weiner J, Nagashima H. 2002. Modelling individual growth and competition in plant populations: growth curves of *Chenopodium album* at two densities. *Journal of Ecology* **90**: 666–671.
- Del Valle H. 1998. Patagonian soils: a regional synthesis. *Ecología Austral* **8**: 103–123.
- Edelin C. 1991. Nouvelles données sur l'architecture des arbres sympodiaux: le concept de plan d'organisation. *Naturalia monspeliensis, Hors-série* **A7**: 127–154.
- Enquist BJ, Brown JH, West GB. 1998. Allometric scaling of plant energetics and population density. *Nature* **395**: 163–165.
- Freitas HMO. 1997. Drought. In: Prasad MNV, ed. *Plant ecophysiology*. New York: John Wiley and Sons, 129–147.
- Gibson N. 1990. The environments and primary production of cushion species at Mt. Field and Mt. Wellington, Tasmania. *Australian Journal of Botany* **38**: 229–243.

- Guo Q, Rundel P. 1998.** Self-thinning in early postfire chaparral succession: mechanisms, implications, and a combined approach. *Ecology* **79**: 579–586.
- Hallé F, Oldeman RAA, Tomlinson PB. 1978.** *Tropical trees and forests*. Berlin: Springer.
- Ishihara MI, Kikuzawa K. 2009.** Annual and spatial variation in shoot demography associated with masting in *Betula grossa*: comparison between mature trees and saplings. *Annals of Botany* **104**: 1195–1205.
- Kikuzawa K. 1999.** Theoretical relationships between mean plant size, size distribution and self-thinning under one-sided competition. *Annals of Botany* **83**: 11–18.
- Kira T, Ogawa H, Shinozaki K. 1953.** Intraspecific competition among higher plants. 1. Competition-density-yield interrelationships in regularly dispersed populations. *Journal of the Institute of Polytechnics, Osaka City University, Series D* **4**: 1–16.
- Kleiman D, Aarssen LW. 2007.** The leaf size/number trade-off in trees. *Journal of Ecology* **95**: 376–382.
- Kozlowski TT, Pallardy SG. 1996.** *Physiology of woody plants*, 2nd edn. San Diego, CA: Academic Press.
- Kytarissis A, Manetas Y. 1993.** Seasonal leaf dimorphism in a semi-deciduous Mediterranean shrub: ecophysiological comparisons between winter and summer leaves. *Acta Oecologica* **14**: 23–32.
- Lambrinos JG, Kleier CC, Rundel PW. 2006.** Plant community variation across a puna landscape in the Chilean Andes. *Revista Chilena de Historia Natural* **79**: 233–243.
- Lauri PE, Kelner JJ. 2001.** Shoot type demography and dry matter partitioning: a morphometric approach in apple (*Malus domestica*). *Canadian Journal of Botany* **79**: 1270–1273.
- Normand F, Bello AKP, Trottier C, Lauri PE. 2009.** Is axis position within tree architecture a determinant of axis morphology, branching, flowering and fruiting? An essay in mango. *Annals of Botany* **103**: 1325–1336.
- Osunkoya O, Omar-Ali K, Amit N, Dayan J, Daud D, Sheng TK. 2007.** Comparative height-crown allometry and mechanical design in 22 tree species of Kuala Belalong rainforest, Brunei, Borneo. *American Journal of Botany* **94**: 1951–1962.
- Prévost MF. 1978.** Modular construction and its distribution in tropical woody plants. In: Tomlinson PB, Zimmermann MH. eds. *Tropical trees as living systems*. Cambridge: Cambridge University Press, 223–231.
- Puntieri JG, Ghirardi S. 2010.** Growth-unit structure in trees: effects of branch category and position on *Nothofagus nervosa*, *N. obliqua* and their hybrids (Nothofagaceae). *Trees* **24**: 657–665.
- Puntieri JG, Pyšek P. 1993.** The effects of physical support and density on biomass production and size hierarchies of *Galium aparine* populations. *Oikos* **67**: 279–284.
- Puntieri JG, Souza MS, Barthélémy D, Mazzini C, Brion C. 2003.** Axis differentiation in two South American *Nothofagus* species (Nothofagaceae). *Annals of Botany* **92**: 589–599.
- Rauh W. 1939.** Über polsterförmigen wuchs. *Nova Acta Leopoldina, Neve Folge* **7**: 267–508.
- Reffye de P, Elguero E, Costes E. 1991.** Growth units construction in trees: a stochastic approach. *Acta Biotheoretica* **39**: 325–342.
- Sabatier S, Barthélémy D, Ducouso I, Germain E. 1998.** Modalités d’allongement et morphologie des pousses annuelles chez le noyer commun, *Juglans regia* L. ‘Lara’ (Juglandaceae). *Canadian Journal of Botany* **76**: 1253–1264.
- Sala OE, Golluscio E, Lauenroth W, Soriano A. 1989.** Resource partitioning between shrubs and grasses in the Patagonian steppe. *Oecologia (Berlin)* **81**: 501–505.
- Soriano A. 1983.** Deserts and semideserts of Patagonia. In: West N. ed. *Temperate deserts and semi-deserts*. Amsterdam: Elsevier Scientific Publishing Company, 420–460.
- Soriano A, Sala OE. 1983.** Ecological strategies in a Patagonian arid steppe. *Vegetatio* **56**: 9–15.
- Thiébaud B, Comps B. 1991.** Repartition de la matière sèche entre les organes végétatifs et reproducteurs dans les pousses annuelles du hêtre européen (*Fagus sylvatica*). *Canadian Journal of Botany* **69**: 2225–2231.
- Valladares F, Niinemets Ü. 2008.** Shade tolerance, a key plant trait of complex nature and consequences. *Annual Review of Ecology, Systematics and Evolution* **39**: 237–257.
- Valladares F, Pearcy RW. 2000.** The role of crown architecture for light harvesting and carbon gain in extreme light environments assessed with a realistic 3-D model. *Anales del Jardín Botánico de Madrid* **58**: 3–16.
- Valladares F, Pugnaire FI. 1999.** Tradeoffs between irradiance capture and avoidance in semiarid environments simulated with a crown architecture model. *Annals of Botany* **83**: 459–470.
- Weiner J. 1985.** Size hierarchies in experimental populations of annual plants. *Ecology* **66**: 743–752.
- Weiner J. 1990.** Asymmetric competition in plant populations. *Trends in Ecology and Evolution* **5**: 360–364.
- Weiner J. 1995.** Following the growth of individuals in crowded plant populations. *Trends in Ecology and Evolution* **10**: 389–390.
- Weiner J, Mallory EB, Kennedy C. 1990.** Growth and variability in crowded and uncrowded populations of Dwarf Marigolds (*Tagetes patula*). *Annals of Botany* **56**: 513–524.
- White J. 1979.** The plant as a metapopulation. *Annual Review of Ecology and Systematics* **10**: 109–145.
- Wilson BF. 2000.** Apical control of branch growth and angle in woody plants. *American Journal of Botany* **87**: 601–607.
- Yagi T. 2000.** Morphology and biomass allocation of current-year shoots of ten tall tree species in cool temperate Japan. *Journal of Plant Research* **113**: 171–183.
- Yagi T. 2009.** Ontogenetic strategy shift in sapling architecture of *Fagus crenata* in the dense understorey vegetation of canopy gaps created by selective cutting. *Canadian Journal of Botany* **39**: 1186–1196.
- Yoda K, Kira T, Ogawa H, Hozumi K. 1963.** Self-thinning in overcrowded pure stands under cultivated and natural conditions. Intraspecific competition among higher plants. *Journal of the Institute of Polytechnics, Osaka City University, Series D* **14**: 107–129.
- Zar JH. 1999.** *Biostatistical analysis*, 4th edn. New Jersey: Prentice Hall.