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Flower removal increases rhizome mass in natural populations of *Alstroemeria aurea* (Alstroemeriaceae)

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ABSTRACT

Plant architecture and phenotypic plasticity under natural conditions remain little known for many rhizomatous species. This study evaluates, in situ, the plastic responses of *Alstroemeria aurea* plants from three Patagonian populations to flower or flowering-shoot removal. The size and architecture of treated and untreated plants were assessed. Nutrient contents (N, P and K) were evaluated for rhizomes and roots developed in two successive years. Those plants that were deprived of their inflorescences developed, on average, a heavier rhizome than both control plants and plants from which flowering shoots had been removed. Neither of the two treatments applied altered the number of metamers or the branching pattern of the rhizomes. The contents of N, P and K were higher in rhizomes than in roots. In summer, nutrients were more concentrated in inflorescences and the new rhizome segment than in the rhizome segment developed in the previous year. The idea that fruiting failure in *A. aurea* promotes resource re-assignment from aerial shoots to rhizomes without altering the architecture of plants is supported. The development of the underground portion of aerial shoots in late summer-autumn allows *A. aurea* plants to take full advantage of short growth periods, but would impose a limit to plasticity.

Introduction

Phenotypic plasticity, i.e., environment-dependent phenotypic expression, is one of the sources of intra-specific morphological variation in plants (Diggle, 2002; Holeski et al., 2012; Sultan, 2000). A high diversity of factors may trigger plastic responses in plants and such responses may involve developmental changes at cell, tissue, organ and ontogeny levels (Sultan, 2003). Other sources of morphological variation are related to genetic and ontogenetic factors that play a major role in the conservative architectural pattern typical of each plant species, which is defined mainly by the level of axis differentiation, the position, orientation and time of development of branches, and the position of reproductive structures (terminal or axillary; Barthélémy and Caraglio, 2007; Hallé et al., 1978). Taking into consideration the occurrence of significant climatic changes worldwide (e.g., UNEP, 2011) a good knowledge about the factors that may cause plastic responses in plants and the kinds of responses involved may help in elucidating the impact of such changes on the functioning of biological communities.

The study of the architecture and phenotypic plasticity of rhizomatous herbs involves logistic complications, since each rhizome portion may degrade months or years after its inception, so that the development of each plant may be difficult or impossible to trace back, especially under natural conditions (Bell and Tomlinson, 1980; Schweingruber and Poschlod, 2005). Scientific interest in the architecture and phenotypic plasticity of rhizomatous plants has increased in recent decades (e.g., Diggle, 2002; de Kroon et al., 1994, 2009; Klimeš and Klimešová, 1999; Puijalon et al., 2008), but important knowledge gaps still remain. For instance, the effects of environmental factors on the reproductive and vegetative development of rhizomatous plants under natural conditions have been little investigated. In the present study we focused on *Alstroemeria aurea* Graham (Alstroemeriaceae, Order Liliales; APG, 2009), a widespread rhizomatous herb that often dominates and plays a key role in pollination webs in Patagonian forests and shrublands (Aizen et al., 2008; Morales and Aizen, 2002). Despite the major relevance of vegetative propagation in the population dynamics of *A. aurea* (Aizen, 2001; Souto and Premoli, 2003), the growth of its rhizomes and roots under natural conditions has been little investigated (but see Buxbaum, 1951). Despite the significant allocation

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of aerial mass devoted annually by *A. aurea* plants to fruits and viable seeds (one-quarter to one-third in dry mass; Puntieri and Gómez, 1992), fruit/seed development are often severely curtailed by pollination shortages (Aizen et al., 2008; Ladio and Aizen, 1999; Morales and Aizen, 2002). In addition, flowering shoots are often cut by people for ornament and damaged by herbivores and seed eaters (Puntieri and Gómez, 1992), like those of other *Alstroemeria* species (Botto-Mahan et al., 2011). The impacts of these factors on the growth of *A. aurea* rhizomes under natural conditions are unknown.

This study was aimed at: (1) determining whether factors preventing the development of viable fruits in *A. aurea* may generate a measurable plastic response at the end of the growth season, and (2) assessing the extent to which such factors affect those plant traits a priori considered as part of the species' architectural pattern. Two levels of intervention were applied to plants growing in otherwise natural conditions: (a) the removal of flowers at early developmental stages, and (b) the removal of flowering shoots. The concentrations of N, P and K in different organs of *A. aurea* plants were also evaluated at two stages of annual growth so as to contribute to the understanding of resource distribution in this species.

Materials and methods

Sampling sites

We selected three natural populations of *A. aurea* developed in communities with low plant cover and plant density. In these populations, the identification of individual plants of this species was possible through the observation of the distribution of vegetative and flowering shoots (Puntieri and Gómez, 1992). These three populations were at least 50 km apart.

One of the selected populations occupies about two hectares of a ski-run at Cerro Catedral, San Carlos de Bariloche (hereafter termed CC; 41° 10′ 08″ S, 71° 26′ 46″ W, 1100 m a.s.l.). The natural vegetation on both sides of the ski-run is a *Nothofagus pumilio* forest with an understory dominated by the bamboo *Chusquea culeou*. At the ski-run, *A. aurea* co-dominates with other herbaceous plants such as *Leucanthemum vulgare*, *Acaena* spp., *Rumex acetosella*, *Achillea millefolium* and several grass species. The second population is located at San Martín de los Andes (SMA; 40° 10′ 20″ S, 71° 21′ 28″ W, 750 m a.s.l.), along 100 m of an open roadside crossing an *Austrocedrus chilensis* forest. *Alstroemeria aurea* in this area is more abundant than other co-existing species, such as *Solidago chilensis* and *Poa* sp. The third population is located alongside the route between San Carlos de Bariloche and Villa La Angostura cities (VLA; 40° 58′ 46″ S, 71° 19′ 59″ W, 870 m a.s.l.), that goes across a woodland dominated by the native species *A. chilensis*, *Maytenus boaria*, *Diostea juncea*, *Schinus patagonicus* and *Lomatia hirsuta*, the climbing species *Mutisia spinosa* and *Vicia nigricans* and the shrubs *Senecio bracteolatus* and *Adesmia boronioides*.

Sampling and measurements

In January 2007 (summer), flowering shoots of *A. aurea* in full bloom were labelled at populations CC, SMA and VLA by means of a numbered plastic flag attached to a 20 cm long wire planted beside each target shoot, and a plastic ring surrounding the target shoot. Previous observations on this species indicated that flowering shoots more that 100 cm apart arise from physically independent individuals (J. Puntieri, unpublished data), so that labelled plants were distant from each other at least this far. Patches of *A. aurea* mixed with other plants were avoided so as to facilitate the sampling of underground organs of the labelled plants. The number of shoots labelled at each site depended on the abundance of *A. aurea* and the density of other species. The total numbers of labelled plants per site were 30 for CC, 36 for SMA and 45 for VLA. One third of the labelled flowering shoots were left intact as controls. Two treatments were applied to the remaining labelled shoots in each population: inflorescence removal and flowering-shoot removal. In the first treatment, the inflorescences of each labelled shoot were cut at their proximal end (including umbel rays, bracts, pedicels and flowers). The second treatment consisted of the removal of the flowering shoot at soil surface.

In April 2007 (early autumn), when the 2006–07 growing season had ended and all aerial shoots had died, all labelled plants were extracted from the soil with a shovel, keeping them as intact as possible. A few flags and labelling rings were lost (probably due to birds, rodents and wind), so that sample sizes were 28 plants for CC, 35 plants for SMA and 44 plants for VLA. Each plant was put in a paper bag. In the laboratory, plants were washed free of soil with a tooth brush and abundant water. The distal end of the main rhizome was identified and the organs formed at each metamer (1 node + 1 internode) of the main rhizome were recorded. Despite the sympodial construction of *A. aurea* rhizomes, throughout the following text aerial shoots (hereafter shoots), roots and lateral rhizomes will be referred to as lateral derivations from the metamers of the main rhizome, so as to simplify data coding. For each metamer of each main rhizome, ranked from the main rhizome's distal end, we recorded the presence/absence of each of these lateral derivations.

By the time of sampling, each plant had extended a new main rhizome segment (i.e., rhizome segment extended in 2007), that could be distinguished by its colour (lighter and more glossy) from the preceding main rhizome segment (Fig. 1). The new main rhizome segment was bearing shoot primordia, roots and, sometimes, a lateral rhizome. Rhizomes extended in 2007 were measured in length (to the nearest 0.1 cm) and diameter (to the nearest 0.1 mm at an intermediate metamer, by means of digital callipers). The metamers making up a rhizome extended in 2007 were counted. Using a razor blade, the rhizome extended in 2007 was detached from older rhizome segments. For each plant, the rhizome extended in 2007, and the roots, shoots and lateral rhizomes derived from it were detached, dried separately at 70 °C to constant weight and weighted to the nearest 0.001 g. The ratios between the dry mass and the number of metamers (i.e., mean dry mass per metamer) of the rhizome extended in 2007, and between the dry mass of the rhizome and the total dry mass developed in 2007 were obtained.

The main rhizome segment initiated in the 2006 growing season could also be identified based on the positions of roots and the scars left by dead shoots. Since the proximal end of this rhizome segment was sometimes not evident (due to the partial degradation of older tissues), its total size could not be accurately determined in all plants. Therefore, only two variables were measured for rhizomes extended in 2006: the ratio between rhizome dry mass and number of metamers (i.e., dry mass per metamer extended in 2006), and the ratio between rhizome dry mass and total dry mass developed in 2006.

Nutrient contents

The total contents of nitrogen (N), potassium (K) and phosphorous (P) were determined for rhizome segments extended in 2006 and 2007 and for roots formed in 2006 and 2007, for a pool of at least 10 of the untreated plants from each of the three populations that were sampled in autumn (April 2007). Total N content was determined with a carbon-nitrogen analyser after combustion at 900 °C, using a Thermo Electron Corporation NC Soil Analyzer Flash EA 1112 (Nelson and Sommers, 1996). Total K content was determined by atomic absorption after sample mineralization through dry digestion (Richards, 1993). Total P content was determined

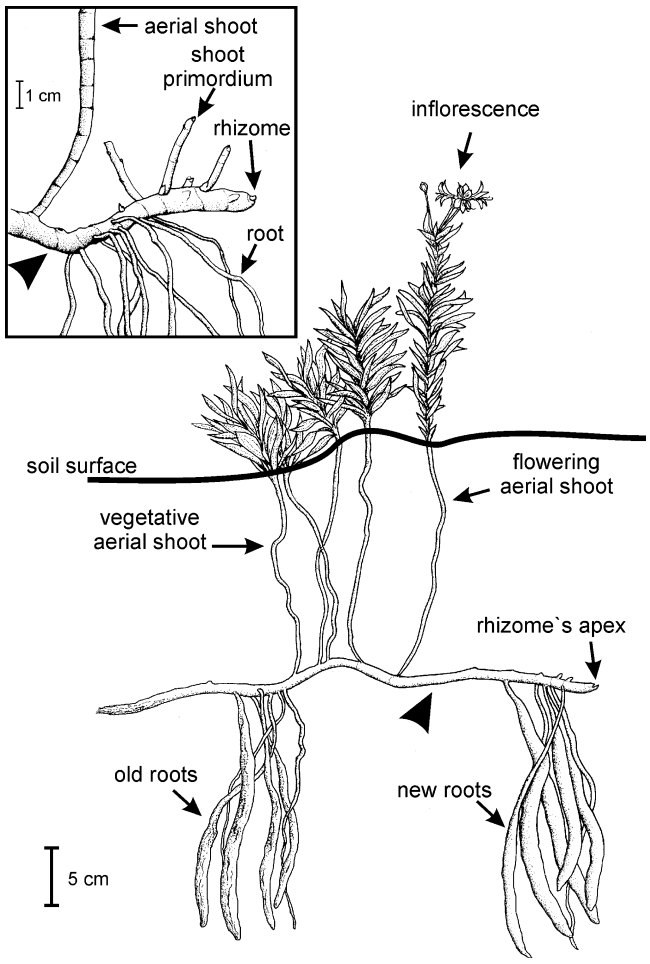

Fig. 1. Diagrams of an *Alstroemeria aurea* plant in early summer (January), and of the distal end of a rhizome as seen at the end of summer (March; outlet). Black arrowheads: approximate limit between old and new growth units of the rhizome.

colorimetrically (ascorbic acid method) after sample mineralization through dry digestion (Richards, 1993).

Nutrient contents in the period of full bloom (January) were assessed in order to have a more complete idea of the growth of *A. aurea* plants. In January 2008, ten plants were randomly selected and sampled from the CC population. In this species, fruit ripening is related to the death of vegetative shoots and leaves of flowering shoots. Since we aimed at assessing the nutrient contents of aerial vegetative organs, this sample was taken before such organs decayed. At that time, the rhizome segment extended in 2008 was differentiated from that extended in 2007. The following compartments were separately dried and weighted: rhizome segments extended in 2007 and 2008, roots developed in 2007 and 2008, vegetative shoots extended in 2007, stem + leaves of flowering shoots extended in 2007, and inflorescences developed in 2007. For each of these compartments, total N, K and P contents were determined.

Statistical analyses

Whenever variance homogeneity (using Bartlett's test) and data normality (Kolmogorov–Smirnov's test) were proved (sometimes after data $\log_e$-transformation), comparisons of all variables were performed by means of two-way ANOVA (GLM procedure for unbalanced designs): plant treatment (inflorescence removal, flowering shoot removal and control) was the main factor and sample site the random factor; the significance of the interaction between these two factors was also assessed. In case any of the assumptions for ANOVA was not met, non-parametric Kruskal–Wallis tests were applied (Sokal and Rohlf, 1981). The frequency of rhizome metamers at each position (rank numbered from the rhizome's distal end) bearing shoots, roots, lateral rhizome and/or none of these organ types, was computed.

The contents of N, K and P were compared between rhizome segments extended in 2006 and 2007 and between roots developed in 2006 and 2007 by means of Kruskal–Wallis tests.

Results

Architecture of A. aurea plants under natural conditions

The horizontal rhizomes of *A. aurea* plants grow between 10 and 40 cm depth (Fig. 1) and have metamers clearly defined by the marks left by cataphylls around each node. Despite their sympodial construction (Buxbaum, 1951), *A. aurea* rhizomes are rather straight. Scarcely branched, often fleshy, roots arise from the rhizome. Lateral rhizomes develop occasionally in axillary positions. Aerial shoots complete their growth in summer, when shoots dry up and seeds are released. In one growing season, between two and five vegetative shoots and one or, less often, two flowering shoots develop from a rhizome's distal end.

The rhizomes of *A. aurea* have a clear structural periodicity evidenced by the distribution along the rhizome of lateral organs: shoots, roots and lateral rhizomes (Fig. 2). In autumn, after the death of the aerial shoots, the rhizome bears shoot primordia, roots and, sometimes, lateral rhizomes. In this study, each rhizome sampled in autumn had one shoot primordium at each of the five to seven distal metamers. These shoot primordia were upturned so that their distal ends were less than 10 cm below the soil surface. At that stage, the distinction between vegetative and flowering shoots could not be made through external observation. Roots emerged both from rhizome metamers that developed shoot primordia, and from metamers that were devoid of shoot primordia (Figs. 1 and 2). The metamers corresponding to the proximal end of a rhizome segment were, in most cases, devoid of lateral organs.

Rhizome segments corresponding to different years were distinguished by colour and texture. The dead remains of the aerial shoots and the presence of roots allowed the evaluation of rhizome growth in the year preceding that of sampling (as shown in Fig. 2). The pattern of lateral organ development described above was similar for rhizome segments corresponding to two successive years (2006 and 2007)

Rhizome size and treatment effects

In autumn 2007, rhizomes extended in 2007 were about 9 cm long and 7 mm thick and consisted, on average, of seven metamers (Table 1). The mean numbers of shoot primordia and lateral rhizomes derived from each main rhizome extended in 2007 were six and one, respectively. The whole plant segment developed in 2007, including rhizome, roots and shoot primordia, had less than 1.5 g in dry mass, although a few plants reached little more than 4.0 g in dry mass. About one-fourth of this mass was in the rhizome, and most of the remaining mass was in the roots. The dry mass per rhizome metamer was, on average, between 0.04 g and 0.05 g for rhizomes extended in 2006 and in 2007 (Table 1).

Inflorescence removal caused a significant increase in the dry mass of the rhizome extended in 2007 and the dry mass per metamer for rhizomes extended in 2006 and 2007 (Table 1). The dry mass of the rhizome extended in 2006 relative to the total dry mass extended in the same year was also higher for the plants subjected to inflorescence removal than for those at the other two

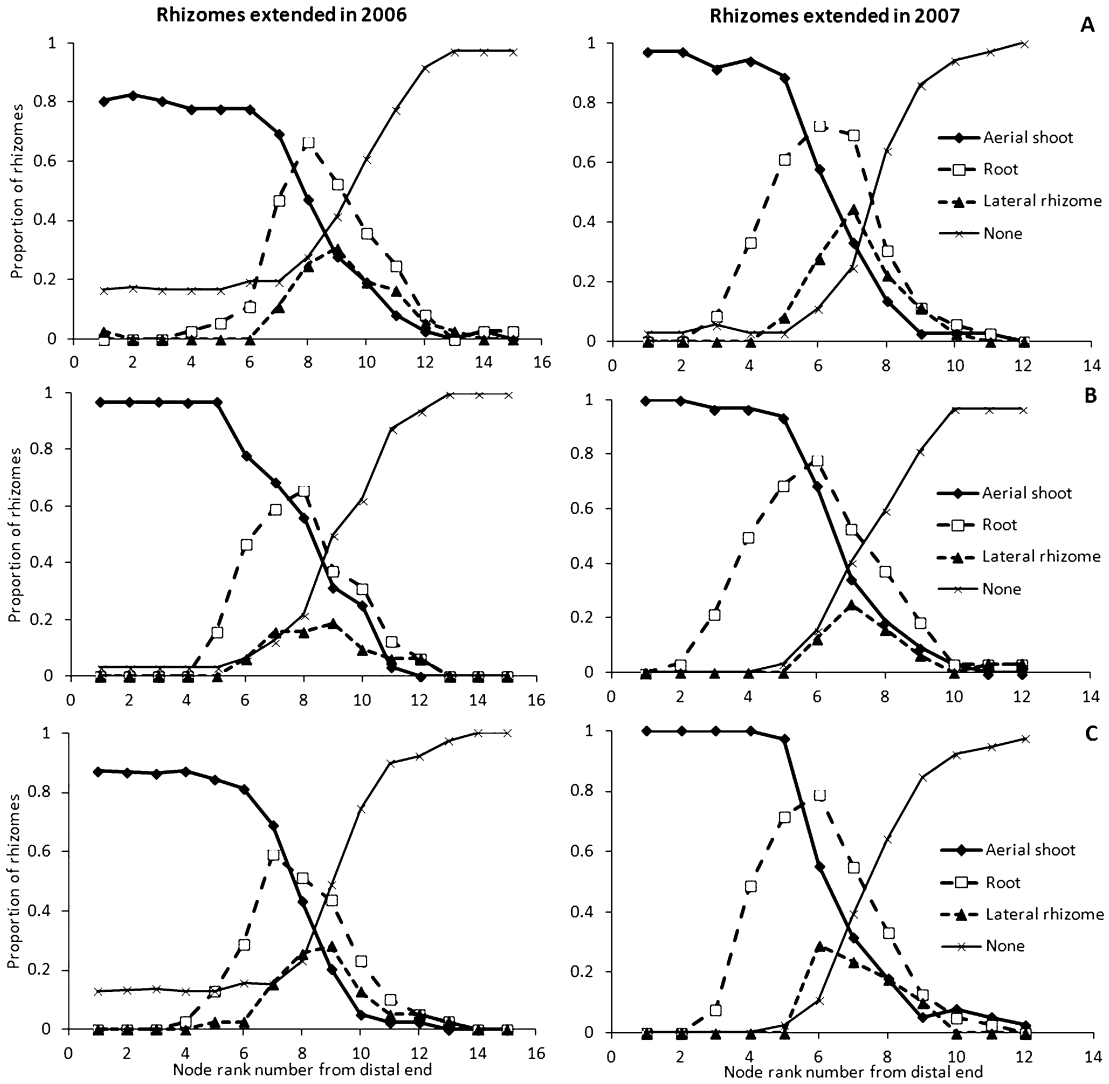

Fig. 2. Distribution of aerial shoots, roots and lateral rhizomes derived from main-rhizome segments of *Alstroemeria aurea* extended in 2006 (left) and 2007 (right). The percentage of plants with each organ type and with no organs associated with each rhizome metamer (counted from the rhizome's distal end) is indicated for plants subject to inflorescence removal (**A**) and flowering-shoot removal (**B**) as well as for control plants (**C**).

conditions. The removal of flowering shoots had no effect on the size and mass of any of the plant compartments. The following variables were not affected by the treatments: length, diameter, number of metamers, number of shoots and number of lateral rhizomes extended in 2007, dry masses of roots, shoots and lateral rhizomes extended in 2007, total dry mass extended in 2007 and the proportion of dry mass in the rhizome relative to the total dry mass extended in 2007 (Table 1).

Significant differences among sampling sites were detected for the length, diameter, number of metamers and number of shoots of the rhizome segment extended in 2007, as well as for the dry masses of roots, branches and shoots derived from these rhizomes. A significant site × treatment interaction was detected only for the number of branches derived from rhizomes extended in 2007 (Table 1).

Nutrient contents

In autumn 2007, after the death of all aerial shoots, the total contents of N and P were higher in rhizomes than in roots (Fig. 3A and B), and broadly similar between rhizomes or roots developed in 2006 and those developed in 2007; K content was, on average, marginally higher in older (2006) than younger (2007) rhizomes and higher in younger (2007) than older (2006) roots.

In summer 2008, when plants were in full bloom, N content in rhizome segments developed in 2007 was lower than in vegetative shoots, flowering shoots and rhizome segments developed in 2008; the N content of inflorescences was higher than in all other plant compartments (Fig. 3C and D). Similar but less sharp differences among plant compartments were found in the cases of K and P. Roots had lower nutrient concentrations than the other organs.

Rhizomes and roots extended in 2007 had higher contents of N, K and P in autumn, soon after their extension (Fig. 3A and B), than in the following summer, when the flowering shoots derived from these rhizomes were in full bloom (Fig. 3C and D).

Discussion

Phenotypic plasticity in A. aurea

The results of the present study indicate that *A. aurea* plants exhibit plasticity in resource allocation when fruit/seed development is impaired. The increase in rhizome dry mass (compared

Table 1
Summary information and statistical comparisons for variables (extended in years 2007 and 2006) describing the size and morphology of *Alstroemeria aurea* plants.

Year	Variable	Inflorescence removal		Shoot removal		Control		Statistical comparisons		
		Mean ± SE	*N*	Mean ± SE	*N*	Mean ± SE	*N*	Treat.	Site	Treat. × site
2007	Length of rhizome (cm)	9.8 ± 0.45	34	8.5 ± 0.49	32	9.0 ± 0.45	39	2.0 ns	4.2*	1.6 ns
	Diameter of rhizome (mm)	7.5 ± 0.33	34	6.5 ± 0.35	31	7.3 ± 0.29	39	2.9 ns	16.8***	0.4 ns
	No rhizome metamers	7.3 ± 0.20	35	7.1 ± 0.29	32	7.1 ± 0.26	39	0.19 ns	15.9***	2.1 ns
	No shoots	5.8 ± 0.28	36	6.2 ± 0.26	32	6.1 ± 0.20	39	5.0 ns	69.5**	0.2 ns
	No branches	1.2 ± 0.21	36	0.7 ± 0.17	32	0.8 ± 0.16	39	0.6 ns	1.1 ns	3.6**
	DM of rhizome (g)	0.40 ± 0.038	36	0.29 ± 0.038	32	0.33 ± 0.031	39	7.6*	3.1 ns	0.4 ns
	DM of roots (g)	0.90 ± 0.092	36	0.85 ± 0.145	32	1.06 ± 0.154	39	*1.7 ns*	*6.6**	–
	DM of branches (g)	0.02 ± 0.012	36	0.03 ± 0.025	32	0.02 ± 0.011	39	*2.4 ns*	*21.3****	–
	DM of shoots (g)	0.07 ± 0.014	36	0.06 ± 0.018	32	0.07 ± 0.012	39	0.7 ns	15.9***	2.2 ns
	DM per rhizome metamer (g)	0.05 ± 0.004	35	0.04 ± 0.004	32	0.04 ± 0.004	39	*4.2**	*0.8 ns*	0.2 ns
	Total DM (g)	1.38 ± 0.120	36	1.23 ± 0.191	32	1.47 ± 0.188	39	*3.9 ns*	*10.2***	–
	Proport. rhizome DM*	0.31 ± 0.021	36	0.32 ± 0.033	32	0.29 ± 0.026	39	0.61 ns	1.5 ns	0.4 ns
2006	DM per rhizome metamer (g)	0.06 ± 0.005	30	0.04 ± 0.004	31	0.04 ± 0.003	34	6.6**	0.7 ns	1.0 ns
	Proport. rhizome DM[a]	0.49 ± 0.045	30	0.38 ± 0.040	31	0.39 ± 0.043	33	3.1*	0.8 ns	1.7 ns

Note. Mean, standard error (SE) and number of sample units (N) are provided for each variable. Experimentally treated (inflorescence removal and flowering shoot removal) and control plants (Treat.), and three sampling sites (Site) are compared with two-way ANOVA whenever variance homogeneity (Bartlett's test) and normality (Kolmogorov–Smirnov's test) were proved; otherwise Kruskal–Wallis tests were applied (italics).
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
[a] DM in the rhizome relative to total DM in the corresponding year.
ns $p > 0.05$. DM: dry mass.

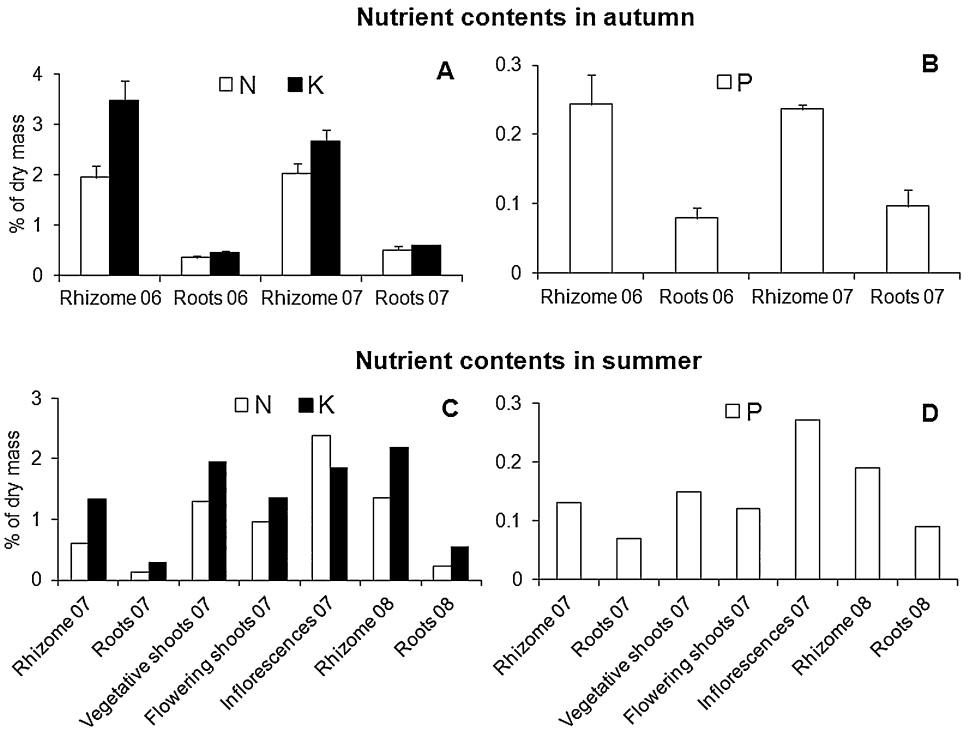

Fig. 3. Contents (% of dry mass) of nitrogen (N), potassium (K; **A** and **C**) and phosphorous (P; **B** and **D**) of *Alstroemeria aurea* organs in autumn 2007 (**A** and **B**) and summer 2008 (**C** and **D**). In **A** and **B**, data for rhizomes and roots extended in 2006 and 2007 are discriminated. In **C** and **D**, rhizomes and roots extended in 2007 and 2008 are discriminated, and data corresponding to vegetative shoots, stem + leaves of flowering shoots (flowering shoots 07) and inflorescences extended in 2007 are indicated.

to control plants) following inflorescence removal clearly suggests that resources originally aimed at fruit and seed setting would then be re-directed to the rhizome. Other geophytes seem to respond similarly to fruit failure (Addai, 2010; Kalin, 1954; Sunmonu et al., 2013). Fruits and seeds constitute a high proportion of the aerial mass of *A. aurea* plants (Puntieri and Gómez, 1992) thus constituting, at their filling stage, strong resource sinks (Wu et al., 2003). Therefore, significant changes in source-sink relationships take place in *A. aurea* plants when fruit and/or seed development fail, which is known to occur frequently due to pollinator deficiencies and fruit-mining by insects (Aizen et al., 2008; Puntieri and Gómez, 1992). This plastic response may be interpreted as an adaptation to unpredictable adverse conditions for seed set. Studies carried out on *in vitro* cultured *Alstroemeria* plants (Pumisutapon et al., 2011, 2012), as well as in other plants (Ida and Kudo, 2009; Ye et al., 2006) support the idea that stressful conditions increase rhizome growth. The present contribution indicates that rhizome mass and, probably, future plant growth, may be promoted by conditions that compromise fruit/seed development without stressing vegetative growth.

Since the increments in the dry masses of rhizomes and rhizome metamers after fruiting failure did not involve changes in the external size and the number of metamers of rhizomes, the increase in starch concentration in underground organs after flower removal seems a likely explanation for such differences in mass. Rhizomes and roots of *A. aurea* are consumed due to their high starch content (Mösbach, 1992). In other species, carbohydrate remobilization to and from storage organs has been found to vary after some organs are damaged either naturally or experimentally (Bowen and Pate, 1993; Kalin, 1954; Kleijn et al., 2005). Other studies indicate that higher storage concentration in rhizomes may have positive effects on future rhizome growth, on the growth rate of shoots and on the number of flowers per plant (Geber et al., 1997). If this were the case also for *A. aurea* plants, it may be predicted that a year of low seed production would be followed by a year of more vegetative growth and/or flower production.

It is interesting to notice that, in this study, root mass was not affected by flower removal, despite the fact that many roots are, like rhizomes, starch storing organs in *A. aurea* (Bond, 1991; Graper and Healy, 1990). The rhizome would act as a stronger resource sink and source than roots, which suggests that rhizomes are metabolically more active than roots in this species. In support of this idea, we found higher contents of N, P and K, and more notable variations in these contents depending on the plant's phenological stage in rhizomes than in roots (Fig. 3). Further studies would be necessary in order to clarify the role of tuberous roots in *A. aurea*.

Interestingly, the removal of flowering shoots applied in this study did not trigger an evident plastic response in *A. aurea* plants. Previous studies on *A. aurea* suggested that flowering shoots have a low leaf area relative to their dry mass, and that assimilates for flower/fruit development would be provided by vegetative shoots (with a proportionally higher leaf area) through the rhizome (Puntieri and Gómez, 1988, 1992). If this were the case, in order to explain the results of the present study it may be proposed that the translocation of resources other than water from rhizome to flowering shoots has already ended by the time flowering shoots are in full bloom, so that these shoots have all the necessary resources for fruit and seed development. In addition, our results suggest that resource translocation from flowering shoots after fruit development would not contribute significantly to rhizome growth.

The branching pattern of *A. aurea* rhizomes was not affected by the removal of either inflorescences or flowering shoots (Fig. 2), although the quantitative expression of rhizome branching in *A. aurea* plants may depend on factors related to each population (as indicated by the significant effect of the treatment × site interaction on the number of rhizome branches; Table 1). This agrees with other studies that considered rhizomatous plants to express plasticity through variations in the extent of rhizome branching (Ye et al., 2006). A possible plastic response unaccounted for in this study was the change in the proportion of vegetative and flowering shoots that were differentiated at the rhizome's distal end following different cutting treatments. This possible effect could not be evaluated in this study as rhizome harvesting was performed at a stage when primordia of vegetative and flowering shoots could be told apart.

Architecture and growth of A. aurea under natural conditions

The investigation of the architecture of rhizomatous herbs under natural conditions faces methodological constraints caused by the fragility and degradation of underground organs (Fitter, 1996; Schweingruber and Poschlod, 2005). *Alstroemeria aurea* plants are suitable for this kind of studies due to the conspicuousness and low extent of branching of their rhizomes and roots, and the persistent scars left by cataphylls, shoots and roots on old rhizome portions. In the present study, the architecture of *A. aurea* under natural conditions was investigated by means of the observation of over 100 plants from several populations. We found that the main rhizome of *A. aurea* plants under unshaded conditions grows an average of 9 cm in length during the summer-autumn period, when aboveground development has ended, as found also in a previous study (Aker and Healy, 1990). Site conditions affect the underground growth of *A. aurea* (Table 1), but its architectural pattern seems to be site-independent. The variations among populations in some of the growth traits evaluated here could be explained by genetic differences, as found for other species (Wang et al., 2013). The distal end of each *A. aurea* rhizome develops, at the end of the season of aerial growth, a new set of organs: a segment of the main rhizome, shoot primordia, root primordia and, sometimes, lateral rhizomes (Fig. 4). Lateral organs on the main rhizome are initiated from the annual main-rhizome segment in an orderly way: the main-rhizome portion extended in the first place is devoid of shoots and roots, the next portion bears roots and, sometimes, one or two lateral rhizomes, and the distal portion develops shoot primordia. By early autumn, the relatively thin (2–4 mm in stem diameter) shoot primordia have grown about 5–10 cm towards the soil surface (Fig. 4a) and remain dormant until spring, when they emerge from the soil surface. Dissections of shoot primordia of *A. aurea* in late summer indicated the presence of leaf primordia (J. Puntieri pers. observation), so that at least some of the metamers making up the aerial shoots of *A. aurea* may be described as preformed organs (Barthélémy and Caraglio, 2007). The preformation of organs in young shoots of rhizomatous plants may be a favourable trait whenever the annual period of aerial growth is short, and may provide a competitive advantage over other herbaceous plants in early spring (Billings and Mooney, 1968; Gómez-González et al., 2009; Rice and Dyer, 2001). Nonetheless, preformation constrains the plastic response of plants

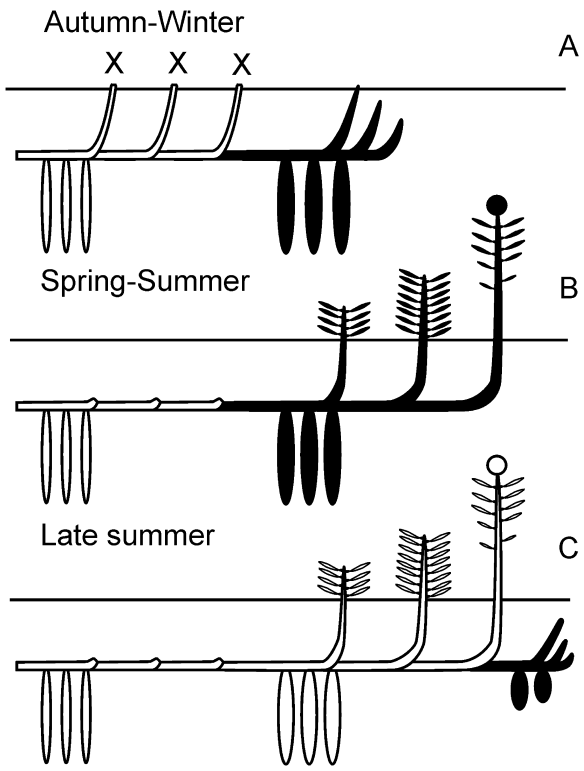

Fig. 4. Schematic representation of an *Alstroemeria aurea* plant in three periods of the year: during autumn-winter (**A**), in the spring-summer period (**B**), and in late summer (**C**). Most recent rhizome segments at right end. Shades of grey indicate resource-sink strength (darker organs are stronger sinks). X: dead aerial shoot or shoot apex. Circle: inflorescence. Horizontal lines correspond to the soil surface. See further details in the text.

to unforeseen conditions (Diggle, 1997; Geber et al., 1997; Werger and Huber, 2006): preformed organs would have anatomical and morphological structures suited for a set of environmental conditions that may differ from those actually occurring at the time these organs complete their growth. In addition, trampling or landslides may cause the breakage of the fragile shoot primordia and compromise plant growth in the following spring. In *A. aurea*, rhizome growth takes place through the succession of sympodially branching metamers, some of which end up upturning distally, thus initiating the development of aerial-shoot primordia (Buxbaum, 1951). Therefore, on morphogenetic grounds, the early initiation of shoot primordia in *A. aurea* is inevitably linked with rhizome growth. In the Andean genus *Alstroemeria* selective pressures for early emergence in spring might be stronger than those favouring plastic responses of rhizomes facing mechanical damage (Williams and Levine, 2004).

Conclusions

In *A. aurea*, environmental factors affecting the production of seeds and fruits may trigger plastic responses resulting in an increase in rhizome mass. Therefore, in a pessimistic scenario regarding pollination and seed development, the occupation of below-ground spaces through vegetative growth would be increased. Developmental rules, including the position of lateral organs on the main rhizome are more resilient to environmental factors acting on aerial shoots. Aerial-shoot preformation in early autumn would set a limit to the plastic response of *A. aurea* in the following growing season.

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