Preslia, Praha, 64:343-355, 1992

Growth analysis of the reproductive shoots of *Alstroemeria aurea* in two contrasting populations

Růstová analýza reproduktivních prýtů u dvou populací *Alstroemeria aurea* z odlišných stanovišť

Javier G. Puntieri[1)] and Isabel A. Gómez[2)]

[1)] *Centro Regional Universitario Bariloche, cc 1336, 8400 San Carlos de Bariloche, Argentina,* [2)] *Grupo de Análisis de Sistemas Ecológicos (Asociado a Fundación Bariloche), cc 138, 8400 San Carlos de Bariloche, Argentina*

Puntieri J. G. et Gómez I. A. (1992): Growth analysis of the reproductive shoots of *Alstroemeria aurea* in two contrasting populations. - Preslia, Praha, 64:343-355.

Keywords: *Alstroemeria aurea*, perennial herb, leaf area, reproductive effort, shoot density, fruit abortion

Dry-weight, leaf area, height, density of shoots and seed-production components were studied for two natural populations of the herb *Alstroemeria aurea* growing in *Nothofagus* forest and shrubland in northern Patagonia. The vegetative development (height, leaf area and vegetative biomass per shoot) was higher in the understory than in the shrubland. The density of vegetative shoots was also higher in the understory. The density of flowering shoots was similar for both populations. The production of seeds per shoot was higher in the shrubland due to the higher number of seeds per fruit. Apparently, a snowfall during the growing season reduced the production of fruits per shoot in the understory population.

Introduction

The study of the growth of different plant populations of the same species in contrasting environments provides vital information about the rules that control intraspecific and interspecific plant interactions (Bradshaw 1965). This information has sometimes been used to support theories on plant competition and evolution (Gadgil et Solbrig 1972, Grime 1979). In addition, the assessment of those traits related with individual survival (e.g. vegetative growth) and seed yield (flowering, fruiting, seed production per fruit) in two or more conspecific populations can also shed light both on their relative degrees of adjustment to their environments (see Turkington et Aarssen 1985) and on the main selective pressures that could have favoured such growth traits.

In the last decade, studies on the ecology of perennial herbs have intensified seeking for generalities in their response patterns under different conditions (Lovett Doust 1981, Ashmum et Pitelka 1985, Hartnett et Bazzaz 1985a,b, Angevine et Handel 1986, Lovett Doust 1987, Slade et Hutchings 1987a,b, among others). Herb species from the temperate forests of South America have received little attention (but see Jaksic et Montenegro 1979, Hancock et Bringhurst 1980, Alpert et Mooney 1986). The amancay, *Alstroemeria aurea* Graham (= *Alstroemeria aurantiaca* D. Don, *Alstroemeriaceae*) is one of these species and an interesting subject for comparative growth studies because of its abundance in several communities of the *Nothofagus*-forest region (see Rothkugel 1916, Dimitri 1972). Despite the horticultural importance of this species and its artificial hybrids both in America and Europe and the actual knowledge about different breeding aspects of hybrids of this species (e.g. Healy et Wilkins 1986, Waithaka et Chepkairor 1988), little is known about its behaviour in the wild (but see Puntieri et Gómez 1988, Puntieri 1991).

A. aurea is a perennial herb with long (up to 30 cm), cylindric, sometimes ramified rhizome, tuberous roots, and upright non-ramified seasonal shoots (up to 120 cm high) with spirally-arranged elliptic-oblanceolate leaves. Some shoots produce an apical 1-10-radius umbrella of 1-3 flowered cymes and, eventually, ovate capsules with ballistic opening. For more details on the morphology and distribution of this species, see the description by Bayer (1987). This species is particularly abundant in the understory of open *Nothofagus pumilio* forests, in parts of which it is one of the most abundant species (Hildebrand-Vogel et al. 1990). However, it is also found in recently disturbed areas with sparse shrub cover (Puntieri 1991). The study of its growth and seed production may give an indication of its relative fitness in each of these communities. This information could provide evidence for theories on the origin of the vegetation of this region.

The proposed aims of this study are: (1) to measure the vegetative and reproductive growth of *A. aurea* flowering shoots and the density of both vegetative and reproductive shoots of this species during one season of development in contrasting natural habitats, and (2) to assess features that contribute to the degree of adjustment of each population to its environment.

Materials and methods

Study areas

Two *A. aurea* populations from contrasting environments were selected for this study; both communities are in the proximity of San Carlos de Bariloche city, Argentina: (1) lenga (*Nothofagus pumilio*) forest community located on the northern slope of Mt. Catedral (41°12'S; 71°31'W), where *A. aurea* dominates the understory (subjective view); (2) community located on the southwestern slope of Mt. Carbón (41°12'S; 71°18'W), without tree cover, composed mainly of sparse shrubs and herbs lower than 50 cm height, where *A. aurea* is one of the most abundant species (subjective view). The most apparent differences between these environments can be summarized as follows: (a) annual precipitations (1400 mm in 1 and 1100 mm in 2); (b) soil water retention capacity (26% at 15 bar in 1 and 12% at 15 bar in 2); (c) orientation (NE for 1, SW for 2); (d) surface organic matter (present in 1, absent in 2).

Data collection and analysis

Weekly, from January to March 1985, 20 *A. aurea* reproductive shoots were collected randomly from each population. The random sampling was carried out by setting up a transect with random direction across the area. The flowering shoot of *A. aurea* closest to a random distance from either side of the transect was selected. Due to the resemblance between vegetative and reproductive shoots in the shrubland at the beginning of their aboveground growth, only four reproductive shoots were collected for that population in the first sample. Height and leaf area (estimated from length and maximum width of each leaf) of each shoot were measured, and its leaves, flowers, viable fruits, aborted fruits and seeds per fruit counted. Fruits containing fully developed seeds (here considered viable

Table 1. - Maximum moving averages (X) obtained for the parameters measured on the shoots of *Alstroemeria aurea* collected from Mt. Catedral and Mt. Carbón. Confidence intervals of 95% (c.i.) and sampling week in which these means were obtained (week) are given. The last column shows the sampling weeks in which differences between both populations were not significant (by Fisher's F-test; $P<0.05$).

	Mt. Catedral			Mt. Carbón			dif.
	X	c.i.	week	X	c.i.	week	
Height (cm)	91	3.1	10	27	1.8	11	-
Stem weight (g)	1.3	0.12	10	0.4	0.05	11	-
Leaf area (cm^2)	301	25.3	10	69	14.4	4	-
Leaf weight (g)	0.69	0.073	6	0.36	0.045	11	-
Number of leaves	23.7	1.33	8	22.9	1.49	6	2
Reproductive weight (g)	0.28	0.035	8	0.56	0.104	11	2-
Reproductive effort (%)	0.13	0.014	8	0.43	0.034	11	-

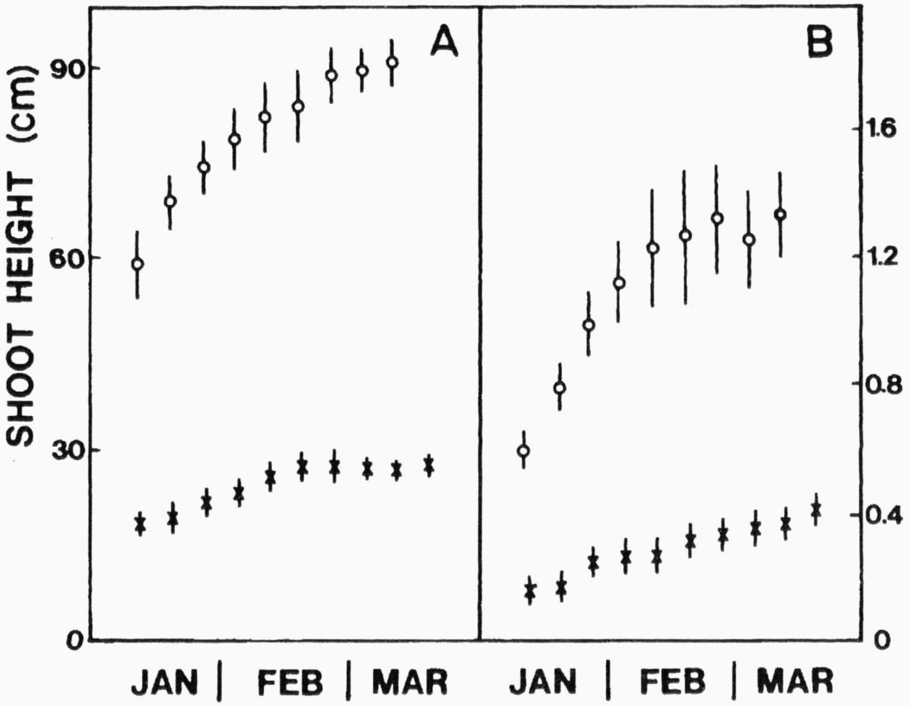

Fig. 1. - Mean shoot height (A) and stem weight (B) of *Alstroemeria aurea* flowering shoots from understory (Mt. Catedral, o) and open shrubland (Mt. Carbón, x) obtained from weekly samples in the 1984/85 growing period. 95% confidence intervals are drawn.

fruits) are egg-shaped and have a smooth surface; fruits containing no seeds (aborted fruits) are usually no more than half the size of viable fruits, and are rough on the outside. Dry weights of leaves, stem and reproductive structures (including floral buds, flowers, fruits and ancillary structures) were obtained after oven-drying at 105°C for 48 hrs. Moving averages of three weeks were calculated for each variable in order to smooth mean value trends (Diggle 1990). The reproductive effort per shoot was estimated as the proportion of the total shoot weight contained either in reproductive structures (flowers, fruits and seeds) or in seeds.

Seasonal maximum mean densities of vegetative and reproductive shoots of *A. aurea* were estimated for each population by counting them in 20 to 27 randomly located plots of 0.25 m^2 in size. The dispersion pattern of each kind of shoot and the significance of the departures from the random pattern were measured by Morisita's index (Morisita 1959). Comparisons between mean values were carried out by analysis of variance when the assumptions of normality and variance homogeneity were demonstrated; otherwise Mann-Whitney paired U-tests were applied.

Results

Stem

Both mean height and mean stem weight of *A. aurea* flowering shoots were greater in the understory than in the shrubland (Fig. 1), with maximum means approximately three times higher in the first habitat (Table 1). Asymptotic trends were recorded for both mean height and stem weight of the understory shoots. For shrubland shoots, in contrast, mean height trend was asymptotic while stem weight followed an almost linear trend. In both populations stem elongation increased relatively more than stem weight during the first part of aboveground growth, including the period of about 3 weeks before the first sample. The stem weight of the shrubland shoots increased notably in the second half of the sampling period, though no shoot elongation was recorded for that period.

Leaves

The leaf area per shoot was always (up to five times) larger in the understory than in the shrubland (Fig. 2A, Table 1). Leaf area development was completed in approximately two months (including the period previous to the first sampling) for the shoots of the understory. In the shrubland shoots the maximum leaf area was reached by the time of the first sampling and no significant differences were found between the means of all samples ($F=0.97$; $P>0.1$). The trends in mean leaf weight were similar to those of leaf area: asymptotic in the understory shoots and almost constant in the open-site shoots (Fig. 2B). The maximum mean leaf weight was twice as great for the understory shoots as for the shrubland shoots (Table 1). In both populations the number of leaves had a similar trend, although moving averages were always higher in the understory (Fig. 2C).

Reproductive structures

The mean weight of reproductive structures per shoot was similar for both populations during the first two months of sampling (Fig. 3). From then on the reproductive weight

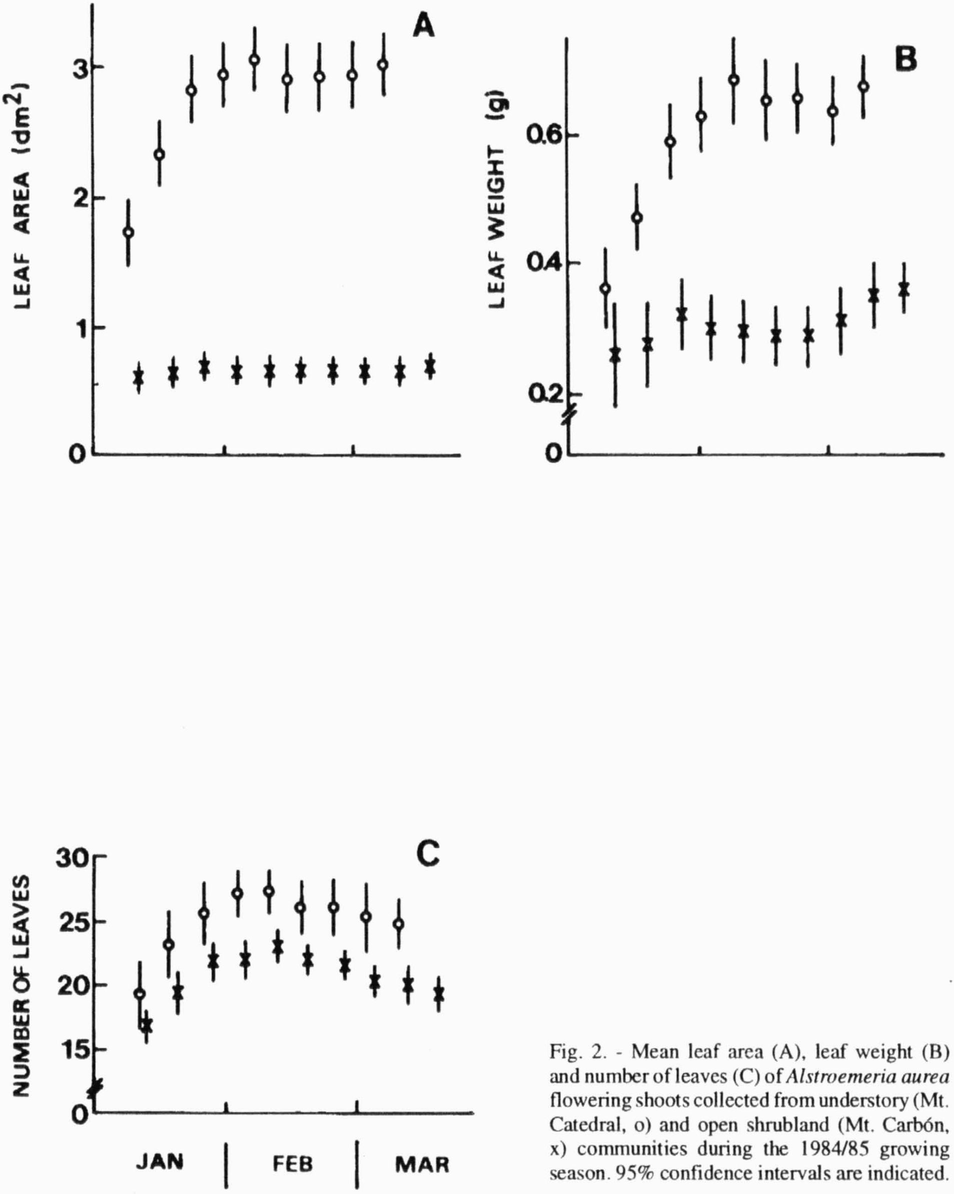

Fig. 2. - Mean leaf area (A), leaf weight (B) and number of leaves (C) of *Alstroemeria aurea* flowering shoots collected from understory (Mt. Catedral, o) and open shrubland (Mt. Carbón, x) communities during the 1984/85 growing season. 95% confidence intervals are indicated.

increased only in the shrubland and reached in that population a maximum mean value twice as high as that reached in the understory (Table 1). Because of the lower biomass of stems and leaves in the shrubland, the reproductive effort was higher in that site during the whole sampling period (Fig. 4).

The median of the number of flowers per shoot resulted significantly higher for the understory shoots than for those from the open community (P<0.05), although in both

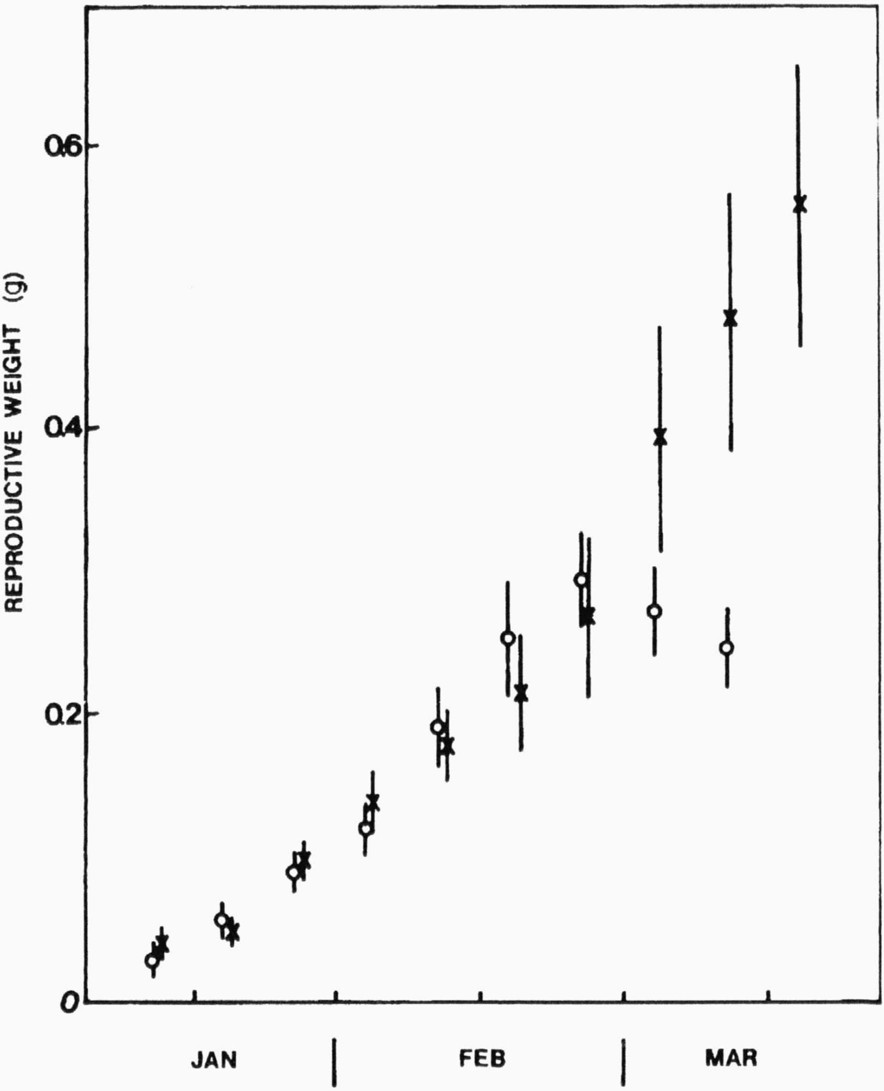

Fig. 3. - Mean reproductive weight of *Alstroemeria aurea* flowering shoots collected from understory (Mt. Catedral, o) and open shrubland (Mt. Carbón, x) communities during the 1984/85 growing period. 95% confidence intervals are indicated.

populations three was the most common number of flowers found (Fig. 5). This difference was mostly due to the more skewed distribution of the number of flowers in the shrubland than in the understory. Neither the mean number of viable fruits nor the mean number of aborted fruits per shoot were significantly different between populations ($P<0.05$; Fig. 5). The seed production per viable fruit was higher in the open site than in the understory (Table 2). Most fruits produced by *A. aurea* shoots of the understory, though judged viable on the base of their size, did not include any seed.

An early snowfall took place in the region on the 14th of February 1985, the intensity of which was similar in both study areas. The flowering shoots of *A. aurea* in the understory were bent down by the weight of the snow, whereas those in the shrubland seemed unaffected.

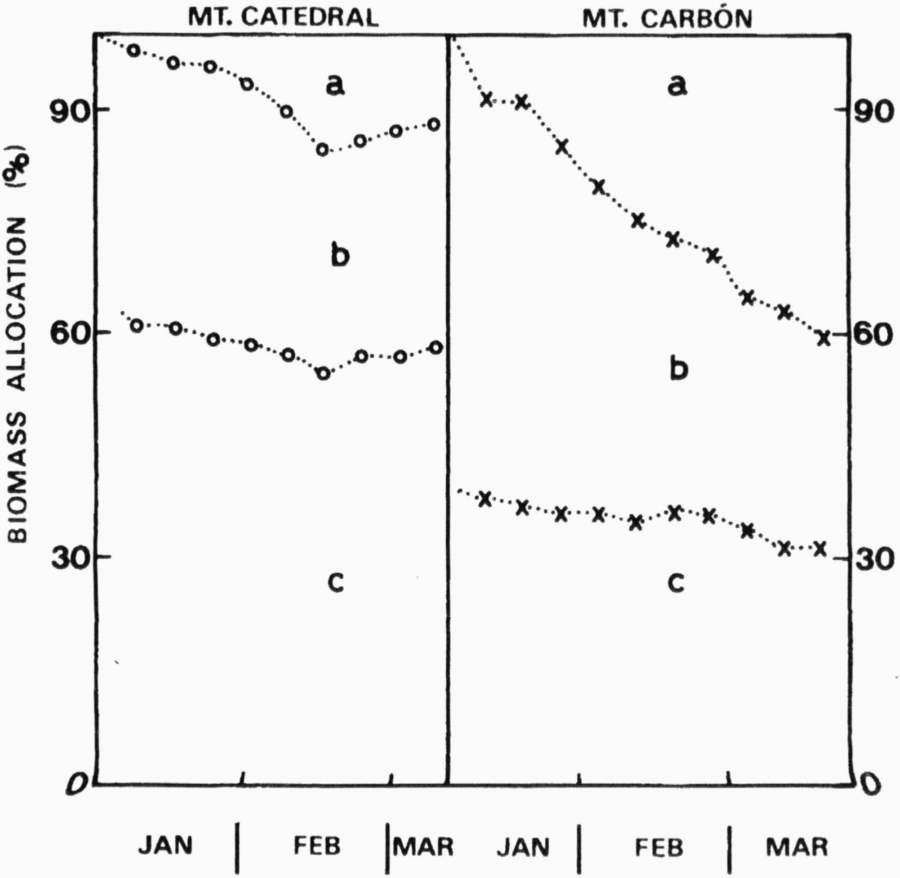

Fig. 4. - Mean percentage of the total weight of flowering shoots contained in reproductive structures (a), leaves (b) and stem (c) during the 1984/85 growing period for understory (Mt. Catedral) and open shrubland (Mt. Carbón) *Alstroemeria aurea* populations.

Shoot density

The mean density of flowering shoots was similar for both populations ($8.8/m^2$ in the understory and $5.2/m^2$ in the shrubland; U=1.52; $P<0.05$). However, the dispersion pattern, measured by Morisita's index (I_d), was random in the understory ($I_d=0.96$) and aggregated in the shrubland ($I_d=1.44$; $P<0.01$). In contrast, the mean density of vegetative shoots was much higher in the understory ($212.6/m^2$) than in the shrubland ($48.1/m^2$). In both cases the dispersion pattern of this kind of shoot was aggregated ($I_d=1.06$ and $I_d=1.86$, respectively; $P<0.01$).

Discussion

Vegetative growth

The growth of *A. aurea* reproductive shoots changes notably between populations developing in contrasting environments. The differences in the growth of stem and leaves of *A. aurea* flowering shoots are similar to those found for the vegetative shoots of these populations (larger height, leaf area and vegetative weight in the understory than in the shrubland; see Puntieri et Gómez 1988). In contrast to the findings for the vegetative shoots, leaf number was higher in the understory flowering shoots than in those of the open site. The development of larger vegetative organs in shaded than in open habitats has commonly been reported for perennial herbs (Gadgil et Solbrig 1972, Abrahamson 1979, Björkman 1981, Bierzychudek 1982) though in some cases the inverse trend has been found (Slade et Hutchings 1987a).

The density of vegetative shoots accounts for a major part of the difference in vegetative development between both populations studied here. Differences in shoot production by perennial herbs can be caused by biotic or abiotic factors which modify the growth pattern of rhizomes (Lovett Doust 1981, 1987, Schmid et Bazzaz 1987, Slade et Hutchings 1987a,b). The higher aggregation of vegetative shoots in the shrubland than in the understory supports the idea that rhizome branching and elongation could change for this species between sites. Studies on the below-ground growth pattern of this species would be necessary in order to test this hypothesis.

Reproductive growth

Studies carried out with *Alstroemeria* hybrids demonstrated that the flower production per shoot is positively related to light intensity while other conditions are held constant (Healy et Wilkins 1982a,b, Healy, Wilkins et Celusta 1982, Healy et Wilkins 1986); this is a common response among herbs (Abrahamson et Gadgil 1973, Grime 1979, Bloom, Chapin et Mooney 1985, Ojala 1985, Mehrhoff 1989). Low soil temperature was also found to be necessary for the production of flowers in hybrids of *Alstroemeria* (Waithaka et Chepkairor 1988). Neither of these factors seems to explain the slightly higher production of *A. aurea* flowers in the understory than in the shrubland. Therefore, assuming a similar response between *A. aurea* and its hybrids with other species, it may be said that one or more factors other than light intensity and soil temperature affect *A. aurea* flower production per shoot. The differences between the two environments chosen for the present study suggest that water availability and soil fertility may play decisive roles.

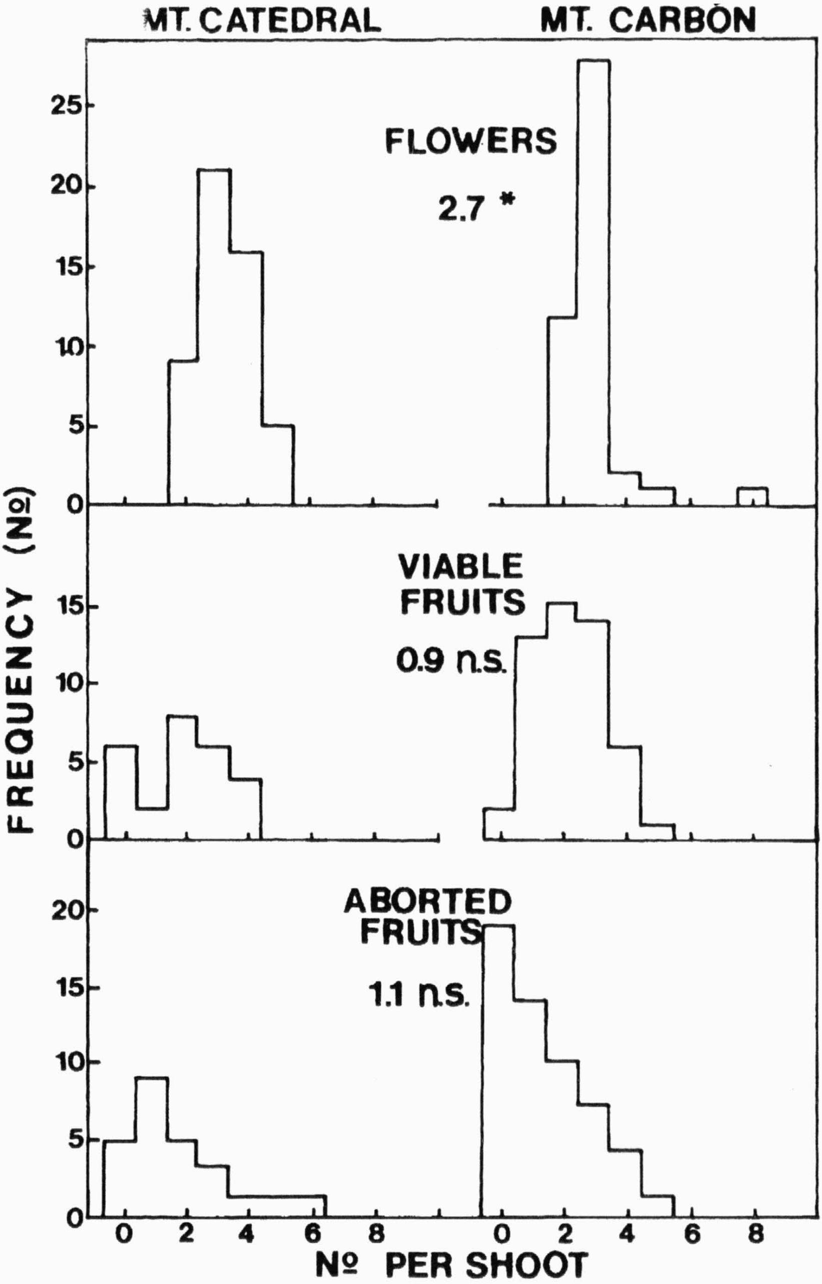

Fig. 5. - Frequency distributions of the numbers of flowers (top), viable fruits (middle) and aborted fruits (bottom) per flowering shoot of *Alstroemeria aurea*, obtained for understory (Mt. Catedral) and open shrubland (Mt. Carbón) populations. U values of Mann-Whitney paired comparisons are indicated (* $P<0.05$, n.s. $P>0.05$).

Table 2. - Productions of fruits per shoot and of seed per fruit for amancay populations of Mt. Catedral and Mt. Carbón in two consecutive growing seasons. X = mean; skew = [(mean-median)/standard deviation]. n = number of samples. Similar letter (a or b) in a row indicate non-significant (P<0.05) difference between mean values (Mann-Whitney's U- tests).

		1984/85		1985/86	
		Catedral	Carbón	Catedral	Carbón
Viable fruits per shoot	X	2.0 b	2.2 b	3.6 a	2.7 ab
	skew	0.00	0.21	0.34	–0.25
	n	20	51	56	54
Seeds per viable fruit	X	0.0 b	11.6 a	1.0 b	14.1 a
	skew	0.00	0.17	0.44	0.06
	n	40	40	69	28
Maximum mean reproductive weight per shoot (g)	X	0.21 b	0.50 a	0.62 a	no data
	skew	0.09	0.39	0.08	
	n	20	20	20	
Mean weight of seeds per shoot (g)	X	0.00 b	0.16 a	0.04 b	no data
	skew	0.00	0.64	0.35	
	n	20	20	20	

Although the number of flowers per shoot was higher in the understory population, both viable and aborted fruit numbers were similar for both populations. This inconsistency may be due to the closeness of the U-values of the comparisons to the critical values. The higher variability in fruit number than in flower number per shoot in both populations may have reduced the power of the test when comparing fruit numbers. Among the factors responsible for the cessation of flower and fruit growth are limited pollination or resource availability (Lloyd 1980, Stephenson 1981, Sutherland 1986a,b, Solomon 1987, 1988, Lee 1988 and references therein). In the present case, the mid-February snowfall could have reduced the number of viable fruits produced by *A. aurea*. Judging by the visual effect of this early snowfall on the flowering shoots of *A. aurea*, it could be hypothesized that the degree of fruit abortion was more affected in the understory than in the shrubland population. This is supported by data obtained during the following growing season (1985/86), in which the study areas were free from snowfalls. The production of viable fruits by understory *A. aurea* shoots in this season was significantly higher than that in the previous season (1984/85) (Table 2). Nevertheless, the effect of the early snowfall on the production of viable fruits in the shrubland seems not to have been significant. This apparent difference between populations in the effects of this snowfall on viable fruit production may have been connected with the phenology of the populations (Fig. 6). During the snowfall most *A. aurea* shoots in the forest were flowering while in the open site some shoots were producing flower buds, others were flowering and the remaining ones were bearing maturing fruits. As the snowfall caused more damage to flowers than to buds and fruits, the understory shoots were more adversely affected than those of the shrubland. Fruit and seed production reduction due to stress have been reported for other species (Stephenson 1980).

Seed production per fruit seems to be the most variable yield-related trait between *A. aurea* populations. The shrubland selected for the present study is by far more appropriate than the forest environment for *A. aurea* seed production (Table 2). Similar results have been reported for other species from woodlands and open sites (Harper 1960, Abrahamson 1979, Lloyd 1980, Bierzychudek 1982).

Like in *Alstroemeria* hybrids, *A. aurea* seems to respond to different habitats by changing not only the allocation of resources to leaves and stem within each shoot, but also by modifying the proportion between vegetative and reproductive shoots produced (see Healy et Wilkins 1986, Waithaka et Chepkairor 1988). Field experimentation should be carried out in order to determine which of the factors known to affect quality and quantity of shoot production in the hybrids is most related to the pattern of development found in natural habitats.

Conclusions

The conditions in the *Nothofagus pumilio* forest community of Mt. Catedral are more favourable for the vegetative development of *A. aurea* than those in the open shrubland of Mt. Carbón. High density of shoots and their vigorous vegetative growth provides this species with high competitive ability (Grime 1979, Björkman 1981). Nevertheless, this population produces few seeds and expends resources on the development of empty fruits. The reproductive structures in this population are apparently more susceptible to environmental stresses (like the snowfall) perhaps due to their longer flowering period (Fig. 6). The less fertile conditions in the shrubland of Mt. Carbón limit the vegetative development of this species (both in density and vigour). However, its shoots may be more resistant to stress and develop more seeds than in the understory. Probably, shrublands like that at Mt. Carbón are affected by natural disturbance and harsh conditions more frequently than the understory communities, so that the development of shorter shoots with smaller leaves (attributes usually connected with harsher environments: Grime 1979) could have been favoured in open areas.

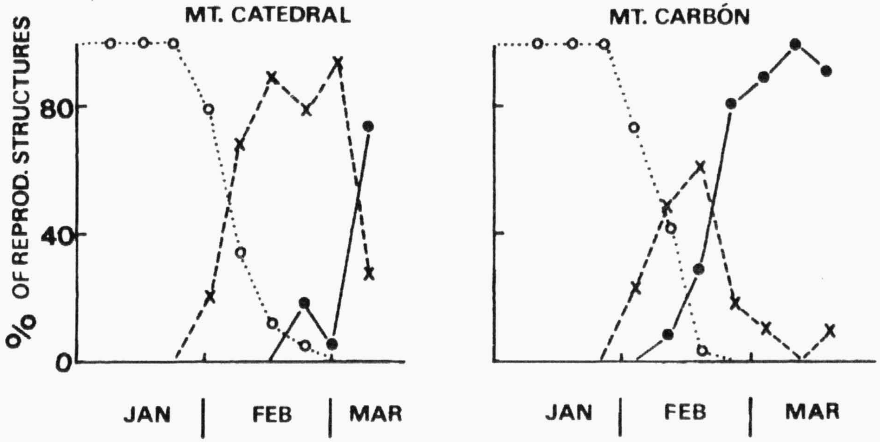

Fig. 6. - Number of flower buds (o), flowers (x) and fruits (•) expressed as percentages of the total number of reproductive structures of *Alstroemeria aurea* populations from understory (Mt. Catedral) and open shrubland (Mt. Carbón) communities, during the 1984/85 growing season.

Acknowledgments

We wish to thank M. Gross, J. Chiapella, S. Pillado and C. Brion for their support during the data analysis, R. Maronna and N. Baccalá for statistical advice and R. L. Hall, T. Veblen, S. Woodell, P. Pyšek and an anonymous referee for comments on different versions of the manuscript. We acknowledge Fundación Bariloche for providing computational facilities and the Administración de Parques Nacionales for authorizing the access to the sampling areas.

Souhrn

Článek se zabývá srovnáním populací byliny *Alstroemeria aurea* (*Alstroemeriaceae*) na dvou odlišných typech stanovišť v okolí San Carlos de Bariloche v Argentině. Prvním stanovištěm byl les s *Nothofagus pumilio* na severním svahu Mt. Catedral, druhým rozvolněné křovinné porosty bez stromového patra na jihozápadním svahu Mt. Carbón. Vegetativní růst (byla měřena výška, listová plocha, biomasa vegetativních orgánů, hustota vegetativních prýtů) byl bujnější v lesním podrostu. Hustota kvetoucích prýtů byla obdobná na obou stanovištích, avšak průměrný počet semen na prýt byl vyšší v křovinném společenstvu díky vyššímu průměrnému počtu semen v plodu. Z práce vyplývá, že podmínky v lesním podrostu jsou pro vegetativní vývoj velmi příznivé, což poskytuje druhu *A. aurea* značnou kompetiční schopnost. Nicméně tato populace vytváří málo semen a produkuje větší počet prázdných plodů. Reproduktivní orgány jsou citlivější vůči stresu, což je v práci rozebíráno na příkladu pozdního sněhu. Naproti tomu, v méně úživných podmínkách křovinného stanoviště je vegetativní růst limitován, ale prýty produkují více semen a zdá se, že jsou odolnější vůči stresu.

References

Abrahamson W. G. (1979): Patterns of resource allocation in wildflower populations of fields and woods. - Amer. J. Bot., Lancaster, 66:71-79.

Abrahamson W. G. et Gadgil M. (1973): Growth form and reproductive effort in goldenrods (*Solidago, Compositae*) - Amer. Nat., Boston, 107:651-661.

Alpert P. et Mooney H. A. (1986): Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. - Oecologia, Berlin, 70:227-233.

Angevine M. W. et Handel S. N. (1986): Invasion of forest floor space, clonal architecture, and population growth in the perennial herb *Clintonia borealis*. - J. Ecol., Oxford, 74:547-560.

Ashmum J. W. et Pitelka L. F. (1985): Population biology of *Clintonia borealis*. II. Survival and growth of transplanted ramets in different environments. - Ibid. 73:185-198.

Bayer E. von (1987): Die Gattung *Alstroemeria* in Chile. - Mitt. Bot. Staatssammlung München 24:1-362.

Bierzychudek P. (1982): Life histories and demography of shade tolerant temperate forest herbs: a review. - New Phytol., London, 90:757-776.

Björkman O. (1981): Responses to different quantum flux densities. - In: Lange O. L. et al. [red.], Physiological Plant Ecology I. Responses to the physical environment, p. 57-107, Berlin.

Bloom A. J., Chapin III S. F. et Mooney H. A. (1985): Resource limitation in plants. An economic analogy. - Ann. Rev. Ecol. Syst., Palo Alto, 16:363-392.

Bradshaw A. D. (1965): Evolutionary significance of phenotypic plasticity in plants. - Adv. Genetics, New York 13:115-155.

Diggle P. J. (1990): Time series. A biostatistical introduction. - Oxford Sci. Publ., Oxford.

Dimitri M. J. (1972): La región de los bosques Andino-Patagónicos. Sinopsis General. - Buenos Aires.

Gadgil M. et Solbrig O. (1972): The concept of r- and K- selection: evidence from wild flowers and some theoretical considerations. - Amer. Nat., Boston, 106:14-31.

Grime J. P. (1979): Plant strategies and vegetation processes. - J. Wiley & Sons, Chichester.

Hancock J. F. et Bringhurst R. S. (1980): Sexual dimorphism in the strawberry *Fragaria chiloensis*. - Evolution, London, 34:762-768.

Harper J. L. (1960): Factors controlling plant numbers. - In: Harper J. L. [red.], The biology of weeds, p. 119-132, Oxford.

Harper J. L. (1977): Population biology of plants. - Academic Press, New York.

Hartnett D. C. et Bazzaz F. A. (1985a): The integration of neighbourhood effects by clonal genets in *Solidago canadensis*. - J. Ecol., Oxford, 73:415-427.

Hartnett D. C. et Bazzaz F. A. (1985b): The regulation of leaf, ramets and genet densities in experimental populations of the rhizomatous perennial *Solidago canadensis*. - J. Ecol., Oxford, 73:429-443.

Healy W. E. et Wilkins H. F. (1982a): The interaction of temperature on flowering of *Alstroemeria* 'Regina'. - J. Amer. Soc. Hort. Science, Alexandria, 107:248-251.

Healy W. E. et Wilkins H. F. (1982b): Responses of *Alstroemeria* 'Regina' to temperature treatments prior to flower-inducing temperatures. - Scientia Hort., Amsterdam, 17:383-390.

Healy W. E. et Wilkins H. F. (1986): *Alstroemeria* culture. - Herbertia, Orlando, 42: 16-20.

Healy W. E., Wilkins H. F. et Celusta M. (1982): Role of light quality, photoperiod, and high intensity supplemental lightning on flowering of *Alstroemeria* 'Regina'. - J. Amer. Soc. Hort. Science, Alexandria, 107:1046-1049.

Hildebrand-Vogel R., Godoy R. et Vogel A. (1990): Subantarctic-Andean *Nothofagus pumilio* forests. - Vegetatio, Dordrecht, 89:55-68.

Jaksic F. M. et Montenegro G. (1979): Resource allocation of Chilean herbs in response to climate and microclimatic factors. - Oecologia, Berlin, 40:81-89.

Lee T. D. (1988): Patterns of fruit and seed production. - In: Lovett Doust J. et Lovett Doust L. [red.], Plant reproductive ecology, patterns and strategies, p. 179-202, Oxford University Press, New York.

Lloyd D. G. (1980): Sexual strategies in plants. I. An hypothesis of serial adjustment of maternal investment during one reproductive session. - New Phytol., London, 86:69-79.

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

Lovett Doust L. (1987): Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). III. Responses to light and nutrient supply. - Ibid. 75:555-568.

Mehrhoff L. A. (1989): Reproductive vigor and environmental factors in populations of an endangered North American orchid, *Isotria medeoloides* (Pursh) Rafinesque. - Biol. Conserv. 47:281-296.

Morisita M. (1959): Measuring the dispersion pattern of individuals and analysis of the distribution patterns. - Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.), Fukuoka, 2:215-235.

Ojala A. (1985): Variation of *Angelica archangelica* subsp. *archangelica* (*Apiaceae*) in northern Fennoscandia. 2. Phenological life strategy and reproductive output. - Ann. Bot. Fenn., Helsinki, 22:183-194.

Puntieri J. G. (1991): Vegetation response on a forest slope cleared for a ski-run with special reference to the herb *Alstroemeria aurea* Graham (*Alstroemeriaceae*), Argentina. - Biol. Conserv. 56:207-221.

Puntieri J. G. et Gómez I. A. (1988): Análisis del crecimiento vegetativo del amancay (*Alstroemeria aurantiaca* D. Don) en dos poblaciones naturales. - Rev. Chil. Hist. Nat., Valparaiso, 61:177-186.

Rothkugel M. (1916): Los bosques Patagónicos. - Buenos Aires.

Schmid B. et Bazzaz F. A. (1987): Clonal integration and population structure in perennials: effects of severing rhizome connections. - Ecology, [New York], 68:2016-2022.

Shao S. P. (1970): Estadística para economistas y administradores de empresas. - México.

Slade A. J. et Hutchings M. J. (1987a): The effects of light intensity on foraging in the clonal herb *Glechoma hederacea*. - J. Ecol., Oxford, 75:639-650.

Slade A. J. et Hutchings M. J. (1987b): Clonal integration and plasticity in foraging behaviour in *Glechoma hederacea*. - Ibid. 75:1023-1036.

Solomon B. P. (1987): The role of male flowers in *Solanum carolinense*: pollen donors or pollinator attractors? - Evol. Trends Plants 1:89-93.

Stephenson A. G. (1980): Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (*Bignoniaceae*). - Ecology, [New York], 61:57-64.

Stephenson A. G. (1981): Flower and fruit abortion: proximate causes and ultimate functions. - Ann. Rev. Ecol. Syst., Palo Alto, 12:257-279.

Sutherland S. (1986a): Floral sex ratios, fruit-set, and resource allocation in plants. - Ecology, [New York], 67:991-1001.

Sutherland S. (1986b): Patterns of fruit-set: what controls fruit-flower ratios in plants? - Evolution, Lancaster, 40:117-128.

Turkington R. et Aarssen L. W. (1985): Local-scale differentiation as a result of competitive interactions. - In: Dirzo R. et Sarukhán J. [red.], Perspectives on plant population ecology, p. 107-127, Sinauer Publ., Sunderland.

Waithaka K. et Chepkairor M. J. (1988): Outdoor growth and flowering patterns of *Alstroemeria* in Kenia. - East Africa Agr. Forest. J., Nairobi, 53: 213-220.

Received 6 August 1992
Accepted 14 September 1992