

# Genetic divergence among natural populations of *Alstroemeria aurea* D. Don: A dominant clonal herb of the understory in subalpine *Nothofagus* forests

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(Received October 2, 2002; Accepted May 27, 2003)

**Abstract.** *Alstroemeria aurea* is a perennial herb with clonal rhizomatous growth, insect pollination, and ballistic seed dispersal that inhabits a range of different environments in the southern Andes. We evaluated the hypothesis that differential selective pressures act together with restricted among-population gene flow result in genetically divergent populations of *A. aurea*. Study sites were located within Nahuel Huapi National Park (41°8'S, 71°19'W) at two mountain ranges and two different elevations. These were Chall Huaco Valley, a pristine site, with populations at 1,250 and 1,100 m, respectively, and Cerro Otto, a disturbed site, with populations at 1,250 and 950 m, respectively. Seeds at each of the four populations were harvested from 20, 1 × 1 m plots. These seeds were counted, weighed, and germinated after a cold and humid stratification for 4 months. Within- and between-mountain ranges differences in seed traits were evaluated by ANOVA. We genetically characterized 30 plants of each population by allozyme electrophoresis and estimated levels of genetic variation and divergence. Seed traits showed different responses to elevation and site conditions. Total number of seeds was greater at low-elevation populations even though they had a higher number of undeveloped seeds. Reduced seed yield at high-elevation populations may result from a short growing season at higher altitudes. Additionally, seed weight, germination rates, and early vegetative spread were significantly greater at Otto, which may suggest a selective strategy to colonize disturbed sites under favorable physical conditions. These between-site differences were supported by allozyme data. High genetic divergence, and thus low gene flow, was estimated among Otto and Chall Huaco whereas within each mountain range among-population divergence depended upon site characteristics. Higher gene flow rates were found in the disturbed site Otto. Our results indicate that restricted pollen and seed dispersal, together with selective forces acting in different habitats, may produce genetic differentiation in populations of *A. aurea*.

**Keywords:** Alstroemeriaceae; Allozyme electrophoresis; Gene flow; Genetic structure; Germination; Patagonia; Seeds.

## Introduction

The ability of a plant species to occupy different environments could be the result of genetic adaptation, environmentally induced phenotypic plasticity, or a combination of these two processes (Jain, 1976). The relative importance of environment and genotype varies in the expression of a character. For example, differences in plant structure, leaf shape, and flowering time are often due to environmental factors while differences in pathogen resistance, flower architecture, and color are largely the result of genetic factors (Levin, 1984). Despite environmental influences, the genetic makeup of populations will directly affect their phenotypic characteristics such as the amount and kind of phenotypic variation, plant function including its interaction with the environment, and ecological tolerances of individuals together with their variation in time and space (Levin, 1984).

The amount and nature of genetic variation within and among populations is strongly affected by the mating system (Hamrick and Godt, 1990) and by the spatial relationship between plants and their parents (Hamrick and Nason, 1996). Populations where mating and seed dispersal occur over substantial spatial distances will have very different genetic properties as well as distinct ecological strategies from those in which these processes are restricted in space. Although random mating is a common assumption in many ecological and evolutionary models, it is unlikely to occur in plants, particularly when insect pollinators have restricted foraging behavior, such as bees tending to move from a plant to its near neighbors (Free, 1970; Levin and Kerster, 1974). In addition, for species with restricted seed dispersal, most progeny are established near their parents (Levin, 1984; Sobrevila, 1988; Redmond et al., 1989). Thus, the more restricted the dispersal of seeds and pollen, the stronger becomes the inverse relationship between distance and genetic kinship (Waser and Price, 1991; Souto et al., 2002). Spatial patterns of genetic variation for morphological, physiological, or phenological traits are the result not only of localized pollen and seed dispersal but also of different selection

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regimes under variable environments (Bazzaz, 1996). The objective of the present study was to analyze the degree of among-population genetic divergence in *Alstroemeria aurea*, a clonal species with restricted pollen movement and seed dispersal that inhabits different habitat types in northwestern Patagonia.

## Material and Methods

### The Species

*Alstroemeria aurea*, D. Don (Alstroemeriaceae) is a perennial herb that is geographically distributed in Argentina and Chile from 36° to 44° S latitude (Sanso, 1996). Outside its natural range, *Alstroemeria aurea* is used in breeding programs for cut flowers and pot plants. This species inhabits different plant communities ranging from woodlands, where mean annual precipitation of mesic *Nothofagus* forests can exceed 4,000 mm, to the dry steppe with only c. 150 mm (Dimitri, 1972). It was suggested that the ability of *A. aurea* to occupy dissimilar habitats was environmentally induced, allowing different phenotypes to colonize areas ranging from pristine and successional advanced to those altered by human and natural disturbances (Puntieri, 1991). This plasticity was related to its capacity to translocate available resources to different plant parts and, in particular, to its below ground storage organs, allowing the species to persist and establish itself as soon as environmental conditions are favorable (Puntieri, 1991).

In Northern Patagonia, Argentina, populations of *A. aurea* reach maximum size in high altitude forests of *Nothofagus pumilio* (southern beech), the dominant and, sometimes, nearly exclusive species of the understory. In these forests, *Alstroemeria aurea* is distributed between 750 and 1,250 m. Along this elevation gradient, different environmental variables—temperature, light intensity, wind exposure, and the amount and persistence of snow cover (Crawley, 1991)—are expected to affect the length of the growing season and, consequently, establishment and growth of *A. aurea*.

*Alstroemeria aurea* is a self-compatible herbaceous plant that reproduces vegetatively by clonal rhizomatous growth and sexually by seeds. Clone identification in the field is often difficult due to the continuous establishment of new individuals via seeds in patches already established (Puntieri, 1991). Using isozyme markers, it was estimated that only 17% of the ramets separated by 1 m belong to the same clone, suggesting a high degree of interdigitation among different genets (Souto et al., 2002). The main pollinators are bumblebees, such as the native *Bombus dahlbomii* (Apidae) and the exotic species *B. ruderatus*. Secondary in importance are the bee *Apis mellifera* (Apidae) and a few other flies of the genus *Tricophthalma* sp. (Nemestrinidae) (Aizen, 1997). Average flight distances between consecutive flower visits of any of these pollinators do not exceed 1 m (Souto, 1999). Flowers that are successfully pollinated mature into capsules with explosive seed dehiscence (Aizen and Basilio, 1995).

In this study we tested the hypothesis that populations of *A. aurea* have a localized genetic structure and significant among-population genetic divergence. These would be the result of different evolutionary processes, such as restricted pollen movement, local seed dispersal, and the ability to propagate vegetatively, together with distinct selective regimes acting in different habitats. Seed characteristics were used as adaptive features to measure differential responses to elevation and site conditions. We used isozyme markers to estimate genetic divergence, useful as an indirect estimator of among-population gene flow.

### Study Sites

Fieldwork was carried out at two mountain ranges within Nahuel Huapi National Park where *A. aurea* is the dominant species of the understory beneath pure *N. pumilio* forests. These are Chall Huaco Valley, a pristine site, and Cerro Otto, a disturbed site, located at 41°15'S / 71°18'W and 41°08'S / 71°21'W latitude/longitude, respectively. In each mountain range, two populations were chosen at different elevations: Chall Huaco high and low (CH and CL) located at 1,250 and 1,100 m, respectively, and Otto high and low (OH and OL) at 1,250 and 950 m, respectively.

### Seed Characteristics

At each population all mature fruits were harvested from each of 20 randomly selected plots (1 × 1 m). Fruits were stored under dark and dry conditions in labeled paper bags until their natural dehiscence. Seeds were then separated from their capsules and for each plot, we quantified the total number of seeds and the number of undeveloped seeds, those which were empty, poorly developed, and/or insect-attacked. Seeds were weighted to ± 0.1 mg in groups of 5 with 10 replicates per plot (N = 1000 seeds/population). To break dormancy, seeds were cold stratified at 4°C using a bed of humid cotton inside plastic bags following Premoli et al. (2000) for 4 months. They were germinated using soil collected from naturally occurring populations of *A. aurea*, assuring that no seeds of this species were present in the soil at the time of sowing. Germination capacity was evaluated at weekly intervals by quantifying the number of emerging shoots over a 150-day period. After 200 days from the initiation of the germination experiment, given that the number of sprouts exceeded the initial number of seeds, new emerging shoots were scored as the number of ramets, including both new emergence as well as possible vegetative spread at the seedling stage.

Seed and seedling characteristics of each plot (dependent variables) were analyzed in relation to elevation and mountain range (independent variables) by two-way ANOVA. Each of these independent variables had two levels: high and low elevation as well as disturbed and pristine, corresponding, respectively, to the Otto and Chall Huaco locations. Germination capacity and total number of ramets in different populations was analyzed by ANCOVA models using the number of pre-treated seeds as a covariate. For further comparisons of populations'

values, we statistically analyzed seed characteristics by the Tukey *post-hoc* test for multiple comparisons of means, adjusting probability levels by the Bonferroni test (Rice, 1989).

### Isozyme Analysis

Genetic characteristics of different populations were analyzed by horizontal isozyme electrophoresis. Fresh leaf material (approximately 1 g) was harvested from 30 randomly selected seedlings grown from seeds collected at each of the four study populations. We extracted enzymes by grinding the leaf material with the buffer of Mitton et al. (1979). Homogenates were stored at  $-80^{\circ}\text{C}$  until electrophoresis on 12% w/v starch gels. Seven enzymes coding for 14 putative genetic loci were resolved using two gel and buffer systems that were reliably scored in previous studies (Souto, 1999; Souto et al., 2002). These were: Isocitrate dehydrogenase (Idh), Malate dehydrogenase (Mdh-1, Mdh-2), Phosphoglucosomerase (Pgi-1, Pgi-2), and 6-Phosphoglucuronate dehydrogenase (6Pgd) on the Morpholine-citrate system (MC) of Ranker et al. (1989) and Malic enzyme (Me-1, Me-2), Menadione reductase (Mnr), and Shikimate dehydrogenase (Skdh) on the Tris-histidine system (HC) by King and Dancik (1983). Electrophoresis was carried out at  $4^{\circ}\text{C}$  with an ice bag on top of the gel until a bromophenol blue dye migrated approximately 10 cm from the origin towards the anode. Staining schedules for particular enzymes followed standard procedures (Soltis et al., 1983). Alleles were sequentially numbered, with the lowest number assigned to the most anodal allozyme.

Isozyme data were used to calculate the following parameters of genetic variability at the population level: mean number of alleles per locus ( $A$ ), the percentage of polymorphic loci ( $P$ ) using the 95% criterion, and the observed ( $H_o$ ) and expected heterozygosity ( $H_e$ ). Isozyme differences among populations were analyzed by Nei's genetic identity (1978), which represents the proportion of genes that are alike between and within populations. In order to graphically portray genetic similarities among all populations, average linkage clustering using the unweighted pair-group method (UPGMA) was performed for all populations using modified Rogers distance coefficient (Wright, 1978).

Genetic diversity was analyzed following Nei (1973) by the total diversity ( $H_T$ ), which can be partitioned within ( $H_S$ ), and the proportion of the total genetic diversity found

among populations ( $G_{ST}$ ). These parameters were estimated for polymorphic loci. The degree of among-population divergence was measured by Wright's  $F_{ST}$ , based on polymorphic loci using FSTAT v. 2.9.1. (Goudet, 2000). Means and confidence intervals (CI95%) for  $F_{ST}$  were computed by jackknifing and bootstrapping over polymorphic loci, respectively, following Weir and Cockerham (1984).  $F_{ST}$  was calculated among different mountain ranges and was compared with the value obtained for populations within each mountain range.

## Results

### Seed Characteristics

We found marked differences in seed characteristics among *A. aurea* natural populations studied. Within each mountain range, the total number of seeds produced per plot was significantly different for populations at different elevations. At both sites, high-elevation populations produced fewer seeds than low-elevation populations (Table 1). This pattern, consistent for Otto and Chall Huaco, resulted in non significant between-site differences (Table 2). Non significant effects, i.e. elevation, site or the interaction between them, were recorded for either the number of undeveloped seeds or seed weight. However, one-way ANOVA indicated that, within each mountain range, low-elevation populations had a greater number of undeveloped seeds, particularly at Otto (Table 1).

The Otto populations' seeds were significantly heavier than those at Chall Huaco (Table 1). In addition, significant site effects were recorded for the germination capacity measured after 150 d. as well as for the total growth measured as the number of ramets after 200 d. at each mountain range. Populations at Otto had significantly greater germination rates as well as a higher number of emerging seedlings and thus greater early vegetative spread than Chall Huaco populations (Tables 1 and 2). However, non significant differences with elevation were recorded for both variables within each mountain range (Table 1).

### Genetic Analysis

Isozyme analysis showed that 5 out of a total of 14 resolved loci were polymorphic in at least one population. Overall, the analyzed populations were similar to each

**Table 1.** Averages of recorded variables measured on populations of *A. aurea* at two sites, Otto (O) and Chall Huaco (C), and two elevations, high (H) and low (L) in NW Patagonia. Standard errors are in parenthesis. Within a row, different letters indicate significant differences (Tukey *post-hoc* test for multiple comparisons of means,  $P < 0.05$  after Bonferroni correction).

Variable	OL	OH	CL	CH
Number of seeds / plot	256.2 (21.6) a	177.1 (14.6) b	310.4 (44.6) a	144.2 (28.5) b
Number of undeveloped seeds	35.1 (6.2) a	14.4 (3.2) b	23.0 (12.4) b	15.2 (6.9) ab
Seed weight (mg)	203 (5.9) a	202 (5.8) a	199 (28.0) b	170 (21.0) b
Number of pretreated seeds	214.15 (22.8) ab	159.8 (12.7) a	282.9 (42.5) b	125.75 (26.2) a
Germination capacity, 150 d	57.4 (30.0) a	50.0 (33.2) ab	29.5 (25.6) b	34.3 (37.0) ab
Total number of ramets, 200 d	71.4 (12.3) a	83.8 (15.0) a	32.15 (8.6) b	29.6 (6.2) b

other in the levels of genetic variation they contained (Table 3). However, high-elevation populations showed a slightly greater mean number of alleles/locus (Otto population, OH) and higher polymorphism and heterozygosity (Chall Huaco population, CH). Genetic identities indicated that populations from the same location were more alike (Otto 0.999 and Chall Huaco 0.983) than were populations from different sites (average of all possible among-site comparisons 0.960; Table 4). This same pattern was obtained in the cluster analysis, where populations were grouped according to their location (Figure 1).

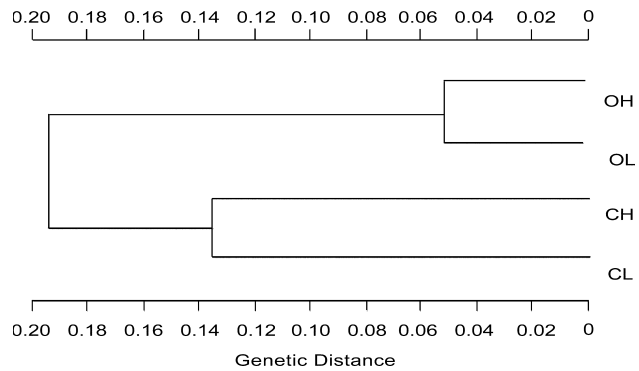
Elevated total genetic diversity was recorded in the studied populations, with  $H_T = 0.310$ , most of which was partitioned within populations ( $H_S = 0.265$  and  $G_{ST} = 14.4\%$ ). Divergence among mountain ranges yielded an  $F_{ST}$  value of 0.288 (95% confidence interval estimated by jackknifing 0.006-0.510). These values correspond to  $Nm = 1 - F_{ST} / 4 F_{ST}$  of about 0.6 migrants per generation, which means limited gene flow rates and thus elevated genetic divergence (Slatkin, 1985) among different mountain ranges. However,

**Table 2.** Results of two-way analyses of variance for seed characteristics showing significant differences in *A. aurea*. Number of pretreated seeds was used as a covariate for germination capacity and total number of ramets. Site (wet and dry corresponding to Otto and Chall Huaco mountains, respectively) and Elevation (high and low) were used as fixed effects. Significant effects are indicated in bold.

Trait	Effect	df	F	P
Number of seeds/plot	Site	1	0.1	>0.01
	Elevation	1	17.2	<b>&lt;0.01</b>
	S × E	1	2.2	>0.01
	Error	76		
Germination capacity, 150 d	Site	1	9.5	<b>&lt;0.01</b>
	Elevation	1	0.03	>0.01
	S × E	1	0.7	>0.01
	Error	76		
Total number of ramets, 200 d	Site	1	15.5	<b>&lt;0.01</b>
	Elevation	1	0.01	>0.01
	S × E	1	0.2	>0.01
	Error	76		

**Table 3.** Genetic variability at 14 isozyme loci in four populations of *A. aurea* at two sites, Otto (O) and Chall Huaco (C), and two elevations, high (H) and low (L). A = Mean number of alleles / locus; P = % polymorphic loci (most common allele does not exceed 0.95);  $H_O$  and  $H_E$  = Mean observed and expected (under Hardy-Weinberg equilibrium) heterozygosity, respectively. Standard error in parenthesis.

Population	A	P	$H_O$	$H_E$
OH	1.3 (0.1)	21.4	0.079 (0.04)	0.097 (0.05)
OL	1.2 (0.1)	21.4	0.081 (0.04)	0.081 (0.04)
CH	1.4 (0.2)	35.7	0.107 (0.05)	0.109 (0.05)
CL	1.4 (0.2)	21.4	0.077 (0.41)	0.083 (0.05)



**Figure 1.** Cluster analysis of the genetic relationships among populations of *A. aurea* using unweighted pair group method UPGMA based on modified Rogers distance coefficient (Wright, 1978). OH= Otto high; OL= Otto low; CH= Chall Huaco high; CL= Chall Huaco low populations.

**Table 4.** Nei's genetic identity between populations of *A. aurea* at two sites, Otto (O) and Chall Huaco (C), and two elevations, high (H) and low (L).

Population	OH	OL	CH	CL
OH	—			
OL	0.999	—		
CH	0.961	0.943	—	
CL	0.975	0.963	0.983	—

greater gene flow rates were indirectly estimated by  $F_{ST}$  values within each mountain range. For Chall Huaco  $F_{ST}$  resulted 0.154 (CI95% = -0.012-0.223), corresponding to a gene flow rate of 1.4 migrants per generation, while  $F_{ST}$  of Otto populations was 0.011 (CI95% = -0.009-0.025), equivalent to 22.5 migrants per generation.

## Discussion

Isozyme and seed characteristics analyzed in this study indicate that among-population divergence exists in natural populations of *A. aurea* and occurs at two levels, site (i.e. mountain ranges) and elevation. Variations in seed weight, germination capacity, and early growth seem related to between-site differences. The studied sites represent different habitats for *A. aurea*. Otto can be characterized as a disturbed site, where individuals of *A. aurea* are weak, sparsely distributed, and share the understory with other species such as the bamboo *Chusquea culeou*. Populations at Chall Huaco, in contrast, can be described as successional advanced where *A. aurea* grows vigorously in dense patches and is the dominant species of the understory. Under this scenario, greater seed weight and high germination capacity, as well as early growth may be beneficial in a competitive environment such as Otto, allowing *A. aurea* to rapidly occupy open habitats as soon as environmental conditions are favorable. Therefore, different selection regimes acting at each site may result in distinct establishment strategies. These differences appear to be genetic, a fact also suggested by

the isozyme analysis that indicated greater similarity between populations from a given site (Figure 1).

Restricted seedling establishment is considered a conspicuous feature of clonal plant population dynamics (Eriksson, 1992). A literature review indicated that 60% of the 68 species for which demographic information was available do not have seed recruitment into established populations (Eriksson, 1989). In *Trifolium repens* module recruitment was shown to far exceed seedling establishment, but at least some new genets are added on a yearly basis (Barret and Silander, 1992). Seedling recruitment may increase particularly at disturbed sites (Cahn and Harper, 1976; Turkington et al., 1979; Ennos, 1981) although establishment rates are higher in undisturbed sites (Barret and Silander, 1992). This suggests that physical disturbances may open sites for seedling recruitment, but these sites are not necessarily favorable for establishment. More studies are needed in *A. aurea* to determine the adaptive features of long-term seedling persistence in different sites.

It has been suggested that seed traits are under maternal control, which in turn is affected by differential environmental conditions. This is because maternal plants growing under benign environments are expected to produce large seeds together with increased germination speed and seedling size. However, this may not be always the case, particularly when maternal ability is not correlated with seed characteristics (Roach and Wulff, 1987). Our results show that, especially at Otto, where such a positive correlation between maternal and seed size traits is not evident, maternal effects would be small. Therefore, seed traits in *A. aurea* may be more affected by the individual genotype and the environment in which it grows, as previously suggested for other species (Weiner et al., 1997).

In addition to between-site differences, within-site differences were also recorded among populations of *A. aurea* separated by short-distances, i.e. hundreds of meters at different elevations. High-elevation populations had smaller seed yields than low-elevation populations. Aizen (2001), for the same Chall Huaco populations of *A. aurea* studied here, found a decline of ~30-40% in seed output between early (e.g. low-elevation population) and late flowers (e.g. high-elevation population). He ascribes this pattern to increasing resource limitation or the short seed-filling period associated with late flowering plants (Schemske et al., 1978; Ågren and Willson, 1992; Bertin and Sholes, 1993; Kudo, 1997). Such seasonal decreases in seed set seem to be quite common among bee-pollinated spring and summer flowering plants (e.g. Schemske et al., 1978; Thomson and Barrett, 1981; Murcia, 1990; Ågren and Willson, 1992; Bertin and Sholes, 1993; Kudo, 1997).

Altitudinal gradients provide differential long-term selection regimes that may lead to changes in life history characteristics (e.g., Clausen et al., 1940; Neuffer and Hurka, 1986; Galen et al., 1991; Mayer and Poljakoff-Mayber, 1989). A few studies have documented intraspecific patterns of altitudinal variation in the southern Andes. In *Nothofagus pumilio*, the dominant overstorey species with windborne

pollen and seeds studied at Chall Huaco, an altitudinal variation for several adaptive features including isozymes was reported (Premoli, 2003; in press). In *Nothofagus antarctica*, a species with marked variation in growth forms associated with different environments, reduced seed weight and decreased germination capacity was measured as elevation increased in northwestern Patagonia (Premoli, 1991). Moreover, isozyme evidence suggests that differences in the growth habit of *N. antarctica* may be genetically determined (Vidal Russell, 2000). Therefore, variable physical conditions probably exert differential selective pressures which, in combination with differences in flowering phenology, reproductively isolate nearby populations of different plant species along elevation gradients.

The heterogeneity recorded in seed traits throughout *A. aurea* populations at different elevations and mountain ranges was also reflected in their low levels of gene flow measured by  $F_{ST}$ . These values and the total genetic diversity were within the range of those obtained for other herbaceous species, particularly those with gravity dispersion of seeds, insect pollination, and sexual and asexual reproduction (Hamrick and Godt, 1990). However, most of the total genetic diversity of *A. aurea* was distributed within sites (75%), suggesting considerable gene exchange between populations within a given mountain range. In particular, Otto populations seem to be maintaining higher gene flow rates than Chall Huaco, as indirectly estimated by  $F_{ST}$  and  $N_m$ . This result is probably related to patch density and pollinator activities. In Chall Huaco, *A. aurea* occurs in large patches, resulting in pollinator foraging that could be restricted to dense flowering patches. In contrast, small and fragmented populations, such as those at Otto, consist of patches with low floral density, and thus flight distances tend to be longer because they do not retain pollinators to the degree larger populations do. Thus, pollinator behavior may result in elevated among-patch gene flow that, in combination with the significantly increased recruitment of seeds at Otto, would explain the greater gene flow measured here.

Understanding the spatial organization of genetic diversity within and among plant populations is of critical importance for the development of strategies designed to preserve genetic variation (Hamrick, 1983; Brown and Briggs, 1991; Hamrick et al., 1991). It has been shown that species with limited gene flow, i.e. with restricted seed and/or pollen movement, have considerably more among-population variation for total amount of genetic diversity (Schoen and Brown, 1991). Thus, conservation strategies for such species as *A. aurea* should be developed with the dispersal ability of the species in mind.

**Acknowledgements.** We thank M. Aizen and one anonymous reviewer for helpful comments on early versions of this manuscript and E. Raffaele who provided statistical assistance. This work was supported by Grant No. B-036 from Centro Regional Universitario Bariloche, Universidad Nacional del Comahue and by a postdoctoral fellowship to A.P. from the National Research Council (CONICET) of Argentina.

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## *Alstroemeria aurea* D. Don 在自然族群中基因的分歧：在次高山下層的山毛櫸森林中的一種優勢且無性繁殖草本植物

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*Alstroemeria aurea* 是一種多年生草本植物有著以地下莖的生長，昆蟲授粉和彈出的種子散布進行繁殖，在南安地斯山脈中可以棲息在不同環境之下。我們假設不同的選擇壓力共同作用限制了 *A. aurea* 族群間的基因交流，以致於導致基因明顯分歧的族群；並對此假設之正確性加以評估。研究的地點位於納威瓦皮國家公園 (41°8'S, 71°19'W) 在兩個山區和兩種不同高度：即 Chall Huaco 谷地，為一原始地方，海拔 1,250 和 1,100 米分別有著族群分佈，和 Cerro Otto 為一已開發的地方，1,250 和 950 米處分別地有著族群分佈。在這四個族群中從 20 個，1×1 米小塊地收集種子。這些種子要算出總數，重量和經過冷和潮濕的四個月的發芽率。在同一山區和不同山區的種子性狀差異，由 ANOVA 來評估。我們使用 30 株的植株經由異型酵素電泳，找到每種族群的基因特性和估算其基因的變化和不同。種子性狀可以顯示不同高度的反應和位置的狀況。種子的總數是以低海拔的族群較多即使含有較高數目的未發育的種子。在較高海拔的族群種子產量的減少可能原因的是在較高的海拔有較短的生長季節。此外，在 Otto 地區種子的重量，發芽率和早期營養生長之擴散顯著地較高，可能的原因為其選擇性的策略到已開發的地方且有物理情況的幫助下去繁殖。這些不同採樣點之間的差異有異型酵素的資料支持。在 Otto 和 Chall Huaco 之間，因高度基因不同和低基因流動已被估計出；然而在每一座山區族群的不同，視地方不同的特性而定。在 Otto 這已開發的地方有較高基因流動。我們的結果顯示，有限的花粉和種子擴散加上不同棲息地之選擇壓力，也許會在 *A. aurea* 的族群產生基因的差別。

**關鍵詞：**阿爾氏科；異型酵素電泳；基因流動；基因結構；發芽；巴塔哥尼亞；種子。