

Negative photoblastism in the invasive specie *Eschscholzia californica* Cham. (Papaveraceae): Patterns of altitudinal variation in native and invasive range

Fotoblastismo negativo en la especie invasora *Eschscholzia californica* Cham. (Papaveraceae): Patrones de variación altitudinal en el rango nativo e introducido

MARÍA L.C. CASTILLO^{1,2*}, RAMIRO O. BUSTAMANTE^{1,2}, FRANCISCO T. PEÑA-GÓMEZ^{1,2}, VÍCTOR L. GUTIÉRREZ^{1,2}, CLAUDIO A. REYES¹, ALICIA ARREDONDO-NÚÑEZ^{1,2} & MARILYN MAREY¹

¹Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile.

²Instituto de Ecología y Biodiversidad, Universidad de Chile, Casilla 653, Santiago, Chile.
mloretocastillo@uchile.cl*

ABSTRACT

Negative photoblastism is defined as the inhibitory effect of light on seed germination. This effect can be modulated by abiotic variables, such as temperature, light condition and water potential. This conditions change notoriously at higher altitudes, could promote differentiations in the photoblastic response among populations. Also, this physiological attribute poses an interesting conflict for plant regeneration, because prevents seed germination on the soil surface, however, it can also to reduce the mortality of seeds germinants in unsuitable conditions and consequently, seedling mortality. *Eschscholzia californica* is one of the few species with negative photoblastism and it is invasive in Chile, growing primarily in open and disturbed places. Some invasive species have the potential to adapt their morphological and ecophysiological characteristics faced to new environmental conditions. In this study, we examined variation in negative photoblastism between populations from central Chile (invasive) and California (native) located at the extremes of their altitudinal distribution. We used common garden experiments where seeds from different origins were germinated under controlled lab condition in Chile. If negative photoblastism is conserved, we would see similar responses among seeds original from this climatic analogues regions. Also, we evaluated whether seed burial increases seed germination of this species as a mechanism for escaping the intense luminosity at the soil surface, by planting seeds at different soil depths. For this experiment, we expected an increase of germination at higher soil depth. The results indicate no differences in negative photoblastism between Chilean and Californian populations. A significant variation across altitudinal range in California suggests the existence of genetic differentiation in the native region, however, the absence of differences across the altitudinal range in Chile suggests trait conservatism at local scale. Seed germination was zero at the soil surface and increased when seeds were experimentally buried, suggesting that negative photoblastism is inhibited. Three possible explanations are given to explain the pattern of establishment of *E. californica* despite having negative photoblastism. This is a fairly specialist trait, related with Mediterranean climates and does not explain by itself the invasiveness described for this specie. In any case, is clear that more studies are necessary to disentangle the adaptive value of this physiological trait.

KEYWORDS: Central Chile, common garden, California poppies, seed burial, seed germination.

RESUMEN

El fotoblastismo negativo es definido como el efecto inhibitorio de la luz sobre la germinación de las semillas. Este efecto puede ser modulado por variables abióticas, tales como temperatura, condición lumínica y potencial hídrico. Estas condiciones cambian notoriamente a mayores altitudes, pudiendo promover diferenciación en la respuesta fotoblástica entre poblaciones. Adicionalmente, este atributo fisiológico presenta un interesante conflicto para la regeneración de la planta, porque previene la germinación de las semillas sobre el suelo, sin embargo también puede reducir la mortalidad de semillas germinantes en condiciones desfavorables y consecuentemente, la mortalidad de plántulas. *Eschscholzia californica* es una de las pocas especies con fotoblastismo negativo y es invasora en Chile, creciendo primariamente en sitios abiertos e intervenidos. Algunas especies invasoras tienen el potencial de adaptar sus características morfológicas y fisiológicas enfrentadas a nuevas condiciones ambientales. En este estudio, examinamos la existencia de variación en el fotoblastismo negativo entre poblaciones de Chile central (invasivas) y California (nativas) localizadas en los extremos de su distribución altitudinal. Utilizamos experimentos de jardín común donde semillas de distintos orígenes fueron germinadas

bajo condiciones controladas de laboratorio en Chile. Si el fotoblastismo negativo es conservado, observaríamos similares respuestas entre semillas originarias de estas regiones climáticas análogas. También evaluamos si el entierro de las semillas incrementa su germinación, como un mecanismo para escapar de la intensidad luminosa de la superficie, plantando semillas a diferentes profundidades del suelo. Los resultados indican que no hay diferencias en el fotoblastismo negativo entre las poblaciones de Chile y California. Una significativa variación a través del rango altitudinal de California sugiere la existencia de diferenciación genética en la región nativa, sin embargo, la ausencia de diferencias a través del rango altitudinal de Chile sugiere conservatismo del rasgo a escala local. La germinación de semillas fue cero en la superficie del suelo y se incrementó cuando las semillas fueron experimentalmente enterradas, sugiriendo que el fotoblastismo negativo es inhibido. Tres posibles explicaciones son entregadas para explicar el patrón de establecimiento de *E. californica* a pesar de poseer fotoblastismo negativo. Este es un rasgo bastante especialista, relacionado con climas mediterráneos y no explica por sí solo la invasibilidad descrita para esta especie. De todas formas, es claro que más estudios son necesarios para dilucidar el valor adaptativo de este atributo fisiológico.

PALABRAS CLAVE: Chile central, jardín común, amapola de California, entierro de semillas, germinación de semillas.

INTRODUCTION

Negative photoblastism is defined as the inhibitory effect of light on seed germination (Vazquez-Yanes & Orozco-Segovia 1993). This effect can be modulated by the type of phytochrome of seeds (in this case the phyA-type which control germination through high radiance responses; Takaki 2001), thus determining the place and moment in which germination is feasible (Casal & Sánchez 1998, Hennig *et al.* 2002); other abiotic variables, such as temperature, light condition and water potential can be important as well (see Takaki 2001 for more details). For instance, in altitudinal gradients abiotic conditions change notoriously, in terms of light radiation, temperature variability and water supply at higher altitudes (Körner 2003), thus imposing different selective pressures that could promote changes in the photoblastic responses of plants.

Negative photoblastism is relatively infrequent in vascular plants (Baskin & Baskin 1998) and poses an interesting conflict for plant regeneration. On one side, it could prevent seed germination on soil surface (and open sites). However, on the other hand, this trait could be viewed as an adaptation to reduce the mortality of germinated seed and consequently, seedling mortality (Thanos *et al.* 1991, 1994). One way to overcome this conflict is the rapid seed burial, thus allowing seed germination under darkness and more favorable conditions (Thanos *et al.* 1991, Fenner & Thompson 2005).

Negative photoblastism has been experimentally documented for *Eschscholzia californica* Cham. (Papaveraceae) (Goldthwaite *et al.* 1971). This species is an herbaceous plant native to California and a successful invader in Mediterranean ecosystems (Cook 1962, Leger & Rice 2003). Its introduction to Chile occurred between mid-1800s and the early 1900s; currently this species has a wide latitudinal (30° S - 38° S) as well as altitudinal distribution (from 0 to 2200 m) (Arroyo *et al.* 2000), growing primarily in open and disturbed environments (Cook 1962, Frias *et al.*

1975). Plant invasion into novel environments may impose new selective pressures (Maron *et al.* 2004) and some species have the potential to adapt their morphological and ecophysiological characteristics faced to new environmental conditions (Caño *et al.* 2008). Comparative ecology studies assessing phenotypic variation between native and invaded range constitute a proper approach to examine adaptive differences (Leger & Rice 2003, Hierro *et al.* 2005).

Comparative studies for invasive plants have registered significant differentiation in physiologic traits between native and invasive ranges (Siemann & Rogers 2001, Quing *et al.* 2011). In the case of *E. californica*, common garden experiments have documented that individuals of this species differ significantly in morphological/functional traits between native and invasive population (Leger & Rice 2003).

In this study, we examine negative photoblastism variation among *E. californica* populations located at different altitudes in Chile and California. For this we used common garden experiment. If negative photoblastism is conserved, we would see similar responses among seeds original from these climatic analogues regions. We also experimentally evaluated whether seed burial can modulate seed germination, by planting seeds at different soil depths. For this experiment, we expected an increase of germination at higher soil depth.

METHODS

California and central Chile share a remarkable climatic similarity (Mooney 1977, Di Castri 1991, Sax 2002, Jiménez *et al.* 2007); with rainfall concentrated during winter, followed by dry and warm summers. Also both regions exhibit similar latitudinal climatic gradients, with an increase in rainfall and a decrease in temperature toward the polar latitudes (Mooney 1977, Di Castri 1991). Furthermore, coastal and interior mountain ranges and central valleys are remarkably comparable between Chile

and California (Mooney 1977).

In central Chile, seeds were collected from reproductive individuals in Algarrobo (33°23'S, 71°41'W; sea level), Lagunillas (33°38'S, 70°20'W; 1200 m; 33°36'S, 70°17'W; 2200 m) and Farellones (33°20'S, 70°21'W; 1200 m; 33°21'S, 70°18'W; 2200 m). In California, seeds were collected at Punta Dume (34°00'N, 118°48'W; 31 m) and Big Bear (34°16'N, 116°48'W; 2050 m). For each population, we collected seeds from capsules of a variable number of plants ranging from 24 to 45 individuals. Seeds were separated by origin and altitudinal range and were stored in paper bags at constant temperature (20 ± 5 °C) and humidity (60%).

In both regions, populations were located at the extremes of their altitudinal distribution. The Algarrobo (Chile) and Punta Dume (California) populations were approximately at sea level and the Farellones (Chile) and Big Bear (California) populations were approximately at 2000 m. We conducted a common garden experiment. Fifteen seeds were placed per Petri dish (n = 30 dishes per treatment), exposed to two light treatments: 24 h light vs. 24 h darkness. Light was provided by a fluorescent tube (400-700 nm) with an intensity of 28.20 μmol m⁻² s⁻¹. For the dark treatment, dishes were covered permanently with aluminum foil. Temperature was maintained in all cases at 15 ± 1 °C and water was provided *ad libitum*. The substrate for the seeds was vermiculite. Experiments were monitored every four days and concluded when no further additional germination was observed; a seed was considered germinated when the radicle was visible to sight. To compare germination between treatments, we conducted a Mann-Whitney test, since data did not meet normality and homogeneity of variance assumptions.

The evaluations of photoblastic responses require to compare seed germination between light and dark conditions. In order to do that, we calculated a Photoblastic Index (PI), defined as

$$PI = (G_D - G_L) / (G_D + G_L)$$

where G_D is the percentage of germination in darkness and G_L is the percentage of germination under light. This index ranges from 1 (negative photoblastism) to -1 (positive photoblastism); PI = 0 indicates that germination is not dependent of light.

We compared PI between regions (Chile and California) at different altitudes. Since the values of PI were normally distributed (K-S, d=0.07), we performed a nested ANOVA (altitude nested within regions). When significant differences were detected between treatments, we performed an *a posteriori* test to discern which pairs of treatments differed significantly.

To determine the effects of seed burial on germination,

we conducted a common-garden experiment, using seeds from two Chilean localities, Farellones and Lagunillas; and from two altitudes, 1200 and 2200 m. Seeds were planted in plastic pots filled with soil (50% dry sand and 50% organic litter). In each pot, we put 2 seeds at 4 depth categories: (i) 0 cm, (ii) 0.2-0.5 cm, (iii) 1-2 cm and (iv) 3-4 cm. For the 0 cm category we used 30 plastic pots and for the remaining depth categories we used 60 pots. The pots were watered every 2-3 days from November to December 2010. The duration of the experiment was one month, until no further seed germination was observed. We assessed seed germination in each pot, assigning 1 if one or both seeds germinated and 0 if neither did. To evaluate the effect of locality, altitude and depth (categorical factors) on the probability of seed germination we used a logistic regression analysis (with logit link and binomial distribution). In this analysis, we consider each pot as an independent replicate. All statistical analyses were performed with Statistica7 (StatSoft 2004).

RESULTS

For Chile, germination percentage was significantly higher under dark conditions (55.1% ± 2.5) than under light conditions (28.2% ± 2.5) (Mann-Whitney, P < 0.001). For California, germination percentage was significantly higher under dark conditions (37.9% ± 3.4) than under light conditions (27.8% ± 3.5) (Mann-Whitney U, P < 0.05). Overall, seed germination was significantly higher in the dark relative to light treatment. Only in California, in populations located at lower altitude, we found no significant differences between treatments (Table I).

No significant differences in PI were detected between central Chile and California (F_{1, 110} = 0.18, P = 0.67). The variance was significantly higher for California than for central Chile (California variance = 0.31; central Chile variance = 0.09; Bartlett test, P < 0.001). We also detected differences between altitudes F_{1, 110} = 9.06, P < 0.01; Fig. 1), but this difference was significant only for California, being PI higher at higher altitude (Tukey, P < 0.001). In central Chile no significant differences were detected between altitudes (Tukey, P = 0.9).

Seed germination was significantly and positively influenced by soil depth (χ²₍₂₎ = 168.78, P < 0.001); locality (χ²₍₁₎ = 62.42, p < 0.001) but not for altitude (χ²₍₁₎ = 2.12, P = 0.15). A significant interaction was detected between locality and depth (χ²₍₂₎ = 41.91, P < 0.001) (Fig. 2), which indicated that the soil depth had a effect more positive on germination at Lagunillas than at Farellones (Fig. 2). In all treatments, no germination was observed at the soil surface (0 cm depth).

TABLE I. Seed germination (%) under two light treatments: constant darkness or constant light of *Eschscholzia californica* populations from different regions (Chile/California) and altitudes (sea level/2000 m). Mean \pm standard error. Values with * indicated not difference at 5% significance level (Mann-Whitney U test).

TABLA I. Germinación de semillas (%) bajo dos condiciones de luminosidad: oscuridad constante o luz constante de poblaciones de *Eschscholzia californica* desde diferentes regiones (Chile/California) y altitudes (Nivel del mar/2000 m). Media \pm error estandar. Valores con * no difieren a un nivel de significancia del 5% (Test de Mann-Withney U).

REGIONS	ALTITUDE (m)	TREATMENTS	SEED GERMINATION (%)
Chile	2000	Dark	61.6 \pm 6.2
		Light	30.2 \pm 5.8
	Sea level	Dark	48.7 \pm 7.4
		Light	26.2 \pm 8.0
California	2000	Dark	18.2 \pm 6.8
		Light	4.7 \pm 2.8
	Sea level	Dark	57.6 \pm 6.0*
		Light	50.9 \pm 6.4*

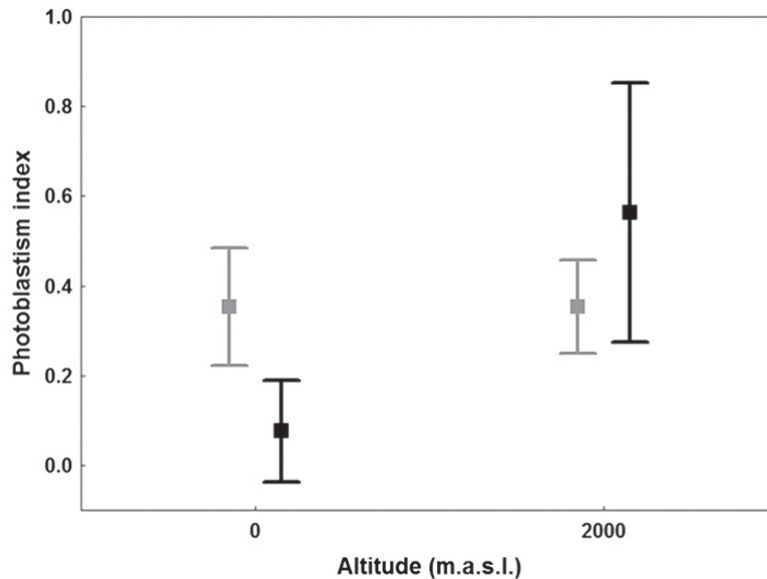


FIGURE 1. Photoblastism index estimated for populations of *Eschscholzia californica* of central Chile and California at different altitudes (California in black/central Chile in gray). Mean \pm 1.96 s.e.

FIGURA 1. Índice de fotoblastismo estimado para poblaciones de *Eschscholzia californica* de Chile central y California a diferentes altitudes (California en negro/Chile central en gris). Promedio \pm 1,96 e.e.

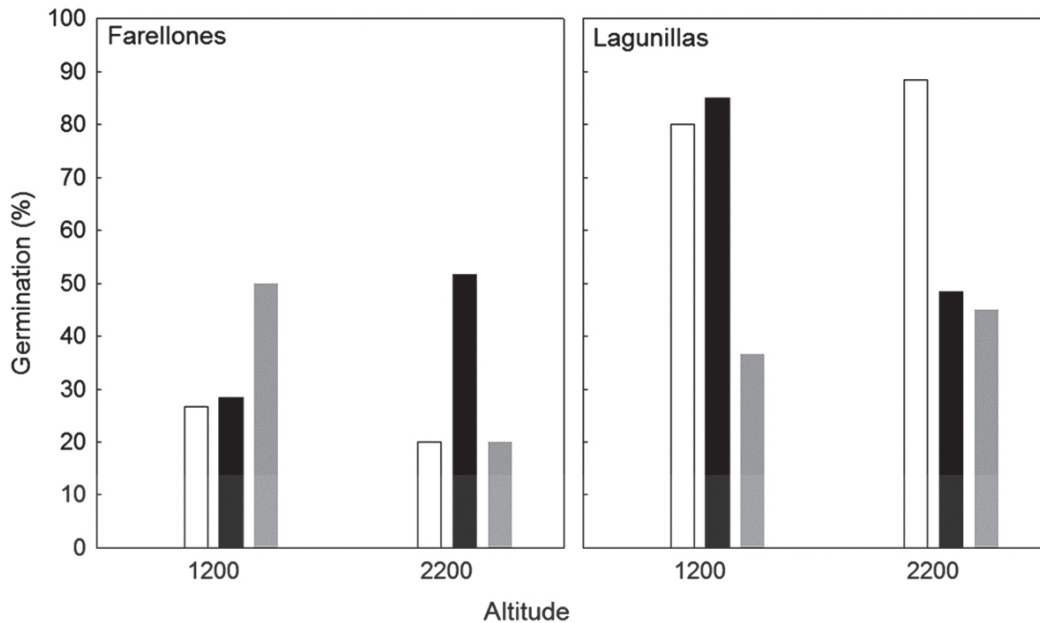


FIGURE 2. Percentage of seed germination of *E. californica* in Farellones and Lagunillas (Central Chile) at three different soil depth categories: 0.2-0.5 cm (white bars), 1-2 cm (black bars) and 3-4 cm (gray bars). At the soil surface (0 cm depth category) no germination was observed at all (results not shown in the figure).

FIGURA 2. Porcentaje de germinación de semillas de *E. californica* en Farellones y Lagunillas (Chile central) a tres diferentes categorías de profundidad de enterramiento: 0,2-0,5 cm (barras blancas), 1-2 cm (barras negras) and 3-4 cm (barras grises). En la superficie del suelo (categoría de profundidad 0 cm) no se observó germinación (resultados no se muestran en la figura).

DISCUSSION

Our result indicated a remarkable similarity in negative photoblastic response between central Chile and California seeds. The notable climatic/topographic similarities between central Chile and California are well known, a fact that suggests that this trait is conserved across population. Another interesting result was that in California the PI variance was significantly higher than in Central Chile. This result suggests that seeds from Chilean localities may constitute a subsample of the Californian seed pool.

In native populations, seeds from higher altitudes presented a greater negative photoblastism than seeds from lower altitude. Given that experiments were conducted under common garden conditions, this altitudinal difference between localities within the native range (California) suggests a genetic basis for the expression of this physiological attribute. Since we did not find differences between altitudes in Chile, we suggest a trait conservatism at local scale, which was not affected by the abiotic variations presented along altitudinal gradients. A causal explanation is that this attribute has an evolutionary inertia and the time from invasion was not enough for local adaptation at the new environment.

The experiments with buried seeds demonstrated that

germination is severely constrained at the soil surface (we observed no germination at all), a fact which is consistent with the negative photoblastism detected in our lab experiments and prove that seed buried could prevent the inhibitory effect of negative photoblastism.

Although results show notable variability between locality and altitude, it is clear that seeds need to be buried just a few cm from the soil surface in order to germinate. The germination variability detected across different soil depths suggests that there is no optimum depth for germination. These results are consistent with the fact that light rarely penetrates more than a few millimeters into the soil (Tester & Morris 1987, Mandoli *et al.* 1990). Even in the case of a clay-loam soil, less than 1% of the incident light penetrates more than 2.2 mm (Woolley & Stoller 1978). However, we cannot discard the possibility that temperature, which can that covariates with soil depth, could affect seed germination as well, a factor that can be relevant for seed germination in some species (Ghersa *et al.* 1992). The significant interaction detected between soil depth and locality of seed origin, indicates that the importance of seed burial for germination varies among localities (it is more important at Lagunillas). We do not have an explanation for these differences as these two localities share similar climatic and edaphic conditions (pers. observ.).

E. californica is commonly well established in open and disturbed sites (Cook 1962, Frias *et al.* 1975) and across Mediterranean ecosystems. How to explain its invasiveness, given negative photoblastism? Three likely explanations (not exclusive) are possible. Firstly, seeds are very small, allowing seed burial and a rapid escape from light. Secondly, buried seeds can increase germination because they have more access to water resource (Thanos *et al.* 1991, 1994, Fenner & Thompson 2005). Thirdly, buried seeds decrease their requirement of water for germination (Del Monte & Dorado 2011). It remains to be tested whether the positive effect of seed burial on seed germination can be propagated to later stages of life cycle.

In summary, negative photoblastism is regarded a fairly specialist trait, a presumed strategy to overcome Mediterranean climates, deserts or disturbed zones (Thanos *et al.* 1991). This trait can be correlated with other attributes such as seed size and water requirements (Fenner & Thompson 2005) and does not explain by itself the invasiveness described for *Eschscholzia californica*. In any case, is clear that more studies are necessary to disentangle the adaptive value of this rare physiological trait.

ACKNOWLEDGEMENTS

We acknowledge the financial support of the FONDECYT, proyect 1100076 to R.O. Bustamante. Partial support was given by the Institute of Ecology and Biodiversity (IEB) project (ICM) P05-002.

REFERENCES

- ARROYO, M.T.K., C. MARTICORENA, O. MATTHEI & L. CAVIERES. 2000. Plant invasions in Chile: present patterns and future predictions. In: H.A. Mooney R.J. & Hobbs (eds.), *Invasive Species in a Changing World*, pp. 385-421. Island Press, Washington DC.
- BASKIN, C. & J.M. BASKIN. 1998. *Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination*. Academic Press, San Diego. 666 pp.
- CAÑO, L., J. ESCARRÉ, I. FLECK, J.M. BLANCO-MORENO & F.X. SANS. 2008. Increased fitness and plasticity of an invasive species in its introduced range: a study using *Senecio pterophorus*. *Journal of Ecology* 96(3): 468-476.
- CASAL, J.J. & R.A. SÁNCHEZ. 1998. Phytochromes and seed germination. *Seed Science Research* 8(3): 317-329.
- COOK, S.A. 1962. Genetic system variation and adaptation in *Eschscholzia californica*. *Evolution* 16(3): 278-299.
- DEL MONTE, J.P. & J. DORADO. 2011. Effects of light conditions and after-ripening time on seed dormancy loss of *Bromus diandrus* Roth. *Weed Research* 51(6): 581-590.
- DI CASTRI, F. 1991. An ecological overview of the five regions of the world with a Mediterranean climate. In: R.H. Groves & F. di Castri (eds.), *Biogeography of Mediterranean Invasions*, pp. 3-16. Cambridge University Press, Cambridge, UK.
- FENNER, M. & K. THOMPSON. 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, UK. 263 pp.
- FRIAS, D.L., R. GODOY, P. ITURRA, S. KOREF-SANTIBAÑEZ, J. NAVARRO, N. PACHECO & G.L. STEBBINS. 1975. Polymorphism and geographic variation of flower color in Chilean populations of *Eschscholzia californica*. *Plant Systematics and Evolution* 123(3): 185-198.
- GHERSA, C.M., R.L. BENECH-ARNOLD & M.A. MARTINEZ-GHERSA. 1992. The role of fluctuating temperatures in germination and establishment of *Sorghum halepense*. Regulation of germination at increasing depths. *Functional Ecology* 6(4): 460-468.
- GOLDTHWAITE, J.J., J.C. BRISTOL, A.C. GENTILE & R.M. KLEIN. 1971. Light-suppressed germination of California poppy seed. *Canadian Journal of Botany* 49(9): 1655-1659.
- HENNIG, L., W.M. STODDART, M. DIETERLE, G.C. WHITELAM & E. SCHAFER. 2002. Phytochrome E controls light-induced germination of *Arabidopsis*. *Plant Physiology* 128(1): 194-200.
- HIERRO, J.L., J.L. MARON & R.M. CALLAWAY. 2005. Abiogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93(1): 5-15.
- JIMÉNEZ, A., A. PAUCHARD, L.A. CAVIERES, A. MARTICORENA & R.O. BUSTAMANTE. 2007. Do climatically similar regions contain similar alien floras? A comparison between the Mediterranean areas of central Chile and California. *Journal of Biogeography* 35(4): 614-624.
- KÖRNER, C. 2003. *Alpine plant life. Functional plant ecology of high mountain ecosystem*. Springer, Berlin. 359 pp.
- LEGER, E.A. & K.J. RICE. 2003. Invasive California poppies (*Eschscholzia californica* Cham.) grow larger than native individuals under reduced competition. *Ecology Letters* 6(3): 257-264.
- MANDOLI, D.F., G.A. FORD, L.J. WALDRON, J.A. NEMSON & W.R. BRIGGS. 1990. Some spectral properties of several soil types: implications for photomorphogenesis. *Plant, Cell & Environment* 13(3): 287-294.
- MARON, J.L., M. VILA, R. BOMMARCO, S. ELMENDORF & P. BEARDSLEY. 2004. Rapid evolution of an invasive plant. *Ecological Monographs* 74(2): 261-280.
- MOONEY, H.A. 1977. *Convergent Evolution in Chile and California: Mediterranean Climate Ecosystems*. Dowden, Hutchinson & Ross. Stroudsburg, Pennsylvania. 224 pp.
- QUING, H., Y. YAO, Y. XIAO, F. HUA, Y. SUN, C. ZHOU & S. AN. 2011. Invasive and native tall forms of *Spartina alterniflora* respond differently to nitrogen availability. *Acta Oecologica* 37(1): 23-30.
- SAX, D.F. 2002. Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions* 8(4): 193-210.
- SIEMANN, E. & W.E. ROGERS. 2001. Genetic differences in growth of an invasive tree species. *Ecology Letters* 4(6): 514-518.
- STATSOFT I. 2004. *Statistica7 for Windows*. Electronic Statistics Textbook. URL: www.statsoft.com/textbook/stathome.html Viewed: June 22, 2011.
- TAKAKI, M. 2001. New proposal of classification of seeds based on forms of phytochrome instead of photoblastism. *Revista Brasileira de Fisiologia Vegetal* 13(1): 103-107.

- TESTER, M. & C. MORRIS. 1987. The penetration of light through soil. *Plant, Cell & Environment* 10(4): 281-286.
- THANOS, C.A., K. GEORGHIOU, D.J. DOUMA & C.J. MARANGAKI. 1991. Photoinhibition of seed germination in Mediterranean maritime plants. *Annals of Botany* 68(5): 469-475.
- THANOS, C.A., K. GEORGHIOU & PINELOPI DELIPETROU. 1994. Photoinhibition of seed germination in the maritime plant *Matthiola tricuspidata*. *Annals of Botany* 73(6): 639-644.
- VAZQUEZ-YANES, C. & A. OROZCO-SEGOVIA. 1993. Patterns of seed longevity and germination in the tropical rainforest. *Annual Review of Ecology and Systematics* 24: 69-87.
- WOOLLEY, J. & E. STOLLER. 1978. Light penetration and Light-induced seed germination in soil. *Plant Physiology* 61(4): 597-600.

Recibido: 24.09.12
Aceptado: 05.08.13