

# Germination ecophysiology for three peri-urban ephemeral weeds

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We determined the environmental requirements leading to germination by three common species found during the summer rainy season in a peri-urban site where construction of a university campus was underway. In particular, we evaluated laboratory responses to low-temperature stratification, day/night air temperature, and water potential for the native Onagraceae *Lopezia racemosa* and *Ludwigia octovalvis*, and the exotic Polygonaceae *Rumex crispus*. Low-temperature stratification had no effect on germination by *L. racemosa*, for which maximum germination averaging 88% was optimal at 25/15 and 30/20 °C. Germination at 21 d was halved at -0.5 MPa and completely inhibited at -1.0 MPa. The seeds of *L. octovalvis* were also insensitive to low temperature stratification and their germination never exceeded 70%, with the two highest temperatures of 30/20 and 35/25 °C being the optimum. For this species germination was maximal at 0.0 MPa, decreasing significantly under every treatment with a minimum germination of 21% for seeds incubated at -0.1 MPa. Germination for the exotic *R. crispus* was delayed by low-temperature stratification, although all of its seeds germinated regardless of the temperature or water potential treatment. While the environmental requirements for germination of ephemeral species often match the typical climate of their growing season, the differential responses found for the species considered in the present study provide some insight into the mechanisms leading to changes in species composition for communities from disturbed environments, including the displacement of native species and the proliferation of exotic, potentially invasive, plants.

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16 Abstract

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36 Keywords: disturbance, land-use change, plant communities, reproductive ecophysiology, seed  
37 bank, stratification, temperature, urban ecology, water potential.

## Introduction

The species composition of annual and ephemeral plant communities can change substantially from year to year (Cousens and Mortimer 1995; Chaideftou et al. 2012). The identities of the species observed in any given growing season depends, of course, on which species are present in the seed bank or have dormant regeneration structures in the soil, but their emergence is greatly modulated by their interactions with the physical environment. Indeed, the prevalent temperature and available water can differentially trigger germination at various times during the growing season of a particular year or along various years (de la Barrera et al. 2009), mediated by structural (such as a thick testa; Debeaujon et al 2000; Dübbern de Souza et al. 2001; Rowarth et al 2007) or physiological (such as the need for cold-vernalization; Larcher 2001; Fenner and Thompson 2005) seed traits that determine both the moment and the rate of germination.

In this respect, the environmental conditions created in habitats resulting from the clearing of vegetation for agricultural purposes, roads, urban development, etc., can restrict the persistence of native species in plant communities, while favoring the establishment of species, native or not, that can tolerate and even thrive under disturbance (Cousens and Mortimer 1995; Dekker 2016). Indeed, landscape modification by human actions is a major threat to global biodiversity (Sala et al. 2000). This is an issue of special concern in Mexico, one of twelve megadiverse countries, that is, however, experiencing a rapid loss of vegetation cover. Indeed, while 62% of the country's surface had vegetation cover in 1976, a mere 38% remained with vegetation by 2002 (de la Barrera and Andrade 2005; Challenger and Dirzo 2009).

Three species that are commonly found in such disturbed sites in Mexico, including as agricultural weeds, are the native Onagraceae *Lopezia racemosa* and *Ludwigia octovalvis*, and the exotic Polygonaceae *Rumex crispus* (Villaseñor and Espinosa-García 1998; Calderón and Rzedowski 2005). *Lopezia racemosa* can be found in various vegetation types including conifer, oak, and cloud forests, in addition to grasslands and thorn scrub. *Ludwigia octovalvis* is mostly restricted to sites with high soil humidity such as riparian ecosystems and along irrigation canals. In turn, *R. crispus*, which is native to Eurasia, has become a common weed throughout the world, especially in the temperate zones of the Northern Hemisphere. These three species were abundant elements of the ephemeral flora of the Universidad Nacional Autónoma de México, Campus Morelia, during the summer growing season of 2009 (unpublished observations). Located in a peri-urban site, the campus was established in 2005 in a former eucalyptus plantation and has been undergoing construction to house various academic entities, which makes its ephemeral flora an interesting research subject as it changes over the years.

In order to determine the environmental conditions leading to seed germination by *L. racemosa*, *L. octovalvis*, and *R. crispus*, three ephemeral plants from a peri-urban site with different ecological niches, a series of controlled-environment experiments were conducted to determine the temperature relations and the influence of water potential on the time and rate of germination.

## Materials and Methods

Seeds of *Lopezia racemosa* Cav. (Onagraceae; hereafter referred to as *Lopezia*), *Ludwigia octovalvis* (Jacq.) Raven (Onagraceae; *Ludwigia*), and *Rumex crispus* L. (Polygonaceae; *Rumex*) were collected during the growing season of June-October 2009 from

areas of the Universidad Nacional Autónoma de México, Campus Morelia (19° 38' 55.9" N; 101° 13' 45" W; 1967 m), where a lack of construction and landscaping allowed the establishment of spontaneous vegetation. Seeds of at least 7 individuals per species were collected by shaking the main stem of plants. The released seeds were placed in cloth bags and mixed into a compound sample. Seeds were kept in black paper bags and stored in a laboratory (in the dark at 23 °C, 40% relative humidity) until utilized within 6 months. Seeds were rinsed with running water during 48 h immediately before the start of each experiment.

Germination was studied for experimental units consisting of 25 seeds placed in covered plastic petri dishes (55 mm in diameter, 15 mm high) with two layers of sterile filter paper as substrate. Usually 5 ml of sterile distilled water were added to each petri dish, with additional water being added over the course of the experiments to keep the filter paper saturated. The petri dishes were placed in an I-35LL germination chamber fitted with fluorescent light tubes (Percival Scientific, Boone, Iowa, USA) for under a photoperiod of 12 h, usually at a day/night temperature of 20/10 °C. Germination, which was scored as seeds with radicle protrusion, was evaluated daily, until no further germination occurred.

Germination responses to low-temperature stratification were evaluated by placing a sample of seeds at 8 °C during 3 months and their germination was compared to that of a control of untreated seeds. The effect of air temperature on germination was evaluated for seeds incubated under day/night air temperatures of 20/10, 25/15, 30/20, or 35/25 °C. In turn, the effect of water potential on germination was evaluated for seeds incubated under water potentials of 0.00, -0.01, -0.05, and -0.1 MPa that were created with aqueous solutions of polyethylene glycol (PEG; molecular weight of 20,000) of various concentrations that were determined following Michel and Radcliffe (1985).

Twelve replicates of 25 seeds each were utilized for each measurement. Statistical analyses for the onset of germination, i.e., the first day significantly higher than 0%, consisted of a Mann-Whitney U test (at  $p < 0.05$ ) for stratification and a Kruskal-Wallis test ( $p < 0.05$ ) for temperature and water potential, which were performed with Statistica 7.0 (StatSoft Inc., Tulsa, Oklahoma, USA). In addition, the process of germination was analyzed with a repeated measures Friedman test followed by *post hoc* Tukey tests ( $p < 0.05$ ) performed with SigmaStat 3.5 (Systat Software, Richmond, California, USA).

## Results

### *Lopezia racemosa*

Low-temperature stratification had no effect on germination for *Lopezia* (Table 1; Fig. 1A). For both the control and treated seeds the onset of germination was observed after  $6.2 \pm 0.7$  days after the start of the experiment. In turn, maximum germination peaked at  $78.7 \pm 1.6\%$  after 21 days of the start of the experiment.

The temperature regime, in turn, had a significant effect on the germination of *Lopezia* (Table 1; Fig. 1D). For instance, the onset of germination occurred after one day of the start of the experiment for seeds incubated under 25/15 °C, after two days for those under 30/20 and 35/25°C, while six days were required to trigger the germination for seeds of *L. racemosa* incubated under 20/10 °C. Final germination averaged  $87.7 \pm 2.7\%$  for seeds incubated under 25/15 and 30/20 °C and they were  $79.0 \pm 2.0$  and  $76.0 \pm 1.3\%$  lower for those under the extremes of 20/10 and 35/25 °C, respectively.

Germination by *Lopezia* responded to the water potential (Table 1; Fig. 1G). The onset of germination occurred at 2 days after the start of the experiment for seeds incubated under 0.0

MPa, the following day for those under  $-0.01$  MPa, and at day six for those under  $-0.05$  MPa, while the seeds incubated under  $-0.10$  MPa failed to germinate. A final germination of  $91.33 \pm 1.69\%$  observed after 21 d of the start of the experiment was maximal for seeds incubated under  $0.00$  MPa, decreasing with increasingly negative water potential until a minimum that was  $41.67 \pm 1.94\%$  lower was observed for seeds incubated under  $-0.05$  MPa.

#### *Ludwigia octovalvis*

Low-temperature stratification improved germination for *Ludwigia* (Table 1; Fig. 1B). Indeed, the onset of germination occurred at  $11.1 \pm 0.7$  days after the start of the experiment for the control, while treated seeds germinated 2.3 days earlier. Also, while the final germination after 21 days of incubation was similar for both groups of seeds, it occurred at a faster rate for stratified seeds.

The temperature regime had a significant effect on germination by *Ludwigia* (Table 1; Fig. 1E). In particular, the onset of germination increased with air temperature and it ranged from  $2.0 \pm 0.0$  days after the start of the experiment for seeds incubated at  $35/25$  °C to 9 days later for seeds under the lowest temperature regime of  $20/10$  °C. Final germination at 21 days after the start of the experiment was also higher and occurred at a faster rate with increasing temperature. For instance,  $68.0 \pm 3.0\%$  of seeds germinated when incubated under  $35/25$  °C, while a mere  $40.3 \pm 3.5\%$  germinated under  $20/10$  °C.

Water potential significantly affected germination by *Ludwigia* (Table 1; Fig. 1H). The onset of germination, which occurred at  $3.5 \pm 1.6$  for seeds exposed to  $0.0$  or  $-0.01$  MPa, was delayed up to 4 days at lower water potentials. In turn, final germination at 21 days after the start



of the experiment was also higher and more rapid at lower water potentials, ranging from  $76.0 \pm 3.4\%$  for seeds incubated under 0.0 MPa to  $20.7 \pm 1.1\%$  for those under  $-0.1$  MPa.

#### *Rumex crispus*

Low-temperature stratification delayed germination for *Rumex* (Table 1; Fig. 1C). The onset of germination occurred at the first day after the start of the experiment regardless on whether the seeds had been exposed to air temperature of  $8^\circ\text{C}$  for three months or not. Maximum germination after 21 days of incubation was not affected either, reaching  $100.0 \pm 0.0\%$ . However, the maximum was reached faster by untreated seeds.

Incubation temperature did not affect the onset of germination by *Rumex*, which occurred at  $1.2 \pm 0.1$  days after the start of the experiment regardless of the treatment, nor the final germination at 21 days of incubation, reaching  $99.7 \pm 0.2\%$  (Table 1; Fig. 1F). However, higher air temperatures led to a faster germination rate, as the seeds incubated at 25/15 and 35/25  $^\circ\text{C}$  reached the germination maxima up to one week faster than those exposed to 20/10  $^\circ\text{C}$  of day/night air temperatures.

The onset of germination for *Rumex* averaged  $2.5 \pm 0.1$  days after the start of the experiment, and it only was significantly delayed for seeds incubated under a water potential of  $-0.1$  MPa, which took up to a day longer (Table 1; Fig. 1I). The final germination of  $99.9 \pm 0.1\%$  after 21 days of incubation was also unaffected by the water potentials tested, but the rate was slower under more negative water potentials. For instance, it took 3-5 days to reach final germination by seeds exposed to 0.0 or  $-0.01$  MPa and up to 12 days for those incubated under  $-0.10$  MPa.

## Discussion

The identity of the species that persist in a community subjected to disturbance depends on which species were originally present in the seed bank and how they respond to the new environmental conditions. Indeed, germination for generalists and species with rapid germination and preference for open sites are likely to be favored by disturbance (Grime 1989; del-Val et al. 2015; Gorgone-Barbosa et al. 2016). In the present study, both the exotic weed *Rumex* and the generalist native *Lopezia* germinated under all the experimental conditions, although their germination was delayed or diminished under the most extreme treatments. In contrast, germination for *Ludwigia*, a specialist of high-humidity environments, only exceeded 50% under the most benign conditions. These differential responses of co-occurring species can provide some insight on potential trends of community composition following disturbance.

Species from regions with marked seasonality, i.e., with distinct dry and wet seasons or with prolonged sub-freezing periods, often display an embryonic dormancy that can delay the onset of germination until the season with environmental conditions favoring seedling establishment (Baskin and Baskin 1988; Benech-Arnold et al. 2000 ). For these plants, germination is often improved by exposing seeds to low temperatures during several weeks, by which germination is avoided during the winter, when the prevailing low air temperatures can be lethal for seedlings, even if some precipitation occurs. This appears to be case for *Ludwigia* whose stratified seeds germinated 2 days faster than untreated seeds, in agreement with previous studies with its congeners *L. alternifolia* and *L. decurrens* (Baskin and Baskin 1998). However, this was not the case for *Lopezia* nor for *Rumex*, suggesting that they either lack primary dormancy or that it had been overcome during storage (Totterdell and Roberts 1979; Chi 2006; Finch-Savage and Leubner-Metzger 2006).

Higher temperatures tended to hasten and increase final germination for the species considered in the present work. However, the the highest temperature resulted in the lowest germination for *Lopezia*. A similar response where germination improves with temperature until an optimum is reached followed by an inhibition of germination was observed for the seeds of *Ludwigia*, which were the most sensitive. In turn, the exotic weed *Rumex* reached maximum germination regardless of the incubation temperature, confirming observations for many weeds, which are able to tolerate and even thrive under high temperatures, an advantageous trait for survival in the extreme environmental conditions of naked soil (Nobel and de la Barrera 2003; Egley 1990).

Germination tended to decrease as the incubation water potentials became more negative, especially at and below  $-0.05$  MPa, similar to responses of other species such as *Campsis radicans* (Chachalis and Reddy 2002). In contrast, germination for *Rumex* was maximal regardless of the water potential, in agreement with the germination behavior of its congeneric *R. acetocella*, which reaches 90% germination under  $-0.1$  MPa (Fani et al. 2013). Considering that substantial amounts of water are required to sustain cell elongation for plants following germination, especially for species that escape or avoid drought by completing their lifecycle during the rainy season, it may be advantageous to restrict germination to times when an adequately high water potential signals that the rainy season is well underway or that at least sufficient water is stored in the soil that will allow seedling development (de la Barrera et al. 2009). However, the water potentials assayed here correspond to a mere ca. 7 days after suspending irrigation for a sandy loam, well above the permanent wilting point of  $-1.5$  MPa, which indicates the sensitivity of germination (Young and Nobel 1986).

The environmental requirements for germination of ephemeral species are often predictable to match those resulting from the typical weather of their growing season (Baskin and Baskin 1988). However, interspecific differences, however small, can determine the identities of the plants that grow in a community during a given year, contributing to the high interannual species variation that has been observed for ephemeral and annual floras (Cousens and Mortimer 1995; Chaideftou et al. 2012; Dekker 2016; Gorgone-Barbosa et al. 2016). The differential responses found in the present study illustrate these interspecific idiosyncrasies and provide insight, for instance, into the mechanisms that enable exotic species to become dominant or for native species to be displaced. The emergence of novel environments resulting from anthropization poses a risk to the prevalence of native floras. Further studies considering larger community subsets or even whole communities are required, including long-term observations aimed at characterizing the rate at which native floras may be shifting in response to anthropic environmental changes.

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## Table 1 (on next page)

Germination parameters for the ephemeral weeds *Lopezia racemosa*, *Ludwigia octovalvis*, and *Rumex crispus*.

The onset of germination (first day statistically different from zero) was evaluated with Mann-Whitney U tests ( $p < 0.05$ ) for stratification and Kruskal-Wallis tests ( $p < 0.05$ ) for the temperature and water potential experiments. In turn, the final germination was evaluated with Tukey tests following a Friedman repeated measures test. Data are shown as mean  $\pm$  S.E. ( $n = 12$  petri dishes with 25 seeds each). For each parameter and experiment different letters indicate statistical differences ( $p < 0.5$ ).

1

2 **Table 1.** Germination parameters for the ephemeral weeds *Lopezia racemosa*, *Ludwigia*  
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8 experiment different letters indicate statistical differences ( $p < 0.5$ ).

<i>Lopezia racemosa</i>	Germination			
	Onset		Maximum	
Control	6.5 $\pm$ 0.31	a	79.0 $\pm$ 1.98	a
Stratification	6.0 $\pm$ 0.0	a	77.3 $\pm$ 2.62	a
20/10 °C	6.5 $\pm$ 0.31	a	79.0 $\pm$ 1.98	a
25/15 °C	1.0 $\pm$ 0.0	b	85.3 $\pm$ 2.48	b
30/20 °C	2.3 $\pm$ 0.14	c	90.0 $\pm$ 3.53	b
35/25 °C	2.0 $\pm$ 0.0	c	76.0 $\pm$ 1.3	c
-0.00 MPa	2.3 $\pm$ 0.14	a	91.3 $\pm$ 1.69	a
-0.01 MPa	3.0 $\pm$ 0.0	a	88.0 $\pm$ 1.78	b
-0.05 MPa	6.1 $\pm$ 0.47	b	41.7 $\pm$ 1.94	c
-0.10 MPa	11.0 $\pm$ 0.58	b	1.0 $\pm$ 0.52	d
<i>Ludwigia octovalvis</i>				
Control	11.1 $\pm$ 0.74	a	40.3 $\pm$ 3.46	a
Stratification	8.8 $\pm$ 0.65	b	41.3 $\pm$ 3.28	b
20/10 °C	11.1 $\pm$ 0.74	a	40.3 $\pm$ 3.46	a
25/15 °C	4.6 $\pm$ 0.15	ab	43.7 $\pm$ 2.85	b
30/20 °C	3.8 $\pm$ 0.11	bc	61.7 $\pm$ 4.52	c
35/25 °C	2.0 $\pm$ 0.0	c	68.0 $\pm$ 2.99	d
-0.00 MPa	3.2 $\pm$ 0.24	a	76.0 $\pm$ 3.38	a
-0.01 MPa	3.8 $\pm$ 0.17	ab	64.0 $\pm$ 1.97	b
-0.05 MPa	5.2 $\pm$ 0.24	bc	47.3 $\pm$ 2.73	c
-0.10 MPa	7.2 $\pm$ 0.41	c	20.7 $\pm$ 1.08	d
<i>Rumex crispus</i>				
Control	1.0 $\pm$ 0.0	a	100.0 $\pm$ 0.0	a
Stratification	1.0 $\pm$ 0.0	a	100.0 $\pm$ 0.0	b
20/10 °C	1.0 $\pm$ 0.0	a	100.0 $\pm$ 0.0	a
25/15 °C	1.0 $\pm$ 0.0	a	100.0 $\pm$ 0.0	b
30/20 °C	1.8 $\pm$ 0.37	a	99.3 $\pm$ 0.45	a
35/25 °C	1.1 $\pm$ 0.08	a	99.7 $\pm$ 0.33	b
-0.00 MPa	2.2 $\pm$ 0.17	a	100.0 $\pm$ 0.0	a
-0.01 MPa	2.4 $\pm$ 0.15	a	100.0 $\pm$ 0.0	ab
-0.05 MPa	2.8 $\pm$ 0.11	ab	99.7 $\pm$ 0.33	b
-0.10 MPa	3.2 $\pm$ 0.11	b	100.0 $\pm$ 0.0	c

# Figure 1

## Seed germination

Germination for the ephemeral weeds *Lopezia racemosa* (A, D, G), *Ludwigia octovalvis* (B, E, H), and *Rumex crispus* (C, F, I), in response to low-temperature stratification (A-C), day/night air temperature (D-F), and water potential (G-I). Data are shown as mean  $\pm$  SE (n = 12 petri dishes with 25 seeds each).

