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Ecological Monographs, Vol. 72, No. 3. (Aug., 2002), pp. 427-443.

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Ecological Monographs, 72(3), 2002, pp. 427–443
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TEMPORAL VARIABILITY MATTERS: EFFECTS OF CONSTANT VS. VARYING MOISTURE AND SALINITY ON GERMINATION

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Abstract. Most ecological experiments test constant environmental conditions instead of the temporally varying conditions that are typical of most ecological systems. This study experimentally evaluated the effects of temporal variations of soil salinity and moisture on the germination of an 11-species annual plant assemblage. In soil-based microcosms with common seed banks, constant conditions were compared to different amplitudes, durations, and seasonal timing of low salinity or high moisture that simulate conditions in the upper intertidal marsh of southern California during periods of germination. The percentage germination of seeds of eight species decreased when low salinity or high moisture lasted for 1 wk before changing to high salinity and low moisture for 3 wk (varying conditions) compared to 4 wk of low salinity or high moisture (constant conditions). The seed germination speed of two species differed (both faster and slower) between the varying and constant treatments. Species responses to varying vs. constant conditions depended on the specific amplitude of temporary low salinity (0, 8, or 17 g/kg) in the varying treatments. Similarly, the duration (1, 2, or 4 wk) of low salinity or high moisture affected the percentage germination (four species) and germination speed (two species). Percentage germination (four species) and germination speed (eight species) also differed according to whether low salinity and high moisture were initiated in November, January, or March. The sensitivity of species seeds to temporally varying conditions could be explained by their germination traits and identity as native or exotic. Seeds of the six exotic species were less sensitive to varying conditions, germinated faster, and were more tolerant of high salinity and low moisture than seeds of the five native species. Varying conditions resulted in different patterns of germination than constant conditions, and environmental factors typically vary through time in the field. Thus, experimenters who are trying to understand or predict plant establishment should consider and simulate, as closely as possible, the variability in field conditions.

Key words: amplitude; duration; exotics; moisture; natives; salinity; salt marsh annuals; seasonal timing; temporal variation.

INTRODUCTION

Most experiments simplify environmental variation by testing constant conditions over time. However, temporal variation of environmental conditions is the norm in most ecological systems, and these fluctuations may have important consequences. Temporal variation influences ecological processes in forest gaps (Bazzaz and Wayne 1994), plant responses to light levels (Pearcy et al. 1994, Bazzaz 1996, Sultan et al. 1998), community invasibility (Davis et al. 2000), and species coexistence (Turpin and Harrison 1979, Chesson and Huntly 1997). For example, the complexities of the intensity, duration, frequency, and seasonality of fire regimes determine the impact of fire on ecological systems (Whelan 1995).

Temporal variation of environmental conditions is also important in wetlands. Interspecific differences in plant response to fluctuating water levels are key to the differentiation of wetland habitats (Olff et al. 1988, Mitsch and Gosselink 1993, Carter et al. 1994). In addition, conceptual models of wetland plant community (van der Valk 1981) and ecosystem dynamics (Zedler and Beare 1986, Odum et al. 1995) include hydrologic fluctuation. Several experiments have identified the effects of temporal hydrologic variance on wetland plants (e.g., Gerritsen and Greening 1989, Smith and Brock 1996, Keeland and Sharitz 1997, Bliss and Zedler 1998, Howard and Mendelssohn 1999*a*, *b*).

In particular, constant levels of abiotic factors are often utilized in plant germination and establishment experiments. This methodology is common despite the importance of temporal variation in environmental conditions to plant germination dynamics. Bazzaz and Wayne (1994) concluded that testing the responses of seedlings with constant environmental factors gives a limited view of the variation that plants experience in the field. For example, Thompson and Grime (1983) found that the germination of 46 of 112 herbaceous species was stimulated by temperature fluctuations and that wetland species were especially responsive. The

Manuscript received 16 October 2000; revised 2 April 2001; accepted 12 April 2001; final version received 19 September 2001.

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germination of many plant species is stimulated by fluctuating light (Bewley and Black 1995), temperature (Bewley and Black 1985, Fenner 1985, Baskin and Baskin 1998), fire regimes (Auld 1986), and moisture (Heydecker 1977, Gerritsen and Greening 1989, Stockey and Hunt 1992, Bliss and Zedler 1998). Few, if any, experiments have contrasted the germination of a large assemblage of species in constant vs. varying conditions.

Plant germination and establishment in the upper intertidal marsh of southern California, USA, occurs during periods of high temporal variability of both soil salinity and soil moisture. Up to 20 annual plant species germinate in this community, including an endangered species, rare species, as well as many abundant exotic species (Noe and Zedler 2001*a*). Germination and establishment occur following winter rainfalls that decrease soil salinity (below 10–35 g/kg) or increase soil moisture (above 40–45%) for a brief period before soil salinity and moisture return to very stressful levels in the dry, hot summer (Noe and Zedler 2001*a*). Soil salinity and moisture fluctuate with varying amplitude, duration, and timing in response to variation in the amount of daily rainfall; tidal inundation is rare in the upper intertidal marsh (Noe and Zedler 2001*b*). Previous research has related the distribution of the species in this assemblage to spatial gradients of soil salinity (Beare and Zedler 1987, Callaway et al. 1990, Kuhn and Zedler 1997, Callaway and Zedler 1998, Noe and Zedler 2001*a*) and soil moisture (Noe and Zedler 2001*a*). The invasion of exotic species in southern California coastal marshes also has been linked to decreased soil salinity arising from increased freshwater inflows from anthropogenic sources (Beare and Zedler 1987, Kuhn and Zedler 1997, Callaway and Zedler 1998). Finally, constant high soil salinity and low soil moisture inhibit the germination of the species in this annual plant assemblage in growth chamber experiments (Noe and Zedler 2000).

Clearly, the annual plant assemblage of the southern California upper intertidal marsh experiences temporal variation in soil salinity and moisture during germination and is responsive to soil salinity and moisture. To further examine the role of varying conditions, I compared the germination of seeds of 11 species of this annual plant assemblage under varying and constant soil salinity and moisture. Specific comparisons and hypotheses of assemblage germination were evaluated with the final percentage germination and speed of germination of each species from a common seed bank in soil-based microcosms. Germination speed was included as a response variable because it can determine future intraspecific and interspecific interactions (Harper 1977, Grace 1987, Bazzaz 1996). Based on field distributions, I hypothesized that a salinity and moisture regime could differentiate the germination requirements of native and exotic species; therefore, differences between the native and exotic species in response to the salinity and moisture treatments were identified. In addition, I hypothesized that the germination traits of species predict which species are sensitive to varying conditions. To evaluate this relationship, the magnitude of each species' difference in percentage germination between the varying and constant treatments was correlated with the species' germination speed, salt tolerance, low-moisture tolerance, and identity as native or exotic. Finally, I compared the ability of experiments with constant vs. varying soil salinity and moisture to explain patterns of assemblage germination in the field.

Methods

Three conditions were tested in microcosms: temporal variations in (1) amplitude, (2) duration, and (3) seasonal timing of low soil salinity or high soil moisture. The amplitude and duration experiments tested treatments with periods of low salinity followed by increased salinity or high moisture followed by low moisture, as would occur in the field following the rainfalls that stimulate germination. These treatments of varying amplitude and duration were compared to constant low salinity or high moisture. Finally, the seasonal timing experiment tested three different times of low salinity and high moisture (November, January, and March) that span the range in the timing of field germination.

Description of the assemblage and species

The most abundant annual species, in descending order, in the upper intertidal marsh of southern California during the 1996–1997 (1996) winter germination season were *Parapholis incurva*, *Mesembryanthemum nodiflorum*, *Juncus bufonius*, *Hutchinsia procumbens*, and *Amblyopappus pusillus* (hereafter species will be referred to by genus; Noe and Zedler 2001*a*). The same five species were also the most abundant species in the 1997 germination season, although their order of ranking changed (Noe and Zedler 2001*a*). The 11 species included in this study (Table 1) accounted for 97% of all annual plant seedlings in the 1996 germination season (Noe and Zedler 2001*a*) and include a mix of native and exotic species.

Microcosm setup

An experimental microcosm consisted of an inner soil-filled pot (14.5 cm diameter × 11 cm depth) resting on a variable number of wooden blocks inside an outer water bath, with a separate water bath for each pot (Fig. 1). Each pot was filled with 0.95 L of mineral, nonwetland soil (48% sand, 41% silt, and 11% clay) that had been passed through a 1-cm sieve. Texture of the experimental soil was similar to that of soils in the upper intertidal marshes of southern California (see Noe and Zedler 2001*b*). An additional 0.1 L of soil that had been passed through a 2-mm sieve was placed on the soil surface to decrease variation in surface mi-

TABLE 1. Description and collection information for the species used in the experiments.

Species	Abbreviation	Family	Growth form	Date(s) of seed collection	Collecting location
Amblyopappus pusillus Hook. & Arn.	*Amb pus*	Asteraceae	n/f	2 June 1997†‡ 2 June 1998‡	SW
Cotula coronopifolia L.	*Cot cor*	Asteraceae	e/f	3 April 1997	LPL
Hutchinsia procumbens (L.) Desv.	*Hut pro*	Brassicaceae	n/f	24 March 1997 31 March 1997	SW
Juncus bufonius L.	*Jun buf*	Juncaceae	n/g	31 March 1997† 21 April 1998‡	SW
Lasthenia glabrata ssp. *coulteri* (A. Gray) Ornd.	*Las gla*	Asteraceae	n/f	31 March 1997 3 April 1997	LPL, SW
Lolium multiflorum Lam.	*Lol mul*	Poaceae	e/g	14 May 1997	LPL
Lythrum hyssopifolium L.	*Lyt hys*	Lythraceae	e/g	3 June 1997	LPL
Mesembryanthemum nodiflorum L.	*Mes nod*	Aizoceae	e/s	21 July 1997	SW
Parapholis incurva (L.) C.E. Hubb	*Par inc*	Poaceae	e/g	5 May 1997 12 May 1997 14 May 1997	LPL, SW, TE
Polypogon monspeliensis (L.) Desf.	*Pol mon*	Poaceae	e/g	14 May 1997	LPL
Spergularia marina (L.) Griseb.	*Spe mar*	Caryophylloaceae	n/s	3 April 1997	LPL

Note: Species descriptions: n = native, e = exotic, f = forb, g = graminoid, s = succulent. Collecting locations: LPL = Los Peñasquitos Lagoon, SW = Sweetwater Marsh National Wildlife Refuge, TE = Tijuana River National Estuarine Research Reserve.

† Date of collection for seasonal timing experiment.

‡ Date of collection for amplitude, duration, and frequency experiments.

crotopography that could result in spatial patchiness of soil salinity. The experimental soil had few viable seeds, and the seedlings were easily distinguished from the 11 experimental species (*personal observation*).

Seeds of the 11 species were collected after plant senescence from three coastal salt marshes in San Diego County, California, USA, in 1997 (Table 1). Additional seeds of 2 species were collected in 1998 for use in the amplitude and duration experiments (Table 1). While seed age can affect germination responses (Baskin and Baskin 1998), salt marsh annual species in southern California most likely develop long-lived seed banks that do not germinate in years with very low rainfall (e.g., Zedler et al. 1992). In addition, a test of the effect of seed age on the percentage germination and germination speed of seeds of 8 of the 11 species found that only the number of *Cotula* seeds germinating changed substantially after 7 mo of dry

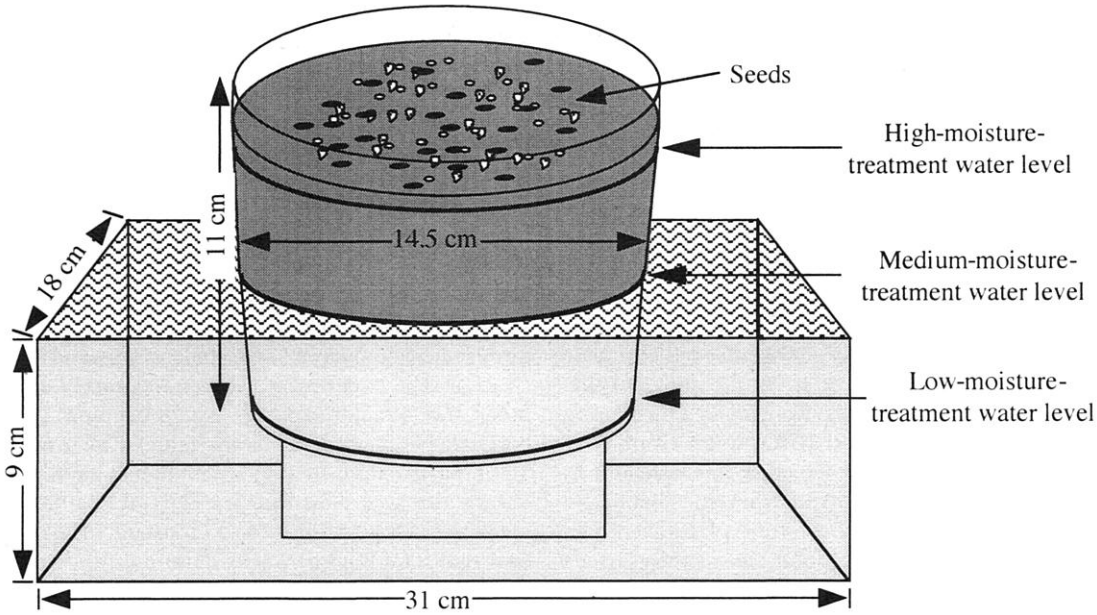

FIG. 1. The design of the experimental microcosms located in the greenhouses of the Pacific Estuarine Research Laboratory, San Diego, California, USA. Each microcosm consisted of a water-filled bath and an inner pot. Each pot had 25 seeds of each species, holes on the bottom, an inner lining of thin muslin cloth, and soil filled to 2 cm from the top. Water levels in the high-, medium-, and low-moisture treatments were 0.5, 4.5, and 8.5 cm below the soil surface, respectively.

storage (Noe and Zedler 2000). Seeds were stored dry in light and ambient room temperatures (16–37°C). Seeds were used only if they had intact seed coats and appeared to have embryos. Seeds of the grass *Polypogon* were removed from the floret to ensure the presence of a seed. *Lolium* and *Parapholis* seeds were left within the floret because their presence could be determined without removal and because they germinate from within the floret in the field (*personal observation*). *Mesembryanthemum* fruits were soaked in deionized water for 15 min to facilitate seed removal. Seed viability was not determined; however, seed germination under optimal conditions for 9 of the 11 species (*Juncus* and *Lolium* were not tested) was reported in another study (Noe and Zedler 2000). In that study, seeds were collected, processed, and stored under similar conditions as in this study but germination tests occurred 3–6 mo prior the study reported here. The maximum percentage germination of seeds was 99% for *Parapholis*, 93% for *Polypogon*, 88% for *Spergularia*, 86% for *Lasthenia*, 81% for *Hutchinsia*, 73% for *Amblyopappus*, 70% for *Lythrum*, 63% for *Cotula*, and 46% for *Mesembryanthemum* (Noe and Zedler 2000). Consequently, it was known a priori that the seeds of most species were largely viable and nondormant.

Twenty-five seeds of each of the 11 species were haphazardly scattered over the soil surface of each microcosm. The number of germinated seeds (defined here as the emergence of the root radicle or cotyledon) of each species was counted every 3 d over the 30-d experiments. Sowing all 11 species in each microcosm allowed simultaneous testing of a large number of species but introduced the possibility for interspecific interactions during germination to influence germination patterns. Control treatments of each species growing in monoculture were not included because interspecific interactions were not the focus of this research.

Three moisture level treatments were achieved by placing the soil-filled pot at differing heights in the water bath (Fig. 1). Filling the outer bath with water of four different salinity levels created different salinity treatments. The moisture and salinity treatments were chosen to represent the range in conditions that occurs during periods of germination in the field (see Noe and Zedler 2001*a*). Preliminary trials indicated that solutions of 0, 5, 10, and 24 g/kg were needed to create target surface soil salinity of 0, 8, 17, and 34 g/kg, respectively. Salinity solutions were created by diluting seawater with reverse osmosis (RO) water (salinity = 0 g/kg). Once the soil surface of a microcosm was wetted, the water was removed from each bath and replaced with RO water. Clear plastic plates were laid on top of each pot to limit evaporation and keep surface soil salinity constant. Treatments with increasing soil salinity had their plates removed and outer baths filled with 34 g/kg seawater at the appropriate time, until the increased target salinity was reached.

The amplitude and duration experiments were conducted in a temperature-moderated greenhouse (mean daily high and low temperatures were 9° and 38°C, respectively). The seasonal timing experiment occurred in three small greenhouse structures designed to prevent rain from falling on the microcosms while minimizing differences from ambient air temperatures. The small greenhouse structures had roofs of the same plastic as in the temperature-moderated greenhouse and walls of flexible translucent plastic that were secured to the ground. The corners of the walls were left open to allow for air circulation and achieve ambient air temperatures. Air temperatures within each of the small greenhouse structures and at each table in the temperature-moderated greenhouse were monitored with Hobo temperature dataloggers (Onset Computer Corporation, Bourne, Massachusetts, USA). Artificial lighting was not used to control photoperiod; consequently, the seasonal timing experiment tested differences in both temperature and photoperiod. The greenhouses were located on the campus of San Diego State University, ~15 km inland from the Pacific coast.

Experimental design

Three experiments were conducted with different types of temporal variation in soil salinity and moisture: amplitude, duration, and seasonal timing. The effects of different amplitudes of variable soil salinity and soil moisture were compared to the effects of constant salinity and moisture (Fig. 2). The experiment used a randomized complete block, 4 × 3 × 2 factorial design with three blocks and one replicate per block (greenhouse table). Treatments consisted of salinity levels of 0, 8, 17, or 34 g/kg, moisture levels of high, medium, or low, and varying or constant salinity and moisture. Varying treatments consisted of each salinity and moisture treatment level combination for 1 wk followed by 34 g/kg (high salinity) and low moisture for 3 wk; constant treatments remained at the salinity and moisture treatment level combination for the duration of the 30-d experiment (Fig. 2). The combination including high salinity and low moisture was identical in the varying and constant treatments because of the fully crossed experimental design. The amplitude experiment was initiated on 15 November 1998.

Differing durations of soil salinity and moisture conditions were compared to constant salinity and moisture (Fig. 2). The experiment used a randomized complete block, 4 × 4 factorial design with three blocks and one replicate per block (greenhouse table). The low salinity and high moisture treatment levels had amplitudes of 8 g/kg and high moisture, respectively. Salinity treatments were low salinity for 0 (constant 34 g/kg), 1, 2, or 4 (constant 8 g/kg) weeks duration, followed by 34 g/kg for the remainder of the study. Likewise, moisture treatments were high moisture for 0 (constant low moisture), 1, 2, or 4 (constant high moisture) weeks duration, followed by low moisture. The duration experiment started on 15 November 1998.

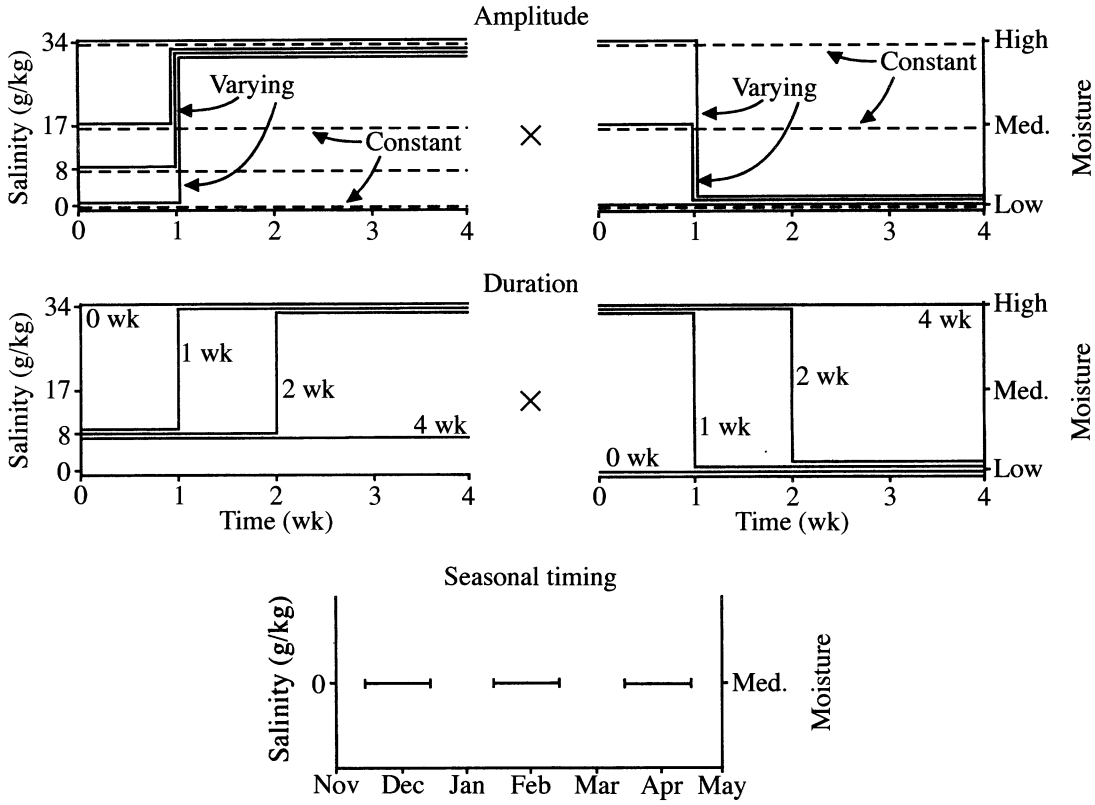

FIG. 2. Schematic diagram of the soil salinity and moisture conditions in the treatments of the amplitude, duration, and seasonal timing experiments. Examples of the varying treatments in the amplitude experiment are shown. The salinity and moisture treatments in the amplitude and duration experiments were fully crossed.

The effects of seasonal timing were tested by comparing medium moisture and low (0 g/kg) salinity beginning on three dates that span the typical period of germination in the field (Fig. 2). Microcosm baths were filled with RO water on 15 November 1997, 15 January 1998, and 15 March 1998. There were six replicates per treatment, with the microcosms blocked by greenhouse.

Soil analysis

To determine the actual moisture and salinity levels in each treatment, soil moisture and salinity were measured every 3 d in seedless microcosms and on the last day (day 30) in the seeded microcosms of the amplitude and duration experiments. The seedless microcosms had two replicates per treatment. A 1.3-cm^2 soil core was taken to a depth of 1 cm in each seedless microcosm each sampling time, and two soil cores were taken to a depth of 1 cm in each seeded microcosm at day 30.

Soil moisture was determined gravimetrically by drying the soil sample at 60°C for 24 h. Soil moisture was calculated as change in mass divided by dry mass (Gardner 1986). In situ soils in the low-moisture treatments were too dry to measure the salinity of the interstitial water. Thus, reverse osmosis water was added to the same dried soil sample until the saturation point was reached (Richards 1954). The saturated soil sample was then added to a 10-mL syringe loaded with filter paper and a drop of water was expressed onto a temperature-compensated salinity refractometer (Pacific Estuarine Research Laboratory 1990). Saturated soil paste extracts underestimate salinity concentrations of field soils, except when soils are saturated, and are a measure of the salt content of the soil. Therefore, the soil salinity treatments are best represented as treatments of differing salt content.

Statistical analyses

The response variables for all experiments were final (day 30) percentage germination and speed of germination of each species. An index of the speed of germination was created that factors out percentage germination and is therefore independent of viability, as compared to Timson's Σn (Timson 1965) and other indexes (e.g., Brown and Mayer 1988). The speed of germination was expressed as $(\Sigma n_t)/(n_f \times t)$, where n_t is the cumulative percentage germination at each sampling time, n_f is the cumulative percentage germination at the end of the experiment, and t is the number of sampling times. When no germination occurs ($n_f = 0$), the index value is defined to be zero. The index ranges

PLATE 1. Temporal variation in salinity and moisture decreased seed germination and plant biomass. Seeds in the mesocosm on the left experienced 17 g/kg salinity and medium moisture for 4 wk, while the mesocosm on the right had 17 g/kg salinity and medium moisture for 1 wk followed by 3 wk of 34 g/kg salinity and low moisture. Photograph by the author.

from zero to one, increasing as germination occurs earlier in the experiment. Cumulative germination was sampled 10 times in this experiment; thus a 0.1 change in the index corresponds to a difference in germination of one sampling time (i.e., 3 d) for the average seed.

Statistical tests of the two germination response variables were performed individually for each species using SYSTAT software (SYSTAT 1992). The amplitude experiment was analyzed with three-way analyses of variance (ANOVAs) with randomized blocking, with the presence or absence of variation, salinity level, and moisture level as the main factors. The duration experiment was analyzed with two-way ANOVAs with randomized blocking, with duration of low salinity and high moisture as the main factors. Finally, the seasonal timing experiment was analyzed with two-way ANOVAs with seasonal timing and block as the main factors. Block was considered as a main factor since the likely mechanisms for seasonal timing effects, light and temperature differences, could also differ among the blocking variables (greenhouses). Percentage germination was arcsine square-root transformed in the ANOVAs to meet the assumptions of homoscedasticity and normality of residuals (Zar 1996). The germination speed index met the assumptions without transformation. All statistical tests were assessed for violations of assumptions with scatterplots. An α of 0.05 was used for all statistical analyses. Differences among treatment levels of significant main factors were assessed with Tukey's hsd multiple comparisons. The P values of each statistical test are reported in the Appendices.

To predict the response of species to varying soil salinity and moisture, correlated germination traits among species were identified, and these traits were related to the difference in percentage germination of each species between the varying and constant conditions. Pearson product-moment correlations ($N = 11$ species) of mean germination speed, salinity tolerance, and low-moisture tolerance were calculated. Relative salinity and low-moisture tolerance were calculated as {1 − [(low stress − high stress)/low stress]}. The high-stress and low-stress values used were the percentage germination at 17 g/kg and 0 g/kg or low moisture and high moisture for salinity and low-moisture tolerance, respectively. Because germination of some species sharply decreased to zero at 34 g/kg, 17 g/kg was used for the high-stress comparison. The mean germination speed of each species was calculated from the seasonal-timing experiment, which tested favorable salinity and moisture conditions, and is therefore independent of salinity and moisture tolerance.

A multiple regression ($N = 11$ species) was performed to determine which germination traits best explained the magnitude of the difference between constant and varying treatments in the amplitude experiment. Relative change in each species' percentage germination under varying compared to constant treatments was related to its germination speed, salinity tolerance, and low-moisture tolerance. Relative change in percentage germination of each species was calculated as [(constant − varying)/constant].

RESULTS

Amplitude experiment

Soil salinity averaged 2.2, 7.1, 14.6, and 30.9 g/kg through the course of the experiment in the constant 0, 8, 17, and 34 g/kg salinity treatments of the seedless microcosms, respectively (Fig. 3). After the seventh day of the experiment, soil salinity began to increase in the varying salinity treatments. Mean surface soil moisture in the seedless microcosms was 45.4%, 41.1%, and 34.8% in the high, medium, and low constant-moisture treatments, respectively (Fig. 3). Soil moisture decreased in the varying high, medium, and low moisture treatments after the seventh day. Soil salinity and moisture in the micrososms were similar to the range in conditions that occur during periods of germination in the field (Noe and Zedler 2001*a*, *b*).

The final percentage germination of seeds of all but

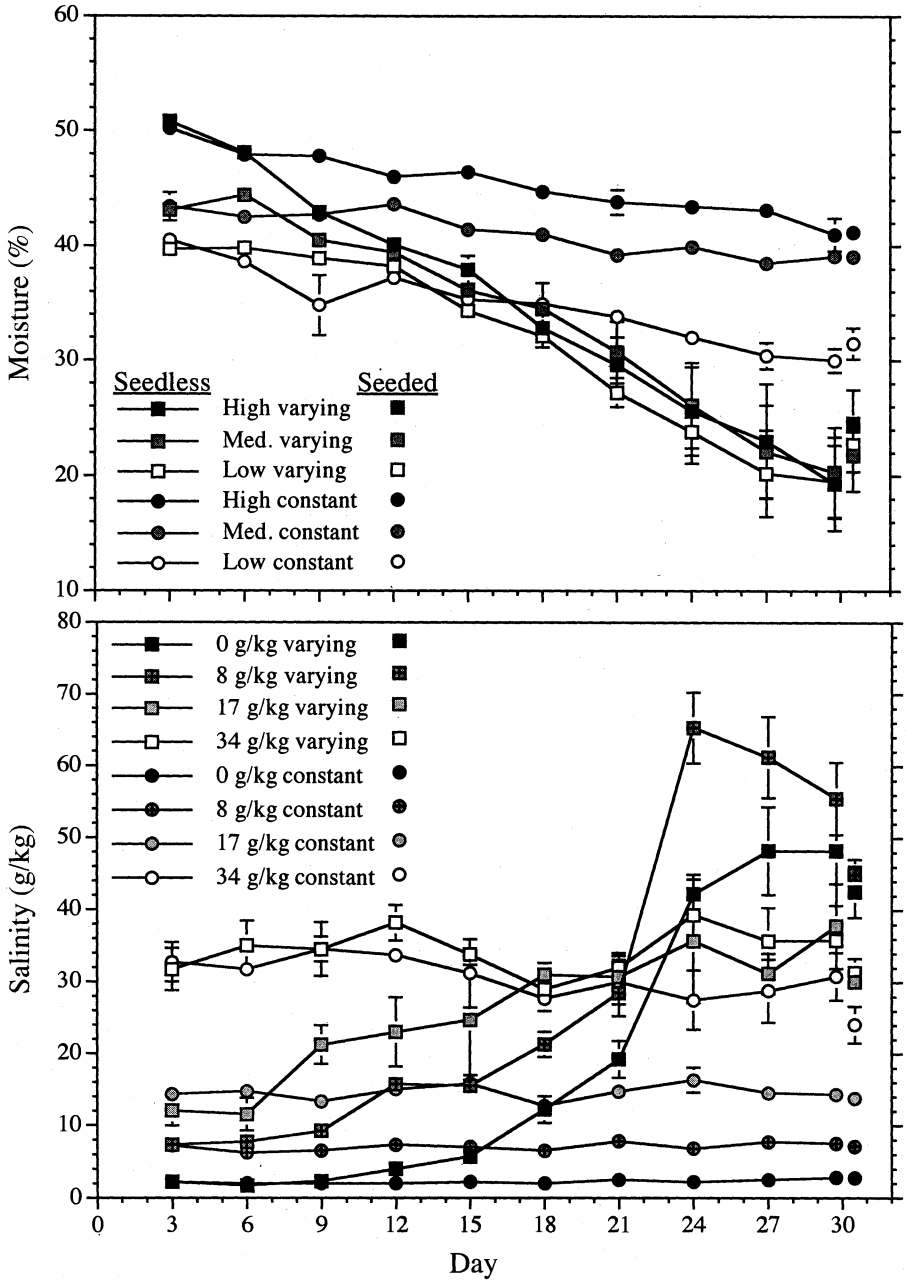

FIG. 3. Surface (1 cm) soil moisture and salinity in the seedless and seeded microcosms of the amplitude experiment (means ± 1 SE). Seeded microcosms were measured only at the end of the experiment.

three species decreased in the varying compared to the constant treatments of the amplitude experiment (Fig. 4; Appendix A; see Plate 1). Percentage seed germination of *Hutchinsia*, *Mesembryanthemum*, and *Polypogon* did not differ between varying and constant treatments, although *Hutchinsia* seeds had a large, but variable, decline in germination. Statistically significant changes in germination ranged from a 72% relative decline for *Lasthenia* seeds (from 13% to 4% of seeds germinating) to a 13% decrease for *Lolium* seeds (from 83% to 73% of seeds germinating). Seed germination speed of only two species responded to the varying treatments in the amplitude experiment (Fig. 5; Appendix B). *Amblyopappus* seeds germinated faster in varying than constant conditions, whereas *Juncus* seeds germinated slower in the varying compared to the constant treatments. The difference in the germination speed index between constant and varying treatments for *Amblyopappus* and *Juncus* seeds was 0.09 (a 16% increase) and 0.08 (a 23% decrease), respectively, and

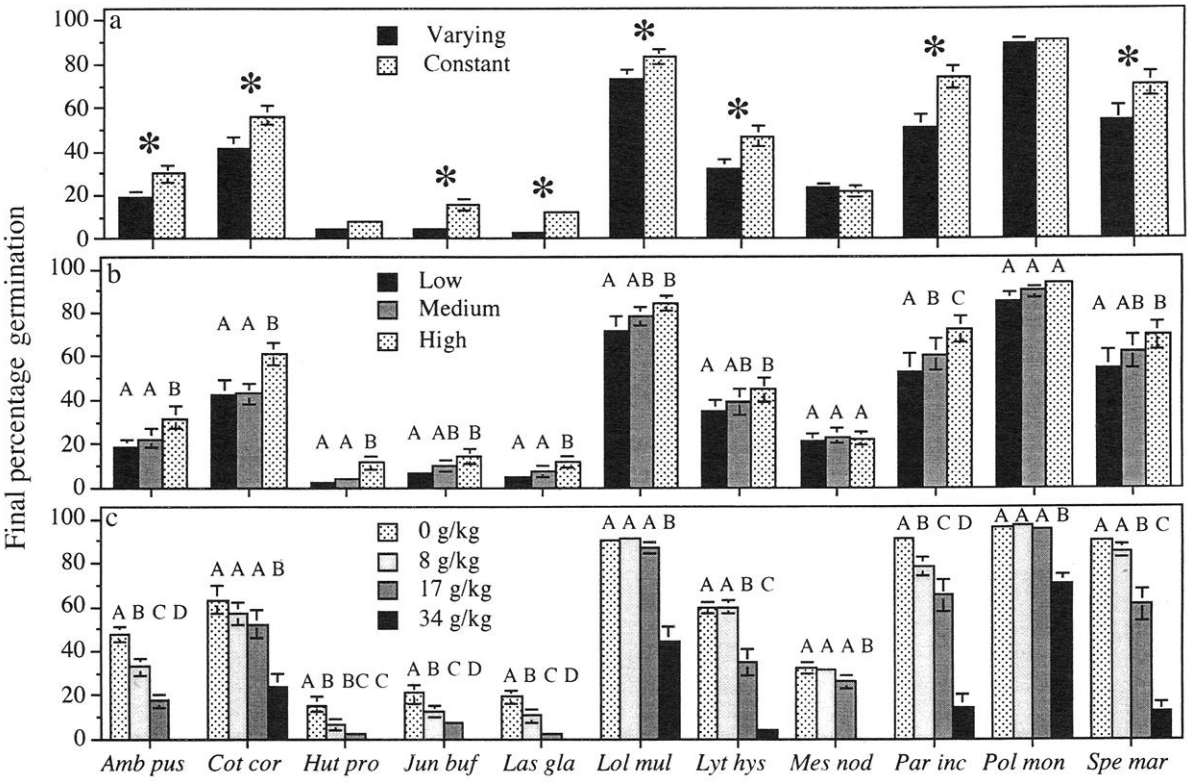

FIG. 4. Final percentage germination of seeds of each species in the (a) constant vs. varying treatments (pooled across salinity and moisture), (b) moisture treatments (pooled across salinity and constant vs. varying), and (c) salinity treatments (pooled across moisture and constant vs. varying) of the amplitude experiment (means ± 1 SE). Asterisks denote a significant difference between the constant and varying treatments, and different letters identify significant differences among moisture or salinity treatments for each species. See Table 1 for an explanation of species abbreviations.

is equivalent to a difference of about one sampling time (3 d).

Interactions between the amplitude of low salinity and the presence or absence of varying conditions affected the percentage germination of seeds of seven species (Appendix A). Differences between the varying and constant treatments occurred in the 0 g/kg salinity treatment for *Juncus* and *Lasthenia* seeds, at 8 g/kg for *Amblyopappus*, *Juncus*, *Lasthenia*, and *Parapholis* seeds, at 17 g/kg for *Amblyopappus*, *Juncus*, *Lasthenia*, *Lythrum*, *Parapholis*, and *Spergularia* seeds, and at 34 g/kg for *Lolium*, *Parapholis*, and *Spergularia* seeds. For example, *Lythrum* percentage seed germination differed among the varying vs. constant comparisons only when salinity in the varying treatment began at 17 g/kg but not 0, 8, or 34 g/kg. Salinity in the varying-34 g/kg and constant-34 g/kg treatments did not differ, but moisture decreased after 7 d in the varying-34 g/kg treatment. Therefore, the response of *Lolium*, *Parapholis*, and *Spergularia* seeds to varying vs. constant treatments in the 34 g/kg salinity amplitude is a response to decreasing moisture levels at high salinity. Fluctuation and salinity amplitude main factors interacted to affect the germination speed of seeds of five species (Appendix B). The presence or absence of varying conditions and moisture treatments interacted for only *Juncus* and *Lasthenia* seeds (Appendix A). For these species, a difference in percentage germination between varying and constant conditions occurred only at the medium- and high-moisture levels.

Percentage seed germination of each of the 11 species responded to the salinity amplitude main factor by decreasing at higher salinity (Fig. 4; Appendix A). Seed germination of the most salt-tolerant species, *Cotula*, *Lolium*, *Mesembryanthemum*, and *Polypogon*, decreased only at the 34 g/kg treatment. *Lythrum*, *Parapholis*, and *Spergularia* seed germination decreased at both the 17 and 34 g/kg treatments but germination occurred at the highest salinity. *Amblyopappus*, *Hutchinsia*, *Juncus*, and *Lasthenia* seeds had rapidly decreasing germination starting at 8 g/kg and did not germinate above 17 g/kg. Seed germination speed of each species was also affected by the salinity main factor (Fig. 5; Appendix B).

Percentage germination of seeds of all species but *Mesembryanthemum* and *Polypogon* differed among the moisture amplitude treatments (Appendix A). For those species that responded to moisture, germination was greatest in the high-moisture treatment; *Cotula* and *Hutchinsia* seeds were most responsive (Fig. 4). Mois-

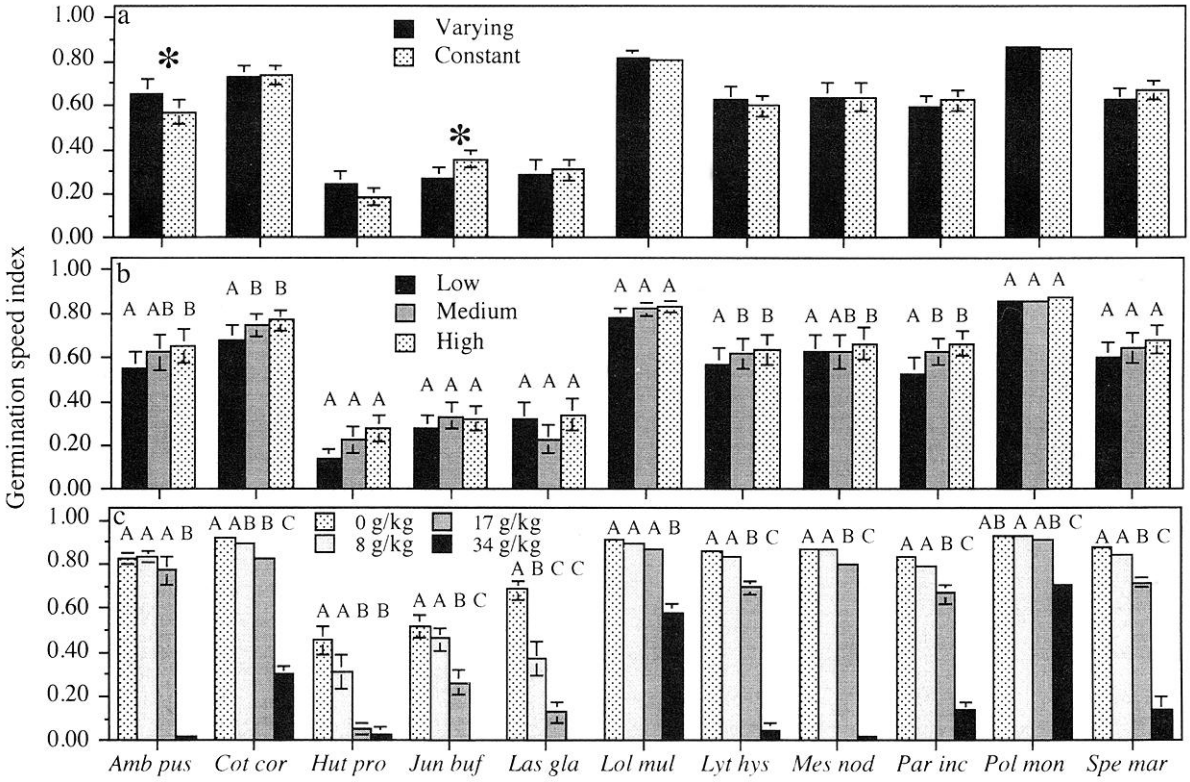

FIG. 5. Germination speed of seeds of each species in the (a) constant vs. varying treatments (pooled across salinity and moisture), (b) moisture treatments (pooled across salinity and constant vs. varying), and (c) salinity treatments (pooled across moisture and constant vs. varying) of the amplitude experiment (means ± 1 SE). Asterisks denote a significant difference between the constant and varying treatments, and different letters identify significant differences among moisture or salinity treatments for each species. See Table 1 for an explanation of species abbreviations.

ture levels had less of an influence on the speed of germination (Fig. 5). Germination speed of seeds of five species differed among the moisture treatments (Appendix B), although the magnitude of response was small.

Percentage germination of seeds of five of the 11 species had a significant interaction between the salinity and moisture treatments (Appendix A). Fewer seeds germinated at low moisture compared to high moisture for *Cotula*, *Lolium*, *Parapholis*, *Polypogon*, and *Spergularia*, but only at high salinity. Soil salinity and moisture interacted to affect the germination speed of only one species, *Cotula* (Appendix B).

The three main factors (variation, salinity, and moisture) interacted to affect the percentage germination of both *Parapholis* and *Spergularia* seeds (Appendix A), indicating that these species are very sensitive to differing combinations of salinity, moisture, and temporal variation regimes. In addition, the percentage germination of *Lolium* and *Parapholis* seeds differed among blocks (Appendix A). One possible source of the block effects was a difference in peak temperatures and the timing of direct sunlight among the greenhouse tables. However, species responses to the main experimental factors were consistent among blocks.

Duration experiment

Mean soil salinity in the 4-wk (constant low salinity) and 0-wk (constant high salinity) low-salinity treatments through the length of the experiment were 7.3 and 28.3 g/kg, respectively (Fig. 6), close to the targets of 8 and 34 g/kg. Salinity of the 1- and 2-wk low-salinity treatments started at 8 g/kg and began increasing after days 7 and 14, respectively. After day 21, soil salinity in the 1- and 2-wk low-salinity treatments increased rapidly and finished at very high salinity levels. Mean soil moisture in the 4-wk (constant high moisture) and 0-wk (constant low moisture) high-moisture treatments were 44.9% and 32.7%, respectively, throughout the experiment (Fig. 6). Moisture of the 1- and 2-wk high-moisture treatments began decreasing after days 7 and 14, respectively, and finished at very low moisture levels (~23%).

Percentage germination of each species' seeds decreased with constant 34 g/kg soil salinity compared to 1, 2, or 4 wk of 8 g/kg followed by 34 g/kg (Fig. 7; Appendix C). More important to the test of small

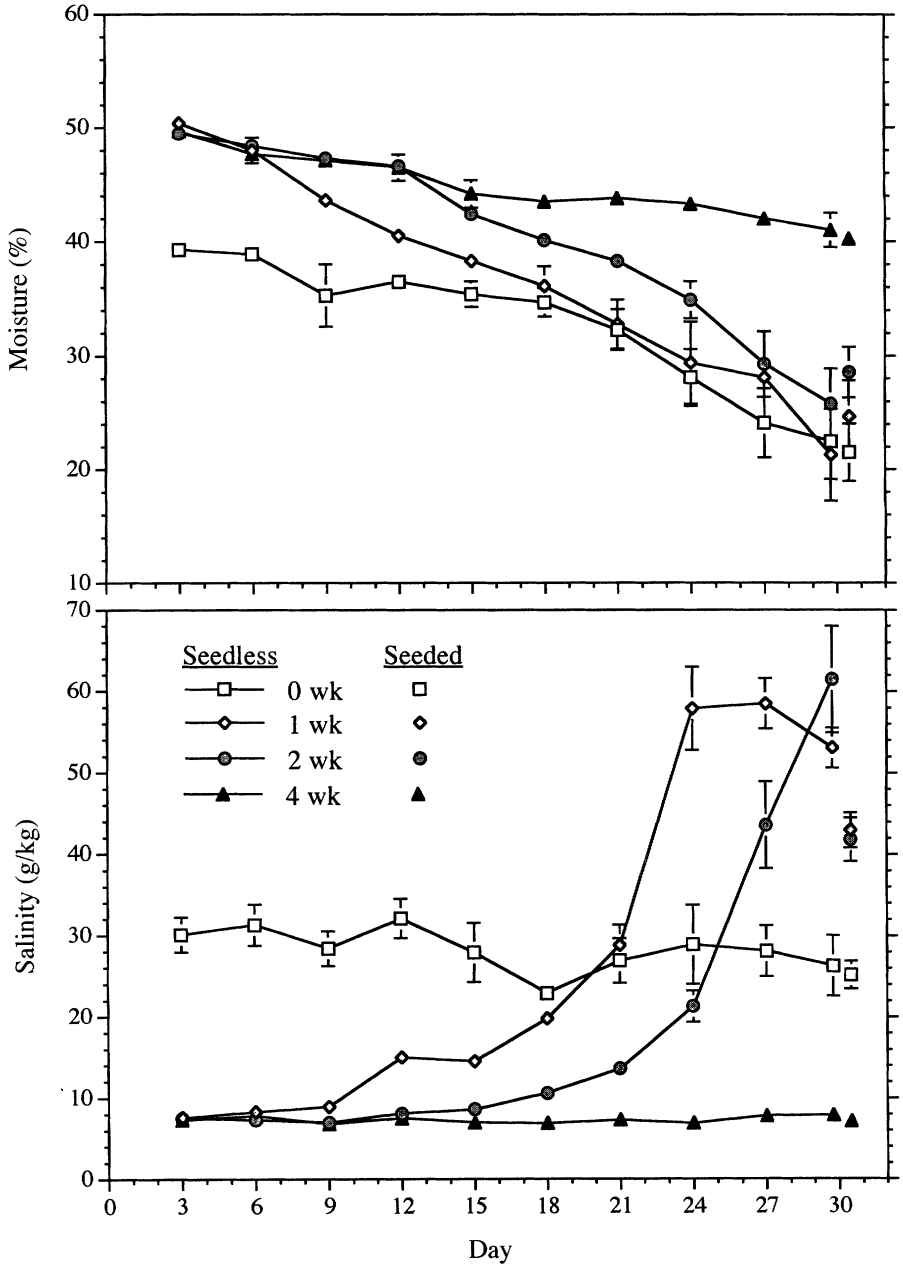

FIG. 6. Surface (1 cm) soil moisture and salinity in the seedless and seeded microcosms of the duration experiment (means ± 1 SE). Seeded microcosms were measured only at the end of the experiment.

differences in the duration of salinity, the percentage seed germination of four species differed among the 1-, 2-, or 4-wk low-salinity treatments. Fewer seeds of *Amblyopappus* and *Juncus* germinated with 1 wk compared to 2 or 4 wk of low salinity. *Hutchinsia* and *Lasthenia* seeds required 4 wk of low salinity for greatest germination, with similar germination in the 1- and 2-wk low-salinity treatments. Some treatment effects were large; for example, *Lasthenia* seed percentage germination was nearly tripled with 4 wk instead of 2 wk of low salinity.

Germination speed of seeds of two species differed among the 1-, 2-, or 4-wk low-salinity treatments (Appendix D). Germination occurred ~5 d earlier with 2 wk compared to 1 wk of low salinity for *Juncus* (index difference = 0.175; Fig. 8). *Amblyopappus* seeds germinated 3 d earlier with 1 wk of low salinity compared to 2 or 4 wk of low salinity (index difference = 0.100 and 0.103, respectively; Fig. 8). It is possible that slower-germinating *Amblyopappus* seeds did not germinate when salinity increased after the first week in the 1-wk treatment. Non-germinating seeds are not included

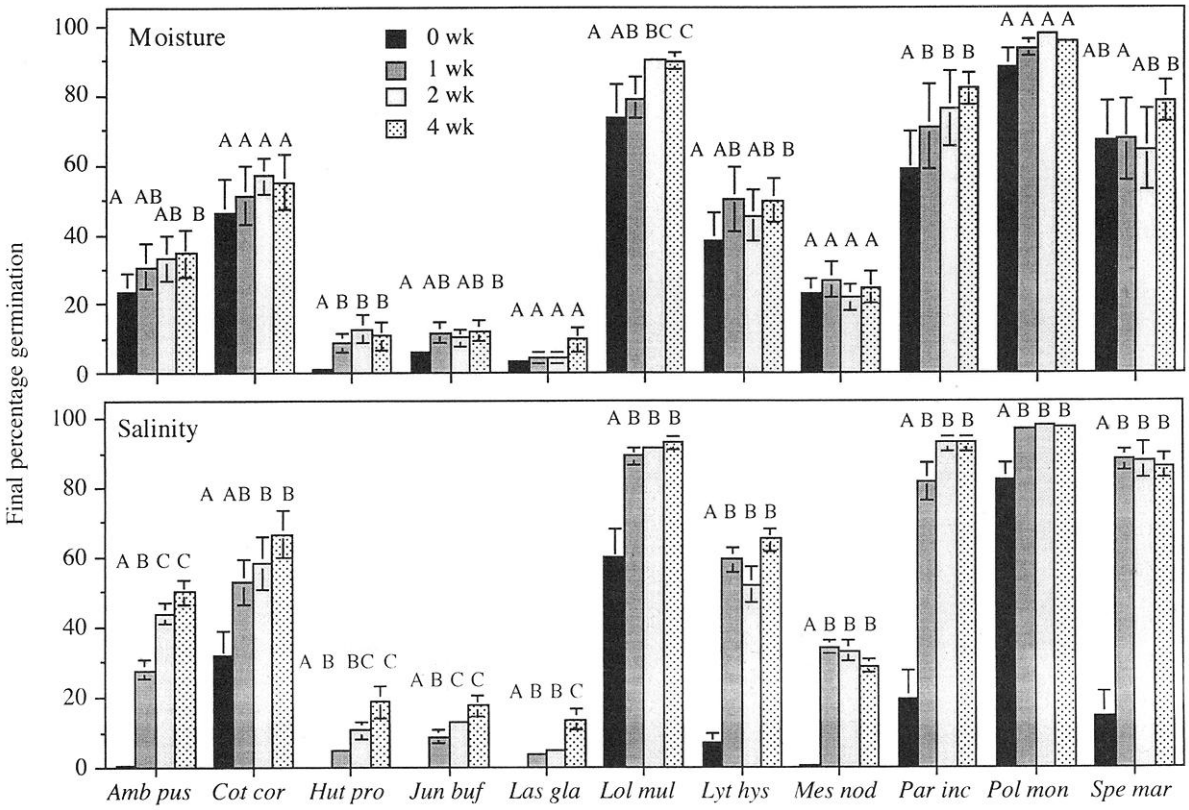

FIG. 7. Final percentage germination of seeds of each species in the moisture and salinity treatments of the duration experiment (means ± 1 SE, pooled across factors). Different letters identify significant differences among moisture or salinity treatments for each species. See Table 1 for an explanation of species abbreviations.

in the calculation of the germination speed index, and thus index values would increase (indicate faster germination). Seeds of all 11 species germinated more slowly with 0 wk (constant high salinity) compared to 1, 2, and 4 wk of low salinity.

The duration of high moisture had less of an effect than the duration of low salinity. The percentage germination of *Lolium* and *Spergularia* seeds decreased with 2 wk compared to 4 wk of high moisture (Fig. 7; Appendix C). However, size of the differences was small relative to the maximum percentage germination of each species. *Lythrum* seeds germinated more slowly with 1 wk compared to 2 wk of high moisture (Fig. 8; Appendix D).

The duration of low salinity and high moisture interacted to affect the percentage germination of seeds of six species (Appendix C). For example, *Juncus* percentage seed germination decreased with 1 wk of high moisture compared to 2 wk of high moisture, but only when the duration of low salinity was 1 wk. In addition, the percentage germination of *Parapholis* and *Spergularia* seeds with 0 wk of low salinity was greater when high moisture lasted 4 wk compared to 0, 1, or 2 wk. At constant high salinity, the germination speed of *Lythrum*, *Parapholis*, and *Polypogon* seeds slowed with 0 wk of high moisture compared to 2 and 4 wk of high moisture (Appendix D). Percentage germination of *Hutchinsia* and *Juncus* seeds and the germination speed of *Cotula*, *Lolium*, and *Polypogon* seeds also differed among blocks (Appendixes C and D).

Seasonal timing experiment

The November, January, and March treatments had differing temperatures and photoperiod. Mean high and low temperatures in the greenhouse structures during the seasonal timing experiment were 34.2° and 10.7°C, 32.7° and 8.3°C, and 40.4° and 12.1°C in November, January, and March, respectively. Daylight (sunrise to sunset) at the beginning of the treatments lasted 10 h, 29 min in November, 10 h, 14 min in January, and 11 h, 57 min in March (Nautical Almanac Office 1965). Percentage germination of *Amblyopappus*, *Hutchinsia*, *Lolium*, and *Parapholis* seeds differed when low salinity and medium moisture treatments were initiated in different months (Fig. 9; Appendix E). Peak germination occurred in different months for each of these species that responded. *Parapholis* seeds germinated more in November, *Hutchinsia* seeds in November and January, *Lolium* seeds in January, and *Amblyopappus* seeds in January and March (Fig. 9). Germination speed of seeds of 9 of the 11 species responded to the seasonal timing of low salinity and high moisture; the germi-

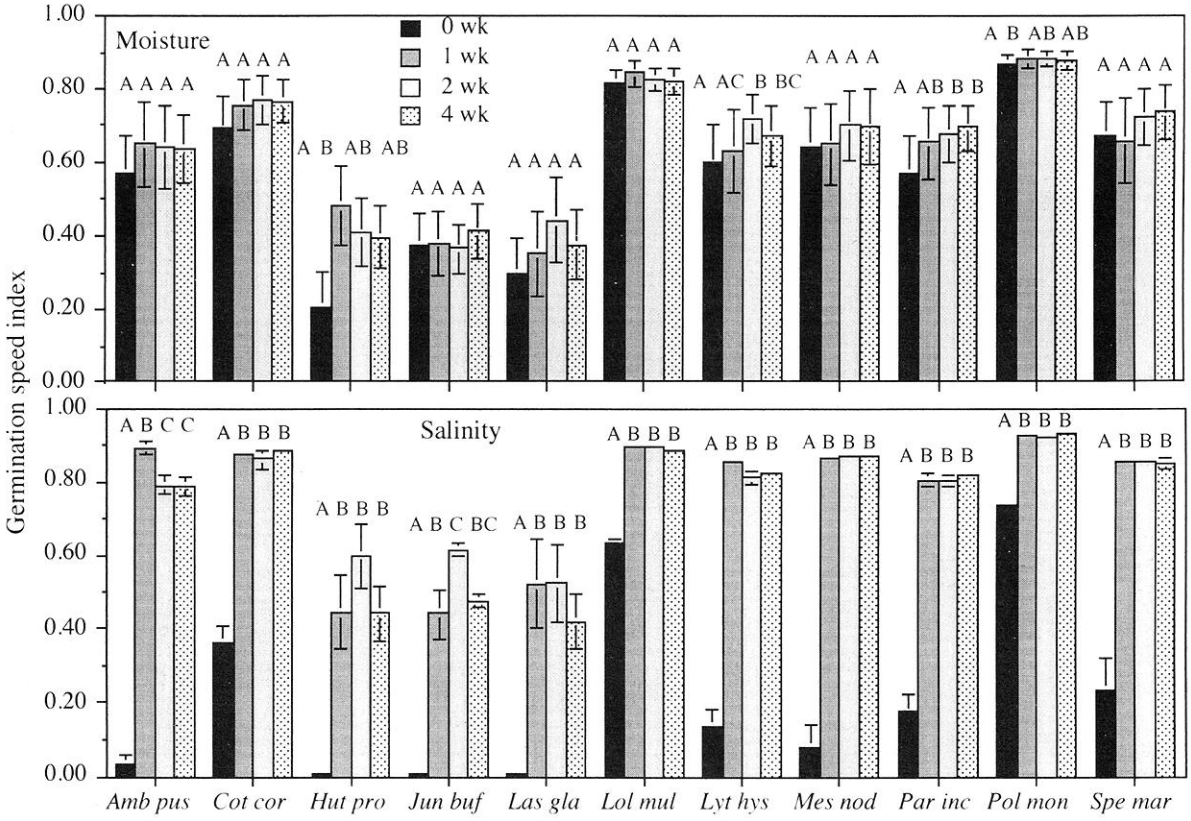

FIG. 8. Germination speed of seeds of each species in the moisture and salinity treatments of the duration experiment (means ± 1 SE, pooled across factors). Different letters identify significant differences among treatments for each species. See Table 1 for an explanation of species abbreviations.

nation speed of *Cotula* and *Hutchinsia* seeds did not respond (Appendix F). Similar to percentage germination, there was no general, consistent response among species seed germination speed to seasonal timing.

Percentage germination of *Cotula* seeds and speed of *Juncus* seed germination differed among blocks (Appendixes E and F). The third greenhouse was on average 2.5°C cooler and was shaded for a longer time than the first two greenhouses. Finally, seasonal timing and block factors interacted to affect *Lolium* percentage seed germination (Appendix E).

Explaining interspecific differences in responsiveness to varying conditions

Germination traits of species explain the magnitude of each species difference in percentage germination between the varying and constant treatments of the amplitude experiment. Speed, salt tolerance, and low-moisture tolerance during germination are correlated traits of species (Table 2). Due to the very strong correlation between salinity and low-moisture tolerance, the latter was dropped from the multiple regression analysis explaining species differences in seed germination between varying and constant conditions. Both the speed of germination ($b' = -0.489$) and salt tolerance of 17 g/kg ($b' = -0.545$) explain the magnitude of species differences in varying vs. constant conditions (df = 2, 8; adjusted $R^2 = 0.813$; $P = 0.001$). Fast germinating species that were also tolerant of high salinity responded less to temporal variation. Seeds of native species, with the exception of *Spergularia*, had larger germination responses to temporally varying conditions compared to seeds of exotic species.

DISCUSSION

Environmental factors vary through time in ecological systems; however, most experiments test the effects of temporally constant factors. Few studies have experimentally tested whether ecological systems respond to temporal variations in environmental conditions. However, such studies have found that the details of how environmental variables fluctuate are important for predicting patterns of germination. For example, Bliss and Zedler (1998) found that the duration of inundation determined the species richness and density of seedlings germinating from vernal pool seed banks. In the seed banks of Okefenokee Swamp, the frequency and timing of drawdown regulated germination and marsh species composition (Gerritsen and Greening 1989). In addition, Stockey and Hunt (1992) found that the germination of a wetland plant species increased

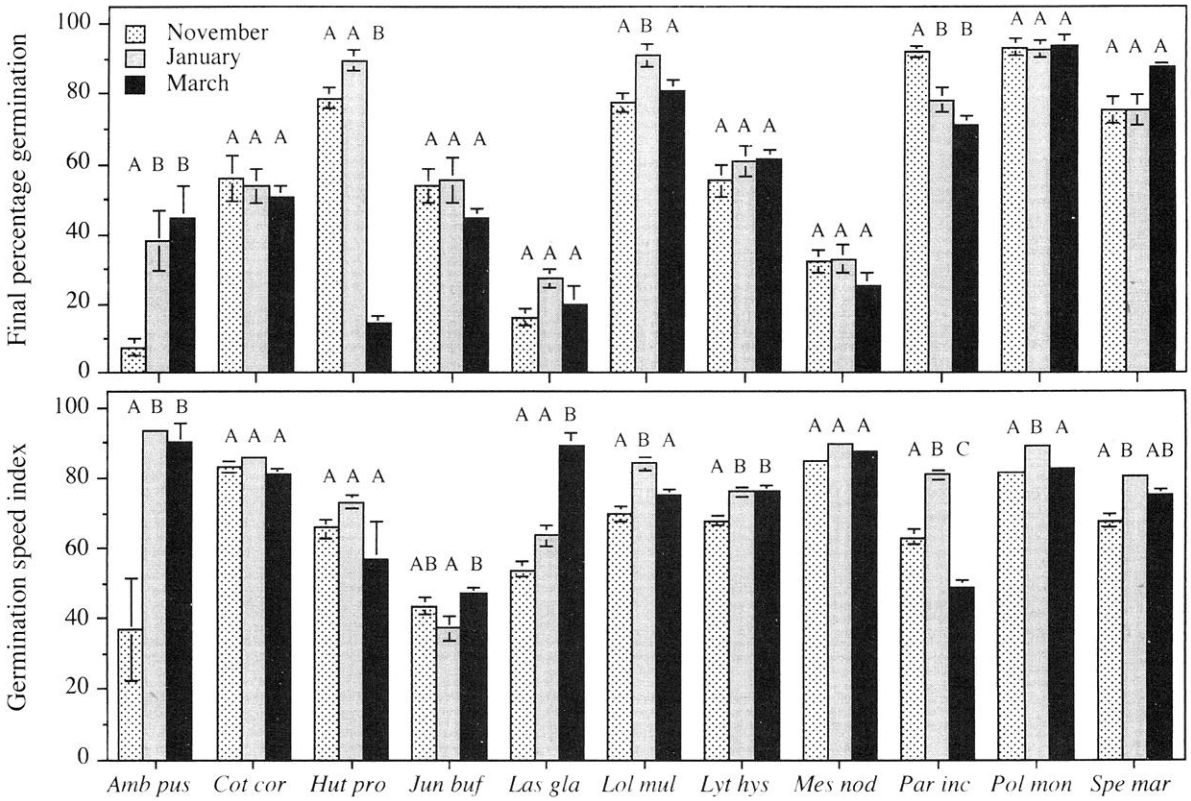

FIG. 9. Final percentage germination and germination speed of seeds of each species in the seasonal timing experiment (means ± 1 SE, pooled across factors). Different letters identify significant differences among treatments for each species. See Table 1 for an explanation of species abbreviations.

nearly tenfold in a fluctuating cycle of flood/wet/flood compared to constant flooded or wet conditions. Finally, the intensity and duration of high temperatures have been shown to affect germination after fires (Auld 1986).

I tested whether temporal variations in soil salinity and moisture result in different patterns of germination compared to constant conditions, utilizing an 11-species annual plant assemblage from the upper intertidal marsh of southern California. The fluctuations of soil salinity and moisture tested in this study were representative of salinity and moisture variation in the field (see Noe and Zedler 2001*b*). The final percentage germination or germination speed of seeds of 10 of the 11 species responded to temporal variations in the amplitude, duration, or seasonal timing of low soil salinity and high soil moisture. Many species responded to small differences in soil salinity and moisture regimes. There were also many interactions among factors and a few block effects (likely due to temperature or light differences) in the experiments. In growth chamber experiments, Noe and Zedler (2000) also found that photoperiod and temperature affect the seed germination of several species of this assemblage. Germination at constant temperature differed from diurnally fluctuating temperatures (Noe and Zedler 2000), further indicating the responsiveness of the species in this assemblage to fluctuations. Thus, the germination response of this species assemblage is sensitive to subtle temporal variation in multiple abiotic factors.

TABLE 2. Correlation matrix of seed germination speed index, high-salinity tolerance, and low-moisture tolerance (N = 11 species).

Germination variable	Speed index	Salt tolerance	Low-moisture tolerance
Speed index	···	0.588	0.658
Salt tolerance	0.057	···	0.911
Low-moisture tolerance	0.028	<0.001	···

Notes: Pearson correlation coefficients (r) are in the upper right of the matrix. P values are in the lower left of the matrix.

The type of temporal variation that resulted in the largest effect (range among treatments) on germination varied among species and response variables. The varying treatments in the amplitude, duration, and seasonal timing experiments had the greatest effect on the percentage seed germination of five, two, and two species, respectively. No type of variation influenced the percentage germination of *Mesembryanthemum* and *Polypogon* seeds. In an unreported, simultaneous experiment, additions of RO water to the soil surface stim-

ulated the percentage germination of *Lasthenia* (65%), *Amblyopappus* (51%), and *Hutchinsia* (36%) seeds to levels much higher than observed in the amplitude, duration, or seasonal timing experiments (Noe 1999). Germination speed of seeds was most affected by the seasonal timing treatments for six species and the duration treatments for two species. The germination speeds of *Cotula*, *Hutchinsia*, and *Mesembryanthemum* seeds were not affected by temporal variations in salinity or moisture. In general, interspecific differences in germination were larger than differences between constant and varying conditions. For example, significant differences in mean percentage seed germination between constant and varying treatments of the amplitude experiment ranged from 9% (*Lasthenia*) to 17% (*Spergularia*) while the mean percentage seed germination of species in the constant treatments of the amplitude experiment ranged from 8% (*Hutchinsia*) to 90% (*Polypogon*; Fig. 4).

Although these experiments ended before the initiation of flowering, individuals were able to grow and would likely have produced seed if they germinated. Any advantage gained by germinating faster in response to a germination cue (e.g., Grace 1987) could be offset if the cue does not reliably predict favorable conditions in the future (Venable 1989). In the upper intertidal marsh of southern California, surface soil salinity fluctuates highly and brief periods of low salinity can be followed by salinity >50 g/kg (Noe and Zedler 2001*b*). If soil salinity and soil moisture in the varying treatments had been more stressful later in the experiment, it is possible that the seedlings germinating in the varying conditions would have died. For most halophyte seeds, exposure to high salinity does not result in seed mortality and seeds that are subsequently exposed to low salinity can germinate (Ungar 1978). It is possible that the slower-germinating species have developed the requirement for long periods of low salinity to germinate and remain dormant during short periods of low salinity. It would be expected that species with a shorter time from germination to seed production would germinate quickly and not be affected by varying conditions. For example, *Hutchinsia* plants flower from 1 to 2 mo after germination and set seed before the other species of the annual plant assemblage (*personal observation*). Contrary to this prediction, *Hutchinsia* was one of the species with seeds that were most salt intolerant, slowest to germinate, and negatively affected by varying conditions.

As was hypothesized, germination traits, quantified to be independent of the varying vs. constant comparisons, predicted which species had larger differences in percentage seed germination between constant and varying conditions. Species with seeds that were more sensitive to temporal variations of soil salinity and moisture also germinated more slowly at low salinity and had larger decreases in percentage germination at both high salinity and low moisture. Seeds of native species tended to possess these traits and had large decreases in percentage germination in varying treatments relative to constant treatments. In contrast, seeds of exotic species germinated fast, were tolerant of high salinity and low moisture, and were insensitive to temporal variations. However, species did not exhibit any discernible strategy to maximize percentage germination or germination speeds of seeds at certain temperatures or photoperiods.

The seeds of exotic species also had higher percentage germination and faster germination speed than the native species. The aboveground biomass of three exotic grasses, *Lolium*, *Polypogon*, and *Parapholis*, dominated the assemblage at the end of the experiment (Noe 1999). *Parapholis* growth was more tolerant of salinity and moisture than its germination, whereas the opposite was true for *Lolium* and *Polypogon* (*unpublished data*). *Spergularia marina*, the native species with similar germination traits as the exotics, is listed as a native species in California but is also found in South America and Eurasia and is a member of a cosmopolitan genus (Hickman 1993). Contrary to what was hypothesized, none of the soil salinity or moisture regimes tested in this experiment favored native species over exotics. The ability of the exotics to outperform the natives during germination may explain why exotic species are so abundant in southern California upper intertidal marshes (up to 92% of all seedlings; Noe and Zedler 2001*a*). These results also suggest that attempts to control exotic species in southern California coastal marshes by increasing soil salinity, such as the addition of salt crystals to the surface of marsh soils (Kuhn and Zedler 1997), will eliminate native annual species if they are present. Other studies found seeds of these exotic species to be less salt tolerant during germination than native species. However, these studies compared exotic annual species to native perennial species (Kuhn and Zedler 1997, Callaway and Zedler 1998); it is possible that native annual species are less salt tolerant than native perennial species. Noe and Zedler (2001*a*) found that exotic annuals, with the exception of *Parapholis* and *Mesembryanthemum*, occurred in areas with lower soil salinity than native annuals in the upper intertidal marshes of southern California. The seeds used in the experiments presented here were collected from the same wetlands. Neither the constant nor varying soil salinity and moisture treatments suggested that exotic annuals would be found at lower salinity than natives in the field. There are three likely reasons for this discrepancy: the importance of other environmental factors, limited seed dispersal, or competition.

The importance of salinity and moisture should be considered relative to other factors that influence the distribution and abundance of species in the field. Noe and Zedler (2001*a*) found that surface (2 cm) soil salinity and moisture explained only 2% of the spatial variation in the distribution of seedlings. Perennial

plant cover, elevation, soil texture, and differences among the wetlands explained much more variation (34%; Noe and Zedler 2001*a*). In addition, germination patterns at different constant soil salinity and moisture levels in a soil-based growth chamber experiment did not predict species densities along spatial gradients of surface soil salinity and moisture in the field (Noe and Zedler 2000). Species tended to occur at lower soil salinity and moisture in the field than would be expected from the results of the growth chamber experiment (Noe and Zedler 2000). This difference between field distributions and germination in constant conditions is consistent with the effects of temporally varying conditions on germination. Germination decreased when salinity varied from low to high, as occurs in the field following rainfall, compared to constant low salinity. Thus, the effects of varying conditions could explain the limitation of species to areas of lower-than-expected mean salinity.

Alternatively, the low abundance of exotics in higher salinity areas might be due to limited seed dispersal. At Los Peñasquitos Lagoon, the major vector for the seeds of invading species is anthropogenically enhanced freshwater flows that increase soil moisture and reduce soil salinity. Less-impacted, high-salinity areas receive less freshwater flow and thus fewer seeds of invading species. The results of the experiments reported here suggest that once the seeds of exotic annual species arrive in higher salinity areas, they will germinate. Because germination is generally more sensitive to salinity than later life history stages (Waisel 1972, Ungar 1978), successful germination should lead to successful establishment and then reproduction.

Finally, competition could also explain why these experiments could not predict field distributions. In this experiment, each microcosm had a common species pool so that the germination of the assemblage could be tested in the absence of seed-bank limitation. There is mixed evidence from other annual plant systems suggesting that the distribution of seeds in the upper intertidal marsh may be influenced by interspecific competition (e.g., Palmblad 1968, Inouye 1980, Inouye et al. 1980, Kadmon and Shmida 1990, Kalisz and McPeek 1992, Casanova and Brock 1996, Rees et al. 1996).

Conclusion

Temporally varying soil salinity or moisture resulted in different germination patterns than constant salinity or moisture. The final percentage germination or speed of germination of seeds of 10 of the 11 species of an annual plant assemblage responded to differing amplitudes, durations, or seasonal timing of low salinity or high moisture. In addition, the responsiveness to temporal variability differentiates the germination requirements of seeds of native and exotic species and is correlated with species germination traits. Because the exotic annuals outperformed the native annuals and tolerated fluctuating saline conditions, it is predicted that exotic species will become more dominant in southern California coastal wetlands. Treatments with temporal variations of soil salinity or moisture more closely approximate variability in wetlands and the varying treatments in this study led to different seedling assemblages than constant treatments. Therefore, future experimenters should carefully choose treatments so that they simulate conditions in wetlands, depending on the specific objectives of the experiment. These results also suggest that the choice of experimental models needs closer scrutiny in ecology. Environmental conditions fluctuate in ecological systems and these variations can have impacts on ecological processes; the inclusion of temporal variation of environmental variables in experiments deserves higher priority.

Acknowledgments

This work was funded in part by the Earth Island Institute, the San Diego State University Joint Doctoral Program, the Achievement Rewards for College Scientists (ARCS) Foundation, and the Sanctuaries and Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanographic and Atmospheric Administration. I thank Joy Zedler for helpful and stimulating insights on study design and Vicki Tripolitis and Meghan Fellows for assisting with the experiments. Boyd Collier, Michael Johnson, Alan Knapp, Joy Zedler, and anonymous reviewers provided constructive reviews of the manuscript.

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APPENDIX A

An ANOVA table presenting the final percentage germination of each species in the amplitude experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A1.

APPENDIX B

An ANOVA table for the germination speed index of each species in the amplitude experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A2.

APPENDIX C

An ANOVA table for the final percentage germination of each species in the duration experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A3.

APPENDIX D

An ANOVA table for the germination speed index of each species in the duration experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A4.

APPENDIX E

An ANOVA table for the final percentage germination of each species in the seasonal timing experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A5.

APPENDIX F

An ANOVA table for the germination speed index of each species in the seasonal timing experiment, giving ANOVA probability values, is available in ESA's Electronic Data Archive: *Ecological Archives* M072-006-A6.