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DIFFERENTIAL EFFECTS OF FOUR ABIOTIC FACTORS ON THE GERMINATION OF SALT MARSH ANNUALS[1]

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Interspecific differences in responsiveness to temperature, photoperiod, soil salinity, and soil moisture confirm the hypothesis that abiotic factors differentially affect the germination of salt marsh plants. In growth chamber experiments, four of eight annual species responded to small differences in temperature or photoperiod. Increasing soil salinity decreased the final proportion of seeds germinating and slowed germination for each of the seven species tested. Higher soil moisture increased the proportion germinating of five species and germination speed of all seven species. Salinity and moisture interacted to affect the proportion germinating of five species and germination speed of all seven species. Although the abiotic factor with the largest effect on germination varied among species, more species responded to, and the magnitudes of the responses were larger for, soil salinity than for the other abiotic factors. These germination tests partially explained interspecific differences in the timing of germination in the field. Patterns of *Hutchinsia procumbens*, *Lythrum hyssopifolium*, *Parapholis incurva*, and possibly *Lasthenia glabrata* ssp. *coulteri* germination in response to a nonseasonal rainfall could be explained by their response to salinity, temperature, or photoperiod. Fine-scale differences in the timing of establishment within the typical germination window and spatial distributions along salinity and moisture gradients were not explained.

Key words: germination; moisture; photoperiod; salinity; salt marsh annual plants; temperature.

A common goal of ecologists is to predict patterns of plant establishment in the field using germination experiments. However, germination studies are frequently performed in ways that make it difficult to extrapolate results to the field (Baskin and Baskin, 1998). This may be due to testing nonmeaningful factors or testing too few factors. There is an understanding in ecology that factors interact and that testing multiple factors may be necessary to predict the dynamics of plant communities (Chapin et al., 1987; Mooney, Winner, and Pell, 1991; Bazzaz and Wayne, 1994; Bazzaz, 1996). For example, the combination of responses to multiple factors is necessary to predict the establishment and composition of the annual community in old fields (Bazzaz, 1996). In wetlands, several authors suggest that testing multiple abiotic factors may be necessary to predict plant establishment (Galinato and van der Valk, 1986; Weiher and Keddy, 1995; Leck, 1996). However, salt marsh studies have emphasized the effect of one factor, salinity, on germination (Kingsbury et al., 1976; Ungar, 1978, 1996; Woodell, 1985; Zedler and Beare, 1986; Callaway et al., 1990; Shumway and Bertness, 1992; Keiffer and Ungar, 1997; Kuhn and Zedler, 1997; Baskin and Baskin, 1998; Callaway and Zedler, 1998) compared to the effects of soil moisture (Baldwin, McKee, and Mendelssohn, 1996; Kuhn and Zedler, 1997; Baskin and Baskin, 1998), or temperature or photoperiod (Pihl, Grant, and Somers, 1978; Khan and Ungar, 1997; Baskin and Baskin, 1998), although there is a larger literature on the influence of temperature or photoperiod on the germination of freshwater wetland species (Thompson and Grime, 1983; Galinato and van der Valk, 1986; Leck, 1989, 1996). Finally, the choice of meaningful treatments is also critical; factors should be tested at levels that can be related to differences in the field at the time of germination. There is a paucity of studies that explicitly test whether multiple interacting abiotic factors, tested at levels found in the field during germination, are necessary to explain observed patterns of establishment in plant communities.

The salt marshes of southern California offer an opportunity to test our ability to predict field seedling establishment based on responses to abiotic factors. The upper intertidal marsh of southern California includes up to 20 annual plant species (Noe, 1999). Germination is highly punctuated due to the region's mediterranean-type seasonality; annual plants typically germinate during the wet, mild winter season and senesce by the dry, hot summer season. In a separate field study, we monitored the density of seedlings (including those with just cotyledons; Noe, 1999). Counts were made weekly during the 1996 period of germination and monthly in 1997. Germination typically occurs between November and March, but individual species establish seedlings either early in, late in, or throughout this ''germination window'' (Table 1). We have shown that temporal variance in soil salinity, and to a lesser degree soil moisture, explains a significant portion of the timing of germination (all species combined) at three southern California coastal wetlands (Noe, 1999). However, annual rainfall totals and the seasonal timing of rainfall are variable (Noe, 1999), and most species' germination does not follow the same strategy every year (Table 1). Additional variability was observed when a rare, early-season rainfall from Hurricane Nora in September 1997 stimulated the germination of selected species (Table 1; Noe, 1999). The seedlings of annual species also segregate along spatial gradients of surface soil salinity and moisture (Noe, 1999).

The variance in the timing of establishment of species is most likely due to temporal differences in soil salinity, soil moisture, photoperiod, or temperature and differential respons-

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TABLE 1. The timing of germination of annual species in the upper intertidal marsh of southern California. Timing of germination and relative density of seedlings are summarized from Noe (1999). Blanks in the table indicate that the species did not occur in the subset of wetlands that were monitored in the 1997 season. The nomenclature follows Hickman (1993).

Species	Nonseasonal germination	Timing within 1996 season	Timing within 1997 season	Density rank
Amblyopappus pusillus Hook. and Arn. (Asteraceae)	slight	prolonged	early	4
Cordylanthus maritimus ssp. *maritimus* Benth. (Scrophulariaceae)	no	late	late	12
Cotula coronopifolia L. (Asteraceae)	yes	early		9
Hutchinsia procumbens (L.) Desv. (Brassicaceae)	no	prolonged	early	5
Juncus bufonius L. (Juncaceae)	no	late	prolonged	3
Lasthenia glabrata ssp. *coulteri* (A. Gray) Ornd. (Asteraceae)	yes	early	prolonged	6
Lolium multiflorum Lam. (Poaceae)	yes	early		11
Lythrum hyssopifolium L. (Lythraceae)	yes	early		8
Mesembryanthemum nodiflorum L. (Aizoaceae)	slight	prolonged	early	2
Parapholis incurva C.E. Hubb. (Poaceae)	no	prolonged	prolonged	1
Polypogon monspeliensis (L.) Desf. (Poaceae)	yes	early		7
Sonchus oleraceus L. (Asteraceae)	slight	late	early	13
Spergularia marina (L.) Griseb. (Caryophyllaceae)	slight	late		10

es of species to these abiotic factors. In the upper intertidal marsh of southern California, soil moisture and salinity fluctuate in response to the amount of daily rainfall during the germination window (Noe, 1999). We expect that soil salinity will have the largest effect on species because levels of salinity during the short germination window are stressful and variable while differences in temperature and photoperiod are small. Additionally, there is a large literature on the influence of salinity on the germination of salt marsh plants. Some annual species in the upper intertidal marsh of southern California likely have a proportion of seeds that are dormant and enter a seed bank (G. B. Noe and J. B. Zedler, personal observation); however, it is unlikely that seeds are buried in this rarely inundated community with low litter production and little soil disturbance. Therefore, the species may not respond to temperature or light like other species with buried seed banks (e.g., Thompson and Grime, 1979, 1983; Grime et al., 1981). For seeds in mediterranean-type climates, cooler temperatures could signal the onset of the wet season and favorable conditions for seedlings.

Experiments determining the effect of salinity on germination are typically conducted at very high moisture levels for the duration of the experiment. Such tests may not be relevant to field conditions because upper intertidal salt marsh soils are rarely saturated for more than a few days at a time. Salinity can have both osmotic and toxic effects on halophyte seeds (Waisel, 1972; Ungar, 1978; Baskin and Baskin, 1998). The interaction of soil salinity and moisture on germination would have important implications for predicting the distribution of salt marsh plants. It would be more appropriate to conduct such laboratory experiments at several moisture levels and to use a factorial experimental design in order to identify the interaction.

The goal of this study was to explain differences in the establishment of species as described in three coastal wetlands in southern California (Table 1; Noe, 1999). To address this goal, we (1) determined the effect of soil salinity, soil moisture, temperature, and photoperiod on germination, (2) compared the magnitude of the effects of each abiotic factor on germination, and (3) assessed the interaction of soil salinity and moisture on germination. We tested ecologically relevant treatments that could be related to field conditions when the annual species germinate in the upper intertidal marsh of southern California. The average climatic conditions of November and March were chosen to represent the beginning and end of the germination window. We also chose a range of soil salinity and moisture levels that is similar to conditions when germination occurs in the field.

We tested ten annual species of the upper intertidal marsh in southern California that accounted for 88% of all seedlings in the 1996 germination window (Noe, 1999). Responses were assessed with both the final proportion of seeds germinating and the speed of germination. The final proportion germinating (''proportion'' hereafter) is a useful measure of establishment and potential community composition and relative abundance. Speed of germination can be an important determinant of intraspecific and interspecific interactions (Harper, 1977; Grace, 1987; Bazzaz, 1996). Because of the potential importance of germination speed, we created an index of the speed of germination that factors out the proportion of seeds germinating and is therefore independent of viability, as compared to Timson's Σn (Timson, 1965) and other indexes (Brown and Mayer, 1988).

MATERIALS AND METHODS

Seed collection, storage, and treatment—Seeds of ten species were collected after plant senescence in 1997 from plants that were growing within the salt marsh (Table 2). Of 20 annual plant species that occur in the system, these ten species produced sufficient seed to permit collection and were selected to include a range of native and exotic, common and rare annual species. Seeds were collected from areas of sparse perennial canopy and along the edges of salt pannes (dominant perennial plant species in both habitats are *Salicornia subterminalis* and *Monanthochloë littoralis*), areas where most seedlings are found in the upper intertidal marsh of southern California. Seeds were collected from three locations in San Diego County, California, USA: the northern arm (Oneonta Slough) of Tijuana River National Estuarine Research Reserve; Sweetwater Marsh National Wildlife Refuge; and Los Peñasquitos Lagoon. All ten species have small seeds (~0.2–5 mm^3).

The seeds were stored dry and under ambient room temperatures (16°–37°C) and a light regime that was typical of summer photoperiod. To our knowledge there is no evidence for recalcitrance among these species. We believe that the storage conditions used in this study are similar to what seeds experience in the upper intertidal marsh of southern California in the period after dispersal in late spring or early summer and prior to germination in the winter. The length of storage varied from 5 to 20 mo depending on the date of seed maturation and collection in the field (Table 2) and the timing of the experiments (Table 3).

Seeds were only used if they had intact seed coats and appeared to have

TABLE 2. Species used in the photoperiod-temperature experiment and salinity-moisture experiment, information on their collection, and the starting date of the salinity-moisture experiment runs. Wetland: LPL=Los Peñasquitos Lagoon, SW=Sweetwater Marsh National Wildlife Refuge, TE=Tijuana River National Estuarine Research Reserve.

Species	Date(s) of seed collection	Seed processing	Wetland	Photoperiod temperature	Salinity-moisture
Amblyopappus pusillus	6-2-97	none	SW		8-22-98
Cordylanthus maritimus ssp. *maritimus*	8-97	none	TE		10-26-98
Cotula coronopifolia	4-3-97	none	LPL	X	
Hutchinsia procumbens	3-24-97, 3-31-97	none	SW	X	7-14-98
Lasthenia glabrata ssp. *coulteri*	3-31-97, 4-3-97	none	LPL, SW	X	10-26-98
Lythrum hyssopifolium	6-3-97	none	LPL	X	
Mesembryanthemum nodiflorum	7-21-97	fruit soaked 15 m	SW	X	9-23-98
Parapholis incurva	5-5-97, 5-12-97, 5-14-97	seed left in floret	LPL, SW, TE	X	9-23-98
Polypogon monspeliensis	5-14-97	seed removed from floret	LPL	X	
Spergularia marina	4-3-97	none	LPL	X	8-22-98

embryos. The seeds of the grass *Polypogon monspeliensis* were removed from the floret to ensure the presence of a seed. *Parapholis incurva* 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 (G. B. Noe, personal observation). *Mesembryanthemum nodiflorum* fruits were soaked in deionized water for 15 min to facilitate seed removal. Seeds of the federal and state-listed endangered *Cordylanthus maritimus* ssp. *maritimus* were collected pursuant to United States Department of the Interior Endangered Species Act recovery permit number PRT 823806 and California Department of Fish and Game Research Permit 96–01-RP. Preliminary attempts to transplant seedlings failed. Therefore, *Cordylanthus maritimus* ssp. *maritimus* seedlings were not returned to the field.

Temperature and photoperiod—Eight upper intertidal marsh annual species (Table 2) were tested for differences in germination between the mean constant temperatures, mean diurnal fluctuating temperatures, and photoperiods of November and March (Table 3). Four comparisons were tested: November vs. March constant mean daily temperature, November constant vs. diurnal fluctuating mean temperature, March constant vs. diurnal fluctuating mean temperature, and 15 November vs. 15 March photoperiod. The three temperature comparisons were run at March photoperiod, and the photoperiod comparison was conducted at November constant mean temperature. The duration of diurnal temperatures treatments corresponded with the length of light and dark in the March photoperiod. Temperatures for coastal San Diego County were determined from the National Weather Service's 30-yr average daily temperature normals for Lindbergh Field (Table 3; National Climatic Data Center, Comparative Climatic Data). Daylengths (sunrise to sunset) on 15 November and 15 March for San Diego were obtained from the Nautical Almanac Office (1965).

The experimental unit consisted of 25 seeds of a species placed in a petri dish (6.0-cm diameter) inside a temperature- and light-controlled Percival® growth chamber. The seeds were evenly placed on a glass fiber filter (4.7-cm diameter) that rested on a thin styrofoam wafer floating on 9 mL of deionized water. The edge of the filter was in contact with the water to keep the filter uniformly moist but not waterlogged. The experiment used a randomized complete block design with four replicates per treatment, with the petri dishes blocked by growth chamber shelf. The number of germinated seeds in each petri dish was counted every 3 d for 30 d. Germination was defined as root radicle or cotyledon emergence. The species in this study germinate with different speeds, although the rank of species' speed of germination is affected by the experimental treatments (see Results). The location of the petri dishes within a block was rerandomized every 6 d. The temperature and photoperiod treatments occurred consecutively (Table 3). To determine the effect of seed aging, the first treatment was repeated at the end of the planned temperature and photoperiod comparisons.

Soil salinity and moisture—Seven upper intertidal marsh annual species were tested for their response to constant moisture and salinity levels (Table 2). Three moisture treatments, high, medium, and low, were fully crossed with four salinity treatments, 34, 17, 8, and 0 ppt. The moisture and salinity treatment levels were chosen to represent a range of conditions found in southern California high salt marsh during periods of germination (Noe, 1999). In order to break any temperature-related dormancy, seeds of each species were cold treated at 5°C for 15 d prior to the start of the experiment. The duration and temperature of the cold treatment were chosen to simulate conditions in coastal San Diego during the winter; minimum temperature rarely reaches 5°C for long periods of time. Species were tested two at a time after the first run with one species (Table 2).

The experimental unit consisted of 25 seeds of a species placed in a microcosm, located inside a temperature- and light-controlled Percival® growth chamber, as above. A microcosm consisted of a soil-filled plastic cup that rested on a wood block inside an outer plastic cup (Fig. 1). The inner cup was filled with 250 mL of mineral soil (48% sand, 41% silt, and 11% clay) that had been passed through a 2-mm sieve. To create the three moisture treatments, the outer cup had a hole at one of three different heights to regulate the depth of water relative to the soil surface. Water of one of four different salinity levels was added to the outer cup to create the different soil salinity treatments. Seeds were evenly placed on flat areas of the soil surface to avoid differences in microtopography. Species with nonspherical seeds were placed with their longitudinal axis flat on the soil surface. The outer cup of each microcosm was covered with a petri dish lid to limit evaporation and maintain constant soil salinity and moisture. The salinity and moisture trials

TABLE 3. Treatments in the temperature, photoperiod, and seed aging tests.

Treatment	Temperature (°C)	Photoperiod (h:min)	Starting date	Experimental order
November constant temperature/March photoperiod	16.7	11:57 light, 12:03 dark	12-3-97	1
November diurnal temperature fluctuation/March photoperiod	21.1/12.2	11:57 light, 12:03 dark	1-20-98	2
March constant temperature/March photoperiod	15.3	11:57 light, 12:03 dark	4-14-98	4
March diurnal temperature fluctuation/March photoperiod	19.1/11.6	11:57 light, 12:03 dark	5-22-98	5
November constant temperature/November photoperiod	16.7	10:29 light, 13:31 dark	2-26-98	3
November constant temperature/March photoperiod (seed age test)	16.7	11:57 light, 12:03 dark	7-8-98	6

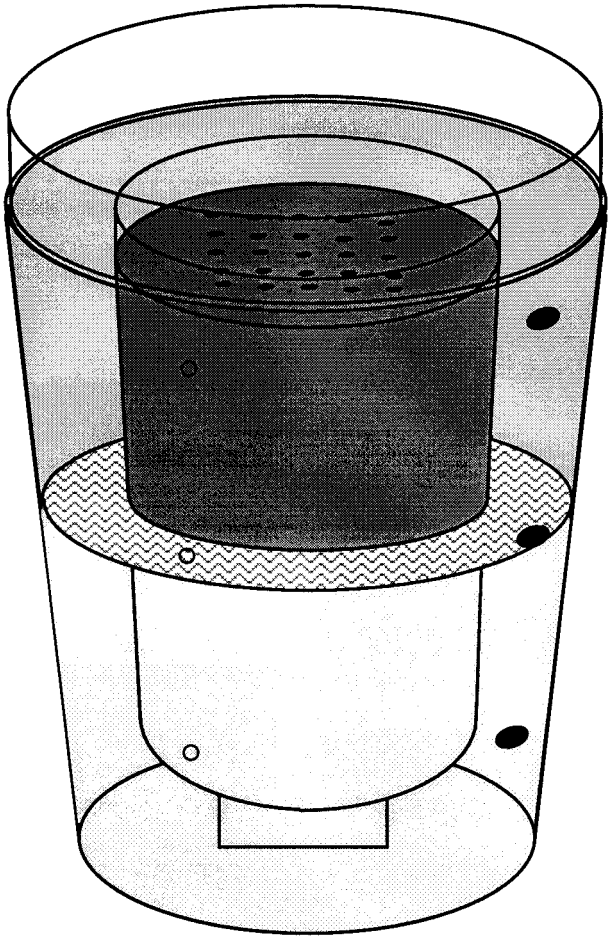

Fig. 1. The design of the soil moisture and salinity experimental microcosms. Holes were placed at 0.5, 3.5, and 7.0 cm from the bottom of a 9.5 cm tall 296-mL plastic inner cup. The inner cup was filled to 1 cm from the top of the cup with mineral soil and rested on a 1.9 cm tall wood block inside a 473-mL outer cup. The outer cup had a hole at 1, 5, or 9 cm from top of the cup for high, medium, and low moisture treatments, respectively. The medium moisture treatment is shown; water is the lighter shade.

Figure Abbreviations: *Ap, Amblyopappus pusillus*; *Cm, Cordylanthus maritimus* ssp. *maritimus*; *Cc, Cotula coronopifolia*; *Hp, Hutchinsia procumbens*; *Lg, Lasthenia glabrata* spp. *couleri*; *Lh, Lythrum hyssopifolium*; *Mn, Mesembryanthemum nodiflorum*; *Pi, Parapholis incurva*; *Pm, Polypogon monspeliensis*; *Sm, Spergularia marina*; SW, Sweetwater Marsh; TE, Tijuana Estuary; LPL, Los Peñasquitos Lagoon.

occurred at November photoperiod and diurnal mean temperature fluctuation (Table 3).

As suggested by preliminary trials, seawater diluted to 25, 12, and 5 ppt and deionized water were added to the outer cup to the level of the hole to create target surface soil salinity of 34, 17, 8, and 0 ppt, respectively. The different salinity waters were added a total of three times on the first day, and once on the second day, to equilibrate water levels in the outer and inner cups. On the third day, the water in the outer cup was replaced with deionized water to maintain constant soil salinity. Seeds were added to the microcosms on the fourth day.

Surface soil moisture and salinity in each run were quantified in nonreplicated seedless micrososms. A 1.3-cm^2 diameter soil core was taken to a depth of 1 cm in each seedless microcosm when the seeds were added to the seeded microcosms (day 0) and on days 3, 6, 9, 15, and 30. A 1-cm deep soil core was taken on day 30 in each of the seeded microcosms.

Soil moisture was determined gravimetrically. The soil sample was dried at 60°C for 24 h. Soil moisture was calculated as change in mass divided by dry mass (Gardner, 1986). Reverse osmosis water (salinity = 0 ppt) 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). All pastes were mixed by one person (G. B. Noe). Saturated soil paste extracts underestimate field soil salinity concentrations, except when soils are saturated. Instead of estimating the salt concentrations of soils, the salinity of saturated soil paste extracts is a measure of the salt mass in soils. Soils in the low-moisture treatments were too dry to measure the salinity of the interstitial water.

The experiment used a randomized complete block design with four replicates per treatment, with the microcosms blocked by growth chamber shelf. The number of germinated seeds in each microcosm was counted every 3 d for 30 d. The location of the microcosms within a block was rerandomized every 6 d.

Statistical analyses—The response variables for all experiments were the proportion of seeds germinating at the end of the experiment (day 30) and the speed of germination. The speed of germination was expressed as $(\Sigma n_t) / (n_f\ t)$, where n_t is the cumulative proportion germinating at each sampling time, n_f is the cumulative proportion germinating 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 from zero to one, increasing as germination occurs earlier in the experiment. Since cumulative germination was sampled ten times in this experiment, a 0.1-change in the index corresponds to a difference in the timing of germination by one sampling time, 3 d, for the average seed.

Four temperature and photoperiod comparisons were tested: November vs. March constant mean temperature, November constant vs. diurnal fluctuating mean temperature, March constant vs. diurnal mean fluctuating temperature, November vs. March photoperiod. Seed age was also evaluated as a potential factor influencing germination by comparing the November constant temperature and March photoperiod treatment at the beginning of the experiment and 7 mo later (Table 3). For each species, the final proportion of seeds germinating and the speed of germination were each analyzed with an analysis of variance (ANOVA) with randomized blocking and photoperiod/temperature treatment as the main factor. Proportion data were arcsine square-root transformed to improve normality and homogeneity of variance in the residuals (Zar, 1996). Significant differences ($P < 0.05$) for each of the five comparisons were tested with Tukey's Honestly Significant Difference (HSD) tests.

The effects of soil salinity and moisture on the final proportion germinating and germination speed of each species were each analyzed with a two-way analysis of variance (ANOVA) with randomized blocking and moisture and salinity treatments as the main factors. Proportion data were arcsine square-root transformed to improve normality and homogeneity of variance in the residuals (Zar, 1996). All significant ($P < 0.05$) main effects were tested for differences between treatment levels with Tukey's HSD tests. However, differences among treatment levels of individual factors are not reported if there was a significant interaction of soil salinity and moisture. All statistical analyses were performed using SYSTAT software (SYSTAT, 1992).

Relative effects of salinity, moisture, temperature, and photoperiod—To compare the magnitude of the effects of the different abiotic variables and seed aging on the proportion and speed of germination, we calculated the range in the means of both response variables for each species in response to each of the four abiotic factor tests (temperature, photoperiod, salinity, and moisture) as well as the seed aging test. The temperature effect for each species was calculated as the largest range among the three comparisons (November vs. March constant, November constant vs. diurnal fluctuating, March constant vs. diurnal fluctuating temperatures). Three of the eight species tested in the temperature, photoperiod, and aging trials in this study were not tested for their response to soil salinity and moisture. In order to compare all of the abiotic factors on all eight species, the response of *Cotula coronopifolia*, *Lythrum hyssopifolium*, and *Polypogon monspeliensis* to different soil salinity and moisture levels was obtained in a separate greenhouse-based microcosm ex-

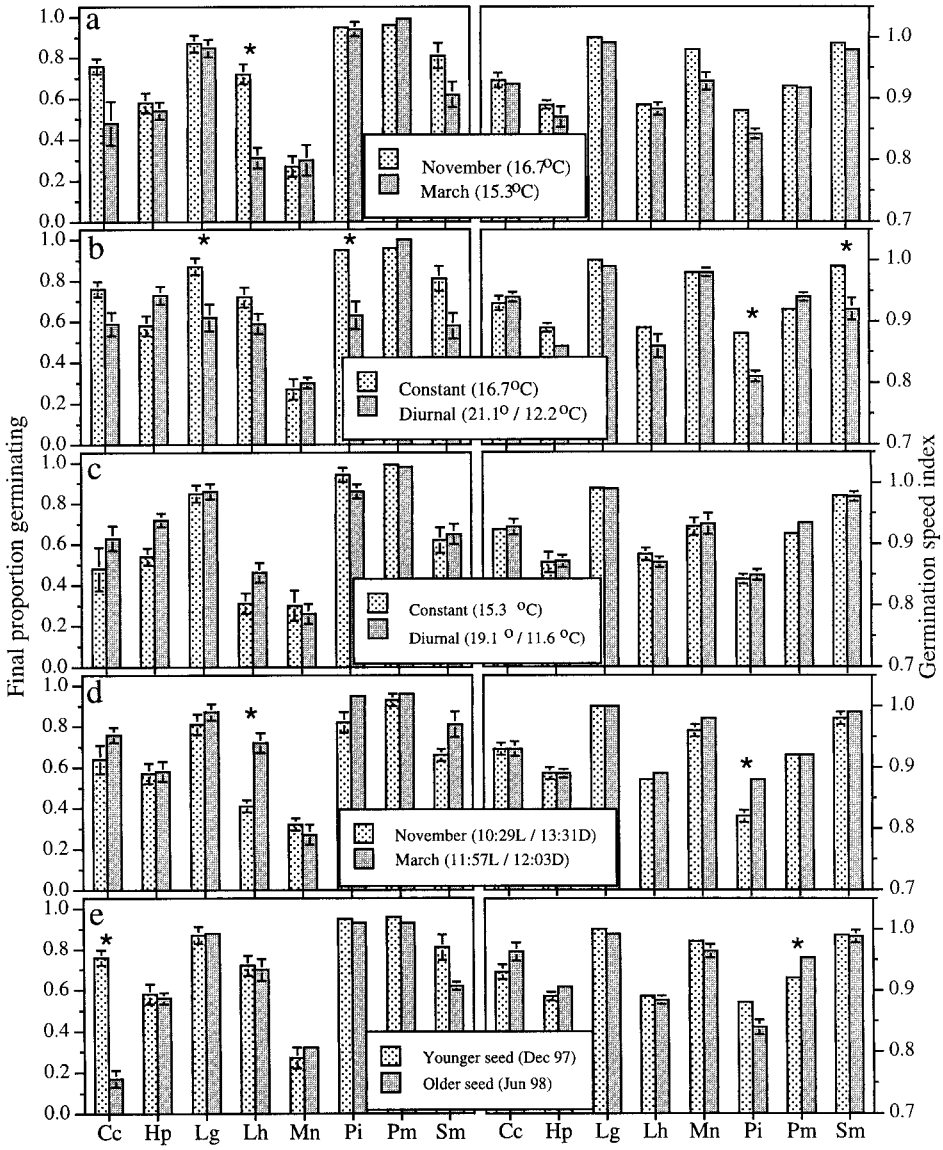

Fig. 2. Species responses to the temperature, photoperiod, and aging comparisons. (a) November vs. March constant temperature, (b) November constant vs. diurnal fluctuating temperature, (c) March constant vs. diurnal fluctuating temperature, (d) November vs. March photoperiod, (e) seed aging comparison. * = significant ($P < 0.05$) difference between treatments.

periment that is reported in Noe (1999). The constant moisture levels in the soil-based microcosms of the greenhouse study (35–45% soil moisture) were similar to moisture contents in the soils of this growth chamber study. The four constant salinity treatments in the greenhouse study were 2, 7, 15, and 31 ppt, with the 31-ppt treatment having higher salinity than the highest salinity treatment in this study (see Results).

RESULTS

Seed age—With one exception, the consecutive arrangement of the temperature and photoperiod treatments had no meaningful effect on species' germination. The proportion germinating of *Cotula coronopifolia* decreased 59% after an additional 7 mo of dry storage ($P < 0.001$) (Fig. 2e). After aging for 7 mo, the germination speed index of *Polypogon monspeliensis* increased 0.03 ($P = 0.007$) (Fig. 2e). This change in germination speed corresponds to a difference of about one day, a shorter time than the sampling interval (3 d).

Temperature and photoperiod—Few species responded to the temperature or photoperiod treatments (Fig. 2a-d). Different constant temperatures had a significant effect on the proportion germinating of *Lythrum hyssopifolium* ($P < 0.001$), with a higher proportion of seeds germinating at constant November (0.72; 16.7°C) than constant March (0.31; 15.3°C) temperature. This species' response to a 1.4°C difference in temperature indicates high sensitivity to temperature during germination, although speed was not affected. A higher proportion of *Lasthenia glabrata* ssp. *coulteri* ($P = 0.029$) and *Parapholis incurva* ($P = 0.004$) seeds germinated at constant November temperature (0.87 and 0.95, respectively) compared to diurnal fluctuating November temperatures (0.62 and 0.63, respectively). In addition, *Parapholis incurva* ($P = 0.002$) and *Spergularia marina* ($P = 0.008$) germinated faster at November constant temperature (0.88 and 0.99, respectively) compared to November diurnal fluctuating temperatures (0.81 and

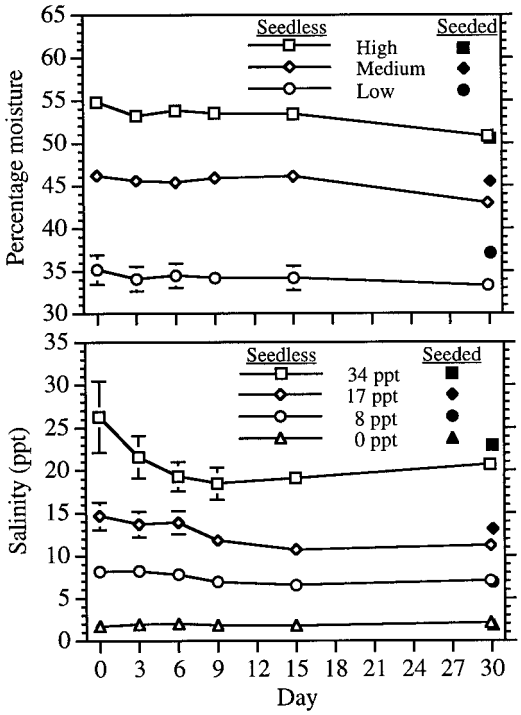

Fig. 3. Mean (±1 SE) surface (top 1 cm) soil moisture and salinity of treatments in seedless and seeded microcosms.

0.92, respectively). However, the proportion and the speed of germination of *Parapholis incurva* and *Spergularia marina* did not differ between the March diurnal temperature fluctuation and the March constant temperature. Seasonal photoperiod differences affected the germination of two species, with March photoperiod resulting in a higher proportion of *Lythrum hyssopifolium* germinating (0.72; $P = 0.009$) and faster *Parapholis incurva* germination (0.88; $P = 0.009$) than the November photoperiod (0.41 and 0.82, respectively). Eight of the nine significant differences among the temperature, photoperiod, and seed age comparisons had $P < 0.001$, indicating that Type I errors are unlikely despite the large number of statistical tests that were performed.

Soil salinity and moisture—Soil moisture levels in the seedless microcosms were relatively constant through time (Fig. 3). Final soil moisture content in the top 1 cm of soil of the seeded microcosms was 37.1, 45.5, and 50.5% in the low, medium, and high moisture treatments, respectively. The three highest salinity treatments fluctuated and decreased slightly during the first week but still exhibited differences among treatments. These decreases in salinity may be due to the frequent removal of soil from the seedless microcosms for sampling; removal of the surface soil decreased the elevation of soil in the inner cup relative to the level of the low salinity water in the outer bath. Final soil salinity was lower than intended. Soil salinity on day 30 in the seeded microcosms was 1.8, 6.8, 13.1, and 22.9 ppt in the 0, 8, 17, and 34 ppt target treatments, respectively. Hereafter, the salinity treatments will be referred to as 2, 7, 13, and 23 ppt.

When a species responded to the soil moisture or salinity treatments, the proportion germinating or germination speed decreased with decreasing moisture or increasing salinity (Fig. 4). The proportion of *Amblyopappus pusillus* germinating was affected by salinity ($P < 0.001$) and moisture treatments ($P = 0.006$). The germination speed of *Amblyopappus pusillus* also responded to salinity ($P < 0.001$) and moisture ($P < 0.001$). However, salinity and moisture treatments interacted for both the proportion ($P < 0.001$) and speed of germination ($P < 0.001$) (Fig. 4). The proportion of *Amblyopappus pusillus* seeds germinating and speed of germination declined drastically at the highest salinity and low moisture (Fig. 4). Although salinity and moisture interacted, the range in germination among the treatments of both soil salinity and soil moisture is a measure of the responsiveness of a species and allows broad comparison between these two factors. In this experiment, the proportion of *Amblyopappus pusillus* germinating responded to salinity treatments more than moisture treatments (Table 4). The range in the proportion germinating in response to the salinity treatments was threefold greater than the range in the moisture treatments. The range in the germination speed index values was similar in the salinity and moisture treatments (Table 5).

The number of *Cordylanthus maritimus* ssp. *maritimus* seeds germinating differed among both salinity ($P < 0.001$) and moisture treatments ($P < 0.001$). Similarly, the speed of *Cordylanthus maritimus* ssp. *maritimus* germination differed among salinity ($P < 0.001$) and moisture levels ($P < 0.001$). Soil salinity and moisture treatments interacted for both the proportion germinating ($P = 0.014$) and the speed of germination ($P = 0.003$), with salinity tolerance much greater under high moisture than low moisture conditions (Fig. 4). The proportion of *Cordylanthus maritimus* ssp. *maritimus* germinating was affected strongly by soil moisture, with a 0.40 difference between the low and high moisture treatments. Moisture was relatively more important than soil salinity, with a larger range in proportion germinating among moisture treatments (0.40) than salinity treatments (0.25; Table 4). However, the range in germination speed was larger among soil salinity treatments (0.25) than soil moisture treatments (0.16; Table 5).

The proportion of *Hutchinsia procumbens* germinating differed among both salinity ($P < 0.001$) and moisture treatments ($P = 0.001$). In addition, germination slowed with increasing salinity ($P < 0.001$) and decreasing moisture ($P < 0.001$). For both the proportion and speed of germination ($P = 0.001$ and $P = 0.048$, respectively), moisture and salinity treatments interacted with differences among moisture treatments becoming much more apparent at high salinity (Fig. 4). The proportion of *Hutchinsia procumbens* germinating was affected more by salinity than moisture, with a fivefold larger range in the salinity treatments compared to the moisture treatments (Table 4). Speed of germination had a nearly twofold higher range in the salinity treatments than the moisture treatments (Table 5).

The proportion of *Lasthenia glabrata* ssp. *coulteri* germinating responded to salinity ($P < 0.001$) and moisture treatments ($P < 0.001$). The speed of germination also differed among salinity ($P < 0.001$) and moisture ($P < 0.001$) levels. Salinity interacted with moisture for both the proportion ($P = 0.012$) and speed ($P < 0.001$) of *Lasthenia glabrata* ssp. *coulteri* germination; there were larger differences in germination among moisture treatments at higher salinity levels (Fig. 4). *Lasthenia glabrata* ssp. *coulteri* was more responsive to salinity than moisture. There was more than a threefold larger range in proportion germinating among the salinity treatments than the moisture treatments (Table 4). In addition, germination speed varied more in response to salinity than moisture (Table 5).

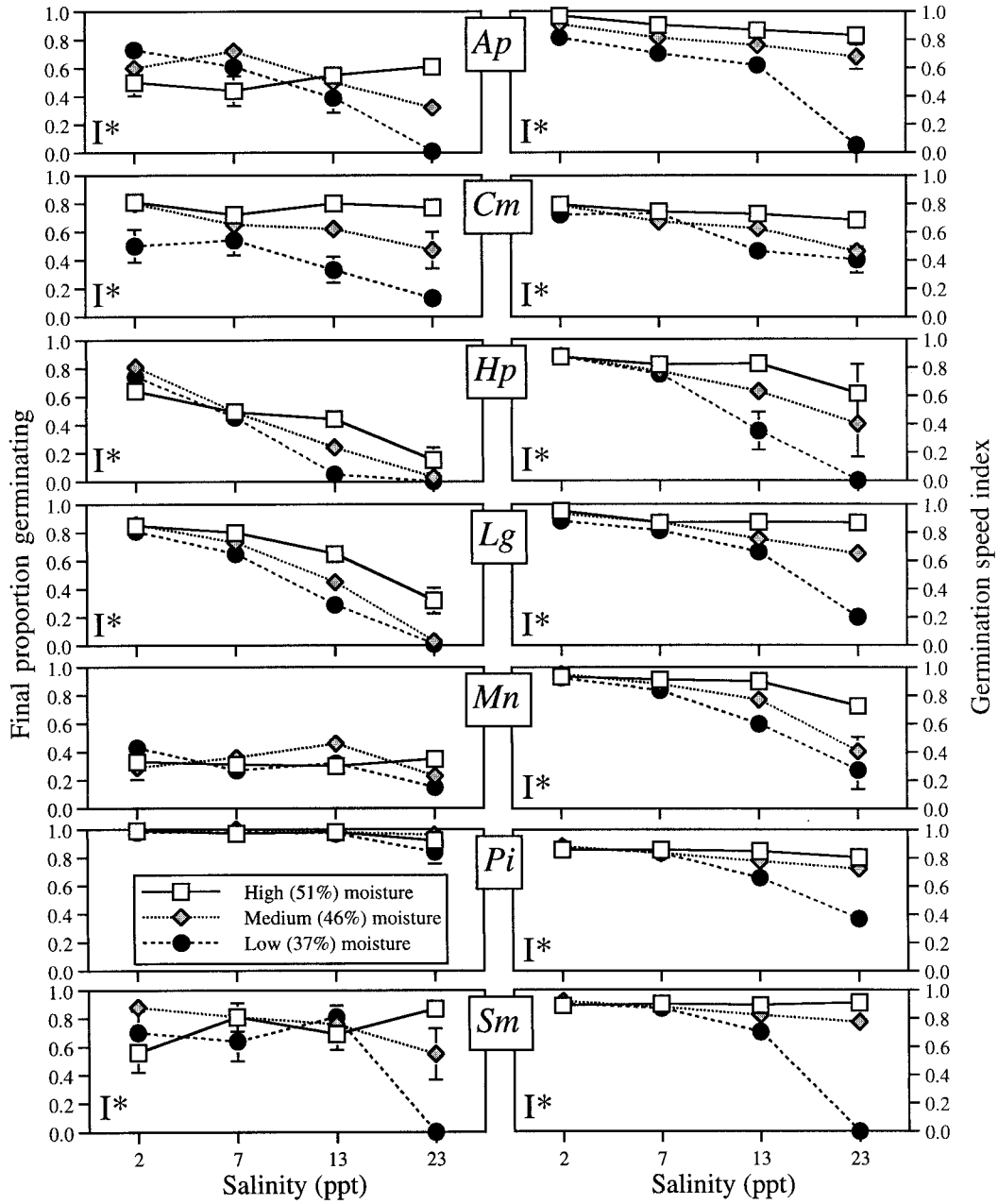

Fig. 4. Interactions of soil moisture and salinity treatments on the mean (±1 SE) final proportion germinating and germination speed index of each species. An "I*" indicates a significant ($P < 0.05$) interaction between soil moisture and salinity.

The interaction of salinity and moisture on the proportion of *Mesembryanthemum nodiflorum* germinating was nearly statistically significant ($P = 0.052$). The proportion germinating responded to soil salinity ($P = 0.035$) and was highest at 13 ppt and lowest at 23 ppt. Soil moisture had no effect on the proportion of *Mesembryanthemum nodiflorum* germinating ($P = 0.429$). The speed of germination responded to salinity ($P = 0.001$) and moisture ($P = 0.001$) and the interaction of salinity and moisture ($P = 0.002$). At high salinity, germination was much slower at low and medium moisture than at high moisture, whereas germination speed did not differ among the moisture treatments at low salinity (Fig. 4). Differences in the proportion of *Mesembryanthemum nodiflorum* germinating were larger among the salinity treatments than the moisture treatments, although there was a maximum difference of only 0.12 among treatments (Table 4). However, salinity had a large effect on the speed of germination (Table 5). *Mesembryanthemum nodiflorum* germination speed index values were halved from 0.94 at 2 ppt to 0.47 at 23 ppt.

The effects of soil moisture and salinity on the proportion of *Parapholis incurva* germinating did not interact ($P = 0.790$) (Fig. 4). The proportion of *Parapholis incurva* germinating decreased at the 23 ppt treatment, but was similar at 2, 7, and 13 ppt ($P = 0.010$) and did not respond to the moisture treatments ($P = 0.254$). The proportion of *Parapholis incurva* germinating was higher than 0.90 for all treatments. However, the speed of germination at different salinity levels did depend on moisture levels ($P < 0.001$). Germination speed responded

TABLE 4. The range in the final proportion germinating of each species among the treatment levels of each abiotic factor and seed age. Boldfaced numbers indicate noteworthy large effects of a factor on a species.

Species	Photo-period	Age	Temper-ature	Salinity	Moisture
Amblyopappus pusillus	—	—	—	**0.30**	0.10
Cordylanthus maritimus ssp. *maritimus*	—	—	—	0.25	**0.40**
Cotula coronopifolia	0.12	**0.59**	0.28	0.35[a]	0.10[a]
Hutchinsia procumbens	0.01	0.02	0.18	**0.67**	0.12
Lasthenia glabrata ssp. *coulteri*	0.06	0.01	0.25	**0.72**	0.22
Lythrum hyssopifolium	**0.31**	0.02	**0.41**	**0.55**[a]	0.12[a]
Mesembryanthemum nodiflorum	0.05	0.05	0.04	0.12	0.05
Parapholis incurva	0.13	0.02	**0.32**	0.08	0.04
Polypogon monspeliensis	0.03	0.03	0.04	**0.21**[a]	0.08[a]
Spergularia marina	0.15	0.19	**0.23**	**0.28**	0.19

[a] Range calculated from data in Noe (1999).

TABLE 5. The range in the germination speed index of each species among the treatment levels of each abiotic factor and seed age. Boldfaced numbers indicate noteworthy large effects of a factor on a species.

Species	Photo-period	Age	Temper-ature	Salinity	Moisture
Amblyopappus pusillus	—	—	—	**0.38**	**0.34**
Cordylanthus maritimus ssp. *maritimus*	—	—	—	**0.25**	0.16
Cotula coronopifolia	0.01	0.04	0.02	**0.57**[a]	0.10[a]
Hutchinsia procumbens	0.01	0.02	0.03	**0.54**	0.28
Lasthenia glabrata ssp. *coulteri*	0.00	0.01	0.01	**0.21**	**0.15**
Lythrum hyssopifolium	0.01	0.01	0.03	**0.76**[a]	0.12[a]
Mesembryanthemum nodiflorum	0.02	0.02	0.05	**0.47**	0.21
Parapholis incurva	0.05	0.04	0.07	**0.24**	0.16
Polypogon monspeliensis	0.00	0.03	0.02	**0.22**[a]	0.01[a]
Spergularia marina	0.01	0.00	0.07	**0.24**	0.08

[a] Range calculated from data in Noe (1999).

to both salinity ($P < 0.001$) and moisture ($P < 0.001$), although differences among salinity treatments were only apparent at low moisture (Fig. 4). Salinity had a larger effect on the proportion germinating than moisture, but both factors had small differences among treatments (Table 4). Salinity affected the speed of germination slightly more than moisture (Table 5).

Both salinity ($P = 0.001$) and moisture ($P = 0.006$) affected the proportion of *Spergularia marina* germinating. Germination speed also responded to salinity ($P = 0.001$) and moisture ($P < 0.001$). Salinity and moisture effects interacted for both the proportion and speed of germination (both $P < 0.001$). When seeds experienced high and medium moisture levels they did not respond to the different salinity treatments (Fig. 4). In contrast, no seeds germinated at low moisture and high salinity. The range in *Spergularia marina* proportion germinating and germination speed index values was similar between the salinity and moisture treatments (Tables 4, 5).

Relative effects of five factors—Of temperature, photoperiod, seed aging, soil salinity, and soil moisture, the speed of germination responded most strongly to soil salinity for all eight species (Table 5). The proportion germinating of four (*Hutchinsia procumbens, Lasthenia glabrata* ssp. *coulteri, Mesembryanthemum nodiflorum,* and *Polypogon monspeliensis*) of the eight species had a greater range among salinity treatments compared to moisture, photoperiod, temperature, or aging treatments (Table 4). Two species (*Lythrum hyssopifolium* and *Spergularia marina*) had similar ranges in their proportion germinating in both the soil salinity and temperature treatments. Temperature had the largest effect on *Parapholis incurva* proportion germinating (Table 4). Finally, the proportion of *Cotula coronopifolia* germinating was affected by seed aging more than the other factors; soil salinity and temperature elicited larger responses in *Cotula coronopifolia* compared to moisture and photoperiod (Table 4).

Two additional species, *Amblyopappus pusillus* and *Cordylanthus maritimus* ssp. *maritimus,* were tested with only soil salinity and moisture. The range in the proportion of *Amblyopappus pusillus* germinating was greatest in response to the soil salinity treatments (Table 4). *Amblyopappus pusillus* germination speed varied the most among soil salinity treatments, although there was a large difference between the high and low soil moisture treatments (Table 5). The proportion of *Cordylanthus maritimus* ssp. *maritimus* germinating was strongly affected by soil moisture and was the only species to be more responsive to soil moisture than soil salinity (Table 4). However, *Cordylanthus maritimus* ssp. *maritimus* germination speed varied more in response to soil salinity treatments than moisture treatments (Table 5).

DISCUSSION

We attempted to explain patterns of field germination by testing multiple factors, interactions among factors, and field-relevant levels of factors on the proportion and speed of germination of half of the annual species in southern California salt marshes. Other studies of wetland plants have found that germination can be affected by several abiotic factors (Leck, 1989). Leck (1996) tested the effects of different soil moisture, light, and temperature regimes on germination and concluded that each species responds to the abiotic environment in a unique manner. Similarly, Galinato and van der Valk (1987) found that each of the species they tested was affected differently by temperature, salinity, and light. Interactions among abiotic factors also occur (Ungar, 1978); Khan and Ungar (1997) determined that temperature, light, and salinity interact to effect germination of halophytes. However, most other experiments on the germination of salt marsh plants have focused solely on the effect of soil salinity. We will discuss the effects of each of the abiotic factors tested, the interaction of salinity and moisture, the differential response of the proportion germinating vs. germination speed, and the ability of these experiments to explain patterns of field germination.

Effects of each factor—Species differed in their responsiveness to abiotic factors, as quantified by the ranges of their proportion germinating and speed of germination (Tables 4, 5). The differing treatments of each abiotic factor corresponded to the range of conditions that the species are exposed to in the field during periods of germination. Therefore, the range of the response variables among the treatments of each of the abiotic factors is a measure of the relative importance of each abiotic factor in determining germination, and therefore influencing population dynamics, in the field. Some species had small ranges among the salinity, moisture, temperature, and photoperiod treatments; others responded with large differences in proportion germinating or germination speed among treatments.

Of the eight species tested, the proportion germinating or germination speed of four (*Lythrum hyssopifolium, Lasthenia glabrata* ssp. *coulteri, Parapholis incurva,* and *Spergularia marina*) responded to the various treatments that tested small differences in either temperature or photoperiod (Fig. 2). The temperatures and photoperiods tested in this experiment represented conditions at the beginning and end of the typical period of germination in the upper intertidal marsh of southern California. Of the three temperature comparisons, the one with the greatest number of significant differences in germination was November diurnal fluctuating vs. constant temperature. Thompson and Grime (1983) found that the germination of many temperate wetland species respond to as small as 1°C fluctuations in temperature compared to constant conditions. A possible explanation for why the germination of the species in this study were less responsive to temperature than those in Thompson and Grime (1983) is that the germination of most species is cued to variations in salinity, not temperature, in salt marshes with a mediterranean-type climate.

The consecutive arrangement of the treatments had little effect on the experiments. Only the proportion of *Cotula coronopifolia* germinating was greatly affected by the 7-mo period between the beginning and ending temperature and photoperiod experimental treatments (both November constant temperature and March photoperiod). Baskin and Baskin (1998) recommend starting germination experiments within 7–10 d of seed collection to prevent changes in germination responses during storage. However, up to six months commonly elapse between seed dispersal and germination in the upper intertidal marsh in southern California (G. B. Noe, personal observation). While seed storage in the laboratory differed from conditions in the field, surface soils in the field are also dry (~5–15%; Fig. 6) during this period of summer dormancy.

The microcosm salinity levels tested in this experiment were similar to those when germination occurs in the upper intertidal marsh of southern California (Noe, 1999). Increasing soil salinity elicited declines in the proportion germinating and slowed the speed of germination for each species. These effects are common among halophytes (Waisel, 1972; Ungar, 1978). However, some species were more tolerant of salt than other species and the degree of slowed germination in response to salinity varied among species. For example, the germination of the average seed of *Lasthenia glabrata* ssp. *coulteri* was delayed ~6 d (0.21 index difference), and *Hutchinsia procumbens* germination was delayed ~16 d (0.54 index difference) at 23 ppt compared to 2 ppt. Such a 10-d difference in the timing of germination between species could shift relative growth rates and alter the outcome of interspecific competition. Grace (1987) was able to measure a competitive advantage between two species with as little as a 2-d difference in the timing of seed sowing. However, the magnitude of the interspecific differences in the delay of germination in this study is not sufficient to explain the 1–3 mo differences in the timing of germination in the field (Noe, 1999).

Others have examined the effect of salinity on the germination of some of the same species. In these studies, seeds of *Lasthenia glabrata* ssp. *coulteri* (Kingsbury et al., 1976; Callaway et al., 1990), *Parapholis incurva* (Callaway et al., 1990), and *Spergularia marina* (Callaway et al., 1990; Keiffer and Ungar, 1997) were less salt tolerant than in this study. Soil paste extracts estimate salt concentrations after dilution; hence, the differences in salt tolerance between this study and other studies are exacerbated by the underestimation of soil salinity in this study. Callaway et al. (1990) used seeds from Carpinteria Marsh, farther north than the seed sources in this study, Keiffer and Ungar (1997) tested seeds from inland salt marshes in Ohio, and Kingsbury et al. (1976) collected seeds from Los Peñasquitos Lagoon. Of these studies, the salt tolerance of *Lasthenia glabrata* ssp. *coulteri* in Kingsbury et al. (1976) is most similar to the results of this study. Kingsbury et al. (1976) found regional differences in *Lasthenia glabrata* salt tolerance and concluded that the salt tolerance of different populations was related to the soil salinity found in the habitat of each population. Beare and Zedler (1987) also found differences in the salt tolerance during germination among different southern California *Typha domingensis* populations. This study is not directly comparable with these other studies because others used filter paper or sand as experimental substrates and collected seeds from populations that may differ genetically from the seeds in this study. Because saline soils are not always saturated, soil-based studies of the salt tolerance of germination may be more realistic and predictive of field patterns.

Microcosm moisture levels were also similar to the range of conditions found in southern California upper intertidal salt marshes during periods of germination (Noe, 1999). Wetter soil resulted in more seeds germinating for five species and the germination speed of all seven species increased in wetter soils. No studies examining the effect of soil moisture content on these species are available for comparison. In addition, most experiments on other wetland species test much higher moisture levels (flooded or saturated conditions) than the moisture levels tested in this study.

Salinity and moisture interaction—Salinity and moisture interacted to affect the proportion germinating of five species and germination speed of all seven species (Fig. 4). The influence of salinity became more evident at low moisture, likewise, moisture effects were largest at high salinity. Salinity and moisture effects were independent of each other for the proportion of *Mesembryanthemum nodiflorum* and *Parapholis incurva* germinating, the two species most tolerant of high salinity and low moisture. The germination of many wetland plant species is also determined by interactions between soil salinity and the duration of soil saturation (Kuhn and Zedler, 1997) or inundation (Baldwin, McKee, and Mendelssohn, 1996).

The interaction in this experiment may be due in part to the method of quantifying soil salinity. The soil paste extracts estimate salt concentrations in saturated soils, and effective salinities were much higher at low moisture than was measurable by this technique. It is difficult to ascertain whether the mechanism of the interaction in this study is due to osmotic effects on water potential or the toxic effects of ions. However, the effects of salinity on the germination of halophytes are most commonly osmotic (Ungar, 1978; Baskin and Baskin, 1998). The interaction of salinity and moisture has implications for studies determining the effect of soil salinity on germination. Most experiments test for effects of salinity on germination by placing seeds on filter paper in water-filled petri dishes, thereby providing very high or saturated moisture levels. Fewer experiments omit the filter paper or use petri dishes with saturated sand. In the upper intertidal zone, where tidal inundation is infrequent and of short duration, soils are often both saline and dry and the interaction of soil salinity and moisture could be important.

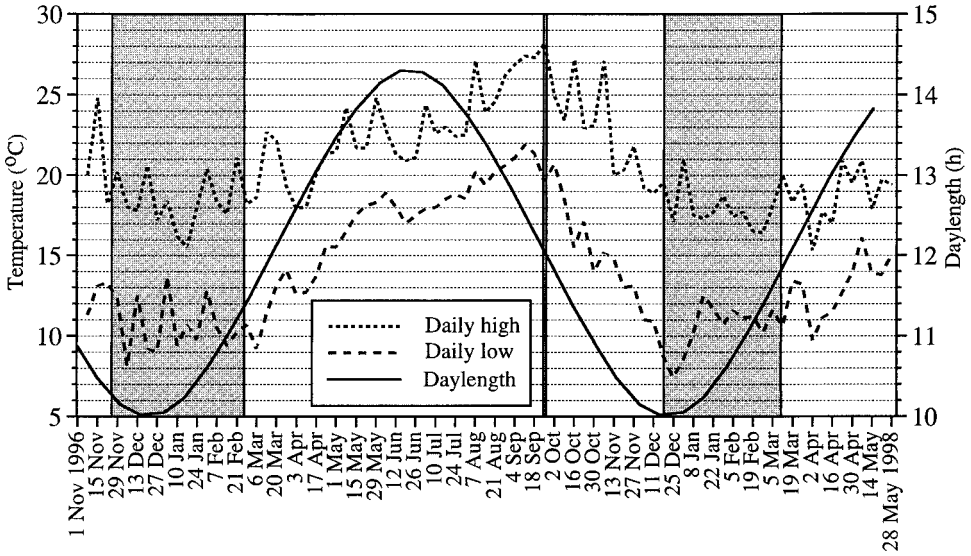

Fig. 5. Daily high and low temperatures at Lindbergh Field and daylength (sunrise to sunset) in San Diego. Shaded boxes indicate the germination windows during the 1996 season, nonseasonal rainfall from Hurricane Nora, and 1997 season.

Proportion vs. speed of germination—The germination speed of each species, but not proportion (at 4 wk), was affected by soil salinity and moisture. At high salinity and low moisture, slowing of germination is a more general trait than decreasing proportion germinating among the species in this study. In the photoperiod and temperature experiments, proportion germinating was more responsive than germination speed (Fig. 2). Statistically significant differences in the proportion germinating ranged from 0.25 to 0.41 between temperature/photoperiod treatments. In comparison, significant differences in the germination speed index ranged from 0.04 to 0.07 in the temperature/photoperiod trials, or a 1.2- to 2.1-d difference in the average time of germination. Despite smaller differences in germination speed than proportion among species and abiotic factors, the time it takes for a seed to germinate can have large effects on interspecific interactions (Grace, 1987). Therefore, while the magnitude of the changes in germination speed could not explain the differences in the timing of germination that were observed in the field, the slowing of some species' germination could affect the competitive balance among species. The lack of concordance between the response of the two traits to abiotic stress suggests that an index of germination speed should be independent of the proportion germinating, as is the index used in this study. This is contrary to the suggestion of Brown and Mayer (1988), who promote combining these aspects of germination into a single, concise index.

Field environmental conditions during germination—Temperatures in each of the 1996 and 1997 germination windows were similar throughout the period of germination (Fig. 5). Daylength increased by about an hour from the start to end of the germination windows. During the germination pulse after Hurricane Nora in late September 1997, high temperatures were ~5°C higher and low temperatures 10°C higher than during the typical germination windows. Photoperiod during this nonseasonal event was similar to conditions in March, the end of the typical period of germination.

Noe (1999) found that soil moisture increased and salinity decreased during the 1996 and 1997 germination windows compared to periods without germination (Fig. 6). Soil salinity and moisture varied during the germination window of both years. A week after the rainfalls from Hurricane Nora in late September 1997, soil salinity was higher and soil moisture was lower than during the germination windows.

Explaining observed field patterns—The upper intertidal marsh of southern California has a germination window of 2–3 mo (Noe, 1999). In general, by testing the germination responses of species to soil salinity, soil moisture, temperature, and photoperiod, we can explain why certain species can germinate outside this germination window. We cannot explain the details of germination timing within this period, nor can we explain the spatial distributions of species. Two species were restricted to the November to March germination window; that is, they did not germinate after Hurricane Nora (Table 1). The absence of *Hutchinsia procumbens* after that nonseasonal rain event is most likely due its low salt tolerance, as soil salinity was high at that time (Fig. 6). However, *Parapholis incurva* is the most salt-tolerant species, so its lack of germination following the hurricane is best explained by its decreased proportion germinating at the highest temperature in this experiment (Fig. 2) and the high temperatures that occurred during and after the hurricane (Fig. 5). The proportion of *Lasthenia glabrata* ssp. *coulteri* germinating also decreased in the highest temperature treatment (Fig. 2) but it germinated following the hurricane. Of the two wetlands where *Lasthenia glabrata* ssp. *coulteri* was found, nonseasonal germination occurred only at the wetland with very low salinity and high moisture (Noe, 1999), indicating that the salinity and moisture conditions may have overridden any effect of temperature on germination. *Parapholis incurva* was found at the same sites as *Lasthenia glabrata* ssp. *coulteri* but did not germinate after the nonseasonal rainfall, suggesting that temperature limitation of *Parapholis incurva* was more important than salinity tolerance. Both the temperature and photoperiod trials correctly predicted that *Lythrum hyssopifolium* would germinate in the conditions following Hurricane Nora.

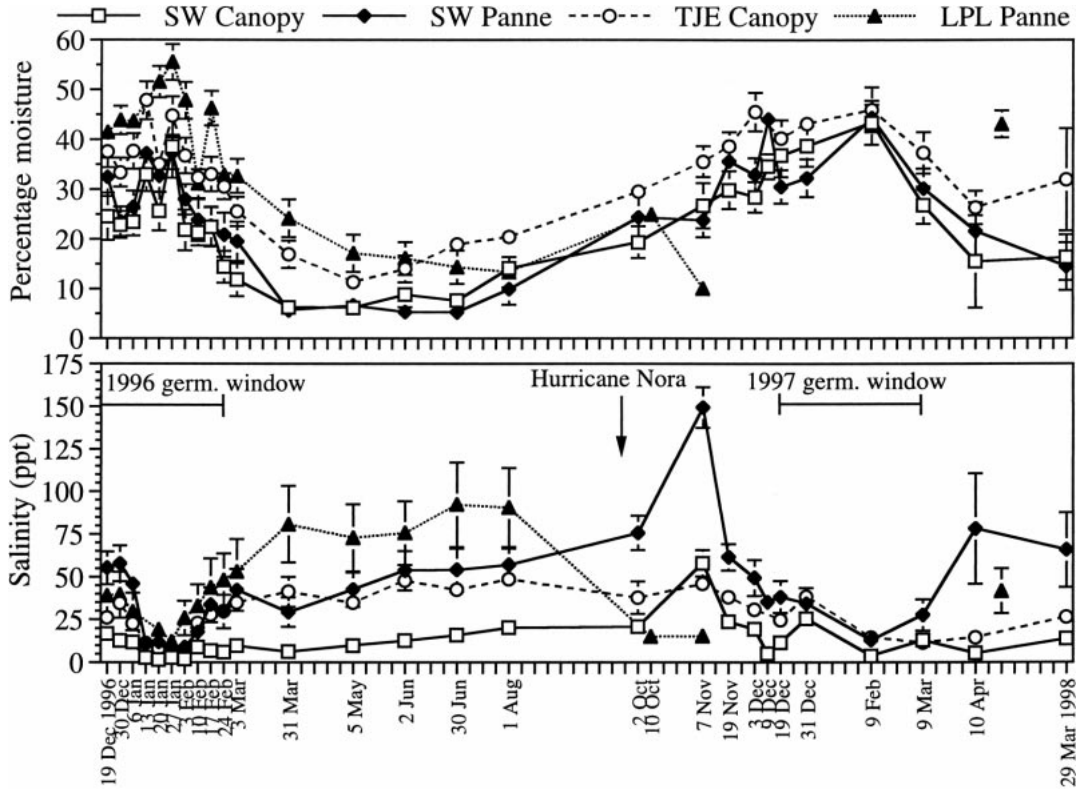

Fig. 6. Mean (±1 SE) soil moisture and salinity in canopy and panne vegetation monitoring transects at three marshes, Sweetwater Marsh, Tijuana Estuary, and Los Peñasquitos Lagoon. Soil cores were taken in the top 2 cm of soil from 19 December 1996 to 3 March 1997, and subsequently in the top 10 cm of soil. Data are reported in Noe (1999).

Variation in the timing of germination within the germination window is less easily explained by the multiple abiotic factors tested in this study than is variation in germination in response to nonseasonal rainfall. Three species, *Amblyopappus pusillus, Hutchinsia procumbens,* and *Mesembryanthemum nodiflorum,* had prolonged germination in the 1996 season and early germination in the 1997 season (Table 1). However, these three species each responded differently to soil salinity, soil moisture, temperature, and photoperiod treatments in the growth chamber (Figs. 2, 4). In addition, both *Hutchinsia procumbens* and *Lasthenia glabrata* ssp. *coulteri* had similar responses to salinity, moisture, and photoperiod, although *Lasthenia glabrata* ssp. *coulteri* responded to temperature fluctuations with high temperature peaks, but the two species had opposite germination timing from each other in both years. The temperature treatments incorrectly predict that both *Lasthenia glabrata* ssp. *coulteri* and *Parapholis incurva* would germinate later in the germination window when temperatures are lower. Finally, the photoperiod trial wrongly predicts that *Lythrum hyssopifolium* would germinate later in germination windows while the temperature trials correctly predict early germination. One correct prediction of the timing of germination within the window is the late germination of *Cordylanthus maritimus* ssp. *maritimus* in both the 1996 and 1997 germination windows. Soil moisture increased later in the germination window of both years, and *Cordylanthus maritimus* ssp. *maritimus* germination is sensitive to soil moisture (Figs. 4, 6).

Annual species segregate along a spatial gradient of surface soil salinity in the upper intertidal marsh of southern California (Noe, 1999). This experiment showed that *Parapholis incurva* and *Mesembryanthemum nodiflorum* are most salt tolerant during germination, *Amblyopappus pusillus, Cordylanthus maritimus* ssp. *maritimus,* and *Spergularia marina* have intermediate salt tolerance, and *Hutchinsia procumbens* and *Lasthenia glabrata* ssp. *coulteri* have relatively low salt tolerance (Fig. 4). However, in the field *Spergularia marina* was found at the highest salinity, followed by *Parapholis incurva, Cordylanthus maritimus* ssp. *maritimus, Hutchinsia procumbens, Mesembryanthemum nodiflorum, Amblyopappus pusillus,* and *Lasthenia glabrata* ssp. *coulteri* at decreasing salinity (Noe, 1999). The juxtaposition of *Mesembryanthemum nodiflorum* from highest salt tolerance in this experiment to greatest abundance at intermediate salinity in the field and *Hutchinsia procumbens* from lowest salinity tolerance in this experiment to intermediate salinity in the field cannot be explained by salinity effects on germination. In addition, the germination response of some species to salinity does not match their pattern of relative abundance along a field salinity gradient (Fig. 7). The data used to characterize the salinity gradient were collected on 27 January 1997, the date of a large germination pulse, and best explained variation in species seedling distributions compared to two other datasets (Noe, 1999). Both *Amblyopappus pusillus* and *Cordylanthus maritimus* ssp. *maritimus* occur at much lower salinity in the field than would be predicted by their salt tolerance under experimental conditions (Fig. 7). The two species that were found in areas with relatively high soil moisture, *Parapholis incurva* and *Spergularia marina,* had the best match between experimental salinity tolerance and abundance along a field salinity gradient compared

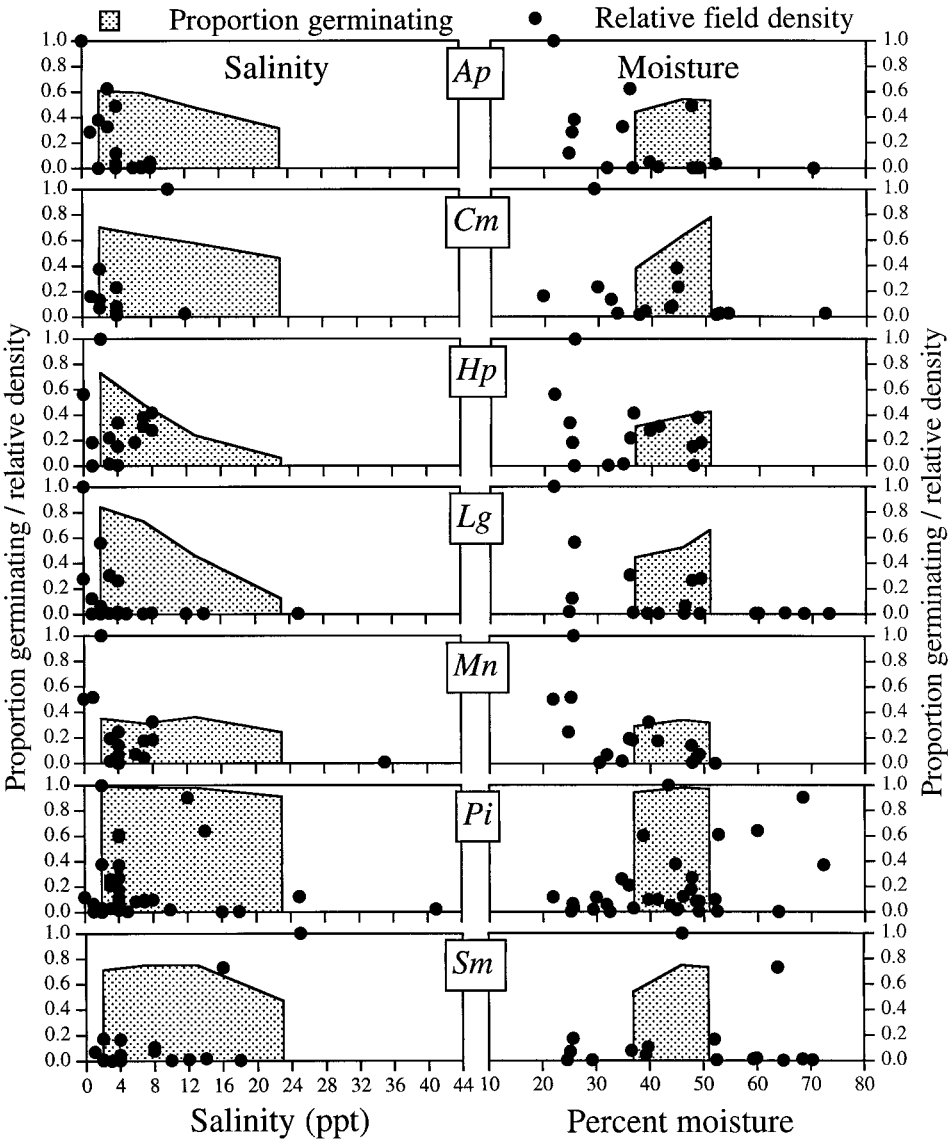

Fig. 7. Final proportion of seeds germinating at different soil salinity and moisture treatments in this study (shaded curves) and relative seedling density (proportional to species maximum density) along gradients of field surface (2 cm) soil salinity and moisture on 27 January 1997 [points; data from Noe (1999)].

to the other species. The other species, found in drier areas, occurred in less saline areas than would be predicted by their experimental salinity tolerance. This may be evidence of the interaction between soil salinity and moisture.

The endangered *Cordylanthus maritimus* ssp. *maritimus* is found at lower (~20 cm) elevations than the other species (Noe, 1999). The large increase in the proportion of *Cordylanthus maritimus* ssp. *maritimus* germinating at high vs. low moisture suggests that drier soils reduce establishment at higher elevations where tidal inundation is infrequent. This finding is corroborated by data from San Diego Bay. There, long-term monitoring indicates that the elevation distribution of *Cordylanthus maritimus* ssp. *maritimus* fluctuates interannually, with most plants found at lower elevations in dry years (Pacific Estuarine Research Laboratory, unpublished report). The germination of *Lasthenia glabrata* ssp. *coulteri* and *Spergularia marina* was also stimulated at high moisture. These two species are found in and along the edges of salt pannes that flood in winter (Zedler, Nordby, and Kus, 1992). The high moisture required for these two species to germinate may explain their association with impounded water. However, the greatly increased germination of *Cordylanthus maritimus* ssp. *maritimus* and *Lasthenia glabrata* ssp. *coulteri* at high moisture does not predict their greatest abundance at low moisture in the field study (Fig. 7).

Including the effects and interactions of other factors on germination or other life history stages could have improved the ability of this study to explain field patterns. Although light has been found to affect halophyte germination (Khan and Ungar, 1997; Baskin and Baskin, 1998), seed burial by sediment or wrack is rare in the upper intertidal marsh of southern California and light stimulation of germination is unlikely. It is possible that additional interactions could improve the ability to explain the timing of the germination. For example, Khan and Ungar (1997) found that salinity, temperature, and light interact to affect the proportion germinating of halo-

phytes. Finally, Casanova and Brock (1996) tested the effects of temperature and moisture on the oospore germination of wetland charophytes and concluded that the germination experiments could somewhat predict field distributions, but other processes working on adults could also be important.

This experiment tested the effects of constant soil salinity and moisture on germination. However, the germination of the same assemblage of species differs when soil salinity and moisture vary through time compared to constant conditions (Noe, 1999). The exotic species are less responsive to the varying soil salinity treatments, which were similar to soil salinity dynamics in the field and more stressful than constant salinity treatments, than the native species (Noe, 1999). Therefore, multiple abiotic factors, as well as the characterization of abiotic factors in experiments, affect the germination of the annual plant assemblage of southern California.

In conclusion, we set out to determine whether we could explain variance in the establishment of an annual species assemblage by testing multiple abiotic factors, interactions between factors, and meaningful levels of factors. Interspecific differences in responsiveness to different abiotic factors confirm the hypothesis that multiple abiotic factors affect salt marsh plant establishment. Soil salinity, soil moisture, temperature, and photoperiod each affected the proportion of seeds germinating and the speed of germination of the salt marsh species in this study. In general, soil salinity had the largest effect on species; more species responded, and the magnitudes of the responses were larger, for soil salinity than for the other abiotic factors. However, the abiotic factor with the largest effect on germination varied among species. These results are contrary to our expectation that the effects of soil salinity would dominate soil moisture, temperature, and photoperiod effects on germination. Historically, most studies have emphasized the effect of salinity on the germination of salt marsh species, but the influence of other abiotic factors should also receive attention. Despite the inability to explain fine-scale differences in temporal and spatial distributions, we were able to explain the restriction of the germination of some species to the germination window of the cool season. Patterns of nonseasonal germination by *Hutchinsia procumbens*, *Lythrum hyssopifolium*, *Parapholis incurva*, and possibly *Lasthenia glabrata* ssp. *coulteri* in southern California wetlands could be explained by their response to salinity, temperature, and photoperiod. Considering the effects of multiple abiotic factors improved the explanation of field patterns compared to testing a single factor. Additionally, small differences in temperature treatments, similar to those that occur in the field during germination, affected germination and explained the temporal distribution of some species.

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