Ecology, 92(12), 2011, pp. 2236–2247
© 2011 by the Ecological Society of America

Seasonal timing of first rain storms affects rare plant population dynamics

Jonathan M. Levine,[1,3] A. Kathryn McEachern,[2] and Clark Cowan[1]

[1]*Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, California 93106 USA*
[2]*U.S. Geological Survey, Western Ecological Research Center, Channel Islands Field Station, 1901 Spinnaker Drive, Ventura, California 93001 USA*

Abstract. A major challenge in forecasting the ecological consequences of climate change is understanding the relative importance of changes to mean conditions vs. changes to discrete climatic events, such as storms, frosts, or droughts. Here we show that the first major storm of the growing season strongly influences the population dynamics of three rare and endangered annual plant species in a coastal California (USA) ecosystem. In a field experiment we used moisture barriers and water addition to manipulate the timing and temperature associated with first major rains of the season. The three focal species showed two- to fivefold variation in per capita population growth rates between the different storm treatments, comparable to variation found in a prior experiment imposing eightfold differences in season-long precipitation. Variation in germination was a major demographic driver of how two of three species responded to the first rains. For one of these species, the timing of the storm was the most critical determinant of its germination, while the other showed enhanced germination with colder storm temperatures. The role of temperature was further supported by laboratory trials showing enhanced germination in cooler treatments. Our work suggests that, because of species-specific cues for demographic transitions such as germination, changes to discrete climate events may be as, if not more, important than changes to season-long variables.

Key words: annual plant; California Channel Islands, USA; climate events; germination; Gilia tenuiflora; *life-history transitions;* Malacothrix indecora; Phacelia insularis; *persistence under climate change; precipitation.*

Introduction

Growing concerns over the biological impacts of climate change have motivated ecologists to explore how changing climate variables influence natural communities (Walther et al. 2002, Root et al. 2003, Thomas et al. 2004). Most of these studies have focused on changing mean conditions, such as annual temperature or rainfall (Jentsch et al. 2007). Many ecological processes, however, may be more sensitive to climate events—discrete, short-term occurrences (Jentsch et al. 2007) such as frosts, storms, and heat waves (Barret et al. 2008, Adams et al. 2009, Miao et al. 2009, Ross et al. 2009, Sorte et al. 2010). Although the severity and frequency of many such events are forecast to increase this century (Karl and Trenberth 2003), our understanding of how these changes will influence populations and communities is only beginning to develop.

Changes to discrete climate events can impact communities via a range of mechanisms. Most obvious are cases where the events influence mortality or growth (Knapp et al. 2008, Adams et al. 2009, Miao et al. 2009, Ross et al. 2009, Albright et al. 2010, Sorte et al. 2010). For example, severe storms and frosts can inflict heavy mortality and reset succession (Ross et al. 2009). Meanwhile, growing seasons with fewer, but larger, rain storms may meet the water demands of vegetation less consistently (Knapp et al. 2002). Our focus here, by contrast, is changes to climate events that cue discrete demographic transitions in a population, such as bud burst, flowering, or seed germination (Adler and Levine 2007, Jentsch et al. 2009, Forest et al. 2010). Changes to these events can shift the timing and length of the growing season, determine the fraction of individuals emerging from dormancy, and thereby influence population growth and persistence. These ecological impacts of climate change may be underappreciated, in part because the life-history cues for demographic transitions are often poorly understood.

For populations with climatically cued life-history transitions, changes in the severity, frequency, and timing of climate events have the potential to overwhelm the impact of changing mean conditions (Jentsch et al. 2007, Levine et al. 2008). However, a recent review by Jentsch et al. (2007) finds that only 20% of experimental climate-change studies focus on events, and very few of these compare the relative importance of changing events to changing mean conditions (but see Fay et al. 2003).

Manuscript received 11 March 2011; accepted 20 June 2011. Corresponding editor: M. J. Lechowitz.
[3] Present address: Institute of Integrative Biology, ETH Zurich, Universitaetstrasse 16, 8092 Zurich, Switzerland. E-mail: jlevine@ethz.ch

Here, we examine how changing the timing and temperature of the first major storm of the growing season influences rare annual plants occurring on the California Channel Islands (USA). Understanding how rare plant species on islands respond to climate change is important because such species cannot shift their range to match future climate. We focus on the first major storm of the season, usually considered ~2.5 cm, because this event triggers the germination of annual plants in the mediterranean climate of the habitat (Bartolome 1979). The temperature, timing, and moisture conditions associated with such storms can determine the fraction of the seed bank germinating that year (Heady 1958, Pitt and Heady 1978, Baskin and Baskin 2001). Meanwhile, the timing of the first rains can strongly influence later life stages by determining the onset of the growing season. Early first rains give plants a longer season to grow and reproduce before soils dry in late spring, but also increase the risk of early-season droughts (Pitt and Heady 1978, Rice 1987). Thus, even though the first major storm typically lasts no more than several days, it may have a disproportionate impact on population fate each year. This is especially true given that individual years differ greatly in the timing and air temperature associated with the first major storm (Fig. 1A, B).

Over the last 20 years the first major rain on the northern Channel Islands has occurred anywhere between mid-September and late February (Fig. 1A). Given that most annual plants in the system complete their life cycle around May, this drives a roughly twofold variation in growing-season length between years. Growing-season length, in turn, has strong potential to influence biomass and therefore fecundity. The nightly low temperature associated with the storm also varies, from 4° to 11°C over the same period (Fig. 1B), a wide range given the sensitivity of germination to temperature for many annual species in the California flora (Went 1948, 1949). Previous work in the Channel Islands study system has shown large between-year variation in germination and fecundity, and, for some species, the temperature associated with the first major storm is negatively correlated with their spring population size across years (Levine et al. 2008). However, these years differ in many factors other than features of the first rain event, motivating our direct manipulation of this factor.

In California, we have several reasons to expect features of the first major storm to shift with climate change, and these changes may affect both germination and post-germination success. First, warmer air temperatures (Dukes and Shaw 2007) will mean warmer conditions surrounding storm events (shifting the distribution in Fig. 1B to the right). Warmer first rains might also be expected with forecasted enhancement of El Niño conditions (Schonher and Nicholson 1989, McFadden et al. 2006); in El Niño years, California derives more of its moisture from warm storms originating in the tropics. Less clear is the effect of changing rainfall itself (Bell et al. 2004, Hayhoe et al. 2004). The most recent regional forecasts predict moderately less annual precipitation in California, with no major change to the Mediterranean pattern of rainfall (Hayhoe et al. 2004, Cayan et al. 2006). Given that storm intensity tends to increase until mid-season, an equal reduction in rainfall through the year might mean that sufficient rain for germination would not come until later in the year (which is also when the storms tend to be cold). Although this prediction remains speculative, it would mean a shorter season for growth and reproduction.

Although considerable uncertainty surrounds the expected changes in the first major rains, better

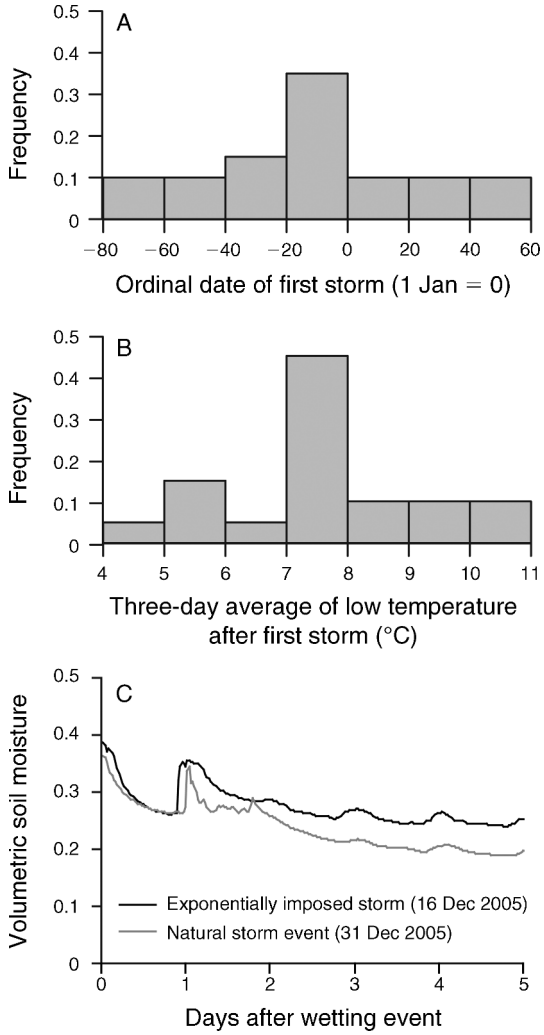

FIG. 1. Variation in (A) ordinal date and (B) average air temperature of the first 2.5-cm rains of the growing season, 1990–2010, on Santa Rosa Island, California, USA. Storm date and temperature are negatively related with an R^2 of 0.25, $P = 0.024$. (C) Comparison of soil moisture (proportion) after an experimentally imposed (5 cm of rain) and naturally occurring (4.24 cm of rain) early storm event at the *Malacothrix* study site.

forecasting the ecological impacts of changing climate requires better understanding the sensitivity of plant populations to early storm events. We thus address four questions in our Channel Islands study system. First, how sensitive are plant population growth rates to the first major rain event of the growing season? Second, which stage of the plant life cycle is responsible for the sensitivity? Third, how do the temperature and the timing of the first storm determine how plants respond? Finally, how do plant responses to the first storm compare to their responses to season-long precipitation?

To answer these questions, we parameterized demographic models with field data to measure the population growth rate of our focal plant species subjected to experimentally imposed and naturally varying first rain events in fall and winter. To determine the extent to which population response to different first storms results from germination or post-germination performance, we conducted a life-table response experiment with the demographic data. To identify storm features determining the plant response, we correlated germination and fecundity with storm temperature and timing, and conducted germination trials at different temperatures. In the *Discussion* we compare the range of population growth rates found in the current study to those in our prior study (Levine et al. 2010) imposing drought and season-long water-addition treatments on the same focal species.

Methods

Study system

We conducted our study on Santa Rosa Island, located off the coast of Santa Barbara, California, USA. Nearly all rainfall occurs between October and April, and averages 32 cm per year. This study extended over two growing seasons: fall 2004 to spring 2005, an El Niño year with significantly more rain than average (51 cm); and fall 2005 to spring 2006, a year with near average precipitation (28 cm) (Levine et al. 2010). Hereafter, we will refer to rainfall years by the year of the spring.

We examined how three rare and endangered annual plants, *Gilia tenuiflora* ssp. *hoffmannii*, *Malacothrix indecora*, and *Phacelia insularis* var. *insularis* (hereafter *Gilia*, *Malacothrix*, and *Phacelia*) responded to manipulations of the first major rain event. The three species are endemic to the northern Channel Islands, and federally listed as endangered. The focal species germinate with the first major rains of the fall or winter ($>\sim$2.5 cm), develop a taproot, and are small statured. All three annuals develop a seed bank, as evidenced by low germination rates and high annual survival of buried seed (Levine et al. 2008) as well as by population recovery in years following seed-set failure. *Gilia* grows on stabilized dune soils, *Malacothrix* on sandy, eroding terraces, and *Phacelia* on stabilized dune headlands. See Levine et al. (2008, 2010) for additional details of the study system.

Manipulation of the first major rain events

We manipulated the first major rain of the season in two ways. In what we call the "natural storm treatments," we took advantage of the natural variation among the first several storms of the growing season. We covered plots with a water barrier, and removed the barriers in a manner that exposed the plants to different "first" storms of the year. Because any year only includes a handful of early storms, we also included "experimental storm treatments." In these, we experimentally imposed a first rain event by watering at different times of the early growing season, after covering plots to exclude the natural first storms. We conducted our manipulations at three field sites, each adjacent to a population of either *Gilia*, *Malacothrix*, or *Phacelia*. These sites were selected to match the physical conditions of the habitat of each focal species without disturbing or overlapping the existing populations.

In fall 2004 we located 64, 60×60 cm plots at 2.5-m intervals along transects at each of our sites (72 plots at the *Malacothrix* site). The following first major rainfall treatments were randomly assigned eight plots (nine at the *Malacothrix* site): (N1) first natural storm, which happened to be 2.8 cm on 19 October; (N2) second natural storm, 6.5 cm on 27 December; (N3) second natural storm repeated, 6.5 cm on 27 December; (N4) third natural storm, 6.7 cm on 7 January; (E1) experimental 1 November storm; (E2) experimental 1 December storm; (E3) experimental 6 January storm; and (E4) experimental 6 February storm. Because natural storm treatment N1 was assigned to receive the first natural storm of the year, it needed no pre-storm water barrier. Natural storm treatments N2, N3, and N4 were covered with a 1×1 m sheet of breathable moisture barrier (Tyvek Home Wrap; DuPont, Wilmington, Deleware, USA) until 13 November, 10 December, and 1 January, respectively. The edges of the moisture barrier were pinned to the ground with irrigation staples. Because no major storm occurred between the time treatments N2 and N3 were uncovered, they were ultimately subject to the same first major rain event (27 December). Treatment N2, however, did experience more sub-germinating moisture (fog and rain events $<$1.2 cm) prior to 10 December, creating a modestly different early-season environment relative to treatment N3.

All plots subjected to the experimentally imposed first storm events (treatments E1–E4) were covered with moisture barrier until their designated experimental rain event. The precise dates of the experimental storms were chosen to spread the treatments through the fall and early winter rather than target any particular climate condition. We imposed the rain events by removing the moisture barrier and using a watering can to distribute water over a 70×70 cm area centered on each plot. To mimic a large storm event, we added 5 cm of water over a two-day period. Over this period, we also covered the plots with a wooden frame supporting wetted burlap.

This helped mimic natural storm conditions by shading the plots and creating a humid environment near the soil surface. Prior to the initiation of each storm treatment, we installed HOBO data loggers (Onset Corporation, Bourne, Massachusetts, USA) fitted with Decagon probes (Decagon Devices, Pullman, Washington, USA) to record soil moisture in the top 5 cm of soil in representative plots. We also logged temperature at the soil surface with temperature sensors (Onset Corporation) and had access to natural air temperature from the island's weather station.

We repeated the entire experiment in the 2005–2006 growing season. Though treatments N1, N2, and N3 were not uncovered until October, November, and December, respectively, the first major rain event of the experiment's second year did not occur until 1 January, a 4.2 cm-event. These three treatments were therefore subject to the same first major rain. They did, however, differ in their exposure to the sub-germinating rains and fog that occurred before this event, and this proves to reasonably affect germination. Treatment N4 was uncovered in January, and the first major storm for plots in this treatment occurred in a 4.7-cm event on 27 February. The experimental storm treatments (E1–E4) followed the methods of the prior year's implementation, imposed on 20 October, 14 November, 19 December, and 21 January. In both years, the dates the experimental storm treatments were imposed differed by several days across sites due to our inability to be in all locations at once (the dates reported are for the *Gilia* site).

Plot design

In each plot we seeded a 15×15 cm area with seed of the focal species for the site. The amount of seed added to each subplot varied across year and species, often limited by seed production the prior spring. Therefore, in the 2005 and 2006 experiments, we sowed the 15×15 cm areas with 40 and 60 seeds, respectively, of *Phacelia*; 100 and 130 seeds, respectively, of *Malacothrix*, and 200 seeds of *Gilia* in both years. Seeds in the first natural storm treatment (N1) were sown in early fall. For all other treatments, seeds were added just after the moisture barrier was removed. Seeds were stored under laboratory conditions between their collection date and the time when they were sown into the experiment. Sowing seeds soon after their production to allow for any influence of summer climate was impractical due to the high loss rates expected with strong winds on the island.

Germination rates and plant size were low enough in all years that interaction with conspecific individuals was minimal. Heterospecific background vegetation was often denser in the experimental sites than in our focal species' natural habitat (where we could not work). We therefore thinned heterospecific density by about half to better match the natural habitat (as in Levine et al. [2010]).

In summer 2005, after the first year of the experiment, the location of all plots was shifted along the transect to be nonoverlapping. This ensured that seed did not carry over between the 2005 and 2006 experiments. In the second year of the experiment (2006) we aimed to better understand how surrounding vegetation influenced the response of the focal annuals to early-season storm events. Thus, in each plot, we sowed the focal species into two 15×15 cm subplots, and randomly selected one of these to have background vegetation cleared. However, results showed that clearing had no effect on any focal species' response to the storm treatments (clearing $\times$ storm interaction $P > 0.50$), causing us to pool the data from the two subplots prior to analysis (as in Levine et al. 2008).

Per capita population growth and vital rate measurement

To assess how different first major rains influenced the per capita population growth rate of our focal annuals, we parameterized an annual plant population model. Mathematical models of annual plant populations are well developed (Watkinson 1980, Pacala 1986, Levine and Rees 2004) and reasonably approximate the life cycle. The yearly per capita population growth rate (λ), including both seed production and carryover in the soil, can be described as follows:

$$\lambda = s(1 - g) + gF \tag{1}$$

where g is the germination fraction, s is the annual survival of ungerminated seeds in the soil, and F is the number of viable seeds produced per germinant (per-germinant fecundity). See Levine et al. (2008) for model details and assumptions.

We measured the germination fraction (g) and per-germinant fecundity (F) in each experimental plot. Seed-bank survival fractions (s) for *Gilia*, *Malacothrix*, and *Phacelia* were 75%, 57%, and 57%, respectively (from Levine et al. 2008), and we assumed these were independent of treatment. We measured germination over a series of censuses by placing a toothpick near each germinant. For the germination rate, the number of germinants was divided by the total number of seeds added, discounted by their viability (98%, 84%, and 90% for *Gilia*, *Malacothrix*, and *Phacelia*, respectively, from Levine et al. 2008). In the spring we measured the total number of flowers produced by the focal species in each subplot. To calculate the seeds per germinant, we multiplied this latter number by the average number of viable seeds per flower (23.3, 28.3, or 8.0 seeds for *Gilia*, *Malacothrix*, and *Phacelia* respectively; Levine et al. 2008) and divided by the number of germinants.

With our parameterized models, we conducted life-table response experiments to evaluate the degree to which variation in population growth rate across treatments was driven by observed variation in germination or per-germinant fecundity (Caswell 2001). We assume that g and F can vary independently and that the difference between the population growth rate in a given storm treatment (λ_{ST}) and the average population growth rate across storm treatments ($\bar{\lambda}$) that year is a

linear combination of the effects of changing g and F:

$$\lambda_{ST} = \bar{\lambda} + (g_{ST} - \bar{g})\frac{\partial\lambda}{\partial g} + (F_{ST} - \bar{F})\frac{\partial\lambda}{\partial F}. \quad (2)$$

The partial derivatives, the sensitivity of λ to changes in g and F, are respectively evaluated at $\bar{g}$ and $\bar{F}$ (the within-year average for these parameters), and the "ST" subscript indicates the storm treatment (N1–N4, or E1–E4). Eq. 2 allowed us to project how the per capita growth rate would change across storms if only the germination rate varied ($F_{ST} - \bar{F} = 0$) or only the per-germinant fecundity (F) varied ($g_{ST} - \bar{g} = 0$). We assessed the contribution of the observed variation in each parameter to cross-storm variation in λ by comparing these two projections to the observed variation in per capita growth rate. Because the seed death rate, s, is assumed to be constant across storms ($s_{ST} - \bar{s} = 0$), not contributing to variation in λ, it is absent from Eq. 2. We conducted separate life-table response experiments for the two years of the study.

Germination trials

Because the first major storms of the season vary considerably in the coincident air temperature (Fig. 1B), we used laboratory trials to evaluate how the temperature at the time of seed wetting influences germination. All trials were conducted by Ransom Seed Laboratory in Carpinteria, California, USA.

For each species, 200 seeds (100 seeds for *Phacelia*) were placed in clear plastic germination boxes on wetted germination paper, and kept for five days in a dark growth chamber at 5°, 10°, 15°, 25°, or 30°C. Seeds were then transferred to a 20°C chamber for two weeks (a neutral temperature). Those that had not germinated were cut, treated with gibberellic acid, and then stained with tetrazolium to check viability (Baskin and Baskin 2001). Although the seed trials are necessarily contrived relative to natural settings, we obtained similar results when we sowed seeds on field or field-mimic soils in a shade house and used ice to impose the different temperature treatments (J. Levine, *unpublished data*).

While this first set of laboratory trials allowed us to assess how temperature at the time of seed wetting influences germination, ungerminated seeds eventually experience a relatively cold event later in the growing season. We were thus interested in whether early exposure to warm conditions enforces dormancy when later cool events arrive. To test this, we simultaneously conducted a parallel set of trials, but before exposing seeds to five days of 5°C, we exposed them to five days of 15°, 25°, or 30°C. This test was not designed to mimic a specific rain sequence, but rather, it tested how seeds respond to cold temperatures after exposure to warmer conditions.

Statistical analyses

We analyzed the effect of the first major storm on species' germination and per capita population growth rates with nonparametric Kruskal-Wallis tests separately conducted for each focal species and year of the study. This choice of test was made due to failure of the data to meet key assumptions of ANOVA. We included all natural storm treatments (regardless of whether the identity of the first major rains differed) and all experimental storms in a single analysis, because each varied the early season conditions for a given year. Moreover, for all species in both years, we found no significant difference in any vital rate between the four natural and four experimentally imposed storms.

To identify the storm features that determined species' germination and per-germinant fecundity, we conducted multiple linear regressions predicting how these demographic rates were predicted by storm date and temperature. In the first model, we used the mean germination proportion (arcsine transformed) in each treatment over the two years as the dependent variable, and the ordinal date of the storm and the three-day average nightly low air temperature after the storm (measured at the island weather station) as predictor variables. We selected this specific temperature measure because, relative to alternative measures, it best predicted germination in univariate regressions. The second model used the mean per-germinant fecundity (log-transformed) in each treatment as the dependent variable.

The influence of temperature on the proportion of seeds germinating in the laboratory trials was tested with a χ^2 test. All analyses were performed in R version 2.9.2 (R Development Core Team 2009).

Results

The experimental storms reasonably mimicked the pattern of water availability after real storm events (Fig. 1C). We also observed that the majority of germination occurred soon after the first major rain in each treatment, and not with later rains in the season.

For all three focal species, the different first rain events drove large differences in germination and per capita growth rate (Figs. 2–4). For *Gilia*, different first storms imposed almost fourfold variation in per capita growth rate in 2005 (Fig. 2A) and twofold variation in 2006 (Fig. 2B), although the 2006 differences were not significant. Germination varied over 10-fold between storms, much more than per capita growth rate (Fig. 2C, D). In addition, we found considerable variation within both the natural storm (N1–N4) and experimental storm (E1–E4) treatments (Fig. 2A, B). Per-germinant fecundity (Appendix; Fig. A1) showed considerably less variation between the first-storm treatments. Life-table response experiments showed that the per capita growth rate variation between first-storm treatments was driven more by variation in germination than variation in per-germinant fecundity (Fig. 2A, B). This is evidenced by the greater proximity of the solid line (where only germination varies between treatments) than the dashed line (where only per-germinant fecun-

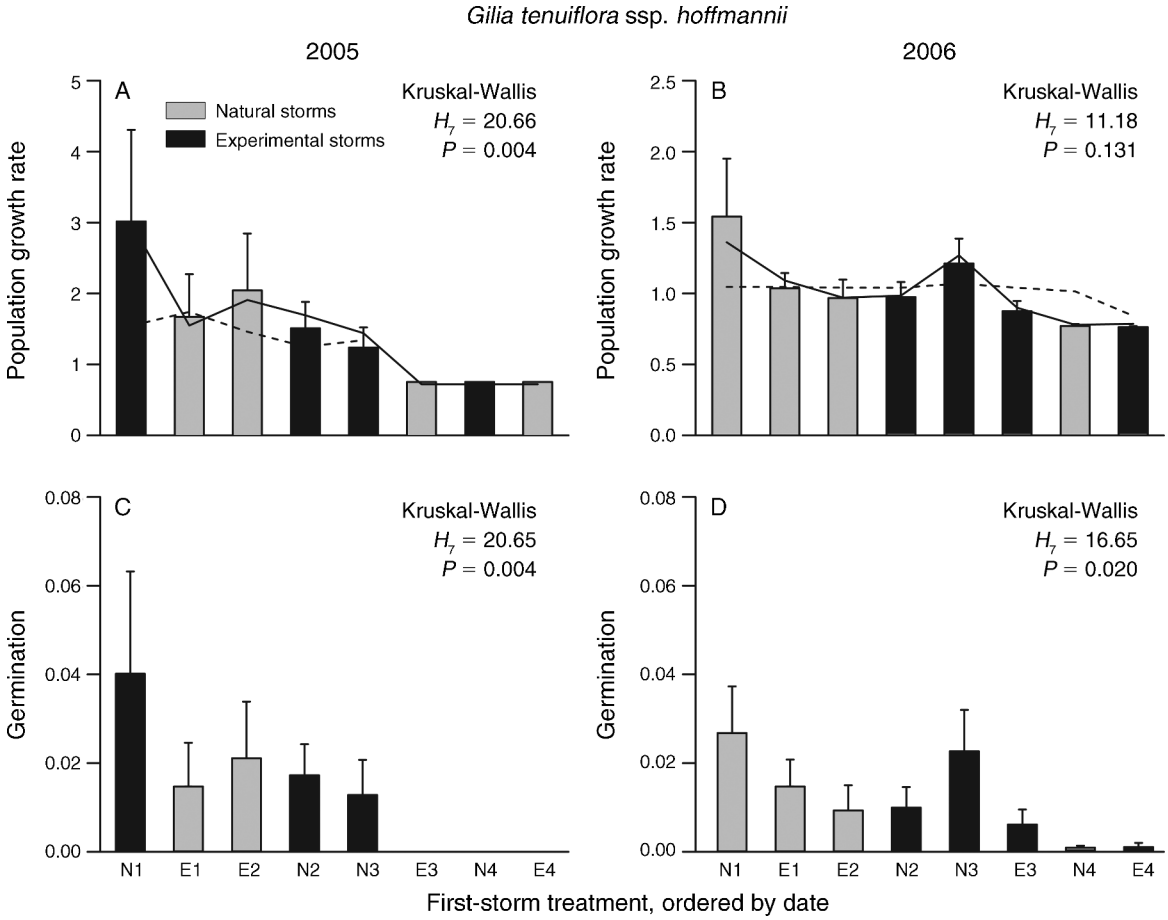

FIG. 2. *Gilia tenuiflora* ssp. *hoffmannii* (A, B) per capita population growth rate and (C, D) germination proportion as a function of the first storm treatments in 2005 and 2006. The first-storm treatments are ordered by date, with the natural storms (N1–N4) shown in black and the experimentally imposed storms (E1–E4) shown in gray. Data are means + SE; Kruskal-Wallis test results are given. In panels (A) and (B) the solid lines show the per capita growth rate predicted by life-table response experiments when only germination varies across the eight treatments. The dashed lines show the predicted per capita growth rate when only per-germinant fecundity varies across the treatments. Gaps in the dashed line arise when per-germinant seed production cannot be calculated because no seeds germinated in a treatment.

dity varies) to the observed per capita growth rates in Fig. 2A and B.

Malacothrix and *Phacelia* also showed large differences in per capita growth rate and germination between different first-storm events, though germination was less responsible for the variation in growth rate. In both years of the study, *Malacothrix* showed threefold variation in per capita growth rate between the first-storm treatments (Fig. 3A, B). Germination varied 6- and 20-fold in 2005 and 2006, respectively (Fig. 3C, D). In the life-table response experiments, neither germination variation nor variation in per-germinant fecundity alone predicted a per capita growth rate that closely matched the observed values (Fig. 3A, B). This indicates that the response of both vital rates contributed to the between-treatment variation in per capita growth rate. *Phacelia* showed a similar pattern of response as *Malacothrix* (Fig. 4), though almost complete germination failure in 2005 left us with only one year of results for *Phacelia*. Again, variation in per capita growth rate (Fig. 4A) and germination (Fig. 4B) was large. However, the life-table response experiment suggested that the high per capita growth rate in treatment N3, the major deviation from the average, corresponded to greater per-germinant fecundity (Appendix: Fig. A1) rather than greater germination.

Results presented thus far show that for each of the three species, different first storms lead to considerably different per capita growth rates, and for *Gilia* and *Malacothrix*, these differences were driven in part by germination. Subsequent multiple-regression analyses showed that species differed in how germination and per-germinant fecundity responded to the temperature and timing of the first storm. *Gilia* germination only responded significantly to the date of the storm (Table 1), with earlier events favoring higher germination than later events (Fig. 5A). *Malacothrix* germination meanwhile, only responded significantly to the temperature

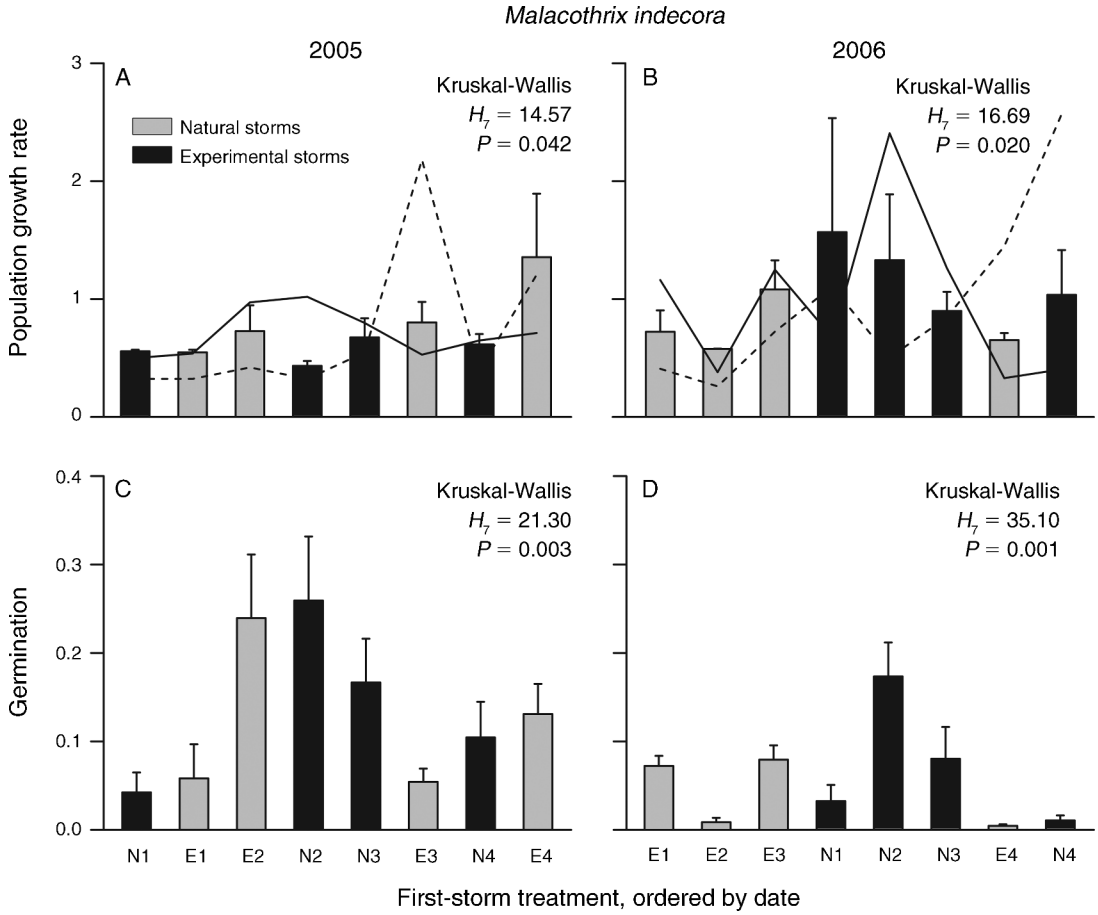

FIG. 3. *Malacothrix indecora* (A, B) per capita population growth rate and (C, D) germination proportion as a function of the first-storm treatments in 2005 and 2006. The format is as in Fig. 2.

associated with the first storm (Table 1); warmer nightly low temperatures after the storm were associated with reduced germination (Fig. 5B). The per-germinant fecundity of *Gilia* declined with later storms (Fig. 5C; Table 1), likely due to the shorter growing season. By contrast, *Malacothrix* per-germinant fecundity increased with later storms (Fig. 5D; Table 1) due to greater survival over the shorter season (Appendix: Fig. A2). *Phacelia* germination and per-germinant fecundity showed no significant correlation with the temperature or the timing of the first major storm, though this may partly reflect a reduced sample size for this species due to the absence of 2005 results.

The storm variables correlated with germination partly match the results of germination trials. All three species showed almost no germination at very high temperatures (30°C), but they differed markedly in how fast germination declined with increasing temperature (Fig. 6). Consistent with its greater germination in cooler storm events, *Malacothrix* was the only species to show declining germination from 5° to 10°C, which covers the range of natural variation in storm events (Fig. 6B). Though *Gilia* and *Phacelia* germination dropped off precipitously at temperatures higher than 25° and 15°C, respectively (Fig. 6A, C), these temperatures are higher than what seeds face in or immediately following natural storm events. In addition, we found that *Malacothrix* seeds subject to initially warmer temperatures (15°C and greater), germinated one eighth as well as unwarmed seeds when subsequently exposed to cool (5°C) temperatures (Fig. 6B). Similar, but weaker effects of initial warming were seen for the other two species (Fig. 6A, C).

DISCUSSION

Large effects of changing the first major rain event

Perhaps the most striking finding of this study is that manipulating the first major rain of the growing season, an event that lasts roughly two to three days, can induce three- to fourfold variation in the focal species' per capita population growth rate, a vital rate that integrates plant performance across the roughly six-month growing season.

In addition, past rainfall manipulations (Levine et al. 2010) allow us to compare the species' response to changes in the first major rain to their response to

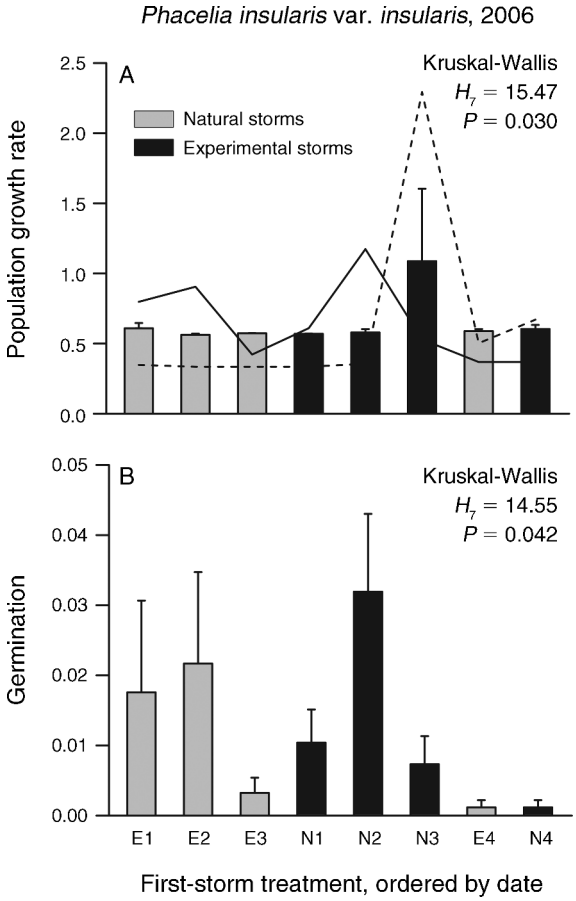

FIG. 4. *Phacelia insularis* var. *insularis* (A) per capita population growth rate and (B) germination proportion as a function of the first-storm treatments in 2006 (2005 saw experiment-wide germination failure). The format is as in Fig. 2.

changes in season-long rainfall. In a prior study, we subjected the same species to rainfall manipulations ranging from season-long drought (75% reductions in ambient rainfall) to season-long doubling of rainfall. This generated an eightfold difference in total annual precipitation between treatments, comparable to natural variation over the last two decades (Levine et al. 2010). Except for *Phacelia* in cleared plots, we saw no more than a twofold per capita growth rate difference between the season-long drought and water-addition treatments. This is modestly less variation than found between the first major rain treatments imposed in the current study. We therefore conclude that changes to the first rains of the growing season are likely to be as important as eightfold changes to season-long rainfall, at least in our study system.

Our conclusion needs to be qualified by the fact that our current experiment allowed the total amount of rainfall to vary with the timing of the first-storm treatments, so that later first-rain treatments had both shorter growing seasons and less total rainfall. Despite this, we still saw no influence of season-long rainfall on vital rates when the current results were combined with past findings. *Gilia* germination was less when the first storm was late (potentially due to less season-long rainfall), but our past work shows that even a 75% reduction in season-long rainfall had inconsistent effects on *Gilia* germination (Levine et al. 2010). And while *Gilia*'s post-germination fecundity was also greater in the early storm treatments, life-table response experiments showed that this vital rate contributed little to its per capita growth rate response. *Malacothrix* germination was independent of storm timing, and its per-germinant fecundity was actually greater with later storms, the opposite of what would be expected if greater rainfall in longer seasons provided an important boost. Finally, our finding that manipulating the first major rains affected population growth rates as much if not more than imposing eightfold variation in season-long rainfall was not restricted to the rare focal annuals. The biomass of the most common annual competitor in each of their habitats showed a similar response (J. Levine, *unpublished data*).

Few other studies have compared the effects of changes to season-long climate variables to the effects of changing discrete climate events (Jentsch et al. 2007). Fay et al. (2003) showed that repacking rainfall in fewer large events (but having no effect on annual totals) reduced tall grass prairie production in the central United States. The reduction in production was comparable to that found with a 30% reduction in total rainfall. In contrast, in a more arid system, concentrat-

TABLE 1. Results of multiple-regression analyses relating the response variables germination and per-germinant fecundity of *Gilia*, *Malacothrix*, and *Phacelia* to the three-day average nightly low temperature and the ordinal date of the storm treatments.

	Gilia			*Malacothrix*			*Phacelia*		
Variable	Slope	t	P	Slope	t	P	Slope	t	P
Germination									
Temperature	−0.0069	−1.23	0.241	−0.0382	−2.44	**0.030**	0.0027	0.36	0.737
Date	−0.0014	−3.79	**0.002**	−0.0013	−1.35	0.200	−0.0008	−1.30	0.250
Per-germinant fecundity									
Temperature	−0.0604	−1.14	0.283	−0.0182	−0.15	0.881	−0.0441	−0.15	0.886
Date	−0.0124	−3.34	**0.008**	0.0240	3.29	**0.006**	0.2579	1.15	0.301

Note: Boldface entries indicate significance at $P < 0.05$. For germination the model R^2 for *Gilia* is 0.53; for *Malacothrix*, 0.32; and for *Phacelia*, 0.41. The per-germinant fecundity model R^2 for *Gilia* is 0.53; for *Malacothrix*, 0.53; and for *Phacelia*, 0.32.

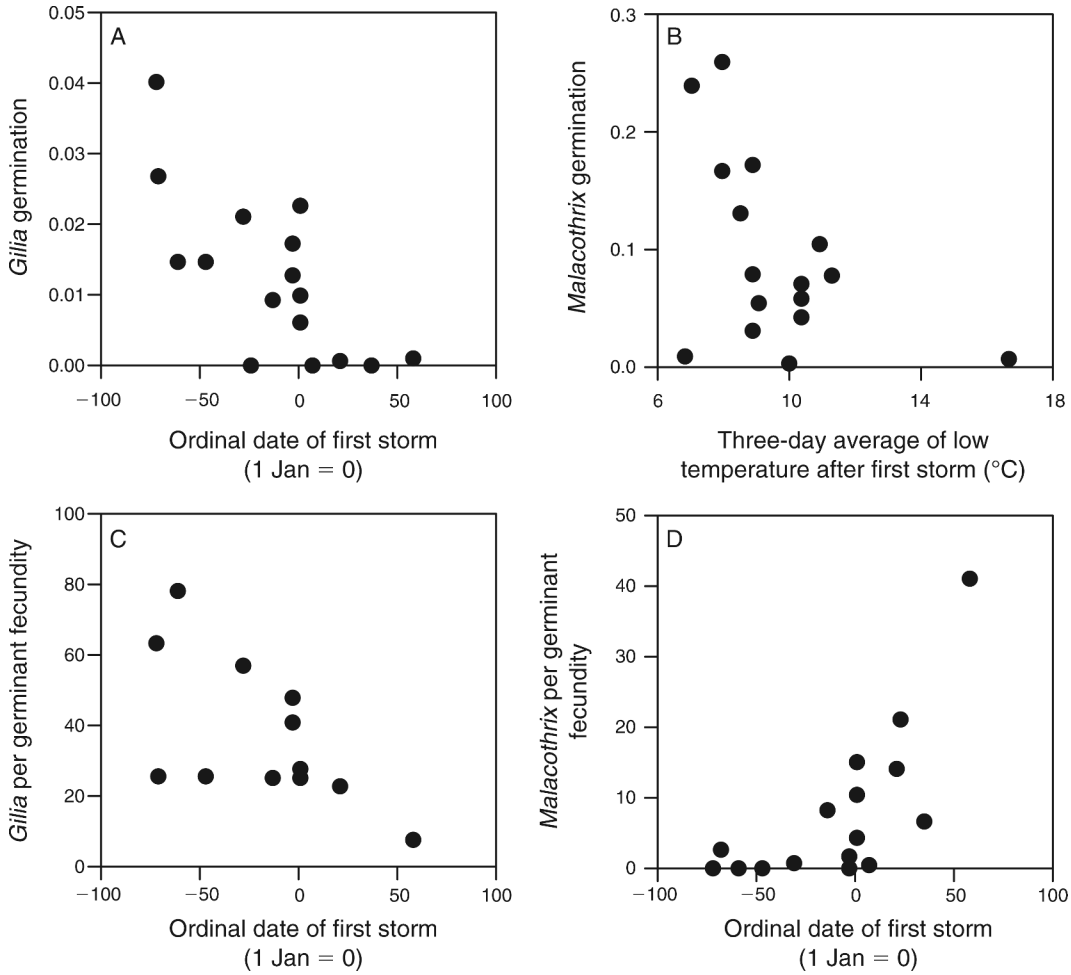

FIG. 5. Germination and per-germinant fecundity responses of *Gilia* and *Malacothrix* to the three-day average nightly low temperature and the ordinal date of the storm treatments (see Table 1 for statistical analysis). Shown are the significant effects of (A) storm date on *Gilia* germination and (B) storm temperature on *Malacothrix* germination. Panels (C) and (D) show the effect of storm date on per-germinant fecundity for each species.

ing storms in fewer larger events actually increased production (Heisler-White et al. 2008).

Underlying mechanisms

Understanding the demographic and climatic processes causing the first major rain to influence population dynamics is critical for predicting the consequences of potential changes to the rainfall regime. With respect to the demographic mechanism, we found that germination responded more strongly than per capita growth rate to the different first-rain treatments. For *Gilia*, life-table response experiments showed that between-treatment variation in germination was sufficient to produce the observed variation in per capita growth rate. For *Malacothrix*, variation in both germination and per-germinant fecundity contributed to its per capita growth rate response, and for *Phacelia* the per-germinant fecundity seemed more important than germination.

Our findings on the relative contribution of germination and fecundity to population-growth variation need to be qualified by the fact that our experiment was designed to minimize intraspecific interactions between the experimental plants. The only exception might be *Malacothrix* individuals in high-germination treatments in 2005, a year in which we saw high mortality of germinants due to damping off. In nature, individuals of all three species sometimes occur at much higher densities than those in our experiment. We might expect intraspecific competition in these locations to dampen fecundity variation between years. Similarly, first rain storms that favor high germination would likely increase intraspecific competition. This might counter the population growth advantage that would arise from greater germination alone.

For the two species that showed some influence of germination on the per capita growth rate differences between storm treatments, we can partly identify the

storm factors associated with greater germination. For *Gilia*, we found no influence of storm temperature, but a significant influence of storm timing, such that early storms showed much greater germination than later storms. Although the mechanism underlying the storm-timing response is unknown (it may relate to day length; Baskin and Baskin 2001, Adondakis and Venable 2004), the absence of a temperature response is consistent with the germination trials for this species. In the laboratory *Gilia* germination declined little between 5° and 15°, a temperature range roughly bracketing the nightly low temperatures measured after real storm events.

In contrast to *Gilia*, *Malacothrix* germination responded significantly to the cold temperatures associated with the storms imposed in our project, but not to their timing. Consistent with its response to field manipulation of the first major rain, *Malacothrix* germination in lab trials declined from roughly 90% at 5°C, to roughly 25% at 10°C, and even less at greater temperatures. Nonetheless, each season eventually presents a cold storm, so *Malacothrix* germination might be expected with the second, third, or fourth storm of the season (as soon as a cold storm occurs). This is not what we observed in the field, however, and may be explained by our finding that seeds initially exposed to warm temperatures (15–30°C) have only 15% germination when subsequently exposed to 5°C (compared with ~90% for unwarmed seeds).

Germination induced by cold temperatures at the time of first seed wetting has long been noted for the annual flora of California deserts (Went 1948, 1949), and is common in desert winter annuals worldwide (Baskin and Baskin 2001, Adondakis and Venable 2004, Facelli et al. 2005). The adaptive significance of this germination cue in coastal California is unknown, but may relate to avoiding germination with late summer rains (Jain 1982, Levine et al. 2008). Such early rain events are rare in coastal California, but when they occur, they are unlikely to be followed by significant rain for several months, a drought long enough to kill any germinants (Rice 1987). Cold temperatures at the time of seed wetting may signal the onset of fall or winter, times of the year when subsequent rainfall is expected within a month. Another consideration is that *Malacothrix* actually made more seeds per germinant with later storms due to greater survival to flowering in the shorter season (Appendix: Fig. A2). Thus, foregoing germination until years with later (cold) first storms may avoid early season droughts, and for species like *Malacothrix*, also enhance fecundity when no drought occurs.

For those species not responding strongly to cold temperatures at the time of seed wetting, seasonal cycles of seed dormancy (Baskin et al. 1993) might allow plants to avoid germination with summer rain. In addition, factors other than the features of the first rains might control germination, including conditions prior to the germination-inducing rains (Baskin and Baskin 2001, Adondakis and Venable 2004). Indeed for all three species in 2006, we saw at least threefold variation in germination between treatments N1–N3 (Figs. 2D, 3D, and 4B), treatments that received the same first rain event. What differed were the climate conditions experienced prior to that event.

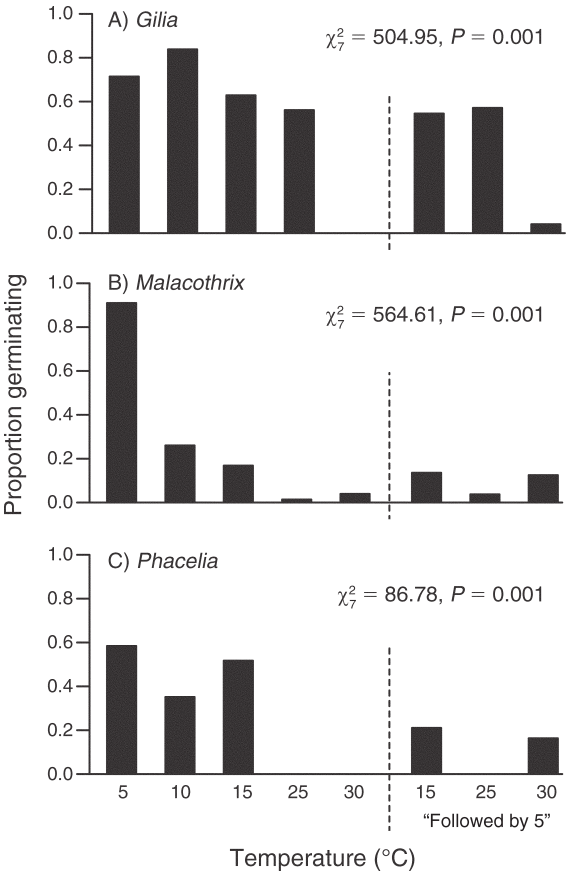

FIG. 6. Laboratory germination trial results for the three rare and endangered annuals, along with χ^2 tests of significant differences between temperature treatments. Tests to the right of the dashed line involved exposing wetted seeds to the noted temperature for five days, followed by exposure to 5°C for five days. See *Methods: Germination trials* for details.

While ecologists generally acknowledge that rainfall is the climate variable that begins the growing season in California annual systems (Bartolome 1979, Rice 1987), the environmental triggers for the end of the growing season (flowering) are less well understood. Nonetheless, for our focal species, we observed high year-to-year consistency in the timing of peak flowering (*Gilia* in late April, *Malacothrix* in mid-June, and *Phacelia* in mid-March). That this consistency emerges despite large year-to-year variability in season-long precipitation suggests a possible photoperiod cue for flowering. If this hypothesis is correct, the start of the growing season is highly variable, driven by the timing of the first rains, while the end of the season is rather fixed. This could be a quite general phenomenon in water-limited systems (Wolkovitch and Cleland 2011), and would lead to the prediction

of less fecundity in years with later growing-season initiation. However, in our study, only one of our three species, *Gilia*, showed less fecundity with later first rains.

In prior work, we have used monitoring data to correlate the springtime plant population size of *Gilia*, *Malacothrix*, and *Phacelia* with the temperature at the time of the first rains (Levine et al. 2008), and these past results are partly consistent with what we found here. In our present study *Malacothrix* germination was highest with cold temperatures in both the storm treatments and laboratory germination trials, and, indeed, this species had its greatest population sizes in years with relatively cold first rains (Levine et al. 2008). By contrast, our past interpretation of the *Gilia* and *Phacelia* monitoring results are not supported by the current experiments. Our past study suggested that, like *Malacothrix*, both species showed greater population sizes in years with cold first rains. Yet in our present study we saw little evidence that these species' germination increased with cold temperatures in either the field manipulation of first rains or the laboratory trials (over a temperature range observed in real storms). The discrepancy likely reflects limitations of the monitoring results. Censuses of the aboveground plant population size in springtime, without a measure of the pre-germination seed bank allow only weak inference of the true germination behavior of the species. Alternatively, *Gilia* and *Phacelia* may indeed have a cold-temperature cue for germination, but only after experiencing the summer conditions bypassed in the experiment.

Persistence under climate change

Our results suggest that changing characteristics of the first rain storm could strongly influence annual plant populations in coastal California. However, the mechanism underlying this response is likely to differ across species. If first storms become warmer, a likely scenario given current climate models, species like *Malacothrix*, which benefit from cold first rains, will likely suffer reduced population growth. Meanwhile, if predictions for less total rainfall (Hayhoe et al. 2004, Cayan et al. 2006) mean that large storms commence later in the year, then species like *Gilia*, which benefit from early storms, will also suffer. Predictions for *Phacelia* are difficult because although the species responded strongly to the field manipulation of first storm events, the mechanism behind its response is unresolved.

The more general conclusion of our study is that changes to discrete climate events such as the timing and temperature of the first major storm may be as—if not more—important than trends in season-long climate variables (Jentsch et al. 2007). The importance of discrete climate events poses several challenges for predicting ecological responses to climate change. Aside from the difficulty of predicting the future of discrete events such as storms and droughts, species' responses to these events can be idiosyncratic, as found here with the germination of our focal species. Finally, our emphasis on species-specific life-history cues in mediating ecological responses to climate events differs from the growth and mortality focus of most studies on this topic (Knapp et al. 2008, Adams et al. 2009, Miao et al. 2009, Ross et al. 2009, Sorte et al. 2010, Albright et al. 2010). This emphasis is important because if species-specific cues for demographic transitions dominate ecological response to climate change, predicting this response may be even more challenging than previously recognized.

Acknowledgments

This work was supported by National Science Foundation grant 0353608. We are indebted to Channel Islands National Park for making our work on Santa Rosa Island possible, and to M. Senning, E. Smith, and D. Burgess for logistical support. We thank N. Vivrette for discussing with us the importance of temperature cues for germination in the Channel Islands annual flora. C. Balzer, O. Godoy del Olmo, E. Mordecai, D. Viola, and J. Williams provided comments on the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Our work was conducted under U.S. Fish and Wildlife Service Recovery Research Permit number TE-044846.

Literature Cited

Adams, H. D., M. Guardiola-Claramonte, G. A. Barron-Gafford, J. C. Villegas, D. D. Breshears, C. B. Zou, P. A. Troch, and T. E. Huxman. 2009. Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. Proceedings of the National Academy of Sciences USA 106:7063–7066.

Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. Oikos 116:221–232.

Adondakis, S., and D. L. Venable. 2004. Dormancy and germination in a guild of Sonoran desert annuals. Ecology 85:2582–2590.

Albright, T. P., A. M. Pidgeon, C. D. Rittenhouse, M. K. Clayton, B. D. Wardlow, C. H. Flather, P. D. Culbert, and V. C. Radeloff. 2010. Combined effects of heat waves and droughts on avian communities across the conterminous United States. Ecosphere 1(5):art12.

Barrett, J. E., R. A. Virginia, D. H. Wall, P. T. Doran, A. G. Fountain, K. A. Welch, and W. B. Lyons. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. Global Change Biology 14:1–13.

Bartolome, J. W. 1979. Germination and seedling establishment in California annual grassland. Journal of Ecology 67:273–281.

Baskin, C. C., and J. M. Baskin. 2001. Seeds. Academic Press, San Diego, California, USA.

Baskin, C. C., P. L. Chesson, and J. M. Baskin. 1993. Annual seed dormancy cycles in two desert winter annuals. Journal of Ecology 81:551–556.

Bell, J. L., L. C. Sloan, and M. A. Snyder. 2004. Regional changes in extreme climate events: a future climate scenario. Journal of Climate 17:81–87.

Caswell, H. 2001. Matrix population models. Sinauer Associates, Sunderland, Massachusetts, USA.

Cayan, D. R., E. P. Maurer, M. D. Dettinger, M. Tyree, K. Hayhoe, K. Bonfils, C. Duffy, P. Santer, and B. Santer. 2006. Climate scenarios for California. Final white paper from California Climate Change Center. CEC-500-2005-203-SF. ⟨http://www.climatechange.ca.gov/climate_action_team/reports/index.html⟩

Dukes, J. S., and M. R. Shaw. 2007. Responses to changing atmosphere and climate. Pages 218–229 *in* M. R. Stromberg,

J. D. Corbin, and C. M. D'Antonio, editors. California grasslands. Ecology and management. University of California Press, Berkeley, California, USA.

Facelli, J. M., P. Chesson, and N. Barnes. 2005. Differences in seed biology of annual plants in arid lands: a key ingredient of the storage effect. Ecology 86:2998–3006.

Fay, P. A., J. D. Carlisle, A. K. Knapp, J. M. Blair, and S. L. Collins. 2003. Productivity responses to altered rainfall patterns in a C_4-dominated grassland. Oecologia. 137:245–251.

Forest, J., D. W. Inouye, and J. D. Thomson. 2010. Flowering phenology in subalpine meadows: Does climate variation influence community co-flowering patterns? Ecology 91:431–440.

Hayhoe, K., et al. 2004. Emissions pathways, climate change, and impacts on California. Proceedings of the National Academy of Sciences USA 101:12422–12427.

Heady, H. F. 1958. Vegetation changes in the California annual type. Ecology 39:402–416.

Heisler-White, J. L., A. K. Knapp, and E. F. Kelly. 2008. Increasing precipitation event size increases aboveground net primary productivity in a semi-arid grassland. Oecologia 158:129–140.

Jain, S. K. 1982. Variation and adaptive role of seed dormancy in some annual grassland species. Botanical Gazette 143:101–106.

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate change experiments: events, not trends. Frontiers in Ecology and the Environment 5:315–324.

Jentsch, A., J. Kreyling, J. Böttcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming – extreme weather events alter flower phenology of European grassland and heath species. Global Change Biology 15:837–849.

Karl, T. R., and K. E. Trenberth. 2003. Modern global climate change. Science 302:1719–1723.

Knapp, A. K., C. Beier, and D. D. Briske. 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. BioScience 58:1–11.

Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, M. D. Smith, J. D. Carlisle, C. W. Harper, B. T. Danner, M. S. Lett, and J. K. McCarron. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. Science 298:2202–2205.

Levine, J. M., A. K. McEachern, and C. Cowan. 2008. Rainfall effects on rare annual plants. Journal of Ecology 96:795–806.

Levine, J. M., A. K. McEachern, and C. Cowan. 2010. Do competitors modulate rare plant response to precipitation change? Ecology 91:130–140.

Levine, J. M., and M. Rees. 2004. Effects of temporal variability on rare plant persistence in annual systems. American Naturalist 164:350–363.

McPhaden, M. J., S. E. Zebiak, and M. H. Glantz. 2006. ENSO as an integrating concept in earth science. Science 314:1740–1745.

Miao, S., C. B. Zou, and D. D. Breshears. 2009. Vegetation responses to extreme hydrological events: sequence matters. American Naturalist 173:113–118.

Pacala, S. W. 1986. Neighborhood models of plant population dynamics. 4. Single-species and multispecies models of annuals with dormant seeds. American Naturalist 128:859–878.

Pitt, M. D., and H. F. Heady. 1978. Responses of annual vegetation to temperature and rainfall patterns in northern California. Ecology 59:336–350.

R Development Core Team. 2009. R: a language and environment for statistical computing, version 2.9.2. R Foundation for Statistical Computing, Vienna, Austria.

Rice, K. J. 1987. Evidence for the retention of genetic variation in *Erodium* seed dormancy by variable rainfall. Oecologia 72:589–596.

Root, T. L., J. T. Price, K. R. Hall, S. H. Schneider, C. Rosenzweig, and J. A. Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57–60.

Ross, M. S., R. L. Ruiz, J. P. Sah, and E. J. Hanan. 2009. Chilling damage in a changing climate in coastal landscapes of the subtropical zone: a case study from south Florida. Global Change Biology 15:1817–1832.

Schonher, T., and S. E. Nicholson. 1989. The relationship between California rainfall and ENSO events. Journal of Climate 2:1258–1269.

Sorte, C. J. B., A. Fuller, and M. E. S. Bracken. 2010. Impacts of a simulated heat wave on composition of a marine community. Oikos 119:1909–1918.

Thomas, C. D., et al. 2004. Extinction risk from climate change. Nature 427:145–148.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. Fromentin, O. Hoegh–Guldberg, and F. Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389–395.

Watkinson, A. R. 1980. Density-dependence in single-species populations of plants. Journal of Theoretical Biology 83:345–357.

Went, F. W. 1948. Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. Ecology 29:242–253.

Went, F. W. 1949. Ecology of desert plants. II. The effect of rain and temperature on germination and growth. Ecology 30:1–13.

Wolkovich, E. M., and E. E. Cleland. 2011. The phenology of plant invasions: a community ecology perspective. Frontiers in Ecology and the Environment 9:287–294.

APPENDIX

Two figures presenting additional demographic responses to the experimental manipulation of the first major rains for the three focal species of the study (*Ecological Archives* E092-194-A1).