



Influences of annual weather variability on vernal pool plant abundance and community composition



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ARTICLE INFO

Article history:

Received 23 June 2015

Received in revised form 1 July 2016

Accepted 6 July 2016

Available online 7 July 2016

Keywords:

Climate change

Precipitation

Topography

Elevation

Lasthenia conjugens

Lolium multiflorum

ABSTRACT

Vernal pools, also termed temporary wetlands, promote key ecosystem services such as floodwater retention and provide unique habitat for many organisms. Despite their ecological value, vernal pools are declining worldwide. Because vernal pools are strongly influenced by variation in annual precipitation that fills the pools, climate change and alterations in precipitation regimes could drastically alter these fragile communities. To understand how annual variation in precipitation and temperature affect vernal pool plant community composition, we examined vernal pool vegetation data collected over a 10 year period. We used native and non-native plant frequencies to explore the dynamics between species frequency and weather variability. We further analyzed fine-scale site topography to explore the effects of spatial variability on ponding. We identified key differences between native and non-native plant species' responses to weather variability and ponding. Over all, most native species tended to respond positively to precipitation accumulations in the early growing season, but some native species frequencies were negatively associated with precipitation accumulations in the late growing season. Some non-native species were negatively associated with increases in precipitation in either the early or late growing season. Inundation appears to act as an ecological filter, impairing the establishment of some non-native species. In addition, elevation was a predictor of ponding—lower elevation pools tended to have higher clay concentrations and promote greater ponding depths, which could enhance the effects of the inundation filter. Together, these findings will assist conservation and management efforts in understanding the climatic and physical factors that influence vernal pool plant community ecology.

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1. Introduction

Vernal pools, which are also referred to as temporary ponds or ephemeral wetlands, are seasonal wetlands commonly found in Mediterranean climates throughout the world (Keeley and Zedler, 1998; Deil, 2005; Williams, 2006; Collinge and Ray, 2009; Fraga i Arguimbau, 2009). These ecosystems typically experience distinct and reoccurring wet and dry phases, often on an annual cycle. The flora in vernal pools consists largely of annual plant species that germinate during the wet phase and reproduce during the dry phase (Deil, 2005). For example, during the wet winter months, vernal pools in California fill with precipitation and flood. The winter rains cue seeds to germinate and produce seedlings that grow and develop under inundation (Keeley and Zedler, 1998; Collinge and Ray, 2009). As winter rains gradually subside and temperatures

begin to increase, water evaporates from the pools in the spring and the predominately annual plants quickly develop, flower, and disperse their seeds prior to or during the summer-autumn dry phase (Collinge and Ray, 2009). The seeds remain in the seed bank throughout the dry months, a mechanism which facilitates propagule survival during unfavorable conditions (Zedler, 2003; Faist et al., 2013), and the vegetative life cycle begins anew with the onset of the winter rains.

Vernal pools provide an array of ecosystem services (McGreavy et al., 2012). Vernal pools act as basins for retaining floodwaters, help recycle nutrients while sequestering toxins, and promote the renewal of ground water (Rhazi et al., 2012). Vernal pools are also home to and support a wide range of endemic flora and fauna. For instance, California's vernal pool communities are made up of over 60 endemic taxa of animals and plants—many of which are rare or in danger of extinction (Croel and Kneitel, 2011).

Despite their ecological value, vernal pools are declining across the globe (Rhazi et al., 2012). In the Central Valley of California in particular, 60–85% of the vernal pools have been destroyed since

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the mid to late 1800s (King, 1998). Two major threats linked to the degradation of vernal pools are well documented: habitat loss and species invasions. In recent years, agricultural development in the Central Valley has surpassed urbanization as the lead cause of vernal pool habitat loss. Much of this development is due to agricultural shifts from traditional field crops like grains to higher priced crops produced in orchards and vineyards (Sleeter, 2008; AECOM, 2009). Of the remaining vernal pools, invasion by non-native species has resulted in significant declines in vernal pool native plant communities. Reports indicate that invasive plants have been observed encroaching into Central Valley vernal pools (Pollak and Kan, 1998; Collinge et al., 2011).

The third, often overlooked, factor that may contribute to shifts in vernal pool plant abundance and composition is increased annual weather variability, potentially resulting from climate change. Plant species around the world are responding to climate change by undergoing range shifts (changes in distribution) and phenological shifts (Walther et al., 2002; Parmesan and Yohe, 2003). Yet despite these general trends, little is known about how plant species found within vernal pools may respond to the changes brought about by climate change. Climate change is projected to result in temperature and precipitation shifts in the Central Valley (Hayhoe et al., 2004; Cayan et al., 2009). Water is a vital element to vernal pool communities and many vernal pools are entirely dependent upon precipitation as the sole source of water (Jokerst, 1990). Year to year precipitation fluctuations often result in different plant community compositions (Bauder, 2005). Because vernal pool plant communities depend upon inundation, climate change may act as a threat to their persistence (Pyke, 2005) and may increase the risk of extinction for many threatened or endangered vernal pool obligate plant species (Bauder, 2005).

In an effort to restore native plant communities and ecosystem function in degraded vernal pool communities, 256 experimental vernal pools were constructed on Travis Air Force Base (TAFB) near Fairfield, CA (38° 15' 00" N, 122° 00' 00" W, 6 m elevation) in 1999 as part of a mitigation effort (Collinge and Ray, 2009). The constructed pools were designed to mimic naturally occurring vernal pools found on TAFB (Collinge and Ray, 2009). Despite the protected habitat on TAFB, native plant abundance has dropped dramatically over the last seven years and non-native species have encroached upon native species within the constructed vernal pools (Collinge et al., 2013). Data suggest that the decline in native plant abundance may be partially explained by extreme weather events in 2006 and 2007. Climate projections for this region suggest that such extreme weather events may become more frequent and intense in the future. Our aim in this study was to better understand how weather variability and spatial variability affect the composition of vernal pool flora. We set out to answer the following two questions: (1) Do changes in annual temperature and precipitation affect the frequency of native and non-native species found in vernal pools? and (2) Does site specific topography, specifically pool elevation and soil type, affect ponding and contribute to changes in community composition within individual vernal pools in the research area?

2. Methods

2.1. Field data collection

We examined plant species frequency data collected for native and non-native plant species found within the 256 constructed vernal pools on TAFB from 2002 to 2012. We excluded the 2000–2001 frequency data because a portion of the constructed pools were still undergoing seeding treatment during this time period. All seeding treatments were completed by the 2002 growing season.

Table 1

A summary of the eleven focal species used in this study (Collinge et al., 2013; plants.usda.gov).

Species Name	Family	Type	Common Name
Native species			
<i>Deschampsia danthonioides</i>	Poaceae	Grass	Annual hairgrass
<i>Downingia concolor</i>	Campanulaceae	Forb	Maroonspot calicoflower
<i>Hemizonia pungens</i>	Asteraceae	Forb	Common spikeweed
<i>Lasthenia conjugens</i>	Asteraceae	Forb	Contra Costa goldfields
<i>Plagiobothrys stipitatus</i> var. <i>micranthus</i>	Boraginaceae	Forb	Stalked popcornflower
Non-native species			
<i>Bromus hordeaceus</i>	Poaceae	Grass	Soft brome
<i>Erodium botrys</i>	Geraniaceae	Forb	Longbeak stork's bill
<i>Hordeum marinum</i>	Poaceae	Grass	Mediterranean barley
<i>Lolium multiflorum</i>	Poaceae	Grass	Italian ryegrass
<i>Vicia villosa</i>	Fabaceae	Forb	Winter vetch
<i>Vulpia bromoides</i>	Poaceae	Grass	Brome fescue

Species frequency data were collected every spring (April–May) under similar conditions; after water had evaporated from the pools and during peak flowering. Frequency data were collected by positioning a 0.5 × 0.5 m grid frame divided into 100 cells over a permanently marked plot found within each of the 256 constructed vernal pools. All the occurring plant species found within the perimeter of the frame were identified using Hickman (1993) and their frequency (the total number of cells out of 100 in which a species was present) was recorded (Collinge and Ray, 2009).

We selected 11 focal plant species for this study. We selected only annual species to allow for a meaningful comparison of germination and life cycle patterns between native and non-native species. The other potential focal native species in the study area (*Eryngium vaseyi* J.M. Coult. & Rose) was excluded because it is a perennial. These focal species were present in the greatest number of constructed pools over the duration of the study and include 5 native species: *Deschampsia danthonioides* Munro, *Downingia concolor* Greene, *Hemizonia pungens* Gray, *Lasthenia conjugens* Greene, and *Plagiobothrys stipitatus* var. *micranthus* Greene and six non-native species: *Bromus hordeaceus* Kerguelen, *Erodium botrys* Bertol, *Hordeum marinum* Thell, *Lolium multiflorum* Lam, *Vicia villosa* Roth, *Vulpia bromoides* Gray (Table 1). We compiled frequency data for all eleven focal species. We then calculated annual arithmetic mean frequency values for the focal plant species by averaging the frequency of each species across all 256 constructed pools for each year.

2.2. Growing season data

We initially used the entire annual growing season (October–March) precipitation and temperature data to examine the effects of these abiotic factors on the annual focal species frequency data. This process proved uninformative and so we considered the results of a previous greenhouse study (Gerhardt and Collinge, 2007) that examined the effects of inundation on vernal pool plant communities, to help identify key annual growing season time intervals that were most appropriate to use for this study. These results suggested that inundation affects the different life stages of the vernal pool vegetative communities. Two stages were particularly affected: (1) plant development and survival and (2) plant growth and reproduction. The first half of the growing season is characteristic of vegetative development and survival at the study site, whereas plants typically grow and reproduce during the second half of the growing season. Thus,

we divided the precipitation and temperature data into early growing season (October–December) and late growing season (January–March). In doing so, we were able to examine the effects of ponding stages and seasonal temperature patterns on the life cycle of the 11 focal species. Specifically, we concentrated specific analyses on early season data, using the relationship between frequency and precipitation/temperature as a proxy to gauge the effects of weather variability on the germination and early survival of the focal species. Similarly, we devoted specific analyses to the late growing season using the relationship between frequency and temperature/precipitation as a proxy to gauge the effects of weather variability on the growth and reproduction of adult focal species.

2.3. Temperature and precipitation data collection

We examined species frequencies in relation to temperature and precipitation using data collected over the course of the study to gain a better understanding of how annual variation in precipitation and temperature affect the frequency of the focal species. We collected monthly precipitation totals and temperature values for Fairfield, CA between the years 2002–2012 from the Western Regional Climate Center's Fairfield climate station (<http://www.wrcc.dri.edu>), located approximately 11.28 km from the study site. We selected the Fairfield climate data because it was the most complete dataset for our study period that was collected closest to our study area. To ensure that these data accurately represented the precipitation accumulated at our research area and were not affected by precipitation variability across the region, we compared the Fairfield precipitation data to the precipitation data collected for 3 other locations near Fairfield: Davis, Lake Solano, and Napa State Hospital. An ANOVA analysis showed that there were no significant differences among climate stations between the mean precipitation accumulations for both early and late growing seasons for the duration of this study (early precipitation: $F_{3,128} = 0.832$, $P = 0.478$; late precipitation: $F_{3,126} = 1.682$, $P = 0.174$). This result supports the use of Fairfield precipitation data for our study area.

To address the effects of temperature on species frequencies we used growing degree days (GDD) data to help gauge key developmental events in the plants' lifecycles. GDD may be understood as the amount of thermal energy that is available to an organism for growth and development. A GDD value is the mean number of degrees that exceed a base temperature within a 24 h period. However, the temperature accumulation of a single day does not typically affect plant development. Rather it is the accumulation of warming days over a period of time that acts on development. Thus, the GDD data were summed for each annual growing season. Because our data (Collinge, *unpub. data*; <http://www.wrcc.dri.edu>) indicated that the mean temperature at which most of the annual vegetation in the constructed vernal pools begins to germinate in December is about 9.44 °C we selected a base temperature of 10.0 °C for our analyses.

2.4. Temperature and precipitation statistical analyses

We performed multiple regression analyses in the R environment (version 3.0.2; R Development Core Team, 2007) using standard statistical procedures (e.g., Zar 2009). Frequency data for each of the focal species were individually modeled by early growing season precipitation totals and GDD totals as well as late growing season precipitation totals and GDD totals. We developed various regression models for our data. We compared the R^2 values obtained from these models and selected the model with the R^2 value closest to 1. The R^2 values produced for the linear models were closer to 1 compared to the R^2 values obtained from the other

models. Thus, it was determined that linear models were the best fit for the data. These linear regression models were then simplified by stepwise deletion. We began with the most complicated model and successively removed variables with the highest P-value until all of the predictors were significant ($\alpha = 0.05$).

Because our sample sizes were limited by the number of growing seasons ($N = 10$) and the Shapiro-Wilk normality test showed that the distribution of the dependent variable was not normal, we performed additional analyses to see if transformations for normality were warranted. Log transformations normalized the data and they were incorporated into the same linear models that were previously used to test the non-parametric data. These models were also simplified by stepwise deletion, until all of the predictors were significant. Once all of the predictors were significant, we removed the transformation from the dependent variables, to explore its effects on the raw data, and calculated the explanatory power for each model. We compared the R^2 values of the previously transformed model to the R^2 values of the untransformed model to determine which model was a better fit for the data. The untransformed models produced R^2 values closer to 1 compared to the R^2 values obtained from the transformed models. As a result, we selected the untransformed models for our analyses. In addition, we also checked to ensure the normality of the residuals for each of the models that carried the higher explanatory power.

2.5. Topographic data collection

We investigated whether fine scale site topography affects the accumulation of water in pools and thus the frequency of native and non-native plant species found within the constructed vernal pools. In April 2014, we used a 2010 Topcon AT-B4 automatic surveying level (Topcon Positioning Systems, Inc., Livermore, CA) (accuracy ± 2 mm) to measure the difference in elevation among pools at our TAFB study site. We systematically moved the survey rod to each of the constructed pools and measured its elevation by placing the rod on a permanent plot marker.

Because soil type also affects water permeability we used data from soil samples collected previously at the study site (Collinge, *unpub. data*) to explore the effects of soil texture on water depth within pools. Soil samples were collected in 2001 from 79 of the constructed vernal pools during peak flowering season (2–3 May). Each sample was collected 10–15 cm outside the permanent plant sampling plot in each pool using a soil auger (2.5 cm diameter, 10 cm deep, volume = 49 cm³). These samples were analyzed for percent sand, silt, and clay as well as chemical characteristics including organic matter, inorganic nitrogen, plant-available phosphorus, pH, cation exchange capacity, and soluble salts at A & L Laboratories (Modesto, CA, USA). Here we focus on soil texture as this trait most closely affects water accumulation in pools.

Finally, we compiled weekly pool depth readings recorded in the winter wet seasons of 2009–2012. From these data we extracted the maximum depth value for each pool. We then took the arithmetic mean of each value to produce an overall maximum pool depth value for each pool.

2.6. Topographic statistical analyses

We used regression analyses to address the relationship between elevation and the mean maximum pool depth values. We performed three individual linear regression analyses, rather than a single multiple regression analysis, to explore the effects of soil type on mean maximum pool depth values because the Pearson's product-moment correlation test indicated a correlation between soil types. The three models explored mean maximum pool water depth by % sand, % silt, and % clay individually. AIC values and Akaike weights were obtained to determine if elevation or soil type was

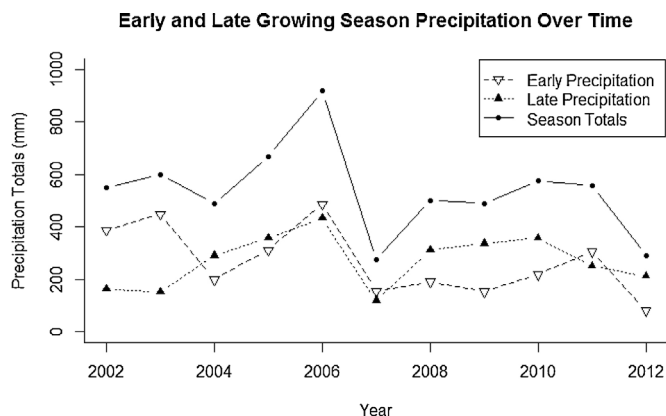


Fig. 1. Early season (October–December) and late season (January–March) precipitation totals are plotted over time. Overall season totals (October–March) are also included.

a better predictor for maximum pool water depth (Burnham and Anderson, 2002).

3. Results

3.1. Temperature and precipitation analyses

Precipitation accumulations fluctuated over the 10 year duration of our study. The average growing season precipitation accumulation for the research area was 537.00 mm of precipitation. The highest growing season precipitation total was 917.20 mm of rain fall, occurring in 2006. The lowest growing season precipitation total occurred in 2007 with 273.60 mm of precipitation (Fig. 1).

3.1.1. Native species

Overall, the native focal species declined in mean abundance from 2002 to 2012 (Figs. 2 a and 3). Generally, the native focal species, including the federally protected species, *L. conjugens*, responded positively to early growing season precipitation totals (Table 2, Figs. 2 a and 3). We found significant positive relationships between annual frequencies of *D. concolor*, *H. pungens*, *L. conjugens*, and *P. stipitatus* var. *micranthus* and early precipitation accumulations (Table 2). As early season precipitation totals increased, species frequency values increased. We also found a significant negative relationship between *H. pungens* and *L. conjugens* frequency and late season precipitation totals (Table 2). In this case, precipitation in the late growing season was associated with decreased species frequency values. There were no significant relationships between native species frequencies and early season GDD totals.

Table 2

Summary of the results from the multiple regression analyses performed on mean species frequency values in relation to early and late season precipitation and temperature totals. The first five species listed are vernal pool natives, and the following six species are non-native to California. Coefficients for an independent variable that has a significant effect on a dependent variable are bolded and the associated individual *p*-value is in parenthesis. Predictor variables that do not have a significant effect on the dependent variable are marked with NS. The significance levels for the overall *p*-values are: **P* < 0.05, ***P* < 0.01, *****P* < 0.001.

	Species Name	Early Precip. Coefficient	Late Precip. Coefficient	Early GDD Coefficient	Late GDD Coefficient	Overall Adj. R ²	Overall F-Statistic	Overall P-value
Native Species	<i>D. danthonioides</i>	NS	NS	NS	0.065 (P = 0.003)	0.610	F _{1,9} = 16.610	0.003**
	<i>D. concolor</i>	0.911 (P = 0.027)	NS	NS	NS	0.374	F _{1,9} = 6.961	0.027*
	<i>H. pungens</i>	0.244 (P = 0.006)	-0.503 (P < 0.001)	NS	NS	0.805	F _{2,8} = 21.590	0.001**
	<i>L. conjugens</i>	0.670 (P = 0.021)	-0.942 (P = 0.021)	NS	0.058 (P = 0.005)	0.805	F _{3,7} = 14.730	0.002**
	<i>P. stipitatus</i> var. <i>micranthus</i>	0.944 (P = 0.009)	NS	NS	0.043 (P = 0.030)	0.600	F _{2,8} = 8.528	0.010*
Non-native Species	<i>B. hordeaceus</i>	NS	NS	NS	NS	0.211	F _{1,9} = 3.680	0.087
	<i>E. botrys</i>	NS	NS	NS	NS	0.020	F _{1,9} = 1.204	0.301
	<i>H. marinum</i>	-1.0196 (P = 0.021)	NS	NS	NS	0.407	F _{1,9} = 7.866	0.021*
	<i>L. multiflorum</i>	-1.102 (P = 0.045)	-1.69 (P = 0.024)	NS	NS	0.568	F _{1,8} = 7.560	0.014*
	<i>V. villosa</i>	NS	NS	NS	NS	-0.067	F _{1,9} = 0.373	0.556
	<i>V. bromoides</i>	NS	NS	NS	NS	0.022	F _{1,9} = 1.229	0.296

However, we found a positive relationship between late growing season GDD accumulations and *D. danthonioides*, *L. conjugens* and *P. stipitatus* var. *micranthus* mean frequencies (Table 2).

3.1.2. Non-native species

In contrast to the patterns observed for native species, non-native species, such as *L. multiflorum*, tended to be negatively associated with precipitation accumulations. There were significant negative relationships between *H. marinum* and *L. multiflorum* frequencies and early season precipitation totals (Table 2). There was also a significant negative relationship between *L. multiflorum* and late season precipitation totals (Table 2). There were no significant associations between non-native species frequency values and GDD totals for either early or late growing seasons (Table 2).

3.2. Topographic effects on pool depths

The difference between maximum and minimum constructed vernal pool elevation at our study site was 1.99 m. There were significant relationships between elevation and soil type in relation to ponding (Table 3) where maximum pool water depths were positively associated with clay concentrations and negatively associated with sand concentrations. There were also significant associations between elevation and concentrations of clay, sand, and silt found in the soil (Table 3). As elevation increased concentrations of clay and silt found in pool basins decreased, while concentrations of sand increased. Maximum pool depth was also negatively associated with pool elevation (Table 3). In comparing the four models that explored the effects of clay, sand, silt, and elevation on ponding, elevation was a better predictor of maximum pool depth compared to concentrations of clay, sand, or silt (Table 3).

4. Discussion

We identified key trends among native and non-native plant species found in constructed vernal pools in response to weather variability and site-specific topography. In general, native forbs responded positively to early precipitation totals. As early season precipitation totals increased, native species frequency values tended to increase, while late season precipitation totals tended to be negatively associated with native species frequency values. These trends are explained by examining the timing of the three key phases associated with ponding, or the process by which vernal pools become filled with precipitation. The first stage of ponding is marked by the moistening of the soil. Precipitation is the primary trigger of seed germination in most vernal pool plant species and the first rains that moisten the soil in October–November typ-

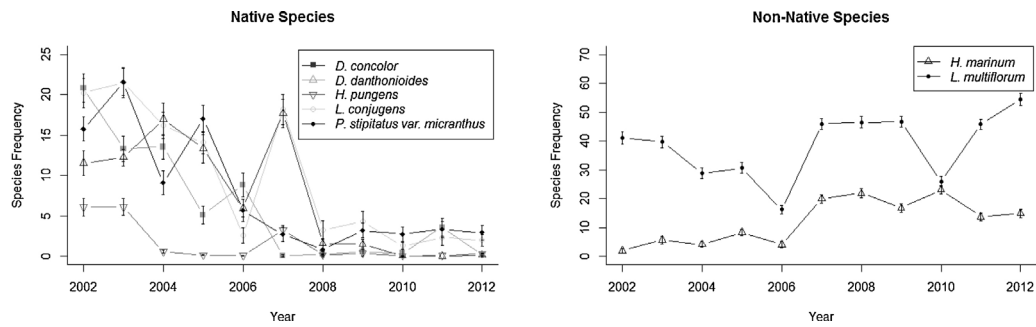


Fig. 2. Mean frequency values with \pm SE for (a) native and (b) non-native focal species which showed significant relationships with temperature and/or precipitation for the 2002–2012 period. Frequency is the total number of cells in which a species is present within the perimeter of a 0.5×0.5 m grid consisting of 100 cells.

Table 3

Summary of the topographic single linear regression analyses. The first four rows describe the effects of soil composition and elevation on mean maximum pool ponding depths. The last three rows describe the relationship between elevation and soil composition. The significance levels are: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. AIC results for the topographic models in relation to mean maximum pool depth are also provided.

Dependent Variable	Independent Variable	Coefficient	Adj. R^2	F-Statistic	P-value	AICc	dAICc	df	Akaike Weight
Pool Depth	% Clay	0.235	0.134	$F_{1,59} = 10.27$	0.002**	181.6	0.0	3	0.686
Pool Depth	% Sand	-0.206	0.124	$F_{1,59} = 9.517$	0.003**	183.9	2.3	3	0.215
Pool Depth	% Silt	0.033	-0.016	$F_{1,59} = 0.079$	0.780	185.5	3.9	3	0.099
Pool Depth	Elevation	-1.906	0.264	$F_{1,59} = 22.520$	<0.001***	198.2	16.6	3	<0.001
% Clay	Elevation	-1.841	0.081	$F_{1,59} = 6.286$	0.015*				
% Sand	Elevation	3.726	0.311	$F_{1,59} = 28.030$	<0.001***				
% Silt	Elevation	-1.86	0.205	$F_{1,59} = 16.430$	<0.001***				

Mean Frequency *L. conjugens* vs. *L. multiflorum* Over Time

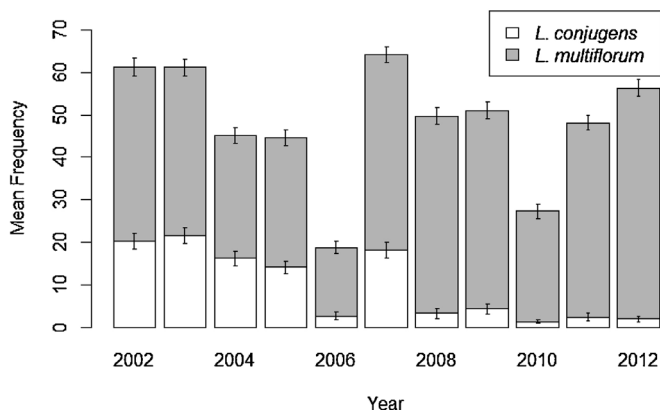


Fig. 3. Details of the mean frequency values and \pm SE for *L. conjugens* and *L. multiflorum*, 2002–2012, extracted from Fig. 2. *L. conjugens* is an endemic and vernal pool obligate plant species currently listed as endangered. *L. multiflorum* is a non-native plant species that has invaded many of the constructed vernal pools on the research site.

ically initiate the germination process (Bliss and Zedler, 1998). Greenhouse experiments conducted using vernal pool plant species indicate that moist soil is adequate for germination (Collinge et al., 2003); furthermore, in these experiments, most species did not require inundation to cue germination (Bliss and Zedler, 1998). Thus, the positive associations between species mean frequency values and increased precipitation in the early growing season that we observed in this study are likely explained by the initiation of germination.

Increased precipitation in the early growing season also promotes the onset of inundation, the second phase of ponding, in which water begins to accumulate in pools. In fact, early ponding acts as an ecological filter, impairing the establishment of non-native species. Greenhouse experiments show that inundation acts as an abiotic pressure that prevents the establishment of non-native species that are not adapted for development under water (Bliss

and Zedler, 1998; Gerhardt and Collinge, 2003, 2007). Although native seedlings are capable of growing and developing under the inundation of water they do not appear to depend on inundation for survival (Bliss and Zedler, 1998).

Additionally, pool depths tended to increase as elevation decreased. Lower elevations potentially receive greater amounts of water due to runoff and underground seepage/flow. Lower elevation pools are often composed of higher concentrations of clay. Clay soils are much more impermeable to water than are other soil types, resulting in greater water retention. The lowest elevation pools are potentially composed of higher amounts of clay due to the different soil horizon types. It is often the case that clay soil is found below the organic and decaying organic layers. The excavation of the constructed pools resulted in the removal of some of the upper organic layers, perhaps resulting in pools that are higher in clay concentrations. Soil horizons extend across the research area and some of the upper layers may be less prevalent at lower elevations. Thus it is likely that lower elevations tend to promote increased ponding and may enhance the effects of the inundation filter.

Finally, the ponding cycle is terminated once water begins to evaporate and the pools become dry. The drying phase is a crucial turning point in the lifecycle of most vernal pool native plant species. This shift into the adult phase of the lifecycle may correspond to the negative association observed between late season precipitation totals and some vernal pool native forbs. The species examined are annuals and would likely incur an ecological advantage if their adult lifecycles were spent in soil that is not inundated. Because of the short growing season, these annual plants are limited to a narrow window of opportunity to produce propagules. Dry soils also help ensure that newly produced seeds are stored in the seed bank until conditions are suitable for germination in subsequent growing seasons (Faist et al., 2013).

Our results also suggest that increased rainfall hinders the viability of some non-native grasses. As early season precipitation totals increased, *H. marinum* and *L. multiflorum* mean frequency values decreased. Similarly, *L. multiflorum* appeared to respond negatively to late season precipitation accumulations. As discussed above, increased water accumulation within vernal pools acts as

an ecological filter, which impairs some non-native species from establishing and proliferating (Gerhardt and Collinge, 2007). However, our data indicate that *L. multiflorum* has thoroughly spread, become established, and often dominates the vegetative communities found in vernal pools at our study site (Collinge et al., 2011). In this case, *L. multiflorum* has bypassed the inundation filter and has invaded many of the constructed vernal pools.

The invasion of *L. multiflorum* in constructed pools may be explained by examining frequency data and precipitation data collected over time and identifying the point at which *L. multiflorum* frequency jumps from relatively low to high values. These data reveal an overall decline in the mean frequency values of *L. multiflorum* from 2002 to 2006. *L. multiflorum* frequency values plummeted in 2006, reaching their lowest recorded levels through the 10 year period. Frequency data collected for other non-native species as well as native plant species also indicate a sharp decrease during the 2006 growing season. The 2006 growing season was marked by extremely high precipitation in both the early and late portions of the growing season, with a total accumulation of nearly 400 mm greater than the average for the duration of this study. The extreme amount of rain that fell in 2006 resulted in abnormally high precipitation accumulations in the late growing season, which ultimately led to delayed drying. Our analyses indicate that some native and non-native species frequencies are negatively associated with increased late season precipitation totals. Thus the intense 2006 precipitation event likely hindered the development of native and non-native species. The 2007 growing season, on the other hand, was marked by extremely low precipitation accumulations. Although both native and non-native species frequency values rebounded during the 2007 growing season compared to the 2006 growing season, non-native species frequency tended to be greater than the native species frequency values for this particular year. We surmised that the extremely low 2007 precipitation event helped the non-native species bypass the inundation ecological filter that normally occurs during average precipitation years. The frequency data also suggests that once a non-native species is able to circumvent the inundation filter it tends to establish, which coincides with results from greenhouse experiments (Gerhardt and Collinge, 2007). This establishment in turn hinders the viability of native species.

Given the increased weather variability that is predicted for this region in the future, many vernal pools may be exposed to altered precipitation and temperature patterns. Most climate change projections agree that average annual temperatures are expected to increase across California with significant warming events in the spring and summer months (Hayhoe et al., 2004; Cayan et al., 2009). There is more variability in precipitation projections for the Central Valley; most projections infer dryer winter months, yet fewer projections suggest increased winter precipitation averages (Hayhoe et al., 2004; Cayan et al., 2009). In light of the current climate projections two growing season climate scenarios may provide insights to assist vernal pool management efforts: (1) hotter and dryer growing seasons or (2) hotter and wetter growing seasons. Under the first scenario, dry conditions in the early growing season would likely have adverse effects on native plant frequencies; native species are dependent upon wet early seasons to trigger seed germination and establish the inundation filter. On the other hand, a dry late growing season may promote vegetative development if sufficient amounts of precipitation were present in the early growing season. Increased temperatures in the late growing season may cause the pools to dry too rapidly and hinder native development. Under the second scenario, wetter early growing seasons are likely to benefit native species while wetter late seasons are likely to hinder native species development. Increased temperatures under this scenario, however, may catalyze the drying phase and benefit native species development. Many native vernal pool

species have mechanisms that allow them to thrive in alternating flooded and drought conditions that are typical of these ephemeral wetland systems. The non-natives at our site also originate in areas with Mediterranean climates – such as Europe, North Africa, and Asia – but are more typical of upland areas and thus lack the mechanisms for tolerating inundation that are present in California native vernal pool species. Given the projected uncertainties in the timing and duration of pool inundation, vernal pool community composition may change and threatened and endangered vernal pool native species may diminish. However, this study identifies key trends that may help land managers identify the ideal timing of management efforts and determine optimal vernal pool conservation and restoration locations where native species are more likely to survive.

5. Conclusion

The current understanding of vernal pool plant species' response to weather variability is limited within the scientific community. We have identified key trends between native and non-native plant species found in constructed vernal pools in response to weather variability. Our analyses reveal an overall trend for many native focal species: a positive response to precipitation accumulations, especially in the early growing season. No such trend was found among the non-native focal species. Inundation acts as an ecological filter impairing the establishment of some non-native species. The Gerhardt and Collinge (2007) study concurs with these results, suggesting that inundation exerts an abiotic pressure that acts to impair the establishment of non-native species in the pools. Lower elevation pools promote deeper ponding and may be more amenable to native species that can tolerate greater inundation depths. As climate change intensifies, precipitation shifts will likely affect vernal pool hydrology and potentially reshape plant community structure. However, this study may help inform land managers of the appropriate timing of vernal pool restoration efforts in relation to the timing of precipitation events and ideal pool location in relation to site specific topography.

Acknowledgements

We thank Dr. Nichole Barger, Dr. Daniel Doak, and Dr. Akasha Faist for their valuable insights, comments, and suggestions. We thank Josilynn Spray for field assistance. This project was funded by the Air Force Center for Environmental Excellence, the US Fish and Wildlife Service, CH2M Hill, NSF LTREB grants (DEB-0744520 and DEB-1257385), and the University of Colorado at Boulder Department of Ecology and Evolutionary Biology.

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