Freshwater Biology (2005) **50,** 2129–2135 doi:10.1111/j.1365-2427.2005.01471.x

The effects of an unpredictable precipitation regime on vernal pool hydrology

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SUMMARY

1. Vernal pools are small precipitation-fed temporary wetlands once common in California. They are known for their numerous narrowly endemic plant and animal species, many of which are endangered. These pools experience the typical wet season/dry season regime of Mediterranean climates. Their hydrological characteristics are determined by a complex interaction between the highly variable climate and topographic relief.
2. Hypotheses regarding the effects on ponding of total precipitation, storm intensity and pattern were examined using long-term weather records combined with two decades of data on the length and depth of inundation in 10 individual pools. Similarly, data on pool landscape position and microtopography allowed examination of the interactions between topography and rainfall amount and pattern.
3. The total amount of precipitation and length of inundation were strongly correlated. Landscape position affected ponding duration, with collector pools holding water longer than headwater pools. Basin microtopography interacted with climatic variability to determine the nature and extent of within-basin microhabitats sufficiently different in hydrological and/or soil conditions to support or exclude individual species. The effect on hydroperiod of precipitation concentrated in a few months rather than spread more evenly over the season depended on total precipitation.
4. Changes in climate, the mound-and-depression landscape or pool microtopography could have profound impacts on the hydrology of individual pools as well as the array of hydrological conditions in the system. Given the individualistic responses of the numerous endemic species supported by vernal pools, any of these environmental changes could diminish their sustainability and increase the risk of species extinction. Conservation, restoration and management decisions should take these factors into account.

Keywords: endangered species, environmental variability, ephemeral ponds, temporary wetlands, vernal pool

Introduction

The effects of environmental variability and/or unpredictability on population dynamics, species coexistence and evolution, have long been the subject of both theoretical (Wiens, 1977; Connell, 1978; Huston, 1979; Venable, 1989; Chesson & Huntly, 1997; Chesson, 2000; Ripley, Holtz & Simovich, 2004) and empirical (Keddy & Reznicek, 1982, 1986; Freas & Kemp, 1983; Ebert & Balko, 1987; Philippi, 1993a,b) studies. By definition, temporary wetlands are highly variable environments. In Mediterranean climates, precipitation is confined to a distinct rainy season during the coolest months of the year, followed by a prolonged drought of 6 months or more, when temperatures are at the highest (Mooney & Parsons, 1973;

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Walter, 1979). The timing of wet and dry seasons is the most predictable aspect of the climatic regime. Unpredictability comes from large differences between years in the amount of precipitation and within years in both the pattern and intensity of storms (Goldman, Jackson & Bursztynsky, 1986). This is typical of arid lands (Le Houérou, 1984). Interactions between this climatic variability and geomorphic variation define the nature of California's temporary wetlands, most of which are vernal pools.

Vernal pools are small precipitation-fed depressional wetlands set in a landscape of high topographic microrelief consisting of mounds; depressions of various sizes, shapes and depths and connecting swales (Smith & Verrill, 1998). Other important geomorphic features are the presence or absence of inlets and outlets, the degree of isolation and topographic position. These factors alone – and in combination – cause each pool to respond in a characteristic manner to the rainfall amount and pattern (Hanes & Stromberg, 1998). The majority of the vernal pools in southwestern California are found on coastal terraces or in cismontane inland valleys and they experience the typical wet season/dry season regime of Mediterranean climates.

To persist in this environment, both plants and animals must cope with a large between-year variation in the longest continuous period of inundation, rising and falling water levels during the rainy season, rapid changes between terrestrial and aquatic conditions, and long periods of high air and soil temperatures coupled with lack of moisture. Various traits have been associated with persistence in such highly fluctuating environments (Salisbury, 1970; Deschamp & Cooke, 1983; Crawley, 1986a,b; Keeley, 1987; Ridge, 1987; Baskin & Baskin, 1989; Crawford, 1989; van der Sman, Joosten & Blom, 1993; Ripley *et al.*, 2004). Differences between pools in hydrological conditions can affect the distribution and population dynamics of the resident species, given their individual life history and other traits (Ritland & Jain, 1984; Bauder, 1987; Holland & Jain, 1988).

Long-term precipitation records and inundation data from individual pools were combined with data on pool microtopography and landscape position to examine hypotheses on the climatic and topographical factors affecting the ponding regime in 10 southern California vernal pools. Specifically: (1) Does a wet season's total precipitation determine ponding length? (2) Do storm pattern and intensity affect the inundation period and fluctuation in water levels? (3) Is a pool's hydrological regime dependent on its position in the landscape? and (4) How does pool microtopography interact with precipitation amount and storm pattern to determine hydrological conditions?

Methods

Ten vernal pools have been monitored for water depth and ponding duration in 20 rainfall years, beginning in 1982/83. The pools are located in San Diego, California, 10–12 km inland from the Pacific Ocean at an elevation of 125 m. Two pools (Pools 5 and 6) were moderately disturbed by cultivation in the first half of the last century. The remaining eight pools have had minimal disturbance.

Climatic data were obtained from the records of the U.S. Weather Bureau for Lindbergh Field 15 km south of the study area. Total yearly precipitation records dating back to 1851 were reviewed to characterise the long-term climate. Water depth was measured at a metal stake at the lowest point in each pool basin. Depth measures were taken within 24 h at the end of a rainstorm and every 3–4 days thereafter, until the pool drained or another storm restarted the cycle. The elevation (relative to the base of the metal bar) was determined in alternating 1-dm^2 quadrats along transects bisecting each basin, using a surveyor's level and stadia rod. These data were used to calculate hydrological variables for each elevation, including depth and duration of standing water and inundation frequency. Each basin's slope was determined using the drop along the transect from the elevation of highest potential water level to the basin's lowest point.

The coefficient of variation (CV) in water depth at pool bottoms and for the elevation points along the transects was calculated using water depth measures at 4-day intervals, either from field-collected data or points on recession curves estimated from the rate of water drop. The correlation between total days of inundation in each pool and total precipitation during the rainfall year (July 1–June 30), the CV of water depth and the number of times pools drained at their deepest elevation was evaluated using Spearman's rank correlation coefficient (r_s). Spearman rank correlations were also used to examine the relationship between precipitation and the difference in inundation period between headwater and collector pools and between precipitation pattern and the number of times pools drained during the wet season. A headwater pool has no inlet and collector pools have no outlet. Inundation period for the 10 pools was compared between years with nearly equivalent total precipitation using the Wilcoxon signed rank test for pairwise comparisons. There were five pairs of equivalent-rainfall years, with the two years of each pair having different seasonal precipitation patterns (1983/84 and 1999/2000, 1996/97 and 1998/99, 1984/85 and 1986/87, 1987/88 and 1991/92 and 1982/83 and 1992/93) . One year had storms concentrated in 2 months (>60% of the year's total precipitation) and one had precipitation more evenly distributed. The same test was used to compare inundation length in the three pairs of headwater/collector pools. Statistical tests were done using Statview 5.0 for Macintosh (SAS, 1998).

Results

Year-to-year variability in precipitation

Over a 153-year period, total yearly (July 1–June 30) precipitation at San Diego's Lindbergh Field ranged from 7.6 to 66.0 cm, with a mean ± SD of 25.5 ± 10.5 cm and a median of 24.5 cm. Exceptionally wet years follow dry ones or vice versa. For example, the 1882/83 rainfall year, the ninth driest with 12.5 cm of precipitation, was followed by 66.0 cm, the wettest year recorded.

There is a strong correlation between total yearly precipitation and the total number of days the water stands in each of the 10 pools ($r_s = 0.77$, $P < 0.0001$). Because of the variable precipitation, individual pools may not pond water for two or more years in a row, then be inundated for 50–90 days in a rainy year. All study pools failed to pond water in 2002, the driest year on record. In the remaining 19 years, five had one or more years without any inundation. The two agriculturally disturbed pools failed to pond in 7 years and one undisturbed pool did not have standing water in 11 of the 20 years. In the 8 years when precipitation was less than the median, average per pool inundation period was less than a week in all but 2 years, suggesting that little or no ponding is more common than generally thought.

As pools fill with water, a strong soil moisture/inundation gradient develops from the upland edge to the bottom of the pool basin. In the average and wet years, there was a steep gradient, and in the dry years, the gradient was gentle or non-existent. Annual differences in the proportion of the study quadrats with any given length of inundation depended on the amount of precipitation (Fig. 1). In a wet year (1982/83), there was a wide array of moisture conditions across the pools, with quadrats distributed quite evenly in 20 classes of increasing length of inundation. Water stood for 30 days or more in 52% of the study quadrats, but in the dry year (1983/84) nearly 50% of the quadrats experienced no inundation at all, and there were no quadrats with a long inundation period.

The most variable moisture conditions within a particular pool were at the upper, dry end of the soil moisture/inundation gradient, where the high water level rose and fell with passing rainstorms. This zone of maximum variability in water depth (CV of water depth) remained at the same elevation along the edge-to-bottom slope during average or wetter-than-average years, but shifted downward in dry years because higher elevations were never inundated. In years of low precipitation, some ponds had no

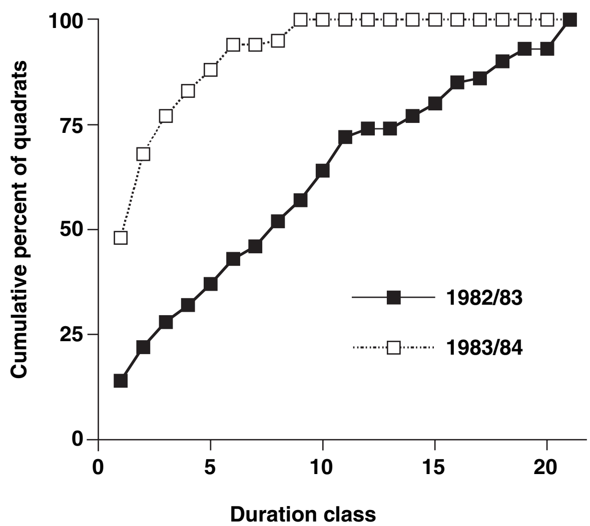

Fig. 1 Distribution of quadrats in water duration classes of 5 days each in two rainfall years. Duration class 1 includes all quadrats >5 cm above the year's high water level and duration class 2 contains quadrats 1–5 cm above high water. Classes 3–20 increase in increments of 5 days' duration, with class 21 containing all quadrats with total days inundation of >90 days. Total precipitation was 46.3 cm in 1982/83 and 14.5 cm in 1983/84.

variability in water depth because no ponding occurred. At the lowest elevations, less variability in water depth was correlated with days inundated ($r_s = -0.70$, $P < 0.0001$), but the soil surface was exposed more often due to the greater number of ponding events in pools that held water longer ($r_s = 0.73$, $P < 0.0001$).

Within-year precipitation patterns

Although the total amount of precipitation falling in a given rainfall year strongly affected the inundation period, the pattern and intensity of storms influenced ponding length as well. During the study period, there were five pairs of years that had total precipitation within 1 cm of each other, but differed in storm pattern. Three pairs had a moderate amount of precipitation ($x \pm 1$ SD), one was wet ($>x + 1$ SD) and the remaining one was very dry ($<x - 1$ SD). Fig. 2 shows an example of a wet, moderate and dry pair. Within each pair, one year had storms concentrated in 2 months (>60% of the year's total precipitation) and one had precipitation more evenly distributed.

In each of the three pairs of moderate years, the total number of days in which pools were inundated was significantly longer in the year with 'concentrated' precipitation (Wilcoxon signed rank test: all comparisons $P = 0.01$). Therefore, years with concentrated precipitation will yield vernal pool hydroperiods that exceed years with equal but distributed precipitation.

In dry (Fig. 2b) or wet (Fig. 2c) years, the effects of 'concentrated' or 'distributed' precipitation changed. In the dry pair of years (1983/84 and 1999/2000; Fig. 2b), ponding was longer when rainfall was 'distributed' as opposed to 'concentrated'. Three pools held no water in either year and two others were tied for number of days with inundation. The remaining five pools all held water longer when the storms were more spread out.

In the two wet years (Fig. 2c), the pools were evenly divided between ones with longer duration in one year or the other. The 1982/83 rainfall year had total precipitation of 46.3 cm spread primarily over 6 months and in 1992/93, 46.5 cm of rain fell mostly over a 4-month period with 76% of the year's total coming in December and January (Fig. 2c). The three pools that held water longer in the 'distributed' year, receive drainage from upslope pools.

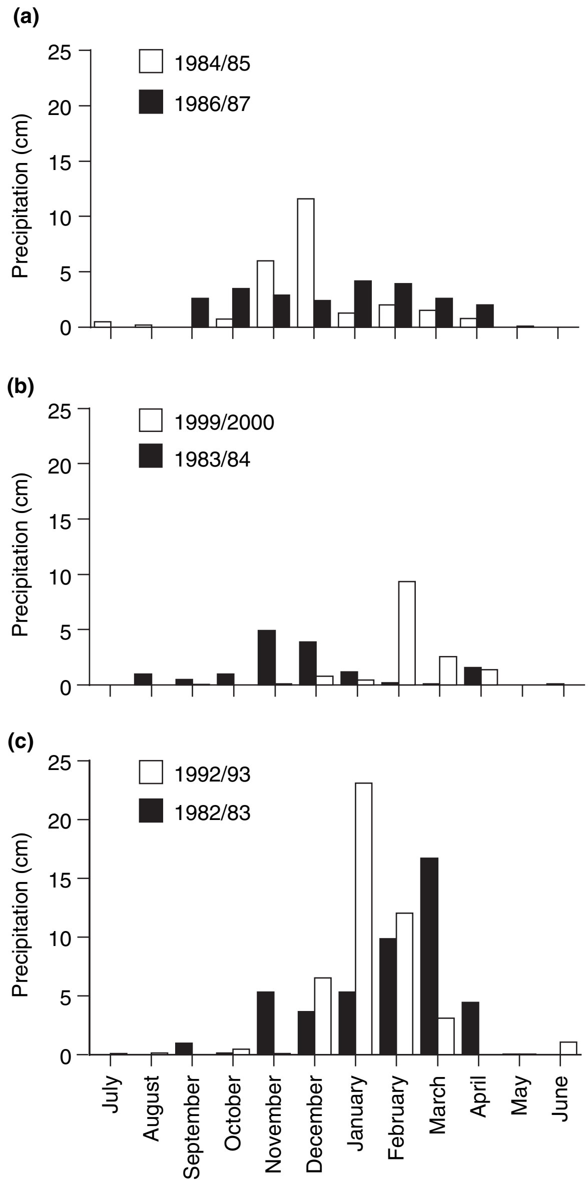

Fig. 2 Monthly distribution of rainfall over three pairs of rainfall years, each with nearly equivalent total precipitation. (a) Moderate precipitation year, (b) dry year and (c) wet year.

In the 9 years when precipitation was greater than the mean, the number of times the soil was exposed in pool bottoms was inversely related to the proportion of the year's total precipitation concentrated in 2 months ($r_s = -0.52$, $P < 0.0001$).

Interaction of weather with geomorphology

Pools that receive surface and/or subsurface water from basins higher in the drainage system generally reach their peak depth a day or two later than topographically higher pools without inlets and, they pond water longer. In the 10-pool study group, there are three pairs of pools with one higher pool draining into the other. The lower pools held water longer than the higher ones (Wilcoxon paired sign test, $P < 0.0001$). One higher–lower pair differed over a month in inundation length in seven of the 20 years. Differences in the inundation period were greater in years with more precipitation ($r_s = 0.32$, $P = 0.02$). There was no apparent relationship of inundation period with a given year's rainfall pattern.

Basin slope (cm decrease per linear m) varied among the study pools from 2.1 to 10.7 cm m^{-1}. Slope combined with rising and falling water levels affected the available microhabitats (i.e. areas within basins having different moisture conditions) on a pool-by-pool basis. In 1982/83, a plant that tolerated (or required) 30–40 days of inundation, could occupy an elevational band 2 cm wide in Pool 51 (slope = 7.6 cm m^{-1}) and one of 5 cm width in Pool 29 (slope = 2.1 cm m^{-1}).

Discussion

Many factors affect ponding in a vernal pool, but the total amount of seasonal precipitation is the most important factor, given a slowly permeable substrate and a sufficiently deep depression. The yearly amount varied widely, and in turn the length of ponding varied as well. As a result, each year new edge-to-bottom soil moisture/inundation gradients formed – gradients that could affect the microdistribution of plants (Bauder, 2000) as well as the presence or absence of species within the pool. Upland species are negatively affected by inundation of any length, limiting them to the upper, drier end of the inundation gradient or excluding them from a pool altogether (Bauder, 1987). Other species are favoured by wetter years (Bauder, 2000). Within the last decade, pools have been invaded by two exotic wetlands grasses, *Agrostis avenacea* Gmelin, an Australasian native, and *Polypogon monspeliensis* (L.) Desf., a native to southwestern Europe. Growth of these grasses is favoured by wet El Niño events, such as the 1997/98 rainfall year. Research in the field and under controlled conditions indicates both grasses negatively affect native pool species in a variety of ways, ranging from survivorship to reproductive success (Bauder, 1988; Bauder, Snapp-Cook & Sakrison, 2002). The effects of this El Niño year suggest possible biological impacts of major climate change.

The most variable hydrological zone within the basin was always at the upper end of the moisture gradient but shifted in response to different rainfall regimes. Some pools had no variability in water level at any elevation because they failed to pond water in a number of years. Pools that held water longer had less variability in water depth at the deepest elevation, but the soil surface was exposed more often due to more ponding events. Seasonal distribution of rainfall and storm intensity create within-year variability that also affects the inundation period (Hanes, Hecht & Stromberg, 1990; Hanes & Stromberg, 1998). In the 20 years of this study, rainfall pattern influenced both the total ponding period and the number of ponding events.

Quadrats with fluctuating water levels have the highest densities of vascular plant species (Bauder, 1987). Theory suggests that temporal fluctuations in the environment may promote co-existence, if species responses are different, non-additive and non-linear (Chesson & Huntly, 1997). Previous work on *Pogogyne abramsi* J. T. Howell, a narrowly endemic pool plant, revealed an important interaction between length of the inundation period and non-linear competitive effects (Bauder, 1987, 1989). Competitive outcomes were also species-dependent (Bauder, 1987). The several dozen endemic plant species which co-occur in southwestern California's vernal pools have different morphologies, growth rates and timing of reproduction during the wet season, suggesting that non-linear responses may be the norm in these communities.

Yearly variability in water depth and duration, interacting with basin morphologies, altered the proportion of each pool experiencing particular moisture conditions in a given year, with implications for species distributions within and among pools. Given the narrow habitat preferences and tolerances of many vernal pool plants, species could be excluded from a pool by the lack of suitable microhabitat due to the slope or depth of the basin (Holland & Jain, 1984).

When a basin's contours are altered by filling, blading, disking or vehicle passage, the hydrology is usually changed in ways that are important to vernal pool plants and animals. Pools that have been repeatedly driven through lose soil and water stands right on the underlying hardpan. They pond with less precipitation and hold water longer (Bauder, 1988). Partially filled pools, such as Pool 6 in this study, require more rain before they pond water, and surface water disappears rapidly after a storm (Bauder, 1987). Within-pool topographical modifications such as ruts, fill or excavations result in uncharacteristic species distributions due to abrupt elevation changes causing sharp boundaries between microhabitats, within-basin areas experiencing significantly different soil and/or moisture conditions.

Pools differing in landscape position responded differently to the same precipitation events. Combined with differences in the pool shape, depth and slope, a wide array of hydrological conditions developed each year and across years. Loss of diversity in pool morphology and the alteration of hydrological properties through destruction of watersheds and hydrological connections could indirectly favour certain species – native or not – at the expense of others and decrease the buffering effects of pools with diverse hydrological properties.

The risk of extinction of characteristic pool species, many of which are endangered, is directly increased by the loss of habitat. Climate changes would be expected to alter pool hydrology and in turn the distributions, population dynamics and interactions of these vernal pool plants and animals. Less obvious threats are related to the loss of structural habitat diversity and the concomitant impacts of such losses on hydrological diversity and in turn species responses.

Subtle changes in any of the examined environmental factors (climate, topographic relief, watershed connections and pool morphology) can have major implications for the long-term persistence of the specialised, endangered species that are a distinctive feature of the vernal pool ecosystem. Preservation, restoration and management decisions need to take this environmental complexity and variability into account.

Acknowledgments

This work was carried out on MCAS Miramar (formerly NAS Miramar) with the permission of the Commanding Officer. I appreciate their cooperation and the opportunity to do research on the Station. Over the 21 years of the study, many people have assisted with field work and I am grateful for their efforts. Clinton Bauder, Ann Kreager, Pam Cannell, Britt Buckner, Larry Hendrickson, Lea Swanekamp and Juda Sakrison made substantial contributions to the collection of field data. Andy Bohonak, George Cox, David Jenkins, Jay Diffendorfer and Stuart Hurlbert commented on drafts of this manuscript and made many useful suggestions, as did two anonymous reviewers. A portion of this work was funded by the Joint Doctoral Program in Ecology of the University of California Davis and San Diego State University. I dedicate this paper to Howie Wier, who inspired me often with his love of plants and vernal pools.

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(Manuscript accepted 11 September 2005)