# Science and Vernal Pool Conservation: Research Questions, Methodologies and Applications Based on a Case Study of *Pogogyne abramsii* in San Diego County, California

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ABSTRACT. As in all areas of ecology, research questions in conservation biology need to be guided by the nature of the habitat and the factors that drive the ecosystem's primary functions. Regional studies of species distributions and their biological and environmental correlates are a critical part of the conservation process. For vernal pools, these factors can be elucidated for each species at the level of an individual pool, as well as in hydrologically connected pool complexes. Particularly when basic research interfaces with policy and management, methodologies need to be carefully tailored to minimize ambiguous conclusions. Consideration of temporal and spatial variability is critically important for vernal pools. Weather patterns (particularly precipitation) vary between and within years. Long-term studies must account for this variation, which can be extreme. The extensive spatial variation among and within individual pools must be accounted for in the sampling scheme, the sampling unit and, the extent of replication. Hypothesis testing is strengthened by the use of complementary methodologies, such as non-destructive field observations paired with controlled experiments in both the field and common gardens. A case study on *Pogogyne abramsii* in San Diego County, California illustrates this use of multiple methodologies. Research that focuses on the basic biology and distributional patterns of vernal pool plants and animals contributes to informed policy decisions related to issues such as the importance of intact catchments, the spatio-temporal scale at which biodiversity must be managed, the potential impacts of systemic climate change and occasional catastrophic events, the role of pool peripheries and uplands, and the consequences of habitat fragmentation.

CITATION. Bauder, E. T. 2011. Science and vernal pool conservation: research questions, methodologies and applications based on a case study of *Pogogyne abramsii* in San Diego County, California. Pages 5-23 in D. G. Alexander and R. A. Schlising (Editors), Research and Recovery in Vernal Pool Landscapes. Studies from the Herbarium, Number 16. California State University, Chico, CA.

## INTRODUCTION

Vernal pools are temporary, rain-fed ponds found primarily, but not exclusively, in regions with a Mediterranean climate (Keeley and Zedler, 1998). California's vernal pools have global significance because they provide habitat for an unusually rich endemic flora and fauna (Thorne, 1976, 1984; Stebbins, 1976). *In situ* speciation appears to have occurred within many vernal pool plant and animal genera (e.g., Simovich, 1998; Stebbins, 1976), and numerous pool species have extremely restricted distributions (Bauder and McMillan, 1998; Griggs, 1981; Griggs and Jain, 1983; King, 1998; Ornduff, 1976; Simovich, 1998; Stebbins, 1976). For these reasons, Californian vernal pools have attracted the interest of botanists for nearly a century (Howell, 1931; Purer, 1939; Ramaley, 1919).

More extensive scientific studies of California's vernal pools began in the 1970s and 1980s (e.g., Bauder, 1987; Brown and Jain, 1979; Griggs, 1980; Griggs and Jain, 1983; Holland and Jain, 1981; Ornduff, 1976; Ritland and Jain, 1984). These studies, and others in more recent years (see other chapters in this volume), have elucidated many factors related to local and regional plant distributions, population connectivity, and the impacts of exotics on the native flora. Nonetheless, many important biological and hydrogeological questions remain unanswered. Rapid urban growth and the expansion of agriculture and other land-altering activities on vernal pool landscapes throughout the state have created an urgent need for more information that will specifically inform and direct conservation and management efforts.

This paper offers suggestions for maximizing the useful information that can be garnered from vernal pool research projects. The first step is to clarify the project goals, along with determination of the universe of interest (e.g., pool, species, watershed, region). Research methodologies must be appropriate for the ecosystem, taking into account climatic variability, unpredictability, habitat heterogeneity and scale, and the characteristic species. Spatial and temporal variability in vernal pools is particularly high in comparison with most other ecosystems. To illustrate the application of specific methodologies to specific research goals in these unique habitats, the chapter concludes with a case study of a long-term research program emphasizing the rare endemic *Pogogyne abramsii* J. Howell (Lamiaceae) found only on the central coastal mesas of San Diego County, California.

## *The Vernal Pool Habitat—Implications for Research*

In California, vernal pools are found in many geographic settings and subclimates (Keeler-Wolf et al*.,* 1998). Due to statewide variation in geomorphology, soil profiles and climate, pools have a wide range of hydrological regimes and substrates that support a diverse and locally adapted flora and fauna. Within- and among-year variability in precipitation amount and pattern creates additional complexity. Understanding the types and levels of variation and variability specific to vernal pools is an important first step to developing a successful research program.

Even within regions, there is exceptional variation in pool origins, substrates, and climate. In Southern California, there are 24 possible types of vernal pools, based on classification by physiographic setting, geomorphologic origin, and age (Bauder et al., 2009) (Table 1). Southern Californian pools are found in over 30 soil series that share important characteristics such as a slope of < 9%, low permeability (< 0.06 inches/hour), a thick clay layer 1-2 feet below the surface and, quite often, a second, less permeable layer below the clay layer (Bauder and McMillan, 1998; Bauder et al., 2009). Substrates in pool basins differ from the surrounding soil series, and vary greatly in both surface and subsurface characteristics. Further variation in soil characteristics exists within and among pool types and soil series. Climate in southern California also varies considerably, even over short distances (Bauder et al., 2009) (Table 2). In general, elevation and distance from the Pacific Coast are the primary factors determining amount of yearly precipitation, likelihood of meaningful summer rainfall, seasonal temperature regimes, and the occurrence of frost.

If the conditions for pool formation are present (a topographic depression with a poorly permeable substrate), sub-regional climate and/or soil series correlate strongly with the distribution of vernal pool species in Southern California, including *Limnanthes gracilis* ssp. *parishii*, *Downingia concolor* var. *brevior* and both *Pogogyne abramsii* and *P. nudiuscula*. The underlying mechanisms restricting species distributions to specific pool complexes include factors such as germination requirements (Bauder, 1992, and unpublished data). The two species of *Pogogyne* may even qualify as highly specialized "double endemics"

TABLE 1. Matrix of vernal pool types in Southern California. All locations are within San Diego County, unless otherwise noted.

| Age and origin | Physiographic setting | | | |
|---|---|---|---|---|
| | Coastal Mesa | Inland Valley | Inland Mesa | Large Depression |
| Pedogenic | • Miramar<br>• Otay Mesa<br>• Wire Mesa (Pendleton)<br>• Isla Vista[a] | • Upper Ramona (Santa Maria Creek)<br>• San Marcos<br>• small pools at Skunk Hollow (Riverside County) | • Valle de las Palmas (Baja Mexico)<br>• Wire Mt./Oscar One (Pendelton)<br>• Sunrise Highway (Mt. Laguna) | • Cuyamaca<br>• Little Lagunas |
| Tectogenic | • no example identified | • Skunk Hollow (Riverside County) | • Moorpark/Tierra Rejada (Ventura County) | • no example identified (uncertain) |
| Landslide | • Otay Mesa<br>• Chiquita/San Clemente (Orange County) | • no example identified | • no example identified | • no example identified |
| Alluviated | • Otay Valley<br>• Proctor Valley | • Lower Ramona (Santa Maria Creek)<br>• Marron Valley<br>• San Marcos<br>• Fairview Park (Orange County)<br>• Hemet (Riverside County) | • no example identified | • Cuyamaca (uncertain) |
| Dune-dammed | • Carlsbad<br>• Carmel Mt. (Del Mar)<br>• Ellwood Beach[a] (Santa Barbara County)<br>• West Bluff (Pendleton) | • no example identified | • no example identified | • no example identified |
| Bedrock | • Colonet (Baja Mexico) | • Tenajas (Riverside County) | • Santa Rosa Plateau (Riverside County) | • North Los Angeles County |

[a] Blend of two pool types: Ellwood Beach and Isla Vista pools are a full continuum between dune-dammed and pedogenic (Bauder et al., 2009).

(i.e., endemic to both temporary wetlands and a particular soil series) (Bauder and McMillan, 1998). Within local areas where the same pool type is found on the same soil series, species distributions may be further restricted by tolerance (of drought or inundation), intraspecific and interspecific competition (taking into account density and competitors' growth

TABLE 2. Climatic variables affecting vernal pools and temporary lakes in southern California (Bauder et al., 2009).

| Pool location | | Elevation (feet) [a] | Annual precipitation (inches) [c] |
|---|---|---|---|
| Coastal mesas | Chula Vista | 56 | 10.9 |
| | La Mesa | 530 | 12.8 |
| | Montgomery Field | 414[b] | 13.1 |
| | Otay Mesa | 510[b] | 10.5 |
| | Oceanside Harbor | 10 | 10.5 |
| | Laguna Beach | 60 | 12.7 [d] |
| | Santa Barbara | 14 | 14.1 [d] |
| Inland mesas | Santa Rosa Plateau [e] | 2,400 | 15.0-16.6 |
| Inland valleys | El Cajon, Gillespie Field (west) | 380[b] | 10.7 |
| | El Cajon (east) | 520[b] | 14.1 |
| | Ramona | 1,450 | 16.1 |
| | San Marcos | 520[b] | 12.6 |
| | Perris | 1,470 | 10.4 [d] |
| | Moorpark | 58 | 13.1 [d] |
| Mountains | Cuyamaca | 4,640 | 38.7 |
| | Palomar | 5,550 | 49.4 |

[a] All elevations from NOAA Climatological Data Station Index, except when footnoted as [b].

[b] Elevations from USGS 7.5 minute quadrangle maps.

[c] Precipitation from County of San Diego (Cartographic Services) rainfall map, except when footnoted as [d].

[d] Precipitation from WRCC.

[e] All data from Lathrop and Thorne (1976).

form and phenology), and dispersal capability.

In common with most arid climates, precipitation varies widely both within and among years, as does the seasonal pattern of storms (Bauder, 2005). This results in a wide and unpredictable range of growing conditions. The unpredictability of hydrological conditions would appear to favor high levels of biodiversity and prevent competitive exclusion in accordance with the classical "intermediate disturbance" hypothesis (Bauder, 1987; Huston, 1979; Chesson and Huntly, 1997). The flora is dominated by annuals and geophytes, which spend the hot, arid summer season as drought-resistant seeds or corms. Much of the aquatic fauna associated with vernal pools has structural equivalents (e.g., encysted embryos in crustaceans) that serve the same function of persistence through the dry phase. As in other temporary wetlands, many plants have adapted to the environmental variability with plastic responses to inundation. These include leaf form (Deschamp and Cooke, 1983, 1984), internodal elongation (Bauder, unpublished data; Ridge, 1987) and shifts in photosynthetic pathways (Keeley, 1987). This allows them to grow under a variety of conditions, ranging from barely moist soil to several months of inundation 10-20 cm deep.

## RESEARCH APPROACHES AND METHODOLOGIES

In outlining and describing the rationale for particular research approaches and methodologies, the following sequence of topics will be discussed: development of goals and establishment of levels of inference, dominant habitat characteristics such as spatial heterogeneity and temporal variability, and the species composition of the flora. Three basic research approaches are then described and evaluated in light of the stated goals, level of inference desired, habitat characteristics, and organisms of interest.

### *Goals, Hypotheses and Levels of Inference*

Research methodologies and sampling schemes should be dictated by the goals or focus of the studies, the hypotheses tested and the chosen level(s) of inference. For example, if the goal is to examine how hydrological disturbance impacts pool community composition, a number of pools with different combinations of hydrology and disturbance regime must be sampled. If the research question deals with the attributes of entire watersheds, then the sampling effort must include data from multiple pools in multiple watersheds. Hypotheses that relate small-scale species distributions to specific conditions of soil or hydrology need to be tested with samples taken at an appropriate scale that reflects the spatial distribution of the phenomenon of interest. If hydrologic impacts within pools vary significantly on scales of < 50 cm, then sampling at 1 m intervals would not be useful.

*Species-specific goals could include the following*:

- Recovery or preservation of a particular species,
- Mechanistic understanding of population dynamics,
- Evaluation of individual plant responses to abiotic factors (e.g., drought/inundation and weather patterns) and biotic interactions (e.g., competition, herbivory and pollination),
- Determining whether critical life history transitions (germination) overwhelm the effects that these factors have on more robust life history stages (flowering), and
- Integration of all information into an estimation of local extinction probability under various scenarios (i.e., conduct a population viability analysis).

*Basin- and ecosystem-scale projects might have their own unique goals:*

- Maintenance or restoration of natural hydrologic regimes,
- Maximization of species diversity (within a pool type, soil series, landscape or region),
- Documentation of the impacts of disturbances (e.g., exotic species, alteration of watersheds or water supply, vehicle intrusions),
- Evaluation of restoration methods or particular restoration sites,
- Preservation of an array of pools in their natural spatial and hydrologic relationships,
- Understanding of the functional relationships between uplands and basins, and
- Identification of the mechanisms that buffer vernal pool systems from occasional extreme natural events such as wildfires, extended drought or exceptionally high rainfall.

### *Consideration of Spatial Heterogeneity and Temporal Variability*

*Spatial heterogeneity*. Pool species occur along a topographic gradient that extends from the potentially moist uplands above the highest possible elevation of inundation to the lowest elevation in the basin. This complex gradient includes a wide range of soil and hydrological conditions over a distance as small as 5-10 m. These gradients must be sampled with sufficient sampling points or plots, and at intervals that take the pool's size, slope and depth into consideration. Sampling units should be scaled to the questions being asked. For example, hydrological conditions and species distributions can change dramatically within pools over only a few decimeters (Bauder, 1987, 2000). Sampling plots larger than 1-2 dm would not capture the gradual changes correlated with changes in elevation.

For purposes of analysis, sampling units within a single pool are not fully independent, since they co-vary in important habitat features such as soil characteristics, depth to hardpan, landscape position, and hydrology. The frequency of sampling, size of sampling units, and number of plots or sampling points may also be affected by within-pool patchiness of cobbles, cracks, mini-depressions, soil discontinuities, and species distributions. Basins with more uniform surfaces require fewer samples compared to those with greater heterogeneity. Within watersheds or regions, individual pools vary greatly in their geomorphology. This variation includes area, depth and volume; slope and shape; presence or absence of inlets and/or outlets; watershed position (isolated, headwater, flow-through, terminal); depth to hardpan or other poorly permeable soil strata; and soil surface features. To avoid results biased by the idiosyncratic or unrepresentative nature of a few samples within a pool or inclusion of an insufficient number of pools when between-pool or regional hypotheses are being tested, variability of critical features should be quantified and the required sample size estimated using the observed variability.

*Temporal variability*. To test many hypotheses, data collection will need to be replicated over years in the same locations because seed germination, plant growth and development, physiognomy (species and community), reproductive output and seasonal progression of development respond to different weather conditions. Similarly, the size, condition and genetic composition of the seed bank vary annually. These hypotheses would include those related to pool, species or community responses over time, to variability in weather or other important environmental variables, and to changes in the habitat (human-caused disturbances or infrequent natural events). Long-term weather data can be consulted to determine what range of total precipitation would be observed in a given time span (e.g., 5 or 10 years). Monitoring of restoration efforts or response to unpredictable events (such as fire) can be aided by baseline data taken prior to the event of interest.

Hydrographs based on water depth readings recorded at regular, short intervals are essential to evaluate the relationship between plant responses and basin hydrology. If there is sufficient rainfall for water to pond, intra-season water levels will rise and fall based on the size of the storms and the length of the between-storm intervals. Pools may pond and dry down several to many times during the wet season, or pond only once and then dry completely. The rising and falling water levels interact with basin morphology, so that positions along the elevation gradient differ in the total number of days inundated, the longest continuous period of inundation, the number of inundation episodes, and the depth of inundation at any time or averaged over time (Bauder, 1987, 2000, 2005). Based on differences in basin morphology (slope, shape and depth) and watershed position, pools within a watershed or area also express a variety of hydrological responses to the same rainfall conditions within a given year.

Vegetation data may need to be collected more than once during the growing season to capture seasonal progression in community composition, quantify each species' maturation rate, make accurate species identifications, and relate frequency, density or survivorship to environmental variables. Plants go through a progression of seasonal changes, regardless of the nature of the rainfall season. Plants may die early due to drought or, at the other end of the moisture gradient, intolerance of inundation. Immature plants may have hollow stems or leaf petioles, and glabrous leaf and stem surfaces. As plants mature, they often develop sclerified stems and leaves, leaf and stem trichomes or spiny structures. Many species are difficult to identify without mature fruits. More fragile species may disappear almost entirely soon after they reproduce. A number of vernal pool species exhibit phenological plasticity of stem length, leaf shape and physiological pathways with rapid responses elicited by standing water (Deschamp and Cooke, 1983; Keeley, 1987; Ridge, 1987).

### *Choice of Species as Study Subjects*

Given the significant differences among vernal pool plant species in life form, morphology, developmental rates and plasticity, life history and other important characteristics, choice of focal species or experimental subjects must be done with care for practical reasons, as well as for reasons related to hypothesis testing.

If studies of a particular species are of primary importance, its limitations as a research subject need to be taken into account from the outset. For example, if the effects of disturbed hydrology are of interest, what hydrological changes are of greatest importance for the species (variability in water levels, water depth, days of inundation), and how will the effects on the species be expressed (germination, survivorship, morphology, reproduction)? Will it be possible to quantify responses? Will response variability or plasticity swamp disturbance-related effects? Can the impacts of different types and levels of disturbances be distinguished?

Inferences about the plant community as a whole require the study of species with different life forms and life histories. Prior observations under a variety of conditions may guide the choice of representative species or groups or guilds of species as surrogates for the entire community. Depending on the choice of research method(s), representative species may be selected because they

- germinate easily,
- grow well under artificial conditions,
- have a morphology that facilitates censusing (plants can be easily separated and counted),
- do not require specific pollinators to fruit,
- retain seeds on the plant as it matures,
- produce sufficient seeds for experimental replicates,
- produce seeds large enough to harvest, manipulate and count, and
- can be reliably identified in the field.

### *Three Research Methodologies*

All research approaches and methodologies have assets as well as tradeoffs and drawbacks, suggesting it is prudent to use more than one research tool to test each hypothesis. Careful formation of testable hypotheses or research questions and appropriate sampling protocols are important to minimize ambiguous results. Three basic approaches to vernal pool research include 1) field observations and sampling, 2) manipulative field experiments and 3) controlled, factorial experiments.

Non-destructive field observations have the advantages of minimal intrusion into the observations and minimal habitat impacts that might affect observations in subsequent years. If carefully planned and executed, destructive sampling of soils, plants and aquatic organisms may not necessarily lead to significant or lasting impacts on the basin habitat, flora or fauna. If non-destructive field observations are carried out over a number of years at the same locations, they can be used both to generate testable hypotheses—especially those related to weather-driven responses—and to validate experimental outcomes. Disadvantages of non-destructive field observations include the difficulty in isolating factors, a heavy reliance on correlation and the difficulty of identifying mechanisms that can account for the patterns observed.

Manipulative field experiments provide an opportunity to test hypotheses by applying factors of interest in semi-natural conditions. In addition to the advantage of setting the primary independent variable at a specific level, many ecologists would argue that only weak inferences are possible from purely observational studies. Presumably, the soils, hydrology, and background vegetation in pools provide a biologically relevant growing environment during the experiments. However, weeding and density manipulations can expose the soil surface to sun and wind, causing higher temperatures and loss of soil moisture. Locating pools that are sufficiently similar to serve as replicates may be difficult or impossible, depending on the size of the area being studied, and on natural and anthropogenic-caused variation. Replicate plots within pools can also be dissimilar in subsurface characteristics (soil texture, depth to hardpan) and surrounding vegetation (species and density), even if they are located at comparable elevations on the upland-basin gradient. To compensate, a split block layout can be used, with replicate blocks located at two or more elevations (Bauder, 1987, 2000). As cautioned above, replicates within pools are not fully independent of each other if the units of inference are a set of pools.

Multi-factorial experiments conducted under controlled conditions are useful to isolate factors, apply them at different levels, and to rigorously examine the effects of the factors individually and in combination. Predictions based on the experimental results may then be evaluated against actual species distributions and behaviors in the field. Disadvantages related to the controlled experimental approach focus around the artificiality of the growing conditions, although these drawbacks can be partially mitigated by growing the plants in-season and outdoors rather than in greenhouses or growth chambers. Although outdoor conditions may reflect those ordinarily experienced by the species being studied, an atypically hot growing season can wreak havoc with the experiment. Vernal pool plants are not adapted to growth under moist, hot conditions, and damping off and other fungal diseases may sharply increase mortality. Chambers, greenhouses or outdoor plots require substantial resources in terms of space and/or equipment. Inundation treatments call for artificial ponds, large tanks or industrial bins where water levels can be manipulated and maintained. Preliminary trials are useful to suggest the number of replicates based on the variability of species' responses. Germination experiments necessitate growth chambers or seed incubators with temperature and day length controls. Both pieces of equipment are costly to purchase and operate. As with replicates within pools, replicates within chambers or incubators are not fully independent. To overcome this drawback, experiments can be run multiple times, with different treatments or species assigned to different chambers with each run. I have not found significant between-chamber differences in germination responses when experiments are repeated several times in close succession.

## *Pogogyne abramsii*, A Case Study In The Use Of Multiple Research Approaches

Over a 25+ year period beginning in 1982, I have pursued a vernal pool research program that utilizes variations of all three research approaches (Appendix). Although over a dozen species have been examined closely, the majority of the experimental work has focused on the diminutive, rare mint, *Pogogyne abramsii*. It is endemic to San Diego County and is found on the central coastal mesas of pedogenic origin, dominated by the Redding soil series. It is on both the federal and California endangered species lists. My work began with three broad goals: to characterize the upland-pool environmental gradient, describe species distributions on the gradient both within and between years, and to test hypotheses on the causes of observed field distributions.

### *Non-destructive, Long-term Transects*

The foundation of my long-term program was a system of permanent transects and water-measuring bars (one transect and bar per pool) established in 12 basins that vary in size, slope, landscape position, and land use history (Bauder, 1987, 2000). Sampling quadrats (1 $dm^2$) were placed along the upland-basin transect. Their elevation relative to each other and to the water bar was determined using a surveyor's level. After 15 years, the elevations were rechecked, and few changes were noted.

Water depth data collected at the water bar are useful to construct seasonal hydrographs for each pool and characterize the hydrology of individual quadrats in relation to their position on the elevation gradient. The data can also be used to compare the responses of different pools within and between years and to relate species' responses to various hydrological metrics such as total days of inundation, longest continuous period of inundation, mean depth of inundation, variation in water depth, and number of times evaporated (soil surface exposed). When pools have evaporated and most species are flowering, each quadrat is scored for vegetative cover. Disturbance by fossorial rodents, siltation or human impacts is noted. Presence of individual species and their phenological state (vegetative, flowering, dead, etc.) is also recorded. After transect sampling is complete, the pool is searched for species not recorded on the transects to determine the total floral species count for the pool. Hydrological and vegetation data were taken continuously in these pools for 20 years, with 3 additional years of vegetation data taken. Data were also taken in a similar fashion for 5 years following a vernal pool restoration project (Bauder and Sakrison, 2001). Additional details regarding specific research questions, methods, and data analysis are provided in the citations for this and the following sections, and summarized in the Appendix.

Even to casual observers, the most obvious feature of vernal pools is the stark difference between ponding water in the depressions (basins) and the absence of standing water in the surrounding uplands. During the period of spring bloom, a second feature becomes apparent: the vegetation gradient from the uplands to the deepest portions of the basin, signaled by zones of flowering plants whose blooms differ in color. Although these rings of flowers can be less apparent or entirely absent in the smaller pools common in San Diego County, small-scale examination of species' distributions along the upland-basin moisture gradient documents the presence of three moderately well-defined floral zones/ species communities: "non-pool," "edge" and "pool" (Bauder, 1987, 2000). In years when pools fail to pond or hold very little water, the moisture gradient fails to establish and species distributions are a function of their dispersability, rather than relative inundation tolerance (Bauder, 2000, 2005).

Each species has a distinctive distributional curve, with curves overlapping along both the elevation and moisture gradients (Bauder, 1987, 2000) (Figure 1). Soil texture and nutrient composition change in parallel with the elevation/inundation gradient (Bauder, 1987; Bauder et al., 2009). Basin soils are higher in clay and nutrients compared to adjacent upland soils. Analysis of the relationship between hydrological conditions and the species present in the quadrats—as well as research

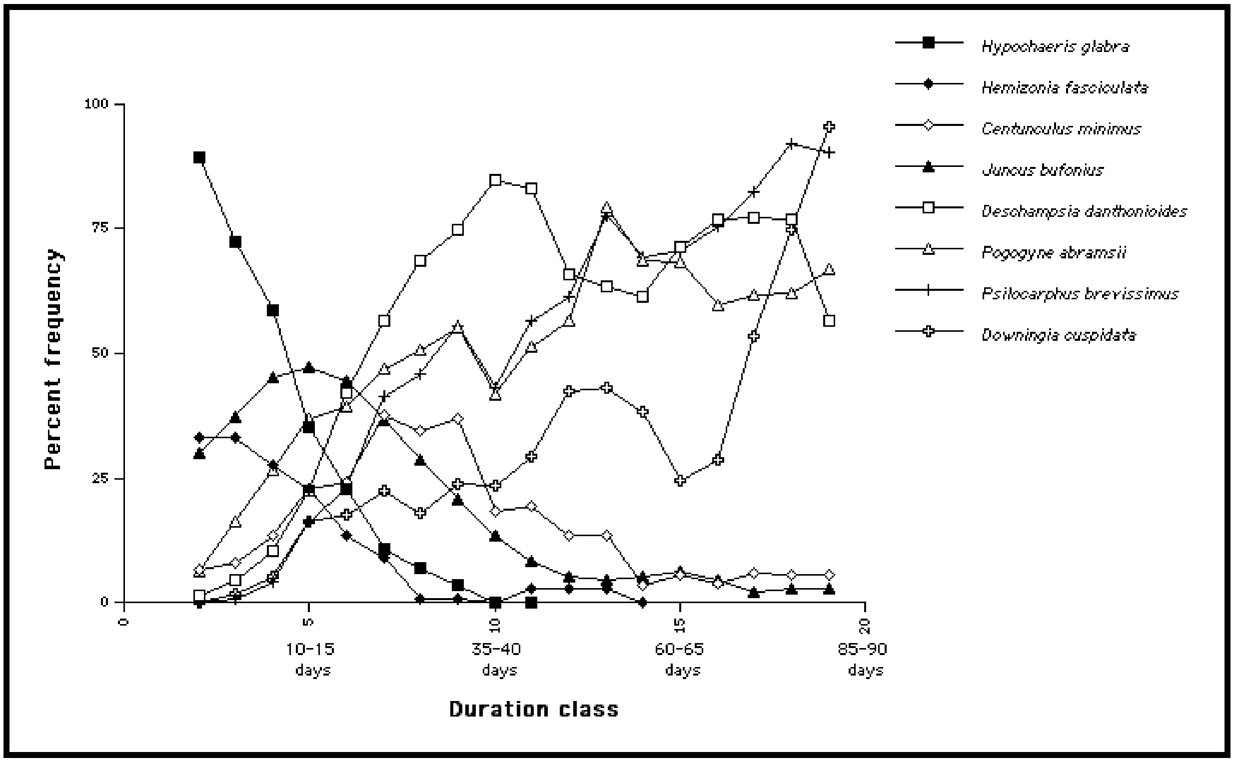

FIGURE 1. Distribution of representative species along the duration of inundation gradient in 1982-1983, a wet year (46.3 cm total precipitation). Duration classes extend from 0 (no inundation) to 20 (85-90 days of inundation). These species re-grow on the elevation gradient anew each year, depending on the precipitation amount and storm pattern.

described below—indicates that a species' position on the gradient can be predicted based on its individualistic response to the total number of days inundated, longest continuous period of inundation, and depth of inundation (Bauder, 1987, 1989a, 2000, and unpublished data). Upland species rarely survive more than 2 weeks of continuous inundation or a month of total days inundated. In coastal San Diego County, most obligate vernal pool species decline in frequency when the total days of inundation exceeds 3 months.

Based on quadrats that span the micro-elevation gradient, it is possible to determine how the hydrological regime drives single-species distributions, areas of greatest species density (# of species per unit area), and total pool diversity. Inferences are strengthened by comparing responses among pools and among years with different rainfall regimes. Species density is greatest near the upper end of the moisture gradient where the fluctuation in water depth (quantified as the coefficient of variation) and total continuous days of inundation are intermediate, and the distributions of the three categories of species overlap (Bauder, 1987, 2000). In drier years, water depth fluctuation is greater, and occurs farther down the elevation gradient (Bauder, 2005). The range of moisture/hydrological conditions within the pool basin and the number of quadrats representing each, varies by year and is rainfall-dependent (Bauder, 2005). The full range of possible conditions is only present during average or wetter than average years.

The 20-year hydrological data set indicates that in Southern California, basins with infrequent ponding may still sustain the flora characteristic of vernal pools. These data also reveal the amount and timing of precipitation required to initiate ponding, and the interaction of rainfall patterns and ponding behavior with a pool's landscape position (Bauder, 2005; Bauder et al., 2009). For example, a pool with a gentle slope is likely to have wider bands under particular hydrological conditions than pools with steeper sides (Bauder, 1987, 2005). Due to the narrow habitat requirements and tolerances of many pool species, rising and falling water levels interact with basin slope edge to affect the presence of individual species, and the total number of species in a pool (Bauder, 1987).

Hypotheses generated by these long-term field observations of plant distributions were tested with manipulative field experiments as well as multi-factorial experiments conducted in growth chambers or in season, in outdoor tubs or tanks. The following hypotheses (stated here simply as questions) were developed from the transect observations and tested in the field or under controlled conditions.

*Inundation/drought*:

- Is inundation required for germination of *Pogogyne abramsii* or growth to maturity?
- Does *P. abramsii* suffer from drought stress, as expressed in higher mortality, reduced biomass or diminished fecundity?
- How does *P. abramsii* respond to different periods of inundation as expressed in survivorship, biomass, fecundity or fitness?
- Are there interactions between intra- and inter-specific density and inundation?

*Neighbor effects (competition)*:

- Is *P. abramsii* excluded from upland habitats by competition with grassland/upland species for moisture and space?
- Is the volume or mass of competitors (i.e., cover, biomass) a better predictor of *P. abramsii* performance than number of competing plants?
- Are different species equivalent in their competitive effects?

*Dispersal*:

- Does the distribution of *P. abramsii* track availability of suitable habitat by seed dispersal?

### *Manipulative Field Experiments*

In a reciprocal soil transplant experiment, three treatments (no disturbance, soil disturbance and soil transplantation) were applied to multiple plots at three elevations (upland, edge and bottom) in two adjacent pools (Bauder, 1987, 2000). In the two disturbance treatments, soil was removed separately from the top 2 cm and the next 2 cm. In the "soil disturbance" treatment, it was stirred and mixed and then replaced in the plot of origination, subsoil first then topsoil. For the "soil transplantation" treatment, surface and subsurface soils were collected from the designated treatment plots at all three elevations, mixed and then replaced as above, subsoil first then topsoil. Plots were sampled using point frames after the first rains, when germination had begun but there had been no ponding. Plots were re-sampled at the end of the season after the two pools had ponded to the overflow elevation, completely dried down, and plants were in flower. Frequency of a particular species was calculated as the proportion of total points intercepted.

Disturbance depressed *P. abramsii* germination/seedling establishment at all three locations (Bauder, 1987). Seedling establishment was greatest in the low elevation, undisturbed plots. During the ponding period, the upland plots were never inundated, edge plots were inundated a total of 2 weeks, and plots in the basin bottom experienced over 2 months of inundation. After inundation, the frequency of *P. abramsii* was highest in the undisturbed edge plots. Bottom plots had less than half the

*P. abramsii* frequency of edge plots and a diminished frequency compared to the pre-inundation sample, suggesting substantial intolerance of the long inundation period. In the upland plots, there were few *P. abramsii* seedlings, other than in the soil transplant plots. This supports the hypothesis that *P. abramsii* seeds are relatively immobile and that they do not maintain a seed bank in upland soils.

To test hypotheses on the relative effects of neighbors, competitor species, and moisture on the apparent restriction of *P. abramsii* to pool basins, this species and three common upland herbs were seeded into circular plots above the overflow elevation of four pools, and brought to various density and species combinations after seedling establishment. Survival of all four species was monitored over the entire season, and final biomass of the competitors and both biomass and fitness of *P. abramsii* were determined at the end of the season. The experiment demonstrated that above the level of inundation, drought overrides density and competitor effects. Thus, I concluded that lack of soil moisture is a primary factor limiting *P. abramsii* to pool basins and their immediate edges (Bauder, 1987, 1989b).

The effects of exotic species on *P. abramsii* frequency were tested in several experiments where two wetlands weeds were removed from belt transects, plots or entire pools—*Polypogon monspeliensis* (Bauder, 1988) and *Agrostis avenacea* (Bauder et al., 2002). Both of these species thrive in conditions that support vernal pool species, unlike most introduced species that are inundation-intolerant. They produce a persistent, abundant thatch that covers the ground to a depth of 1 dm or more. *Polypogon monspeliensis* seed heads, dead plants and duff were removed in the fall, and live *A. avenacea* plants, plus the prior years' duff were removed in the summer. Non-removal controls were included in both experiments. In the *A. avenacea* experiment, removal of *A. avenacea* duff and plants nearly doubled the number of *P. abramsii* plants in the next growing season (Figure 2).

### *Controlled, Factorial Experiments*

Two multi-factorial experiments examined the single and combined effects of length of inundation, competitor species and density on *P. abramsii* survivorship, total biomass and fitness (Bauder, 1987). Each factor was applied at multiple levels, and the plants were grown outdoors and in-season. *Pogogyne abramsii* survivorship was negatively affected by both inundation and high density. Biomass and seeds per plant were reduced in high-density treatments. Competitors differed in their effects. *Pogogyne abramsii* fitness (mean survivorship times mean number of seeds per survivor) was greatest when the inundation period was long or the initial planting density was low. Within inundation treatments, plants grown at low density out-performed those in high density plantings.

*Pogogyne abramsii* and two other vernal pool species were planted with *A. avenacea* sown at three densities (none, low and high). Plants were grown outdoors and in-season. The first year was warmer and drier than usual (increasing mortality and stunting plant growth), so the experiment was repeated the following year. Despite the unfavorable growing conditions in the first year, the results from both experiments were similar. *Pogogyne abramsii* biomass decreased significantly with increasing density of *A. avenacea*, as did the number of branches and total length of the three longest branches (Bauder et al., 2002) (Figure 3). As part of the same study, seeds of four species (*P. abramsii, A. avenacea, Downingia cuspidata,* and *Deschampsia danthonioides*) were germinated under five temperature regimes, each in both the light and the dark.

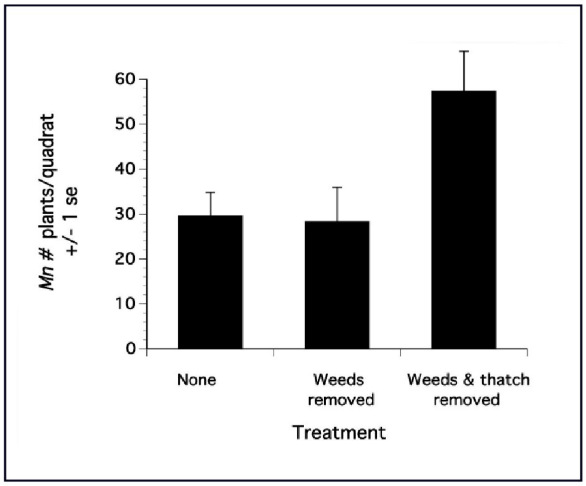

FIGURE 2. Response of *Pogogyne abramsii* in the field to removal of *Agrostis avenacea* plants and thatch.

Germination of all four species was depressed by the dark treatment, with *D. cuspidata* most affected. It did not germinate in the dark. All species germinated well in the light, but germination was depressed by high temperatures, most notably for *D. cuspidata* followed by *P. abramsii* (Bauder et al., 2002).

### *Comparison of Experimental Results with Field Distributions*

Monitoring of field transects confirms the inhospitable environment of the peripheral uplands for *P. abramsii*. Over 25 years, *P. abramsii* has rarely been observed in quadrats above the basin overflow elevation and never observed, even as seedlings, more than a meter distant from pool margins or connecting swales. The upland field experiment confirmed the ability of *P. abramsii* to germinate without inundation, as did the reciprocal soil transplant experiment (Bauder, 1987, 1989b, 2000). Survivorship and performance of seedlings in upland circular plots improved significantly with supplemental watering, implicating drought as a primary factor in restricting this species to pool basins (Bauder, 1987, 1989b).

The presence or absence of *P. abramsii* in specific pools is unchanged over decades, even when pools with and without this species are in close proximity to each other. Presumably this is due to the lack of between-pool seed dispersal or establishment of infrequent seed migrants carried by animals, water or wind. Lack of establishment in unoccupied pools has been documented by the long-term monitoring program. In the soil transplantation experiment, upland plots without soil transplantation had zero to few seedlings. This supports the hypothesis that *P. abramsii* seeds fail to migrate outside of basins. Evidence for frequent and extensive dispersal of upland exotic species is abundant, including data taken on the long-term transects and the soil transplant experiment (Bauder, 1987, 2000, and unpublished data).

Field distributions also reveal the static nature of *P. abramsii* populations along the elevation gradient within basins (Bauder, 2000). Although drought demonstrably reduces survivorship and fitness, plants can survive to reproduction with minimal moisture (Bauder, 1989b, 2000). Plants can survive extended periods of standing water, aided by their hollow juvenile stems, adventitious roots and capacity for stem elongation (Bauder, unpublished data). Therefore, this species can cope with a wide array of moisture conditions but is most abundant where the likelihood of standing water and partial inundation is high but water does not stand for more than three months (Bauder, 1987, 2000, unpublished data).

In the field, *P. abramsii* occurs at highest frequency in dry years where water stands for a total of 10-35 days (Bauder, 1987, and unpublished data). In average or wetter than average years, it peaks in locations with 45-75 total days of ponding (Bauder, 1987, 2000, and unpublished data) (Figure 1).

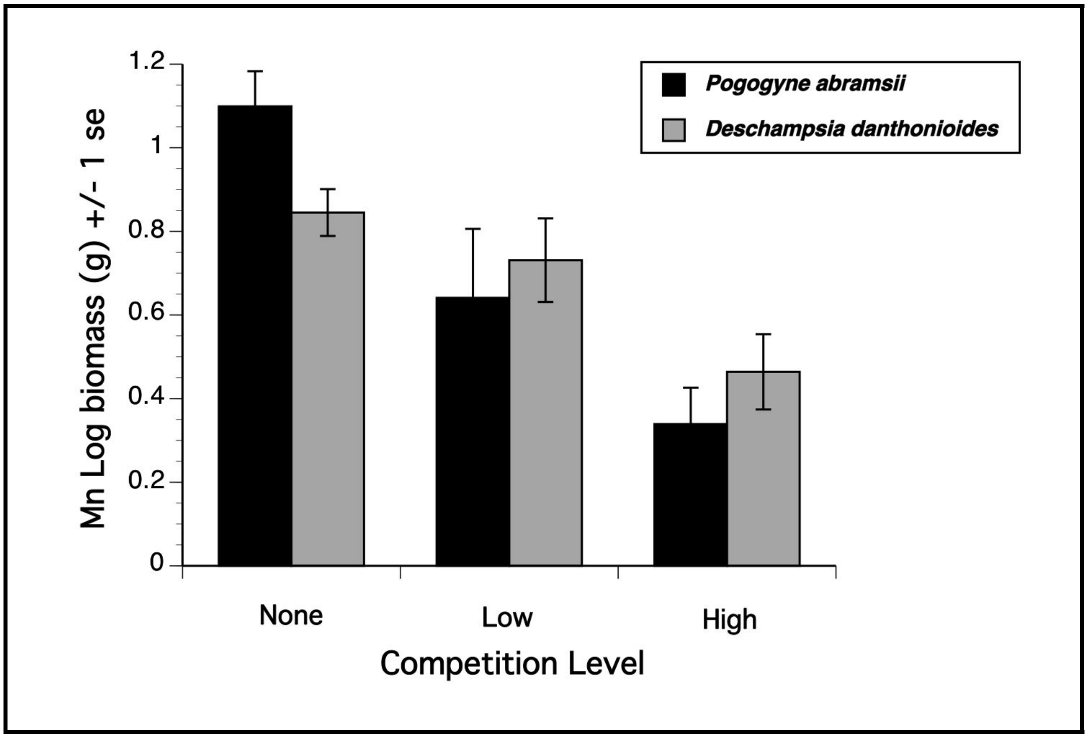

FIGURE 3. Response of *Pogogyne abramsii* and *Deschampsia danthonioides* when grown with three densities of *Agrostis avenacea*.

In controlled experiments, P. abramsii had the highest survivorship in pots with moist soil but no inundation (Bauder, 1987) (Table 3). This apparent discrepancy between field observations and experimental results is explained by the increased fitness of *P. abramsii* when density (regardless of competitor) was fixed at a low level or diminished by inundation-related mortality. Under artificial growing conditions, fitness was greatest when plants were inundated for 2 months, and lowest when plants experienced no inundation at all but were grown in moist soils (Table 3). These results correspond with *P. abramsii* distributions along the wet year moisture/inundation gradient (i.e., years where a seasonal total of 60-75 days of inundation is usually associated with one period of 60 or more days of continuous inundation).

## IMPLICATIONS FOR CONSERVATION AND MANAGEMENT

Over two decades of non-destructive observations, field experiments, and experiments in more controlled and simplified artificial habitats have yielded recommendations for the conservation and management of San Diego vernal pools and of *P. abramsii* in particular. Even the most tolerant of the vernal pool natives persists on a proverbial knife's edge, balanced between dry, nutrient-poor upland habitat and more productive, permanent ponds and lakes. Maintenance of the typical range of hydrological conditions is critical to the establishment, survivorship, biomass production, seed set, and fitness of *P. abramsii*. Disturbances to the watershed and uplands of a vernal pool or pool network can have significant impacts on the hydrology of the pools and on their flora and fauna. Because most exotic

TABLE 3. Growth responses of *Pogogyne abramsii* grown under different moisture conditions.

| Growth responses | Moisture conditions | | | |
|---|---|---|---|---|
| | Dry[a] | Moist[b] | Short inundation[b] (15 days) | Long inundation[b] (60 days) |
| Survivorship (Proportion surviving) | 0.34 | 0.85 | 0.80 | 0.61 |
| Biomass (g dry wt/survivor) | 0.018 | 0.088 | 0.122 | 0.161 |
| Fitness (# seeds/survivor x proportion surviving) | 1.38 | 1.12 | 1.34 | 4.07 |

[a] Upland manipulative field experiment conducted in 1984 (Bauder, 1987, 1989b).
[b] Controlled multi-factorial experiment conducted in 1983 (Bauder, 1987).

plants in the Southern Californian vernal pool landscape are upland species, even occasional inundation for as little as two continuous weeks serves to temporarily eliminate them from pool basins. Most of these upland exotics disperse readily and are able to exploit suitable habitat as it becomes available. The wetland weeds *Polypogon monspeliensis* and *Agrostis avenacea* pose a more serious threat than upland exotics and present an intractable management challenge. Because they thrive in conditions similar to those preferred by vernal pool species, inundation does not keep them in check. Hand removal is effective, but labor-intensive and not appropriate for large areas. When removal programs are interrupted or terminated, the weeds can quickly return via wind dispersal. Herbicides cannot be used without impacts to other pool species, including amphibians and invertebrates (Bauder et al., 2002). Pools with unnaturally long inundation periods support *Typha* species and other perennial marsh taxa, to the exclusion of the typically diminutive pool species.

If climate change leads to changes in total annual precipitation, seasonality of rainfall or storm patterns, or alters the yearly temperature range and mean, vernal pools could experience species extinctions, conversion to an entirely different community or one composed of different species with different biotic interactions (Bauder, 2005; Pyke, 2005a,b). This suggests that conservation must occur at the scale of intact watersheds that contain pools with a range of hydrological conditions, as well as representative groups of pools from different climatic sub-regions. In Southern California, this would include coastal mesas, inland valleys, inland mesas and montane meadows and forests.

Intensive work on the crustacean faunal community, combined with the above work on pool hydrology and vegetation, has made it possible to develop a comprehensive method, based on the U. S. Army Corps of Engineers hydrogeomorphic approach, to assess important vernal pool functions in southern Californian pools (Bauder et al., 2009; Bohonak and Bauder, 2011). Pool assessment has always been hampered by the lack of tools to deal with the region's extremely variable precipitation. The development of tools to estimate function through a variety of direct and indirect means has made it possible to assess vernal pools throughout the entire year, even when they may not be holding water. During development of these assessment methods, I was able to incorporate many of the lessons described here, including use of long-term data under a complete range of precipitation regimes.

Many information gaps remain for vernal pool ecosystems. Importantly, we know little about biogeochemical cycles, subsurface hydrological connections in pool networks, biological interactions such as herbivory and pollination, and the functional biological and hydrological relationships between the basins and adjacent uplands. Because several papers in this volume address these topics (Leong, 2011; Rogers, 2011; Searcy and Shaffer, 2011), this publication will hopefully stimulate further research in these areas to further improve management and conservation practices.

## ACKNOWLEDGEMENTS

I am grateful to dozens of people for their contributions over the many years I have spent studying San Diego County's vernal pools. There are so many who assisted, often as volunteers, I am unable to list all of them here. However, I would like to single out Juda Sakrison for her decade of careful work in the field, the lab and at the greenhouses. She also contributed to the design of many of the experiments, and supported data reduction. Without her able assistance, as well as her companionship, this work would not have been completed. Andrew Bohonak also deserves recognition and thanks for his extensive contributions to the development and editing of this manuscript. The U. S. Navy gave me access to their land for most of the fieldwork reported here, and I deeply appreciate their cooperation. They also provided financial support for several of the field experiments. The California Department of Fish and Game and California Department of Parks and Recreation provided financial support for several other projects. A large portion of the work was done under the University of California, Davis/San Diego State University joint doctoral program in Ecology. For the duration of this work, San Diego State University's Department of Biology provided me with laboratory and office space, outdoor growing space, the use of growth chambers, and technical support. I thank my S.D.S.U. colleagues for those years of support and encouragement. The remainder of the work was unfunded and depended on the labors and expertise of many volunteer assistants, including my eldest son, Clinton Bauder.

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APPENDIX. List of goals, research methodologies used, and relevant citations of work completed. Long-term non-destructive, observational studies of coastal mesa vernal pools have been conducted for over 20 years. These pools are located on MCAS Miramar at 32° 50' latitude and 117° 07' longitude. The distance of the pools from the coast is 9-16 km inland at an elevation of ca. 130 m. Much of the material has not been reported or published. Some manipulative experiments have likewise not been reported.

| Goals | Research methodology[1] | Citations |
|---|---|---|
| Characterize within-pool gradients | | |
| Hydrology | Non-destructive field observations | Bauder, 1987, 1988, 1989a, 1994, 1999, 2005; Bauder and Sakrison, 2001; Bauder, et al., 2009 |
| Soils | Destructive field sampling | Bauder, 1987; Bauder et al., 2009 |
| Species distributions | Non-destructive field observations | Bauder, 1987, 1988, 1989a, 1999, 2000, 2005; Bauder and Sakrison, 2001 |
| Compare pools within one pool type | | |
| Hydrology | Non-destructive field observations | Bauder, 1987, 2000, 2005; Bauder and Sakrison, 2001; Bauder et al., 2009 |
| Species composition | Non-destructive field observations | Bauder, 1986, 1987, 2000; Bauder and Sakrison, 2001; Bauder et al., 2009 |
| Basin morphology/network position | Non-destructive field observations | Bauder, 1987, 1988, 1989a, 2005; Bauder et al., 2009 |
| Describe and compare pool types within the San Diego region | | |
| Geomorphology/origin/age | Non-destructive field observations | Bauder, et al., 2009 |
| Associated soil series | Non-destructive field observations | Bauder and McMillan, 1998; Bauder et al., 2009 |
| Sub-regional climate | Non-destructive field observations | Bauder, 1992, 1999; Bauder and McMillan, 1998; Bauder et al. 2009 |
| Species distributions | Non-destructive field observations | Bauder, 1986, 1992; Bauder and McMillan, 1998; Bauder et al., 2009 |
| Multi-year/long-term monitoring | | |
| Species distributions/ abundances/frequencies | Non-destructive field observations | Bauder, 1987, 1992, 1999, 2000; Bauder and Sakrison, 2001 |
| Hydrology | Non-destructive field observations | Bauder, 1987, 1992, 1999, 2000, 2005; Bauder and Sakrison, 2001; Bauder et al., 2009 |
| Restoration/disturbance | Non-destructive field observations | Bauder, 1988, 1989; Bauder and Sakrison, 2001 |
| Test hypotheses | | |
| Moisture | | |
| Drought stress | Manipulative experiment (field) | Bauder, 1987, 1989b |
| Inundation effects | Manipulative experiment (field) Controlled factorial experiment | Bauder, 1987, 1992; Bauder et al., 2002 |
| Temperature and day length | Controlled factorial experiment | Bauder, 1992, 1999; Bauder et al., 2002 |
| Neighbors | | |
| Upland habitats | Manipulative experiment (field) | Bauder, 1987, 1989b |
| Basin habitats | Manipulative experiment (field) Controlled factorial experiment | Bauder, 1987; Bauder et al., 2002 |
| Dispersal | Manipulative experiment (field) | Bauder, 1987 |

[1] Refer to “***Three Research Methodologies***” under “RESEARCH APPROACHES AND METHODOLOGIES” in the preceding text.