Water (or the lack thereof), management, and conservation of an endangered desert wetland obligate, *Lilaeopsis schaffneriana* var. *recurva*

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Huachuca water umbel, *Lilaeopsis schaffneriana* var. *recurva*, is a federally endangered desert wetland plant restricted to southeastern Arizona, USA, and adjacent portions of Mexico. Very little is known about the factors that influence the species presence, absence, and abundance, including the effects of wetland drying caused by drought or water withdrawals. We conducted three lines of research to address the lack of information about the species' ecology using observational field research and controlled experiments. First, we examined ecological correlates of the species presence and absence along a perennial stream in Southeast Arizona where the species has been established for over a decade. Next, we used a full-factorial experiment to examine the species' drought resistance and drought resilience. Last, we monitored transplanting efforts of the species along the upper Rio Yaqui. We found that distance to the nearest water umbel patch centroid—a measure of historical factors—and distance to surface water were the best predictors of the species' presence and leaf density. The drought experiments demonstrated that leaf density is an important factor influencing both resistance and resilience: low leaf-density was associated with replicates reaching critical conditions approximately one full day before high leaf-density plants, and high leaf-density plants rebounded at nearly twice the rate of low-density plants when water became available. Transplants appeared to be most successful in areas where water levels remained relatively constant, herbaceous-layer competitors were rare, and water velocity was low. These results indicate that protecting existing populations by ensuring stable water sources is the most important action for conserving the species in current locations and future transplant locations.

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Abstract

Huachuca water umbel, *Lilaeopsis schaffneriana* var. *recurva*, is a federally endangered desert wetland plant restricted to southeastern Arizona, USA, and adjacent portions of Mexico. Very little is known about the factors that influence the species presence, absence, and abundance, including the effects of wetland drying caused by drought or water withdrawals. We conducted three lines of research to address the lack of information about the species' ecology using observational field research and controlled experiments. First, we examined ecological correlates of the species presence and absence along a perennial stream in Southeast Arizona where the species has been established for over a decade. Next, we used a full-factorial experiment to examine the species' drought resistance and drought resilience. Last, we monitored transplanting efforts of the species along the upper Rio Yaqui. We found that distance to the nearest water umbel patch centroid—a measure of historical factors—and distance to surface water were the best predictors of the species' presence and leaf density. The drought experiments demonstrated that leaf density is an important factor influencing both resistance and resilience: low leaf-density was associated with replicates reaching critical conditions approximately one full day before high leaf-density plants, and high leaf-density plants rebounded at nearly twice the rate of low-density plants when water became available. Transplants appeared to be most successful in areas where water levels remained relatively constant, herbaceous-layer competitors were rare, and water velocity was low. These results indicate that protecting existing populations by ensuring stable water sources is the most important action for conserving the species in current locations and future transplant locations.

Keywords: Huachuca water umbel, ecology, drought, competition, endangered species

Introduction

Conserving rare species and their ecosystems requires knowing the threats they face. Desert wetlands are among the most endangered ecosystems in the world because water withdrawals for anthropogenic uses have accelerated over the past century, and will likely continue into the future (Hendrickson and Minckley 1984). Numerous wetland species in the U.S. Southwest and adjacent portions of Mexico are protected under state and federal laws specifically because of altered hydrology (e.g., Rio Yaqui fishes [USFWS 1995], Chiricahua leopard frog [USFWS 2002]), with water withdrawals as the primary driver. If regional climate change projections (Seager et al., 2007) are realized, then the threats posed to these species by hydrological changes will be further exacerbated. Understanding the drought ecology of imperiled wetland obligates is needed to devise conservation and management strategies that may allow such species to survive and recover.

The Huachuca water umbel (*Lilaeopsis schaffneriana* var. *recurva* (Hill) Affolter; hereafter, water umbel) is listed as an endangered species under the U.S. Endangered Species Act because of, "degradation and destruction of habitat resulting from livestock overgrazing, water diversions, dredging, and groundwater pumping" (USFWS 1997). The species is known from over two dozen sites in the U.S., including San Bernardino and Leslie Canyon National Wildlife Refuges, sites in Coronado National Forest, along the San Pedro River, and adjacent parts of Mexico (USFWS 2014). Desert wetlands (cienegas) in the region have attracted attention for over a century, but the water umbel has not been studied extensively. Research since Affolter's monograph on the genus (Affolter, 1985) has included the phylogenetic relationships of *Lilaeopsis*, demonstrating the uniqueness of *L. s.* var. *recurva* (Bone et al., 2011, Fehlberg and Allen, 2014), and the threat to *L. s.* var. *recurva* posed by livestock trampling (Malcom & Radke, 2008). But very little quantitative information exists on the basic ecological correlates or requirements of the species. Titus and Titus (Titus & Titus, 2008a,b) examined water umbel monitoring and prospects for reintroducing the species to sites from which it had been extirpated. They found evidence for interspecific competition, negative effects of drought conditions, and general success for transplants as long as drought was not too severe. The same authors also evaluated the seed bank of an historical cienega and showed that water umbel seeds were present and germinated in a greenhouse even though the plant was no longer growing at the site (Titus & Titus, 2009).

Here we address three basic questions about water umbel ecology:

1. What are the ecological correlates of water umbel presence, absence, and abundance in a natural setting?
2. What characteristics of water umbel morphology are associated with variation in the species' drought resistance and resilience?
3. What factors influence water umbel transplant success and failure?

Answering the first question is important to managing habitat conditions that can help improve the conservation status of the water umbel. If overhead canopy is the most important determinant of water umbel presence, absence, and abundance, then local vegetation management may be of first order; if soil saturation is more important, then watershed-level management will be critical. Answers to the second question are needed to know what characteristics to measure in monitoring programs and to inform management targets for the umbel. If leaf density is predictive of resistance or resilience to drying conditions, then measures of leaf density are needed to complement measurements of aerial extent in a water umbel status monitoring program. Third, because the water umbel has already been lost from many sites where it was once found, determining the factors that improve transplant success can help identify the best reintroduction sites. We show that historical factors and distance to surface water are primary determinants of water umbel presence and abundance; that leaf density is a strong predictor of drought resistance and resilience; and transplant success is associated with sites exhibiting stable water levels, low-velocity water, and relatively few herbaceous competitors. We discuss how these results inform management and conservation decisions across the species' range.

Materials & Methods

<u>Study areas</u>

In 2007, Huachuca water umbel occurred in thirteen discrete patches along 100 meters of Leslie Creek in Leslie Canyon National Wildlife Refuge (LCNWR), Cochise County, Arizona, at an elevation of 1,900 m. Most of the extant patches are the result of transplanting that occurred in the mid-1990s from stock collected at San Bernardino National Wildlife Refuge (SBNWR), but no records are available to differentiate transplanted versus natural patches. The riparian canopy of the Creek is dominated by *Fraxinus velutina*, with a few interspersed *Salix gooddingii* and

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Populus fremonti. Understory vegetation includes young *Fraxinus* and *Salix*, but is otherwise lacking. Potential direct competitors of the water umbel include *Rorippa nasturtium-aquaticum* and *Sporobolus giganteus*. Leslie Creek is subject to annual flash flooding, with peak flows of ca. 10,000cfs common, but is also subject to periods of very low water levels during the droughts that characterize the region. Leslie Canyon is deep and steep-walled, but the gradient of Leslie Creek is very low where the water umbel lives.

Huachuca water umbel formerly occurred along Black Draw, SBNWR, but was extirpated by the late 1990s as surface waters receded with a long drought. Restoration work, however, has increased and stabilized the local water table to create conditions that may be ideal for re-establishing the water umbel. The transplant sites at SBNWR all occur in or near Black Draw, the northernmost tributary of the Rio Yaqui, at an elevation of 1,190m. Transplants occurred in a *Populus*-dominated corridor with little understory vegetation and in the shallow portion of a palustrine wetland dominated by a mix of *Typha dominigensis* and *Scirpus americana*. Black Draw, like Leslie Creek, is subject to annual flooding, with peak flows of >10,000cfs. Black Draw is deeply incised and the terrain adjacent to the stream thalweg is relatively steep compared to the areas of Leslie Creek where the water umbel grows.

Ecological correlates

We studied the ecological correlates of the Leslie Creek water umbel population using a systematic-random sampling design. Samples were taken every 10m along the creek from a random starting point near the downstream end of the plant's local distribution. We took three samples perpendicular at distances of 0.1, 0.25, and 0.75m from the water's edge at each 10m point. We visually estimated canopy cover in five directions for each group of three samples: 45 and 135 degrees from horizontal parallel to the stream, 45 and 135 degrees from horizontal perpendicular to the stream, and 90 degrees (directly overhead). That is, we estimated canopy cover for all three samples at a point using five subsamples.

At each of the three points we measured the density of water umbel leaves and any competitors, if present, using a 5x5-cm wire frame. Additionally, we collected a 5cm deep, 1.75cm diameter soil plug and placed it in a Whirl-Pak that we tightly sealed. We returned the soil samples to the lab and massed them to the nearest milligram the same day as the collection. These samples were dried at 52°C for 48h, then re-massed to the nearest milligram. We determined water content by mass by subtracting the dry mass from the wet mass, then dividing by the wet mass.

We hypothesize that history plays a strong role in determining the local patch distribution, but we need to disentangle the roles of spatio-temporal dependency of water umbel presence, absence, and abundance, versus the ecological causes of current variation. To do so, we measured the distance from each sample point to the nearest patch centroid as a surrogate for history. That is, if we assume that patches expand outward from the original transplant location (or a small refuge that survived a drought) as ecological conditions allow, then the closer we are to the nearest patch centroid the more likely water umbel is to be detected. This variable may seem tautological, but the fact that we sampled at sites very near patch centroids that lacked water umbel highlights that informative variation is captured.

We defined eight models to examine the relationship between water umbel densities and the environmental variables (Table 1) before any analysis. These models were constructed based on our observations of the conditions in which the water umbel occurs along Leslie Creek. The distribution of water umbel densities highlights the need to consider the factors that affect both presence/absence and leaf densities (Figure 1). We intended to include potential herbaceous-layer competitors in the models to investigate interspecific competition, but when we attempted to use a zero-inflated negative binomial model to fit both the presence/absence and count components simultaneously to all measured variables, the resulting matrices were singular. The offending predictor variable was herbaceous-layer competitor; we found no strong relationship to water umbel densities and therefore excluded competitor from the models (see Article S1 for a variety of analysis supplements). We compared models using Akaike's Information Criterion, corrected for small sample size (AIC_C; Burnham & Anderson, 2002) using the `AICcmodavg` package (Mazerolle, 2016) for R 3.2.3 (R Core Team, 2015). We calculated the Akaike weights (w_i, for each i^{th} model), to evaluate the degree of support for the models, given the data.

Drought resistance and resilience

During field work with the water umbel we observed that patches or significant portions of patches are often characterized by either high- or low-density leaves. We used a full-factorial experimental design with two treatments to determine if leaf density is an accurate representation of the species' drought resistance (i.e., ability to withstand drying conditions) and resilience (i.e., ability to recover from drought). The first treatment was high versus low leaf density, reflecting the densities observed in the field. The second treatment was the water umbel's condition in each replicate: green, ¼-wilted, ½-wilted, wilted, and dead, with plants considered "dead" when no green coloration was visible. We randomized treatments among the replicates. These treatments resulted in forty replicates in full crosses, including four controls per leaf density treatment.

Water umbel plugs measuring 5x5cm were taken from plants kept in cultivation at the Wildlife Refuge headquarters starting in 2003. Visual inspection of the stock readily revealed two distinct densities among the stocks. We extracted plugs from the stock and randomly assigned each plug to either the high or low leaf-density treatment, then counted all leaves from the replicates to describe those leaf densities. Mean leaf densities = 8 leaves per cm^2 for high leaf density and 2 leaves per cm^2 for low leaf density (see Article S1). We placed replicates in individual 600-mL containers, maintained the experiment outdoors under a sunshade, and randomized placement on shelves daily to avoid any systematic day-lighting or weather bias.

We watered the experimental replicates for three days to ensure that each was well-established, and recorded each plant's condition daily. To test drought resistance, we began withholding water from all replicates (except the eight controls) starting on the fourth day. Water was withheld from each replicate until it reached the pre-assigned critical value for the second treatment. For example, if a replicate was designated as ½-wilted, then water was withheld until the first day that a ½-wilted condition was recorded. The time from experiment initiation until the critical value was reached was the response variable "drought resistance" portion of the experiment.

After the critical condition was reached, we watered each plant daily for fifteen days to quantify recovery from a given drought-induced condition. We recorded the condition—using the same 5-level index used in the drought resistance experiment—of each plant daily. We watered the controls daily throughout the experiment, until the final replicate had reached the 15th day of recovery in the resilience phase of the experiment. Because the resilience portion of the experiment immediately followed the resistance experiment, and because the time-to-critical for individual replicates was staggered, the ending times for the 15-day recovery were staggered as well.

The drought response variable of interest was time-to-critical condition, and the drought resilience response was the rate of recovery. We analyzed the data from both experiments using a general linear model and used AIC$_C$ to evaluate model parsimony (see Article S1). Statistical significance was set at $\alpha = 0.05$.

Transplants

We transplanted fourteen water umbel plugs measuring 7.5x15cm at three locations on SBNWR between 2005 and 2007. We placed four at the “Minckley” site in Black Draw, which is a low-gradient lotic system; seven at the “Twin Overflow” site in Black Draw, which is a higher-gradient lotic system; and three in the “Twin II” site, a palustrine lentic site. We monitored plug conditions weekly for the first month following transplant, and monthly or bi-monthly thereafter. The small number of suitable transplant sites, coupled with the small number of plugs available for transplanting, precluded rigorous quantitative analysis; we therefore examine the outcomes qualitatively.

Results

Ecological correlates

We collected data at 53 points along Leslie Creek in July 2007. Models 4 and 1 accounted for 93% of model selection uncertainty and the remaining six were relatively uninformative (Table 2). Both distance to nearest centroid (presence-absence of the zero-inflated model; Figure 1) and distance to the edge of the creek (count component of model; Figure 2) were informative variables (Table 3). Although canopy cover measures were included in Model 1, the variables were not well-supported in any models. Our second *post hoc* model (“Post-2” in Table 1) was substantially better than Model 4 (Δ AIC$_C$ = 5.02), and the parameter estimates were very similar to estimates weighted by the w_{AIC} for Models 1 and 4 (see Article S1).

Drought resistance and resilience

We conducted the drought resistance and resilience experiments between June and July 2007. All controls for both high- and low-density leaf treatments survived and maintained their condition during the experiment. The interaction model (AIC$_C$ = 79.8) provided a much better fit to the data than the no-interaction model (AIC$_C$ = 153.1). Water umbel leaf density was strongly related to drought resistance ($F_{7,24} = 12.3$, $P = 1.38e^{-6}$): high leaf density conferred over one additional day of drought resistance over low leaf densities ($\beta = -1.5$, SE = 0.46, $p = 0.003$). On average, the pre-assigned critical condition (treatment 2 in *Materials & Methods*) was reached 1.5 d earlier by low leaf density treatments than by high leaf density treatments (Figure 3).

Water umbel leaf density was also directly related to drought resilience. The model with an interaction between leaf density and day of recovery had a substantially better fit (AIC_C = 1394; $F_{6,473} = 102$, $P < 2e^{-16}$) than a purely additive model (AIC_C = 1398.8) or a full interaction model (AIC_C = 1401.5). On average, high density treatments recovered at twice the rate of low density treatments (Figure 4), with the day estimate = 0.108 (SE = 0.015) and the day × low-density term estimate = -0.056 (SE = 0.022, $p = 0.009$).

Transplants

Of the fourteen water umbel plugs transplanted during the study, eleven were extant as of mid-2007 and four showed signs of expansion. The three patches at the Twin II site were apparently out-competed by *Typha* and *Scirpus*, and have disappeared from the site. One of the four 2005 transplant plugs was lost at the Twin Overflow site when soil moisture dropped in association with water flow cessation. Three of four 2007 transplant plugs at the Minckley site and one at Twin Overflow, all on relatively level micro-sites adjacent to slow water (water velocity $\bar{x}$ = 0.01m/s), expanded approximately two-fold. The five remaining Twin Overflow transplants and the one remaining Minckley plug remained alive for several years, but either contracted or never expanded; these patches are on higher-gradient micro-sites and are adjacent to faster-flowing water (water velocity $\bar{x}$ = 0.21m/s). Over the longer term, water umbel transplants were negatively affected by extended drought conditions, herbaceous competitors, trampling by ungulates (*Pecari tajacu*), removed by severe flood events, and buried by sediment loads from floods. By 2015, the transplants survived only at the Minckley site, but had expanded in area occupied.

Discussion

Conserving and managing imperiled species and their ecosystems requires understanding the species' ecology. The Huachuca water umbel, a wetland obligate, is clearly limited in its extent by water availability. Despite this general knowledge, very little is known about the ecology of the water umbel. How much soil saturation is enough? How important are competitors to limiting the species' extent? We used a combination of observational field research, greenhouse experiments, and transplants to fill in some of the gaps in our knowledge about the species.

The results from the observational research suggests two basic filters act on water umbel presence, absence, and abundance. First, the data illustrate the role of history in determining whether the species is present at any given area. On one hand this isn't terribly surprising, but the biology of the water umbel suggests that colonization might be faster. Specifically, the water umbel's primary mode of reproduction is vegetative, but Leslie Creek is not lined by water umbel even though patches are found along a significant portion of the perennial section. The drying and wetting cycles of the creek may drive water umbel patch contractions and expansions. When the water level of Leslie Creek dropped drastically because of extended drought in 2005 and 2006, the water umbel responded by extensive lateral contraction. After 2006, when water levels rose again, the water umbel once again began to spread. This effect is similar to that observed for other riparian species (Stromberg et al. 1996, Busch and Smith 1995), including *Populus* spp. (Rood et al. 2003) and *Carex* sedges (Budelsky and Galatowitsch 2000).

The second filter we observed was distance from surface water. Mean water umbel leaf density declines rapidly over a very short distance as one moves laterally away from the edge of Leslie Creek. While we also observed that soil moisture declines with increasing distance, our soil moisture measurements and water umbel leaf density weren't strongly correlated. We do not know if this is because there is one or more other limiting factors that we did not measure. There was limited support for the hypothesis that herbaceous competitors or the extent of canopy cover explained significant variation in either the presence/absence or the density of the water umbel. Given the regular flooding of Leslie Creek, which could homogenize soil conditions, systematic variation in other limiting resources such as nutrients seems unlikely. Future work should assay the water umbel's growth across a variety of realistic nutrient concentrations to determine the extent to which nutrients can be a limiting factor. If a strong factor, then this work would need to be followed by detailed soil analyses from field sites where the species' presence, absence, and abundance varies over short distances.

Our drought resistance and resilience experiments further refine our understanding of the species' ecology with relation to water. As Titus and Titus (2008a,b) showed in their work, drought patterns are critical to understanding water umbel ecology. Considerable research has examined the physiological and photosynthetic consequences of drought stress (see Chaves et al.

2002 and Chaves et al. 2003 for reviews). The pattern of water umbel leaf senescence observed during the experiments follows the results of Munne-Bosch and Alegre (2004), who describe how senescence aids survival in drought conditions. As the water umbel became drought-stressed, peripheral leaves were the first to begin wilting and witnessing chlorophyll degradation; they may have transferred nutrients to the core leaves and delayed their wilting. The high leaf density treatments likely possessed greater nutrient reserves by virtue of additional leaves, providing a possible explanation of their increased drought resistance and resilience. Hydrological conditions in desert wetlands are critical for many plant species' survival (Busch and Smith 1995), and a variety of adaptations protect individuals against the negative impacts of low water levels (Rood et al. 2003). When water umbel grows in conditions that are better-than-marginal—that is, when water (and presumably nutrients) are readily available, and resultant leaf densities are high—individuals are more resistant to drought. Furthermore, the fact that the water umbel plants recovered from drought conditions twice as quickly at high leaf densities than at low leaf densities underscores the importance of strong growth and establishment. We do not know at this time whether the differences in the low- and high-density water umbels used in the transplant experiments had an effect on their medium- or long-term survival.

Our qualitative analysis of transplants suggests that water permanence is of greatest importance to Huachuca water umbel re-establishment. Several transplant patches were lost when water from a wetland outflow was suppressed, and growth did not resume when water was eventually re-introduced. This finding is in line with the drought experiment, but contrasts with the results of Titus and Titus (2009), who were able to sprout the water umbel from seeds in the seed bank. It may be that our transplants had not yet fruited by the time the artificial drought occurred, and therefore the species was not part of the seed bank. Patches introduced adjacent to slow water appeared to survive and expand, while patches introduced adjacent to faster-flowing water typically survived for a time but did not expand. These transplant results reinforce the idea that soil must remain saturated for the species to survive and expand, but that the details of the water movement may be important.

Although our ecological correlates research did not detect a strong relationship between water umbel presence or density and the presence or abundance of competitors, the transplant experiments suggest a relationship. Patches introduced at lentic sites were consistently out-competed by *Scirpus*, *Typha,* and other herbaceous species. The degree of water umbel exposure to direct sunlight throughout the year also appears to impact survivability. Patches restricted to shaded sites appear to lose viability over time and eventually disappearing, and patches exposed to direct sunlight or mixed shade typically surviving well. Competition among herbaceous-layer waterline species is well documented (see, e.g., Gaudet and Keddy 1995), and is suggested as a potential negative influence on water umbel (USFWS 1997, Zuhlke et al. 2002, Titus and Titus 2008a). Thus, despite the lack of statistical evidence of the interaction, our transplant experiments suggest that competition has a real negative effect on water umbel.

Previous workers have suggested that monsoon-associated flooding is important to the water umbel because such floods disproportionately affect potential competitors (e.g., Stromberg and Tellman 2009). We have made similar observations, and the fact that transplants protected from seasonal flooding appears to have been out-competed provides further support for the proposed relationship of the water umbel to flooding. However, the transplant experiments indicate that flood events can negatively affect the water umbel. Plants that are otherwise thriving can be buried by aggraded sediment and killed, plants can be directly uprooted and relocated downstream, and severe erosion can remove plants from water saturated sites and ultimately deposit them on drier locations where they desiccate and die. Additionally, we have observed water umbel that was uprooted during a severe flood event and subsequently re-deposited at a suitable location downstream, where it survived to root and establish a new population. Additional work is needed to understand the full diversity of the water umbel's relationship to seasonal flooding that is characteristic across its range.

Conclusion

The importance of protecting water sources for conserving and recovering the Huachuca water umbel is well recognized (USFWS 2014). Our research reinforces this conclusion, and suggests that maintaining water levels over extended periods is important because of the role history plays in shaping presence and absence. While small, short-duration events such as trampling by javelina or cattle can have a negative impact on the species, water loss and wide fluctuations likely have a larger impact. In fact, the livestock damage described by Malcom and Radke (2008) was no longer visible along Leslie Creek by late 2008. While competitors may have local negative effects on water umbel, the effects might be managed by transplanting in areas that regularly flood to minimize the establishment of potential competitors (but see below). Because the subsurface (root competition) impacts are difficult to ascertain, the relationship between leaf density and drought resistance and resilience underscores the need to measure water umbel leaf density as a part of monitoring programs because it is predictive of survival in fluctuating environments. Lastly, we propose that using high leaf density plugs for transplants may be preferable to low density plugs because high leaf density plugs exhibit better short-term survival.

Numerous ecological research questions surrounding Huachuca water umbel remain. Although we have observed flowering of the water umbel plugs kept in cultivation (during one season only), what are the environmental conditions that trigger flowering? Rare species buffer ecosystems against non-native species invasion (Lyons and Schwartz 2001) and can be important in wetland resilience to disturbance (Englehardt et al. 2001); does the water umbel assist in these respects? In areas where the water umbel occurs, and where stream flows can be managed, is there a specific flood regime that benefits the species (Richter and Richter 2000)? To what degree does leaf litter from trees along Leslie Creek and Black Draw affect the soil nutrients available to the water umbel, as Andersen and colleagues (2003) investigated in a general sense? Is nutrient deficiency a significant issue for strong growth and development? Answers to these questions can only help with the recovery of this rare desert wetland species.

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Tables

Table 1. Eight models relating predictor variables to *Lilaeopsis schaffneriana* var. *recurva* presence / absence and density using zero-inflated count models.

Model	Description
1	distance to water + soil moisture + canopy PC1 + canopy PC2 + dist. to centroid
2	soil moisture + canopy PC1 + canopy PC2 + dist. to centroid [1]
3	dist. to water + canopy PC1 + canopy PC2 + dist. to centroid
4	dist. to water + dist. to centroid
5	soil moisture + dist. to centroid
6	soil moisture + canopy PC1 + canopy PC2
7	canopy PC1 + canopy PC2
8	can_45perp + can_135perp + can_45para + can_135para + can_90deg [2]
Post-1	soil moisture + dist. to centroid | dist. to centroid [3]
Post-2	dist. to water + dist. to centroid | dist. to centroid [3]

[1] Canopy PC1 and PC2 are the first two principal components of the five riparian canopy measures.

[2] "perp" = measurement perpendicular to Leslie Creek; "para" = measurement on the axis parallel to Leslie Creek; "deg" = measurement 90 degrees (directly over) each patch

[3] Post-hoc models separated the count portion of the zero-inflated model before the vertical bar, |, and the presence / absence portion after the bar.

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Table 2. Model selection results for the eight *a priori* models evaluated, as described in Table 1.

Model	**K**	**AICc**[1]	**Δ AICc**[2]	**Mod Lik.**[3]	**AICcWt**[4]	**logLikel.**[5]
Mod 4	9	151.46	0.00	1.00	0.64	-64.53
Mod 1	15	153.10	1.64	0.44	0.28	-54.69
Mod 3	13	155.83	4.37	0.11	0.07	-60.00
Mod 5	7	174.37	22.92	0.00	0.00	-78.88
Mod 2	11	179.04	27.58	0.00	0.00	-75.14
Mod 7	7	195.17	43.71	0.00	0.00	-89.28
Mod 6	9	195.35	43.89	0.00	0.00	-86.48
Mod 8	13	206.42	54.97	0.00	0.00	-85.29

[1] AIC$_C$ = Akaike's Information Criterion, adjusted for small samples

[2] The AIC$_C$ difference from the best (lowest AIC) model

[3] Unscaled likelihood of the model

[4] Scaled model likelihood

[5] log maximum-likelihood of the model

Figure 1.

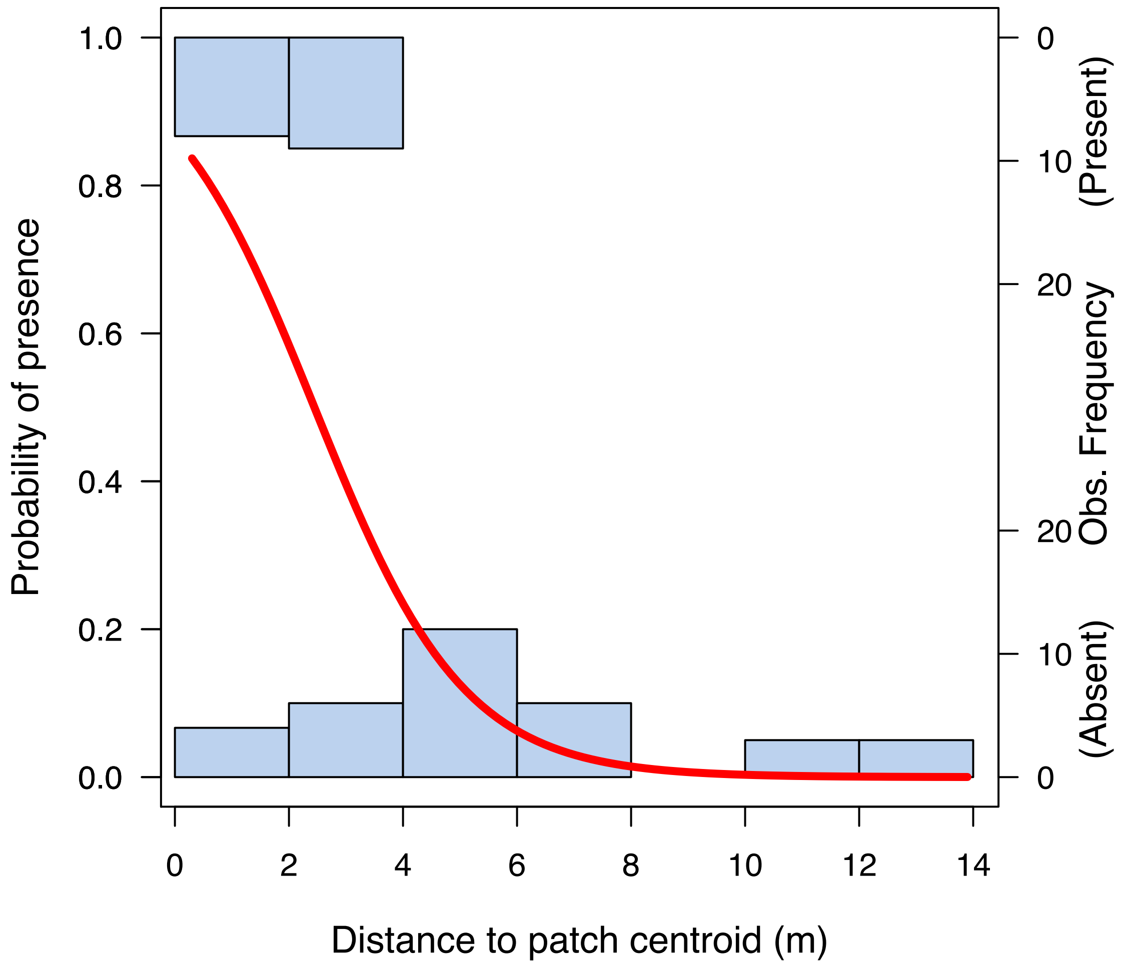

Figure 1. The probability of Huachuca water umbel presence and absence appears to be strongly constrained by history. The probability of occurrence (red line) drops to 50% by approximately 3m from the nearest patch centroid, which likely represents transplant locations from the early-mid 1990s. The histogram bars show the counts of occurrences (top) and absences (bottom) as a function of distance from the nearest patch centroid.

Figure 2.

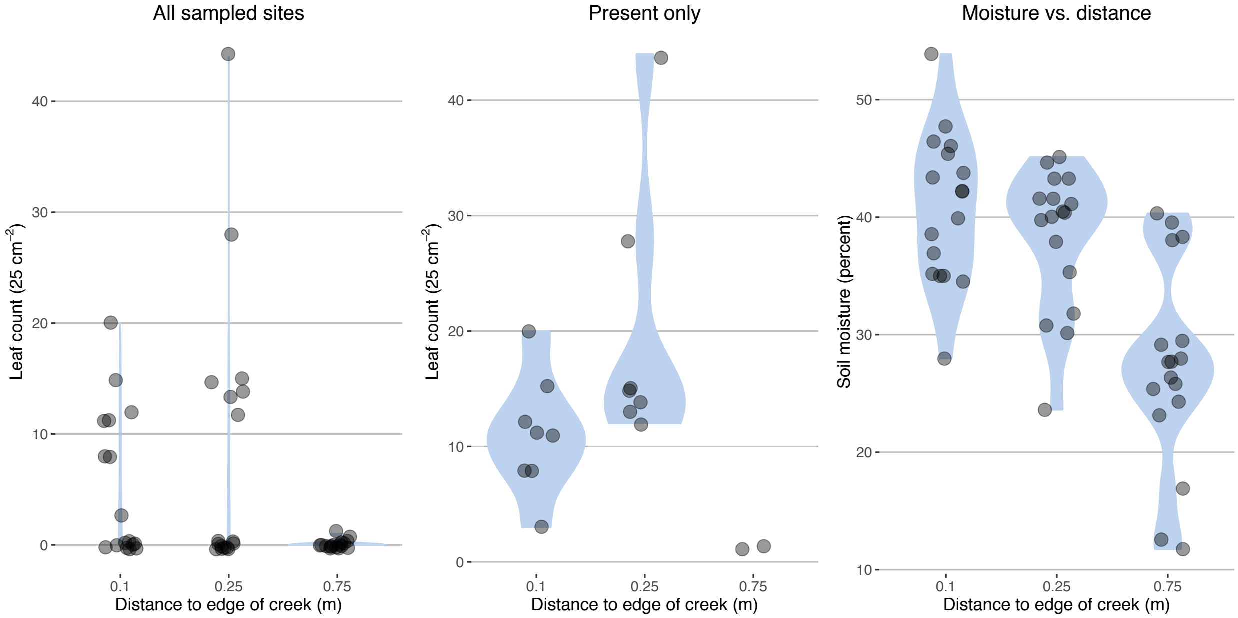

Figure 2. The density of Huachuca water umbel leaves covaries with distance from surface water. The density of Huachuca water umbel leaves peaked 0.25m from the creek (left and center panels) and the distance from the creek corresponds to a strong soil moisture gradient (right panel). The left panel highlights that several sample sites at the water's edge lacked the water umbel, as did almost all sample sites 0.75m from the water. Excluding samples lacking water umbel the relationship to distance from Leslie Creek is a bit clearer. And the left panel shows that soil moisture content covaries strongly with distance from the creek (as expected).

Figure 3.

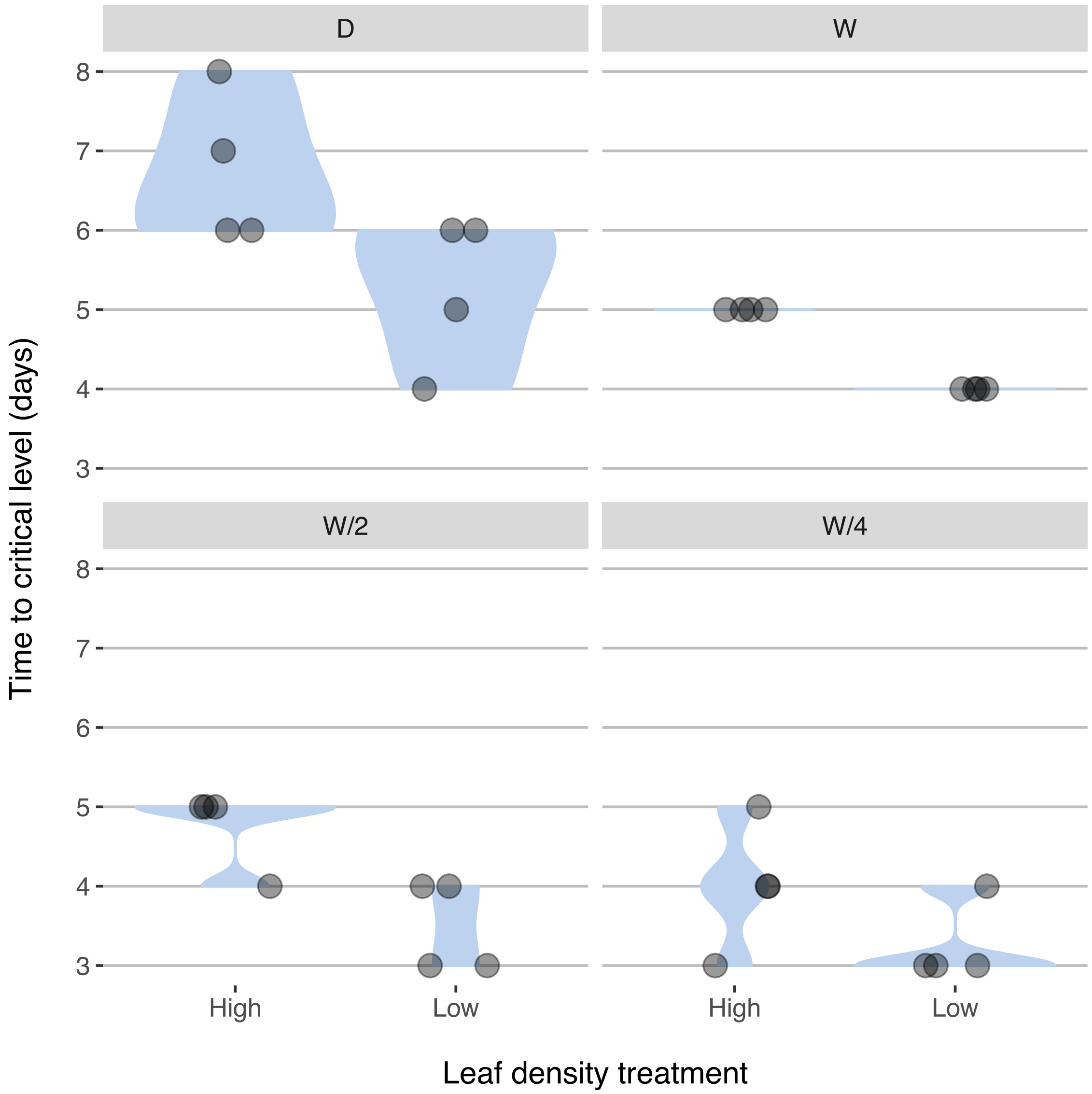

Figure 3. High leaf density confers resistance to drought conditions for Huachuca water umbel. High density Huachuca water umbel reaches apparent leaf death (D), fully wilted (W), and ½-wilted (W/2) conditions significantly later than low-density water umbel, but the time to ¼-wilted (W/4) is similar.

Figure 4.

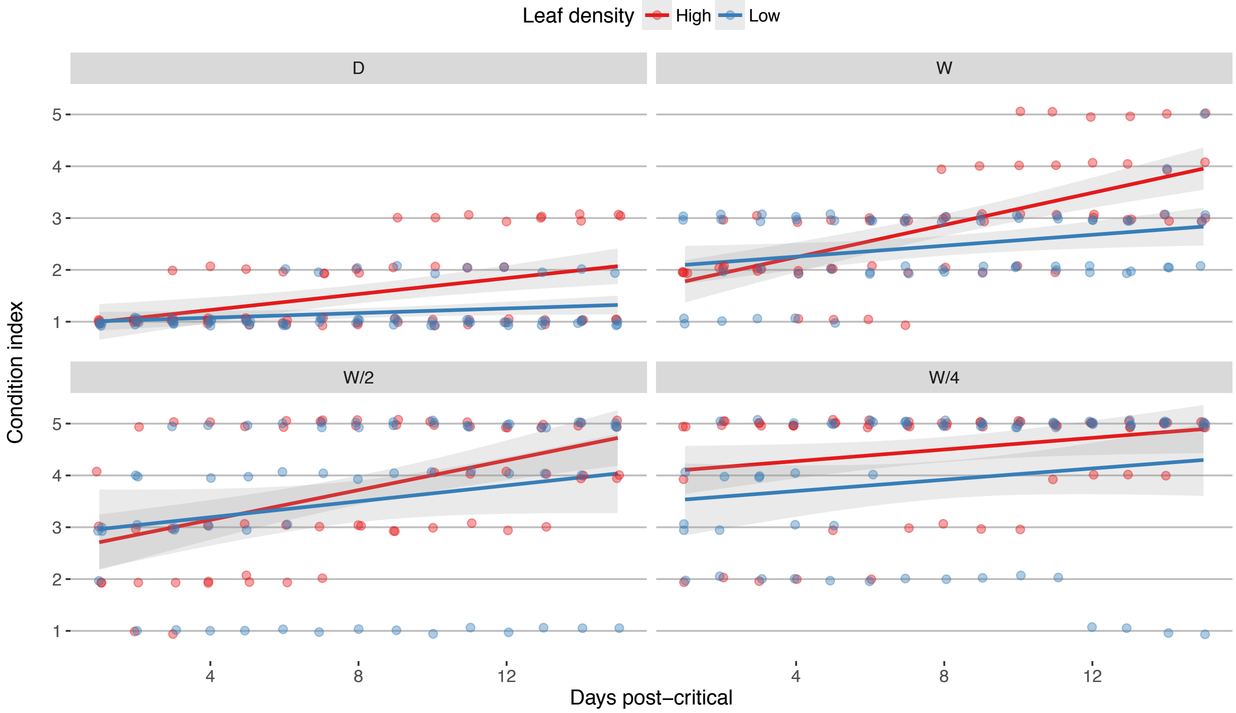

Figure 4. High leaf density confers resilience to drought conditions for Huachuca water umbel. High density Huachuca water umbel recovers significantly faster from apparent leaf death (D), fully wilted (W), and ½-wilted (W/2) conditions low-density water umbel, but the recovery rate from ¼-wilted (W/4) is similar.