Screwbean Mesquite (*Prosopis pubescens*) Die-off: Population Status at Restored and Unrestored Sites in the Lower Colorado River Watershed

by

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ABSTRACT

Die-off of screwbean mesquite (*Prosopis pubescens*), a species native to the American Southwest, has been documented regionally within the last decade. Historical causes for episodic mortality of the more widely distributed velvet mesquite (*Prosopis velutina*) and honey mesquite (*Prosopis glandulosa*) include water table declines and flood scour. Causes of the recent die-offs of *P. pubescens* have received little study. Numerous riparian restoration projects have been implemented regionally that include screwbean mesquite. Restoration propagules from foreign sources can introduce diseases, and low genetic diversity plantings may allow for disease irruptions. I asked: 1) Are die-offs associated with a particular age class, 2) Is die-off suggestive of a pathogen or related to specific environmental stressors, 3) Are mortality influences and outcomes the same between restoration and local populations, 4) Are particular land uses and management associated with die-off, and 5) Are populations rebounding or keeping pace with mortality?

I documented the screwbean mesquite population status at rivers and wetlands in Arizona with varying levels of restoration. I used logistic regression and Pearson correlation analysis to explore mortality response to site factors and disease related variables. I compared mortality response and disease severity between local and restoration populations.

Biotic damage surfaced as the most important factor in statistical analyses, suggesting that mortality was caused by a pathogen. Mortality was greatest for young size classes (3 to 14 cm), and biotic damage was higher for individuals at infrequently flooded areas. Strong differences were not found between local and restoration populations – however restoration populations were less stressed and had lower biotic damage. Novel urban and restored sites may provide refuge as site conditions at other

locations deteriorate. A culmination of past water diversion, development and land use may be surfacing, rendering riparian species vulnerable to diseases and triggering such events as region-wide die-off.

DEDICATION

This Masters thesis is dedicated to my family and friends. First, to my loving parents Michelle and Art Gerardo, whose words of encouragement and continued support has been invaluable to my success in graduate school and life. I also dedicate this thesis to my fellow labmates who provided moral support throughout the process: Dustin Wolkis, Brenton Scott, Danika Setaro, Lane Butler, Amanda Suchy and Frankie Coburn. A special thanks to Lia Clark and Tyna Yost for the many hours of fieldwork assistance, moral support, laughs and adventures in the field. And lastly, thank you to my good friends for their encouragement and support through my many career changes and educational endeavors: Pat Garcia, Teresa Miro Martin, Matthew Clark, Gwynne Sullivan, Shay Albert, Kendra Wake, Estela Dimas, Eugene Young and Dr. Veysi Demir.

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INTRODUCTION

Large-scale regional die-off of screwbean mesquite (*Prosopis pubescens*), a species native to the American Southwest, has been documented at numerous localities (Anderson 2007; Foldi 2014). The first accounts of mortality were documented in 2005 along the Lower Colorado River at the Goose Flats area, near Blythe, California. Tree health declined rapidly after 2-3 months following the onset of yellowing leaves and dead branches, and many trees died within a year (Anderson 2007). An unknown pathogen was suspected, as healthy individuals of other riparian tree species were growing alongside afflicted screwbean mesquite, with the exception of reduced vigor among tamarisk (*Tamarix chinensis*) at a few locations. A similar pattern has been noted along the Lower Gila River (from the Quigley Wildlife area to the confluence of the lower Colorado and Gila rivers), Cienega de Santa Clara and adjacent playas in Sonora Mexico (Linden Piest, 2014, AZGFD, personal communication). Populations in southeastern California, however, appeared to be unaffected (Linden Piest, 2014, AZGFD, personal communication). Recent surveys have documented a 53 percent reduction of screwbean mesquite's former range (Foldi 2014).

Our general understanding of tree die-off among desert riparian systems is limited. Riparian tree mortality is a complex process that can result from many interacting abiotic (e.g., water stress, heat stress, flood scour, anoxia) and biotic factors (e.g., root structure, senescence, herbivory, disease) (Shafroth et al. 2000; Baird et al. 2005). A culmination of seemingly unimportant factors (e.g., injuries) can predispose trees to disease-causing agents (Franklin 1987). Forest stand-level die-off can be gradual, sudden or in stages brought on by fluctuation in site factors (Franklin et al.

1987). Episodic die-off or 'pulses' of mortality have become more apparent for some tree species in the Southwest (Bowers & Turner 2001). The ability for populations to rebound and keep pace with mortality depends on the rate of regeneration and key processes (e.g., flood scour events, soil wetting) that create suitable regeneration niches (Stromberg 1993).

Pioneer riparian vegetation at the Lower Colorado River and Lower Gila River, where *P. pubescens* reached its greatest abundance regionally, relied heavily on periodic flooding to flush salts from the river channels, create seed beds for establishment and regenerate populations (Busch & Smith 1995; Howe & Knopf 1991; Lytle & Merritt 2004). The low reproduction and dominance of senescent stands among riparian vegetation at these rivers today are the direct result of flood control measures (Friedman & Lee 2002). Senescent populations are generally more susceptible to stand-level die-off owing to their reduced ability to combat insect and disease outbreaks (Franklin et al. 1987).

Climate change in the Southwest is causing increasing aridity and reduced surface flow and groundwater recharge (Seager et al. 2007). Urban expansion is placing more demands on rivers through water withdraws and may increase disease incidence through "pathogen corridors" from nearby land use (Meentemeyer et al. 2012; Tubby & Webber 2010). The increase in transport of biological material globally poses challenges for species, increasing the probability of disease epidemics (Burdon & Chilvers 1982). It is not uncommon for parasites to drive host populations to very low numbers, but over long periods of time parasites and host populations oscillate, ultimately reaching quasi-equilibrium (Burdon & Chilvers 1982). The past century of water control measures and land management decisions may have placed many pathogen-host dynamics in disequilibrium among desert riparian areas (Meentemeyer et al. 2012).

Numerous riparian restoration and mitigation projects (revegetation for wildlife habitat), including several with screwbean mesquite plantings, have been conducted in the American Southwest. At the Yuma East Wetlands along the Lower Colorado River, *P. pubescens* is abundant within habitat planted for threatened and endangered species protected by the Lower Colorado River Multi-Species Conservation Program. The Rio Salado Monitoring and Adaptive Management Plan for the urban Salt River identifies screwbean, honey and velvet mesquite as useful adaptive management species – targeted species for habitat if site conditions deteriorate, such as increased salinity and decreased flows (Rio Salado 2007). A large dense screwbean mesquite grove was installed by the Army Corps of Engineers along the Salt River just west of Tempe Town Lake where stormwater provides near perennial flows.

Depending on site conditions, replanting alone may not be sufficient in establishing riparian vegetation. In Arizona, only one out of six riparian restoration projects with planted vegetation dependent on irrigation experienced a survival rate greater than 20 percent (Briggs 1996). Understanding the causes responsible for site deterioration and adopting recovery plans aimed at improving conditions are paramount for successful restoration. Recovery plans or restoration that promotes self-sustaining ecosystems by restoring processes that encourage natural recruitment, establishment and regeneration, are more sustainable over the long term (Briggs 1996). Restoration plantings or propagules should be carefully selected because populations from one location may introduce unfamiliar localized diseases or pests to another (Briggs 1996). Also, the degree to which remnant and restoration-planted populations are susceptible to pathogen-related mortality may differ.

The objectives of this research were to examine *P. pubescens* population status and site conditions at rivers and wetlands regionally in Arizona. Specifically, I address the following research questions: 1) Are die-offs associated with a particular age class, 2) Is die-off suggestive of a pathogen or related to specific environmental stressors, 3) Are mortality influences and outcomes the same between restoration and local populations, 4) Are particular land uses and management associated with die-off, and 5) Are populations rebounding or keeping pace with mortality?

MATERIALS AND METHODS

Study sites

I selected seven study sites within central and southern Arizona along major rivers and wetlands to capture the range of conditions in which *P. pubescens* is found (Figure 11). Populations were sampled at riverine and lacustrine (seasonally flooded depressions, created and spring-fed wetlands) habitats. Study sites and populations were also selected by the level or degree of restoration. "Low restoration" sites were sites with little to no active restoration (i.e., wildland locations). "Moderate restoration" sites were sites where restoration activities such as revegetation were implemented, but were generally limited in scope. "High restoration" sites were areas where restoration such as extensive earthmoving and ongoing management (irrigation, intentional flooding, etc.) has been implemented.

Identified in the field, patches represent an age cohort or population growing in a distinct environment, paralleling the river channel or wetland. Within each study site, I sampled one to three patches or populations that differed in apparent age (size) and fluvial setting for a total of 21 populations.

Trees were also classified by population source (restoration-planted or local), based on local knowledge (land managers, expert opinion). To explore differences within populations I classified plants as either restoration volunteers or local volunteers. Identified in the field, volunteers were trees that had recently established from either local or restoration seed sources. For example, restoration such as earthmoving at Yuma East Weltands resulted in many *P. pubescens* volunteers from seeds already at the site – therefore these trees were classified as local volunteers. Other sites where volunteers established and the surrounding trees were predominately restoration plantings, trees were classified as restoration volunteers.

The Lower Colorado River

Downstream from the Hoover Dam, the Lower Colorado River flows from Bullhead City south 280 miles to the Mexico-U.S. border near San Luis, Arizona. Historically, high sediment erosion and deposition occurred across the alluvial valley as a result of large spring-to-summer flooding, creating a series of terraced bottoms that supported large expanses of mesquite bosques and other riparian vegetation (Ohmart et al. 1988). With the construction of the Hoover Dam, flooding (magnitude and timing) and fluvial processes were practically eliminated from the Lower Colorado River. Today, water sources from incidental releases and unlined canals provide perennial flows for riparian vegetation from the Hoover Dam to the Imperial Dam (Webb et al. 2007). Tamarisk, arrowweed and mesquite (*P. glandulosa*) are abundant along many reaches of the river, while willows and cottonwoods are rare. Historically, *P. pubescens* was locally abundant at many reaches of the Lower Colorado River.

Study Site 1. Goose Flats area (the Lower Colorado River)

Goose Flats is one of a number of revegetation projects that have been conducted along the Lower Colorado River. As part of a mitigation project, revegetation was conducted in 2008 at the Goose Flats area along the river just outside Blythe, California. Rows of screwbean mesquite were planted using seeds and cuttings from local populations and irrigated for three growing seasons. At two locations, marsh habitat was created by digging a depression to the water table – palms, cottonwood, Goodding willow, sandbar willow and screwbean mesquite all grew as volunteers (Bert Anderson, 2015, personal communication). Three populations were sampled: restoration plantings (lcr 1) and restoration volunteers (lcr 2) at marsh habitat, and local remnant at a first terrace along the main channel of the Lower Colorado River (lcr 3).

Study Site 2. Yuma East Wetlands (the Lower Colorado River)

Restoration of local wetlands along the Colorado River near downtown Yuma, Arizona, began as part of a partnership among the City of Yuma, the Quechan Tribe, Yuma Crossing National Heritage Area, Arizona Game and Fish Commission, and other federal agencies. Yuma East Wetlands consists of 373 acres of restored habitat that abuts the confluence of the Gila and Lower Colorado rivers. Restoration began in 2004, supported by grants from the Arizona Water Protection Fund and Reclamation. Extensive salt cedar stands were cleared. Fallow agricultural land was replaced by backwater, marshes and sheet-irrigation to restore riparian forests. Screwbean mesquite was planted at sheet-irrigated terraces near banks and grew as volunteers at the north channel restoration site at flood-irrigated cells.

Heavy equipment, such as backhoes and bulldozers, were used for pushing earth. Native plant cuttings were collected by hand and propagated. Salt cedar was removed on site, chipped and used as groundcover throughout the area. Planting sources were collected locally, including bulrushes, cottonwoods, willows and native salt grass (plugs or poles). Honey mesquite (*P. glandulosa*) was the most commonly planted mesquite species.

In 2013, the Lower Colorado River Multi-Species Conservation Program joined the restoration partnership to support long-term management of the Yuma East Wetlands. The Yuma East Wetlands are in close proximity to the Pacific Flyway, an important migratory route for threatened and endangered species, such as the Southwestern Willow Flycatcher and Yellow-billed Cuckoo. Many regionally endemic and sensitive species have also been confirmed using the restored cottonwood-willow habitat types in the area. Three populations were sampled: two local volunteers at a large flood-irrigated cell (yew1) and along a pond edge (yew2), and restoration plantings along a drip-irrigated terrace (yew3).

The Gila River

Historically, the Gila River had intermittent flows, with flows being present during the spring months from melting snow in the upper basin and again in later summer from monsoonal rains. In 1921 water was diverted for agriculture and flows were suppressed to prevent flooding following the construction of the Gillesipe and Painted Rock Dams. Much of the Lower Gila River has undergone dramatic riparian vegetation change – most reaches now flow only in response to precipitation or when waters are released from upstream dams (Webb 2007).

Study Site 3. The Gila River, near its confluence with the Lower Colorado River

Irrigation returns (flows from the Mohawk Irrigation District) support riparian vegetation from the confluence of the Gila and Lower Colorado rivers east to Wellton, Arizona. In 1993, wet winter storms produced large statewide floods. 2.8 million acre-feet of water filled the Painted Rock Reservoir resulting in the highest flood level since 1961, producing large floods along the Lower Gila River. As a result, screwbean mesquites established 20 miles east of the confluence of the Gila and Lower Colorado rivers near Wellton, Arizona, and have since attained very large size. The river is moderately channelized and nearby land use in the area is primarily agricultural. All populations sampled were from local sources: a recent recruit at the river bottom (Gila 1), and two at higher terraces (Gila 2 and Gila 3).

The urban Salt River

Historically, the Salt River flowed westward through bedrock canyons (Upper Salt River) to its confluence with the Verde River where it flowed in a meandering fashion downstream through the Phoenix Valley with a floodplain reaching widths as great as 80 km (Graf 2000). Following a century of water diversion and control measures and urban expansion, the Lower Salt River in the Phoenix area is now a narrow, highly channelized river. While water control measures upstream have almost completely eliminated flows downstream, occasional releases (floods: 1978, 1993), dam failures (Tempe Town Lake), stormwater runoff and the decision not to dam the Verde River have all supported riparian vegetation in an otherwise dry channel bed.

Study Site 4. Urban Salt River – Rio Salado Restoration Priest, Tempe, Arizona

Assemblages of plants have established at a number of reaches along the urban Salt River, usually located near stormwater outfalls (Stromberg et al. 2015). The perennial supply of water near Priest Road in Tempe is a result of re-routed and combined stormwater following the construction of Tempe Town Lake. As part of the Tempe Rio Salado Restoration Project, the U.S. Army Corps of Engineers planted a number of screwbean mesquite along the channel bed and at high terraces just west of Tempe Town Lake. Recent studies indicate high recruitment of screwbean mesquite at this location (Stromberg et al 2015).

Study Site 5. Urban Salt River – Rio Salado Habitat Restoration Area, Phoenix, Arizona

The Phoenix Rio Salado Habitat Restoration Area (between 19th Avenue and 24th Street) includes five miles of the urban Salt River just south of downtown Phoenix. Wetland ponds, drip-irrigated terraces and low flow channel stabilization were installed in 2005 by the City of Phoenix and the U.S. Army Corps of Engineers. The following vegetation complexes were installed: cottonwood/willow, mesquite bosques (velvet, honey and screwbean), wetlands (including aquatic stands), lower Sonoran mesquite, lower Sonoran palo verde and shrubs (salt, quail, and burro bush) (Rio Salado 2007). Stormwater outfalls provide significant intermittent to perennial flows throughout the area. All populations at this site were established from planted-restoration sources: two along artificial ponds along the low flow channel at 7th Street (Rio 1) and Central Avenue (Rio 3) and another at a drip-irrigated terrace at Central Avenue (Rio 2).

Study Site 6. Quitobaquito Springs, Organ Pipe Cactus National Monument

Located at the U.S.-Mexican border (near Lukeville, Arizona), Quitobaquito Pond is a flat-bottomed pond of 0.22 hectares by 1 meter deep that supports wildlife, riparian vegetation and the endangered Arizona pupfish, *Cyprinodon macularius* (Fisher 1992). Water feeds the pond from nearby springs originating from Quitobaquito Hills in the Organ Pipe Cactus National Monument. Abundant healthy screwbean mesquites have been documented at Quitobaquito Pond, with their status unknown today (last surveyed 1991, SEINet). All populations at this site were established from remnant/local sources: one along the main pond (Quito 1), two at a secondary channel/stream feeding main pond (Quito 2, Quito 3) and another along a gently sloping alkali bed about 40 meters higher in elevation from the main pond (Quito 4).

Study Site 7. Gilbert Riparian Preserve, Gilbert, Arizona

Located at Guadalupe and Greenfield Roads in Gilbert, Arizona, The Gilbert Riparian Preserve at Water Ranch was developed to increase groundwater recharge (using reclaimed water), provide habitat for wildlife and create recreational opportunities. The 110-acre wildlife habitat, installed in 1999, is the second wastewater storage site the Town of Gilbert created. It attracts thousands of visitors annually. In addition to the Riparian Preserve, the Water Ranch has a library, fishing lake, park, fire station and water treatment plant. There a total of seven 10-acre storage ponds that are designed to mimic wetlands while also recharging groundwater sources. Fourteen different habitat areas support a variety of wildlife. Populations from this site were restoration-plantings: two sampled at pond/wetland edges (Gilbert 1, Gilbert 2).

Data collection

Prosopis pubescens population structure

For patches of relatively small size (less than 100 meters), starting at one end, walking the length of the patch, every encountered tree was sampled until reaching a goal of 20 trees. For larger patches, the area was divided into four 30-meter sections, using meter tape laid parallel to the length of the patch. Five trees were randomly sampled in each section, to reach a goal of 20 trees. To assess the population structure of *P. pubescens*, stem diameter was measured at 10 cm up from the base of the trunk (due to branching nature) for each tree (dead or alive) per patch. Trees were grouped into size classes that represent broad demographic life stages: seedling/sapling (0.5-2 cm), young (3-14 cm), mature (15-30 cm) and old (31-45 cm).

Health status

To assess the health status, a score was assigned for each tree to describe healthy, stressed and dead individuals. A score of 1 represented dead trees with no signs of leafing out and with dead stems greater than 90% (brittle branches). A score of 2 represented highly stressed individuals with significant yellowing and wilting (> 60%), signs of damage and significant branch pruning (very few branches leafing out). A score of 3 represented individuals with poor health: significant leaf yellowing and wilting (> 30%), signs of damage and branch pruning. A score of 4 represented moderately healthy individuals with few yellowing or wilting leaves (< 10%), and with a slightly stunted growth form or shrub-like appearance. A score of 5 represented individuals with very little signs of damage (leaf wilting or yellowing). A score of 6 was the highest health score and represented individuals with little to no signs of damage (physical and biotic; < 5%), having healthy leaves of a bluish-green color, with no wilting or yellowing, with well-developed canopies.

Physical tree factors

Physical tree factors measured included physical and biotic damage (presence of biological wounds and insects). Biotic damage scores ranged from 1 (low; < 5%) to 3 (high; > 60%) and physical damage scores ranged from 1 (low; no damage) to 3 (high; large cuts, tree uprooted, broken stems).

Soil factors

Two composite soil samples were collected at the soil surface to a depth of 5 cm near the trunk of adult *P. pubescens* trees (randomly selected) per patch/population. Soil samples were sent to a local analytical laboratory to obtain information on EC (Electroconductivity) and pH. EC measures the conductance of liquid in a sample and is influenced by the concentration and composition of dissolved salts. Gravimetric soil analysis was also conducted at ASU to obtain information on soil moisture.

Data analysis

Data reduction

Scores for biotic damage, physical damage and health status were averaged by population level, resulting in a continuous interval range used for statistical analysis (logistic regression and Pearson correlation analysis). Health scores were also collapsed for descriptive purposes (e.g., to show health status by size class categories): dead (1), stressed (2,3) and healthy (4,5,6). Populations were classified by the frequency (2 levels: frequent and infrequent) of high water flows to explore the effects (positive or negative) of disturbance on mortality. To assess the broad landscape pattern of water availability at sites, populations were classified by the estimated frequency (2 levels: frequent and infrequent) of soil water present in the root zone. Only size class 2 was present at all sites, and therefore the only size class used in the Pearson correlation analysis and logistic regression analysis. Correlation between land use (urban, agriculture/cultivated and wild) and its influence on disease severity and mortality is explored descriptively due to the small sample size and lack of replication.

<u>Logistic regression</u>

Logistic regression using the beta regression model proposed by Cribari & Ferrari (2004) was used to model mortality response (percent mortality). The beta distribution can take on various shapes depending on the combinations of parameter values that index the distribution, resulting in a flexible model that naturally incorporates heteroskedasticity or skewness in the data. The beta regression model allows for stronger statistical inference among small datasets, specifically proportional data, where traditional Gaussian-based approximations for hypothesis testing can lead to misleading inferences (Cribari & Ferrari 2012). A set of models were constructed to determine which set of variables (soil, water and physical tree factors) were most correlated with mortality response (percent mortality by population); a full saturated model containing all variables, a nested model containing only soil and water factors and another nested model containing only physical tree variables. Soil and water-related variables included percent soil moisture (surface soil), frequency (frequent and infrequent) of soil water present in root zone, frequency (frequent and infrequent) of high water flows, EC (dS m^{-1}) and pH. Physical tree variables included biotic damage score and physical damage score. All statistical analyses, logistic regression and Pearson correlation analysis, were conducted using R, version 3.2.1.

<u>Recruitment index</u>

Little is known regarding the recruitment processes for *P. pubescens*, therefore the weighted recruitment index is used to measure active recruitment and approximate the regeneration potential among populations. More weight is given to seedlings and saplings (a) and small trees (b) than to midsize (c) and old (d) trees to express recent recruitment. The weighted sum among size classes is then divided by the total trees per population to obtain the final recruitment index (proportion) per population:

$$Recruitment\ Index = \left(\frac{a(.75)+b(.15)+c(.05)+d(.05)}{n}\right)$$

RESULTS

Question 1: Are die-offs associated with a particular age class?

A chi-square goodness-of-fit test indicated that die-offs were not equal among size classes, X^2 (6, N = 369) = 79.65, $p < 0.05$. Size class two (young individuals, 3-14 cm in diameter) was the group with the highest mortality (19%), followed by mature (11%) and then seedlings (5%). Mortality was not present among old individuals (Figure 3). Size class two was the most dominant and only size class present at all sites (Figure 1). Among sites, mortality followed similar distribution with the exception of Goose Flats where mortality was higher for mature trees – however, this size class was poorly represented (less than 10 trees) compared to young individuals (Figure 3). Seedling mortality was only present at Priest, most likely attributed to recent flood damage for some trees. With the exception of Goose Flats, seedlings were healthy at all sites (Figure 3).

Question 2: Is die-off suggestive of a pathogen or related to specific environmental stressors?

There was a positive correlation between biotic damage and mortality, indicating that trees with a high severity of biotic damage had higher mortality (Table 5). For size class two, biotic damage varied among sites from 1.0 (Gilbert Riparian) to 2.1 (Quitobaquito Springs). The highest score for an individual population was at the Gila River at 2.83 (Appendix 1). While the strength of association was not high, there also was a positive correlation between physical damage and biotic damage, indicating that trees with high physical damage had a higher severity of biotic damage (Table 5).

<u>Logistic regression analysis</u>

In the full model, high water flows, biotic damage and physical damage were all significant. In the nested soil and water model, only high water flows and pH were significant. In the nested tree model, both biotic damage and physical damage were significant (Table 4). While Pseudo R-squared was nearly equal between the soil and water model and tree model, the tree model did have a lower AIC_c value (i.e., better fit of the data).

<u>Physical and biotic damage</u>

Physical and biotic damage were significant in both the full and nested tree models. While physical damage was significant in the regression, the coefficient was negative indicating high damage among populations with low mortality. Also, while physical damage was not statistically correlated with mortality, $r = -0.17$, $p > 0.10$, it showed the same relationship, evident by the negative coefficient (Table 5). While physical damage was not correlated with mortality, it was negatively correlated with health status. In other words, highly stressed individuals had high physical damage (Table 5). However, this was only the case for size class two (Table 6). In a separate analysis an interaction between physical damage and biotic damage was modeled, however the interaction was not significant.

<u>EC</u>

EC was negatively correlated with mortality but was not statistically significant in logistic regression analysis. The negative correlation between EC and mortality suggests low EC values to be correlated with high mortality going against the expected trend. Only three observations had EC values greater than 10.6 dS m^{-1} and mortality for these populations was less than 10 percent, whereas a majority of observations with EC values less than 3 dS m^{-1} had mortality ranges from 0 to 67 percent (Figure 6). EC values ranged from 0.25 dS m^{-1} to 13 dS m^{-1} with a mean EC value of 3.4 dS m^{-1} and 79 percent of the values were less than 5 dS m^{-1} (Figure 6).

pH

pH was positively correlated (Pearson correlation) with mortality. The variable was not statistically significant in full logistic regression model, but was significant in the nested tree model (Table 4). pH values ranged from 7.3 to 8.8 with a mean pH value of 8.2. While pH was positively correlated with mortality, there were a number of observations with low mortality at mid to high pH values (Figure 6).

High water flows

The high water flows variable was significant in both the full and nested model (soil and water). Trees experiencing infrequent high water flows had higher mortality values but only represented data above the third quartile or 25 percent of the data (Figure 7). Median biotic damage was much higher for trees at infrequent high water flows. Half of the observations for trees at infrequent high water flows, data above the second quartile, had higher biotic damage than all trees at frequent high water flows (Figure 7). Health status followed a similar trend – trees at infrequent high water flows had higher stress (Figure 7, Figure 8).

Question 3: Are mortality influences and outcomes the same between restoration and local populations?

Differences between restoration and local populations

While restoration and local populations had nearly equal mortality, restoration populations were less stressed and had slightly less biotic damage than local populations (Table 7). The same trend was observed for all size classes with the exception of size class one where local trees were slightly healthier and had less biotic damage than restoration trees (Table 8). Mortality distribution among size classes was similar for restoration and local populations (Figure 4). In particular, both had higher mortality among size class two. Only restoration populations had mortality among size class one (seedlings) – many caused from recent flood damage at Priest. However, of note, with the exception of seedlings, stress was notably higher among local populations (Figure 4).

Differences between volunteers and established individuals

With the exception of slightly higher health scores among local volunteers, strong differences between established trees and volunteers were not detected within restoration and local populations (Table 7). Mortality was nearly equal for both volunteers and established trees among local sources, whereas volunteers had higher mortality (23 percent) compared to established trees (13 percent) among restoration sources. Perhaps more importantly, biotic damage was not significantly different between established trees and volunteers for both restoration and local populations (Table 7).

Question 4: Are particular land uses and management associated with die-off?

Land use

Overall, trees at urban locations were the healthiest and had the lowest severity of biotic damage (Table 1). On average, Priest had the healthiest trees followed by Yuma East Wetlands, then Gilbert Riparian Preserve and lastly Rio Salado (Table 2). Trees at agricultural sites had the second healthiest trees on average with the healthiest at the Gila River (Table 1, Table 2). Quitobaquito Springs was the only wild sampled population and had the highest stressed individuals (i.e., low health scores) and severity of biotic damage. While trees at Quitobaquito Springs had the highest stress and severity of biotic damage, mortality was actually higher for trees at agricultural areas (Table 1).

Active restoration

Sites were also classified by the degree or level of active restoration. Low restoration describes sites where little or no active restoration is occurring. Moderate restoration describes restoration activities such as revegetation but is generally limited in scope. High restoration describes restoration where extensive earthmoving and ongoing management (irrigation, intentional flooding, etc.) has been implemented (Table 2).

Trees were healthier and had less biotic damage where active restoration is high (Yuma East Wetlands, Gilbert Riparian and Rio Salado). The exception to this was Priest, where restoration is moderate and tree health was the highest. Interestingly, both Priest and Goose Flats have moderate levels of restoration. However, trees at Priest were much healthier than those at Goose Flats. On average, where restoration is nonexistent or low trees had higher stress and severity of biotic damage.

Question 5: Are populations rebounding or keeping pace with mortality?

Potential regeneration

A majority of populations had recruitment indices between 10 and 30 percent, indicating that seedlings and young individuals are well represented among a number of populations. Only three populations (Gila River, Yuma East Wetlands and Priest) had recruitment indices greater than 30 percent. These populations were also the healthiest on average (Figure 9). Populations at Quitobaquito Springs and Gilbert Riparian Preserve had the lowest recruitment indices (Figure 9).

Restoration versus local sources

Eight out of eleven (72 percent) restoration populations had both high health scores and moderate to high recruitment indices. In contrast, only four out of ten (40 percent) local populations were healthy, and only half, or 50 percent of these, had high recruitment (Figure 9).

Spatial pattern of die-off and health status

Mortality does not appear to follow a point origin spread (Figure 11). Die-offs were first noted to occur at the Lower Colorado River near Blythe, California (Goose

Flats). While the severity of die-off was greatest at Goose Flats, both Quitobaquito Springs and Goose Flats (> 150 miles between sites) had a significant number of stressed individuals that shows a similar die-off pattern to those at the Lower Colorado River sites.

DISCUSSION

Biotic damaged surfaced as the most significant variable in the full and nested regression models, indicating that biotic damage has a high “explanatory” power compared to the other variables. Physical damage was the least “important” variable as it was not directly correlated with mortality (Pearson correlation) and the regression coefficient suggested populations with high physical damage had lower mortality incidence (i.e. did not follow ecological realism). While the frequency of the high water flows variable was statistically significant in both the full and nested models, the influence on mortality was low compared to biotic and physical damage (i.e. lower T-ratio compared to biotic and physical damage). Taken all together, these findings support a disease or pathogen as a likely agent of region-wide *P. pubescens* die-off.

On average, restoration populations were healthier than local populations and had slightly less biotic damage. Although restoration volunteers had higher mortality than planted trees, overall there were no significant differences between established trees (remnant and planted) and volunteers.

Urban sites had the healthiest trees and lowest severity of biotic damage. Agricultural areas and wild areas had moderate and high stress levels, respectively. Areas where active restoration is moderate (revegetation, planted trees without irrigation) tree health and biotic severity varied between sites. In areas where active restoration is high (Yuma East Wetlands, Rio Salado), trees had consistently higher health status and lower biotic severity than areas with low restoration.

Question 1: Are die-offs associated with a particular age class?

Contrary to expectations of mortality being higher for seedlings and old individuals, mortality was the highest for mid-size or young individuals. The type of disease and age of the plant can have strong influences on mortality outcomes (Burdon &

Chilvers 1982), and it may be that seedlings and old individuals are out of the "window of vulnerability." Also, if a pathogen is acting on populations, sites with low mortality and high stress (Quitobaquito Springs) may represent early "invasion" stages where effects have yet to manifest.

Question 2: Is die-off suggestive of a pathogen or related to specific environmental stressors?

Biotic damage (Figure 12) was detected at all sites and was found to be highly significant in all statistical analyses. Biotic damage was also the most influential (high T-ratio value) in logistic regression analysis. While both physical damage and biotic damage were statistically significant in both the full and nested tree model, biotic damage had a higher influence on mortality response than physical damage among the nested tree model, evident by the higher T-ratio (Table 4).

Physical damage was the least "meaningful" variable in the logistic regression analysis for several reasons. The coefficient for physical damage in the regression on mortality did not follow ecological realism (i.e. low mortality was observed among trees with high physical damage). Also, physical damage alone was not statistically correlated with mortality (Table 5). And lastly, physical damage included trees uprooted from flood damage, mechanical cuts and broken branches; therefore, physical damage did not always result in direct mortality.

Mean EC values were found to be low (3.4 dS m^{-1}) with 79 percent of data below 5 dS m^{-1}. Only much higher salinity values, approaching 94 dS m^{-1}, have been documented to cause reduced growth and survival of *P. pubescens* (Jackson et al. 1990). While the variable was statistically correlated with mortality, the negative coefficient suggested low salinity was correlated with high mortality, which is highly unlikely. Also, the variable was not significant in the logistic regression analysis. For these reasons it is unlikely EC has a strong influence on mortality. However, soil samples were collected at the soil surface (depth of 5 cm) and healthy riparian vegetation was growing in close proximity to *P. pubescens* at many sites. Native riparian species have been found growing among highly saline surface soils along the Lower Colorado River (up to 162 dS m^{-1}), but because the roots are at deeper soil horizons where salinity levels are low they are able to persist (Merritt & Shafroth 2012). Other factors, such as the ongoing lack of overbank flooding, irrigation inputs, capillary rise and evaporative concentration of salts among highly regulated stream reaches (Gila River, Lower Colorado River), are most likely impacting riparian vegetation. More research is needed to understand the effects of soil chemistry on *P. pubescens* mortality and health status.

Extreme high or low pH values can have significant indirect effects (e.g., nutrient availability, microbial activity) on plant health. For example, certain metals (e.g., aluminum, manganese) are more soluble at low pH values, rendering them toxic to plants. The influence of pH on *P. pubescens* mortality is questionable as the variable was only statistically significant when the influence of biotic and physical damage was excluded (nested soil and water model). Also, *P. pubescens* can tolerate strongly alkaline soils with pH values ranging from 8.5 to 10.6 (Vilela & Ravetta 2001). A majority of the observations had pH values below 8.5. Only four observations were in the extreme range that *P. pubescens* is known to tolerate and mortality varied substantially from 5 to 67 percent.

The high water flows variable was statistically significant in both the full and nested (soil and water) logistic regression models, suggesting that disturbance may influence disease severity. Trees at areas with infrequent high water flows had notably lower tree health scores (i.e. high stress) and higher severity of biotic damage.

Question 3: Are mortality influences and outcomes the same between restoration and local populations?

While there were no strong differences (biotic damage and mortality) between restoration and local populations, a majority of the populations with high vigor and recruitment were restoration populations (Figure 9). Selecting foreign propagule sources can introduce localized pests or disease. Where propagule sources were selected from seed sources in the area (Goose Flats, Yuma East Wetlands), there were no strong differences observed for remnant/local and restoration populations. Seed sources for Priest are unknown and identifying such may provide insights on potential genotypes best suited for targeted restoration, given the high vigor and number of recent recruits at this site.

Question 4: Are particular land uses and management associated with die-off?

Mortality does not appear to follow a point origin spread (Figure 11). In other words, mortality rates varied substantially from site to site and did not follow a spatial pattern. In an epidemiological landscape context, the spread of disease through landscapes is determined by the degree of structural connectivity (arrangement of host plants, connectivity through water courses), as well as the heterogeneous nature of the landscape (Meentemeyer et al 2012). While it is unclear what type of disease or pathogen is responsible for *P. pubescens* die-off, the examination of corridors through land use or structural connectivity may illuminate potential disease pathways. No clear pathosystems appear to be affecting die-off. Downstream from Goose Flats (where die-offs where first noted), populations were healthier and had less stress (Yuma East Wetlands). Also, Quitobaquito Springs and Goose Flats are separated by a great distance (over 150 miles) with little to no structural connectivity and both had a significant amount of stressed individuals and similar die-off patterns.

Human-induced land changes, such as road construction, irrigation, urban expansion, agricultural encroachment and wetland modification, can significantly increase pathogen introductions and infectious disease outbreaks (Patz et al 2004). Ornamental plants in the urban environment can act as conduits for disease invasion to the wider rural environment (Tubby & Webber 2012). While no clear pattern of die-off was associated with a particular land use, trees at cultivated areas (Goose Flats and the Gila River) had high stress and biotic damage. However, trees at Yuma East Wetlands had a mixture of cultivated and urban land use in close proximity and had less stress and biotic damage.

Question 5: Are populations rebounding or keeping pace with mortality?

While little is known of the recruitment requirements for *P. pubescens*, tree health and recruitment indices can provide an estimate of the regeneration potential and target areas that may rebound. Healthy trees with high recruitment indices have a high regeneration potential, whereas those with high stress and low recruitment indices have a low regeneration potential. Populations at the Gila River, Yuma East Wetlands and Priest had the highest regeneration potential. At the Lower Gila River, the removal of riparian vegetation for flood conveyance along with the near perennial flow from irrigation returns may be inadvertently creating establishment sites at some reaches. At other sites, stormwater delivery (Priest) and periodic flooding (Yuma East Wetlands) appear to be supporting existing and new *P. pubescens* recruits. These sites may have genotypes best suited for changing environmental conditions, potentially providing ideal propagules for targeted restoration. A number of populations at Quitobaquito Springs and the Lower Colorado River had low regeneration potential and may be at risk of extirpation given their low recruitment index, high stress and mortality.

CONCLUSIONS

When considering all potential factors (soil, water and physical tree factors), soil conditions were not found to be as influential on *P. pubescens* mortality as physical tree factors (biotic damage). However, the elimination of flood pulses and overbank flooding may be influencing mortality and disease through indirect effects not sufficiently captured in the data (i.e. small sample size). This was exemplified by the significance of pH and high water flows when excluding the influence of biotic and physical damage (nested soil and water logistic regression models). Additionally, trees at areas with infrequent high flows had notably higher stress and severity of biotic damage. Biotic damage was detected at all sites. It was statistically correlated with mortality and was the most influential factor in logistic regression analysis; this supports the assumption that a pathogen is the likely agent of *P. pubescens* die-off.

There have been accounts of large-scale episodic die-offs among desert trees in the Southwest, suggesting pulses of mortality to be more common for certain species (Bowers & Turner 2001). While there is strong evidence of a pathogen or disease influencing region-wide die-off among *P. pubescens*, the degree to which predisposing factors have influenced mortality is complex and involves many interacting factors such as catastrophic events, parasites, tree physiology and the successional stage of the species (Franklin et al. 1987). Older trees and seedlings are generally more vulnerable to biotic and abiotic perturbations. However, findings showed the opposite, with young to mature *P. pubescens* trees being more vulnerable. While puzzling, tree age and the type of disease can have a strong influence on plant health and mortality (Burdon & Chilvers 1982).

Other researchers found no evidence of high salinity levels, disease symptoms or signs of a pathogen. However, several new beetle-transmitted fungal pathogens causing similar diseases have been described by Dr. Akif Eskalen at the University of California Riverside (personal communication, Linden Piest 2015). Of particular concern has been the recent dieback occurring throughout southern California from the invasive ambrosia beetle, polyphagous shot hole borer (PSHB). This Asian beetle (*Euwallacea* sp.) vectors three fungi (*Fusarium euwallacea, Graphium* sp. and *Acremonium* sp.) resulting in Fusarium Dieback. This dieback was first documented in 2003 among avocado trees, but the fungal damage was not discovered until 2012 (Eskalen et al. 2013). Adult females tunnel galleries to lay their eggs and grow the fungi to use as a food source for both adults and larvae. This compromises the tree's vascular system by intercepting the transport of water and nutrients, resulting in branch die-off and eventually tree death (Eskalen et al. 2013). A number of reproductive hosts are dominant members among several important plant communities, including riparian habitats, in southern California (detected throughout Orange and San Diego Counties). Over 300 species have been determined to be susceptible to the disease. It is suggested that the disease has the potential to establish in a number of plant communities locally and worldwide given the number of reproductive hosts among urban landscapes (Eskalen et al. 2013).

Landscape connectivity directly affects plant-pathogen disease processes. Diseases or pathogens can inadvertently spread through connected habitats, such as revegetated areas connected to urban rivers (Meentemeyer et al. 2012). Urban development can create dispersal shortcuts and increase range dispersal of pathogens (Tubby & Webber 2012). Cultivated and urban areas at some sites (Goose Flats, Gila River) may be acting as "dispersal corridors," increasing pathogen introduction and spread.

A significant reduction in *P. pubescens'* historic range has been documented across the species range, with large gaps between sites (Foldi 2014). Several site visits to the Hassayampa River Preserve confirmed there are no trees remaining in areas where they have been previously documented (Wolden et al. 1995). Large, instantaneous floods are capable of lowering population numbers in the area. However, it is unlikely these events alone would result in extirpation. Propagule sources at upstream sites may have disappeared, potentially reducing or eliminating populations downstream. Over time, isolated patches can lower the genetic and physiological diversity, making populations more susceptible to large severe stand-level die-offs (Franklin et al. 1987). While the sample size was small, trees at urban areas were far less stressed than trees at wild locations. Restoration sites and novel urban environments (Priest, Yuma East Wetlands) may provide refuge for *P. pubescens* while remnant locations lack the necessary site conditions for population renewal and persistence.

Whether or not populations rebound depends on a better understanding of the ecology of *P. pubescens* and future monitoring at sites identified in this study. For example, do sites with high stress and significant biotic damage represent early disease invasion stages where effects have yet to manifest? Also, do restoration-planted populations with low stress and high recruitment have "suited genotypes" at impounded rivers and wetlands? Future monitoring at these sites would provide valuable insights on *P. pubescens* population viability and persistence.

Wetlands in Arizona are among the most important ecosystems in the Southwest and present great challenges in restoration. Revegetation projects alone are generally limited in scope. There is increasing desire among restoration practitioners to shift from classic rehabilitation projects to instating functional self-sustaining ecosystems (Briggs 1996; Perring et al. 2015). These ecosystems would address past, current and future conditions and the suite of species best adapted for changing conditions. While techniques to overcome poor site conditions have been employed, such as leaching salts through irrigation, these activities will only offer a temporary solution as the underlining factors (e.g., lack of overbank flooding that wash salts from the channel) are generally not addressed. Also, in light of the apparent disease and large-scale die-off of a species typically capable of withstanding less desirable conditions than other riparian species, land managers may have to rethink the species best suited for these sites. For example, *Parkinsonia aculeata* has become established at surface-water-dominated urban rivers (Salt River) where groundwater is too deep for native riparian taxa (Stromberg et al. 2015). Perhaps *Parkinsonia aculeata* may be a better choice as an "adapted management species" to changing environmental conditions than *P. pubescens* at some locations. Upland problems are intricately connected to bottomlands (Briggs 1996), and activities from a distance can take decades to manifest at the floodplain (Webb et al. 2007). A culmination of past water diversion, development and land use may be surfacing, rendering riparian species vulnerable to diseases and triggering such events as region-wide die-off at impounded rivers and wetlands in Arizona. Reports that document widespread die-offs are critical as desert riparian trees support a variety of wildlife and a disproportionate level of biodiversity. The loss of riparian trees, such as *P. pubescence*, are likely to have devastating impacts to ecosystems region-wide.

Table 1. Average health scores, biotic damage and percent mortality of *P. pubescens* by hydrologic type, land use type and level of restoration.

Grouping	Category	Health score	Biotic damage	Mortality
Hydrology	Lacustrine	3.26	1.71	16
	Riverine	4.04	1.44	13
Land use	Urban	4.29	1.29	9
	Agricultural	3.06	1.75	27
	Wild	2.61	2.26	9
Active restoration[1]	High	3.99	1.32	7
	Moderate	3.82	1.52	23
	Low	3.04	1.96	15

[1] Describes the level of restoration. Low (L) describes sites with little or no active restoration. Moderate (M) describes restoration activities such as revegetation but generally limited in scope. High (H) describes restoration where extensive earth moving and ongoing management (irrigation, intentional flooding, etc.) has been implemented.

Table 2. Site averages for average health scores, biotic damage and percent mortality of *P. pubescens*.

Site	Health score	Biotic damage	Mortality	Land use[1]	Hydrology[2]	Active Restoration[3]
Priest	4.95	1.22	14	U	R	M
Yuma East Wetlands	4.20	1.20	10	U	L	H
Gilbert Riparian Preserve	4.13	1.40	0	U	L	H
Rio Salado	3.75	1.42	7	U	R	H
Gila River	3.43	1.68	20	A	R	L
Goose Flats area	2.68	1.82	33	A	L	M
Quitobaquito Springs	2.61	2.26	10	W	L	L

[1] Land use categories: agricultural (A), urban (U) and wild (W).
[2] Hydrology categories: river (R) and lacustrine (L).
[3] Describes the level of restoration. Low (L) describes sites with little or no active restoration. Moderate (M) describes restoration activities such as revegetation but generally limited in scope. High (H) describes restoration where extensive earth moving and ongoing management (irrigation, intentional flooding, etc.) has been implemented.

Table 3. Pearson correlation between soil, water, physical tree factors and mortality between restoration, local and all populations for size class 2 of *P. pubescens*.

	Biotic damage			Mortality		
	Res[1]	Local[2]	All	Res[1]	Local[2]	All
Physical damage	**0.68**	NS	**0.41**	NS	NS	NS
Biotic damage	--	--	--	NS	**0.61**	**0.60**
Soil moisture	NS	**-0.72**	**-0.45**	NS	NS	NS
EC	NS	**-0.67**	NS	NS	NS	**-0.41**
pH	NS	**0.88**	**0.41**	NS	**0.64**	**0.57**
Canopy cover	NS	NS	NS	NS	NS	NS
Mortality	NS	**0.61**	**0.60**	--	--	--
Health status	**-0.57**	**-0.81**	**-0.75**	**-0.76**	**-0.80**	**-0.79**

[1] Includes: RP: restoration planting and RV: restoration volunteer
[2] Includes LR: local Remnant and LV: local volunteer
NS = P value > 0.10

Table 4. Mortality response to soil, water and physical tree factors for size class 2 trees of *P. pubescens* (population level).

	Full model		Soil and water model		Tree model	
Variable	Estimate	T-ratio	Estimate	T-ratio	Estimate	T-ratio
Soil moisture	-0.95	-0.43	-0.74	-0.31		
Soil water (infrequent)	0.27	0.62	0.38	0.72		
High water flow (infrequent)	**1.19[1]**	2.54	**1.05[1]**	2.12		
EC	-0.09	-1.54	-0.04	-0.54		
pH	1.05	1.47	**1.78[1]**	2.24		
Biotic damage	**1.58[1]**	3.25			**1.99[1]**	4.97
Physical damage	**-2.82[1]**	-4.01			**-1.96[1]**	-2.66
Psuedo R^2	**0.67**		0.55		0.48	
AICc	-1.68		-3.82		**-17.93**	

[1] $p < 0.05$
Coefficients are represented as log odd ratios.

Table 5. Correlation matrix of soil, water and physical tree factors (size class 2). Correlations for which P <0.01 are shown in bold text/shaded cells.

	Soil moisture (gravimetric)	EC	Biotic damage	Physical damage	pH	Mortality	Canopy
EC	**0.45**						
Biotic damage	**-0.45**	-0.25					
Physical damage	-0.34	-0.18	**0.41**				
pH	-0.29	0.03	**0.41**	0.25			
Mortality	-0.33	**-0.41**	**0.60**	-0.17	**0.57**		
Canopy cover	0.02	0.03	-0.27	-0.25	-0.29	0.04	
P. pubescens health status	0.23	0.32	**-0.75**	-0.22	-0.33	**-0.79**	0.11

Table 6. Correlation coefficients between biotic damage, physical damage and average health score for all size classes (data pooled across sites).

	Health score[1]			
	Size class 1	Size class 2	Size class 3	Size class 4
Biotic damage	-0.65[3]	-0.55[3]	-0.69[3]	-0.53[2]
Physical damage	NS	-0.32[3]	NS	NS

[1] Health score is measured on a unit interval scale: 1(dead) – 5 (healthy).
[2] $P < 0.10$
[3] $P < 0.05$
NS = $P > 0.10$

Table 7. Percent mortality, average health scores and biotic damage for local and restoration populations (all size classes and size class 2).

Population source	Mortality	Health score	Biotic damage	N[1]
All Size Classes				
Local	**15**	**3.26**	**1.79**	**174**
Local remnant	15	3.08	1.93	134
Local volunteer	15	3.88	1.30	40
Restoration	**15**	**3.98**	**1.40**	**195**
Restoration planting	13	4.08	1.41	155
Restoration volunteer	23	3.58	1.33	40
Size Class 2				
Local	**20**	**3.01**	**1.71**	**112**
Local remnant	19	2.98	1.80	84
Local volunteer	21	3.11	1.43	28
Restoration	**18**	**3.92**	**1.39**	**130**
Restoration planting	15	4.16	1.39	101
Restoration volunteer	28	3.07	1.41	29

[1] Number of trees

Table 8. Percent mortality, average health scores and biotic damage for local and restoration populations (all size classes).

Size class	Population source	Mortality	Health score	Biotic damage	N[1]
1	Local	0	5.70	1.00	23
	Restoration	5	4.84	1.06	32
	All	**5**	**5.20**	**1.04**	**55**
2	Local	9	3.01	1.71	112
	Restoration	10	3.92	1.39	130
	All	**19**	**3.50**	**1.54**	**242**
3	Local	6	2.45	2.48	31
	Restoration	5	3.33	1.70	30
	All	**11**	**2.89**	**2.10**	**61**
4	Local	0	3.00	2.50	8
	Restoration	0	4.00	2.00	3
	All	**0**	**3.27**	**2.36**	**11**

[1] Number of trees

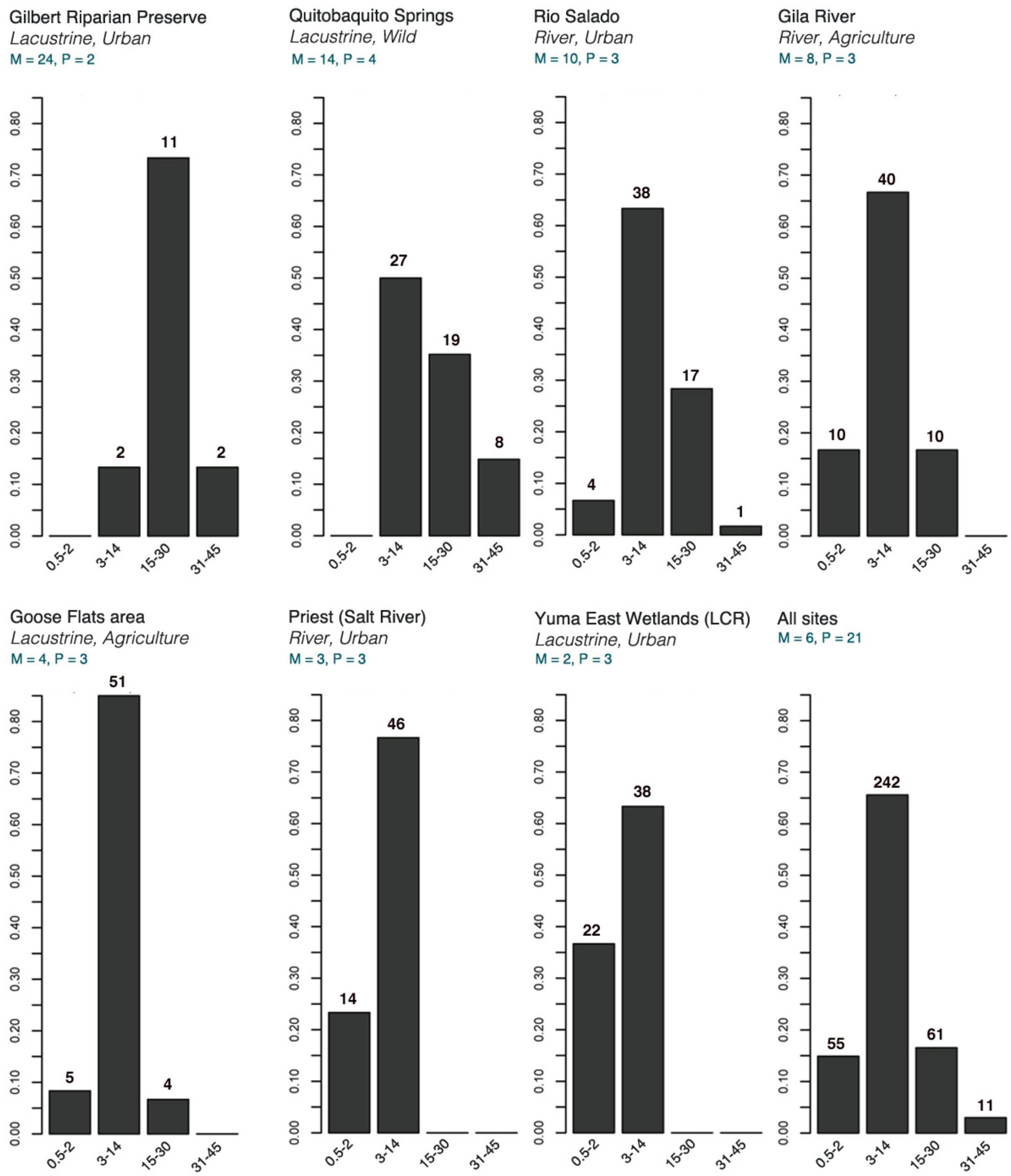

Figure 1. *Prosopis pubescens* size class distribution at study sites in central and southern Arizona. Bars display proportion of trees within each of four stem diameter size classes (seedling and sapling = 0.5-2 cm, young = 3-14 cm, mature = 15-30 cm and old = 31-45 cm). Number of populations (P) and median tree diameter size (M) are displayed below site names. Number of trees listed above bars.

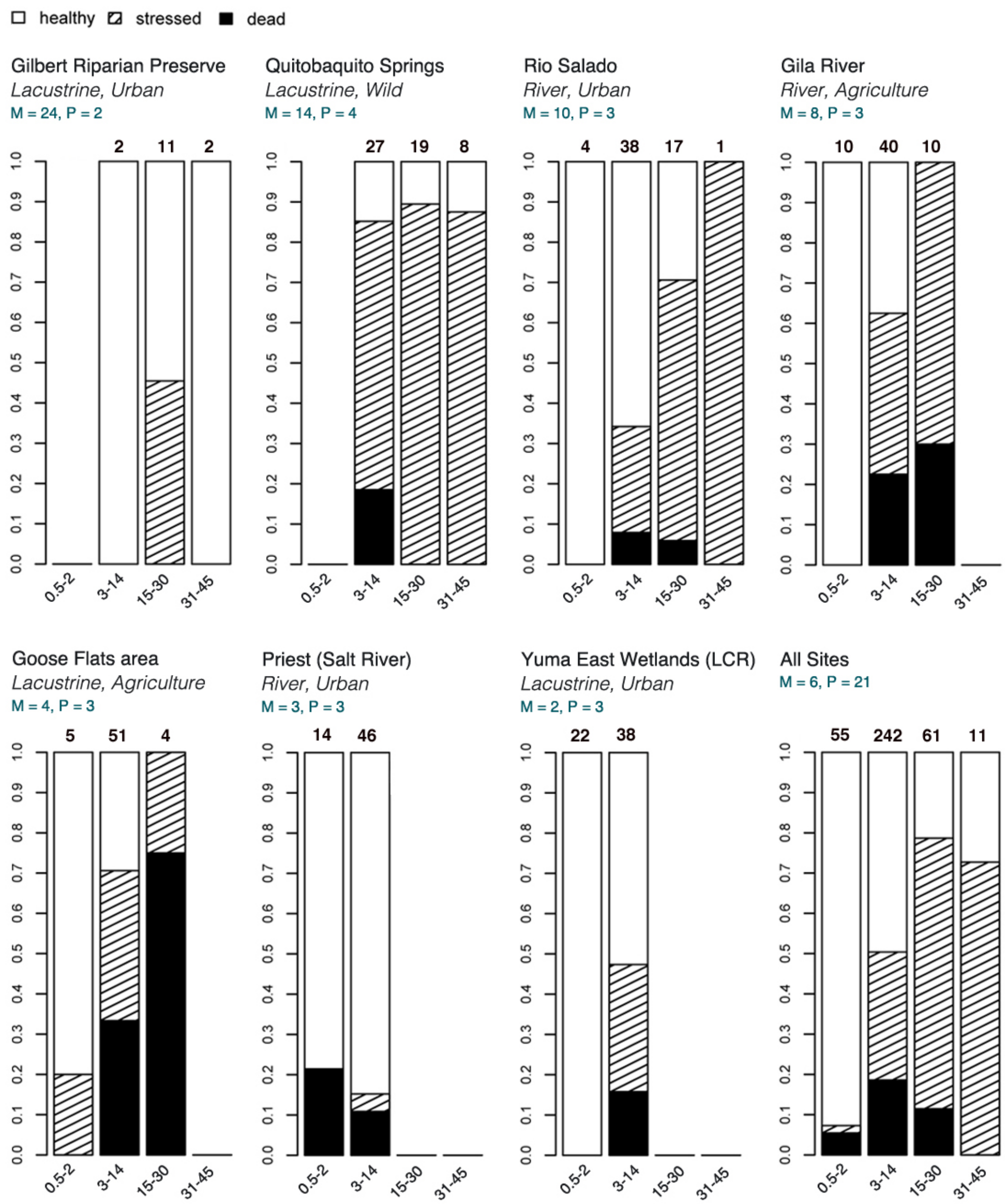

Figure 2. *Prosopis pubescens* health status by size class (seedling and sapling = 0.5-2 cm, young = 3-14 cm, mature = 15-30 cm and old = 31-45 cm). Bars display proportion of healthy, stressed and dead trees for each size class category. Number of populations (P) and median tree diameter size (M) are displayed below site names. Number of trees listed above bars.

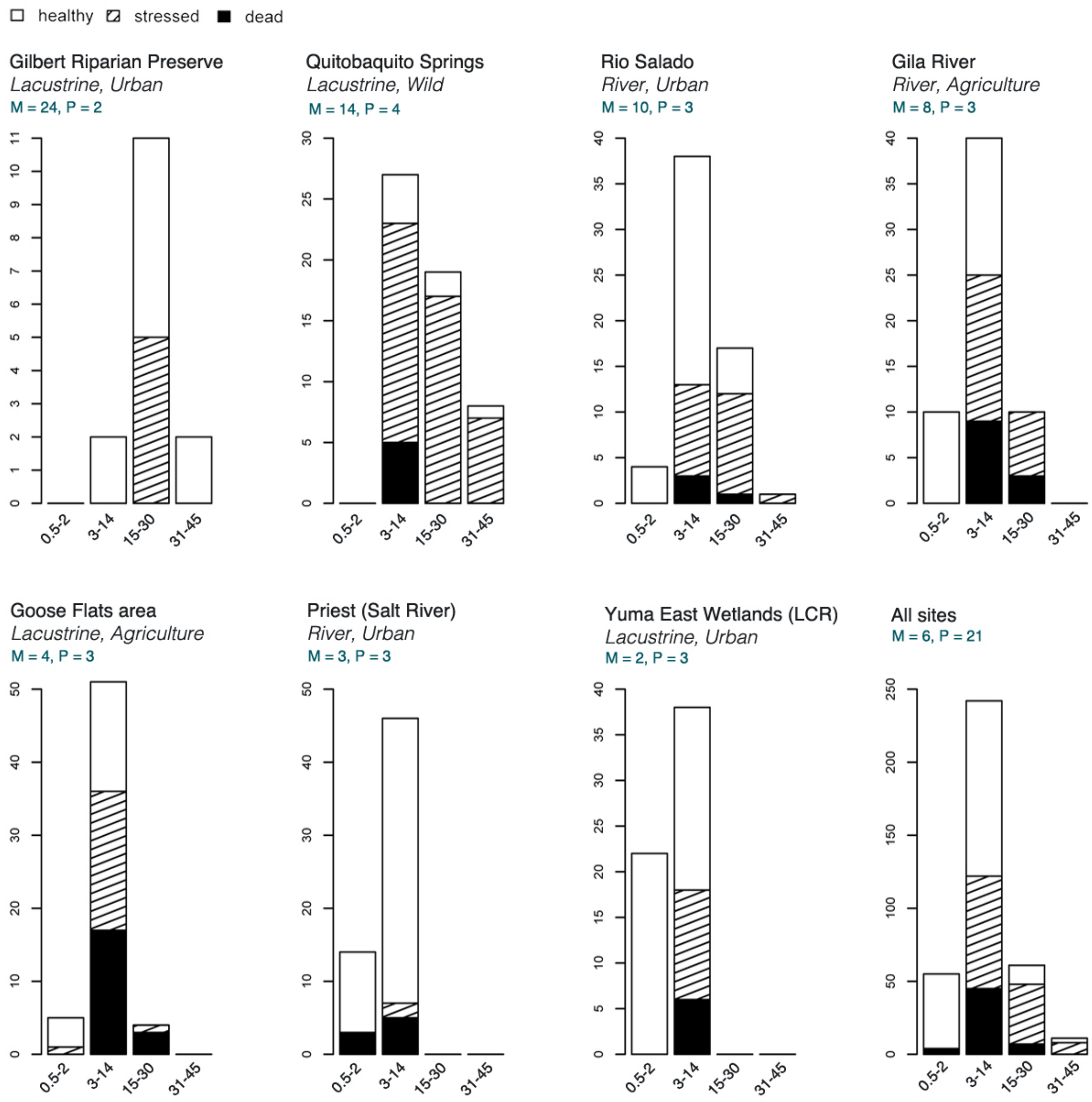

Figure 3. *Prosopis pubescens* health status by size class (seedling and sapling = 0.5-2 cm, young = 3-14 cm, mature = 15-30 cm and old = 31-45 cm). Bars display number of healthy, stressed and dead trees for each size class category. Number of populations (P) and median tree diameter size (M) are displayed above bars.

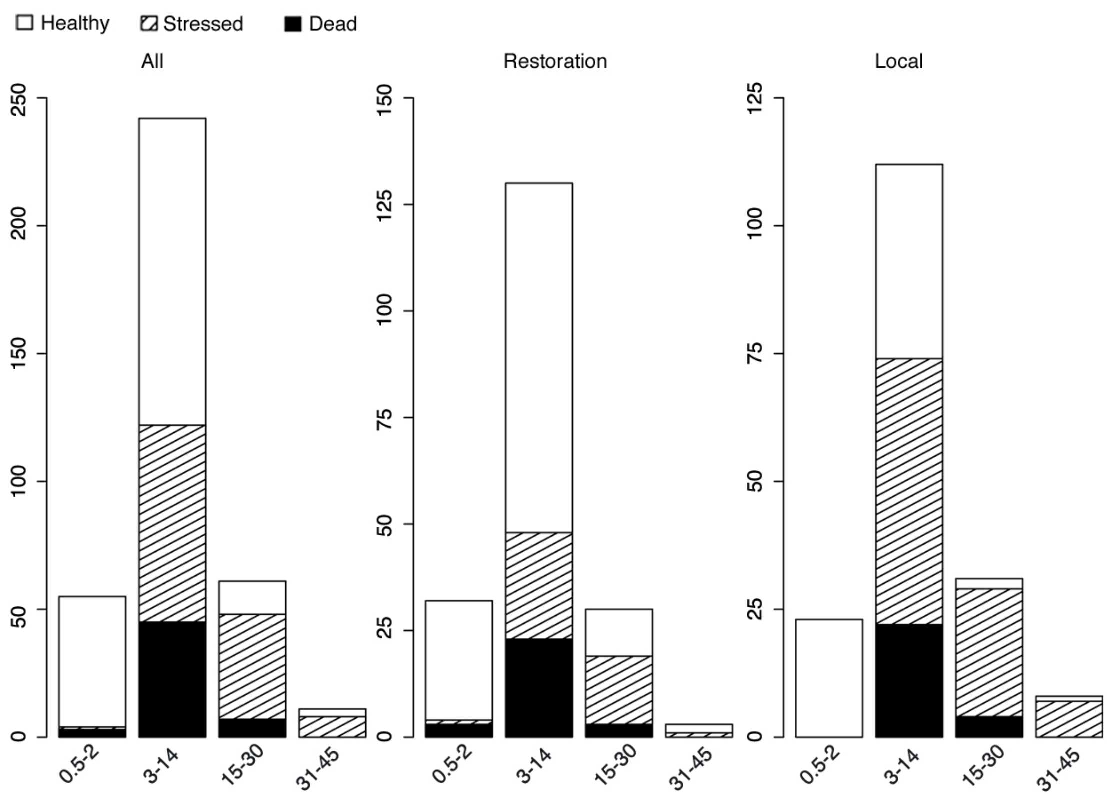

Figure 4. *Prosopis pubescens* health status by size class for restoration, local and all populations.

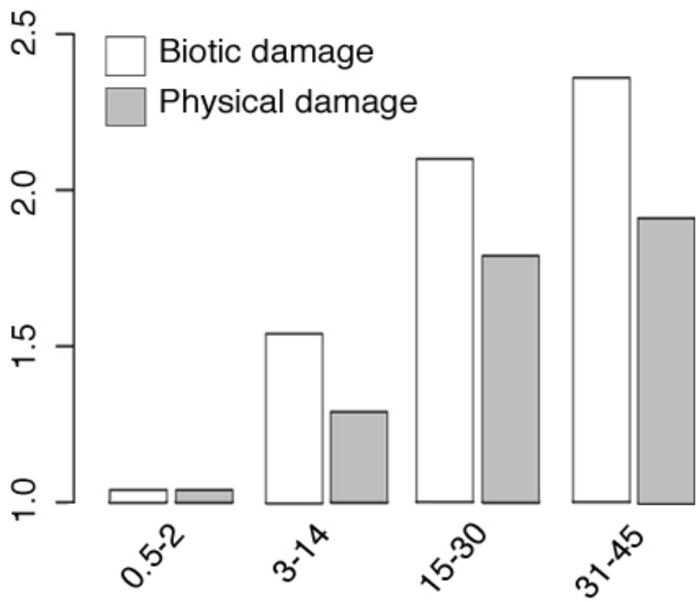

Figure 5. Average biotic and physical damage by size class of *P. pubescens* (cm). The scales range from 1 to 3.

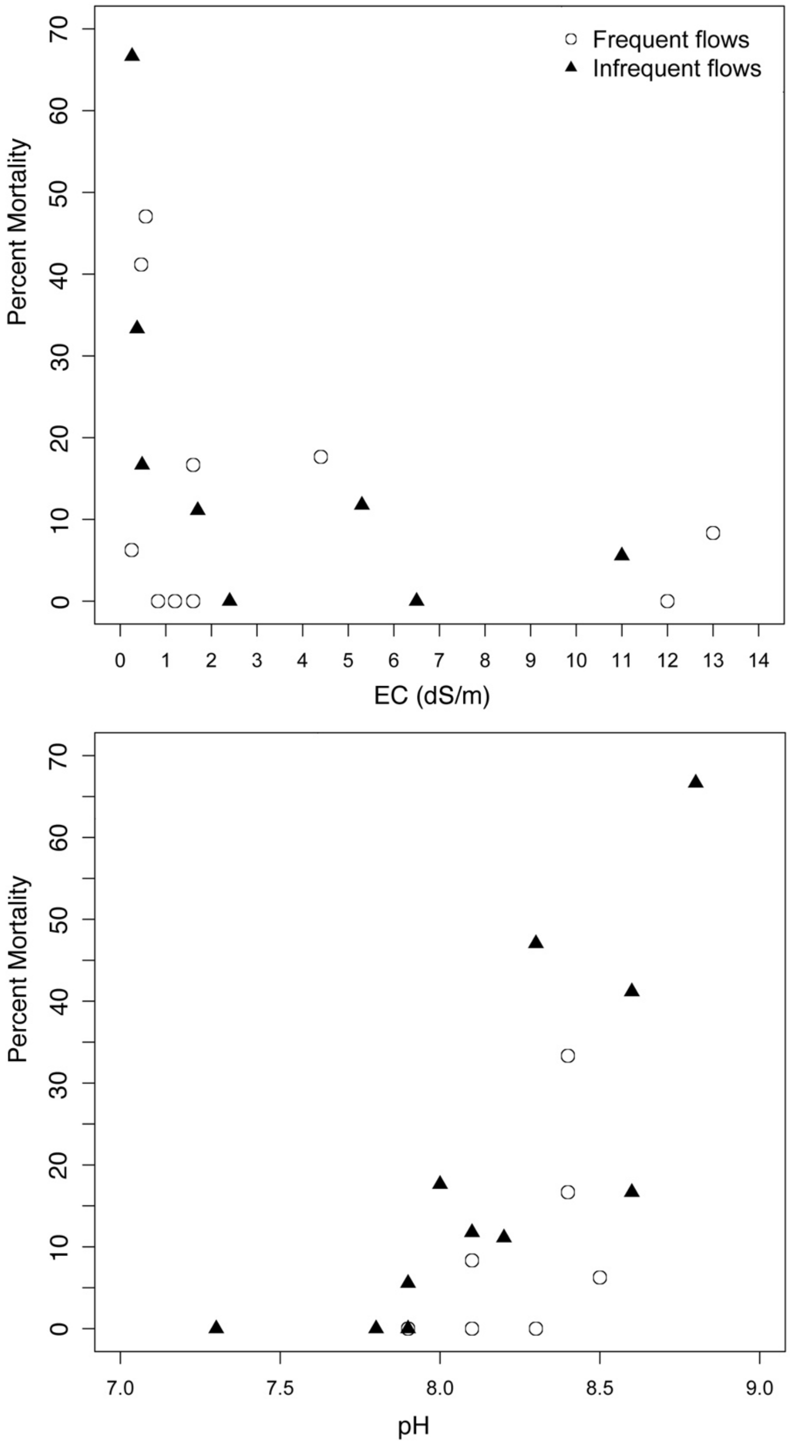

Figure 6. Mortality of *P. pubescens* in relation to EC (top) and to pH (bottom) for sites with frequent and infrequent flood flows (size class 2 averages).

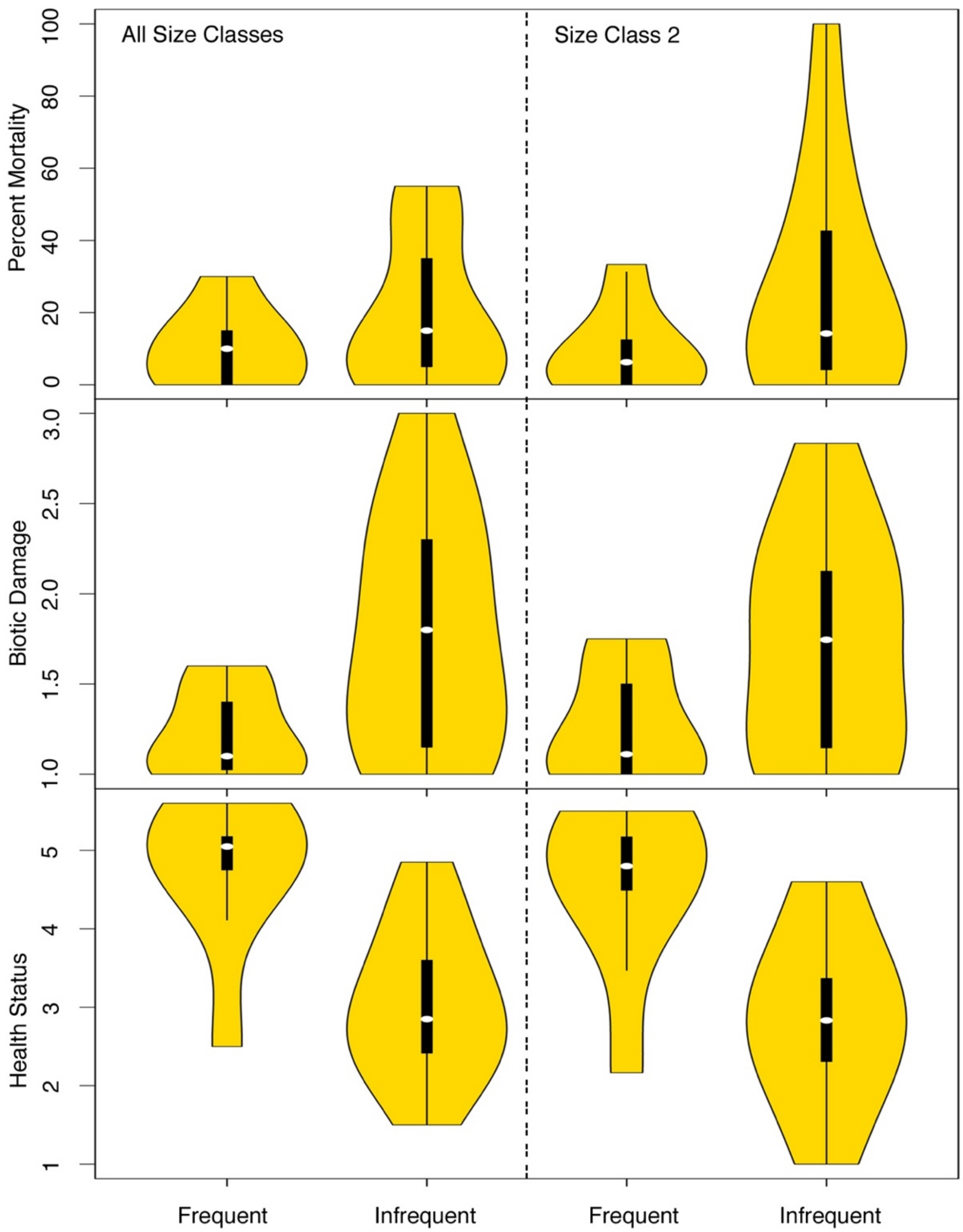

Figure 7. Violin plot of percent mortality and biotic damage. Biotic damage (1 is < 10%, 3 is > 60%) and health status (1 is dead, 6 is healthy) of *P. pubescens* at sites with frequent and infrequent flood flows for all trees (left of dotted line) and size class 2 trees (right of dotted line).

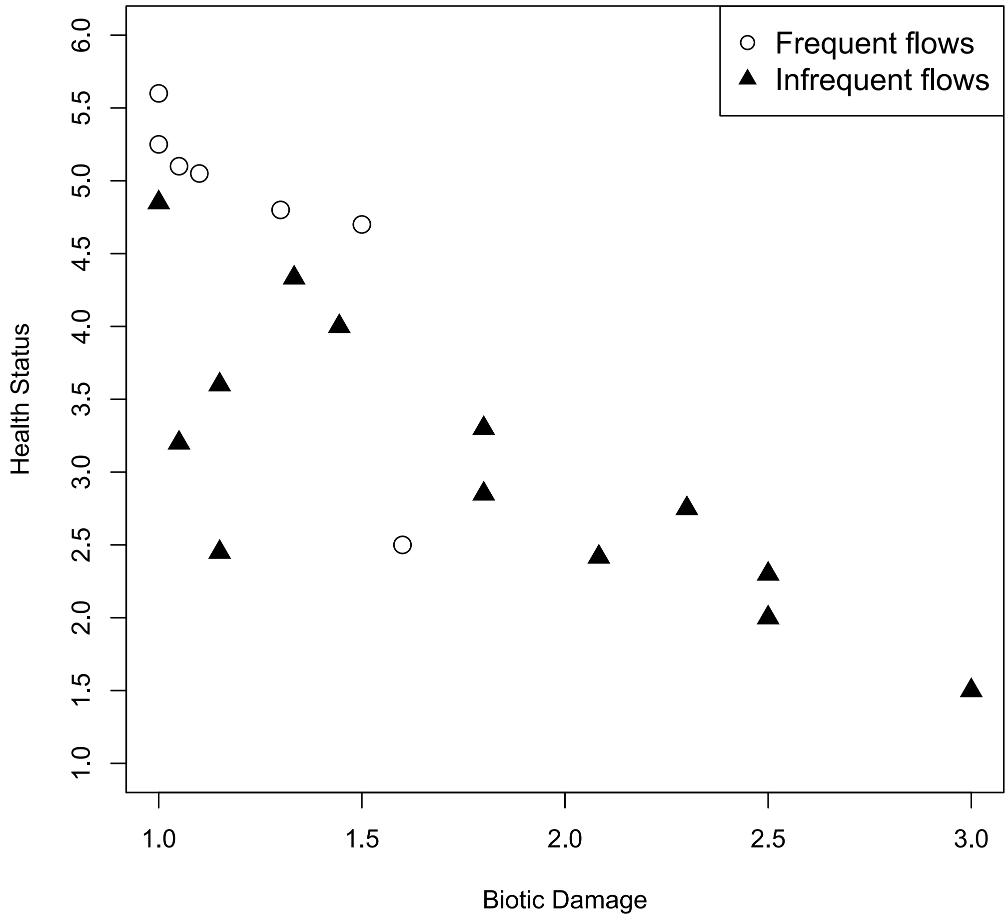

Figure 8. Biotic damage and health status of *P. pubescens* at sites with frequent and infrequent flood flows (all size classes). Health status ranges from 1 (dead) to 6 (healthy).

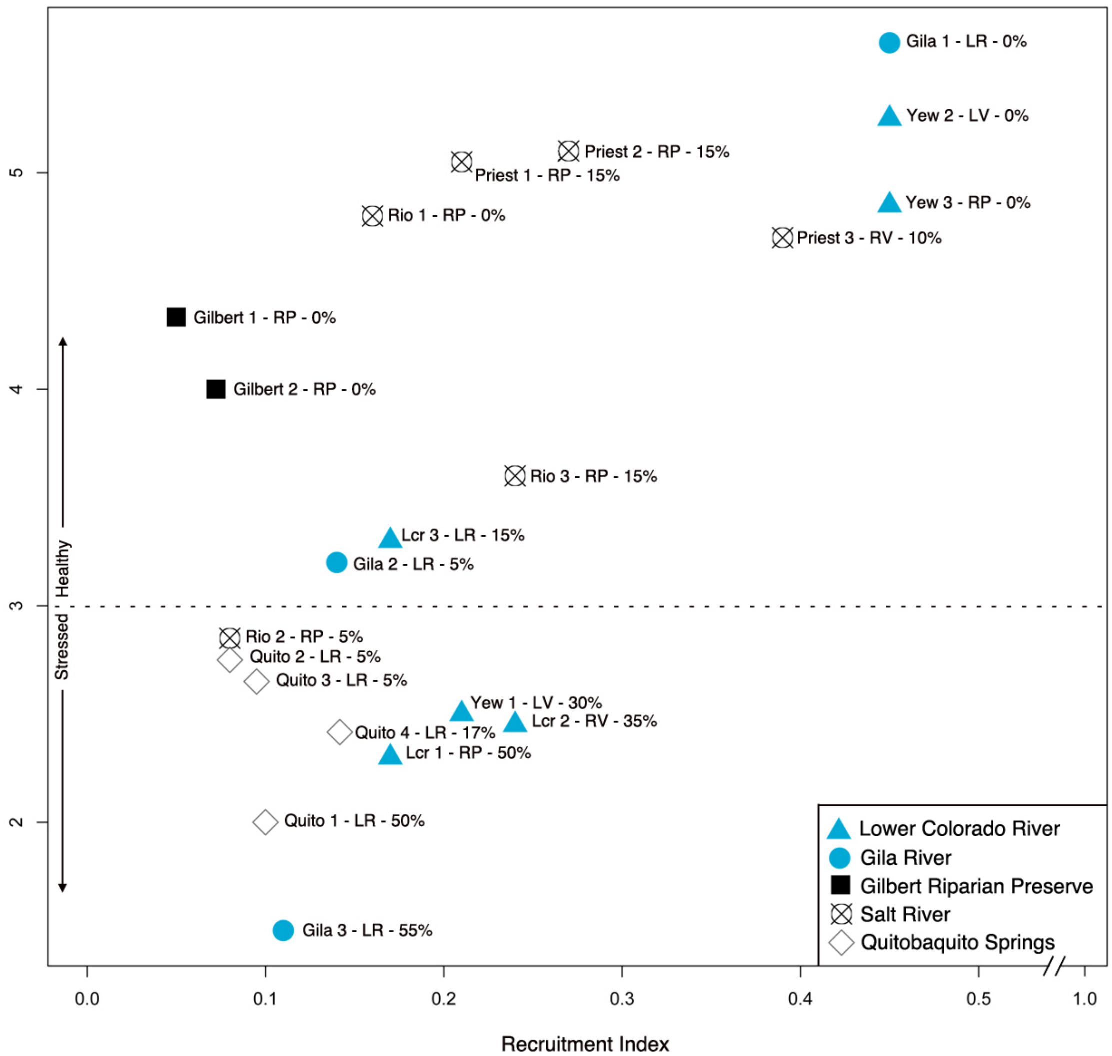

Figure 9. Population health status, recruitment index and mortality of *P. pubescens* by major River/Wetland and site. Data points (population) are grouped by color by geographic location. Cyan: southwest Arizona. Black: central Arizona. Grey: south central Arizona (Quitobaquito Springs). Data points are labeled by population name, population source (RP: restoration planting, RV: restoration volunteer, LR: local remnant, LV: local volunteer), and percent mortality. Health status: stressed < 3 (below dotted blue line) and healthy > 3 (above dotted blue line). The recruitment index describes the recruitment or "regeneration" potential for each population.

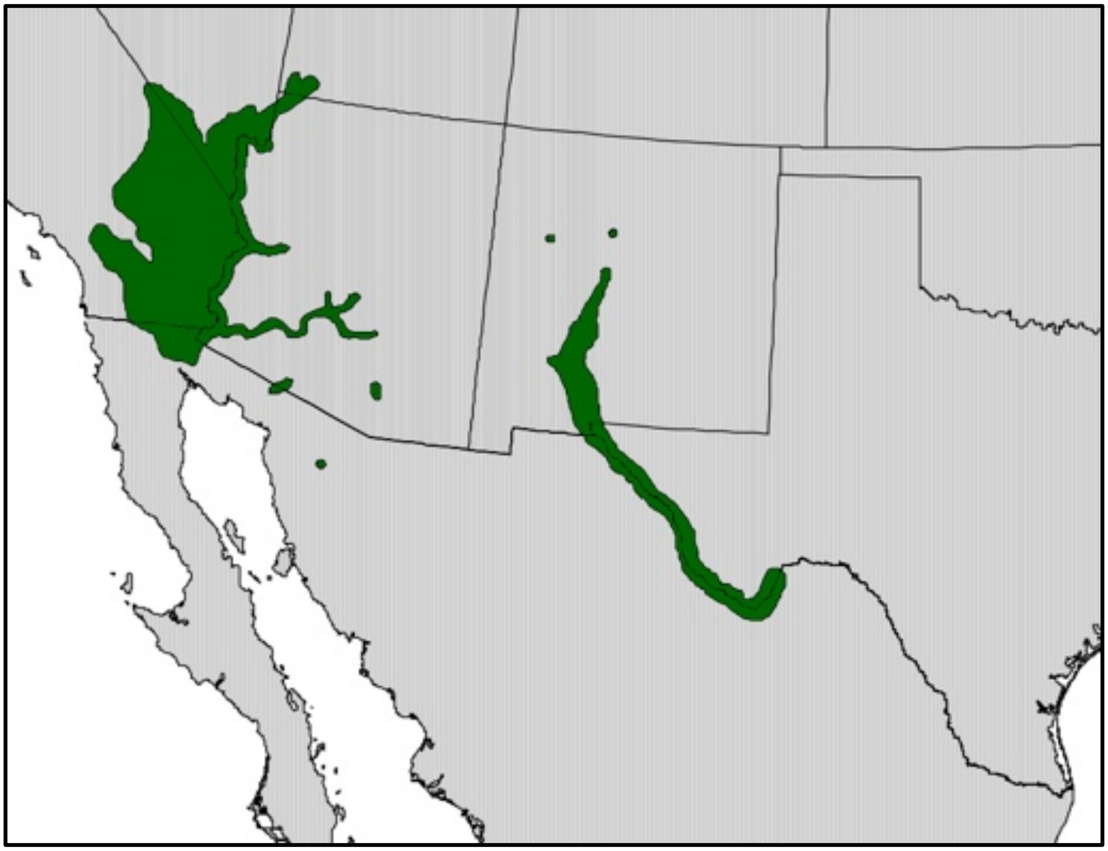

Figure 10. *Prosopis pubescens* Range Map. Obtained from USGS (http://esp.cr.usgs.gov/data/little/).

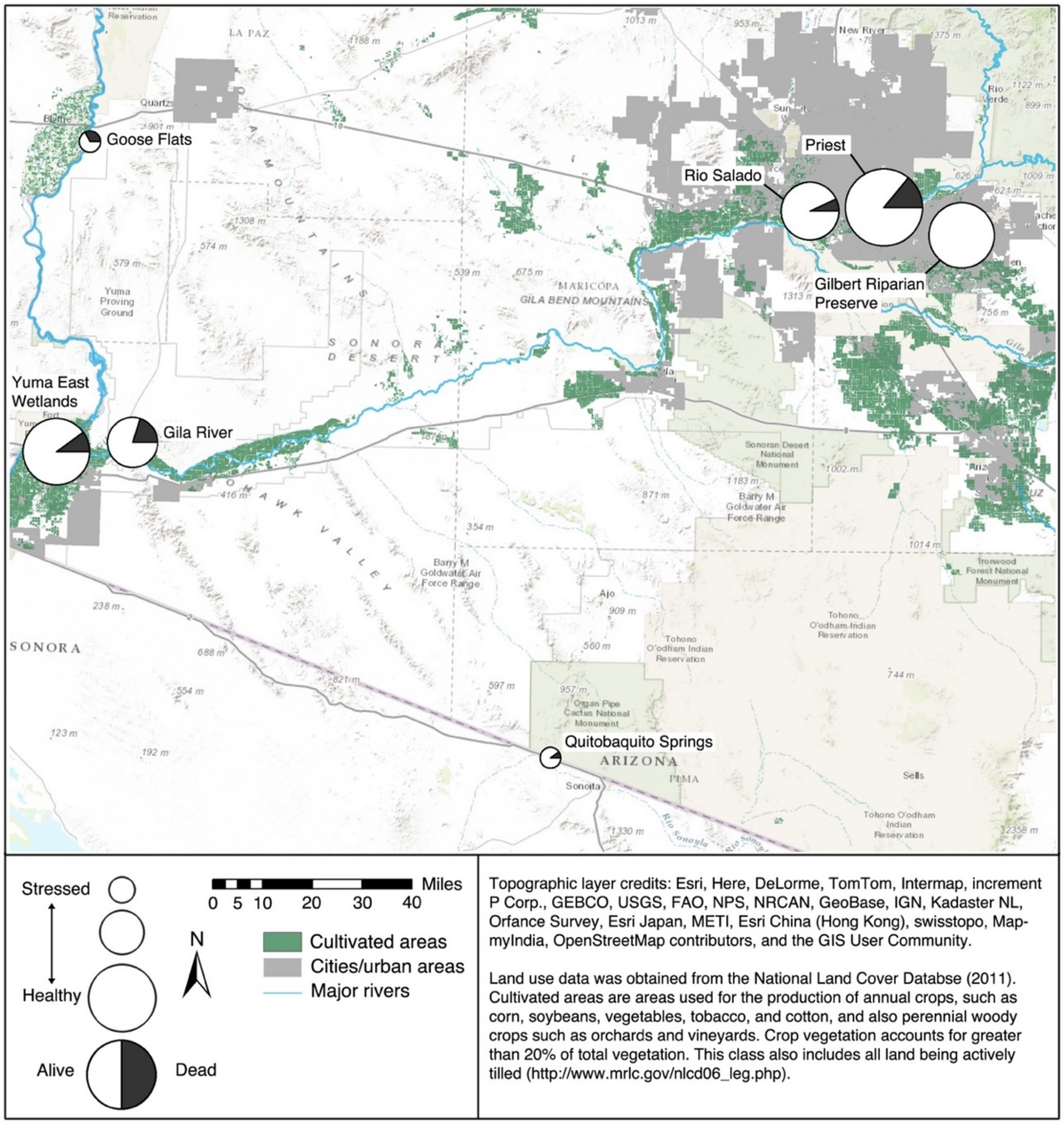

Figure 11. Study sites, health status and mortality.

Figure 12. *Prosopis pubescens* Biotic Damage. A: unusual black spots observed on fruits of several trees at Rio Salado. B: abnormal/deformed fruit at Quitobaquito Springs. C: example of severe biotic damage (beetle activity and curious bleeding) near Goose Flats area (LCR). D: typical example of yellow leaves with small brown spots, observed at several sites. E: bleeding among a mature individual at Priest. F: leaves bunched together and curling inward at Rio Salado, observed at several sites.

CHAPTER TWO: A REVIEW ON SCREWBEAN MESQUITE ESTABLISHMENT, TREE MORTALITY, RIVER MANAGEMENT AND RESTORATION

SCREWBEAN IMPORTANCE

Riparian zones in dryland deserts provide wildlife a retreat from the surrounding desert. Mesquite trees are an important riparian species in the American Southwest. Unless otherwise noted, in this chapter "mesquite" refers to the regionally native velvet (*Prosopis juliflora* var. *velutina*), honey (*Prosopis juliflora* var. *glandulosa*) and screwbean (*Prosopis pubescens*) mesquite. Vast forests of mesquite once spanned hundreds of kilometers across the floodplains of desert rivers throughout Arizona and provided a structure somewhat similar to cottonwood-willow forests (Stromberg 1993). Found along washes, rivers and alluvial floodplains, as well as upland areas with adequate precipitation, mesquite produces productive and wildlife-rich habitats. Velvet and honey mesquite are common and well-studied compared to the less researched and less common screwbean mesquite. Like other mesquites, screwbean provides valuable wildlife habitat. In desert riparian systems, the tall canopy and shade from screwbean mesquite provides high relative use as nest sites among wildlife compared to honey mesquite (Austin 1970).

DISTRIBUTION AND ECOLOGY

Screwbean mesquite range encompasses central Arizona; southeast California; parts of Baja California and Sonora, Mexico; southeast Nevada; southern Utah; central and southwest New Mexico; and western Texas (Figure 10). Historically, screwbean mesquite reached its greatest abundance along the Lower Colorado River, where it was commonly found in desert riparian woodlands with scattered willows and cottonwood and among scrub habitats. Considered mostly an obligate riparian species across its range, screwbean can be found along first terraces of rivers, old oxbow ponds, springs and in areas where backwaters have formed. In arid settings where summer rainfall is sparse, mesquite depend on flooding for recruitment and groundwater sources for persistence (Stromberg 1993). Mesquite germination is triggered by late summer monsoonal rains. Fruit ripen and drop throughout the summer and fall, reaching peak production during early July (Ohmart et al. 1988).

Animal dispersal is a strong factor in mesquite establishment. Nearly two-thirds of a mule deer's diet comes from woody fruits from leguminous shrubs (Urness & McCulloch 1973 in Ohmart et al. 1988). Significant amounts of screwbean seeds were found in mule deer pellets along screwbean and willow stands at first terrace bottoms along the Lower Colorado River, indicating that *P. pubescens* seed pods are an important forage for mule deer (Ohmart et al. 1988). With the removal of vegetation at second terraces (honey mesquite) that connect mountainous areas to the riparian zone, mule deer are likely to disappear from the Lower Colorado River (Ohmart et al. 1988).

HISTORIC DECLINE

Mesquite forests were some of the most abundant riparian vegetation types in place prior to land conversion and water control measures instituted in the past century. Mesquite were historically well represented along the Gila, San Pedro, Santa Cruz and Lower Colorado rivers in Arizona. Past and current water management practices (water diversion from dams, groundwater withdraws), agricultural land conversion and wood cutting have resulted in dramatic shifts among many riparian systems, causing reduction of some taxa and expansion of others (Busch & Smith 1995; Stromberg 1993). Screwbean mesquite bosques, once common along the Lower Colorado River, today have mostly been eliminated or greatly reduced. Large screwbean mesquite groves reaching heights greater than the mature honey mesquite have been extirpated from the Lower Colorado and Bill Williams rivers (Ohmart et al. 1988; Hunter et al. 1987). The almost complete extirpation of mesquite bosques at some localities in Arizona, including the Gila and Lower Colorado rivers, has been well documented (Judd et al. 1971; Ohmart et al. 1998).

RIVER MANAGEMENT

Key disturbances, such as flooding, are critical in structuring vegetation and creating opportunities for species to colonize an area. Distinct species establish across fluvial surfaces from island bars to terraces. The result is a highly dynamic system in which populations and communities are in constant flux following hydrogeomorphic and spatio-temporal patterns. Altered flows have strong effects on composition, community and population dynamics – all of which influence mortality and, potentially, disease outcomes. In addition to animal dispersal, flooding can play an equally important role in mesquite establishment by scarifying the seed coat and increasing germination rates (Stromberg 1993). Historically, screwbean was common among habitats (e.g., Sonoran cottonwood-willow forests) in which flooding was a frequent disturbance (Holland 1986). Regulated flows can lead to low reproduction among riparian trees and increase the probability of local extinction (Friedman & Lee 2002; Lytle & Merritt 2004). Where fluvial disturbances have been reduced, senescent populations dominate sites (Webb et al. 2007). The open park-like structure of screwbean mesquite forests was the result of frequent flooding (Holland 1986).

GROUNDWATER DECLINES AND DISEASES

Severe groundwater declines and drought can reduce resilience, growth and crown volume, as well as increase the mortality of riparian trees (Stromberg & Patten 1992; Scott et al. 1999). Rapid water-level drawdown can induce cavitation resulting in the loss of water from roots to branches. For short periods of withdraw, mature individuals (cottonwood, willow) have a much higher chance of survival than saplings (Shafroth et al. 2000). Mortality can occur with as little as one meter of water-level decline over the course of 14 days (Scott et al. 1999). Mesquite can generally handle larger fluctuations in groundwater levels than other riparian trees (Webb et al. 2007). Extensive groundwater table declines over a 50-year period coupled with dense mistletoe growth are suspected to be the primary factors leading to massive mortality of velvet mesquite along the Gila River (Judd et al. 1971). While mesquite can generally access deep water sources, dense bosques depend on shallow groundwater sources for persistence (Stromberg et al. 1992). Conditions such as persistent drought that cause gradual water level declines are less likely to cause immediate tree death. This allows plant roots the time to adjust, with negative impacts generally limited to branch pruning (Webb et al. 2007). When conditions create sudden and rapid declines in water levels, such as large-scale agricultural use, trees can die within a few days (Webb et al. 2007). Screwbean tends to be restricted where depth to the water table is less than 4 meters (Anderson 1996). However, little is known about screwbean mesquite's capacity to survive water table decline.

PATHOGENS

Pathogens can persist at low levels in vigorous populations but can induce disease outbreaks in weakened or stressed trees (Mattson & Haack 1987). Prolonged stress reduces capacity to fight diseases or parasites. Beetles can act as primary or secondary agents of mortality, entering through the roots or bark (beetle borers). Girdling beetles were found to reduce mesquite stub survival and reproduction at dry sites, whereas increased stub survival and reproduction were observed for trees at wet sites (Martinez et al. 2009). High-intensity floods can cause physical tree damage, making trees more susceptible to diseases (e.g., wound pathogens). The type of disease (e.g., cankers, vascular, root rot) and age of the plant affect health and mortality outcomes. Foliar diseases rarely kill large plants, but can negatively affect growth and reproduction (Burdon & Chilvers 1982).

In dammed systems where flood regimes are regulated, forest density can increase, perhaps facilitating disease spread. High stand densities directly modify the microclimate, increase competition for resources and increase disease incidence. Lowered host tolerance to rust infection was observed among plants growing in high stand densities (Burdon & Chilvers 1982). Leaf rust (*Revenelia arizonica*) and leaf blight (*Sclerophysnium aureum*) are common diseases among mesquite (Judd et al. 1971). The composition and characteristics of the stand (e.g., isolated patches versus connected forests) can also affect pathogen transmission and disease (Burdon & Chilvers 1982).

EFFECTS OF SOIL CHEMISTRY ON PLANT HEALTH

Screwbean mesquite is described as having a high salinity tolerance, growing at areas with EC values approaching 94 dS m^{-1}. However, plant growth and survival was greatly reduced at these levels (Jackson et al. 1990). Screwbean can be found growing alongside other halophytes such as arrowweed *(Pluchea sericea*) and tamarisk (*Tamarix chinensis*) (Ohmart et al. 1988; Marks 1950). Water stress and salinity gradients are among the main determinates in structuring riparian vegetation. With the loss of overbank flooding, salts accumulate and can build to lethal levels for some riparian species. Additionally, fires, runoff from agriculture, construction of canals and drainage ditches can all affect soil salinity, pH and texture (Busch & Smith 1995; Campbell & Dick-Peddie 1964). While elevated levels of salinity may not act as primary factors of mortality, it can induce stress, trigger early senescence, inhibit germination and lower resilience to diseases or physical damage (Busch & Smith 1995; Glenn et al. 1998). Species tolerance to salinity can vary between populations of the same species (Briggs 1996). Although riparian species are adapted to periods of waterlogging or saturated soil conditions, their tolerance is greatly reduced among high salinity soils (Briggs 1996). Boron, a micronutrient required for plant health, can reach toxic levels, specifically among soils with boron-laden irrigation water (Nable et al. 1997). This results in lowered plant growth, visible symptoms including stem die-back, bark necrosis, and fruit disorders.

EXTIRPATION

The probability of local extinction (extirpation) is dependent in part on species life history traits, genetics and perturbations (e.g., diseases, prolonged stressors). Many Sonoran woody plants have been known to rebound following large declines in population numbers (Goldberg & Turner 1986). However, over the past three decades, temperatures at some locations in central Arizona have been well above the optimal level for growth of desert riparian trees, with some populations experiencing temperatures great enough to denature photosynthesis enzymes (Grady et al. 2011). As part of a common garden experiment, populations of desert riparian trees (*Populus fremontii, Salix goddingii* and *Salix exigua*) growing at the limit of their tolerance to high temperatures were more productive than trees from provenances experiencing lower maximum temperatures, a difference of 5°C (Grady et al. 2011). Under future climate change scenarios, these findings suggest many populations will experience conditions outside optimal growing levels over a large percentage of the growing season. Additionally, climate change can bring about changes in interspecific competition, shifting dominance of species locally, depending on life history traits (e.g., generation time, seed dispersal, fecundity). Probability of extinction is low when populations sizes are large (maintaining genetic variability) and seed sources (e.g., from unaffected groups of individuals, seed banks) are available (Aitken et al. 2008). Highly fragmented areas may be at risk of local extinction as populations may lack efficient propagule sources following an epidemic.

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APPENDIX A

MORTALITY AND BIOTIC SEVERITY OF *P. PUBESCENS* BY SIZE CLASS, SITE AND POPULATION (PERCENTAGE TOTALS BY SITE AND POPULATIONS)

land use	Restoration	Hydrologic setting[1]	Population source[2]	Population[3]	Mortality by size class[4]					Biotic damage by size class[5]				
					1	2	3	4	All	1	2	3	4	All
Agriculture	No	R		**Gilla (all)**		**20**	**43**		**22**	**1.0**	**1.6**	**2.8**		**1.7**
			LR	Gila 1					0	1.0	1.0			1.0
			LR	Gila 2		2			2		1.1	1.0		1.1
			LR	Gila 3		18	43		20		2.8	3.3		3.0
Urban	Yes	L		**Gilbert (all)**							**1.0**	**1.4**	**2.0**	**1.4**
			RP	Gilbert 1								1.2	2.0	1.3
			RP	Gilbert 2							1.0	1.5	2.0	1.4
Agriculture	Yes	L		**Lcr (all)**		**38**	**43**		**36**	**1.0**	**1.8**	**2.8**		**1.8**
			RP	Lcr1		18	29		18	1.0	2.5	3.5		2.5
			RV	Lcr2		16			13	1.0	1.2			1.2
			LR	Lcr3		4	14		5	1.0	1.8	2.0		1.8
Urban	Yes	L		**Yew (all)**		**13**			**11**	**1.0**	**1.3**			**1.2**
			LV	Yew1		13			11	1.0	1.7			1.6
			LV	Yew2						1.0	1.0			1.0
			RP	Yew3						1.0	1.0			1.0
Urban	Yes	R		**Rio (all)**		**7**	**14**		**7**	**1.0**	**1.3**	**1.7**	**2.0**	**1.4**
			RP	Rio1						1.0	1.3	1.3		1.3
			RP	Rio2			14		2		1.7	1.9	2.0	1.8
			RP	Rio3		7			5	1.0	1.2			1.2
Urban	Yes	R		**Priest (all)**	**100**	**11**			**15**	**1.1**	**1.2**			**1.2**
			RP	Priest 1		7			6	1.0	1.1			1.1
			RP	Priest 2	67	2			5	1.3	1.0			1.2
			RV	Priest 3	50	2			4	1.1	1.8			1.5
Wild	No	L		**Quito (all)**		**11**			**9**		**2.1**	**2.4**	**2.5**	**2.3**
			LR	Quito 1		2			1		2.0	3.0		2.5
			LR	Quito 2		2			2		2.2	2.4	2.3	2.3
			LR	Quito 3		2			2		2.1	2.3	2.6	2.3
			LR	Quito 4		5			4		2.1	2.0		2.1
				ALL SITES	5	19	11	0	15	1.0	1.5	2.1	2.4	1.6

[1] Hydrologic setting: river (R) and lacustrine (L)
[2] Population source: local Remnant (LR), local volunteer (LV), restoration planting (RP), restoration volunteer (RV)
[3] Population labels: the Gila River (Gilla), Gilbert Riparian Preserve (Gilbert), Goose Flats at the Lower Colorado River (Lcr), Yuma East Wetlands (Yew), Rio Salado Habitat restoration area at the Lower Salt River (Rio), Priest at the lower Salt River (Priest) and Quitobaquito Springs (Quito)
[4] Percent mortality by size classes: 1 (seedling, sapling; .5-2cm), 2 (young; 3-14cm), 3 (mature; 15-30cm), 4 (old; 31-45)
[5] Average biotic damage scores by size classes