

Is drought altering plant populations in the mountainous region of Northeastern Mexico?

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Abstract – Mortality in six plant species was examined in the vegetation of a mountain region in Northeastern Mexico and hypotheses of survival pathways within populations in the ecosystem were tested. Significant differences in the general mortality pattern were found among species indicating species-specific responses to stress gradients. Average mortality differed among species: *Yucca carnerosana*, 33.8%; *Pinus cembroides*, 29.9%; *Larrea tridentata*, 25.9%; *Hechtia podantha*, 13.7%; *Agave lechuguilla*, 13.0%; and *Thelocactus santaclarensis*, 9.0%. Within populations, mortality increased with water stress and survivorship increased with less stressful environments. Results from this study may be useful for the development of a management plan to support the conservation and sustainable use of forest vegetation in this mountain community.

Keywords: *Agave lechuguilla*, climate change, *Hechtia podantha*, *Larrea tridentata*, *Pinus cembroides*, *Thelocactus santaclarensis*, water stress, *Yucca carnerosana*

Introduction

Climate change has been linked to drastic vegetation shifts (VITOUSEK et al. 1997, HUGHES 2000, MENZEL et al. 2006), which could alter plant (MCLACHLAN et al. 2005) and animal (PETERSON et al. 2002) distributions. Projected changes include increased frequency and severity of droughts (IPCC 2001). This in turn could have numerous consequences for ecosystems (WRIGHT 1992, CORLETT and LAFRANKIE 1998, CURRAN et al. 1999, HARRISON 2000), because severe or frequent droughts may cause drastic changes in the vegetation, mainly in arid and semi-arid ecosystems (ALLEN and BRESHEARS 1998, HANSON and WELTZIN 2000). The research required to provide a better understanding of the effect of drought is necessarily complex (VAN NIEUWSTADT et al. 2005). Plants in Northeastern México are adapted to regularly occurring droughts and inter-annual variation in rainfall (GARCÍA

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2011). For the mountain vegetation of Northeastern México there are no studies examining the effects of drought on plant survival, and little is known about what factors affect the probability of mortality in woody plants during a severe drought. Furthermore, it is unknown how the vegetation of the mountains in Northeastern Mexico will respond to climate change. Mortality rates of species may be decisive for future predictions of climate change effects. The aim of this research was to examine the factors associated with plant mortality and pathways to survival (plant size, nursery, competition, soil type, shade, understory plants and nurse stones). Nursery, shade and understory vegetation are mechanisms of plant-plant facilitation and promote plant establishment. Two major hypotheses were tested: (1) mortality among species differs due to species-specific responses and to genetic variability in resistance to stressors, and (2) between populations, plant survival varies throughout the ecosystem due to environments that are more or less stressful. Determining the effect of drought on mortality and survival of the species studied across the region will contribute to predicting future vegetation distributions on regional scales and incorporate climate change predictions into conservation efforts.

Materials and methods

Study site and species

High mortality of trees of an entire ecosystem subjected to the adverse effects of drought can be exacerbated by climate change, but at the same time provides an opportunity to test hypotheses on present and future plant composition. To examine drought effects on plant species in this mountain community, a study was conducted in Ascension Aramberri Nuevo Leon Mexico (24°20'14"N, 99°56'35.9"W, at 2190 m a.s.l.). The climate is cool, medium dry with an annual rainfall of 423 mm. Rain falls mainly in late summer and early autumn. Mean annual temperature is 14.9 °C, with a maximum of 22.8 °C in summer and a minimum of -3 °C in winter. Examination of patterns of mortality and survival of plants was conducted between summer 2007 and the winter of 2012. The most frequent and abundant plant species distributed in the area were chosen: (1) *Pinus cembroides* Zucc. (Pinaceae), which in the mountain region represents a dominant plant that provides habitat and ecosystem structure; (2) *Larrea tridentata* (Moç. & Seseé ex DC.) Coville (Zygophyllaceae), dominant in the semiarid zone, and four species distributed in both ecosystems; (3) *Yucca carnerosana* (Trel.) McKelvey (Agavaceae); (4) *Hechtia podantha* Mez (Bromeliaceae); (5) *Agave lechuguilla* Torr. (Agavaceae), and (6) *Thelocactus santaclarensis* Halda, Kupcák & Sladk. (Cactaceae). The seeds of the first species are collected for human consumption and species 3 and 5 are used for the extraction of natural fiber.

Mortality among species

To test for differences in mortality levels among species due to drought effects, in the fall of 2008 a minimum of 40 plots for each species were established. For all species eight different locations were selected in areas where the species are widely distributed; in each site, five plots were established. Plot size varied between species: (i) for *Yucca carnerosana* 50 × 50 m; (ii) 40 × 40 m for *Pinus cembroides*; (iii) 20 × 20 m for *Larrea tridentata*, *Hechtia podantha* and *Agave lechuguilla*; and (iv) for *Thelocactus santaclarensis* plots were of 10 × 10 m. The 240 plots were within a radius of 25 km. Each plant was classified as living or dead, with the assumption that a lack of living structures was evidence of mortality.

Survival pathways within populations

To determine survival pathways, mortality events and factors associated with increased survival such as: plant size, nursery, competition, soil type, shade, understory plants and nurse stones, were documented.

According to FRANCO et al. (1994), *L. tridentata* extracts ground water near the surface and small shrubs recover faster from drought than large shrubs. To test whether smaller plants were more resistant to drought, in spring 2010, in four randomly selected chaparral systems, mortality was estimated along six 50-m transects and plants were classified each as living or dead and plant size for *L. tridentata* ≤ 1.0 and > 1.0 m was recorded.

To test whether mortality of *Y. carnerosana* is decreased if it grows in association with *P. cembroides*, mortality rates of *Y. carnerosana* in an area visually dominated by *P. cembroides* were contrasted with those in an adjacent area nearly devoid of *P. cembroides*. In the spring of 2009 we chose twelve sites that included both *P. cembroides* sites and sites without *P. cembroides*. In each site we sampled along two 200 m by 50 m belt transects across the study area. Plants were classified as living or dead and whether they occurred: (i) with *P. cembroides* or (ii) not.

To determine whether soil type had an effect on mortality and survival of *H. podantha*, three soil types were chosen: Lithosols, soil with small trees; rendzina, soil with high organic matter associated with *P. cembroides*, and griese (gypsisol) without trees. In summer of 2011 ten random (20 × 20 m) plots were established, on each soil type in three communities. Every *H. podantha* within a plot was classified as living or dead, and mortality levels between the three soils were compared.

To determine if *A. lechuguilla* grows more often under other plants, and whether shade is an important factor determining survival, in the fall of 2009 twenty plots of 20 × 20 m were established in areas where the studied species was abundant. Each *A. lechuguilla* was recorded as growing: (i) in direct sunlight or (ii) under the canopy of another plant, and each individual in the plots was classified as living or dead.

To test the hypothesis that seedlings of *P. cembroides* growing in association with understory vegetation had a higher survival rate, in the winter of 2008, (a year with high seed production) four locations were selected in each site. Seedlings of *P. cembroides* were located along twenty 100-m transects and classified as growing in association with: (i) understory vegetation (forbs, grasses, shrubs and cacti, Tab. 1), (ii) under the *P. cembroides* canopy, and (iii) on cleared soil, devoid of vegetation. Seedling survival was monitored each season recording live and dead individuals in each environment until the winter of 2011. The percentage of seedling survival based on the number of live plants/total seedling × 100 was calculated.

The nurse association may be biotic, as with nurse-plants, or abiotic, as with rocks, where there are some reports of cacti growing preferentially near rocks, and hence the rocks provide a microhabitat that favors seedling establishment and survival (PARKER 1987). Rocks act as moisture-collectors and delay evaporation by shading (REYES-OLIVAS et al. 2002). To test whether *T. santaclarensis* populations increased with distance to small semi-buried stones, or those growing at least 0.5 cm from a small stone fixed to the ground, in the summer 2007 seven localities were chosen with similar elevations and slopes, and four 100 m-long transects 2 m wide were randomly placed. Recruitment levels of *T. santaclarensis* with three levels of stoniness (low $\geq 25\%$; medium < 25 and $\leq 50\%$ and high $> 50\%$) were correlated.

Tab. 1. Taxonomical list of seedlings of understory vegetation found in the summers between 2009–2011; seedlings were within a 20-cm radius of seedlings of *Pinus cembroides*.

| Family species | 2009 | 2010 | 2011 |
|--|------|------|------|
| Acanthaceae | | | |
| <i>Justicia runyonii</i> Small | 76 | 81 | 52 |
| <i>Ruellia rudiflora</i> (Gray) Urban. | 14 | 89 | 21 |
| <i>Stenandrium dulce</i> (Cav.) Nees | 43 | 112 | 25 |
| Agavaceae | | | |
| <i>Agave lechuguilla</i> Torr. | 37 | 61 | 55 |
| <i>Agave striata</i> Zucc. | 34 | 42 | 36 |
| <i>Yucca carnerosana</i> (Trel.) McKelvey | 17 | 22 | 19 |
| <i>Yucca filifera</i> Chabaud | 10 | 18 | 15 |
| Amaranthaceae | | | |
| <i>Amaranthus</i> sp. | 21 | 98 | 37 |
| Asteraceae | | | |
| <i>Aster subulatus</i> Michx. | 55 | 143 | 66 |
| <i>Helianthus annuus</i> L. | 47 | 95 | 0 |
| <i>Sanvitalia ocyroides</i> DC. | 109 | 222 | 56 |
| <i>Verbesina encelioides</i> (Cav.) Gray. | 55 | 93 | 16 |
| <i>Viguiera stenoloba</i> Blake. | 45 | 211 | 55 |
| Boraginaceae | | | |
| <i>Heliotropium angiospermum</i> Murray | 72 | 109 | 66 |
| <i>Heliotropium curassavicum</i> L. | 23 | 69 | 17 |
| Cactaceae | | | |
| <i>Opuntia engelmannii</i> Salm-Dyck ex Engelm. | 7 | 11 | 9 |
| <i>Opuntia leptocaulis</i> DC. | 21 | 33 | 33 |
| <i>Opuntia tunicata</i> Lehmann | 10 | 13 | 12 |
| <i>Thelocactus santaclarensis</i> Halda, Kupcák & Sladk. | 56 | 57 | 56 |
| Chenopodiaceae | | | |
| <i>Chenopodium album</i> L. | 27 | 76 | 17 |
| <i>Suaeda torreyana</i> S. Watson | 74 | 145 | 62 |
| Convulvulaceae | | | |
| <i>Convolvulus arvensis</i> L. | 26 | 92 | 76 |
| <i>Evolvulus alsinoides</i> L. | 18 | 54 | 21 |
| Euphorbiaceae | | | |
| <i>Croton torreyanus</i> Muell. Arg. | 32 | 44 | 41 |
| <i>Euphorbia dentata</i> Michx. | 45 | 56 | 49 |
| <i>Tragia ramosa</i> Torr. | 29 | 45 | 31 |
| Fabaceae | | | |
| <i>Acacia greggii wrightii</i> (Benth.) Isely | 9 | 11 | 10 |
| <i>Canavalia villosa</i> Benth. | 17 | 20 | 18 |
| <i>Desmanthus virgatus</i> (L.) Will | 7 | 8 | 7 |

Tab. 1. – continued

| Family species | 2009 | 2010 | 2011 |
|--|------|------|------|
| Lamiaceae | | | |
| <i>Salvia coccinea</i> Juss. | 27 | 31 | 30 |
| Malvaceae | | | |
| <i>Abutilon</i> sp. | 47 | 61 | 41 |
| <i>Hibiscus cardiophyllus</i> Gray. | 12 | 34 | 29 |
| <i>Sida neomexicana</i> Gray. | 31 | 35 | 29 |
| Papaveraceae | | | |
| <i>Argemone echinata</i> Ownb. | 66 | 79 | 74 |
| Poaceae | | | |
| <i>Aristida</i> sp. | 28 | 31 | 29 |
| <i>Botriochloa</i> sp. | 42 | 45 | 33 |
| <i>Botriochloa</i> sp.2 | 28 | 38 | 36 |
| <i>Bouteloua trifida</i> Thurb | 19 | 21 | 32 |
| <i>Cenchrus incertus</i> M.A. Curtis | 99 | 145 | 139 |
| <i>Chloris submutica</i> H.B.K. | 30 | 29 | 32 |
| <i>Pennisetum ciliare</i> (L.) Link. | 45 | 138 | 131 |
| <i>Tridens</i> sp. | 98 | 119 | 121 |
| <i>Rhynchelitrum repens</i> (Willd) C.E. Hubb. | 79 | 99 | 84 |
| Solanaceae | | | |
| <i>Physalis pubescens</i> L. | 78 | 99 | 92 |
| <i>Solanum rostratum</i> Dunn. | 40 | 48 | 31 |
| Urticaceae | | | |
| <i>Urtica dioica</i> L. | 34 | 33 | 24 |
| Verbenaceae | | | |
| <i>Lantana velutina</i> Mart. & Gal. | 29 | 38 | 27 |

To test whether microhabitat had an effect on *T. santaclarensis* survival, three experiments were conducted: (1) in early autumn of 2007 four sites were chosen; at each site, ten plots of 10 × 10 m were established. Percentage of seedling survival was recorded, on three contrasting microhabitats where this species is distributed: (i) on ground with few stones, (ii) on bare soil, and (iii) under a dense canopy. In each environment (2) soil moisture and (3) dew were determined; the gravimetric method was used to determine moisture, and dew was determined with the method used by REYES-OLIVAS et al. (2002), collecting water on pairs of 95 cm² disks of Whatman filter paper no. 1 placed on polyethylene plates; 10 plates were placed in bare soil and beneath the canopy and 10 at stony sites. Disks were opened on one occasion in December 26, 2008, from 7.00 pm to 7.00 am. Seedling survivors were monitored each month in each plot until the winter of 2010; each individual of *T. santaclarensis* in the plots was classified as living or dead.

To avoid double counting of new seedlings; seedlings were referenced on sketches in the winter of 2008 for *P. cembroides* and early autumn of 2007 for *T. santaclarensis*.

Statistical analyses

To contrast mortality levels among species, average percent mortality was compared using ANOVA ($\alpha = 0.05$). All data were arcsine transformed to conform to a normal distribution assumption, previous to ANOVA (SOKAL and ROHLF, 1995). Tukey multiple means of comparisons were used when the ANOVA indicated significant differences. Ninety-five percent confidence intervals were used in graphics to highlight differences for each species. To determine whether *L. tridentata* mortality occurred more often than expected by chance, mortality levels of *L. tridentata* ≥ 1.0 m and < 1.0 m were compared with goodness-of-fit test for Poisson χ^2 -test. Wilcoxon test for paired samples was conducted to determine mortality and survival levels of *Y. carnerosana* in and out of *P. cembroides* areas. The Kruskal-Wallis test for comparison of k independent samples was used to determine mortality and survival between soil types for *H. podantha*. A t-test for paired means of two samples was used to determine whether individuals occurred under other plants more often than expected by chance, and to determine if *A. lechuguilla* grew more often under other plants. All data were log transformed to conform to the normal distribution assumption, previous to t-test. To test the hypothesis that seedlings of *P. cembroides*, in association with understory vegetation, had increased survival rates, Friedman test was carried out. To test whether *T. santaclarensis* populations increased with distance to small stones, recruitment levels of *T. santaclarensis* with the percentage of *T. santaclarensis* associated to small stones were correlated. A regression analysis and an ANOVA ($\alpha = 0.05$) were carried out to test if the slope b1 differed from 0. ANOVA ($\alpha = 0.05$) was used to determine the effect of microhabitat on seedling survivors of *T. santaclarensis*; previous to ANOVA ($\alpha = 0.05$) data were transformed to conform to a normal distribution assumption. Differences in soil moisture and dew were determined with Friedman test.

Results

Plant mortality between species

The effect of drought on plant mortality significantly differed among species ($F = 6.82$, d. f. = 239, $p < 0.001$; Fig. 1). *Y. carnerosana*, *P. cembroides* and *L. tridentata* had greater mortality (33.8.0%, 29.9% and 25.9%), than *H. podantha* (13.7%), *A. lechuguilla* (13.0%),

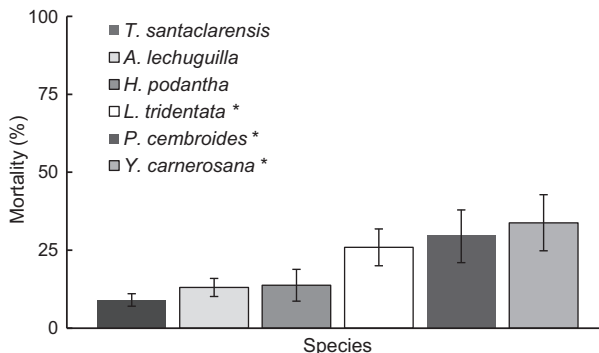


Fig. 1. Mortality between species. * indicates significant differences detected with Tukey's test. Error bars represent the confidence intervals ($\alpha = 0.05$).

and *T. santaclarensis* (9.03%). Percentage of mortality by species exhibited significant variability, indicating that the effects of drought although widespread, differed among species.

Survival pathways within populations

A total of 1324 *L. tridentata* plants were recorded, from which 105 plants > 1.0 m and 33 plants ≤ 1.0 m died, giving 7.93 and 2.49% mortality levels, respectively. Plants > 1.0 m died more often than expected by chance ($\chi^2 = 945$, d. f. = 1, $p < 0.0001$, Fig. 2a). The higher survival of plants ≤ 1.0 m, may be the result of a morphological modification to provide protection from drought.

A total of 1950 plants of *Y. carnerosana* were recorded on the plots and 403 of them died (20.6 % mortality). Plants had higher survival rates when growing with *P. cembroides* (approximately 70.2%); on bare soil areas only 29.7% survived ($Z = 6.48$, $p < 0.001$; Fig. 2b). In the association *Y. carnerosana*-*P. cembroides* the mortality gradient of *Y. carnerosana* may be sharply lower than that present on bare soil, so the increased facilitation by association with *P. cembroides* seems to be related to the provision of moisture.

There were a total of 3158 *H. podantha* plants, of which 2498 survived, providing a 20.9% mortality. Soils devoid of trees (lithosols and gypsisol) were significantly associated with mortality ($\chi^2 = 12.06$, d. f. = 2, $p < 0.0002$; Fig. 2c). In mountain vegetation when suitable microsities are common, low mortality of *H. podantha* on rendzina soil associated to *P. cembroides* indicates that favorable microsities increase survival. A positive interaction among *P. cembroides* and *H. podantha* may ameliorate stress caused by drought.

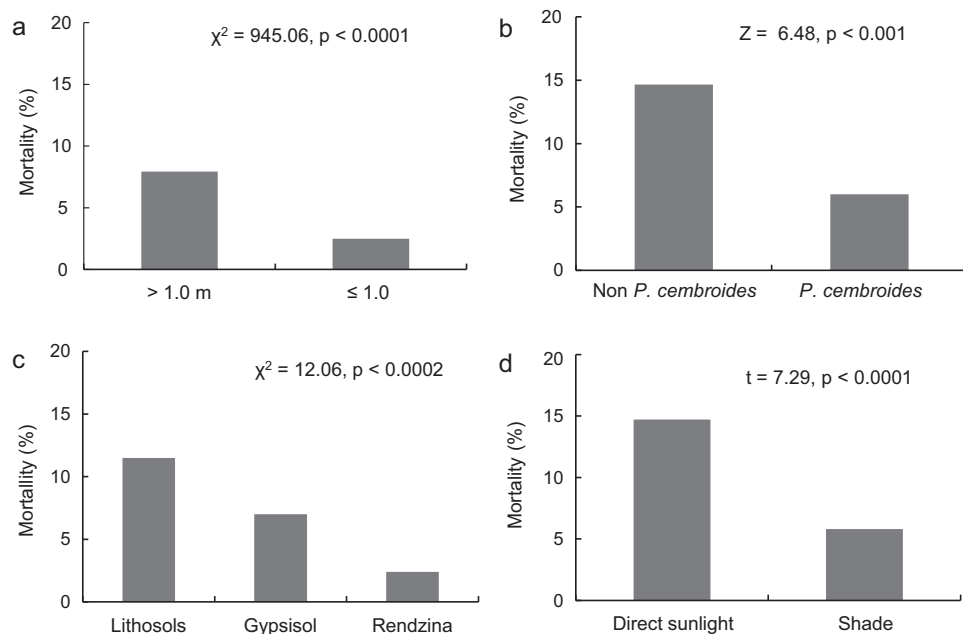


Fig. 2. Plant mortality is a function of: (a) plant size > 1.0 m for *Larrea tridentata*; (b) non-association with *Pinus cembroides* for *Yucca carnerosana*; (c) soil type (lithosols and gypsisol) for *Hechtia podantha* and (d) direct sunlight for *Agave lechuguilla*.

A total of 1427 plants of *A. lechuguilla* were detected in shade and under direct sunlight from which 293 were recorded as dead (20.52% mortality). Shaded plants showed low mortality (5.81%), whereas those exposed to direct sunlight showed high mortality (14.71%; $t = 7.29$, d. f. = 19, $p < 0.0001$; Fig. 2d).

Survival of *P. cembroides* differed according to the environmental conditions ($X^2_r = 12.31$, d. f. = 2, $p < 0.05$; Fig. 3a). It was higher for seedlings in understory vegetation (36.1%), lower under canopy (19.5%) and lowest on bare soil (8.8%). In this environment stress due mainly to drought might have caused the death of most of the seedlings. Results indicate that survival was higher under nurse plants that might provide a shield against stressful environmental conditions.

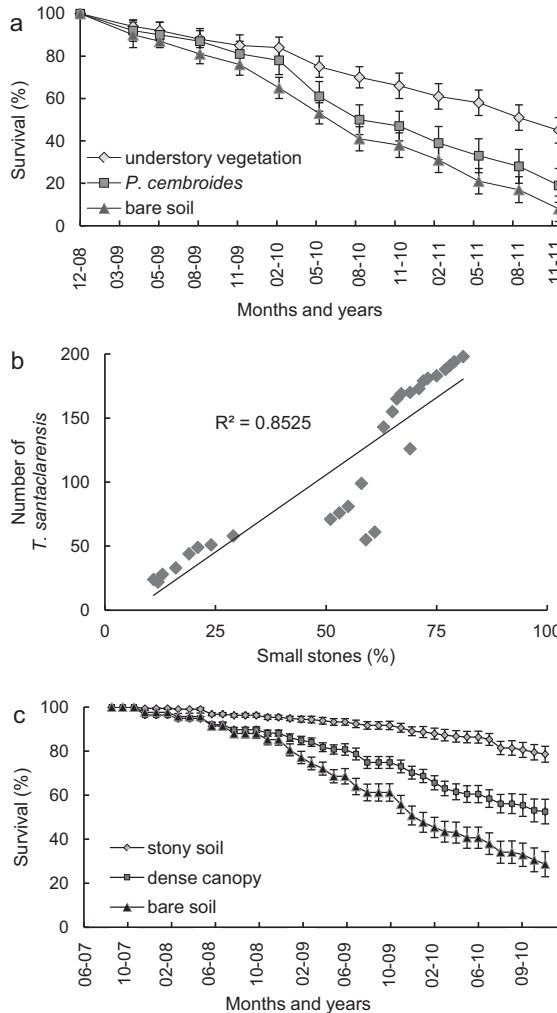


Fig. 3. Plant recruitment and seedling survival as a function of understory vegetation for *Pinus cembroides* (a) increased % of small stones (b) and association with stony soil for *Thelocactus santaclarensis* (c).

Recruitment of *T. santaclarensis* was positively correlated with small stones ($F = 113.07$, $p < 0.001$, $R^2 = 0.8525$; Fig. 3b). A total of 3167 individuals of *T. santaclarensis* were recorded on transects where there were a greater number of seedlings.

There were a total of 1214 *T. santaclarensis* plants: 566 on stony soils, 390 under the canopy of *P. cembroides* and 258 on bare soil respectively. Survival differed among habitats, with higher survival of *T. santaclarensis* ($F = 49.63$, d. f. = 15, $p < 0.001$, Fig. 3c) on stony soil than under dense closed canopy and on bare soil. Low moisture in the soil might have caused death of most of the seedlings. On stony soil, positive interactions between rocks and *T. santaclarensis* influenced seedling survival during consecutive years (Fig. 3c). Soil moisture differed according to the microenvironment ($X^2_r = 7.45$, d. f. = 2, $p < 0.05$) (stony soil $14.13 \pm 1.11\%$; border $10.55 \pm 0.97\%$ and under a dense canopy $8.31 \pm 1.45\%$). Dew collected differed between microenvironments ($X^2_r = 9.31$, d. f. = 2, $p < 0.05$) with 1.41 ± 0.22 g collected on stony soil; 1.39 ± 0.30 g on bare soil and 0.71 ± 0.11 g under dense closed canopy.

Discussion

Mortality among species

Except for *Y. carnerosana* mortality was lower for species growing in both ecosystems (*H. podantha*, *A. lechuguilla* and *T. santaclarensis*), with dominant species and *Y. carnerosana* showing localized patterns of very high mortality (23 to 81%). Water stress may cause changes in plant community composition and structure (SHILO-VOLIN et al. 2005, WEIGELT et al. 2005), and in some cases, they may also reverse the competitive hierarchies of plant species (FYNN et al. 2005). Drought effects caused widespread high mortality among species (9.03 to 33.8%, Fig. 1). Shrubs and tree species (*Y. carnerosana*; *P. cembroides* and *L. tridentata*, Fig. 1) were more susceptible to drought due to the inherent differences among species, to species-specific responses and to genetic variability in resistance to stressors. Changes in patterns of mortality may also modify plant populations in this mountain community, and affect the entire ecosystem, which could have major impacts on local diversity (GITLIN et al. 2006).

Survival pathways within populations

L. tridentata plants ≤ 1.0 m were more resistant to drought effects (Fig. 2a). Low moisture and water limitation due to stressful conditions limited survival of plants > 1.0 m, because of size differences among plants (both above and belowground). Plant response may vary according to microenvironmental differences (FRAZER AND DAVIS 1988). In the arid and semi-arid regions where the species is distributed, soil wetting does not penetrate to a depth of 0.6 m (FRANCO et al. 1994). Therefore, small plant roots may be exposed to greater soil water availability. Previous studies have determined that adult trees are more sensitive than juveniles, with more positive responses to precipitation, and more negative responses to temperature (SUAREZ et al. 2004).

Mortality was higher in *Y. carnerosana* growing outside *P. cembroides* vegetation (Fig. 2b), and this positive interaction between *P. cembroides* and *Y. carnerosana*, suggests positive survival effects through increased water or nutrient availability (HOLZAPFEL and MAHALL 1999) inducing an increase in seedling survival.

Mortality of *H. podantha* was higher on lithosol and gypsisol soils (Fig. 2c), and survival was higher in rendzina, perhaps because this soil is rich in humus and soil fertility (JOERGENSEN 1991).

Death of *A. lechuguilla* plants was attributed to stress on bare soil (Fig. 2d). Shade provided by *P. cembroides* improved survival of *A. lechuguilla*. Seedling survival of *A. lechuguilla* has been shown to be higher under reduced direct solar radiation (FRANCO and NOBEL 1989), and lower soil temperatures (FLORES-MARTÍNEZ et al. 2004). Shade from nurse plants reduces thermal amplitudes and decreases soil water evaporation (DOMINGO et al. 1999), and also reduces thermal stress and transpiration of understory plants, thereby protecting them from photo-inhibition (NOBEL 1980, VETAAS 1992, MORO et al. 1997). This in turn may further increase plant survival. SEMCHENKO et al. (2012) determined a positive effect of shade on plant growth by amelioration of stress or active regulation of growth rate. Moreover, high light intensity may promote seedling survival through fungal pathogen suppression (AUGSPURGER 1983). These findings indicate stage-specific patterns of plant survival in environments that experience severe drought. However higher frequency of severe drought may increase plant mortality, which may occur in rapid pulses rather than gradual declines (GITLIN et al. 2006). Hence high plant mortality may inhibit the ability of local populations to recover and expand into more hospitable environments (HEWITT and KELLMAN 2004).

Understory plants increased the survival of *P. cembroides* (Tab. 1; Fig. 3a), where nurse plants ameliorated environmental conditions that affected seedling survival. Previous studies have shown that the presence of vegetation may protect establishing seedlings against high radiation, high temperatures and losses of soil moisture, thereby increasing survival (CALLAWAY 1995, CASTRO et al. 2002, GÓMEZ-APARICIO et al. 2004).

Recruitment of *T. santaclarensis* was positively correlated with small stones (Fig. 3b) due to the plants' ability to develop root systems close to rocks (NOBEL et al. 1992; NOBEL and ZUTTA 2005). A positive interaction between *T. santaclarensis* and small stones promoted survival (Fig. 3b), where small stones act as collectors of dew (LARMUTH and HARVEY 1978). Higher soil moisture and dew under stones than under *P. cembroides* and on bare soil suggests that water availability (Fig. 3c) is key for survival. In dry habitats such as those found in this mountain vegetation, drought is the major constraint on seedling survival and competition for water is often more important than competition for light or nutrients (CASPER and JACKSON 1997).

Mortality patterns were a function of plant size > 1.0 m for *L. tridentata*; non-association with *P. cembroides* for *Y. carnerosana*; soil type for *H. podantha* and direct sunlight for *A. lechuguilla* (Figs. 2a–d). Survival within populations increased with size ≤ 1.0 m for *L. tridentata*; association with *P. cembroides* for *Y. carnerosana*; rendzina soil type for *H. podantha* and shade for *A. lechuguilla* (Figs. 2a–d). The high variation in mortality within populations shows high-stress sites and might be utilized to investigate the role of sites of increased stressor conditions for seedling survival. The overall patterns of survivorship found are consistent with the hypothesis that greater survival is associated with less stressful environments.

Results from this study show that seedlings of *P. cembroides* died on bare soil and under *P. cembroides*, with understory plants having a higher survival (Tab. 1; Fig. 3a). When abiotic stress is high due to drought exacerbated by climate change, positive interaction by facilitation is important (BERTNESS and CALLAWAY 1994, CALLAWAY et al. 2002) to mitigate those negative effects.

A positive interaction between small stones and *T. santaclarensis* increased survival (Figs. 3b–c). Stony soil favors plant survival due to its capacity to retain moisture (Fig. 3b), while under dense closed canopy and in bare soil habitats (Fig. 3c) mortality is attributed to lack of moisture. It has been suggested that rocks may act as good moisture-collectors (REYES-OLIVAS et al. 2002). While facilitation of recruitment by ‘nurse’ plants has been widely documented (FLORES and JURADO 2003), nurse rocks have been poorly documented. However research does report positive interactions between cacti and rocks (PARKER 1987, 1989, NOBEL et al. 1992), where rocks ameliorate stressor conditions; this provides a fresh and moist environment without reducing sunlight (PETERS et al. 2008). Furthermore small rocks protect seedlings from freezing temperatures (NOBEL 1980).

Implications for management

The effects of drought on plants can affect associated community members across trophic levels (GITLIN et al. 2006, JOHNSON et al. 2011) and can be expected to affect entire ecosystems (WIMP et al. 2004, BANGERT et al. 2005). Changes in above-ground–below-ground linkages in response to drought may influence plant communities in the future (JOHNSON et al. 2011) and have evolutionary consequences (GRANT and GRANT 1993, 2002, NEVO 2001). In the context of climate change, ecosystem managers should consider the promotion of plant recruitment through intensification of activities such as soil conservation. High stress sites could be used to determine implications on changes in plant diversity and abundance.

The ecosystem of the mountains of this region could be especially sensitive to climate change (RISSER 1995, HANSON and WELTZIN 2000), due to high tolerance to low water levels, and may act as barometers of change currently going on in other ecosystems (BROWN et al. 2001, GITLIN et al. 2006).

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