Plant dieback under exceptional drought driven by elevation, not by plant traits, in Big Bend National Park, Texas USA

In 2011, Big Bend National Park, Texas, USA, experienced the most severe single year drought in its recorded history, resulting in significant plant mortality. We used this event to test how perennial plant response to drought varied across elevation, plant growth form and leaf traits. In October 2010 and October 2011, we measured plant cover by species at six evenly-spaced elevations ranging from Chihuahuan desert (666 m) to oak forest in the Chisos mountains (1920 m). We asked the following questions: what was the relationship between elevation and stem dieback and did susceptibility to drought differ among functional groups or by leaf traits? In 2010, pre-drought, we measured leaf mass per area (LMA) on each species. In 2011, the percent of canopy dieback for each individual was visually estimated. Living canopy cover decreased significantly after the drought of 2011 and dieback decreased with elevation. There was no relationship between LMA and dieback within elevations. The negative relationship between proportional dieback and elevation was consistent in shrub and succulent species, which were the most common growth forms across elevations, indicating that dieback was largely driven by elevation and not by species traits. Growth form turnover did not influence canopy dieback; differences in canopy cover and proportional dieback among elevations were driven primarily by differences in drought severity. These results indicate that the 2011 drought in Big Bend National Park had a large effect on communities at all elevations with average dieback for all woody plants ranging from 8% dieback at the highest elevation to 83% dieback at lowest elevations.

1   Elizabeth F. Waring Texas Tech University, Department of Biological Sciences, Lubbock, TX

2   USA

3   Dylan W. Schwilk Texas Tech University, Department of Biological Sciences, Lubbock, TX USA

4   Corresponding Author: Dylan W. Schwilk, Texas Tech University, Department of Biological

5   Sciences, Lubbock TX USA. Email: dylan.schwilk@ttu.edu

1. INTRODUCTION

The study of plant community structure over elevational gradients has played an important role in plant ecology (Merriam 1890, Whittaker 1965, Whittaker & Neiring 1964, 1968). In arid environments, water availability can increase dramatically with elevation and can drive turnover in plant species over short geographical distances (Whittaker & Neiring 1968, Allen, Peet, & Baker 1991). Drought can result in plant mortality or in stem death and partial dieback (Sperry & Ikeda 1997, Jacobson et al. 2008) and can lead to changes in the plant community structure (Lloret, Siscart, & Dalmases 2004). Although precipitation in arid and semi-arid ecosystems is highly variable from year to year (Noy-Meir 1973, Schwinning & Sala 2004), a major decrease in annual precipitation could cause dramatic mortality or dieback for species near the limit of their ecological tolerance (Pockman & Sperry 2000).

The Chisos Mountains of Big Bend National Park in southwest Texas have dense oak-juniper forest communities in the higher elevations while the lower elevation Chihuahuan desert communities are dominated by grasses, succulents, and drought-tolerant deciduous shrubs. The various plant communities in Big Bend National Park would be expected to respond to environmental stress differently due to different species morphology and physiology. Leaf traits can vary greatly among species and across plant communities. A leaf trait commonly used to measure energy invested per photosynthetic return is leaf mass per area (LMA, g/cm^2). Adaptations to prevent water loss, such as fibrous content and pubescence, will cause a thickening of the leaf, increasing its LMA (Monneveux & Belhassen 1996) and there is usually a positive correlation between leaves with a high LMA and drought tolerance (Wright, Reich, & Westoby 2001). However, if a severe drought does cause dieback in plants with high LMA, the greater carbon investment per leaf may require longer post-drought recovery times for

29 construction of new leaves for those species than for species with low LMA (Witkowski &

30 Lamont 1991, Wright et al. 2004).

31   In 2011, Texas experienced the most severe drought in its recorded history (Neilsen-

32 Gammon 2011, Combs 2011), which led to dramatic plant mortality in Big Bend National Park

33 (Poulos 2014, Waring & Schwilk personal observation). This drought was coupled with an

34 unusual multi-day, severe freeze in February 2011, which likely exacerbated the effects of

35 drought in addition to directly causing freezing damage (Poulos 2014). We used this event to test

36 how perennial plant response to extreme drought varied across elevations, plant growth forms

37 and leaf traits. We asked the following questions: What was the relationship between elevation

38 and stem dieback; and were any elevational patterns driven by turnover in functional groups or in

39 leaf trait changes? To answer the second question, we investigated if susceptibility to drought

40 differed among functional groups or by species leaf traits. These questions lead to two competing

41 hypotheses regarding the interaction of drought and elevation. First, we would expect there to be

42 higher proportional dieback at the lower elevational sites due to absolutely lower precipitation

43 during the drought. However, the plants at the lower elevations may have greater physiological

44 tolerances to drought conditions, so a second hypothesis is that we could see less proportional

45 dieback at lower elevations, especially as the 2011 departure from average conditions was greater

46 at higher, rather than lower, elevations.

47 2. METHODS

48 2.1 Site description

49   Plant communities at Big Bend National Park range from succulent and deciduous shrub

50 dominated lowlands, to desert grasslands at mid elevations, to juniper, oak, and pine forest at

51 higher elevations. Precipitation in Big Bend National Park is seasonally uneven (NOAA 2013).

52 There is higher precipitation in the summer and fall months with very little precipitation in the

53 winter and spring (Robertson et al. 2010). After years of wetter than normal conditions, 2011 was

54 an extraordinarily dry year for Big Bend National Park (Neilson-Gammon 2011). The average

55 annual precipitation increases with elevation: at the Chisos Basin meteorological station (1617 m

56 above sea level) annual precipitation averaged 441.7 mm between 1947 and 2012, Panther

57 Junction (1143 m) averaged 333.04 mm between 1955 and 2012, and Rio Grande Village (566

58 m) averaged 167 mm annually in 2006 through 2012 (NOAA 2013). In 2011, however, the

59 Chisos Basin received only 109 mm of precipitation, the Panther Junction Station received 64

60 mm precipitation and Rio Grande Village received 59 mm (NOAA 2013). This drought was

61 coupled with extremely high temperatures in 2011 in Big Bend National Park. Prior to 2011, the

62 Chisos Basin averaged 22 days with temperatures above 32ºC, while Panther Junction averaged

63 106 days, and Rio Grande Village averaged 154 days (NOAA 2013). However in 2011, the

64 Chisos Basin experienced 63 days, Panther Junction had 151 days, and the Rio Grande Village

65 had 234 days above 32ºC (NOAA 2013). In addition to the severe drought, there was a multi-day

66 freeze event in February of 2011 that probably contributed to plant dieback (NOAA 2013, Poulos

67 2014 for the Chisos Basin freeze).

68 We collected data at six elevations within the park (~250 m apart vertically) in autumn of

69 2010 and 2011 (Table 1, conducted under permit BIBE-2010-SCI-0019 to DWS). The lower

70 elevation sites were located along the Ross Maxwell Scenic Drive while the high elevation sites

71 were along the Pinnacles Trail. Sites were selected to be near hiking trails and roads in 2010.

72 Sites were chosen with a north to northwest aspect with the exception of the lowest elevation site

73 which was nearly level. In each of the two sampling years, fifty-meter-long transects were placed

74   randomly within a 500 m radius of the GPS location for each site. The six sites are described in

75   Table 1. Species were identified using Powell (1997) and Mueller (1940).

76   2.2 Canopy cover measurements

77   In 2010 and 2011, 4 to 12 fifty-meter-long line-intercept transects were run perpendicular

78   to the slope at each site. The number of transects was dependent on the density of the cover at

79   each site: sites with higher cover had fewer transects because we aimed for relatively even

80   sampling effort at each site (number of transects per site in Table 1). Transect starting points were

81   selected randomly each year. The intercepted distance of canopy cover was recorded for each

82   individual woody plant. Overlapping canopies were measured individually leading to the

83   possibility of having canopy cover >1. Herbaceous species were not identified to species but

84   were grouped together and bare ground was recorded. In 2011, for each individual woody plant

85   or succulent, the proportion of the total canopy that was dead was visually estimated and

86   recorded as "dieback proportion" for each individual plant (tested by bending small twigs in the

87   case that leaves were missing). Dieback data were not estimated in 2010 after preliminary

88   observations indicated very little dieback (<2% of cover). We classified species according to

89   growth form: tree, shrub, subshrub, or succulent. We defined trees as species that regularly grew

90   as single stemmed individuals > 2 m tall; shrubs as species with mostly multi-stemmed

91   individuals < 2 m; subshrubs as individuals with some above ground woody stem and herbaceous

92   growth above the base that would die back annually (e.g. equivalent to "chamaephyte" in

93   Raunkiær classification, du Rietz 1931), and succulents included individuals of the families

94   Agavaceae, Cactaceae, and Nolinaceae. Transects were treated as replicates nested within a site.

95   All measurements were expressed on a per transect basis for analysis.

96   Total canopy cover for each individual was determined using equation 1.

$$C_i = \frac{\sum L_i}{50} \tag{1}$$

97 Where i represents the individual species, L is the intercepting length of the canopy and 50

98 represents the length of the transect (50 m).

99   The total canopy cover for each transect was determined by equation 2.

$$C_t = \sum_{i=1}^{n} C_i \tag{2}$$

100 Where the sum of all individual plant is determined for each transect. Relative canopy cover was

101 determined using equation 3:

$$R_i = \frac{C_i}{C_t} \tag{3}$$

102   After calculating the total cover of each transect and relative cover, the amount of dieback

103 per individual was calculated using equation 4:

$$D_i = \frac{\sum d_i L_i}{50} \tag{4}$$

104 In equation 4, the nomenclature is the same as equation 1 and d_i is the proportion of observed

105 canopy dieback per individual. Using the dieback per individual, we were able to calculate total

106 dieback (equation 5) and total living canopy cover (equation 6):

$$TD = \sum_{i=1}^{n} D_i \tag{5}$$

$$C_i - ¿ \sum_{i=1}^{n} D_i = C_t - TD \tag{6}$$

$$C_l = \sum_{i=1}^{n} ¿$$

107   Lastly, we calculated the amount of proportional dieback per transect using equation 7:

$$PD_i = \frac{D_i}{C_i} \qquad (7)$$

108   Proportional dieback for a single growth form was the total dieback distance of species in

109   a particular growth form divided by the total cover of that growth form. Proportional dieback was

110   used in all analyses of dieback.

111   In 2010 (pre-drought), we collected 3-8 leaves per individual for 2-3 individuals per

112   species at each elevation. We did not collect leaves from succulents (Cactaceae, Nolinaceae and

113   Agavaceae). We used a flatbed scanner and LAMINA software (Bylesjö et al. 2008) to calculate

114   leaf area. After leaf area was recorded, the leaves were dried for 24 hours at 85 °C and then

115   weighed to determine the dry mass of the leaf. The LMA was calculated as dry mass over area

116   (g/cm^2). The weighted LMA on each transect was the average of the species' LMA values on that

117   transect weighted by each species relative cover.

118   2.3 Statistical Analysis

119   All data were analyzed using R (R Development Core Team 2013). All data were tested

120   using a Shapiro-Wilk test of normality in R which confirmed that the response variables were

121   normally distributed. Statistical differences across elevations were determined using ANCOVA

122   models. For the analysis of total, living, and relative canopy cover, hierarchical linear models

123   were run with elevation and year of data collection as fixed effects. Transects were nested within

124   elevations: with one site per elevation, we have a sample size of six with which to detect

125   elevational trends. Models were fit with the nlme package in R (Pinheiro et al. 2013). For models

126   predicting relative canopy cover and dieback by elevation and growth form, transect was a

127   random effect (due to multiple dieback estimates per transect) within elevation. The data for total

128   and living cover were untransformed because they met the assumption of normality and were not

129   true proportions. However prior to analysis, proportional dieback and relative cover were

130   transformed using an empirical logit transformation $(\ln((p + \varepsilon)/(1-(p + \varepsilon), \text{ where } \varepsilon = 0.0001)$ as

131   those measurements were true proportions (Warton & Hui 2011). For the analysis of wLMA by

132   proportional dieback across elevations, a nested linear model was used (transects nested within

133   elevation). Post-hoc analyses were done on the wLMA and proportional dieback including and

134   excluding the conifer species. Additional analyses where the sites were grouped by high and low

135   elevation were also performed.

136   3. RESULTS

137   Total canopy cover (both living and dead canopy combined) for all growth forms

138   increased significantly with elevation (F=17.34, p=0.014). In 2010 and 2011, the lowest elevation

139   had ~80% less cover than the highest (Fig 1). Total canopy cover did not change significantly

140   between years (F=1.549, p=0.217), but there was a significant interaction between elevation and

141   year (F=6.895, p=0.010) with the highest elevations dropping slightly in total cover by the 2011

142   measurement (possibly a result of a slight underestimation of total cover for trees with some

143   dieback and with leafless canopy that year). The relative cover of the four perennial woody

144   growth forms (trees, shrub, subshrub, and succulent) differed significantly across elevation

145   (empirical logit transformed, F=69.36, p<0.0001, Fig 2). There was no significant difference in

146   relative cover between years and no interaction between year and growth form. Succulent and

147   shrub species were present at all elevations. Subshrubs were present at all elevations except the

148   highest elevation, 1920 m. Tree species were present at the two highest elevations, 1920 and 1690

149   m. Growth forms showed differing elevational patterns in relative cover (significant interaction

150   between growth form and elevation, F=36.57, p<0.0001, Fig 2).

151   Living canopy cover of all woody plants (shrubs, succulents, subshrubs and trees)

152   increased with elevation (F=18.33, p=0.013, Fig 3). Living canopy cover decreased significantly

153   post-drought (F=103.6, p<0.0001) and there was no interaction with elevation: the absolute

154 amount of dieback was consistent across elevations. Because high elevations had much higher

155 initial cover, however, this resulted in much lower proportional dieback at the higher elevations:

156 living canopy cover decreased by 17% at the highest elevation, 1920 m, and by 83% at the lowest

157 elevation, 666 m.

158 Proportion dieback decreased significantly with elevation in succulent and shrub species

159 (logit transformed, F=8.867, p=0.04). There was no effect of growth form on proportional

160 dieback (F=0.844, p=0.473), but there was an interaction between growth forms and elevation

161 (F=7.245, p=0.0002, Fig 4). Proportional dieback for each site varied from 0.90 (succulents at

162 1132 m) to 0.03 (succulents at 1920 m) (Untransformed means, Table 2). The overall elevational

163 trend was driven by succulent and shrub species for which dieback decreased with elevation (Fig

164 4).

165 There was no relationship between wLMA and dieback across transects within elevations

166 (nested ANCOVA, F=2.096, p=0.152). Because conifer and angiosperm leaves differ in gross

167 morphology, we also conducted a similar nested ANCOVA which excluded conifers. Those

168 results were consistent with the analysis including conifers: there was no relationship between

169 wLMA and dieback (F=0.034, p=0.855) nor was there an interaction wLMA and elevation

170 (F=0.550, p=0.463). We also grouped sites into two elevation classes and ran the nested

171 ANCOVA with elevation class ("high" = 1920, 1690, and 1411 m and "low" =1132, 841, 666 m)

172 as a factor. There was no relationship between wLMA and dieback (F=0.992, p=0.326) nor was

173 there an interaction between wLMA and elevation class when conifers were included (F=0.017,

174 p=0.898) or excluded (F=0.088, p=0.768).

175 4. DISCUSSION

176   As in most arid mountain ranges, total woody plant cover increased with elevation

177   (Whitaker & Neiring1964 1965, Fig 1). The lack of significant difference in total canopy cover

178   across years indicates that our sampling methods were consistent across years despite the large

179   amount of dead canopy at some elevations in 2011—with the possible exception that we may

180   have slightly underestimated total cover in 2011 at the highest elevation site (Fig 1). The change

181   in canopy cover from dominantly trees at higher elevations to shrubs at lower elevations was the

182   expected community turnover in Big Bend National Park (Fig 2). Living canopy cover was

183   affected by the drought of 2011 and living cover was significantly reduced in 2011 at all

184   elevations, as would be expected (Fig 3). However, the large degree to which living cover

185   decreased in 2011 (largest decrease at 1411 m from 0.65 to 0.35) was striking. We expected the

186   extreme drought event to overwhelm some of the adaptations that the lower elevation species had

187   for drought. However, as the dieback data indicates, this drought affected all growth forms at all

188   elevations. The impacts of drought across growth forms resulted in the relative abundance of each

189   growth form at a given elevation (measured by living cover) not changing as a result of the

190   drought. Because most of our sites were on a north to northwest facing aspect with less solar

191   radiation than southern aspects, it is likely that the dieback measured in this study is a

192   conservative estimate of the amount of dieback that occurred in Big Bend National Park in 2011.

193   By the end of 2011, the Chisos Basin (1615 m), the Panther Junction (1140 m), and the

194   Rio Grande Village (566 m) meteorological stations had only received about 22%, 21%, and 39%

195   of their normal average precipitation at each location annually (NOAA 2013). This decrease in

196   available water would have increased the likelihood that all woody species experienced stress in

197   xylem transport potentially leading to hydraulic failure. Kukowski, Schwinning, & Schwartz

198   (2012) reported extensive tree dieback due to hydraulic failure in the Edwards Plateau of Central

199   Texas after the 2011 drought. Our study showed total dieback did decrease significantly with

200 elevation and increasing precipitation. Additionally, this drought was coupled with an unusual

201 multi-day freezing event in February 2011 (Poulos 2014, NOAA 2013). The freeze in 2011

202 affected the various elevations differently (Table 3). The interaction of freezing and drought may

203 have exacerbated hydraulic failure (Langan, Ewers, & Davis 1997, Cavender-Bares & Holbrook

204 2001, Martinez-Vilata & Pockman 2002). It is likely that the freeze also contributed to the

205 extensive succulent mortality we witnessed, but there is not an obvious difference in the

206 departure from average across the elevations: at all three meteorological stations, there were

207 about 1.5 times as many freezing days as normal in February 2011 (Table 3).

208   Although the greatest reduction in precipitation and the most prolonged freezing

209 temperatures were at the highest elevations, the effect of the drought (and possibly freezing) were

210 most severe at the lower elevations in terms of proportional canopy dieback (NOAA 2013).

211 Therefore, it seems likely that the more severe effects at low elevation are due to species at those

212 sites being closer to physiological thresholds. This is consistent with our first hypothesis that the

213 lower elevations would experience more dieback due to lower precipitation and/or soil moisture.

214 One site (871 m) defied the trend: this site had less dieback than the next higher site (1132 m, Fig

215 4). This was most likely due to the topography of the site at 871 m. That site was characterized by

216 a gentle slope, but in a drainage that could have led to extra water being funneled to the site

217 through runoff.

218   Overall, the degree to which the drought affected the different growth forms varied with

219 elevation (Fig 4). The overall trend was decreasing dieback with elevation, but this was driven by

220 the dominant shrub and succulent growth forms. Trees only occurred at two elevations and we

221 therefore cannot test an elevational effect. Tree dieback levels were intermediate in comparison

222 with the range of values seen for shrubs across elevations (Fig 4). There was no effect of

223 elevation on dieback in subshrub species. For subshrub species, the lack of differences in dieback

224 was due to where they were located and their responses to drought. There were very few

225 subshrubs at 1690 m, so their dieback would have little influence on the overall dieback for the

226 subshrubs. Additionally, subshrubs have a woody base and herbaceous annual growth. We

227 hypothesize that there was little canopy dieback in subshrubs because, while the woody stems

228 persisted, the herbaceous growth on the subshrubs never leafed out in 2011 due to the drought.

229 The previous year's growth dried and abscised prior to our measurements, therefore there was

230 less cover to measure in 2011. The drought did not affect subshrubs through canopy dieback, but

231 rather through preventing growth.

232 The shrubs were greatly affected by the drought at all elevations lower than 1690 m (Fig

233 4). Plants exhibit different strategies to deal with drought including variation in rooting depth,

234 variation in ability to prevent water loss, and differences in tissue-specific drought resistance

235 (Schwinning & Ehleringer 2001, Chesson et al 2004, Ogle & Reynolds 2004). Despite this, we

236 saw significant mortality across both evergreen and deciduous species. Significant change in total

237 living cover across elevations was driven by the magnitude of dieback in shrub species (Fig 4).

238 The succulent species were expected to be able to tolerate the drought better than the other

239 growth forms as a result of water efficient CAM photosynthesis and large reservoirs of water

240 stored in their stems. However, even for succulents, there was significant dieback at the lower

241 elevations and little dieback at the higher elevations. The severity of the drought (or the

242 combination of drought and freezing) at Big Bend National Park was too stressful for the

243 succulents at the lower elevations.

244 The relationship between elevation and dieback is not explained by differences in

245 wLMA among species for which leaf traits were collected. Leaf traits were only collected on

246 shrub, subshrub, and tree species. There was no relationship between LMA and dieback on a

247 species or growth form basis. The species at the lower elevations are adapted to drought by

248 producing small, easily replaceable leaves, and while investment per leaf area was generally

249 higher at higher elevations, there was no effect of wLMA on dieback within elevations (data not

250 shown). This does not mean that growth form and wLMA were not factors in tolerance to the

251 drought, but with our data, elevation alone is the strongest predictor of the impact of the 2011

252 drought and freeze event. Despite the desert species in the lower elevations having adaptations

253 for drought tolerance, the historic severity of the 2011 drought overpowered those adaptations

254 which led to higher dieback in drought tolerant species.

255 5. CONCLUSION

256   The 2011 drought in Big Bend National Park had a large impact on all plant

257 communities, with the relative effects decreasing with elevation. Our data imply that differences

258 in canopy cover and dieback among elevations were probably driven by differences in absolute

259 drought and freezing severity and not by turnover in growth forms and not by turnover in growth

260 forms, or leaf trait differences. Species turnover within growth forms (e.g. variation in drought

261 tolerance within the diverse shrub group) may have played a role in the elevational trend, but we

262 cannot test that with our data. We can say, however, that the decreasing dieback with elevation

263 was not driven by shifts in the relative abundance of shrubs, succulents and trees. Nor was an

264 easily measurable leaf trait, LMA, driving the observed trend.

265   We cannot distinguish the relative influence of drought and freezing on these

266 communities, but we suspect that freezing may be an important environmental factor in this

267 system. One possibility is that the freezing event most severely impacted low elevation species,

268 and the resultant low elevation mortality masked differences in drought susceptibility (although

269 meteorological data suggest that, historically, winter freezes are just as common at low elevations

270 as they are at the higher). We believe the most likely explanation is that this extreme drought

271 pushed all species to the edge of their tolerances. The widespread dieback of slow-growing shrub

272 and succulent species in the lower elevations of Big Bend National Park will likely have long-

273 term effects on the plant community.

274 Acknowledgements

275 We thank Joe Sirotnak at Big Bend National Park for his assistance and we thank Brandon

276 Pratt and the students in Ecological Strategies of Plants; Will Brewer, Tony Cullen, Shirali Davé,

277 Thomas Fitzgibbons, Maria Gaetani, Nathan Geiger, Hasitha Guvvala, Audrey Harrell, and Caleb

278 Hill for their contributions to data collection. We thank Michael Huston, Rita Quiñones-

279 Magalhães, Susanne Schwinning and an anonymous reviewer for their comments which

280 improved this manuscript.

281 References

282 Allen, R. B., R.K. Peet, & W. L. Baker. 1991. Gradient analysis of latitudinal variation in

283   southern Rocky Mountain forests. Journal of Biogeography. 18:123-139.

284 Bylesjö, M., V. Segura, R.Y. Soolanayakanahally, A.M. Rae, J. Trygg, P. Gustafsson, S. Jansson,

285   & N.R. Street. 2008. LAMINA: a tool for rapid quantification of leaf size and shape

286   parameters. BMC Plant Biology. 8:82. DOI:10.1186/1471-2229-8-82.

287 Cavender-Bares J. & N.M. Holbrook. 2001. Hydraulic properties and freezing-induced cavitation

288   in sympatric evergreen and deciduous oaks with contrasting habitats. Plant, Cell and

289   Environment. 24: 1243-1256. DOI: 10.1046/j.1365-3040.2001.00797.x

290   Chesson, P., R.L.E. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M.S.K. Ernest, A. Sher, A.

291   Novoplansky, & J.F. Weltzin. 2004. Resource pulses, species interactions, and diversity

292   maintenance in arid and semi-arid environments. Oecologia. 141: 236-253

293   Combs, S. 2011.The Impact of the 2011 Drought and Beyond. The office of the State

294   Comptroller of Public Accounts, Texas. Publication No. 96-1704.

295   Du Rietz, G. E. 1931. Life-forms of terrestrial flowering plants. I. Acta Phytogeographica

296   Suecica. 3: 95 pp.

297   Kukowski, K.R., S. Schwinning, & B. F. Schwartz. 2012. Hydraulic responses to extreme

298   drought conditions in three co-dominant tree species in shallow soil over bedrock. Acta

299   Oecologica. 171:1-12.

300   Jacobsen, A. L., R.B. Pratt, S.D. Davis, & F.W Ewers. 2008. Comparative community

301   physiology: nonconvergence in water relations among three semi-arid shrub communities.

302   New Phytologist. 180: 100-113.

303   Langan, S.J., F.W. Ewers, & S.D Davis. 1997. Xylem dysfunction caused by water stress and

304   freezing in two species of co-occurring chaparral shrubs. Plant, Cell & Environment 20:

305   425-437.

306   Lloret, F., D. Siscart, & C. Dalmases. 2004. Canopy recovery after drought dieback in holm-oak

307   Mediterranean forests of Catalonia (NE Spain). Global Change Biology. 10:2092-2099.

308   DOI: 10.1111/j.1365-2486.2004.00870.x

309   Martinez-Vilalta J. & W.T. Pockman. 2002. The vulnerability to freezing-induced xylem

310   cavitation of *Larrea tridentata* (Zygophyllaceae) in the Chihuahuan desert. American

311   Journal of Botany. 89: 1916–1924.

312   Merriam, C. H. 1890. Results of a biological survey of the San Francisco Mountain region and

313   desert of the Little Colorado in Arizona. North American Fauna. 3:1-4.

314   Monneveux, P. & E. Belhassen. 1996. The diversity of drought adaptation in the wide. Plant

315   Growth Regulations. 20:85-92.

316   Muller, C.H. 1940. Oaks of Trans-Pecos Texas. American Midland Naturalist 24: 703–728. DOI:

317   10.2307/2420868.

318   Neilsen-Gammon, J. W. 2011. The 2011 Texas Drought; A Briefing Package for the Texas

319   Legislature. Page 43. Office of the State Climatologist.

320   NOAA. 2013. National Climatic Data Center. http://www.ncdc.noaa.gov/oa/ncdc.html (Accessed 15

321   August 2013)

322   Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual review of ecology

323   and *systematics*. 4:25-51.

324   Ogle, K. & J.F. Reynolds. 2004. Plant responses to precipitation in desert ecosystems: integrating

325   functional types, pulses, thresholds, and delays. Oecologia. 141: 282-294.

326   Pinheiro, J, D. Bates, S. DebRoy, D. Sarkar & the R Development Core Team. 2013. nlme:

327   Linear and Nonlinear Mixed Effects Models. R package version 3.1-109.

328   Pockman, W.T. & J.S. Sperry. 2000. Vulnerability to xylem cavitation and the distribution of

329   Sonoran desert vegetation. American Journal of Botany. 87:1287-1299.

330   Poulos H.M. 2014. Tree mortality from a global-change type drought coupled with a short-

331   duration freezing event in a Southwestern piñon-juniper woodland, USA. PeerJ

332   *PrePrints* 2:e237v1 DOI:http://dx.doi.org/10.7287/peerj.preprints.237v1

333   Powell, AM 1997. Trees & Shrubs of the Trans-Pecos and Adjacent Areas. University of Texas

334   Press, 517 pp.

335   R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for

336   Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

337   Robertson, T.R., J.C. Zak, & D. T. Tissue. 2009. Precipitation magnitude and timing differentially

338   affect species richness and plant density in the sotol grassland of the Chihuahuan Desert.

339   Oecologia. 162:185-197.

340   Schwinning, S. & J.R. Ehleringer. 2001. Water use trade-offs and optimal adaptations to pulse-

341   driven arid ecosystems. Journal of Ecology, 89:464-480. DOI: 10.1046/j.1365-

342   2745.2001.00576.x

343   Schwinning, S. & O.E. Sala. 2004. Hierarchy of responses to resource pulses in arid and semi-

344   arid ecosystems. Oecologia. 141: 211-220. DOI: 10.1007/s00442-004-1520-8

345   Sperry, J. S. & T. Ikeda. 1997. Xylem cavitation in roots and stems of Douglas-fir and white

346   fir. Tree Physiology. 17: 275-280.

347   Warshall, P. 1995. The Madrean Sky Island archipelago: a planetary overview. Biodiversity

348   management of the Madrean Archipelago: the Sky Islands of southwestern United States

349   and northwestern Mexico. USDA Forest Service 5-18.

350   Warton, D.I. & F. K.C. Hui. 2011. The arcsine is asinine: the analysis of proportions in ecology.

351   Ecology. 92:3–10.DOI:http://dx.doi.org/10.1890/10-0340.1

352   Whittaker, R.H. & W.A. Niering. 1964. Vegetation of the Santa Catalina Mountains, Arizona. I.

353   Ecological Classification and Distribution of Species. Journal of the Arizona Academy of

354   Science. 3: 9-34.

355 Whittaker, R.H. & W.A. Niering. 1965. Vegetation of the Santa Catalina Mountains, Arizona: A

356   Gradient Analysis of the South Slope. Ecology. 46:429-452.

357 Whittaker, R. H. & W.A. Niering. 1968. Vegetation of the Santa Catalina Mountains, Arizona III.

358   Species Distribution and Floristic Relations on the North Slope. Journal of the Arizona

359   Academy of Science. 5:3-21.

360 Witkowski, E. T. F. & B.B. Lamont. 1991. Leaf specific mass confounds leaf density and

361   thickness. Oecologia. 88: 486-493.

362 Wright, I.J., P.B. Reich, & M. Westoby. 2001. Strategy shifts in leaf physiology, structure and

363   nutrient content between species of high-and low-rainfall and high-and low-nutrients

364   habitats. Functional Ecology. 15:423-434.

365 Wright, I. J., P.B. Reich, M. Westoby, D. D. Ackerly, Z. Baruch, F. Bongers, J. Cavender-Bares,

366   T. Chapin, J. H.C. Cornelissen, M. Diemer, J. Flexas, E. Garnier, P. K. Groom, J. Gulias,

367   K. Hikosaka, B. B. Lamont, T. Lee, W. Lee, C. Lusk, J. J. Midgley, M.L. Navas, U.

368   Niinemets, J. Oleksyn, N. Osada, H. Poorter, P. Poot, L. D. Prior, V. I. Pyankov, C.

369   Roumet, S. C. Thomas, M. G. Tjoelker, E. J. Veneklaas, & R. Villar. 2004. The worldwide

370   leaf economics spectrum. Nature. 428: 821-827.

Figure 1

Total canopy cover by elevation in 2010 and 2011.

Symbols represent the mean ± 1 standard deviation. Circles and a solid line represent 2010 while triangles and a dashed line represent 2011. There was a significant increase in cover with elevation (F=17.34, p=0.014) and interaction in cover between years and elevation (F=6.895, p=0.010).

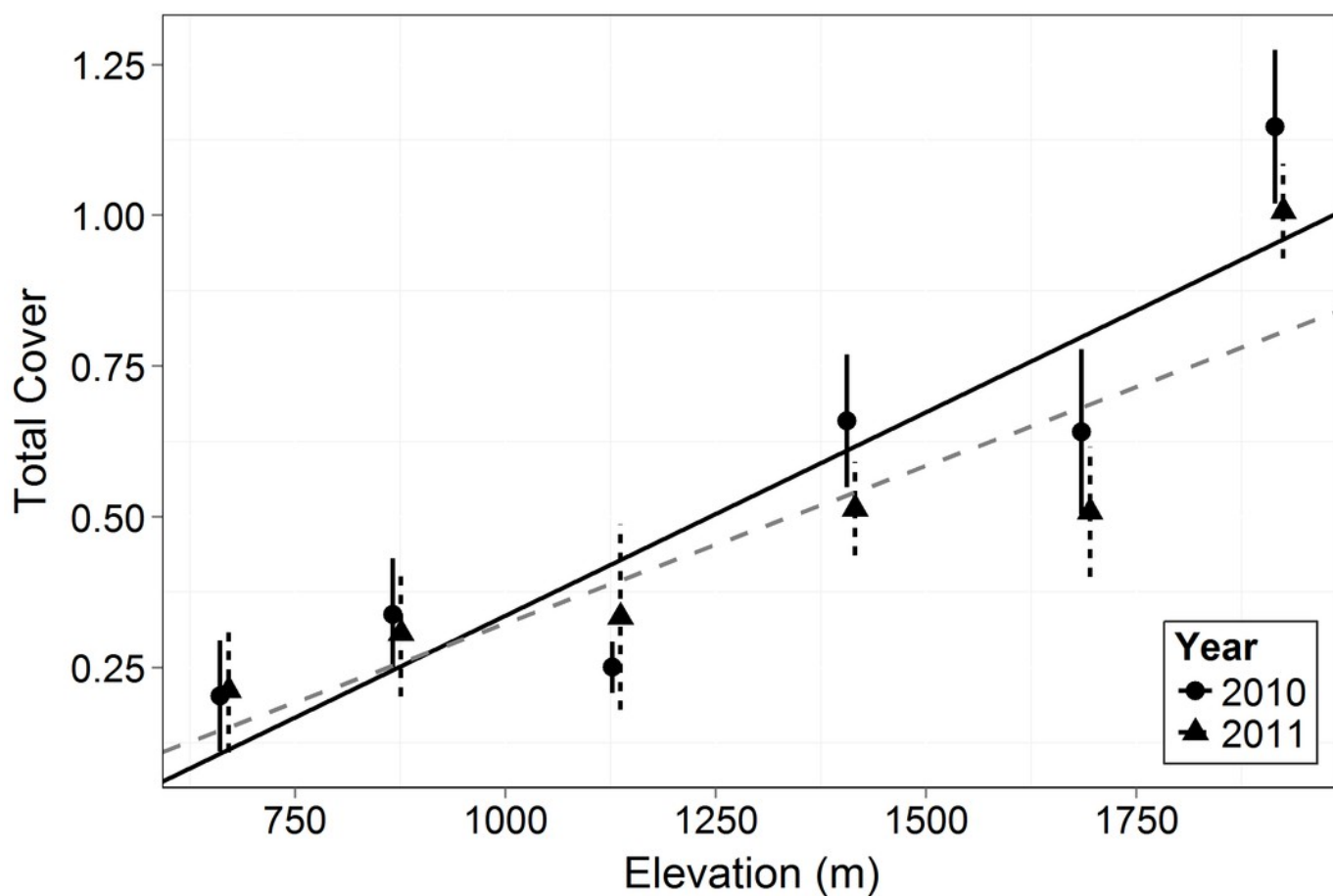



Figure 2

Relative cover (logit transformed) of different growth forms by elevation in 2010.

Figure shows the cover of each growth form relative to the total canopy cover (see equation 3). This figure shows the changes in growth forms on an elevational gradient. Circles represent the mean ± 1 standard deviation. Only 2010 is shown in the figure as there was no significant difference between years ($F=3.473$, $p=0.064$). There was no significant difference among the growth form cover across elevations ($F=0.0466$, $p=0.840$). However, there was a significant difference in the relative cover of the growth forms ($F=69.36$, $p<0.0001$) and in the interaction of growth form with elevation ($F=36.57$, $p<0.0001$).

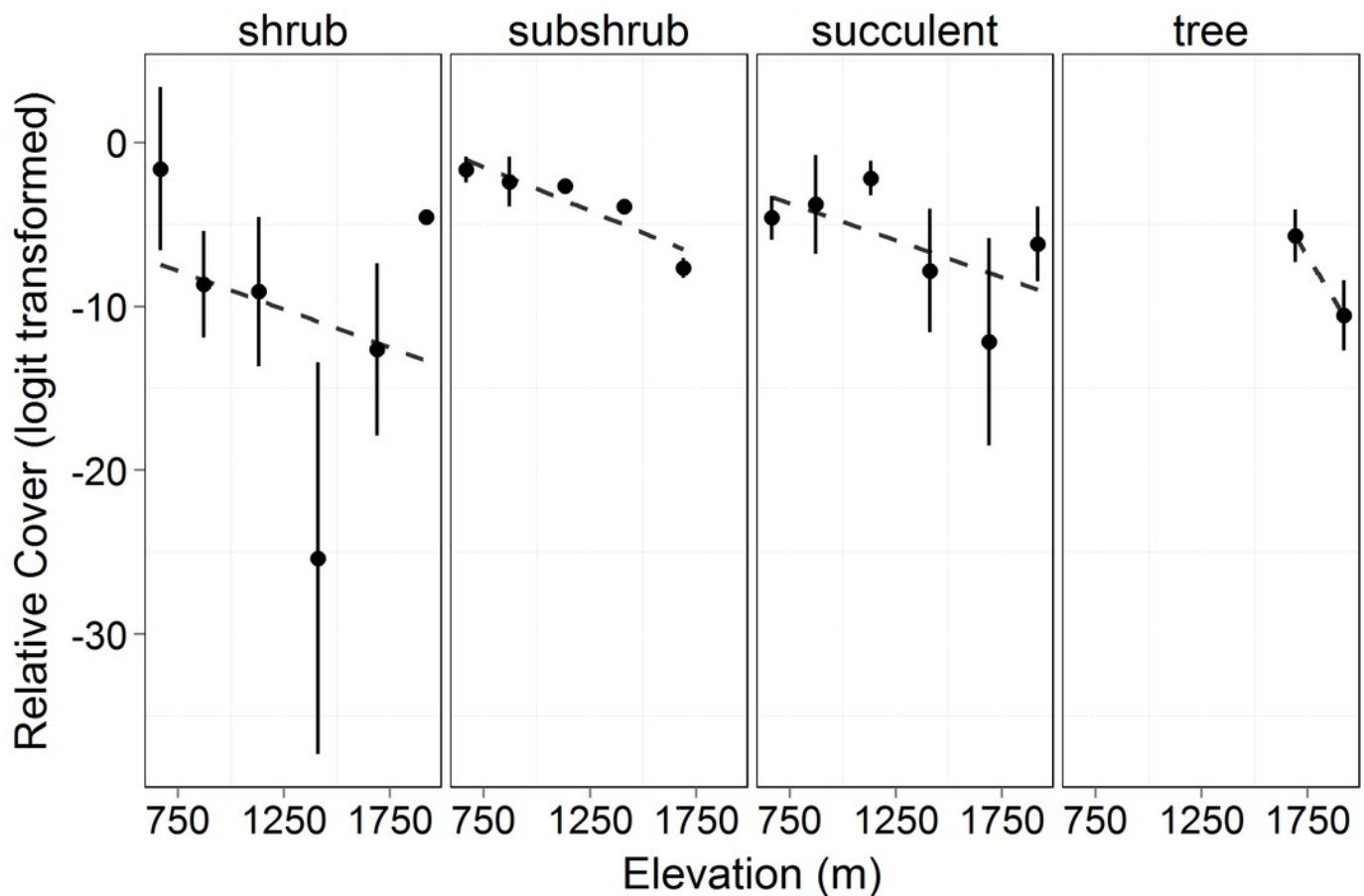



Figure 3

Total living canopy cover by elevation in 2010 and 2011.

Symbols represent the mean ± 1 standard deviation. Circles and a solid line represent 2010 while triangles and a dashed line represent 2011. Living cover increased significantly with elevation (F=18.33, p=0.013) and there was a significant decrease in 2011 compared to 2010 across elevations (F=103.6, p<0.0001).

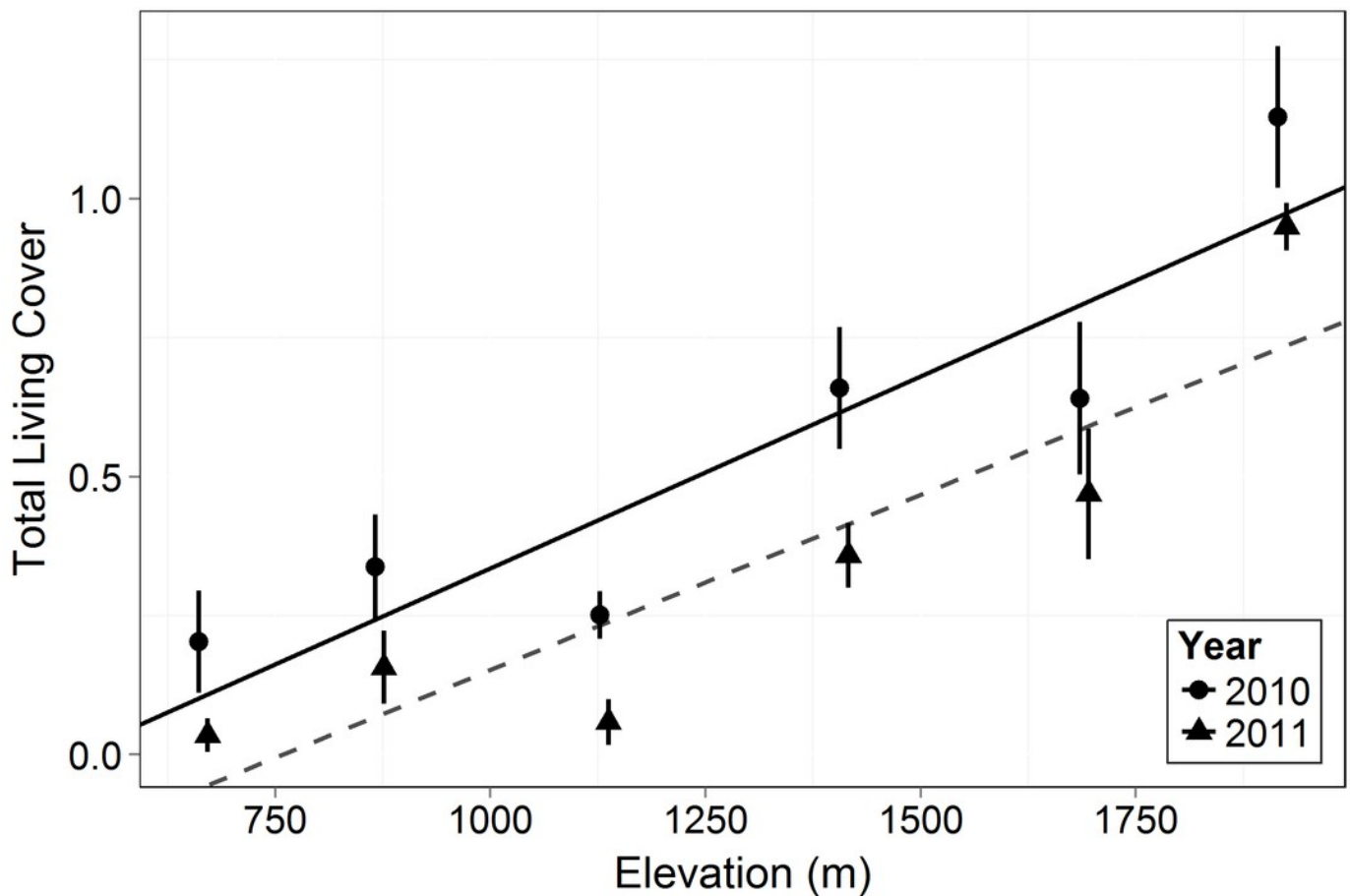
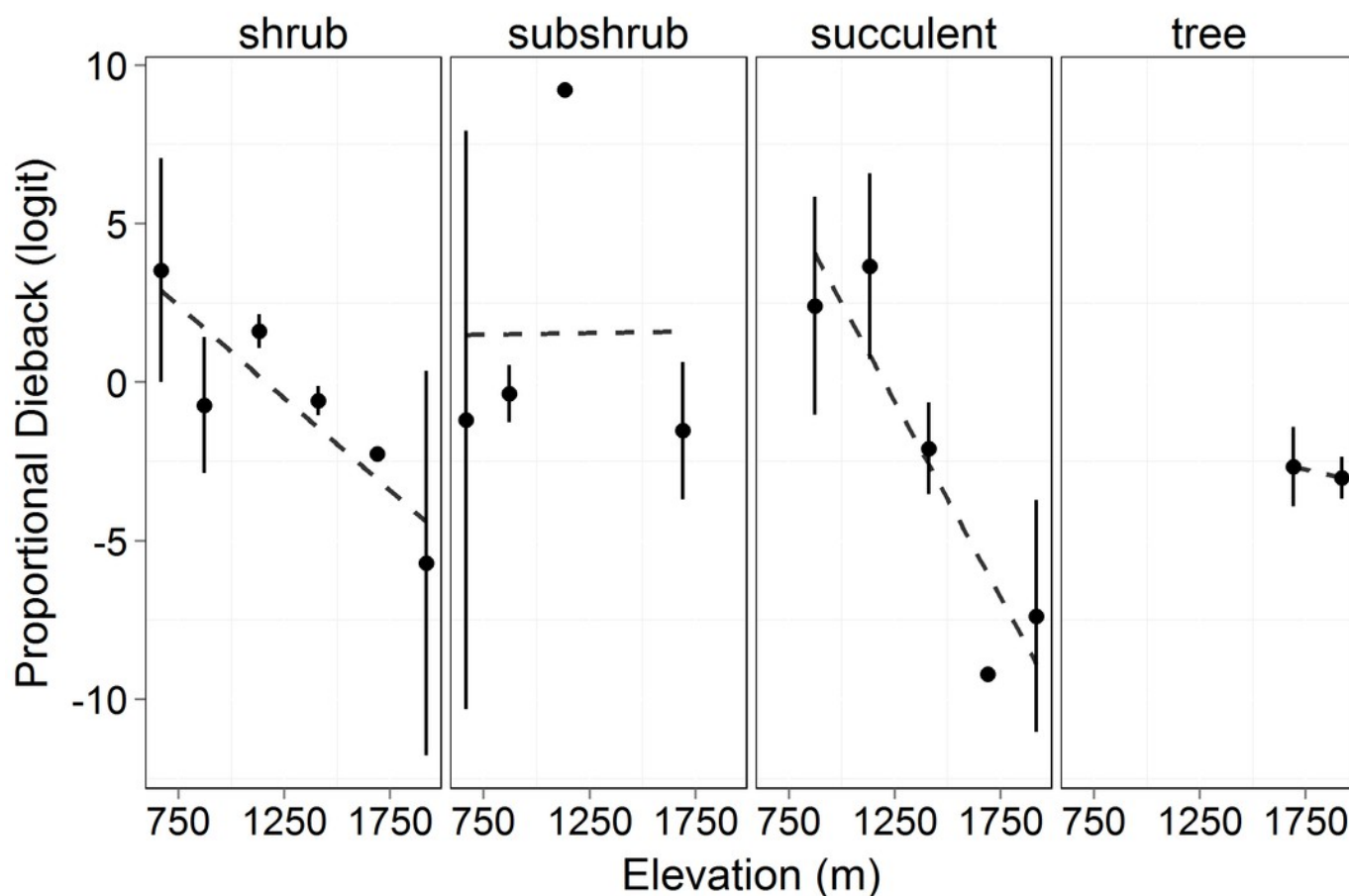



Figure 4

Proportional canopy dieback (logit transformed) in 2011 by elevation.

Circles represent the mean ± 1 standard deviation. Figure shows the amount of dieback at each elevation in proportion to the amount of total cover measured (see equation 7). Transformed proportional dieback decreased with elevation across all growth forms (F=8.867, p=0.04). There was no significant difference in proportional dieback among growth forms (F=0.844, p=0.473), but there was an interaction between growth form and elevation (F=7.245, p=0.0002).

Site descriptions.

A description of the each collection site as well as information of the woody species that were

present at each site.

Elevation (m)	Location (latitude and longitude)	Number of Transects	Dominant Growth Form	Most Common Species in Transects	Aspect
666	29° 8.24' N 103° 30.8' W	12	Deciduous shrub	*Larrea tridentata*	Flat
871	29° 10.8' N 103° 25.8' W	10	Desert shrub	*Agave lechuguilla* *Jatropha dioica* *Larrea tridentata*	Flat
1132	29° 21.2' N 103° 16.7' W	9	Desert shrub	*Acacia greggii* *Agave lechuguilla*	Flat
1411	29° 18.2' N 103° 15.9' W	7 (2010) 5 (2011)	Shrub	*Acacia constricta* *Dasylirion leiophyllum* *Opuntia chisosensis*	North
1690	29° 16.0' N 103° 18.1 W	4 (2010) 5 (2011)	Tree	*Juniperus* species (*J. coahuilensis, deppeana,flaccida,* and *pinchotii*) *Opuntia chisosensis*	Northwest
1920	29° 15.2' N 103° 18.0' W	4	Tree	*Juniperius deppeana* *Quercus* species (*Q. emoryii, gravesii,* and *grisea*)	Northwest

Proportional dieback of growth forms by elevation.

Each cell shows the untransformed mean proportional dieback of each growth form across elevations ± 1 standard deviation. The bottom row is the total mean of proportional dieback for all growth forms at each elevation. If a growth form was not measured at an elevation, it is represented with a NA.

	1920 m	1690 m	1411 m	1132 m	871 m	666 m
Shrub	0.26±0.45	0.10±0.02	0.36±0.11	0.82±0.08	0.35±0.28	0.85±0.12
Subshrub	NA	0.29±0.20	NA	1.00±0	0.42±0.19	0.42±0.49
Succulent	0.03±0.07	0±0	0.17±0.14	0.90±0.11	0.74±0.32	NA
Tree	0.05±0.03	0.10±0.07	NA	NA	NA	NA
Total	**0.10±0.23**	**0.11±0.14**	**0.27±0.16**	**0.88±0.11**	**0.50±0.31**	**0.68±0.38**

	Chisos Basin (1615 m)			Panther Junction (1140 m)			Rio Grande Village (566 m)		
	Average Minimum Temperature (°C)	Zero Degree Days	Freezing Days	Average Minimum Temperature (°C)	Zero Degree Days	Freezing Days	Average Minimum Temperature (°C)	Zero Degree Days	Freezing Days
Nov	7.2 (6.2)	0 (0.45)	1 (9.0)	7.4 (6.8)	0 (0.11)	1 (2.6)	3.5 (4.0)	0 (0)	3 (5.4)
Dec	4.7 (3.4)	0 (0.26)	4 (5.9)	4.4 (3.0)	0 (0.19)	4 (7.8)	-1.9 (-0.6)	0 (0)	21 (17.8)
Jan	3.3 (2.8)	0 (0.05)	6 (3.0)	2.6 (2.3)	0 (0.46)	10 (10.0)	-1.5 (-1.2)	0 (0.2)	21 (20.6)
Feb	3.3 (4.0)	3 (0.11)	10 (3.7)	2.4 (4.1)	2 (0.23)	10 (5.7)	-1.8 (-1.2)	2 (0.5)	15 (11)
Mar	12.0 (6.8)	0 (0.31)	0 (8.4)	11.1 (7.6)	0 (0)	0 (2.2)	8.5 (6.0)	0 (0)	0 (3.8)
Total	**6.1 (4.6)**	**3 (1.18)**	**21 (30)**	**5.6 (4.8)**	**2 (0.99)**	**21 (29.29)**	**1.4 (1.4)**	**2 (0.7)**	**60 (58.6)**