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Variability in needle morphology and water status of *Pinus cembroides* across an elevational gradient in the Davis Mountains of west Texas, USA[1]

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POULOS, H. M. AND G. P. BERLYN (Yale School of Forestry and Environmental Studies, Yale University, Greeley Memorial Laboratory, 370 Prospect St., New Haven, CT 06511, USA). Variability in needle morphology and water status of Pinus cembroides across an elevational gradient in the Davis Mountains of west Texas, USA. J. Torrey Bot. Soc. 134: 281–288. 2007.—The pinyon pines (Pinaceae, Pinus subsections Cembroides and Rzedowskianae) are a widely distributed group of site generalist species that dominate many of the middle to upper elevation semi-arid regions of North America. We investigated the physiological and morphological response of Pinus cembroides var. bicolor Little across an elevational gradient in the Davis Mountains of west Texas to test the hypothesis that variability in needle morphology, relative water content, and transpiration allow this species to exist across a range of elevations and local site conditions. Results from our study showed significant increases in P. cembroides needle length, mass, and area and plant water status (relative water content and transpiration) with elevation. Our findings suggested that this species is able to adapt to changes in local environment over short distances, which is an important factor responsible for the wide distribution of pinyon pines in North America.

Key words: elevation gradient, gradient analysis, needle morphology, *Pinus cembroides*, pinyon pine, transpiration, pinyon-juniper woodlands, water relations.

Pinyon pines (Pinaceae, *Pinus* subsections *Cembroides* and *Rzedowskianae*) are some of the most widely distributed trees in the semi-arid regions of the northern hemisphere (Fig. 1). They dominate over 325,000 square kilometers in North America. Their latitudinal range spans from southern Idaho in the United States (42°N) to southern Puebla, Mexico (18°N), and their longitudinal distribution covers a similarly large portion of North America from Puebla (97°W) to California (120°W) (Fig. 1) (Aldon and Springfield 1973, Barger and Ffolliot 1972, Little 1999). The biogeographic range of the pinyon pines is large compared to many other pine species in southwestern North America (i.e., *Pinus strobiformis* Englem., *P. arizonica* Englem., *P. flexilis* James, *P. leiophylla* Schltdl. & Cham., *P. engelmannii* Carrière, *P. ayacahuite* Ehrenb. ex Schltdl.), which are generally more restricted in their geographic and elevational distributions (Hanawalt and Whittaker 1976, Neiring and Lowe 1984, Bailey and Hawskworth 1987, Allen et al. 1991, Poulos et al. in press).

Water availability is the most limiting factor to tree growth in the Southwest (Meko et al. 1995, Hidalgo et al. 2001, Adams and Kolb 2005), and the drought tolerance of pinyon pines in this region is considered the primary factor regulating their distributions across climatic and soil moisture gradients (Barton 1993, Barton and Teeri 1993, Lajtha and Getz 1993, Linton et al. 1998). Moisture and temperature can vary more than twofold over elevational gradients inhabited by Southwestern pinyon pines (West 1988), with a generally increasing trend in moisture and decreasing trend in temperature with elevation (Barry 1992). These changes in local environmental conditions with elevation are presumed to increase water availability to plants, allowing for increased carbons sequestration and growth (Barnes 1986, Padien and Lajtha 1992, Lajtha and Getz 1993).

The wide distribution of pinyon pines across the elevational gradients of southwestern North America has been quantified in a range of studies (St. Andre et al. 1965, Whittaker and Niering 1965, 1968, 1975, Niering and

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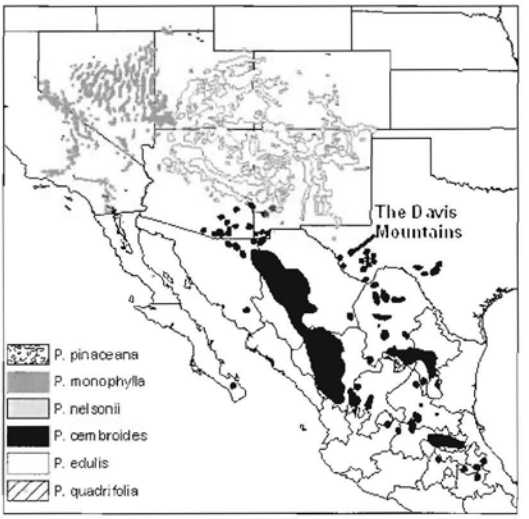

FIG. 1. Distributions of the dominant pinyon pine species in North America. Derived from Little (1999).

Lowe 1985, Barton 1993, Martens et al. 2001, Poulos et al. in press). However, virtually no information exists that identifies the anatomical, morphological, and physiological variability in pinyon pines that underscores their wide distribution across North America (but see Jaindl et al. 1995).

This study examined the ecophysiological mechanisms responsible for the extensive range of Mexican pinyon pine (*Pinus cembroides* var. *bicolor* Little) by measuring a suite of morphological and physiological traits on adult trees that spanned the elevational gradient of The Nature Conservancy Preserve of the Davis Mountains in west Texas (DMTNC). To our knowledge, no previous studies have been conducted on the physiological ecology of this species, though it is the most common and economically important pinyon pine in Mexico (Suzán-Aspiri et al. 2002). We hypothesized that Mexican pinyon pine would respond to changes in environmental conditions along the elevational gradient through variation in needle morphology, plant water status, and transpiration.

Materials and Methods. SITE DESCRIPTION. The Nature Conservancy Preserve of the Davis Mountains is located in Jeff Davis County in the Trans-Pecos region of western Texas (Fig. 1). The Davis Mountains (30° 50′ N; 103° 50′ W) comprise the largest mountain range in Texas, spanning from 1525 to 2555 m in elevation. The forests of DMTNC are dominated by pinyon-juniper-oak and mixed-conifer woodlands. Chihuahuan desert grasslands bound the site at lower elevations, and relict montane conifer forests form the upper elevational boundary (Hinckley 1944). The Davis Mountains are 35–39 million years old, and originated in the same Eocene to Oligocene orogeny that formed most of the Front Range of the Rocky Mountains (Turner 1977). Geologic substrates in DMTNC are derived from the erosional remnant of the once widespread Davis Mountains volcanic field, and consequently, the underlying rocks are predominantly extrusives, consisting of lavas and pyroclastics (Savage and Morin 2002). Soils are generally shallow to moderately deep, and are volcanic in origin.

Pinus cembroides is distributed across the entire elevational gradient of DMTNC. It is the dominant pine species at low elevations, where it exists in association with *Juniperus deppeana*-Steud., and several oak species (*Quercus grisea* Liebm. and *Q. emoryi* Torr.). At middle and upper elevations, it mixes with *P. ponderosa* Douglas ex C. Lawson var. *arizonica* (Engelmann), *P. strobiformis* Engelm., and other oak associates (*Q. grisea, Q. hypoleucoides* A. Camus, and *Q. rugosa* Nee), and it is the highest elevation tree species in the Davis Mountains. We sampled a low (1820 m), an intermediate (2113 m), and a high (2513 m) elevation stand of *P. cembroides* trees to test the hypothesis that leaf morphology and water relations in *P. cembroides* vary according to elevation, and that such variation allows this species to colonize the range of available sites in DMTNC.

The distribution of *P. cembroides* is limited to west Texas and southern New Mexico in the United States, though it spans a wide geographical range in Mexico (Fig. 1) (Little 1999). The Davis Mountains form part of the northern limit of the distribution of *P. cembroides*, being replaced by *Pinus edulis* Engelm. in the Guadalupe Mountains, which is the next mountain range 200 km to the north.

The climate is arid, characterized by cool winters and warm summers. Mean annual precipitation is 400 mm in Ft. Davis, Texas, and is distributed bi-modally in late-summer and winter with the majority of precipitation falling as rain in the summer as part of the

North American Monsoon System (Bomar 1995). Mean monthly minimum temperatures range from 0.0 °C in January to 17.7 °C in July, while mean monthly maximum temperatures range from 15.5 °C in January to 32.6 °C in June.

FIELD SAMPLING. Sun needles of *Pinus cembroides* were sampled on the top branches of 15 trees at 1820 m, 2113 m, and 2513 m elevation ($n = 45$) at DMTNC on May 24, 2004. The 1820 m site represented the lower end of the range of *P. cembroides* in these mountains, and the 2513 m site represented the highest elevation stand of trees in the Davis Mountain Range. Branches were chosen from vigorous canopy trees that were approximately 15 cm diameter at breast height and 8 m tall in an effort to sample trees that were similar in size and age. Tree height was measured using a Laser Tech Impulse 200 (Laser Technology Inc., Centennial, CO). Branches were cut with a pole cutter from the top of the canopy with a southern exposure following DeLucia and Berlyn (1984).

RELATIVE WATER CONTENT AND TRANSPIRATION DECLINE CURVES. Leaf relative water content (RWC) was determined for 5 needles on 15 trees at each elevation ($n = 75$). RWC for needles on each tree were averaged, providing a sample size of $n = 45$. While, two and three needle fascicles were present on *Pinus cembroides*, only three needle fascicles were chosen for use in this experiment to preserve uniformity in the sampling design. Needles were detached and immediately weighed on a portable digital balance (Acculab model PP-2060, Newtown, PA) to obtain their fresh weight (FW). Needles were then saturated in water to full turgor by immersing them in water and leaving them in the dark for 24 h. Needles were reweighed to obtain their turgid weight (TW) and put into an oven at 70 °C to dry the needles while preventing case hardening. After 3 days, the needles were weighed. Then, needles were placed in a 100 °C oven for 2 days and reweighed. Needles were placed back in the 100 °C oven until they reached a constant mass to obtain their dry weight (DW). RWC was calculated as: $RWC = (FW - DW)/(TW - DW) \times 100$.

The rate of water loss was measured gravimetrically on 2 twigs of 15 trees at each elevation ($n = 30$). Samples were recut under degassed distilled water immediately after returning from the field. They were then placed upright in test tubes and left in diffuse light for 48 hours prior to the experiment. At the onset of the experiment, twigs were removed from the test tubes, blotted dry, weighed, and placed horizontally on screen racks. Twigs were reweighed on an electronic balance periodically for the next 15 h. The temperature ranged from 16.7–20.5 °C during the course of the experiment. The relative humidity was not controlled, and ranged from 16–30 %. At the end of the experiment, twigs were oven dried at 70 °C until they reached a constant mass, and weighed a final time to obtain their dry mass.

Transpiration was measured using transpiration decline curves as the rate of water loss over time (mg min^{-1} g dry $mass^{-1}$) (Jarvis and Jarvis 1963). It was assumed that the stomata were fully open at time 0, and that stomatal and cuticular transpiration could be differentiated by a slowing in the transpiration rate upon closure of the stomata based on previous work by DeLucia and Berlyn (1984), who found this to be true for *Abies balsamea* (L.) P. Mill.

MORPHOLOGICAL MEASUREMENTS. Morphological measurements were made on 75 needles from each elevation. Needle area (cm^2) and needle length (mm) were measured using a CID-202 Leaf Area Meter (CID Inc., Camas, WA). Leaves were then oven dried at 70 °C to a constant mass to determine their dry mass. LMA (mg cm^{-2}) was calculated as the ratio of leaf dry weight to leaf area.

STATISTICAL ANALYSES. Differences in RWC, leaf area, needle length, needle mass and LMA among the three sites were analyzed using a general linear model procedure (GLM). Elevational differences in stomatal and cuticular transpiration were analyzed by a mixed model repeated measures procedure with elevation as a fixed effect. All statistical analyses were performed using the R Statistical Language (R Development Core Team 2006).

Results. All measures of needle morphology showed significant linear, increasing trends with elevation ($P < 0.05$) except LMA (Table 1, Fig. 2). Low elevation (1820 m)

Table 1. Needle morphology and relative water content (RWC) of *Pinus cembroides* along the elevational gradient in DMTNC. Mean values for the traits are reported for each elevation. Standard errors are reported in parentheses.

Site	RWC (%)	Needle area (cm^2)	Needle length (mm)	Needle mass (mg)	LMA (mg cm^{-2})
1820 m	44.46 (2.07)	1.25 (0.02)	30.69 (0.05)	106.9 (7.13)	82.9(19.21)
2113 m	66.05 (1.83)	2.07 (0.06)	33.85 (0.03)	132.1 (8.81)	74.6 (14.03)
2513 m	70.58 (1.25)	2.29 (0.05)	36.88 (0.03)	223.3 (14.89)	122.6 (38.92)
P	0.041	0.0001	0.0001	0.0400	n.s.

pinyons had the smallest (1.25 cm^2) and shortest (20.69 mm) needles with the least mass (132.1 mg). Pinyon needle morphology was intermediate at middle elevations (2113 m) compared to the other two sites, with mean values of 2.07 cm^2 for needle area, 33.85 mm for needle length, and 132.1 mg for mass. High elevation (2513 m) pinyon needles were the largest (2.29 cm^2), longest (22.85 mm), and heaviest (223.3 mg) of all needles, suggesting greater carbon assimilation in needles of high elevation pinyons relative to other elevations.

Needle RWC also showed a significant increasing trend with elevation ($P = 0.04$), indicating a rise in plant water status along the elevational gradient of DMTNC. Mean values were 44.46% at 1820 m, 66.05% at 2113 m, and 70–58% at 2513 m elevation.

Stomatal and cuticular transpiration did not exhibit linear relationships with elevation. The stomatal and cuticular phases of transpiration were differentiated by the slowing in water loss that took place 60 minutes after excision (Fig. 3). Stomatal transpiration did not differ by elevation ($P = 0.12$). Cuticular transpiration differed between the sites ($P = 0.05$), and the rate of branch water loss increased with elevation ($P = 0.05$) (Fig. 3). Middle elevation branches had the lowest transpiration throughout the experiment. Transpiration was highest for low elevation branches during the stomatal phase of transpiration, followed by high-, and then mid-elevation branches. High elevation branch transpiration surpassed middle and low elevation water loss during the cuticular phase of transpiration after stomatal closure.

Discussion. The variability in *Pinus cembroides* morphology and water relations was manifested by a positive relationship between elevation and RWC, needle length, needle mass, and needle area. The changes in *P. cembroides* needle morphology and plant water status with elevation potentially reflect the adaptation of each pinyon pine population to local environmental conditions, explaining why this species is able to exist across a wide range of site conditions.

The low stomatal and cuticular transpiration of mid-elevation pinyon pine branches relative to other elevations suggests that these individuals may have been the most adapted to variable environmental site conditions.

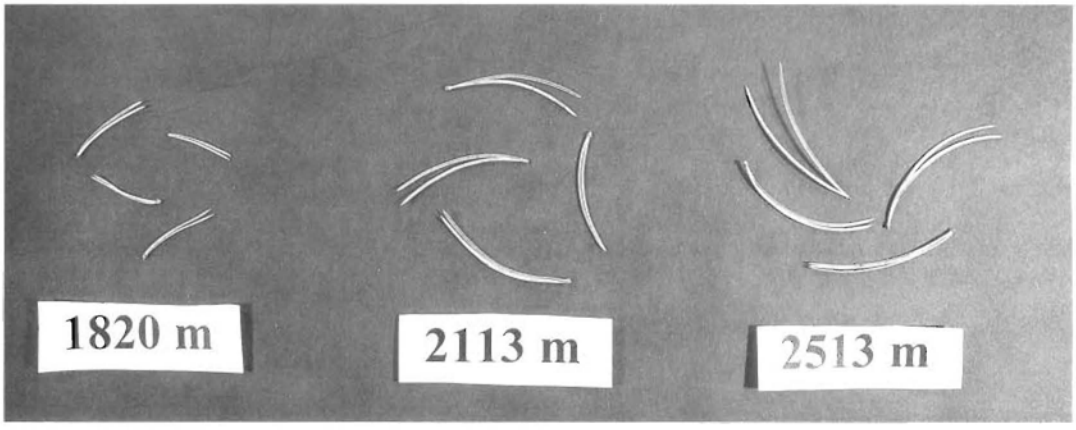

FIG. 2. Morphological characteristics of *Pinus cembroides* needles at 1820 m, 2113 m, and 2513 m elevation.

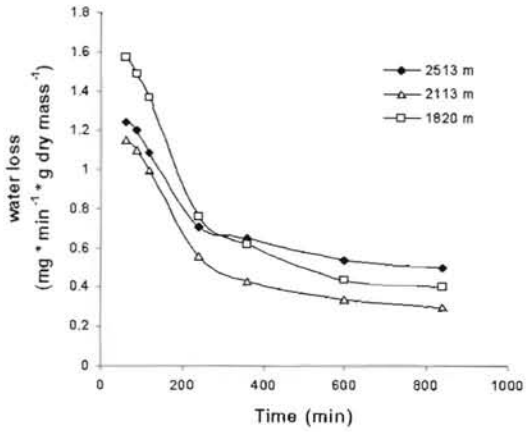

FIG. 3. The rate of water loss per gram dry weight of needles excised from mature twigs of *Pinus cembroides*. Each point represents a mean rate for that time interval and was plotted at the center of that interval. Means were calculated from 15 individuals from 1820 m, 2113 m, and 2513 m elevation.

Their location in between the hot, dry conditions of low elevations and the cooler, wetter environments of upper elevations in DMTNC may mean that these individuals were exposed to a wider range of environmental conditions than Mexican pinyon pines at other elevations, and their low transpiration rates during the experiment may have reflected this adaptation.

Middle elevations in DMTNC also probably provided more optimum conditions for photosynthesis. The cuticles and total cuticular layer are laid down after the upper cell wall is developed (see Berlyn et al. 1993). This is a secondary allocation and requiring additional carbon. Optimal allocation to the total cuticular layer requires adequate carbon reserves that stressed foliage at low elevations may not provide, which potentially explains the high cuticular transpiration by low-elevation relative to mid-elevation needles.

RELATIVE WATER CONTENT AND NEEDLE MORPHOLOGY. For pines, differences in needle morphology have been suggested as adaptations to water stress (Haller 1965, Neilson 1987, Tausch and West 1987, Jaindl et al. 1995). The trend of increasing needle length, area, and mass with elevation changed in accord with local environmental variability across the elevational gradient. The environmental lapse rate causes lower temperatures and higher relative humidity at higher elevations in montane ecosystems (Barry 1992), resulting in ameliorated growing conditions at high elevations in southwestern North America. Low elevations in the Davis Mountains are hot and dry most of the year. In contrast, high elevations of the Davis Mountains have a more varied climate, with cooler and wetter summer weather, and intermittent below freezing conditions in winter.

Temperature and water availability have major effects on plant growth and carbon assimilation (Taiz and Zeiger 2006). Leaves that develop under conditions of low water supply are usually correspondingly smaller and have a smaller surface area (Billings and Mooney 1968, Larcher 2003, Fitter and Hay 2002). The ameliorated climatic conditions at middle and upper elevations during the growing season in DMTNC were probably responsible for the greater RWC, needle length, needle mass and needle area of Mexican pinyon pine at high elevations. Likewise, the hot, dry environments of low elevations in DMTNC probably similarly limited carbon assimilation.

The relationship between needle morphology and elevation that we observed in *Pinus cembroides* was consistent with other work on conifers in semi-arid regions, although the opposite trend has been observed in montane conifers at higher latitudes. Callaway et al. (1994) found a similar trend of increasing biomass allocation in high versus low elevation *P. ponderosa* var. *scopulorum* Engelm. in another semi-arid locale in Nevada. Leaf mass, sapwood mass, and total tree height increased with elevation and precipitation, and decreased with temperature, suggesting a general trend of increased plant growth with elevation in semi-arid regions of western North America. Yet, the opposite trend has been documented in other alpine regions of North America, where needle area, length, mass, LMA, and epicuticular wax content showed decreasing trends with elevation (DeLucia and Berlyn 1984, Berlyn et al. 1993, Richardson et al. 2001) in response to harsher winter climatic conditions than those in the Davis Mountains, suggesting that these patterns vary with latitude and the length of the elevational gradient

TRANSPIRATION. The low transpiration of middle elevation branches relative to low elevation branches is surprising in light of the smaller needle size of low elevation versus middle elevation Mexican pinyon pines. How-

ever, the trend of greater water loss of *Pinus cembroides* at higher elevations during cuticular transpiration was potentially the product of needles having thinner needle cuticles at high elevations. While we did not measure needle cuticle thickness, it can vary dramatically with elevation and is known to have pronounced effects on transpiration (Gale 1972, Smith and Geller 1979, Berlyn and DeLucia 1984, Berlyn et al. 1993, Apple et al. 2000). Berlyn and DeLucia (1984) and Berlyn et al. (1993) obtained results similar to ours on the relationship between transpiration and needle epicuticular wax content at treeline (~ 1450 m) in *Abies balsamea* on Mt. Moosilauke, NH and in *Picea rubens* Sarg. on Whiteface Mountain, NY, respectively. Likewise, Tranquillini (1979) reported that *Picea abies* (L.) H. Karst. twigs growing at 1940 m had three times the transpiration rate of shoots growing at 1000 m. This suggests that high elevation trees may be more stressed than trees at intermediate elevations, making them unable to allocate carbon to wax production. However, our results appear to be unique for pinyon pine. Previous work on *P. monophylla* Torr. & Frem. in the Great Basin showed no significant seasonal or elevational variation in transpiration, suggesting that this pattern may not be a general trend for pinyon pines as a whole (Jaindl et al. 1995).

Middle elevations likely represented the most favorable growing conditions in DMTNC. This environment probably facilitated greater carbon fixation (i.e., higher photosynthesis) leading to thicker cuticles, greater total cuticular thickness, and reduced transpiration by middle elevation needles. Low elevations represented the hottest and driest growing conditions in DMTNC. The lighter color of low elevation pinyon needles (Poulos, pers. obs.) and the harsher growing conditions probably resulted in lower needle chlorophyll content and photosynthesis, yielding less available carbon for growth. This in turn, could have led to thinner cuticles at low versus intermediate elevations, and higher transpiration by low elevation needles.

Pinus cembroides transpiration was also much lower than other transpiration studies on other short-needle conifers in the United States, highlighting its high drought tolerance relative to other, more-temperate conifers. Stomatal transpiration of *P. cembroides* was half that of *Abies balsamea* on Mt. Moosilauke, NH, though it had needles that were almost twice as long (DeLucia and Berlyn 1984). Similarly, *P. albicaulus* Engelm. had higher transpiration than *P. cembroides* (Adams and Kolb 2005), suggesting that this species is also more drought hardy than other species that are also adapted to harsh, dry conditions near treeline.

PINYON PINE AS A SITE GENERALIST. Results from this study confirm the hypothesis that leaf morphology and water relations in *Pinus cembroides* vary according to elevation, and that such variation allows this species to colonize the range of available sites in DMTNC. This suggests that the wide distribution of pinyon pines across North America is related to its high drought tolerance relative to other pine species, and its ability to adapt to changes in local growing conditions over short distances. The morphological variability in needle characteristics and differences in transpiration of *P. cembroides* across the elevational gradient of DMTNC suggest that this species has the potential to survive under a wide range of climatic conditions. Furthermore, studies of historical (Lanner and VanDevender 1998, Gray et al. 2006) and contemporary (Blackburn and Teuller 1970, Lanner 1981, Bahre 1991) range expansions of pinyon pine support the idea of its ability to thrive under a variety of climate scenarios.

This research represents the only study that has investigated the morphological response of pinyon pine to changes in local environmental conditions across an elevational gradient in North America, and it represents only the second study to examine the influence of elevation on pinyon pine physiology (i.e., Jaindl et al. 1995). Further studies that investigate the morphological, anatomical, and physiological mechanisms that underscore pinyon pine distribution patterns across larger biogeographic areas, in addition to studies of niche differentiation by the range of pinyon pine species, are warranted for furthering our understanding of the mechanisms that underscore the distribution patterns of the pinyon pines of across North America.

Literature Cited

ADAMS, H. D. AND T. E. KOLB. 2005. Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. J. of Biogeog. 32: 1629–1640.

ALDON, E. F. AND H. W. SPRINGFIELD. 1973. The southwestern pinyon-juniper ecosystem: A bibliography. USDA Forest Service Gen. Tech. Rep. RM-4. Ft. Collins, CO.

ALLEN, R. B., R. K. PEET, AND B. L. BAKER. 1991. Gradient analysis of latitudinal variation in Rocky Mountain forests. J. Biogeog. 11: 123–139.

APPLE, M. E., D. P. ORMROD, J. D. LEWIS, D. M. SOUTHWORTH, D. M. OLSZYK, AND D. T. TINGEY. 2000. Morphology and stomatal function of Douglas-fir needles exposed to climate change: elevated CO_2 and temperature. Int. J. Plant Sci. 161: 127–132.

BAHRE, C. J. 1991. Legacy of change: historic human impact on vegetation in the Arizona Borderlands. University of Arizona Press, Tucson, AZ.

BAILEY, D. K. AND F. G. HAWKSWORTH. 1987. Phytogeography and taxonomy of the pinyon *Pinus* subsection *Cembroides*. *In* M. F. Pasini, D. C. Tovar, and E. Peidra [eds.], Proceedings of II Simposio Nacional Sobre Pinos Piñoneros, August 6–8, 1987. Mexico City, Mexico.

BARGER, R. L. AND P. F. FFOLLIOT. 1972. Physical characteristics and utilization of major woodland species in Arizona. USDA Forest Service. USDA Forest Service Res. Pap. RM-83. Ft. Collins, CO.

BARRY, R. G. 1992. Mountain Weather and Climate. 2nd Edition. Routledge, London, UK.

BARTON, A. M. 1994. Gradient analysis of relationships among fire, environment and vegetation in a southwestern USA mountain range. Bull. Torrey Bot. Soc. 121: 251–265.

BARTON, A. M. AND J. A. TEERI. 1993. The ecology of elevational positions in plants: drought resistance in five montane pine species in southeastern Arizona. Am. J. Bot. 80: 15–25.

BERLYN, G. P., A. O. ANORUO, A. H. JOHNSON, D. R. VANN, G. R. STRIMBECK, R. L. BOYCE, AND W. L. SILVER. 1993. Effects of filtered air and misting treatment on cuticles of red spruce needles on Whiteface Mountain, NY. J. Sust. For. 1: 25–47.

BILLINGS, W. D. AND H. A. MOONEY. 1968. The ecology of arctic and alpine plants. Biol. Rev. 43: 481–529.

BLACKBURN, W. H. AND P. T. TUELLER. 1970. Pinyon and juniper invasion in black sagebrush communities in east central Nevada. Ecology 51: 841–848.

BOWMAR, G. W. 1995. Texas Weather. University of Texas Press, Austin, TX.

CALLAWAY, R. M., E. H. DELUCIA, AND W. H. SCHLESINGER. 1994. Biomass allocation of montane and desert ponderosa pine: An analog for response to climate change. Ecology 75: 1474–1481.

DELUCIA, E. H. AND G. P. BERLYN. 1984. The effect of increasing elevation on leaf cuticle thickness and cuticular transpiration in balsam fir. Can. J. Bot. 62: 2423–2431.

FITTER, A. H. AND R. K. M. HAY. 2002. Environmental Physiology of Plants. Academic Press, New York, NY.

GALE, J. 1972. Elevation and transpiration: Some theoretical considerations with special reference to Mediterranean-type climate. J. Appl. Ecol. 9: 691–702.

GRAY, S. T., J. L. BETANCOURT, S. T. JACKSON, AND R. G. EDDY. 2006. Role of multidecadal climatic variability in a range extension of pinyon pine. Ecology 87: 1124–1130.

HALLER, J. R. 1965. The role of 2-needle fascicles in the adaptation and evolution of ponderosa pine. Brittonia 17: 354–382.

HANAWALT, R. B. AND R. H. WHITTAKER. 1976. Altitudinally coordinated patterns of soils and vegetation in the San Jacinto Mountains, California. Soil Sci. 121: 114–124.

HIDALGO, H. C., J. A. DRACUP, G. M. MACDONALD, AND J. A. KING. 2001. Comparison of tree species sensitivity to high and low extreme hydroclimatic events. Phys. Geogr. 22: 115–134.

HINCKLEY, L. C. 1944. The vegetation of the Mount Livermore area in Texas. Am. Midl. Nat. 32: 236–250.

JAINDL, G. J., L. E. EDDLEMAN, AND P. S. DOESCHER. 1995. Influence of an environmental gradient on physiology of singleleaf pinyon. J. Range Manag. 48: 224–231.

JARVIS, P. G. AND M. S. JARVIS. 1963. The water relations of tree seedlings. IV. Some aspects of the tissue water relations and drought resistance. Physiol. Plantarum 16: 501–516.

LAJTHA, K. AND J. GETZ. 1993. Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94: 95–101.

LANNER, R. M. 1981. The Piñon Pine: A Natural and Cultural History. University of Nevada Press, Reno, NV.

LANNER, R. M. AND T. R. VANDEVENDER. 1998. The recent history of pinyon pines in the American Southwest. *In* D. M. Richardson [ed.], Ecology and biogeography of *Pinus*. Cambridge University Press, Boston, MA.

LARCHER, W. 2003. Physiological Plant Ecology: Ecophysiology and Stress Physiology of Functional Groups. 4th Edition. Springer, New York, NY.

LINTON, M. J., J. S. SPERRY, AND D. G. WILLIAMS. 1998. Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. Funct. Ecol. 12: 906–911.

LITTLE, E. L. 1999. Digital representation of "Atlas of United States Trees.". U.S. Geological Survey.

MARTENS, S. N., D. D. BRESHEARS, AND F. J. BARNES. 2001. Development of species dominance along an elevational gradient: Population dynamics of *Pinus edulis* and *Juniperus monosperma*. Int. J. Plant Sci. 162: 777–783.

MEKO, D. M., C. W. STOCKTON, AND W. R. BOGGESS. 1995. The treering record of severe sustained drought. Water Res. Bull. 31: 789–801.

NEILSON, R. P. 1987. On the interface between current ecological studies and the paleobotany of pinyon-juniper woodlands, p. 93–98. *In* R. L. Everett (comp.), Proc. Pinon-Juniper Conference. USDA Forest Service Gen. Tech Rep. INT-215. Intermountain Research Station, Ogden, UT.

NIERING, W. A. AND LOWEC. H. 1984. Vegetation of the Santa Catalina Mountains: Community types and dynamics. Vegetatio 58: 3–28.

POULOS, H. M., A. H. TAYLOR, AND R. M. BEATY. In press. Environmental controls on dominance and diversity of woody plant species in a Madrean, Sky Island ecosystem, Arizona, USA. Plant Ecol.

R DEVELOPMENT CORE TEAM. 2006. Retrieved June 25, 2006. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>

RICHARDSON, A. D., G. P. BERLYN, AND T. G. GREGOIRE. 2001. Spectral reflectance of *Picea rubens* (Pinaceae) and *Abies balsamea* (Pinaceae) needles along an elevational gradient, Mt. Moosilauke, New Hampshire, USA. Am. J. Bot. 88: 667–676.

SAVAGE, W. Z. AND R. H. MORIN. 2002. Topographic stress perturbations in the southern Davis Mountains, west Texas. J. Geophys. Res. 107: ETG 5-1-3.

SMITH, W. K. AND G. N. GELLER. 1979. Plant transpiration at high elevations: Theory, field measurements, and comparisons with desert plants. Oecologia 41: 109–122.

ST. ANDRE, G., H. A. MOONEY, AND R. D. WRIGHT. 1965. The pinyon woodland zone in the white mountains of California. Am. Midl. Nat. 73: 225–239.

SUZÁN-ASPIRI, H., J. SÁNCHEZ-RAMOS, J. G. MARTÍNEZ-AVALOS, S. VILLA-MELGAREJO, AND M. FRANCO. 2002. Population structure of *Pinus nelsoni* Shaw, an endemic pinyon pine in Tamaulipas, Mexico. For. Ecol. Mgmt. 165: 193–203.

TAIZ, L. AND E. ZEIGER. 2006. Plant Physiology, 4th Edition. Sinauer Associates Inc. Sunderland, MA.

TAUCH, R. J. AND N. E. WEST. 1987. Relationships of Great Basin single-needled pinyon, p. 86–91. *In* R. L. Everett [ed.], Proc. Pinon-Juniper Conference. USDA Forest Service Gen. Tech Rep INT-215. Intermountain Research Station, Ogden, UT.

TRANQUILLINI, W. 1964. The physiology of plants at high altitudes. Annu. Rev. Plant Phys. 15: 345–362.

TROMBULAK, S. C. AND M. L. CODY. 1980. Elevational distributions of *Pinus edulis* and *P. monophylla* (Pinaceae) in the New York Mountains, Eastern Mojave Desert. Madroño 27: 61–67.

TURNER, A. J. 1977. Soil survey of Jeff Davis County, Texas, USDA, Soil conservation Service. US Geological Survey. 2005. National Elevation Dataset. US Geological Survey, Sioux Falls, SD.

WEST, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands, p. 209–230. *In* M. G. Barbour and W. D. Billings [eds.], North American terrestrial vegetation. Cambridge University Press, Cambridge, UK.

WHITTAKER, R. H. AND W. A. NIERING. 1965. Vegetation of the Santa Catalina Mountains, Arizona: II. A gradient analysis of the south slope. Ecology 46: 429–452.

WHITTAKER, R. H. AND W. A. NIERING. 1968. Vegetation of the Santa Catalina Mountains, Arizona: IV. Limestone and acid soils. J. Ecol. 56: 523–544.

WHITTAKER, R. H. AND W. A. NIERING. 1975. Vegetation of the Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. Ecology 56: 771–790.

WILKINS, S. C. AND J. M. KLOPATEK. 1987. Plant water relations in ecotonal areas of pinyon-juniper and semi-arid scrub ecosystems, p. 412–417. *In* R. L. Everett (comp.), Proc. Pinon-Juniper Conference. USDA Forest Service Gen. Tech Rep. INT-215. Intermountain Research Station, Ogden, UT.