

Pinyon pine (*Pinus edulis*) mortality and response to water addition across a three million year substrate age gradient in northern Arizona, USA

Christopher E. Looney · Benjamin W. Sullivan ·
Thomas E. Kolb · Jeffrey M. Kane ·
Stephen C. Hart

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Abstract

Background and aims Pinyon pine (*Pinus edulis* Engelm.) is an important tree species in the western United States that has experienced large-scale mortality during recent severe drought. The influence of soil conditions on pinyon pine response to water availability is poorly understood. We investigated patterns of tree mortality and response of tree water relations and growth to experimental water addition at four sites across a three million year soil-substrate age gradient. **Methods** We measured recent pinyon mortality at four sites, and tree predawn water potential, leaf carbon isotope signature, and branch, leaf, and stem radial growth on 12 watered and unwatered trees at each

site. Watered trees received fifty percent more than growing season precipitation for 6 years.

Results Substrate age generally had a greater effect on tree water stress and growth than water additions. Pinyon mortality was higher on intermediate-aged substrates (50–55%) than on young (15%) and old (17%) substrates, and mortality was positively correlated with pinyon abundance prior to drought.

Conclusions These results suggest high soil resource availability and consequent high stand densities at intermediate-age substrates predisposes trees to drought-induced mortality in semi-arid regions. The response of tree water relations to water addition was consistent with the inverse texture hypothesis; watering reduced tree water stress most in young, coarsely textured soil, likely because water rapidly penetrated deep in the soil profile where it was protected from evapotranspiration.

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C. E. Looney · B. W. Sullivan (✉) · T. E. Kolb · J. M. Kane
School of Forestry, Northern Arizona University,
Flagstaff, AZ 86011, USA
e-mail: ben_sullivan@nau.edu

S. C. Hart
School of Natural Sciences & Sierra Nevada Research
Institute, University of California,
5200 North Lake Road Merced,
Merced, CA 95343, USA

Present Address:
B. W. Sullivan
College of Forestry and Conservation,
The University of Montana,
Missoula, MT 59812, USA

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Abbreviations

SAGA	Substrate Age Gradient of Arizona
Ψ_{pre}	Predawn water potential
$\delta^{13}\text{C}$	Leaf carbon isotope ratio
DRC	Diameter at root collar
SDI	Stand density index
BA	Basal area

Introduction

Pinyon pines are a key component of woodland ecosystems that occur on over 24.7 million hectares in the United States (Ronco 1990). Commonly associated with various juniper species (*Juniperus spp.*), pinyon pine woodlands support a diverse array of plant and animal species, as well as economic uses (Ronco 1990). Drought driven by climate warming threatens the health of Colorado pinyon pine (*Pinus edulis* Engelm.) (Breshears et al. 2005; Mueller et al. 2005; Shaw et al. 2005). For example, between 2000 and 2005 in northern Arizona drought-associated mortality in pinyon pine ranged from 15 to 30% of live tree basal area (Shaw et al. 2005), and some models predict large reductions in pinyon pine range over the next century of warming (Rehfeldt et al. 2006). Outside of the Southwest, reports of recent tree mortality due to drought and heat stress are increasing globally (Allen et al. 2010). The frequency and severity of such droughts are predicted to increase as a result of warming temperatures associated with global climate change (Seager et al. 2007).

Predisposing factors such as soil nutrient and water availability can increase tree susceptibility to stresses such as drought (Manion 1991). The Walker and Syers (1976) model of ecosystem development proposes that as soils develop, nutrient limitation to plant growth shifts from nitrogen (N) to phosphorus (P) limitation. Young substrates are rich in rock-derived nutrients, such as P, and deficient in atmospherically-derived nutrients, such as N (Walker and Syers 1976; Chadwick et al. 1999). As substrates age, P is lost through erosion, leaching, and occlusion, while N accumulates (Wardle et al. 2004). These changes in resource availability cause forest productivity to initially increase with substrate age and peak at intermediate soil ages (Wardle et al. 2004). Productivity subsequently declines during a retrogressive phase attributed to P limitation in old substrates (Peltzer et al. 2010).

Water storage capacity increases as soil develops and soil particles become finer (Selmants and Hart 2008). Most studies of tree growth and productivity associated with substrate age have focused on humid ecosystems (e.g., Wardle et al. 2004). Few studies have examined the possible link between substrate age and tree growth and mortality in arid or semi-arid ecosystems (but see Fravolini et al. 2003). This is of particular interest because soil texture may affect

tree water stress differently in arid ecosystems. The “inverse texture hypothesis” originally proposed by Noy-Meir (1973) suggests that plants growing in fine-textured soil experience greater water stress than those in coarse-textured soil because precipitation is lost from the surface of fine-textured soils via evaporation or runoff. Sala et al. (1988) further refined this hypothesis by proposing that below an annual precipitation of 370 mm, plant growth would be impeded rather than facilitated by finer soil texture. The inverse texture effect has been reported in arid ecosystems worldwide (e.g., Sala et al. 1988; Seagle et al. 1993; Dodd et al. 1997; Yang et al. 2009). Recent support for this hypothesis includes the greater response of mesquite (*Prosopis velutina*) water relations to simulated rainfall events on coarse-textured compared to fine-textured soils (Fravolini et al. 2005). Woody species with relatively deep rooting habits may be particularly capable of utilizing pulse summer rainfall through the inverse texture effect (Fravolini et al. 2003).

Variations in nutrient availability associated with substrate age also have influenced tree mortality in humid environments. Walker et al. (1983) linked mortality of *Eucalyptus* species in Australia to land clearing and subsequent grazing on ancient, phosphorus-poor soils. Mortality of *Metrosideros polymorpha* in Hawaii has been associated with young, nitrogen-deficient soils (Gerrish et al. 1988). In eastern North America, Horsley et al. (2002) suggested that old calcium-poor soils may predispose sugar maple (*Acer saccharum* L.) to decline.

Availability of soil nutrients and water can influence the growth, vigor, and mortality of pinyon pine. Compared with trees growing on fine-textured sandy loam soils, trees on nutrient- and water-deficient coarse-texture soils have been reported to have greater herbivory (Cobb et al. 1997). Radial growth response to drought (Adams and Kolb 2004) and post-drought mortality (Koepke et al. 2010) were similar for pinyon pines growing on coarse-textured soils derived from volcanic cinders and finer-textured soils derived from flow basalts and sedimentary parent materials, but canopy dieback of live trees was greater for coarse-textured soils (Koepke et al. 2010). Pinyon pine in the Southwest shows temporal and local variations in use of summer precipitation (Williams and Ehleringer 2000). Pinyon pine displays a drought-avoiding hydraulic strategy, the success of which may be influenced by the effect of soil on summer rainfall utilization

(McDowell et al. 2008). Studies are lacking that investigate the influence of substrate age, independent of changes in soil parent material, on pinyon pine tree growth, water stress, and mortality.

Selmants and Hart (2008) used the Substrate Age Gradient of Arizona (SAGA) to validate Walker and Syers' (1976) model of soil development in a semi-arid ecosystem. The sites that comprise the SAGA have substrate ages ranging from ~930 to 3,000,000 y, while other soil forming factors (Jenny 1941) are similar. With mean annual precipitation less than the 370 mm threshold defined by Sala et al. (1988), the SAGA represents an opportunity to examine the relationship between a naturally occurring gradient of soil water and nutrient availability and pinyon pine water stress, growth, and mortality with the potential influence of the inverse texture effect. In addition, pinyon pines at each of the SAGA sites were watered for 6 years, providing a strong framework to experimentally explore the relationships described above.

Walker and Syers' (1976) model of ecosystem development and the inverse texture hypothesis (Noy-Meir 1973) lead to potentially contradictory predictions for this study. Hence, we structured our hypotheses to examine the applicability of each to pinyon pine at the SAGA. Our first hypothesis was that trees growing at the youngest substrate age (0.93 ky) would have higher water supply, as indicated by higher predawn water potential (Ψ_{pre}) and a lower leaf carbon isotope ratio ($\delta^{13}C$), than trees growing at older substrate ages due to the inverse texture effect. Our second hypothesis was that Ψ_{pre} and $\delta^{13}C$ of trees at the 0.93 ky substrate age would be more responsive to water additions than trees at older substrate ages due to rapid penetration of water deep into the rooting zone where the effects of evapotranspiration would be lessened. Our third hypothesis was that tree growth would be highest at intermediate substrate ages (55 ky and 750 ky), where soil nutrient concentrations were more available than at younger and older substrate ages. Our fourth hypothesis was that the positive effects of water additions on growth would be most pronounced at the 750 ky substrate age, as that substrate age has the highest pools and fluxes of soil C and N prior to retrogression (Selmants and Hart 2008). Our fifth hypothesis, based on studies linking forest health to substrate age, was that recent tree mortality would be higher at the 0.93 ky and 3,000 ky substrate ages, where water and/or

nutritional deficits increase tree susceptibility to drought.

Methods

Study area

The SAGA is a soil chronosequence derived from basalt cinder parent material within the San Francisco Volcanic Field near Flagstaff, AZ (Selmants and Hart 2008). Soil parent material ages at the four sites that comprise the SAGA were ~0.93 ky, 55 ky, 750 ky, and 3,000 ky (Tanaka et al. 1986). All sites support a pinyon pine and one-seed juniper (*Juniperus monosperma* Engelm.) woodland, with canopy interspaces dominated by blue grama grass (*Bouteloua gracilis* (Wild. ex Dunth) Lag. ex Griffiths) except at the youngest site where woody shrubs (*Fallugia paradoxa* and *Rhus trilobata*) dominate the intercanopy spaces. The 0.93 ky, 55 ky, and 750 ky sites had evidence of light grazing, wood cutting, and off-road motorized travel, but otherwise were not directly impacted by human disturbance. Portions of the 3,000 ky site were disturbed by the process of chaining (Ansley and Rasmussen 2005) several decades ago, presumably in an attempt to stimulate grass production by toppling trees. The chaining did not cause a substantial loss of tree cover and did not shift the area to a grassland. The site currently supports a woodland dominated by pinyon pine and junipers.

The sites experience similar climate (Selmants and Hart 2008; Table 1), characterized by cold, wet winters and a wet "monsoon" precipitation pattern in late summer (Sheppard et al. 2002). Approximately half of the annual precipitation occurs during winter. Notable dry periods occur in late spring/early summer and fall. Annual precipitation was different during the years 2008 and 2009, during which the bulk of our measurements focus. At the Flagstaff, AZ airport, located within 50 km of the four SAGA sites and approximately 150 m higher in elevation (2,134 m), mean annual precipitation between 1950 and 2010 was 537 mm. Precipitation in 2008 was slightly less (483 mm) than average. However, 2009 was the fourth driest year recorded since 1898, with only 296 mm of precipitation, largely due to a dry monsoon season that had only 72.9 mm of precipitation (National

Table 1 Substrate ages, elevations, mean annual precipitation (MAP), mean annual temperature (MAT), potential evapotranspiration (PET) for the years 2002–2005, precipitation measured with bulk precipitation collectors between December 1st 2008

and November 30th 2009, percent soil clay content, soil total nitrogen (N) concentration, and soil total phosphorus (P) concentration at the four sites that comprise the Substrate Age Gradient of Arizona

Substrate age (ky)	Elevation (m)	MAP 2002–2005 (mm) ^a	MAT 2002–2005 (°C) ^a	PET (mm a ⁻¹) ^a	2009 precipitation (mm) ^b	% Clay ^a	Soil total N (g kg ⁻¹) ^a	Soil total P (g m ⁻²) ^c
0.93	1905	328	12	1325	186	1.13	0.5	375
55	1941	352	11	1328	166	8.38	1.1	250
750	2073	325	11	1334	224	31.84	2.0	165
3,000	2003	338	11	1324	253	37.15	1.3	150

^aSelmants and Hart 2008; ^bEmerson 2010; ^cSelmants and Hart 2010

Weather Service, Flagstaff). During the 365-day period between December 1st 2008 and November 30th, 2009, annual precipitation measured by bulk precipitation collectors was lowest at the 55 ky site and highest at the 3,000 ky site (Table 1, Emerson 2010).

Water addition experiment

We assessed the effect of substrate age and experimental water additions on pinyon pine growth and water relations. Trees used for these measurements averaged 2.4 m in height and 8 cm in diameter at root collar (DRC). For 6 years prior to sampling (2004–2009), 12 trees per site received experimental water additions, while 12 trees per site received no treatment and served as controls. Seventy liters of water were applied evenly within 1.8 m of the bole of the tree every 2–3 weeks between early May and mid July, and between late August and early October in each year. On average, 55 mm y⁻¹ of water was applied to watered trees, which was approximately 50% of growing season precipitation. Watering did not occur between mid-July and late August because of concerns that heavy rains would mute the effects of watering during the late summer monsoon season.

Pinyon water relations

We measured tree xylem predawn water potential (Ψ_{pre}) using a Scholander-type pressure bomb (Plant Moisture Stress Inc, Albany, OR, USA) for 12 watered and 12 unwatered trees in early July 2009 shortly after water addition. All samples were collected between 1 h before and 0.5 h after sunrise. We sampled the

0.93 ky and 3,000 ky sites 1 d after watering and the 750 ky and 55 ky sites 2 and 3 d after watering, respectively. Samples were stored in cool humid conditions until Ψ_{pre} measurement, which took place in the field immediately after collection. We averaged the Ψ_{pre} measurements of two needles collected from the west side of each of 10 trees per treatment at each site.

We measured soil volumetric water content at a depth of 0–30 cm in the mineral soil beneath the canopy edge of half the trees in each treatment at each site ($n=6$) using time-domain reflectometry (TRASE System 1, model number 6050x1, Soil Moisture Equipment Corp., Santa Barbara, CA) on the same day as the measurements of Ψ_{pre} . The majority of pinyon pine roots are found within the top 30 cm at the study sites (G.S. Newman, Northern Arizona University, unpublished data).

We analyzed leaf carbon isotope ratio ($\delta^{13}C$) and N concentration using whole-tissue foliage samples collected from 2008 and 2009 branch sections of all watered and unwatered trees at each site. The $\delta^{13}C$ ratio is a time-integrated indicator of leaf internal CO₂ concentration and leaf-level water use efficiency (Farquhar et al. 1989), which is affected by drought in pinyon pine (Adams and Kolb 2004). We used leaf N concentration to evaluate the possible influence on $\delta^{13}C$ of varying carboxylation capacity, which may influence $\delta^{13}C$ independently of water availability (Dawson et al. 2002). We sampled foliage halfway between the crown base and top of each tree, using only unshaded branches growing in the four cardinal directions. We pooled the needles to create a single sample per tree. After drying at 70°C for 24 h, we ground each pooled sample using a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA)

with a 40 mesh screen and sent them to the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University for measurement of leaf $\delta^{13}\text{C}$ and N concentration using a DELTA plus XL gas isotope-ratio mass spectrometer.

Pinyon growth

We quantified annual branch elongation and leaf area production for 2008 and 2009. We measured annual branch elongation with a ruler as the length between bud scale scars on one mid-canopy branch on the north side and one branch on the south side of eight randomly selected trees per treatment per site, for a total of 64 trees. On the same branches, we removed the needles from each branchlet and determined the projected leaf area of needles formed in 2008 and 2009 using a flatbed scanner and WinFolia software (Regents Instruments Inc., QC, Canada).

We measured the radial growth of the unwatered and watered pinyon pines by coring each tree close to the base using an increment borer. Cores were processed using standard dendrochronological techniques (Stokes and Smiley 1968). By scanning each core, we created a high-resolution image (2400 dpi) that we imported into WinDendro software (Regent Instruments). We then assigned annual ring boundaries and measured ring widths (mm yr^{-1}). All ring width series were then visually cross-dated by site and COFECHA (Grissino-Mayer 2001) was used to assess the strength of cross-dating. Samples that could not be cross-dated and were poorly correlated with the remainder of the samples ($r < 0.15$) at a given site were removed from subsequent radial growth analyses.

Vegetation survey and pinyon mortality

To quantify pinyon pine abundance and mortality, we recorded the status (live or recently dead) and measured all pinyons greater than or equal to 2.5 cm in DRC (Grier et al. 1992), on ten 0.405 ha circular plots randomly distributed across each site. We defined recently dead trees as those that had retained some bark and/or fine twigs. We used the DRC measurements to calculate basal area (BA) and stand density index (SDI; Reineke 1933) for both live and dead trees. We calculated SDI using the summation method (Long and Daniel 1990). Stand density index represents a relative measure of tree density that incorporates

tree size and frequency, and is robust against differences in site quality (Jack and Long 1996; Long et al. 2004).

To characterize the density, BA, and SDI of junipers we used the line-intersect method (Meeuwig and Budy 1980), which is more efficient for measuring junipers than conventional methods (Fox and Raskob 1992). At the center of each fixed-area plot used to measure pinyon pine density, we established a pair of 22.7 m long transects (for a total of ten pairs per site) arranged perpendicularly so that both transects shared the same mid-point. Along each transect, we counted and measured all live junipers greater than or equal to 2.5 cm. We did not sample dead junipers, as they were both rare and difficult to classify as recent or old mortality. We summed data from transect pairs; however, when the same tree fell on both transects, we only counted it once (Meeuwig and Budy 1980).

Data analysis

We calculated a relative change in mean annual stem radial growth during years of water addition relative to years before water addition on the watered and unwatered trees by calculating the mean annual radial growth during the treatment period (2004–2009) divided by the mean annual radial growth during the pre-treatment period (1998–2003). We used two-way analysis of variance (ANOVA) with substrate age, watering treatment, and their interaction as factors for analysis of Ψ_{pre} , soil water content, stem radial growth during the treatment period (2004–2009), and relative change in stem radial growth. We used two-way repeated measures analysis of variance (RMANOVA) where the year of interest (2008 or 2009) represented a non-independent time effect to simultaneously investigate the effects of substrate age, treatment, time, and their interactions on pinyon leaf area production, branch elongation, leaf N concentration, and leaf $\delta^{13}\text{C}$. We used a natural log transformation to normalize the distribution of radial and shoot growth, though we present untransformed means and standard errors for ease of interpretations. For the pinyon pine growth and water relations data, we used Tukey's HSD to separate means when appropriate as indicated by significant factors in the ANOVA or RMANOVA models. For all ANOVA, RMANOVA, and Tukey's HSD tests, we set statistical significance, a priori, at $p \leq 0.05$. Tree mortality was calculated based on the percentage of BA and tree

density comprised of dead trees. We used pair-wise Wilcoxon/Kruskal-Wallis tests with Bonferroni corrections (6 comparisons, $\alpha=0.0083$) in all mortality comparisons because the data violated assumptions of normality. Substrate age was not independently replicated in our study and replications consisted of measurements on trees within sites. Therefore, results and inferences apply only to our specific study area and should not be extrapolated to other sites without caution (Hurlbert 1984).

Results

Substrate age and water addition effects on soil and pinyon leaf characteristics

Sites with older substrate ages had higher soil water contents in the top 30 cm in July 2009 than sites with younger substrates, and experimental water additions to soil under pinyon pines increased soil water content compared to soil under unwatered pinyon pines (Fig. 1a). July soil volumetric water content was significantly different among substrate ages ($F=36.90$, $p<0.01$). Watering significantly increased soil water content ($F=20.69$, $p<0.01$) and the effect of watering was similar among substrate ages (soil age \times treatment interaction $F=0.69$, $p=0.56$).

Higher soil water content at older substrates did not result in a detectable change in water availability to pinyon pines in mid July 2009 based on Ψ_{pre} , which did not differ significantly among substrate ages (Fig. 1a; $F=1.90$, $p=0.14$). Watering, however, significantly increased Ψ_{pre} at all substrate ages ($F=18.66$, $p<0.001$), and the effect of watering was similar among substrate ages (treatment \times substrate age interaction, $F=1.29$, $p=0.29$).

Results for leaf $\delta^{13}C$ suggest a substrate age effect on pinyon pine water stress. The leaf $\delta^{13}C$ value increased between the 0.93 ky site and the 750 ky site and then decreased between the 750 ky site and the 3000 ky site (Fig. 2a). Values of $\delta^{13}C$ differed significantly among substrate ages ($F=9.03$, $p<0.01$) and between 2008 and 2009 ($F=107.37$, $p<0.01$). The substrate age \times year interaction was significant ($F=19.26$, $p<0.01$). Leaf $\delta^{13}C$ was higher in 2009 than 2008, and was higher at the 750 ky site than the other soil ages (Fig. 2a). There was no overall significant effect of the watering treatment on leaf $\delta^{13}C$ ($F=0.02$,

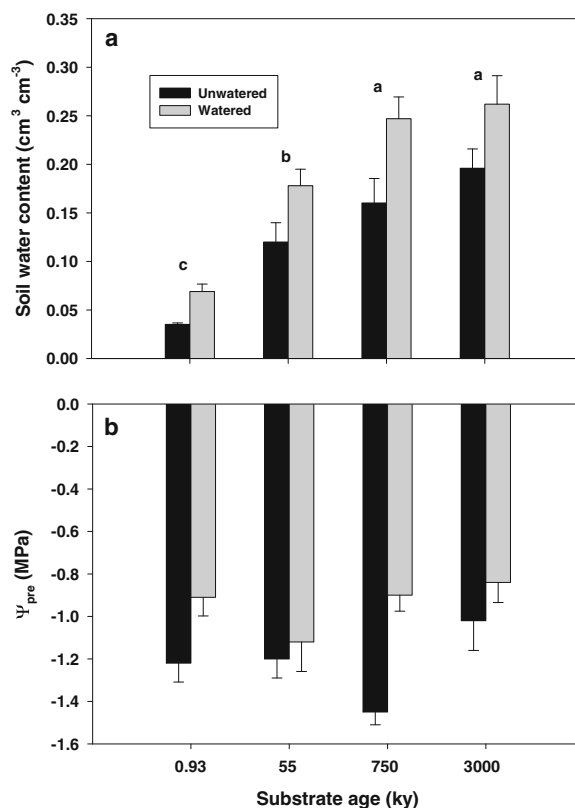


Fig. 1 Mean soil volumetric water content by substrate age and watering treatment (**a**) and pinyon pine predawn leaf water potential (Ψ_{pre} ; **b**). Error bars denote one standard error of the mean. Panel **a**: Watering over a six year period (2004–2009) increased soil water content ($F=20.69$, $p<0.01$). Soil water content varied among substrate ages ($F=36.9$, $p<0.01$); substrate age means labeled with different letters differ significantly. Panel **b**: Watering increased Ψ_{pre} ($F=18.66$, $p<0.01$) and was the only significant effect on Ψ_{pre}

$p=0.88$), but there was a significant substrate age \times treatment interaction ($F=3.33$, $p=0.03$); this interaction was the result of a significant decrease in leaf $\delta^{13}C$ at the 0.93 ky site, a significant increase in $\delta^{13}C$ values at the 750 ky site, and no significant change in $\delta^{13}C$ values at the 55 ky and 3,000 ky sites in response to watering treatment (Fig. 2b).

Leaf N concentration increased from a minimum at the 0.93 ky site to a maximum at the 3,000 ky site in both 2008 and 2009 (Fig. 2c). Leaf N concentration differed by substrate age ($F=4.01$, $p=0.01$) and year ($F=13.01$, $p<0.01$), but there were also significant substrate age \times year ($F=3.26$, $p=0.03$) and substrate age \times year \times treatment ($F=3.03$, $p=0.04$) interactions. Differences in leaf N concentration among substrate

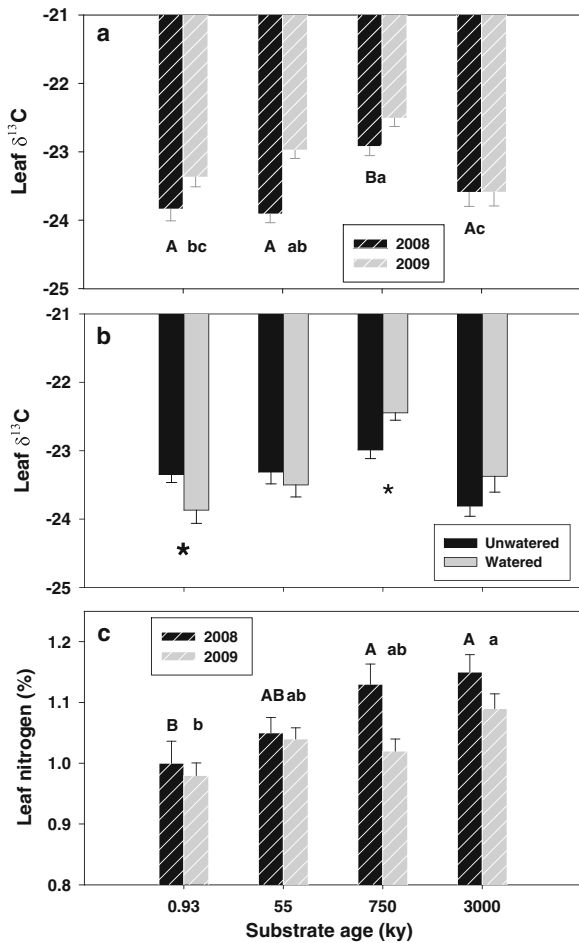


Fig. 2 Patterns of mean leaf-level traits of pinyon pine across the Substrate Age Gradient of Arizona and in response to 6 years of watering treatments (2004–2009). Error bars denote one standard error of the mean. Panel a: Leaf $\delta^{13}\text{C}$ values differed among substrate ages ($F=9.03$, $p<0.01$) and years ($F=107.37$, $p<0.01$), and the soil age \times year interaction was significant ($F=19.26$, $p<0.01$). The substrate age means from 2008 and 2009 labeled with different upper or lower case letters, respectively, were significantly different. Panel b: Effects of water amendments on mean leaf $\delta^{13}\text{C}$ values. The substrate age \times watering treatment interaction was significant ($F=3.33$, $p=0.03$); asterisks denote substrate ages with significant treatment effects. Panel c: Leaf nitrogen concentrations varied significantly among soil ages ($F=4.01$, $p=0.01$) and years ($F=13.01$, $p<0.01$), and the soil age \times year ($F=3.26$, $p=0.03$) and year \times soil age \times treatment ($F=3.03$, $p=0.04$) interactions were significant. The substrate age means from 2008 and 2009 labeled with different upper or lower case letters, respectively, were significantly different

ages were consistent in both 2008 ($F=4.56$, $p<0.01$) and 2009 ($F=4.77$, $p<0.01$), though these differences were more pronounced in 2008 than 2009 (Fig. 2c).

Simple linear regressions of individual tree data indicated weak relationships between leaf N concentration and leaf $\delta^{13}\text{C}$ in both 2008 ($r^2=0.03$, $p=0.12$) and 2009 ($r^2=0.03$, $p=0.08$).

Pinyon growth

In both 2008 (Fig. 3a) and 2009 (Fig. 3b), leaf area production per branch generally increased from the 0.93 ky site to the 55 ky site, and then declined as substrate age increased. Leaf area production was significantly affected by substrate age ($F=7.32$, $p<0.01$), and year ($F=7.73$, $p<0.01$), and the effect of substrate age varied between 2008 and 2009 (substrate age \times year

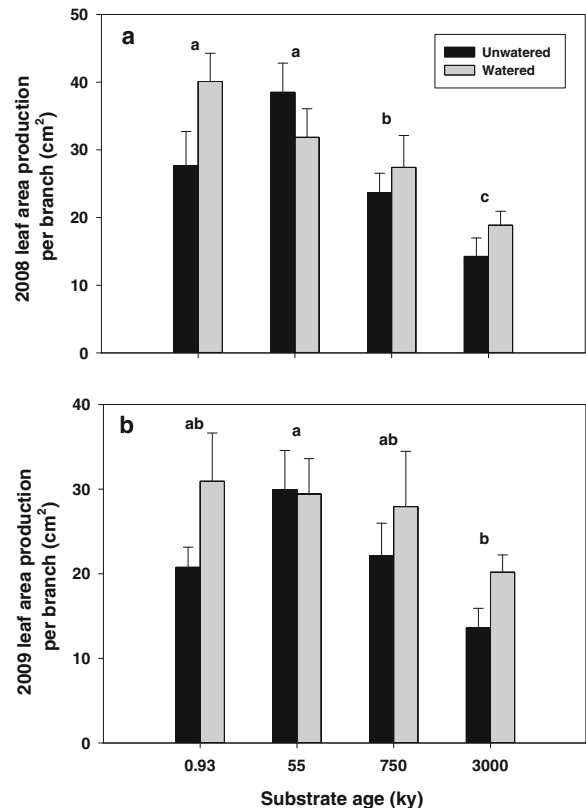


Fig. 3 Patterns of mean leaf area production per branch of pinyon pine for years 2008 (a) and 2009 (b) across the Substrate Age Gradient of Arizona and in response to 6 years of watering treatments (2004–2009). Error bars denote one standard error of the mean. The substrate age \times year interaction was significant ($F=2.76$, $p=0.05$) and leaf area production differed significantly among substrate ages in both 2008 ($F=9.42$, $p<0.01$) and 2009 ($F=3.62$, $p=0.02$). Watering did not significantly affect leaf area ($F=2.65$, $p=0.11$). In each panel, substrate age means labeled with different letters differed significantly

interaction $F=2.76$, $p=0.05$). There was no significant substrate age \times year \times treatment interaction. Leaf area production was significantly higher in 2008 than 2009 and the difference between years was greatest at the 0.93 ky site. Watering had no significant ($F=2.65$, $p=0.11$) or consistent effect on leaf area production (Fig. 3). The substrate age \times treatment interaction and year \times treatment interaction were not significant sources of variation for leaf area production ($F=0.08$, $p=0.23$; $F=2.37$, $p=0.13$, respectively).

Branch elongation increased from the 0.93 ky site to the 55 ky site, and then declined as substrate age increased in both 2008 (Fig. 4a) and 2009 (Fig. 4b). Branch elongation significantly varied by substrate age ($F=14.97$, $p<0.01$), year ($F=44.75$, $p<0.01$), and the substrate age \times year interaction ($F=3.50$, $p=0.02$). The three-way substrate age \times year \times treatment interaction was also significant ($F=2.75$, $p=0.05$). Watering caused a 20% increase of average branch elongation in 2009 (Fig. 4b; $F=8.72$, $p<0.01$) but not in 2008 (Fig. 4a; $F=0.02$, $p=0.89$). Average branch elongation was greater in 2009 than 2008 at every substrate age, and unwatered pinyon branch elongation was 7% greater in 2009 than 2008 when all substrate ages were pooled.

Mean annual radial growth (Fig. 5a) during the treatment years (2004–2009) had a similar relationship to substrate age as branch elongation. Radial growth differed significantly among substrate ages ($F=19.14$, $p<0.01$), but not treatment ($F=0.04$, $p=0.83$), and the substrate age \times treatment interaction was significant ($F=3.23$, $p=0.03$). A significant difference in radial growth due to treatment was detected only at the 750 ky-old site, where watering caused a 36% reduction in growth compared to unwatered trees.

Because comparing mean annual radial growth among substrate ages does not consider pretreatment differences in pinyon pine growth among substrate ages, we relativized the mean annual radial growth of each tree during the treatment period (2004–2009) by dividing by the mean annual radial growth prior to treatment (1998–2003). This measure of relative change in radial growth provided similar results to the unrelativized radial growth. Relative change in radial growth differed significantly by substrate age ($F=4.11$, $p<0.01$), but not treatment ($F=0.65$, $p=0.42$), and the substrate age \times treatment interaction was significant ($F=2.68$, $p=0.05$). At the 0.93 ky site, radial growth of watered and unwatered pinyons was $\sim 30\%$ higher during the

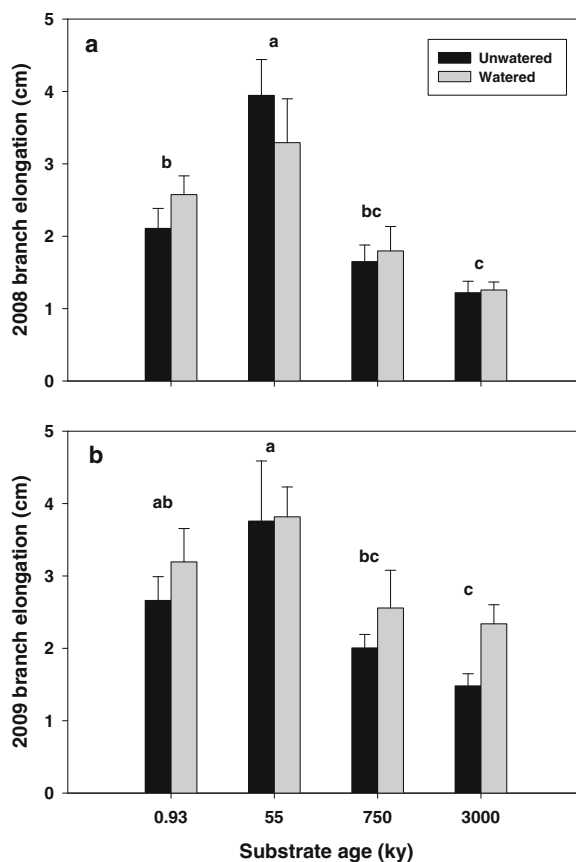


Fig. 4 Patterns of mean pinyon pine branch elongation for 2008 (a) and 2009 (b) across the Substrate Age Gradient of Arizona and in response to 6 years of watering treatments (2004–2009). Error bars denote one standard error of the mean. Branch elongation was significantly different between years ($F=44.75$, $p<0.01$) and substrate ages ($F=14.97$, $p<0.01$), and the substrate age \times year ($F=3.50$, $p=0.02$) and substrate age \times year \times treatment ($F=2.75$, $p=0.05$) interactions were significant. Substrate age effects were significant in both 2008 ($F=19.60$, $p<0.01$) and 2009 ($F=4.82$, $p=0.03$). There was a significant positive effect of watering in 2009 (Panel b, $F=8.72$, $p<0.01$) but not in 2008 (Panel a, $F=0.02$, $p=0.89$). In each panel, substrate age means labeled with different letters differed significantly

treatment period relative to the pre-treatment period (Fig. 5b). At the 55 ky site, growth was similar for pre-treatment and treatment periods. The 750 ky site was the only substrate age where relative growth significantly differed between watered and unwatered trees; watered trees had 30% less radial growth during the treatment period than the pre-treatment period whereas unwatered trees had 30% more radial growth during the treatment period than the pre-treatment period. At the 3,000 ky site, growth was 20% lower during

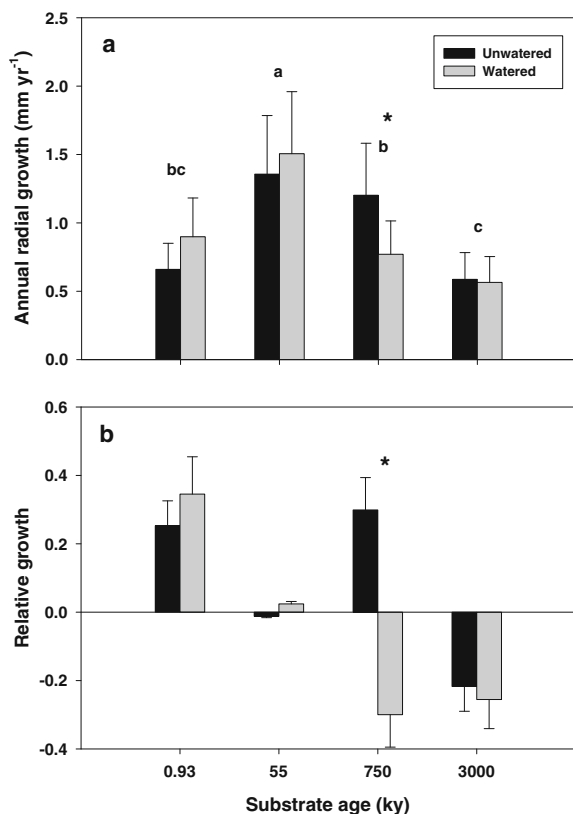


Fig. 5 Patterns of mean annual radial growth of pinyon pine during the treatment period (2004–2009) across the Substrate Age Gradient of Arizona and in response to 6 years of watering treatments (2004–2009). Error bars denote one standard error of the mean. Panel **a**: Radial growth differed among substrate ages ($F=19.14$, $p<0.01$) but not treatment ($F=0.04$, $p=0.83$) and the substrate age \times treatment interaction was significant ($F=3.23$, $p=0.03$). Substrate age means labeled with different lower case letters differed significantly. The asterisk denotes the substrate age with a significant treatment effect. Panel **b**: Annual pinyon pine radial growth during the treatment period (2004–2009) relative to annual radial growth prior to the treatment period (1998–2003). Relative growth differed significantly among substrate ages ($F=4.11$, $p<0.01$) but not treatment ($F=0.65$, $p=0.42$), and the substrate age \times treatment interaction was significant ($F=2.68$, $p=0.05$). The asterisk denotes the substrate age with a significant treatment effect

the treatment period relative to the pretreatment period for both watered and unwatered trees (Fig. 5b).

Pinyon abundance and mortality

All measures of total pinyon pine abundance (BA, tree density, SDI) increased with increasing substrate age between the 0.93 ky and 750 ky sites and decreased

between the 750 ky and 3,000 ky sites (Table 2). However, the pattern of live pinyon pine abundance among substrate ages was more complicated. Although live pinyon pine tree density followed the pattern of total pinyon pine tree density, live pinyon pine BA was lowest at the 750 ky site and live pinyon pine SDI increased to a maximum at the 3,000 ky site. The dominance of pinyon pine relative to juniper changed with increasing substrate age, where pinyon pine comprised the most live BA (70%) at the 0.93 ky site and the least (18%) at the 750 ky site.

The 750 ky site had the highest pinyon pine mortality (as indicated by % mortality by both density and BA), followed closely by the 55 ky site. Mortality was similar at the 0.93 ky and 3,000 ky site, and was substantially lower at these substrate ages than the two intermediate-aged substrate ages (Table 2). Live tree diameter was significantly smaller at the 750 ky site than the 0.93 ky and 3,000 ky sites (Table 2), but dead tree diameter was similar among substrate ages. Percent pinyon pine mortality at the plot scale ($n=40$ pooled over all substrate ages) was significantly and positively related to live pinyon pine abundance indicated by SDI ($r^2=0.34$, $p<0.01$), basal area ($r^2=0.31$, $p<0.01$), and tree density ($r^2=0.12$, $p=0.03$). In contrast, percent pinyon pine mortality was not significantly related to any measure of juniper abundance (results not shown).

Discussion

Our results suggest that three million years of soil development affected pinyon pine water relations, growth, and mortality in strong but unexpected ways. We also found that 6 years of experimental watering, which increased growing season precipitation by 50%, had inconsistent and unexpected effects on pinyon pine water relations and growth. These findings were remarkable given that watering significantly increased soil water content in an ecosystem where potential evapotranspiration substantially exceeds annual precipitation (Selmants and Hart 2008). These results emerged from the integration of two experimental designs: a long-term experimental watering treatment and a well-constrained substrate age gradient, where topography, climate, and soil parent material, were similar.

Table 2 Mean (and standard error) basal area (BA), tree density, stand density index (SDI), percent mortality, and diameter at root collar (DRC) for live and dead pinyon pines (*Pinus edulis*) and live junipers (*Juniperus monosperma*) at four sites that

comprise the Substrate Age Gradient of Arizona. Substrate age means that share the same letter do not differ significantly (paired Wilcoxon/Kruskal-Wallis with Bonferroni corrections; $p < 0.0083$)

	Substrate age			
	0.93 ky	55 ky	750 ky	3,000 ky
<i>Pinus edulis</i>				
Total BA (m ² ha ⁻¹)	4.2 (0.7) a	5.2 (1.7) ab	11.4 (1.8) b	5.1 (0.8) a
Total density (# ha ⁻¹)	155.6 (47.7) a	168.0 (34.9) a	659.5 (125.0) b	232.2 (38.7) a
Total SDI	66.7 (14.2) a	114.8 (34.6) ab	284.4 (39.8) b	124.3 (17.5) a
Live BA (m ² ha ⁻¹)	3.5 (1.4) a	3.5 (1.2) a	2.1 (1.0) a	4.4 (0.8) a
Live density (# ha ⁻¹)	113.6 (21.5) a	117.3 (21.5) a	291.5 (82.7) a	182.8 (35.0) a
Live SDI	84.7 (22.9) ab	51.1 (21.1) a	58.6 (24.7) ab	154.0 (17.5) b
Dead BA (m ² ha ⁻¹)	0.7 (0.5) a	3.6 (1.8) ab	9.2 (2.2) b	0.7 (0.4) a
Dead density (# ha ⁻¹)	34.6 (29.3) a	91.4 (31.0) a	363.1 (105.8) a	46.9 (25.36) a
Dead SDI	14.8 (9.44) a	75.9 (37.1) ab	212.4 (45.6) b	19.1 (11.1) a
% mortality by BA	16.6 (7.3) a	58.3 (12.0) a	71.6 (12.8) a	13.9 (6.8) a
% mortality by density	15.3 (6.6) a	50.0 (10.4) a	54.5 (11.1) a	17.2 (7.6) a
Live tree DRC (cm)	15.2 (3.1) b	13.0 (3.1) ab	6.8 (1.8) a	16.9 (1.4) b
Dead tree DRC (cm)	7.3 (5.2) a	14.7 (3.6) a	14.0 (2.9) a	6.5 (2.3) a
<i>Juniperus monosperma</i>				
BA (m ² ha ⁻¹)	1.5 (0.8) a	6.4 (2.3) ab	9.3 (2.0) b	13.2 (2.0) b
Density (# ha ⁻¹)	27.5 (12.4) a	166.2 (92.9) ab	126.9 (24.6) b	502.1 (97.8) c
SDI	24.7 (11.7) a	84.9 (78.5) ab	173.5 (28.1) bc	314.1 (49.1) c

Pinyon water relations

Our results for pinyon pine water stress differed between the short-term measurement of leaf Ψ_{pre} during one week in early July 2009, and the time-integrated assessment of leaf $\delta^{13}\text{C}$. In our study, the leaf $\delta^{13}\text{C}$ value included plant water stress over 2 years (2008–2009) of leaf formation. While substrate age did not significantly affect Ψ_{pre} , the results for leaf $\delta^{13}\text{C}$ suggest greater chronic water stress at the 750 ky site than at other substrate ages. This result is inconsistent with our first hypothesis that pinyon pines growing at the 0.93 ky substrate age would have lower water stress compared with pinyon pines growing at older substrate ages.

Results of experimental water additions to pinyon pines also differed between the short-term (Ψ_{pre}) and longer-term ($\delta^{13}\text{C}$) indicators of tree water stress. The short-term indicator, Ψ_{pre} , showed that water additions reduced pinyon water stress in mid July 2009 at all

substrate ages 2–3 days after watering (Fig. 1b). However, leaf $\delta^{13}\text{C}$ suggested that water additions reduced pinyon water stress at the youngest substrate ages and increased water stress at the two oldest substrate ages. This interpretation is supported by previous research on pinyon pine, which found greater stomatal conductance and lower $\delta^{13}\text{C}$ values associated with increased water availability (Williams and Ehleringer 2000; Adams and Kolb 2004; West et al. 2007). The results for leaf $\delta^{13}\text{C}$ support our second hypothesis that trees at the 0.93 ky substrate age would be more responsive to water additions than trees at older substrate ages. While we did not find a significant effect of watering on $\delta^{13}\text{C}$, the significant substrate age \times treatment interaction suggests summer rainfall may be of greater importance to trees growing on young, coarse-textured substrates than on old, fine textured substrates.

These results provide the first evidence that the inverse texture effect occurs at the SAGA. Mean annual precipitation at the SAGA is 336 mm, below the

370 mm threshold proposed by Sala et al. (1988) as the upper boundary of the inverse texture effect, above which the retention of soil water from higher water storage capacities of fine-textured soils outweighed the loss of water from lower infiltration rates. Further evidence supporting the inverse texture hypothesis at the SAGA is the lower soil water content in the surface soil (0–30 cm) at the two youngest soil ages, compared to the two oldest soil ages. The water at these two youngest substrate ages may drain from the top 30 cm into deeper soil, where it is less likely to be lost via evaporation.

In addition to water limitation, nutrient deficiencies can affect mesophyll conductance and thus leaf internal CO_2 concentration and $\delta^{13}\text{C}$. For instance, studies of other pine species growing in mesic habitats have found higher $\delta^{13}\text{C}$ on water-limited substrate ages following fertilization (Guehl et al. 1995; Korol et al. 1999). However, N fertilization had little effect on pinyon leaf $\delta^{13}\text{C}$ (Lajtha and Getz 1993), and $\delta^{13}\text{C}$ has been previously shown to be a robust measure of pinyon pine response to water availability (West et al. 2007). Differences in carboxylation capacity, as suggested by leaf N concentration (Field and Mooney 1986), can alter $\delta^{13}\text{C}$ (Dawson et al. 2002). The lack of a correlation between leaf N concentration and $\delta^{13}\text{C}$ in our study suggests that enzymatic effects on carboxylation capacity and mesophyll conductance did not appreciably affect $\delta^{13}\text{C}$ across the substrate age gradient. While P deficiency can affect leaf $\delta^{13}\text{C}$ of pines via changes in photosynthesis, stomatal conductance, and intercellular CO_2 concentration (DeLucia et al. 1989), there is little evidence for an effect of P availability on leaf $\delta^{13}\text{C}$ in our study because leaf $\delta^{13}\text{C}$ was similar at the two youngest and oldest soil ages (Fig. 2A), which differ substantially in plant-available soil P (Table 1, Selmants and Hart 2010).

Pinyon growth

The results of our tree growth measurements indicate that substrate age had a greater effect on pinyon growth than 6 years of experimental water additions. The stem radial growth results were consistent with the leaf $\delta^{13}\text{C}$ results in suggesting that on older substrates, the experimental watering stressed pinyon pines. We used several measurements of the growth of watered and unwatered pinyon pines that integrated tree responses to water availability over different time scales. Annual branch elongation and branch-level leaf

area production were indicators of canopy growth in 2008 and 2009. Stem radial growth measured whole-tree aboveground biomass during the treatment period and retrospectively, as stem diameter has been strongly correlated with aboveground biomass of pinyon pines (Grier et al. 1992).

All three growth metrics were consistent with our third hypothesis that tree growth would be greatest at intermediate-aged substrates. However, we expected the 750 ky site, not the 55 ky site, to have the greatest individual-tree growth because pools and fluxes of soil carbon and N, which indicate soil resource availability, were greatest at that substrate age (Selmants and Hart 2008). Additionally, tree growth at the 0.93 ky site was greater than or equal to the 750 ky site (depending on the metric), despite the 0.93 ky site having the lowest soil nutrient availability and water holding capacity of the surface soil of all substrate ages (Selmants and Hart 2008, 2010). One possible explanation for this result is that the coarse-textured surface soil at the 0.93 ky site may promote pinyon pine water uptake from deep soils, which is consistent with the inverse texture hypothesis. Another explanation is that there may be an interaction between resource availability and competition within the SAGA sites. For instance, though soil N availability is much lower at the 0.93 ky site than the 750 ky site, live pinyon density was highest at the 750 ky site. Resource availability per tree may be higher at the 0.93 ky site than the 750 ky site. A final explanation is that pinyon pines may shift production from above- to below-ground growth in older soils to obtain P. Such a shift from above- to below-ground production with increasing substrate age has been reported for *Metrosideros polymorpha* in Hawaii (Ostertag 2001). Research on pinyon pine is less clear. Though pinyon root biomass was not significantly different among the SAGA sites at the profile level, younger substrates had greater root biomass in the A horizon than older substrates (G.S. Newman, unpublished data). Gehring and Whitham (1994) found greater root growth at the 0.93 ky site compared to older, finer-textured soils, though soil parent materials differed. However, a study of the similar species singleleaf pinyon (*Pinus monophylla* Torr and Frem.) found little influence of soil nutrient availability on root/shoot ratio (DeLucia et al. 1989). Clearly, more research on the response of pinyon root morphology and productivity to water and nutrient availability is needed.

At most substrate ages, our experimental water additions had unexpectedly small effects on pinyon pine growth. The only growth metric that was significantly increased as a result of watering was branch elongation in 2009. Watering had no significant effect on annual stem radial growth over the entire treatment period (2004–2009), except for a significant reduction in growth at the 750 ky site. This growth reduction does not support the fourth hypothesis, which predicted watering effects on growth would be both positive and most pronounced at the 750 ky site due greater soil nutrient pools and fluxes at that substrate age (Selmants and Hart 2008, 2010). To our knowledge, no other study that added water to trees observed reductions in above-ground growth. Our study was not designed to explore the mechanisms behind such an effect. Because this unexpected result only occurred at one substrate age, we speculate it may be the result of an interaction with other characteristics unique to that substrate age, such as competition or nutrient availability, or a shift in resource allocation from above- to below-ground tissues. A shift in resource allocation is consistent with the above explanation that as substrate age increased, aboveground growth of unwatered pinyon pines declined because of an increase in belowground growth. It is important to note that we studied and applied water to relatively small trees at the SAGA; larger pinyon pines may show different responses to watering treatments and substrate age. Mature pinyon pines allocate less growth to new foliage (Grier et al. 1992) and are more susceptible to drought than young trees (Mueller et al. 2005).

Pinyon mortality

Because the 750 ky site had the greatest nutrient pools and fluxes of any of the SAGA sites (Selmants and Hart 2008, 2010), we expected that pinyon pine mortality would be lowest at that site. However, contrary to our prediction, the 750 ky site had the highest pinyon mortality of all SAGA sites. This result neither supports our fifth hypothesis that recent tree mortality would be higher at extremes of substrate age, nor is it consistent with evidence from more humid ecosystems that extremes of soil age promote greater tree mortality (Walker et al. 1983; Mueller-Dombois 1986; Gerrish et al. 1988; Horsley et al. 2002). Our study, however, is not the first to report low pinyon pine mortality on young, low-N soils. Ogle et al. (2000) reported lower pinyon pine mortality on flat, young cinder-derived

soils near our 0.93 ky site than on older, sandy loam soils derived from limestone parent material.

We propose two non-exclusive hypotheses based on our tree mortality results: 1) high stand density increased mortality, and 2) high water stress increased mortality. Regarding the first explanation, the 750 ky site had the highest pinyon pine abundance prior to the droughts of 1996 and 2002 and the highest recent tree mortality of all SAGA sites. However, percent pinyon mortality estimated by pinyon abundance was nearly as high at the 55 ky site as at the 750 ky site, despite the fact that the 55 ky site had lower pre-drought pinyon abundance than the 750 ky site. The percentage of dead pinyon pine was positively but weakly correlated with all measures of pinyon pine abundance for plot-level data. Regarding the second explanation, pinyon pine mortality and water stress, as measured by leaf $\delta^{13}\text{C}$, were higher at the 750 ky site than the other substrate ages (Fig. 2a), but our water addition experiment did not decrease leaf $\delta^{13}\text{C}$ at the 750 ky site as would be expected if water more strongly limited tree physiological processes at that substrate age than the other substrate ages. The experiment showed that tree growth at the 750 ky site was lower for watered compared with unwatered trees. It is also likely that these two explanations are interrelated: high stand density at the 750 ky site may have increased tree water stress during drought (e.g., Kolb et al. 1998; Skov et al. 2004), which led to higher mortality.

Conclusions

We made several unexpected discoveries about controls over pinyon pine water relations, growth, and mortality via a long-term watering experiment at multiple sites along a well-constrained substrate age gradient with measurements of tree performance that integrated over different time scales. First, pinyon water stress was higher at intermediate substrate ages than young and old substrate ages. Second, pinyon mortality was greatest on intermediate substrate ages, which may be related to intraspecific competition prior to the onset of mortality. Third, growth of individual pinyon trees was greatest at the intermediate 55 ky site, an earlier date than would be expected based on evidence of ecosystem retrogression (Peltzer et al. 2010) from soil nutrient availability (Selmants and Hart 2008). Fourth, high soil nutrient availability and

consequent ecosystem productivity at intermediate substrate ages may predispose trees to drought-induced mortality in semi-arid regions. As the southwestern U.S. can be expected to experience an increase in temperature and a decrease in precipitation resulting from climate change (Seager et al. 2007; Solomon et al. 2009), understanding the response of pinyon pine to water availability will be critical in predicting the spatial distribution and intensity of large-scale tree mortality events.

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