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concentrations. Our findings demonstrate the potential for delayed phenological development and reduced growth with higher temperatures and drought in tree species that are vulnerable to drought and reveal potential mechanistic links to physiological stress responses. Climate change projections of an earlier and longer growing season with higher temperatures, and consequent increases in terrestrial C sink strength, may be incorrect for regions where plants will face increased drought stress with climate change.

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Experimental drought and heat can delay phenological development and reduce growth in semiarid trees.

Running Head: Drought and heat affect phenology and growth

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Keywords: phenology, climate change, *Juniperus monosperma*, Juniper, *Pinus edulis*, piñon pine, non-structural carbohydrate, water potential, drought experiment.

Primary Research Article

Abstract.

Higher temperatures associated with climate change are anticipated to trigger an earlier start to the growing season, which could increase the terrestrial C sink strength. Yet greater variability in the amount and timing of precipitation are also expected with higher temperatures, bringing increased drought stress to many ecosystems. We experimentally assessed the effects of higher temperature and drought on the foliar phenology and growth of mature trees of two semi-arid conifer species. We exposed field-grown trees to a ~45% reduction in precipitation with a rain-out structure, a 4.8°C temperature increase with open-top chambers, and a combination of both simultaneously (heat+drought). Over the 2013 growing season, heat, drought, and heat+drought treatments reduced shoot and needle growth in piñon pine (*Pinus edulis*) by ≥39%, while juniper (*Juniperus monosperma*) had low growth and little response to these treatments. Needle emergence on primary axis branches of piñon pine was delayed in heat, drought, and heat+drought treatments by 19 to 57 days, while secondary axis branches were less likely to produce needles in the heat treatment, and produced no needles at all in the heat+drought treatment. Growth of shoots and needles, and the timing of needle emergence correlated inversely with xylem water tension and positively with non-structural carbohydrate concentrations. Our findings demonstrate the potential for delayed phenological development and reduced growth with higher temperatures and drought in tree species that are vulnerable to drought and reveal potential mechanistic links to physiological stress responses. Climate change projections of an earlier and longer growing season with higher temperatures, and consequent increases in terrestrial C sink strength, may be incorrect for regions where plants will face increased drought stress with climate change.

Introduction.

The phenology of plants, i.e. the timing of development and growth, has a strong influence on the atmospheric concentration of CO_2 at both short and long time scales. Interannual fluctuations of atmospheric CO_2 concentrations illustrate the dominance of terrestrial phenology on earth's atmosphere (Keeling 1960, Keeling et al. 1996). At longer-time scales changes in the phenology of the terrestrial biosphere could affect planetary climate regulation, as changes in growing season length and associated increases in terrestrial primary production are an important feedback to climate change (Richardson et al. 2010, 2012, 2013, Keenan et al. 2014). The potential effects of climate change on growing season shifts, typically estimated as a negative feedback on warming, are represented in the global vegetation components of earth system models used in climate change projection (Richardson et al. 2012, Oleoson et al. 2013, Keenan et al. 2014).

Studies of long-term records have consistently found that increased temperatures are linked to an earlier and longer growing season in temperate (Aono and Kazui 2008, Miller-Rushing and Primack 2008, Primack et al. 2009) and Mediterranean ecosystems (Peñuelas et al 2002, Ogaya and Peñuelas 2004, Gordo and Sanz 2009). Warming experiments have often shown the same effect of earlier growth and an extended growing season in trees (Norby et al. 2003, Morin et al. 2010, Han et al. 2014). There is also evidence from experiments that increased temperatures do not always produce the typical response but can have no effect on phenological timing (Guak et al. 1998, Kuster et al. 2014). A potential explanation for such atypical responses could be that temperature increases can be associated with an increase in drought stress (Overpeck and Udall 2010, Williams et al. 2013). Observations of reduced growth, decreased branching rate, and delayed leaf development have been reported in trees subjected to rainfall exclusion experiments (Borghetti et al. 1998, Ogaya and Peñuelas 2004, Peñuelas et al. 2004, Girard et al. 2011, 2012, Limousin et al. 2012).

Investigation of the physiological causes of phenological responses may be a useful approach for improving climate change predictions, given the variation in temperature and drought effects on tree growth and development, (Schaber and Badeck 2003). Growth and development are highly sensitive to stress from water availability (Körner 2003, Fatichi et al. 2014). Following the sink limitation hypothesis, reduced growth from drought is thought to be caused by the direct effects on turgor necessary for cell wall expansion at active meristems, not through any source limitation of C assimilation or availability of stored C resources (Körner 2003, Würth et al. 2005, Fatichi et al. 2014, Palacio et al. 2014). This hypothesis is supported by much work demonstrating that drought, reflected in high xylem water tensions, limits growth more than photosynthesis, and that non-structural carbohydrates (NSC) tend to increase in response to stress and are reduced when environmental conditions favor growth, consistent with change in C sink demand (Tissue and Wright 1995, Körner 2003, Würth et al. 2005, Oberhuber et al. 2011, Gruber et al. 2012, Deslauriers et al. 2014, Fatichi et al. 2014, Dickman et al. 2015). Changes in carbon supply through reduced photosynthesis serve to exacerbate these impacts (McDowell 2011, Adams et al. 2013, Sevanto et al. 2014, Dickman et al. 2015, Hartmann et al. 2015).

Few studies have examined the combined effects of increased temperature and drought on phenological responses in mature trees, despite the need for improved phenology models in global change assessments (Richardson et al. 2012). Even fewer studies have investigated the physiological processes behind the phenological responses to these environmental stresses. In this study, we measured phenological, growth, and physiological responses to an experimental field manipulation of temperature and drought in mature trees of two semi-arid conifer species, *Juniperus monosperma* and *Pinus edulis*. These tree species are widespread across the Southwest USA, a semi-arid region where tree phenological responses to climate have not been well studied. Our objectives were to determine the effect of temperature and drought, separately and in combination, on tree phenology, and to investigate the causal links between physiological and phenological responses to these treatments. We tested the following hypotheses:

1. Increased temperature will cause earlier phenological development and increased growth.
2. Drought will delay development and reduce growth.
3. In combination, the effects of drought will counteract any heat effects, resulting in no change in development and growth relative to ambient conditions.
4. Growth and development will be constrained primarily by xylem tension and will be either unrelated or negatively correlated with NSC concentration.

Methods.

Site description and experimental design.

The Los Alamos Survival-Mortality experiment (SUMO) is located on Frijoles Mesa near Los Alamos, New Mexico, USA, at an elevation of 2150 m (Garcia-Forner et al. 2015). The experiment is located in a piñon-juniper woodland near the ponderosa pine (*Pinus ponderosa*) forest ecotone. The tree community at SUMO is dominated by piñon pine (*Pinus edulis* Engelm.) and one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) with Gambel oak (*Quercus gambelli* Nutt.) and the occasional ponderosa pine (*Pinus ponderosa* Douglas ex C.Lawson), alligator juniper (*Juniperus deppeana* Steud.) and rocky mountain juniper (*Juniperus* *scopulorum* Sarg.) are also found. Soils are Hackroy clay loam and range in depth from 40 to 80 cm above a parent material of volcanic tuff.

The SUMO experiment includes a below canopy rain-out structure that diverts ~45% of precipitation and 18 transparent open-top chambers (OTCs) regulated by heating and cooling units (RJPL Package Heat Pump and RLPL Package Air Conditioner, Rheem Manufacturing Company, Atlanta GA, USA) to enable temperature control (Garcia-Forner et al. 2015). The rainout structure is similar in design to that described by Pangle et al (2012), but with troughs at ~1.3 m above the ground. Piñon pine and one-seed juniper trees were assigned to 5 treatments, drought (~45% rain-out), heat (~+5°C OTC), heat+drought (~45% rain-out and ~+5°C OTC), ambient (ambient precipitation and temperature) and ambient chamber control (ambient precipitation and ~+0°C OTC; Fig S1). OTCs maintained at ambient temperatures allowed testing for any chamber effects independent of heating. Temperature was monitored by two weather stations at the site and in each OTC at two height locations (1 m and 2/3 tree height; CS215 Temperature and Relative Humidity Probe and CR1000 datalogger, Campbell Scientific, Logan, UT, USA). This system was used as a thermostat to set desired temperature conditions in chambers. Over the course of this study, the mean effect in the heated treatments (heat and heat+drought) was +4.77°C (Fig S2) and in the ambient chamber control was -0.13°C, relative to ambient site conditions.

Environmental Conditions.

Treatments were initiated in June 2012 (Garcia-Forner et al. 2015), approximately nine months prior to initial phenology and growth measurements in March of 2013. From 1987-2012, mean annual temperature at SUMO was 10.5°C, varying on average from -0.6°C in December to

21.6°C in July, with a mean annual precipitation total of 414 mm (http://environweb.lanl.gov/weathermachine/). Precipitation at the site is influenced by the North American Monsoon season and is highest from July to September with a relatively even distribution throughout the rest of the year. Mean annual temperature in 2012, the year prior to the study, was 12.2°C and total precipitation was 198 mm. Mean annual temperature in 2013, the year of this study, was 9.7°C and total precipitation was 426 mm. However, 45% of annual precipitation in 2013 (194 mm) fell in September (Fig S2), such that the majority of the 2013 growing season and study measurements occurred during a period of drought continuing from 2011 (Williams et al. 2014).

Phenology and Growth.

For each treatment, eleven branches were selected among four piñon pine and juniper trees (2-3 per tree) for phenology and growth measurements. On each branch, we made measurements on the primary axis of growth, and also on a secondary axis that had 3-5 years of growth (measured in piñon pine, estimated in juniper) following the methods of Girard et al. (2011, 2012). After branch selection, initial measurements were made on March 16, 2013 (day of year (DOY) 75) and measurements were repeated periodically (every 9 to 29 days, mean sampling interval was ~18 days) throughout the 2013 growing season until November 19, 2013 (DOY 323). In branches of piñon pine, we noted phenophase (developmental stage) and measured the length of any new needles with a digital caliper. We described shoot phenophase using a numerical classification scheme adapted for piñon pine from the methods of Girard et al. (2011, 2012; Table 1, Fig S3). This scheme included the following stages: 1) bud dormant and unchanged in size, 2) bud swelling or growth observed, 3) needle scales open (budbreak), 4) new needle emergence and growth, 5) needle pairs separate. From these measurements we determined the day of needle emergence for each branch (phenophase 4), and calculated the proportion of branches which had needle growth for each piñon pine tree for each sampling date.

Concurrently, measurements of shoot length were also made with a digital caliper. For piñon pine, we measured shoot length from the visible boundary that can be easily discerned in this species between the previous year's growth and the base of the bud. As prior annual shoot growth cannot be discerned visually in juniper, we marked the transition between green and brown shoot tissue with ink, and measured from this mark to the tip of the growing shoot. In both species we also noted the appearance of male and female reproductive structures and calculated the percentage of measured branches with these. In juniper, male cones grow in late summer for pollen release the following early spring, and we quantified the presence of both 2013 and 2014 pollen cones in 2013. Branches of both species were also photographed approximately each month.

Water potential

Plant water potential on each tree (four per treatment) was measured monthly during the 2013 growing season to assess xylem water tension. Two twig samples were excised from the south side of each tree before dawn and kept in a refrigerator at the site until measurement within 2 hours of collection. Water potential was measured with a Scholander pressure chamber (PMS Instruments, Albany, OR) and determined as the mean of the two samples for each tree. A growing season mean in pre-dawn plant water potential was calculated from monthly measurements taken in March through October 2013.

Non-structural carbohydrates.

On June, 19 2013 (DOY 170), approximately 1 year after experimental treatments were initiated, tissue samples were collected from all trees in the study for non-structural carbohydrate (NSC) analysis. Foliar and shoot (twig) samples were collected by clipping recent canopy tissue. Bole and large root samples were collected with an increment borer. Roots samples were not obtained for some trees when roots of sufficient size for coring could not be found. All NSC samples were placed in liquid N_2 after collection, transported to the laboratory on dry ice, stored at -70°C, microwaved for 5 minutes at 800 W, and then dried at 65°C for 48 hours. All samples were ground into a fine powder using a ball mill (VWR, Radnor, PA), and woody samples were pre-ground with a Wiley mill (Thomas Scientific, Swedesboro, NJ). NSC, defined as soluble sugars (glucose, fructose, and sucrose) and starch, were assayed with water extraction and enzymatic quantification following a protocol modified from Hoch et al. (2002). Complete details of our NSC protocol were described by Dickman et al. (2015). Extraction was performed on ~12 mg of sample with 1.6 mL of deionized water for 1 hour in a 100°C water bath. Quantification was achieved via NAD-linked enzymatic assay and spectral assessment at 340 nm (Varian Cary 50 UV-Vis spectrophotometer, Palo Alto, CA).

Data analysis.

Prior to data analysis, time series of phenology and growth data for each branch were checked and inconsistent or missing data were corrected from branch photographs if possible, or removed. All statistical analyses were performed in SPSS Statistic 22.0 (IBM, Amonk, NY) with an α of 0.05. Before analysis, missing data were imputed conservatively by substituting the measurement recorded at the previous sampling date on the same branch. Repeated measures

ANOVA was used in time series analysis of proportion of branches with needles, needle growth, and shoot growth, with treatment (5 categories) and time as main fixed factors, and with Fisher's LSD for post-hoc analysis. We used the Huynh-Feldt correction (Huynh and Feldt 1976) to determine significance of results when unequal variance assumptions were violated (as determined by Mauchly's test for sphericity). For day of needle emergence and percent of branches with reproductive structures, data were analyzed with ANOVA using treatments as factors and Fisher's LSD for post-hoc analysis. Data were analyzed using Kruskal-Wallis with Dunn's test for post-hoc analysis if a Levene's test for unequal variance was significant. For analysis of the relationships of NSC and water potential with phenology and growth metrics, we calculated tree means of multiple branch data separately for the primary and secondary axes and used linear regression.

Results.

Phenophase and needle emergence timing in piñon pine.

The proportion of piñon trees that had needle emergence was highest in ambient and chamber control treatments for both primary and secondary branch axes ($p < 0.001$, Fig 1). For the primary axis, this proportion was lower than ambient in the drought and drought+heat treatments ($p < 0.05$), but not in the heat treatment ($p > 0.05$, Fig 1). For the secondary axis branches, the proportion of trees that had needle emergence was lower in the heat, drought, and drought+heat treatments than in ambient or chamber controls ($p < 0.05$). No needle emergence was observed in selected secondary axis branches on trees in the drought+heat treatment (Fig 1). Needle emergence on primary axis branches occurred earliest in ambient and control chamber treatments, on average at DOY 196 (July 15) and 205 (July 24), respectively (Fig 2). Relative to ambient, needle emergence in primary axis branches in the drought, heat, and drought+heat treatments was delayed on average by 19, 39, and 57 days, respectively ($p < 0.05$, Kruskal-Wallis and Dunn's test, Fig 2). There were no significant differences in the emergence timing of secondary axis branches among treatments, likely due to the large variability in responses and the absence of needle growth in the drought+heat treatment ($p > 0.05$). For both axes, standard error around needle emergence timing is higher in heat, drought, and drought+heat treatments relative to ambient, indicating increased variability with climate stress.

Needle and shoot growth.

In primary axis branches, piñon needle growth in the ambient and chamber control treatments was greater than that in the drought, heat, and drought+heat treatments ($p < 0.05$, Fig 3). For the secondary axis, there were no significant differences in piñon needle growth among ambient, heat and drought trees ($p > 0.05$). However, no piñon needle growth was observed in drought+heat trees, and control chamber trees had higher needle growth than trees in the heat and drought treatments for the secondary axis ($p < 0.01$, Fig 3). Shoot growth of piñon pine over the course of 2013 was higher, and increased earlier, in the ambient and chamber control treatments relative to the heat, drought, and drought+heat treatments for both primary and secondary axes ($p < 0.05$, Fig 4). For juniper, there was no difference in shoot growth among treatments ($p > 0.05$), and shoot growth was much lower than for piñon pine ($p < 0.001$, Fig 4).

Reproductive structures.

Observed differences in the growth of reproductive structures among treatments in both species was minimal. We observed no female cone production for either species, and only one piñon branch in the control chamber treatment had male cones. We observed substantial production of male cones in juniper, both early (cones produced in 2012 which released pollen in early 2013) and later in the year (cones produced in 2013 for pollen release in early 2014, Fig S3). There were no significant treatment effects on juniper male cone production for either year, likely due to the high variability among trees and branches. In the drought+heat treatment, male pollen cones were reduced from 2012 to 2013 on secondary axis branches ($p < 0.05$, Fig S4, Kruskal-Wallis analysis with posthoc Dunn's test).

Phenology and Physiology Correlations.

Shoot and needle growth of piñon were positively correlated with pre-dawn water potential while needle emergence timing was negatively correlated with water potential ($p < 0.05$, Fig 5a and c, Table S1). There were no correlations for juniper between shoot growth and water potential ($p > 0.05$). Correlations between shoot growth, needle growth, and needle emergence timing were also found with soluble sugars, starch, and total NSC in bole, needle, and shoot tissues ($p < 0.05$, Fig 5b and d, Table S2). Growth measurements were positively correlated with NSC components with one exception, an inverse relationship for primary axis shoot growth with shoot glucose and fructose ($r = -0.48$, $p < 0.05$). Needle emergence timing was negatively correlated with NSC variables in primary axis branches ($p < 0.05$), but this relationship was not significant for secondary axis branches ($p > 0.05$). Shoot growth, needle growth and needle emergence timing were most consistently correlated with shoot starch content and these relationships generally had the highest correlation coefficients (Table S2, Fig 5c and d). Although the distribution of points in Fig 5c and d suggests a non-linear relationship, non-linear regression did not result in a statistical improvement over a linear trend. For juniper, only two correlations with NSC were found, shoot growth in secondary axis branches with shoot glucose and fructose ($r = -0.53$, $p < 0.05$) and with shoot total NSC ($r = -0.46$, $p < 0.05$; data not show). Monthly and mean growing season pre-dawn water potential were correlated with June NSC variables by tissue in piñon pine (Table S3). Soluble sugars were inversely correlated with water potential, but a greater number of tissue starch and total NSC variables were positively correlated with water potential ($p < 0.05$, Table S3).

Discussion.

Overall, we found that experimental drought and heat reduced growth and delayed phenological development of piñon pine, while juniper growth was unresponsive to treatment. We hypothesized that increased temperature would lead to earlier development and increased shoot and foliar growth. We found no support for this hypothesis in any measured phenological or growth variable. In contrast, the heat treatment (+4.8°C) reduced phenological development in secondary axis branches (Fig 1), delayed needle emergence in primary axis branches (Fig 2), reduced foliar growth (Fig 3), and reduced shoot growth (Fig 4) in piñon pine relative to the ambient treatment. These results contrast starkly with findings from much phenological research, predominately from more mesic ecosystems where increased temperature was associated with earlier development and/or increased growth (Aono and Kazui 2008, Miller-Rushing and Primack 2008, Gordo and Sanz 2009, Primack et al. 2009, Richardson et al. 2013, Keenan et al. 2014). Our results demonstrate that this paradigm may not apply for trees in drier regions.

Drought alone delayed phenological development and reduced foliar growth (primary axis), and shoot growth, relative to the ambient treatment, consistent with our hypothesis (Figs 1-

4). Moreover, there were no differences in any measured variable between the heat and drought treatments in either branch axis, indicating that these two stresses affected the growth and phenology of piñon pine similarly. Our results were consistent with the phenological and growth responses of several Mediterranean tree species to experimental and natural drought (Borghetti et al. 1998, Ogaya and Peñuelas 2004, Peñuelas et al. 2004, Girard et al. 2011, 2012).

Given that the heat and drought treatments both delayed development and reduced growth it was surprising that the drought+heat treatment did not have more of a synergistic effect on piñon pine (Figs 1-4). The effects of heat and drought were most striking for foliar development, where heat delayed emergence by 19 days, drought by 39 days, and drought+heat by 57 days in the primary axis branches (Fig 2), while in secondary axis branches in the drought+heat treatment had no needle growth at all in 2013 (Figs 1 and 2). Although evergreen conifers can still photosynthesize with previous years' foliar growth, these trees went without the higher photosynthetic efficiency of younger foliage for part or all of the growing season (Ethier et al. 2006, Warren 2006).

Experiments have been found to under predict advances in leaf-flushing from warming, perhaps due to treatment artifacts (Wolkovich et al 2012). We found no differences in response between our ambient and chamber control treatment making this explanation for our results less likely. Previous research has shown that advances in development from heating can be reduced as temperature increases from ~+1 to ~+3°C (Repo et al. 1996, Morin et al. 2010, Kuster et al. 2014), and our temperature treatment was ~+4.8°C. Our result of reduced growth in the heated treatment is consistent with previous research finding that that radial growth of piñon pine and other conifers in the southwest US is negatively correlated with temperature (Adams and Kolb 2005, Williams et al. 2013).

Our phenology and growth results should be considered in the context of the unusually dry climate of 2011, 2012, and 2013 prior to September (Fig S2; Williams et al. 2014). From January through August 2013 the SUMO experiment site received only 146 mm of precipitation, 51% of the 25-year mean of 284 mm for the same period. Prior to this, 2012 annual precipitation was only 48% of the 25-year mean. Thus for the majority of 2013, our heat and drought treatments were imposed on top of an already strong drought. Effects of this background drought on the ambient trees in our experiment may explain why we did not observe any earlier development or increased growth in the heat treatment for piñon pine, relative to the ambient treatment. The lack of any reproductive development in ambient piñon, despite our observations that male pollen cones were common in 2012 in these trees, could also be explained by the dry start to 2013. The low precipitation in 2011-2013 may also explain the low shoot growth of juniper, relative to piñon pine, and also the lack of any treatment effect in juniper shoot growth. Juniper is known for its highly conservative growth in dry years (Howell 1941, Herman 1956). This conservative growth strategy likely enables juniper's survival at hotter and drier sites than piñon pine. Notably, the conditions in the drought+heat treatment during the already dry 2013 were not unrealistic, but analogous to those anticipated with future warming in megadrought climate conditions projected for later in the century (Williams et al. 2013, Cook et al. 2015).

Consistent with our hypothesis, lower values of water potential appeared to constrain growth and timing of needle emergence in piñon pine (Fig 5, Table S1). Correlation coefficients were typically highest for mean growing season water potential, and values in the months of March, May, June, and August were consistently correlated with growth and phenology, indicating that physiological drought stress over the entire growing season influenced growth and development (Fig 5, Table S1). In juniper, low observable variability in growth likely contributed to the lack of correlation with water potential.

We hypothesized that non-structural carbohydrates (NSC) would be unrelated to growth and phenology, or that reduced growth and delayed development due to drought stress would be associated with increased NSC, consistent with a reduction in C sink demand preceding a C source limitation (Körner 2003, Fatichi et al. 2014). However, low NSC in June was correlated with reduced growth and delayed needle emergence in piñon pine (Table S2). Correlations were strongest and most consistent across growth and phenology variables for shoot starch (Fig 5), indicating that trees with higher NSC reserves in shoots in the dry early growing season were more likely to show earlier needle emergences and greater growth over the rest of the season. This relationship, while unexpected given previous results from some species (e.g. Körner 2003), is consistent with reduced NSC in piñon pine observed in response to seasonal and prolonged drought stress (Adams et al. 2013, Sevanto et al. 2014, Dickman et al. 2015). The response of piñon is not unique; Mediterranean *Arbutus unedo* with low lignotuber NSC following 14 years of experimental drought had reduced basal area increment growth (Rosas et al. 2013). Despite low variability in juniper growth, we found two significant positive correlations of shoot growth with shoot glucose and fructose, and total NSC, indicating that higher juniper growth was related to increased NSC. Glucose and fructose have been shown to increase in juniper in response to drought and may be important for osmotic adjustment that enables growth under drought conditions in this species (Dickman et al. 2015). The paucity of significant relationships in this species is consistent with our hypothesis that NSC would be primarily unrelated to growth.

We urge caution in interpreting positive (inverse) relationships between growth (needle emergence timing) and NSC in these trees as a source limitation. We have correlated growth with NSC from relatively early in the growing season (June 19th, DOY 170). At this time for piñon pine, some shoot growth had been observed in the ambient and control chamber treatments, but needle emergence had not yet occurred in any measured branches. It is possible that NSC increased later in the growing season in trees which had reduced growth. June NSC and its components were correlated with shoot water potential across the growing season (Table S3), complicating the attribution of causation. For all cases where a significant relationship was found for both mean growing season water potential and shoot starch with growth or needle emergence (Fig 5), the adjusted r^2 from a linear regression was always higher for the correlation with water potential than for that with shoot starch concentration. This indicates that direct drought stress on xylem water tension was a stronger constraint for growth and development than NSC.

Our results demonstrate that a 4.8C increase in temperature, a change consistent with climate projections for 2100 in many regions with increasing anthropogenic CO_2 emissions (IPCC 2013), can cause phenological delay and reduced growth. Moreover, drought in combination with elevated temperature resulted in either a ~2 month delay in needle emergence or a complete lack of needle growth in piñon pine, which would cause a severe reduction in tree vigor over multiple growing seasons. These strong effects were observed after only ~1 year of treatment, demonstrating that phenological and growth responses to temperature and drought stress can be rapid. Our results indicate that projections based on typical phenological responses of an earlier and longer growing season in response to higher temperatures, and consequent increased ecosystem C sink strength, may not be valid for regions where plants will face increased drought stress with future climate change (Weiss et al. 2012). Trees that experience growth reductions from drought and temperature stress have reduced vigor and are often more prone to drought-induced mortality (Manion 1980, Waring 1987, Macalady and Bugmann 2014). Outside of the Mediterranean region, phenological responses of semi-arid tree species to drought and temperature have not been well-studied, and our results highlight the need to evaluate these tree responses in other dry regions. The physiological link between xylem tension and phenological response could provide a mechanistic, process-based approach to account for drought- and temperature-induced developmental delay and reduced productivity in global vegetation models. Correctly representing such phenological feedbacks on the terrestrial C sink with a changing climate is necessary for robust projections of global climate change.

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References.

Adams HD, Kolb TE (2005) Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. Journal of Biogeography, 32, 1629-1640.

Adams HD, Germino MJ, Breshears DD, Barron-Gafford GA, Guardiola-Claramonte M, Zou CB, Huxman TE (2013) Nonstructural leaf carbohydrate dynamics of *Pinus edulis* during drought-induced tree mortality reveal role for carbon metabolism in mortality mechanism. New Phytologist*,* 197, 1142-1151.

Aono Y, Kazui K (2008) Phenological data series of cherry tree flowering in Kyoto, Japan, and its application to reconstruction of springtime temperatures since the 9th century. International Journal of Climatology*,* 28, 905-914.

Borghetti M, Cinnirella S, Magnani F, Saracino A (1998) Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. Trees-Structure and Function*,* 12, 187-195.

Cook BI, Ault TR, Smerdon JE (2015) Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances, 1, e1400082.

Deslauriers A, Beaulieu M, Balducci L, Giovannelli A, Gagnon MJ, Rossi S (2014) Impact of warming and drought on carbon balance related to wood formation in black spruce. Annals of Botany*,* 114, 335-345.

Dickman LT, McDowell NG, Sevanto S et al. (2015) Carbohydrate dynamics and mortality in a piñon-juniper woodland under three future precipitation scenarios. Plant Cell and Environment, 38, 729-739.

Ethier GJ, Livingston NJ, Harrison DL, Black TA, Moran JA (2006) Low stomatal and internal conductance to CO2 versus Rubisco deactivation as determinants of the photosynthetic decline of ageing evergreen leaves. Plant Cell and Environment*,* 29, 2168-2184.

Fatichi S, Leuzinger S, Körner C (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. New Phytologist, 201, 1086-1095.

Garcia-Forner N, Adams HD, Sevanto S *et al.* (2015) Response of two semi-arid conifer tree species to reduced precipitation and warming reveal new perspectives for stomatal regulation. Plant, Cell, and Environment, In review.

Girard F, Vennetier M, Guibal F, Corona C, Ouarmim S, Herrero A (2012) *Pinus halepensis* Mill. crown development and fruiting declined with repeated drought in Mediterranean France. European Journal of Forest Research, 131, 919-931.

Girard F, Vennetier M, Ouarmim S, Caraglio Y, Misson L (2011) Polycyclism, a fundamental tree growth process, decline with recent climate change: the example of *Pinus halepensis* Mill. in Mediterranean France. Trees-Structure and Function, 25, 311-322.

Gordo O, Sanz JJ (2009) Long-term temporal changes of plant phenology in the Western Mediterranean. Global Change Biology, 15, 1930-1948.

Gruber A, Pirkebner D, Florian C, Oberhuber W (2012) No evidence for depletion of carbohydrate pools in Scots pine (*Pinus sylvestris* L.) under drought stress. Plant Biology, 14, 142-148.

Guak S, Olsyzk DM, Fuchigami LH, Tingey DT (1998) Effects of elevated CO(2) and temperature on cold hardiness and spring bud burst and growth in Douglas-fir (*Pseudotsuga menziesii*). Tree Physiology, **18**, 671-679.

Han S, Chung H, Noh NJ *et al.* (2014) Effect of open-field experimental warming on the leaf phenology of oriental oak (*Quercus variabilis*) seedlings. Journal of Plant Ecology*,* 7, 559-566.

Hartmann H, McDowell NG, Trumbore S (2015) Allocation to carbon storage pools in Norway spruce saplings under drought and low CO2. Tree Physiology, In press.

Herman FR (1956) Growth and phenological observation of Arizona junipers. Ecology*,* 37, 193-195.

Hoch G, Popp M, Körner C (2002) Altitudinal increase of mobile carbon pools in *Pinus cembra* suggests sink limitation of growth at the Swiss treeline. Oikos*,* 98, 361-374.

Howell J (1941) Piñon and juniper woodlands of the Southwest. Journal of Forestry*,* 39, 542-545.

Huynh H, Feldt LS (1976) Estimation of the box correction for degrees of freedom from sample data in randomized block and split-plot designs. Journal of Education and Behavioral Statistics, 1, 69-82.

Intergovernmental Panel on Climate Change (IPCC) (2013) Climate Change 2013: The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the IPCC. Cambridge, UK: Cambridge University Press.

Keeling CD (1960) The concentration and isotopic abundances of carbon dioxide in the atmosphere. Tellus*,* 12, 200-203.

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO2 measurements. Nature, 382, 146-149.

Keenan TF, Gray J, Friedl MA *et al.* (2014) Net carbon uptake has increased through warming-induced changes in temperate forest phenology. Nature Climate Change, 4, 598-604.

Körner C (2003) Carbon limitation in trees. Journal of Ecology, 91, 4-17.

Kuster TM, Dobbertin M, Gunthardt-Goerg MS, Schaub M, Arend M (2014) A phenological timetable of oak growth under experimental drought and air warming. Plos One, 9.

Limousin J-M, Rambal S, Ourcival J-M *et al.* (2012) Morphological and phenological shoot plasticity in a Mediterranean evergreen oak facing long-term increased drought. Oecologia, 169, 565-577.

Macalady AK, Bugmann H (2014) Growth-mortality relationships in piñon pine (*Pinus edulis*) during severe droughts of the past century: shifting processes in space and time. Plos One, 9, 17.

Manion PD (1980) Tree Disease Concepts. Prentice Hall Career & Technology, Englewood Cliffs, New Jersey.

McDowell NG (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. Plant Physiology, 155, 1051-1059.

Miller-Rushing AJ, Primack RB (2008) Global warming and flowering times in Thoreau's concord: A community perspective. Ecology, 89, 332-341.

Morin X, Roy J, Sonie L, Chuine I (2010) Changes in leaf phenology of three European oak species in response to experimental climate change. New Phytologist, 186, 900-910.

Norby RJ, Hartz-Rubin JS, Verbrugge MJ (2003) Phenological responses in maple to experimental atmospheric warming and CO2 enrichment. Global Change Biology, 9, 1792-1801.

Oberhuber W, Swidrak I, Pirkebner D, Gruber A (2011) Temporal dynamics of nonstructural carbohydrates and xylem growth in *Pinus sylvestris* exposed to drought. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere, 41, 1590-1597.

Ogaya R, Peñuelas J (2004) Phenological patterns of *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo* growing under a field experimental drought. Ecoscience, 11, 263-270.

Oleoson KW, Lawrence DM, Bonan GB (2013) Technical description of version 4.5 of the Community Land Model (CLM). Technical Note, NCAR/TN-503+STR, National Center for Atmospheric Research,

Overpeck J, Udall B (2010) Dry Times Ahead. Science, 328, 1642-1643.

Palacio S, Hoch G, Sala A, Körner C, Millard P (2014) Does carbon storage limit tree growth? New Phytologist, 201, 1096-1100.

Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. Global Change Biology, 8, 531-544.

Peñuelas J, Filella I, Zhang XY *et al.* (2004) Complex spatiotemporal phenological shifts as a response to rainfall changes. New Phytologist, 161, 837-846.

Pangle RE, Hill JP, Plaut JA *et al.* (2012) Methodology and performance of a rainfall manipulation experiment in a pinon-juniper woodland. Ecosphere,3, Article 28.

Primack RB, Higuchi H, Miller-Rushing AJ (2009) The impact of climate change on cherry trees and other species in Japan. Biological Conservation, 142, 1943-1949.

Repo T, Hanninen H, Kellomaki S (1996) The effects of long-term elevation of air temperature and CO2 on the frost hardiness of Scots pine. Plant Cell and Environment, 19, 209-216.

Richardson AD, Anderson RS, Arain MA *et al.* (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. Global Change Biology, 18, 566-584.

Richardson AD, Black TA, Ciais P *et al.* (2010) Influence of spring and autumn phenological transitions on forest ecosystem productivity. Philosophical Transactions of the Royal Society B-Biological Sciences, 365, 3227-3246.

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. Agricultural and Forest Meteorology, 169, 156-173.

Rosas T, Galiano L, Ogaya R, Peñuelas J, Martinez-Vilalta J (2013) Dynamics of non-structural carbohydrates in three Mediterranean woody species following long-term experimental drought. Frontiers in Plant Science, 4.

Schaber J, Badeck FW (2003) Physiology-based phenology models for forest tree species in Germany. International Journal of Biometeorology*,* 47, 193-201.

Sevanto S, Mcdowell NG, Dickman LT, Pangle R, Pockman WT (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. Plant Cell and Environment*,* 37, 153-161.

Tissue DT, Wright SJ (1995) Effect of seasonal water availability on phenology and the annual shoot carbohydrate cycle of tropical forest shrubs. Functional Ecology*,* 9, 518-527.

Waring RH (1987) Characteristics of trees predisposed to die. Bioscience, 37, 569-574.

Warren CR (2006) Why does photosynthesis decrease with needle age in *Pinus pinaster*? Trees-Structure and Function*,* 20, 157-164.

Weiss JL, Betancourt JL, Overpeck JT (2012) Climatic limits on foliar growth during major droughts in the southwestern USA. Journal of Geophysical Research-Biogeosciences*,* 117, 15.

Williams AP, Allen CD, Macalady AK *et al.* (2013) Temperature as a potent driver of regional forest drought stress and tree mortality. Nature Climate Change*,* 3, 292-297.

Williams AP, Seager R, Berkelhammer M *et al.* (2014) Causes and implications of extreme atmospheric moisture demand during the record-breaking 2011 wildfire season in the southwestern United States. Journal of Applied Meteorology and Climatology*,* 53, 2671-2684.

Wolkovich EM, Cook BI, Allen JM *et al.* (2012) Warming experiments underpredict plant phenological responses to climate change. Nature*,* 485, 494-497.

Würth MKR, Pelaez-Riedl S, Wright SJ, Körner C (2005) Non-structural carbohydrate pools in a tropical forest. Oecologia*,* 143, 11-24.

Supporting Information.

Table S1. Correlations between water potential and shoot growth, needle growth, and emergence timing.

Table S2. Correlations between NSC and components and shoot growth, needle growth, and emergence timing.

Table S3. Correlations between water potential and NSC components.

Fig S1. Design of the Los Alamos Survival-Mortality experiment.

Fig S2. Daily means in temperature and vapor pressure deficit for the ambient and heated treatments, and total daily precipitation at the SUMO experiment in 2013.

Fig S3. An illustration of phenological phases in our classification scheme for piñon pine

Fig S4. Pollen cone production in one-seed juniper by treatment.

Figures and Tables

Table 1. Phenophase descriptions of piñon pine shoot development. This classification scheme was adapted for piñon pine from Girard et al. (2011, 2012). Photographic examples of phenophases in piñon pine are shown in Fig S3.

Phenophase	Description
1	Bud dormant and unchanged in size
2	Bud swelling or growth observed
3	Needle scales open (budbreak)
4	Needle emergence
5	Needle pairs separate

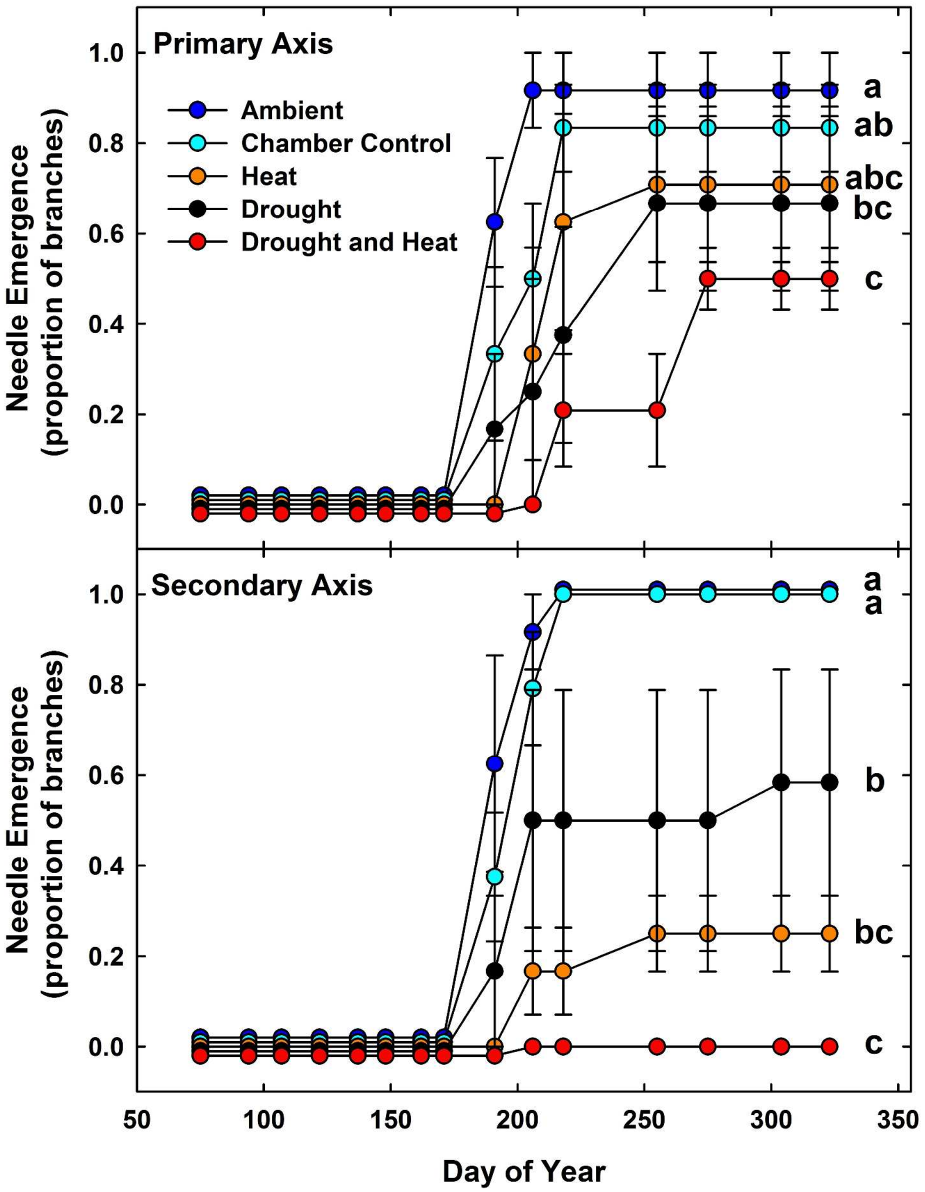
Fig 1. The proportion of piñon pine shoots with needle emergence (phenophase > 4, Table 1) on primary and secondary branches over the 2013 growing season under 5 environmental treatments. Significant differences among treatments (over the growing season) are indicated by letters separately for both primary and secondary axis branches (repeated measures ANOVA, $p < 0.05$). Phenophase classification is defined in Table 1 and illustrated in Fig S3. Overlapping values are offset slightly to illustrate all treatments. Error bars are standard errors.

Fig 2. Timing of needle emergence for primary (black) and secondary (gray) axis branches. Significant differences were found for needle emergence timing in the primary, but not secondary, axis branches, and are indicated with letters (Kruskal-Wallis analysis and posthoc Dunn's test). Note that no needle growth was observed in secondary axis branches in the drought+heat treatment during the 2013 growing season. Error bars are standard errors.

Fig 3. Piñon pine needle elongation on primary and secondary axis shoots over the 2013 growing season under 5 environmental treatments for shoots that had needle emergence. Significant differences among treatments (over the growing season) are indicated by letters separately for both primary and secondary axis branches (repeated measures ANOVA, $p > 0.05$). Piñon pine trees under ambient conditions had greater needle elongation than trees in the heat, drought, and drought+heat treatments on the primary axis, and the drought treatment on the secondary axis. A line is shown at zero for the lack of needle growth observed on secondary axis shoots in the drought+heat treatment; this was not included in statistical analysis. The occasional appearance of decline in mean needle growth over the growing season is due to the error in the growth measurement. Error bars are standard errors.

Fig 4. Shoot growth on primary and secondary axis branches of piñon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) over the 2013 growing season under 5 environmental treatments. Shoot growth increased significantly in both species over the growing season (repeated measures ANOVA, $p < 0.001$). Treatment effects and treatment by time interactions were significant only for piñon pine ($p <0.001$). Letters indicate significant differences in effects among treatments for piñon pine over the growing season; shoot growth was reduced in the heat, drought, and drought+heat treatments, relative to control treatments ($p < 0.05$). The occasional appearance of decline in mean shoot growth over time is a due to the error in the growth measurement. Error bars are standard errors.

Fig 5. Relationships in piñon pine between mean growing season pre-dawn water potential (Ψ_{pd}) and growth (**a**), June twig starch concentration and growth (**b**), mean growing season Ψ_{pd} and timing of needle emergence (**c**), and June twig starch concentration and timing of needle emergence (**d**), for primary (red) and secondary axis (blue) branches. Relationships with growth are shown for both shoots (circle, solid line) and needles (triangle, dashed line) in **a** and **b**. Significant linear regressions between water potential and primary axis shoot ($r^2 = 0.39$) and needle ($r^2 = 0.45$) growth, secondary shoot ($r^2 = 0.51$) and needle ($r^2 = 0.68$) growth, and primary needle emergence timing ($r^2 = 0.49$) are shown in **a** and **c**. Significant linear regressions between June twig starch concentration and primary axis shoot ($r^2 = 0.24$) and needle ($r^2 = 0.29$) growth, secondary shoot ($r^2 = 0.39$) and needle ($r^2 = 0.59$) growth, and primary needle emergence timing ($r^2 = 0.43$) are shown in **b** and **d**. Additional growth and phenology correlations with water potential and non-structural carbohydrate components for bole, needle, root and twig tissues are found in Tables S1 and S2. Analogous relationships for juniper shoot growth were not observed and are not shown ($p > 0.05$).



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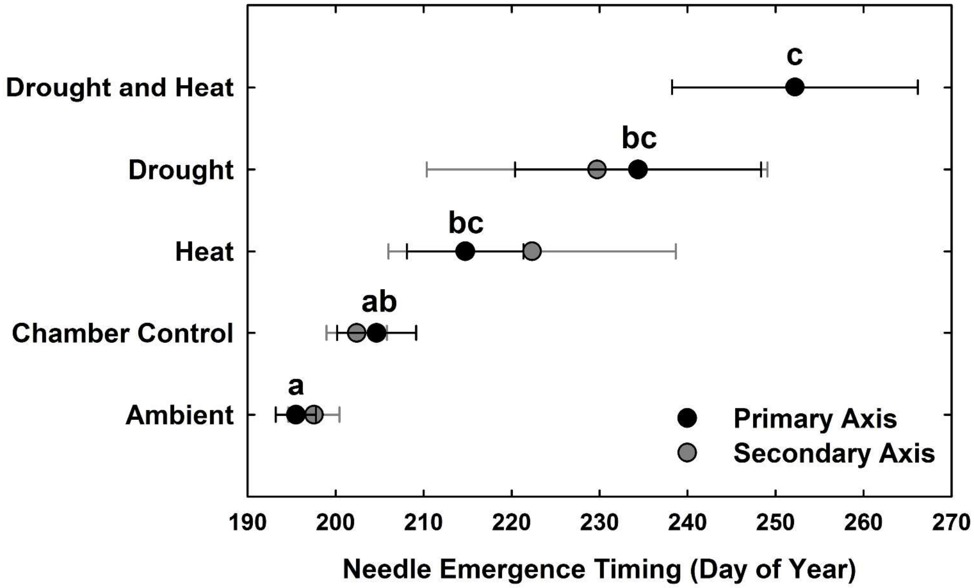

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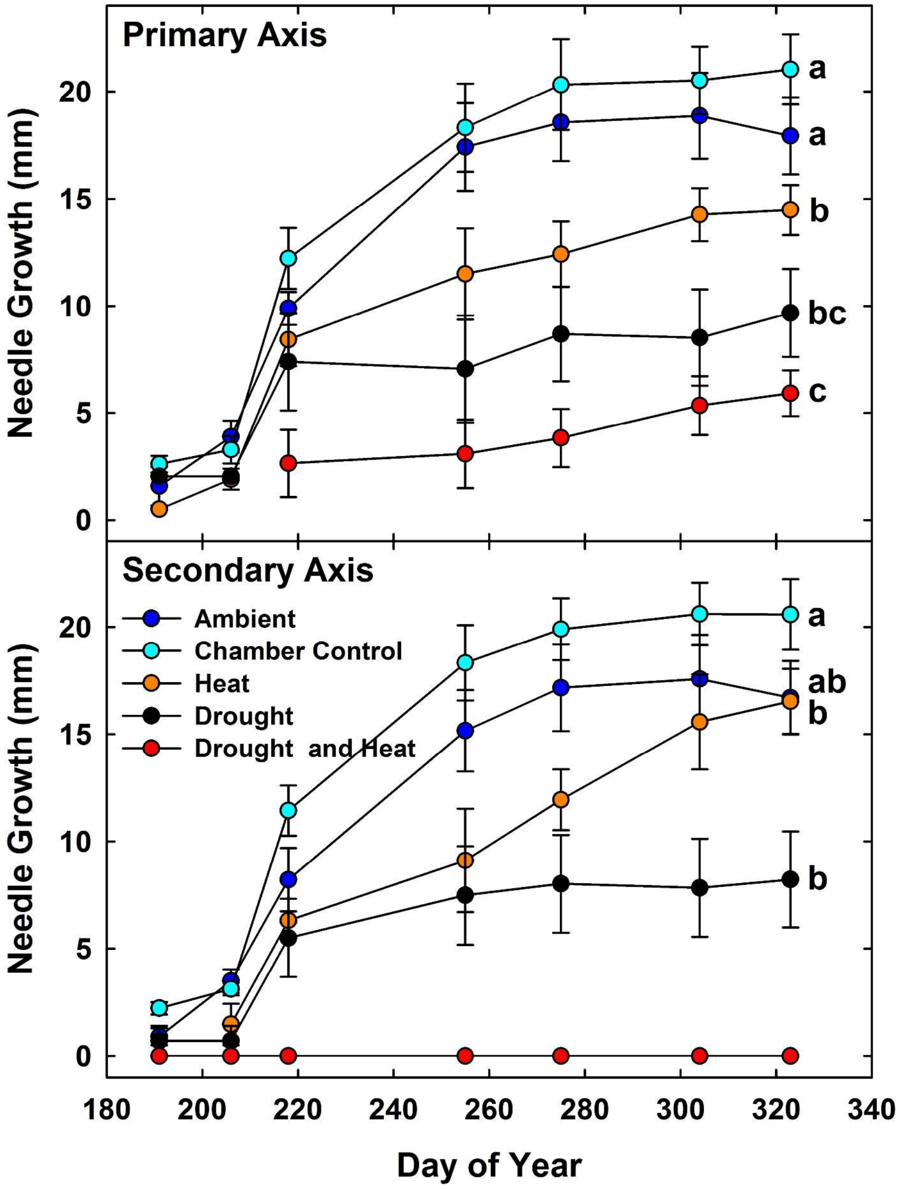

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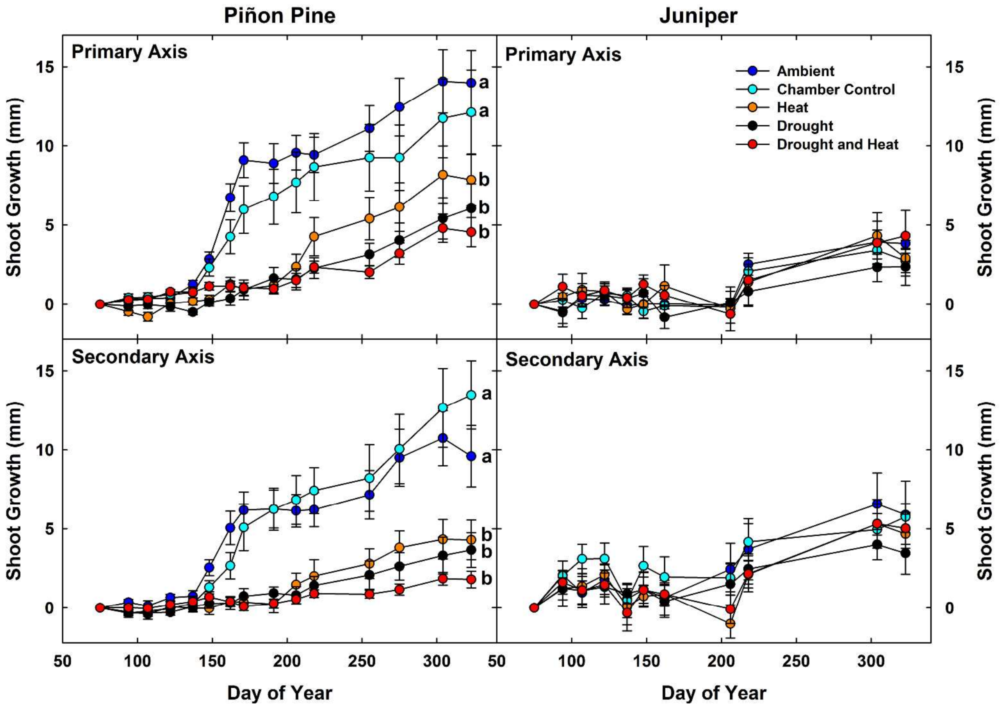

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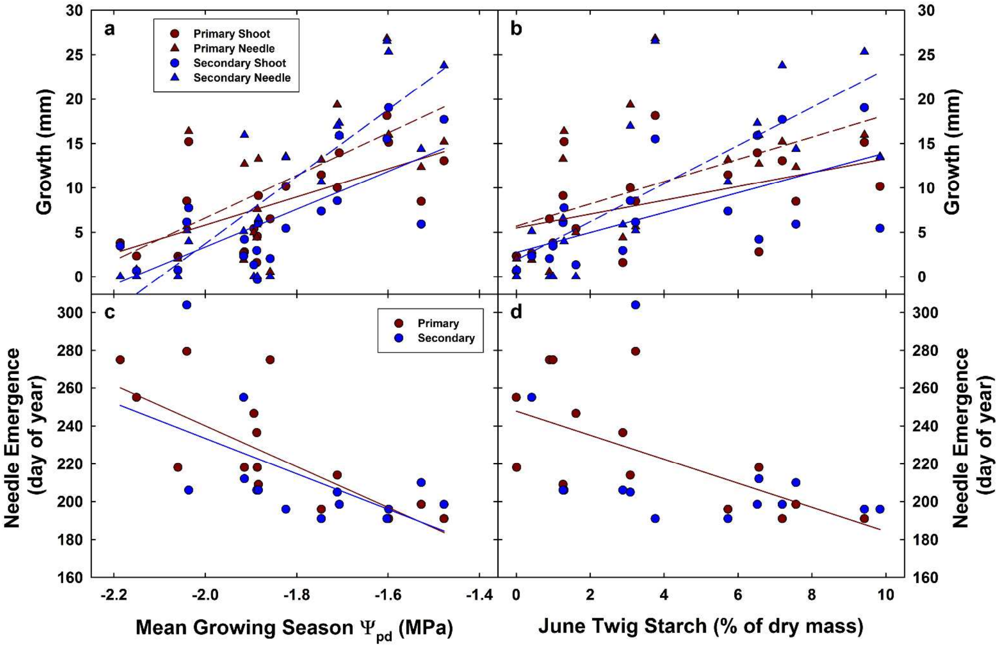

Fig 5. Relationships in piñon pine between mean growing season pre-dawn water potential (Ψpd) and growth (a), June twig starch concentration and growth (b), mean growing season Ψpd and timing of needle emergence (c), and June twig starch concentration and timing of needle emergence (d), for primary (red) and secondary axis (blue) branches. Relationships with growth are shown for both shoots (circle, solid line) and needles (triangle, dashed line) in a and b. Significant linear regressions between water potential and primary axis shoot (r2 = 0.39) and needle (r2 = 0.45) growth, secondary shoot (r2 = 0.51) and needle (r2 = 0.68) growth, and primary needle emergence timing (r2 = 0.49) are shown in a and c. Significant linear regressions between June twig starch concentration and primary axis shoot (r2 = 0.24) and needle (r2 = 0.29) growth, secondary shoot (r2 = 0.39) and needle (r2 = 0.59) growth, and primary needle emergence timing (r2 = 0.43) are shown in b and d. Additional growth and phenology correlations with water potential and non-structural carbohydrate components for bole, needle, root and twig tissues are found in Tables S1 and S2. Analogous relationships for juniper shoot growth were not observed and are not shown (p > 0.05).

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Experimental drought and heat can delay phenological development and reduce growth in semiarid trees.

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Supporting Information.

Supporting Figures

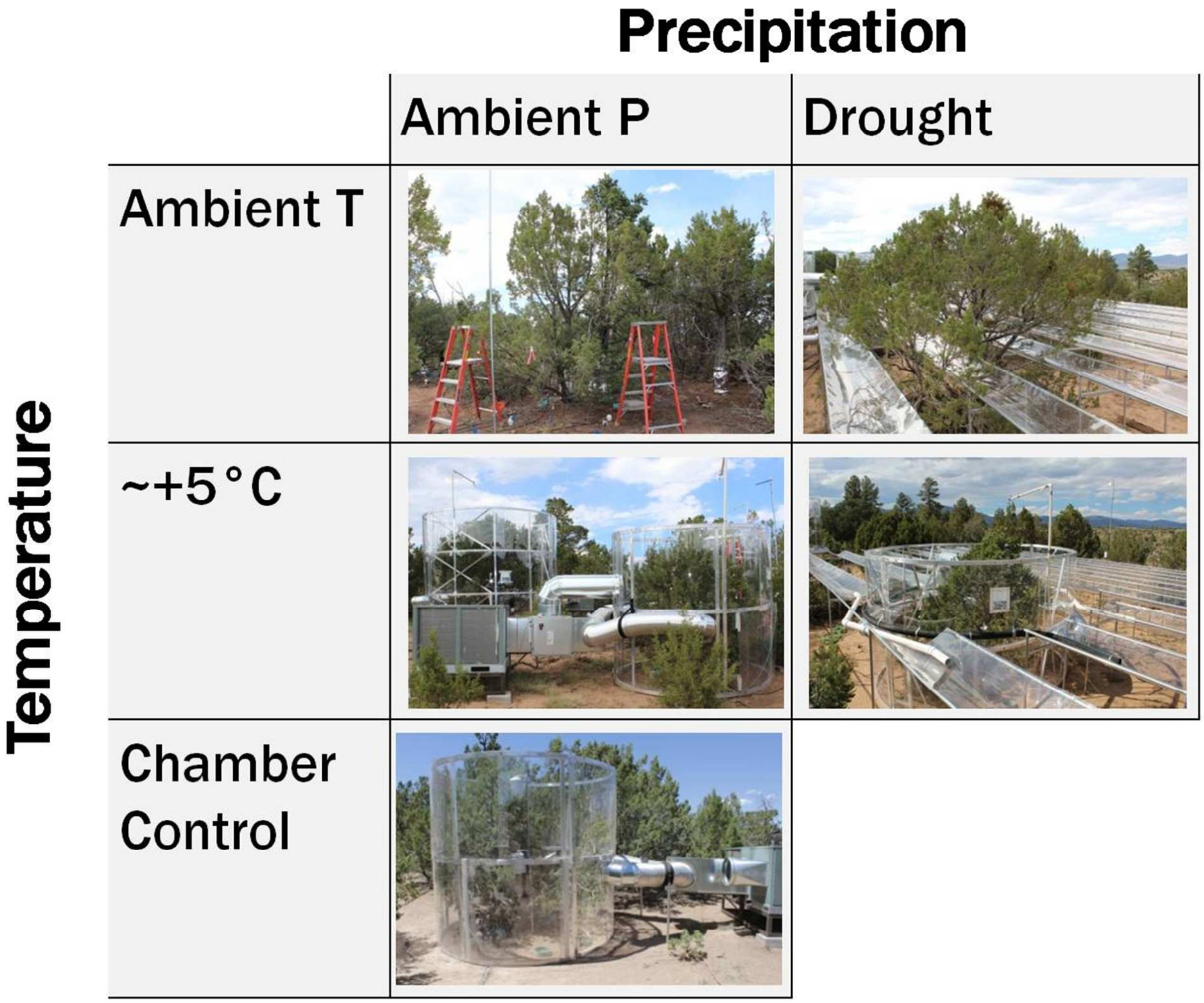

Fig S1. Design of the Los Alamos Survival-Mortality experiment (SUMO). Drought was induced with a ~45% throughfall rain-out structure and temperature was modified with transparent plastic open-top chambers regulated by heating and cooling units. Precipitation and temperature factors were combined to provide ambient, drought, heat, and drought+heat treatments. A chamber control treatment was implemented with an additional set of open-top chambers regulated to ambient field air temperature.

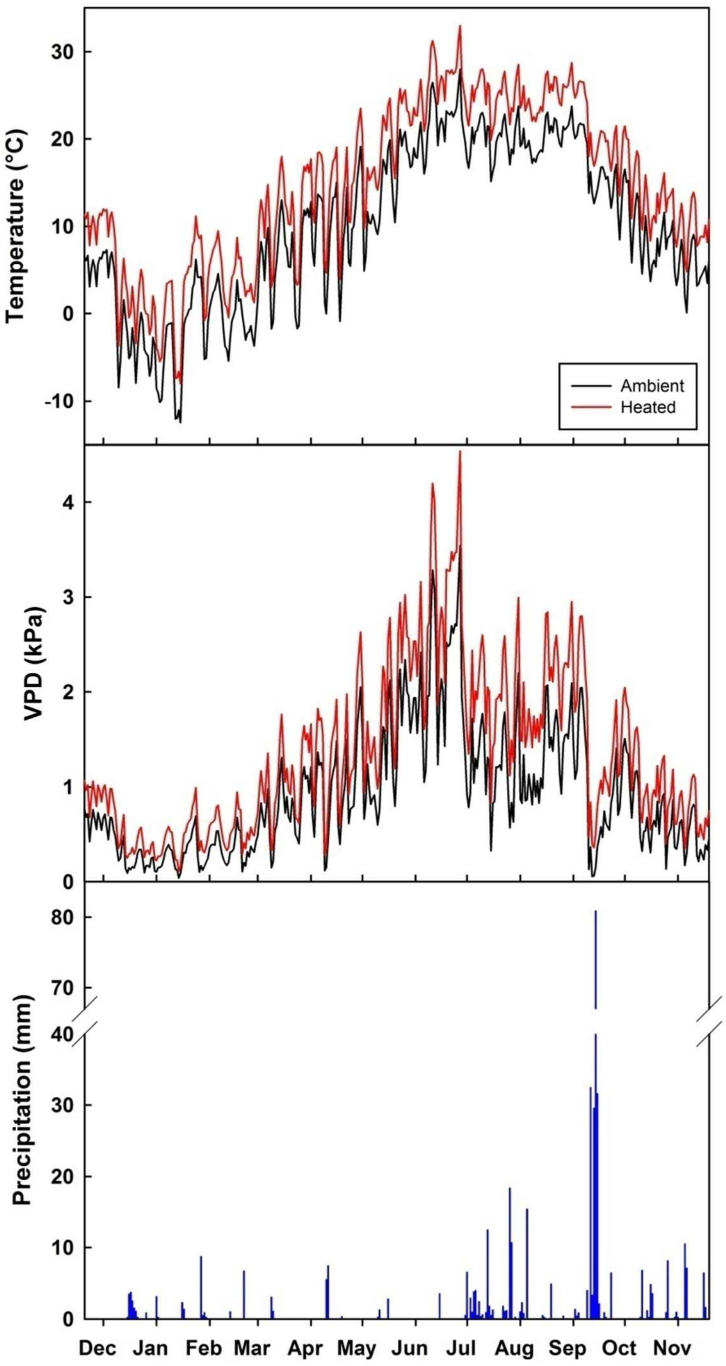

Fig S2. Mean daily temperature and vapor pressure deficit (VPD) for the ambient and heated treatments (heat and drought+heat), and total daily precipitation at the SUMO experiment from December 2012 to November 2013.

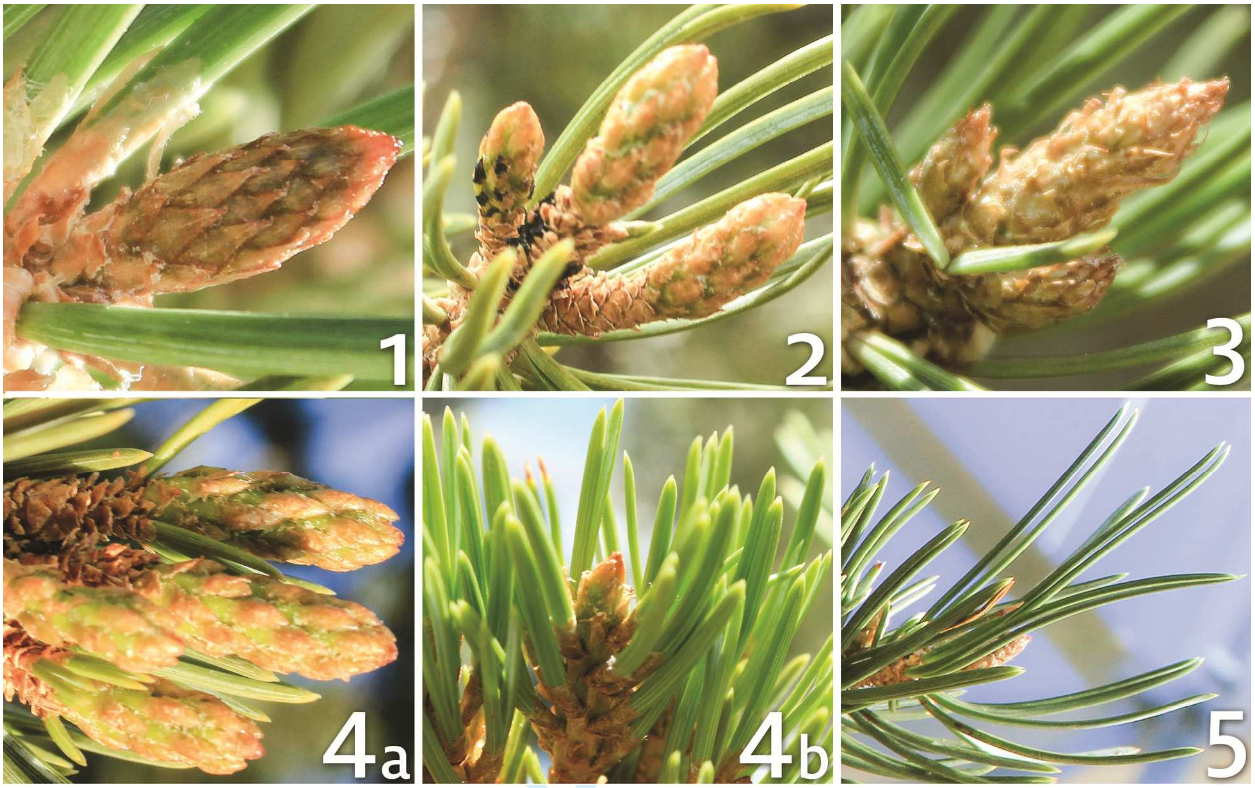

Fig S3. Phenological phases in our classification scheme for piñon pine: 1) bud dormant and unchanged in size, 2) bud swelling or growth observed, 3) needle scales open (budbreak), 4) new needle emergence and growth (both early (4a) and later (4b) examples of this stage are shown), 5) needle pairs separate.

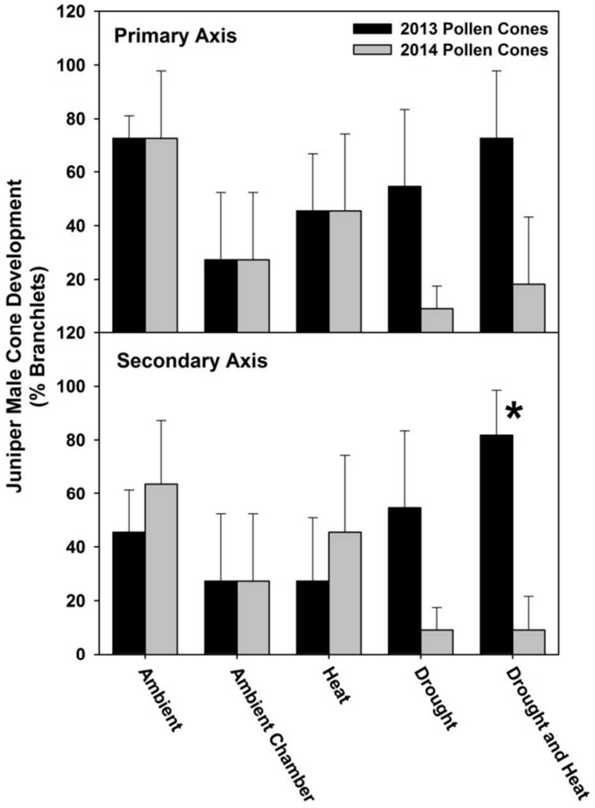

Fig S4. Pollen cone production in one-seed juniper by treatment. Pollen cones observed releasing pollen in early 2013 and also those developed late in the growing season for 2014 pollen release are shown. Significant differences between 2013 and 2014 cones are noted with an asterisk (Kruskal-Wallis test, $p < 0.05$). Error bars are standard errors.

Supplemental Tables

Table S1. Correlations are shown between pre-dawn shoot water potential (monthly and mean growing season) and shoot growth, needle growth, and needle emergence timing in primary and secondary axis branches of piñon pine. Only significant correlation coefficients are shown ($p < 0.05$). The relationships between mean growing season water potential and shoot growth, growth, and needle emergence timing are also shown in Fig 5. There were no significant correlations for juniper between shoot growth and water potential.

	Phenology	**Correlation coefficient with water potential**								
Axis	**Measurement**	**March**	**April**	**May**	**June**	**July**	**August**	**Sept.**	**Oct.**	**Mean**
Primary	Shoot growth	0.59		0.70	0.49		0.46			0.62
	Needle growth	0.66		0.66	0.48		0.59			0.66
	Needle emergence	-0.61		-0.60			-0.65			-0.70
Secondary	Shoot growth	0.73		0.64	0.48			0.50		0.71
	Needle growth	0.79		0.60	0.57		0.60	0.45		0.82
	Needle emergence									-0.55

Table S2. Correlations between June non-structural carbohydrate (NSC) concentrations and shoot growth, needle growth, and needle emergence timing in primary and secondary axis branches of piñon pine. Correlations are shown separately for NSC components of glucose and fructose (Gluc & Fruc), sucrose, starch, and total NSC concentrations. Only significant correlation coefficients are shown ($p < 0.05$). The relationships between shoot starch content and shoot growth, growth, and needle emergence timing are also shown in Fig 5. Significant correlations were found for juniper shoot growth in secondary axis branches with shoot glucose and fructose ($r = -0.53$, $p < 0.05$) and shoot total NSC ($r = -0.46$, $p < 0.05$; data not show).

Tissue	**NSC Component**	**Primary Axis**			**Secondary Axis**		
		Shoot growth	**Needle growth**	**Needle emergence**	**Shoot growth**	**Needle growth**	**Needle emergence**
Bole	Gluc & Fruc						
	Sucrose						
	Starch					0.54	
	Total NSC						
Needle	Gluc & Fruc						
	Sucrose						
	Starch			-0.45	0.51	0.55	
	Total NSC				0.47	0.46	
Root	Gluc & Fruc						
	Sucrose						
	Starch						
	Total NSC						
Shoot	Gluc & Fruc	-0.48					
	Sucrose					0.52	
	Starch	0.49	0.55	-0.65	0.62	0.77	
	Total NSC		0.51	-0.57	0.58	0.77	

Table S3. Correlations between pre-dawn shoot water potential (monthly and mean growing season) and June NSC and components in piñon pine. Only significant correlation coefficients are shown ($p < 0.05$).

	NSC	**Correlation coefficient with water potential**								
Tissue	**Component**	**March**	**April**	**May**	**June**	**July**	**August**	**Sept.**	**Oct.**	**Mean**
Bole	Gluc & Fruc									
	Sucrose	-0.51	-0.68							-0.52
	Starch					0.55				
	Total NSC		-0.58							
Needle	Gluc & Fruc							0.47		
	Sucrose									
	Starch	0.55						0.44		0.55
	Total NSC							0.53		
Root	Gluc & Fruc									
	Sucrose									
	Starch					0.60	0.61			0.59
	Total NSC									0.58
Shoot	Gluc & Fruc			-0.61	-0.53					
	Sucrose									
	Starch	0.50			0.67	0.58	0.49			0.70
	Total NSC	0.49			0.54	0.56	0.45			0.63