Drought characteristics' role in widespread aspen forest mortality across Colorado, USA

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Abstract

Globally documented widespread drought-induced forest mortality has important ramifications for plant community structure, ecosystem function, and the ecosystem services provided by forests. Yet the characteristics of drought seasonality, severity, and duration that trigger mortality events have received little attention despite evidence of changing precipitation regimes, shifting snow melt timing, and increasing temperature stress. This study draws upon stand level ecohydrology and statewide climate and spatial analysis to examine the drought characteristics implicated in the recent widespread mortality of trembling aspen (*Populus tremuloides* Michx.). We used isotopic observations of aspen xylem sap to determine water source use during natural and experimental drought in a region that experienced high tree mortality. We then drew upon multiple sources of climate data to characterize the drought that triggered aspen mortality. Finally, regression analysis was used to examine the drought characteristics most associated with the spatial patterns of aspen mortality across Colorado. Isotopic analysis indicated that aspens generally utilize shallow soil moisture with little plasticity during drought stress. Climate analysis showed that the mortality-inciting drought was unprecedented in the observational record, especially in 2002 growing season temperature and evaporative deficit, resulting in record low shallow soil moisture reserves. High 2002 summer temperature and low shallow soil moisture were most associated with the spatial patterns of aspen mortality. These results suggest that the 2002 drought subjected Colorado aspens to the most extreme growing season water stress of the past century by creating high atmospheric moisture demand and depleting the shallow soil moisture upon which aspens rely. Our findings highlight the important role of drought characteristics in mediating widespread aspen forest mortality, link this aspen die-off to regional climate change trends, and provide insight into future climate vulnerability of these forests.

Keywords: Climate change, drought, forest mortality, plant ecophysiology, *Populus tremuloides*, stable isotopes, water use

Introduction

Anthropogenic changes in climate are expected to increase the frequency and duration of droughts across much of western North America over the 21st century (Seager *et al.*, 2007; Cayan *et al.*, 2010), significantly influencing the composition, distribution, condition, and productivity of many ecosystems (Easterling *et al.*, 2000). Abrupt ecosystem shifts, especially through widespread vegetation mortality, could be among the most striking impacts of increased drought and climate change, with growing evidence of widespread forest die-off from drought and heat stress around the globe (Allen *et al.*, 2010). While climate-influenced processes

such as natality and growth can shape species distributions and ecosystem structure over long time periods, rapid mortality due to climate extremes can induce range shifts in a matter of years (Allen & Breshears, 1998). In addition, regional tree die-offs driven by top-down climate factors can have drastic effects on ecosystem function, land-atmosphere interactions, nutrient-cycling, ecosystem services, and carbon sequestration (Anderegg *et al.*, 2012a). Yet we currently lack sufficient understanding of these mortality processes to model and predict tree die-off based on easily observed or modeled climate variables. Filling this knowledge gap is particularly important given that many species around the world appear to have narrow hydraulic safety margins and may thus be vulnerable to future climate stress (Choat *et al.*, 2012).

Climate projections indicate that changes in winter temperature, snow pack, and spring run-off may be some of the stronger and earlier impacts of climate

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change, especially in the western United States (Hayhoe *et al.*, 2004; Field *et al.*, 2007). Declines in mountain snow pack and advances in the timing of snow melt-driven runoff have already been detected across much of the region (Mote *et al.*, 2005) and attributed to anthropogenic climate change (i.e. Pierce *et al.*, 2008; Stewart, 2009). Winter and spring precipitation and infiltration can play a large role in forest water supply (e.g. Debyle & Winokur, 1985). Thus, the impacts of these changes in seasonality of precipitation and seasonal availability of water could play an important role in widespread forest mortality, yet they have received relatively little attention.

A wealth of ecophysiological studies in grassland, desert, and Mediterranean-type ecosystems suggests that moisture availability including seasonality, form, timing, and sequence of precipitation are very important for ecosystem processes (e.g. Schwinning *et al.*, 2005a,b; Chimner *et al.*, 2010). In particular, drought characteristics can be critical to understanding how much water is available to plants during severe drought, influencing both the temporal and spatial availability of soil moisture and when, where, and how forests experience drought. Yet, with the exception of recent tree ring studies (e.g. Linares & Camarero, 2012) most work on drought-induced forest mortality to date has focused on what occurs once a plant experiences drought stress without taking into account the time-course of water stress (e.g. Mcdowell *et al.*, 2008).

Widespread drought-induced die-off of trembling aspen (*Populus tremuloides* Michx.) forests recently occurred across much of the western United States and parts of Canada (Worrall *et al.*, 2008; Michaelian *et al.*, 2011). Triggered by a severe drought from 2000–2003 and continuing multiple years post-drought, this widespread, multi-year die-off has been termed sudden aspen decline (SAD) and has been estimated to affect up to 17% of Colorado aspen forests (Worrall *et al.*, 2008; Anderegg *et al.*, 2012b). While the drought was unusually warm, it was not the most extreme precipitation deficit on record in most Colorado locations (Pielke *et al.*, 2005). Yet previous droughts with more extreme precipitation deficits do not appear to have initiated widespread aspen mortality. Thus, SAD provides a timely and relevant example to test the role of drought characteristics, particularly drought seasonality and the rolls of precipitation deficit and temperature-driven atmospheric moisture demand, in inducing widespread forest die-off. Growing season atmospheric moisture demand in particular has been found to be key in explaining drought stress in the tree ring record (Williams *et al.*, 2012) and in distinguishing the droughts in the 2000s from previous droughts (Weiss *et al.*, 2012). Yet how evaporative demand integrates with forest ecohydrology and forest ecophysiology is largely unknown.

An understanding of plant-available water dynamics is critical for establishing the link between drought characteristics and tree mortality. Plant-available water is influenced not just by the meteorological inputs and evapotranspirative outputs, but also by plant functional rooting depth and rooting plasticity. Thus, to understand when and how aspens became critically water stressed, we draw on two complementary approaches here to explore critical aspects of aspen ecohydrology that define what water sources are available for aspen use (a bottom-up physiology approach) and to identify the characteristics of the 2000–2003 drought that were truly extreme and that posed critical limitations to water availability (a top-down geographic approach).

Stable isotope techniques are a powerful tool for examining plant ecohydrology and use of seasonal water sources. The $^{18}O/^{16}O$ and D/H ratios of soil water vary spatially and temporally due to both seasonal variation in the abundance of oxygen and hydrogen isotopes in precipitation (summer rain is more enriched than winter snow) (Dansgaard, 1964) and evaporative enrichment at the soil surface. Because no fractionation occurs when plant roots take up water, the isotopic content of plant xylem water can be used to trace the water transpired by a plant to isotopically distinct sources such as deep vs. shallow soil moisture (Phillips & Ehleringer, 1995) or seasonal precipitation (Williams & Ehleringer, 2000). Thus, while water isotope analyses have yet to be applied specifically to the investigation of drought-induced mortality, they can provide insight into the vulnerability of forests to various meteorological drought characteristics such as summer vs. winter drought, by revealing if and when plants rely on different seasonal water sources.

In this study, we ask the following four questions concerning ecological mechanisms and patterns of aspen decline: (1) Which layers of the soil do aspens draw on during seasonal and experimental water stress? (2) Do isotopic analyses provide insight into specific characteristics of drought detrimental to aspens? (3) What drought characteristics, especially seasonality and atmospheric demand vs. precipitation deficit, defined the 2000–2003 droughts in Colorado? (4) Can lessons learned in this study about aspen ecohydrology be used to identify relevant drought variables that can estimate coarse biogeographic patterns of drought-induced aspen die-off?

Materials and methods

Field measurements were undertaken in the summer of 2010 in the San Juan National Forest (SJNF), in southwestern

Colorado, USA. The San Juan National Forest holds extensive aspen forests and experienced some of the most severe aspen mortality in Colorado due to SAD (Worrall *et al.*, 2008). SJNF has a mean annual temperature of 3.2 °C and receives around 508 mm of annual precipitation (Elliott & Baker, 2004). The precipitation regime is generally bimodal, with precipitation falling either as winter snow between November and May or as monsoonal summer rains originating from the Gulf of Mexico and California and beginning in early July, with 50–60% of precipitation typically falling as snow (Keen, 1996).

Water source and stable isotope methods

To characterize aspen water source use, we sampled five aspen stands over the course of the growing season, 12 aspen stands of varying edaphic and stand characteristics during the height of a growing season drought, and one aspen stand in which precipitation was artificially reduced via rain-out troughs. Plant and soil samples were gathered from five mature, healthy aspen stands between 2600 and 2800 m in elevation in the SJNF at three time intervals over the 2010 growing season: (1) early summer (23–26 June), (2) midsummer/premonsoon (16–18 July), and (3) following the onset of the monsoon in late summer (17–19 August). Soils in all five stands were Mollisols greater than 0.5 m in depth. In each stand, xylem samples were collected from three dominant aspen trees using an increment corer. The phloem and innermost sections of each tree core were discarded to avoid contamination from heartwood and phloem water, and the core was rapidly placed in a plastic pop-top vial, wrapped with parafilm, and frozen until analysis. Soil samples were collected from a soil pit at 5, 10, 25, 50, and (where possible) >60 cm depth and stored in the same manner as tree cores.

Predawn and midday xylem tensions were measured in the five stands as well as seven additional stands at each sampling event. Twig xylem tension was assessed between 03:00 and 05:00 hours and again between 12:30 and 15:00 hours in at least one twig from at least two of the isotopically sampled trees in each stand using a Scholander-type pressure chamber (PMS Instruments, Corvallis, Oregon, USA). On the same day that xylem tension was measured, soil cores were collected from a depth of 10, 25, and 50 cm in each of the 12 stands and assessed for gravimetric water content (weighed, oven dried to a constant weight, and weighed again).

The SJNF received nominal precipitation (<0.5 cm) between the snow free date in mid-May 2010 and the onset of monsoonal rains in late July 2010, contributing to a moderate growing season drought (see Results). To examine the spatial variation in water source use by aspens during moisture stress, isotope samples were collected during pre monsoonal conditions from the initial five study stands as well as the seven additional aspen stands in which xylem tensions were measured. The combined 12 aspen stands varied in aspect, slope (from 3.5° to 18°), aspen basal area (24.8–118.4 m² ha⁻¹), aspen height (11.6–29.8 m), depth to bedrock (from 0.4 to >2 m), and understory cover and composition (herbaceous dominated with 0% shrub cover to 85%

shrub cover of almost entirely *Symphoricarpus albus*). We assessed shrub cover in each stand via 16 randomly located quadrats of 1 m² area.

To better understand the response of aspen to strong summer moisture stress, we performed an amplified drought experiment by collecting aspen xylem samples in a plot receiving only half of summer precipitation. In mid-June 2010, we built rain-out troughs using wood and clear plastic in two 12 m × 18 m plots (each containing 12 mature aspen ramets) that had been isolated from the aspen forest via 50–80 cm deep trenches (to bedrock) prior to leaf out. The troughs in the control plot were perforated with multiple holes to allow precipitation to pass through, while the troughs in the drought plot diverted roughly half of incoming precipitation outside of the plot (for full description of methods, see Anderegg *et al.*, 2012b). Isotopic samples were taken from three to five trees per plot three times during the summer (not coincident with the early summer, midsummer, and monsoon samplings of the five stands described above). Samples were first collected 1 week prior to the onset of monsoonal rains, when both control and drought treatments had received no measurable rainfall since snow melt. Samples were then collected 6 days after the onset of the monsoons, when the control treatment had received 2.5 cm and the drought treatment 1.25 cm of rain. Final samples were collected 16 days into the monsoonal rains, when 13 and 7.5 cm of rain had fallen on the control and drought treatments, respectively. While not a perfect analog to the drought that incited SAD, this experimental drought was sufficient to induce significant physiological damage in drought trees compared to control trees (Anderegg *et al.*, 2012b).

Ground water samples were collected from one potable well central to the 12 stands at three times during the summer, as well as one potable well and two natural seeps once during the summer. Samples were stored in plastic screw top vials, wrapped with parafilm and frozen until analysis. Three snow cores sampling the entire snow profile were collected from the area on 25 March 2010, allowed to melt in sealed plastic bags, and then frozen in plastic vials. We collected roughly weekly precipitation samples as well as a few samples of individual rain events from the beginning of the summer monsoons (21–27 July) in plastic screw top vials partially filled with mineral oil to prevent evaporation. Deuterium (D) and ¹⁸O values from these precipitation samples ($n = 12$) were used to construct a Local Meteoric Water Line.

Water from soil and xylem samples was extracted via cryogenic distillation (Ehleringer *et al.*, 2000). The amount of ¹⁸O in all extracted samples was determined through mass spectrometry by CO_2 headspace equilibration using a Gas Bench II (GB, ThermoFinnigan) connected to a Delta Plus XL mass spectrometer (ThermoFinnigan, Bremen, Germany) at the Center for Stable Isotope Biogeochemistry (CSIB), University of California, Berkeley, CA. The deuterium content of precipitation samples, samples from the five repeatedly sampled stands, and xylem samples from the induced drought experiment was determined via injection into a H/Device (HDEV, Thermo-Finnigan, 30 Bremen, Germany) coupled to a Delta Plus mass spectrometer (ThermoFinnigan), also at CSIB. Due to a freezer

failure after some samples had been processed for [18]O content, we were unable to process seven samples for deuterium content and these samples were removed from analyses involving deuterium. All isotopic compositions are reported in delta (δ) notation in parts per thousand (‰) relative to the V-SMOW standard

$$\delta^{18}O \text{ or } \delta D = (R_{sample}/R_{standard} - 1) \times 1000 \qquad (1)$$

where R = [18]O/^{16}O or D/H.

Soil moisture data from the five observed stands and xylem isotope data from the experimental drought were analyzed using repeated measures ANOVAS. The relationship between predawn xylem tension and soil moisture at different depths was tested using linear regression, as was the relationship between stand characteristics and midsummer aspen xylem $\delta^{18}O$ content. All statistical analysis of isotopic, water potential, and soil moisture data was performed using the R statistical package (R Development Core Team 2011).

Statewide climate analysis

We drew upon two climate datasets to examine the characteristics of the 2000–2003 severe droughts in Colorado. Daily snow water equivalent (SWE) was acquired from 110 SNOTEL stations in Colorado for 1990–2009, primarily located at elevations near or above aspen forests. Secondly, long-term (1900–2009) monthly precipitation and maximum and minimum temperature and dew point temperature from Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 1994) were extracted using bilinear interpolation of 4-km raster data to each SNOTEL site, to provide a longer term retrospective analysis of the 2000–2003 droughts at aspen elevation.

To analyze the characteristics of the severe drought, we calculated a set of climate variables that capture the seasonality and type of drought across the region: total spring (March–May) and total summer (June–August) precipitation (PRISM dataset), mean spring and mean summer temperature (PRISM dataset), maximum SWE between November and May and first snow free day after March 1 within each water year (SNOTEL dataset; Table S1).

In addition to the above raw climate variables, we also calculated four modeled variables pertinent to the ecohydrological and climatological analyses: potential evapotranspiration (PET), actual evapotranspiration (AET), evaporative deficit (here defined as PET-AET), and surface soil (0–10 cm) moisture (Table S1). We estimated monthly PET using PRISM data for the SNOTEL locations from 1900 to 2009 using the energy-balance Penman-Monteith method (Allen et al., 1998) parameterized with seasonally unvarying aerodynamic and surface conductance's of 77.9 and 9 mm s^{-1} calculated in aspen forests, respectively (Hogg et al., 2000; Blanken & Black, 2004). Due to the lack of long-term spatially explicit observations of downward solar radiation, we bilinearly interpolated climatological monthly downward surface short-wave radiation from NLDAS-2 (Mitchell et al., 2004) to SNOTEL sites. The use of monthly meteorological data may result

in slight biases in PET calculations, but these methods were applied consistently throughout the period of record. To supplement our estimation of atmospheric moisture demand, we utilized daily hydrologic output from the Variable Infiltration Capacity (VIC, Liang et al., 1996) macroscale hydrologic model at 1/8th degree resolution bilinearly interpolated to the SNOTEL sites covering the same 1916–2009 period of record. VIC data begin in 1916 due to limitations in station records. Output from VIC includes soil moisture summed over the uppermost soil layer (top 10-cm) and actual evapotranspiration (AET). As a caveat, we note that unlike our calculations of PET that are parameterized for aspen, AET output from VIC was not specifically parameterized for aspen, but rather generalized vegetation categories; however, we found the variables mirrored one another when moisture was not limiting suggesting a robust approximation that is consistent across the period of record. Finally, we estimate evaporative deficit as the difference between atmospheric demand (PET) and AET.

Patterns of regional forest die-off

To examine whether seasonal climate variables were associated with sudden aspen decline die-off patterns around Colorado, we subdivided Colorado into watershed units and used a multiple linear regression model to predict the percentage of aspen mortality per watershed using climate data from a SNOTEL weather station within each watershed. We downloaded USGS 12-digit HUC Watershed boundaries for Colorado, and then dissolved these watersheds into the coarser 10-digit HUC code watersheds for our analysis. We calculated the area of aspen forest cover-type in each watershed from ReGAP Analysis data (Lowry et al., 2007), which provides a relatively conservative estimate of aspen forest distribution and extent in watersheds because we did not include mixed aspen-conifer cover classes. We then overlaid the distribution of 'SAD cover class' forest die-off from US Forest Service Forest Health aerial survey data (also called aerial sketch-map data) collected for Colorado in 2009 (Worrall et al., 2010). These data delineate geo-referenced polygons identified by aerial survey to be affected by severe and visually obvious SAD mortality, which is easily identified because SAD-affected areas exhibit complete branch or tree canopy die-back while other stressors (i.e. insect or frost damage) leave a thin but visible canopy (Worrall et al., 2008). While survey data are collected yearly, because surveys only identify areas with severe mortality they conservatively sum all tree mortality that has occurred since the inciting drought (e.g. the 2009 survey includes areas that died in previous years) and appear relatively robust through time to the removal or blow-down of dead trees.

Aerial survey data have been used extensively to identify sudden aspen decline in previous research and they agree well with satellite remote-sensing metrics of SAD (Worrall et al., 2008, 2010; Huang & Anderegg, 2012). We chose to use 2009 data because this was the first year that these aerial surveys explicitly delineated SAD as a cover class. In addition, SAD induced mortality both lagged the 2000–2003 droughts

and extended over multiple years, increasing through 2008 (Worrall *et al.*, 2010). Therefore, 2009 data were used as an integrated measure of SAD mortality. We then calculated the percentage of aspen mortality in each watershed by dividing the area delineated as SAD by the GAP derived aspen cover-type area. We removed incomplete watersheds that crossed state boundaries and masked our analysis for areas not flown in the aerial surveys.

For each watershed with a SNOTEL weather station we examined nine climate variable anomalies (z scores) in 2002 that capture a wide set of drought characteristics and seasonality: mean spring (March–May) and summer (June–August) temperatures, spring and summer precipitation, annual PET, maximum SWE, first snow free day, growing season (April–August) evaporative deficit, and growing season surface soil moisture (climatological mean 1900–1999 for PRISM variables, 1916–2009 for VIC variables, 1990–1999 for SNOTEL variables; see Table S1). In addition, we included annual precipitation anomaly, annual temperature anomaly, and annual PET anomaly averaged over the extended 2000–2003 period. Although interactions between these climate variables are likely important, given the sample size of our current analysis ($n = 65$) and the large number of potentially pertinent interaction terms, we chose not to include interactions between variables in our model.

We used a multiple linear regression algorithm to relate these climate variables to the percentage SAD mortality calculated in each watershed, treating the climate values calculated at each SNOTEL site as independent variables and the mortality level of the watershed, log transformed for normality, in which the SNOTEL site is located as the dependant variable. We averaged climate variables where two or more SNOTEL sites fell within the same watershed. Before constructing our multiple regressions model, we first utilized two standard algorithms to remove multiple collinearity among our climate predictor variables (Rockwell, 1975). The first method consisted of testing the Variance Inflation Factor of each explanatory variable, and variables are removed from the analysis if VIF > 3. The second method created a matrix of correlation coefficients among all combinations of the remaining predictor variables. If any two variables were highly correlated ($r > 0.7$), the algorithm calculated the correlation of each against the dependent variable (percent mortality in a watershed) and removed the less effective predictor variable from all subsequent analyses. We tested the robustness of this method to remove collinearity by varying the cutoff of correlation from $r = 0.5$ to 0.7.

We then used a backward stepwise multiple linear regression model to predict watershed level aspen mortality across Colorado with the climate variables from each watershed's SNOTEL site. This model sequentially removes independent variables from the model and calculates the reduction in the Akaike's Information Criteria score for each variable. The resultant model is reasonably parsimonious with this many data points ($N = 65$ watersheds). We tested that residuals of the final model were normally distributed with a Shapiro Wilkes test. All statistical analyses were performed in R statistical environment (R Development Core Team 2011).

Results

Isotopic analysis

At the study area, winter snow had a $\delta^{18}O$ value of -17.48 ± 0.23‰ ($\pm$SE) and δD value of -129.3 ± 1.8‰ while summer precipitation ranged from $\delta^{18}O = -12.35$‰ ($\delta D = -88.1$‰) to $\delta^{18}O = -3.96$‰ ($\delta D = -19.16$‰) with a flux weighted average of $\delta^{18}O = -10.65$‰ ($\delta D = -73.7$‰). The Local Meteoric Water Line (LMWL, $N = 15$ including snow) had an equation of $\delta D = 8.06*\delta^{18}O + 12.08$ ($r^2 = 0.9941$). In the study year, the western San Juan National Forest received slightly above average snowfall (Figure S1), followed by a dry late spring and early summer, and then a strong monsoon beginning in late July (Figure S2). This resulted in the study region receiving 87% of average precipitation, 65% of which fell as snow. Ground water had an isotopic value of $\delta^{18}O = -14.29 \pm 0.13$‰ ($\delta D = -104.3 \pm 0.6$‰).

In the five stands analyzed over the entire growing season, $\delta^{18}O$ isotopic soil profiles with depth showed evaporative enrichment of the surface layers approaching a value intermediate between snow and rain and similar to groundwater (Fig. 1a). Following the monsoonal rain, the isotopic soil profile showed a pulse of enriched rain water that infiltrated to 25 cm, but not 50 cm depth. The lack of early growing season rain (snow free date around mid-May to mid-July) resulted in considerable dry-down of soils in the study stands between early summer and midsummer (Fig. 1b). A repeated measures ANOVA on soil moisture showed a significant time and depth effect ($P = 0.0025$, 0.0015, respectively), as well as a significant time-by-depth interaction ($P = 0.0025$). Post hoc student's t tests showed that 10 cm soil moisture was significantly wetter than 25 cm soil moisture at early summer ($P = 0.0078$) and significantly wetter than both 25 cm soil moisture ($P = 0.0005$) and 50 cm soil moisture ($P = 0.0001$) during the post monsoon sampling. However, neither 25 cm nor 50 cm soil moisture differed significantly from 10 cm soil moisture at midsummer.

Predawn and midday xylem tensions also became increasingly negative from early summer to midsummer (Fig. 2). Mature aspen branches from these and other nearby stands lost 50% of hydraulic conductivity at an average xylem tension of -2.3 MPa (WRL Anderegg, unpublished data). At midsummer, three stands had even predawn xylem tensions more negative than -1.0 MPa and five stands had midday xylem tensions below -2.0 MPa. Moreover, following an influx of almost 16 cm of rain between the midsummer and post monsoon samplings, midday xylem tensions became more negative or did not recover to above -2.0 MPa by the end of the summer in five of 12 stands. Thus, the
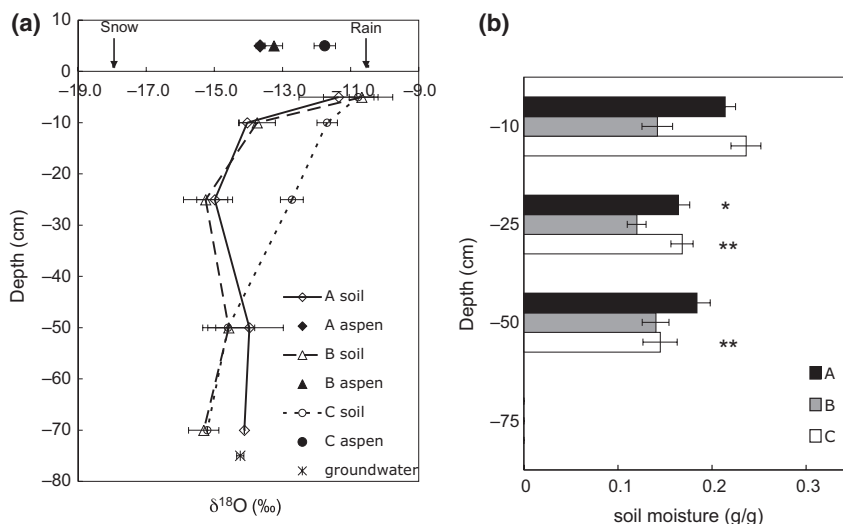
Fig. 1 (a) Average (±SE) soil and aspen xylem $\delta^{18}O$ values from five aspen stands sampled three times over the growing season (A: early summer, B: midsummer/premonsoon, and C: postmonsoon). (b) Average (±SE) gravimetric soil moisture with depth from 12 aspen stands sampled at the same three times during the growing season (A: early summer, B: midsummer/premonsoon, and C: postmonsoon). Stars denote significant differences from the 10 cm soil moisture of the same sampling event (*$P < 0.01$, **$P < 0.001$).
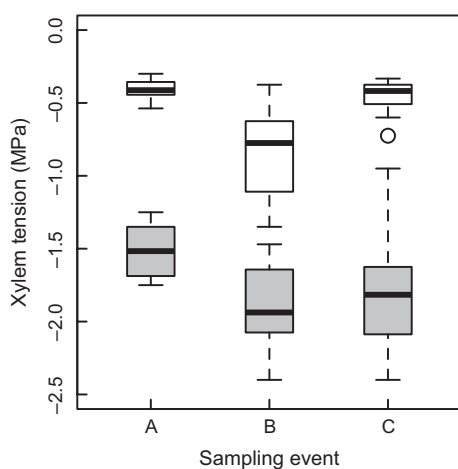
Fig. 2 Boxplot of predawn (white) and midday (gray) xylem tensions from 12 aspen stands sampled three times over the growing season (A: early summer, B: midsummer/premonsoon, and C: postmonsoon). Whiskers represent minimum and maximum values without outliers (circles), defined as twice the interquartile range subtracted and added from the first and third quartile (the bounds of boxes), and the solid lines are median values.

studied stands were likely under at least moderate physiological water stress when sampled for xylem isotopes at midsummer, though considerable variation in xylem tensions between stands at midsummer suggests that water stress was not even across different microsites. Comparing predawn xylem tension to soil moisture from 10, 25, and 50 cm, no soil moisture at any depth predicted predawn xylem tension during the

lower-stress early and post monsoon sampling events (linear regression, all $R^2 < 0.13$ and all $P > 0.25$). However, during the high-water-stress midsummer sampling event, predawn xylem tension was strongly related to 10 cm soil moisture ($R^2 = 0.58$, $P = 0.0038$), less strongly related to 25 cm soil moisture ($R^2 = 0.38$, $P = 0.03$), and not significantly related to 50 cm soil moisture ($R^2 = 0.19$, $P = 0.15$).

Isotopic analysis revealed that aspen xylem water typically fell near very shallow (5 and 10 cm) soil moisture. This can be seen both in relation to single isotope soil profiles (Fig. 1a), and the location of soil moisture in dual isotope space (Fig. 3a–c). While xylem isotope values likely represent a mixture of soil moisture isotopes from multiple depths, the general evaporative enrichment (distance to the right of the LMWL, Fig. 3) of aspen values, and their proximity to shallow soil moisture values suggests that aspens derived a large fraction of their water from shallow soil layers during all three sampling events. Surprisingly, this delineation was most obvious at the height of the growing season drought (midsummer sampling event, Fig. 3b), when aspens were more enriched in ^{18}O and fell farther from the LMWL than any soil values deeper than 10 cm or even 5 cm.

Because aspen xylem often fell slightly outside (below to the right) of the dual isotope space defined by soil moisture (e.g. Fig. 3b and c), especially when each stand was analyzed individually, it was not possible to quantify shallow vs. deep water source use using typical mixing models. Instead, to support the visual interpretation of our results we used a simple
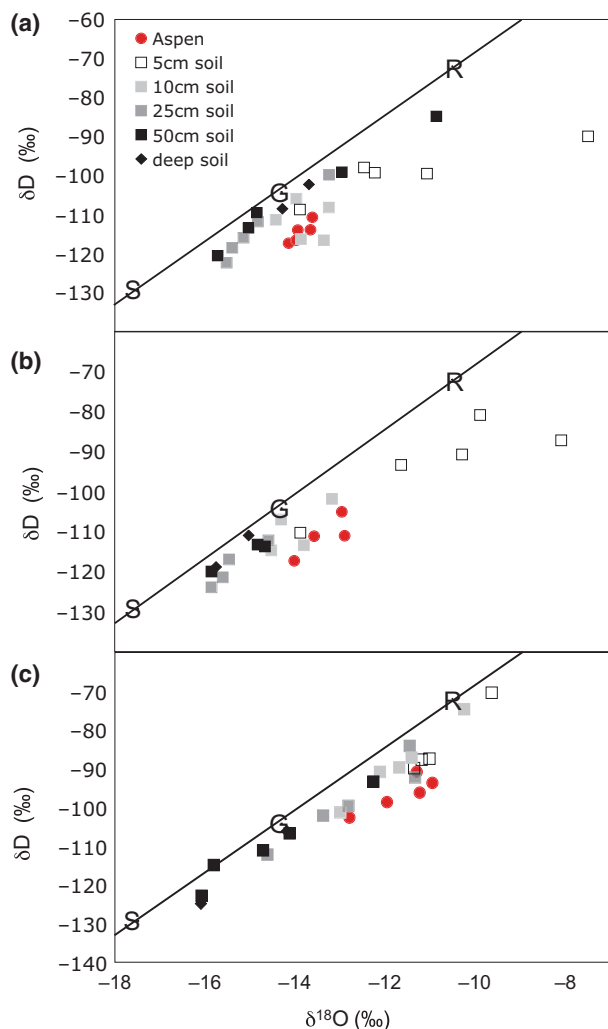
Fig. 3 Soil and aspen xylem $\delta^{18}O$ and δD values from five aspen stands sampled three times over a growing season: (a) early summer, (b) midsummer/premonsoon (c) late summer/postmonsoon. Solid line represents the Local Meteoric Water Line (calculated from local precipitation samples). 'R', 'G', and 'S' represent the average or flux weighted average rain, groundwater, and snow values (respectively) for the study site.

two end-member linear mixing model based on the soil evaporation line (SEL) for each sampling event and deep and shallow soil moisture end members (see Supporting Information: Isotope Mixing Model). For each sampling event, we also calculated the deuterium excess (*d*-excess = $\delta D - 8 \times \delta^{18}O$) of soil moisture layers in each stand and compared them to the *d*-excess of aspen xylem. Deuterium excess is a previously used indicator of the relative influence of nonequilibrium fractionation (in this case, evaporation) on a water sample, with more negative *d*-excess indicating a greater influence of evaporation (Dawson & Simonin, 2011).

Both the simple mixing model and the *d*-excess calculations indicated considerable shallow soil moisture use throughout the summer. Using the isotopic value of 10 cm soil moisture as the shallow end member, the mixing model indicated greater than 60% shallow moisture use throughout the summer (see Supporting Information: Isotope Mixing Model). Even using extremely shallow soil moisture (5 cm) as the shallow end member, aspen shallow water use fluctuated from $25 \pm 9\%$ at early summer, to $45 \pm 11\%$ at midsummer, to $49 \pm 13\%$ post monsoon. Throughout the summer, median aspen *d*-excess was more negative than the *d*-excess of all soil layers (see Figure S3), suggesting that aspens were transpiring water that was considerably influenced by evaporation.

The pattern of shallow soil moisture use during the driest point of the growing season appeared robust across stands with a wide variety of edaphic and stand characteristics. In eight of the 12 stands sampled at midsummer, aspen xylem $\delta^{18}O$ values were more enriched than either 50 or 10 cm soil moisture (Fig. 4), indicating use of extremely shallow, evaporatively enriched water. In the four remaining stands, all aspen $\delta^{18}O$ values were closer to 10 cm soil values than 50 cm soil values, even in two stands (GN2 and SN2) in which 10 cm soil was more depleted in ^{18}O than 50 cm soil. No stand characteristics (slope, depth to bedrock, basal area, understory structure, etc.) were significantly associated with xylem $\delta^{18}O$ content, nor were predawn or midday xylem tensions.

Finally, trees experiencing experimental drought fell in roughly the same dual isotope space as control trees during all three sampling periods (Fig. 5). Isotopic differences were greatest during the second sampling (Sampling 2), when drought trees were enriched in both ^{18}O and deuterium compared to control trees, though repeated measures ANOVAS for
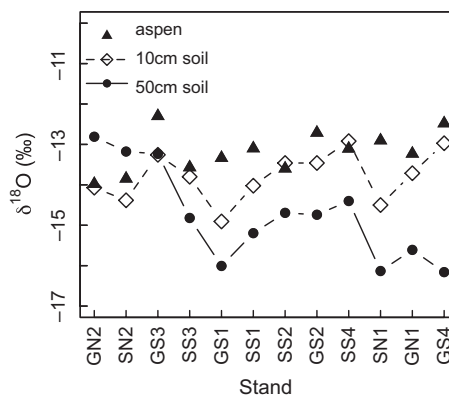
Fig. 4 $\delta^{18}O$ values of aspen xylem, shallow (10 cm) soil moisture, and deep (50 cm) soil moisture from 12 aspen stands during the height of a growing season drought.
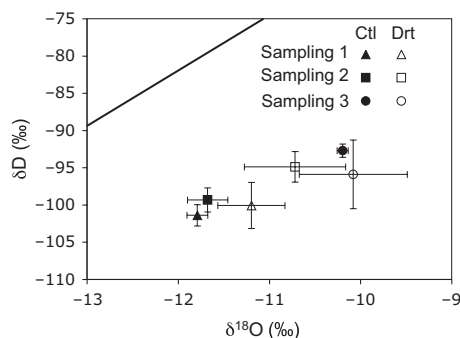
Fig. 5 $\delta^{18}O$ and δD values ($\pm$SE) of aspen xylem of trees placed under experimental drought. Filled symbols denote control trees, and open symbols drought treated (1/2 incident precipitation) trees. Shape of symbol denotes sampling event (triangle: first sampling prior to monsoonal rain, square: 6 days after start of monsoons, circle: 16 days after start of monsoon). Solid line is the Local Meteoric Water Line. There was no significant effect of treatment (control vs. drought) on either $\delta^{18}O$ or δD as determined by repeated measures ANOVAS.

both $\delta^{18}O$ and δD showed only significant sampling event effects ($\delta^{18}O$: F = 15.28, df = 2, P = 0.013; δD: F = 10.13, df = 2, P = 0.027), and no significant treatment effects or treatment x event interactions (all P > 0.4).

Characteristics of drought and patterns of aspen forest mortality

While the extended 2000–2003 drought period exhibited lower than average precipitation, precipitation patterns revealed 2002 as a single severe year of

precipitation deficit throughout the Colorado Rocky Mountains at 40–50% of climatology values (−1.7 to −2 SD; Fig. 6). Max SWE fell below average every year during 2000–2003, but was around 50% of average (−1.2 SD) during 2002 (Fig. 6b). First snow free date at Colorado SNOTEL stations was approximately 24 days earlier than average (−1.1 SD) in 2002 (Fig. 6b). Growing season evaporative deficit (PET-AET) at SNOTEL sites reached a record high during 2002, bracketed by high levels in 2001 and 2003 (Fig. 7a). Similarly, growing season soil moisture of the top 10 cm soil reached a record low during 2002 at these sites (Fig. 7b). Seasonal analysis of the progression of soil moisture indicated that soil moisture departed from normal conditions in early May and remained at record lows until mid-July (Fig. 7c).

Regional forest die-off patterns

The final regression model of SAD patterns across Colorado included six variables and explained 32% of the variance in spatial patterns (R^2 = 0.32, P = 0.005; for scatterplot of predicted vs. observed mortality levels, see Figure S4). Residuals of the final model were normally distributed (P = 0.16) and showed no obvious pattern. Summer temperature anomaly for 2002 was the most significant predictor variable, followed closely by 2002 growing season 10 cm soil moisture anomaly (Table 1). The final model also contained 2002 summer precipitation anomaly and 2000–2003 annual temperature anomaly as marginally significant variables, and 2002 maximum snow water equivalent as a variable that improved model fit, but had a nonsignificant
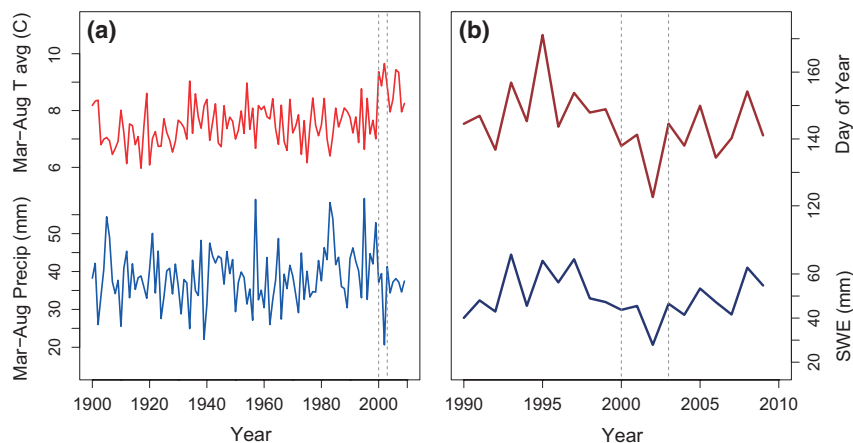
Fig. 6 (a) Average growing season (March–August) temperature (red) and precipitation (blue) value across Colorado's National Resources Conservation Service Snowpack Telemetry (SNOTEL) weather stations from 1900 to 2009 based on Parameter-elevation Regressions on Independent Slopes Model (PRISM) data. (b) Average first snow free date (brown) and average maximum snow water equivalent (SWE, dark blue) at Colorado SNOTEL weather stations from 1990–2009, based on SNOTEL data. Dotted lines outline the 2000–2003 drought period in both (a) and (b).
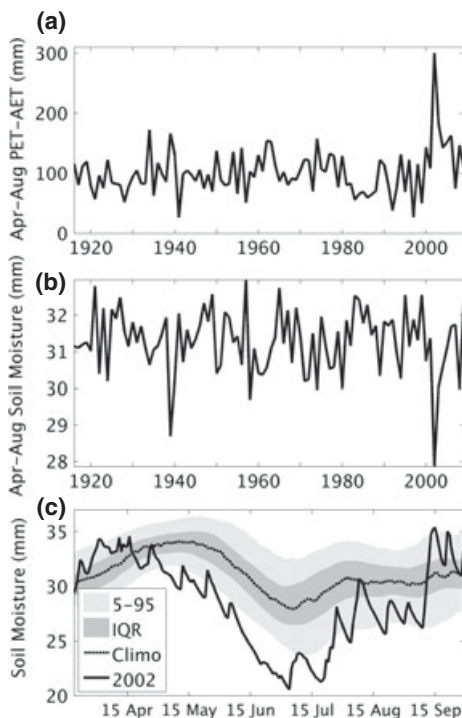
Fig. 7 (a) Average April–August evaporative deficit – defined as potential evapotranspiration (PET) minus estimated actual evapotranspiration (AET) – at Colorado Snowpack Telometry (SNOTEL) weather stations from 1916 to 2009. (b) Average April–August surface (top 10 cm) soil moisture modeled via the Variable Infiltration Capacity soil model at SNOTEL stations from 1916 to 2009. (c) Average seasonal surface soil moisture modeled via the Variable Infiltration Capacity soil model at SNOTEL stations for 2002 (black), 1916–1999 climatology (dashed), interquartile range of climatology (dark gray), and 5–95 percentiles of climatology (light gray).

Table 1 Significant variables in regional regression model of aspen forest die-off (collinearity cutoff $r = 0.7$).

Variable	Coefficient	SE	t value	P value	Rank
(Intercept)	7.568	1.039	7.283	<0.0001	—
Summer (JJA) T_{mean} 2002	3.10	1.46	2.13	0.02	1
Growing season 0–10 cm soil moisture 2002	−3.27	1.50	−2.09	0.03	2
Summer Precip 2002	−2.38	1.36	1.86	0.05	3
Annual Temp 2000–2003	2.66	1.41	1.80	0.06	4
Max SWE, 2002	−2.02	1.30	1.55	0.12	5

coefficient (including only the top three significant variables, model $R^2 = 0.24$, $P = 0.007$). Variance Inflation Factor analysis removed 2002 PET from the analysis.

Varying the correlation cutoff for removing collinear variables from $r = 0.7$ to 0.5 resulted in fewer variables included in the final model. However, the top three variables (summer temperature, growing season soil moisture, and summer precipitation) were included as statistically significant ($P < 0.05$) and in the same order in the model, regardless of cutoff level. This suggests that the primary model results were largely robust to the selection of input climate variables and criteria of removing collinearity.

Discussion

We present here an analysis of the role of drought characteristics in a widespread regional forest die-off of trembling aspen based both on inference from plot level tree ecohydrology and region level climate and spatial analysis. Isotopic analysis of forests in southwest Colorado indicated that aspens relied heavily on surface water throughout the growing season and across a large variation in aspect, understory cover, depth to bedrock, and xylem tension. Furthermore, these forests appeared to display little plasticity in water source use, with xylem water closely resembling 5–10 cm soil moisture while under natural water stress.

Even when this natural water stress was exacerbated by experimental drought, xylem isotopes of aspen trees experiencing artificial water exclusion did not differ significantly from control trees. Indeed, if anything, drought affected trees were more isotopically enriched than control trees (Fig. 5). Assuming a soil profile similar to all stands in which soil samples were taken (Fig. 1a), any increased use of deeper soil moisture would have resulted in depletion rather than enrichment of water isotopes compared to controls. Although the seasonal water stress examined here was not as severe as the 2002 drought because 2010 winter and spring precipitation preceding the experiment were near average, the experimental drought created nearly identical total summer precipitation as 2002 (10.5 cm of precipitation by the end of August in drought treatment compared to 10.3 cm in 2002, Figure S2).

While it is possible that aspen ecohydrology changes under extreme drought, none of our analyses show any indication that aspen trees draw on deeper water resources. Trembling aspen have been documented to have sinker roots to a depth of 3 m in some soils (Sucoff, 1982), and previous studies have found soil moisture depletion under aspen to a depth of 2.7 m in northern Utah (Johnston, 1970) and 2.1 m in Minnesota (Mital & Sucoff, 1983). However, our isotopic results, as well as the observed relation between shallow soil

moisture and xylem tension during moisture stress suggest that aspens may be functionally tied to shallow soil moisture reserves even during drought despite drawing some water from deeper soil layers. Moreover, the lack of relationship between midsummer xylem tension and xylem $\delta^{18}O$ across 12 stands indicated that there was no trend toward deeper water use with increased water stress. Thus, multiple lines of evidence from isotopic analyses and xylem tensions connected aspen water source use to shallow soil layers, which are heavily influenced by temperature-driven evaporation and summer precipitation during the growing season.

Building on aspen stand level ecohydrology, the drought that precipitated SAD appears to have exposed aspens to the most extreme single growing season shallow moisture stress experienced in the last century. This was caused by a combination of poor snow pack and early snow melt encouraged by above average spring temperatures, followed by a prolonged dry spell resulting from poor summer precipitation and the highest atmospheric evaporative deficit on record (Figs 6 and 7). As a result, modeled soil moisture suggests that the shallow soil water to which aspens are tied reached record lows during 2002 and remained extremely low for almost the entire 2002 growing season.

The statistical model of aspen mortality across the state of Colorado generally supports the bottom-up insights from isotopic analyses and begins to allow us to rank the ecophysiological importance of some drought characteristics. Our regional analysis of drought characteristics yielded a model that captured 32% of the spatial variance in mortality between watersheds. Acute 2002 summer temperature stress and shallow soil moisture during the 2002 growing season best explained this variance (Table 1). As one might predict from the climate analysis, some measures of 2002 snow pack and summer precipitation were included in the final model, although only as marginally significant or nonsignificant variables.

The high significance of summer temperature, and inclusion of 2000–2003 temperatures as the only multiyear variable in the model suggests the potential salience of temperature both directly (e.g. respiration requirements, damage to photosynthetic capability) and indirectly through vapor pressure deficit (VPD) in stressing tree physiology. In fact, growing evidence suggests that temperature could play a pivotal role in tree mortality under drought (Adams *et al.*, 2009) and in SAD (Anderegg *et al.*, 2012b). Sap flow data from southwest Colorado suggest that aspen may be more vulnerable to VPD changes than changes in soil moisture (Anderegg, 2012), which aligns well with damage to hydraulic function documented in SAD (Anderegg

et al., 2012b) and the prominence of temperature in our model. This also aligns well with a recent forest drought stress index based on tree ring width of conifer species in this region (Williams *et al.*, 2012), which included the central role of growing season temperature-driven vapor pressure deficit. High growing season vapor pressure deficit was also associated with tree mortality in other conifer species throughout the region (Weiss *et al.*, 2012).

Notably, both PRISM derived spring and summer temperatures showed a strong warming trend at Colorado SNOTEL sites over the last 40 years (spring: 0.57 C/decade; R^2 = 0.31; P < 0.0001, summer: 0.31 C/decade; R^2 = 0.22; P = 0.002). This suggests that long-term increases in spring and summer temperature due to climate change played a role in exacerbating the drought and inducing the die-off. Our results present clear evidence that high summer temperatures drove record atmospheric water demand and, including recent and continuing trends in spring temperatures and early snow melt, indicate that recent aspen die-off in the western United States may be an increasing phenomenon rather than a passing extreme.

Spatial estimates of forest mortality over a large region are by nature heterogeneous and difficult to quantify, and thus several caveats are worth keeping in mind. Our estimates of forest mortality were derived from aerial surveys of this region, which are categorical in nature and may not be as accurate as satellite remote-sensing of die-off. Comparisons between aerial survey estimates of aspen mortality and satellite estimates of biomass loss, however, indicate that aerial surveys do capture high mortality relatively effectively (Huang & Anderegg, 2012). In addition, considering mortality at the watershed level to leverage snow pack station data could obscure smaller scale spatial variation in mortality across elevation and aspect within and among watersheds (e.g. Worrall *et al.*, 2008). Our methods of standardizing climate variables to z values from each watershed's climatology, and standardizing mortality to a percentage of a watershed's aspen cover-type were aimed to minimize confounding factors of differential elevation, aspects, and aspen cover among watersheds in our analysis. These factors matter, of course, in determining spatial patterns and, along with other variables absent in our spatial model such as soil characteristics, likely contribute to the variance unexplained by the selected climate variables.

The ecohydrological results presented here correspond well with the results of our spatial analysis of mortality across Colorado. We report our findings with the caveat that our isotopic data come from one mountain region in southwestern Colorado. It is possible that functional rooting depth and water source use changes

across trembling aspen's range in Colorado. For example, Williams & Ehleringer (2000) found a decrease in the use of summer rain by trees in pinyon-juniper woodlands as the proportion of annual precipitation falling as summer rain decreased from southern Arizona to northern Utah. However, the rooting distribution of aspen judged via root trenches did not differ markedly between our study stands (LDL Anderegg, unpublished data) and studies from other locations in the intermountain west (see Sucoff, 1982) or Minnesota (Mital & Sucoff, 1983) and suggested that the majority of aspen roots occur in shallow soil layers. While the proportion of total precipitation that falls as summer rain does decrease from southern Colorado to Northern Colorado, this decrease is considerably less (22–14%) than the trend studied by Williams and Ehleringer (60–18%). Nevertheless, the variation in aspen ecohydrology across a large geographic scale is an important uncertainty in our analysis, and warrants additional study.

This study links a nuanced climatological understanding with an ecohydrological understanding of how drought causes water stress in trembling aspen. If we ultimately hope to use climate data such as meteorological observations or climate model outputs to predict future drought-induced forest mortality, we believe that such an ecohydrological perspective is critical for translating such data into meaningful physiological impacts. Recent research suggests that SAD is associated with xylem cavitation and loss of hydraulic conductivity in drought stressed trees (Anderegg *et al.*, 2012b). Our results suggest that acute single growing season drought in 2002 could lead to the water stress that initiated this deterioration of hydraulic function. This indicates that single season or short time period drought experiments may be a reasonable analog for sudden aspen decline, though this is not likely true for all systems. The only similar spatial analysis of plant mortality in relation to climate variables that we are aware of found that woody plant death in the Sonora and Mojave Deserts following the same drought was most related to long-term (60 month) drought indices rather than short-term drought metrics (Mcauliffe & Hamerlynck, 2010).

We highlight here the sensitivity of trembling aspen forests to acute drought and present an ecohydrological perspective that can inform mechanistic models of forest mortality. Our analysis utilized physiological understanding derived from a field study to guide and model drought-induced aspen mortality at a regional scale. In addition, we document a trend of warming spring temperatures that together with earlier snow melt observed in the western United States suggests a strong climate change signal on this aspen die-off that is likely to

increase in coming decades (Mote *et al.*, 2005; Knowles *et al.*, 2006; Wi *et al.*, 2012). Ultimately, improved understanding of both the physiological mechanisms through which trees succumb to drought and the characteristics of drought that determine water availability hold great potential for projections of forest persistence and mortality with climate change in the coming decades.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Table S1 and S2, Figures S1, S2, S3, and S4, and description of isotopic mixing model.