

# Complex aspen forest carbon and root dynamics during drought

## A letter

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**Abstract** Drought-induced vegetation mortality has been documented on every vegetated continent in recent decades and constitutes a major uncertainty in climate change impacts on terrestrial ecosystems and carbon cycle feedbacks. While recent research has focused on specific failure mechanisms during drought-induced forest die-off, a broader understanding of the physiology of trees under drought, especially changes in growth and carbon allocation, is needed for determining the sensitivity of forests to drought and interacting mechanisms during forest mortality. I present here multi-tissue and high-resolution temporal dynamics of tree carbon resources during moderate experimental and natural drought in trembling aspen (*Populus tremuloides*) forests, a major forest type in western North America that recently experienced widespread drought-induced die-off. Drought led to substantial declines in inferred carbon uptake. Tree carbohydrate concentrations, however, largely increased in concert with substantial decreases in growth and severe declines in root biomass. These findings highlight that growth declines, especially in fine roots which are important to water uptake, and increased carbon allocation to root non-structural carbohydrates are key responses to drought in aspen and could play an important role in widespread die-off. They suggest multi-year consequences of drought and carbon-hydraulic interconnections. They underscore the need for a more integrated multi-tissue, multi-process, and multi-year perspective of climate-induced forest mortality.

## 1 Introduction

Changes in drought severity and frequency with climate change are expected to have far-reaching consequences on the world's ecosystems. Forest ecosystems, which store almost half

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of the carbon found in terrestrial ecosystems, are likely to be vulnerable to drought and increasing temperatures (Bonan 2008). Large portions of the Amazon rainforest have been vulnerable to drought in the last decade, and elevated levels of mortality in tropical and temperate forests have been linked to drought and temperature (van Mantgem et al. 2009; Phillips et al. 2009). Drought-induced forest mortality has been documented on every vegetated continent in recent decades (Allen et al. 2010). Forest mortality can have substantial consequences for regional land-cover, biosphere-atmosphere interactions, biodiversity, carbon sequestration, and climate policy (Dale et al. 2000; Breshears et al. 2005; Kurz et al. 2008a; Kurz et al. 2008b).

Understanding the physiology of forests under drought and temperature stress is critical to projecting the future of forests ecosystems. A recent synthesis suggested two prominent physiological pathways of drought-induced tree mortality, known as hydraulic failure and carbon starvation (McDowell et al. 2008). *Hydraulic failure* due to drought occurs when low soil and atmospheric moisture cause xylem tensions to exceed critical levels and cavitate with air, compromising the water transport system. In *carbon starvation*, drought induces stomatal closure in trees, which suppresses carbon uptake, leading eventually to tissue-level carbon starvation (Adams et al. 2009; Sala 2009).

Yet focus on these two mechanistic pathways may be premature (Sala et al. 2010; Hartmann 2011; McDowell et al. 2011). Carbon and hydraulic changes during drought are likely highly interrelated and could interact in multiple ways (McDowell et al. 2011). More importantly, research to date has largely not examined the time course of the full spectrum of physiological changes under drought, especially changes in fine root growth or changes in carbon allocation to non-structural carbohydrates, that could influence the hypothesized mechanisms. Interactions between biotic attacks, carbon reserves and allocation, phloem transport impairment, tissue growth and stress repair, and hydraulic changes may all play a role in distinct tissues or stages of tree death. Furthermore, we currently understand very little of feedbacks and multiyear changes that could mediate mortality.

Rather than specifically testing hydraulic failure and carbon starvation in a given forest die-off, examining physiological responses to drought with temporal and multi-tissue dynamics holds substantial promise for improving our understanding of drought impacts on forests (Hartmann 2011). I present here a multi-tissue (roots, bole xylem, bole bark, branches, and leaves), high resolution temporal analysis of carbon dynamics in trembling aspen (*Populus tremuloides*) forests during moderate seasonal drought. These forests recently experienced a severe and widespread drought-induced die-off in western North America (Worrall et al. 2010), termed sudden aspen decline (SAD). While carbon starvation and hydraulic failure in SAD have been examined elsewhere (Anderegg et al. 2011), my aim here is to examine a broader spectrum of processes that occur during moderate and seasonal drought, especially changes in carbon uptake, stem growth, fine root growth, and carbon allocation to non-structural carbohydrates. These processes have generally not been considered in the two main mortality mechanisms or in SAD. Understanding aspens' seasonal drought response provides a foundation for characterizing physiological changes during drought-induced die-off. The processes examined here provide a more complete and integrated perspective of aspen's drought response that complements direct tests of mortality mechanisms, and may be highly relevant for SAD.

I compare an experimental drought manipulation of potted trees with two contrasting mature aspen clones at different elevations and aspects under seasonal drought and landscape patterns of root biomass to examine four components of aspen carbon dynamics during drought: 1) stomatal response and its effects on carbon uptake, 2) changes in non-structural carbohydrate (NSC) concentrations across tissues and over time, 3) changes in growth that accompany drought, and 4) changes in coarse and fine root biomass during experimental drought in relation to observed landscape patterns of root biomass in SAD.

## 2 Methods

I acquired 30 potted 3 m tall trembling aspen trees and destructively sampled a randomly-selected 8 for baseline morphological and biomass measurements. I located the remaining 22 trees in a meadow in the San Juan National Forest, Colorado. Twelve trees experienced drought stress by excluding natural precipitation and receiving 2 L-water/day from June 15–August 16, 2010. The remaining ten trees constituted the control treatment and received 4 L/day during that period.

I measured stomatal conductance, net photosynthesis, and non-structural carbohydrate (NSC) reserves on roughly bi-weekly intervals and growth and morphological characteristics at the conclusion of the experiment. Net photosynthesis and stomatal conductance were measured at noon in 5 of the 12 drought trees and 5 of the 10 control trees at six points between July 1 and August 15, 2010 using a LiCOR 6,400 gas exchange system with ambient CO<sub>2</sub> and relative humidity, and a fixed LED light source of 1,500 μmol photons/m<sup>2</sup>s. For morphological responses to drought, I measured basal growth, apical growth, average leaf size and leaf shedding (see [Supporting Information](#) for full details). I collected branch, leaf, and root samples on roughly bi-weekly intervals during drought and analyzed tissues for glucose, sucrose, and starch concentrations via enzymatic digestion ([Supporting Information](#)). At the conclusion of the experiment, I assessed fine and coarse root density in the potted trees by tallying the number of root intersects with a transverse plane through the rootball to compare against the 8 baseline trees.

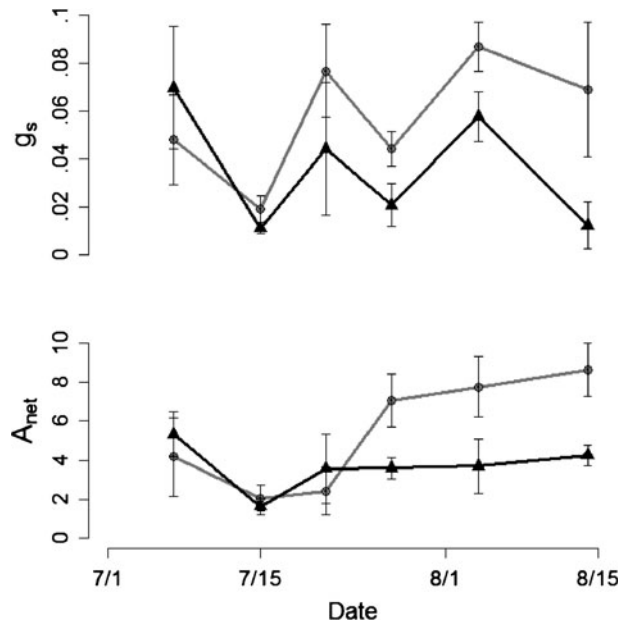
In addition, I examined sap-flow and NSC content in multiple tissues in two contrasting mature aspen forest sites under differential climatic stress due to site and elevation characteristics during a moderate seasonal drought. Site H was at higher elevation, northwest-facing, and exemplified a healthy stand. Site S was at lower elevation, south-facing, and typical of a vulnerable or stressed stand ([Supporting Information](#)). I collected tissue samples in all major tissues (leaf, branch, bole xylem, bole bark, and roots) in three ramets per stand at roughly bi-weekly intervals from June 15–August 20. I analyzed these tissues for glucose, sucrose, and starch concentrations. Comparisons in fine root biomass were made between ten healthy and five SAD sites in the San Juan National Forest, Colorado, during July 2010 ([Supporting Information](#)).

## 3 Results

Drought-treated potted trees experienced moderate drought during the experiment, which, as previously reported, led to more negative leaf water potentials and higher loss of hydraulic conductance than controls (Anderegg et al. 2011), though it did not lead to tree mortality during the drought period. Mature aspen forest experienced moderate seasonal drought between May 1 and July 20, due to no precipitation and warm temperatures. Soil moisture probes revealed that soil moisture levels reached the driest decile of June soil moisture levels compared to a gridded monthly dataset of soil moisture at these sites (Maurer et al. 2002). Midday water potentials measured via pressure chamber suggest that xylem tensions in these two stands reached stressed levels (−2.0 to −2.5 MPa) in this species (Anderegg et al. [In Review](#)).

While stomatal conductance varied in both treatments of potted trees over the course of the summer, partial stomatal closure occurred after July 25 as drought severity increased (*t*-test:  $p < 0.04$ ; Fig. 1). Accompanied by decreases in internal leaf CO<sub>2</sub> concentrations, stomatal closure drove significant decreases in net photosynthesis of drought trees relative to control trees during this time period (*t*-test:  $p < 0.02$ ; Fig. 1).

**Fig. 1** Gas exchange measurements of stomatal conductance (mean  $\pm$  SEM; mol/m<sup>2</sup>s) and net photosynthesis (mean  $\pm$  SEM;  $\mu$ mol CO<sub>2</sub>/m<sup>2</sup>s) in control (*gray*) and drought (*black*) potted trees over the course of induced drought

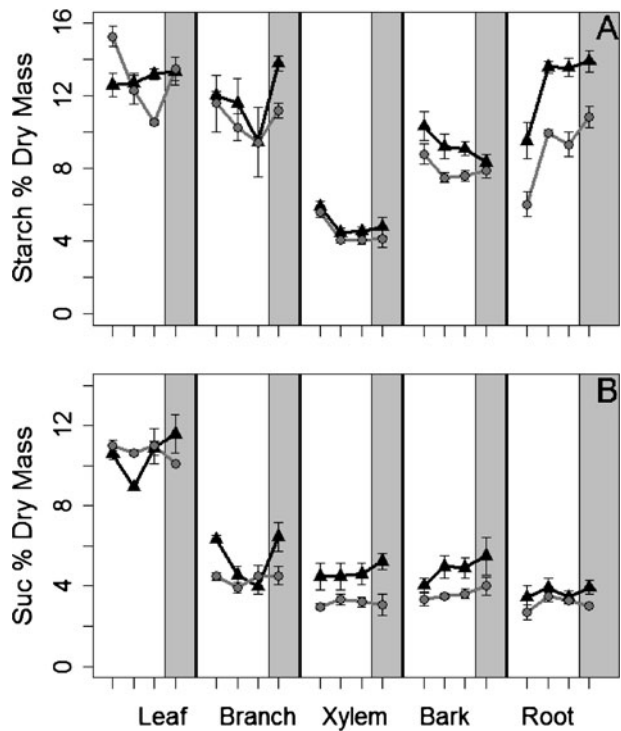


Similarly, both mature forest sites exhibited large declines in sap flow during seasonal drought, likely decreasing carbon uptake. Sap flow declined in both sites as soil moisture fell and summer drought progressed (Fig S1). Sap flow declined more at the more stressed south-facing site (59%) compared to the healthier northwest-facing site (52%) ( $t$ -test;  $p=0.01$ ), indicating stronger decreases in carbon uptake at the drier site. Furthermore, total daily sap flow (averaged across all trees measured) in both sites combined responded much more strongly to soil moisture (linear regression,  $r^2=0.49$ ;  $p<10^{-8}$ ) than to atmospheric vapor pressure deficit ( $r^2=0.06$ ;  $p=0.04$ ) over this period. A strong response indicates the stems are able to respond to and thus minimize potential stress via adjusting transpiration. Conversely, a weak response indicates less ability to regulate transpiration in response to high VPD. Thus, sap flux data suggest that aspens may be more vulnerable hydraulically to changes in atmospheric water vapor demand (e.g. temperature-driven changes in VPD) than to declines in soil moisture.

Both potted trees and mature forest stands showed complex changes in tissue NSCs during moderate drought. Leaf starch and sucrose levels remained relatively constant over the summer (Repeated-Measures ANOVA;  $p_{mature}=0.58$ ;  $p_{potted}=0.77$ ) and between levels of drought severity in both mature and potted trees ( $p_{mature}=0.97$ ;  $p_{potted}=0.81$ ) (Fig. 2, S2). In the mature native stands, xylem and bark starch concentrations declined early in drought and then remained constant while sucrose concentrations increased, though both non-structural carbohydrates were consistently higher in the more vulnerable site ( $p_{xylem}=0.01$ ;  $p_{bark}=0.001$ ) (Fig. 2). Root starch levels increased over the summer in these stands despite drought stress ( $p_{mature}=0.002$ ) and, in fact, drought-treated trees generally exhibited higher levels of starch than control trees ( $p_{mature}=0.0006$ ;  $p_{potted}=0.03$ ) (Fig. 2a, S2). Sucrose levels increased in drought-stressed branches, xylem, bark, and roots (Fig. 2b, S2), which could be due to osmotic regulation of turgor at higher levels of xylem tension in those tissues.

Potted trees revealed substantial changes in morphology and growth due to drought. Average leaf area per leaf of control trees was slightly greater (4.54 cm<sup>2</sup>) than that of drought

**Fig. 2** (a) Starch levels (mean  $\pm$  SEM; percent dry mass) of five plant tissues during drought (white region) and following drought (shaded region). Grey points indicate the healthier, northwest-facing stand (Site H); black points indicate the more stressed, south-facing stand (Site S). (b) Sucrose levels (mean  $\pm$  SEM; percent dry mass) of five plant tissues during (white region) and following (shaded region) drought



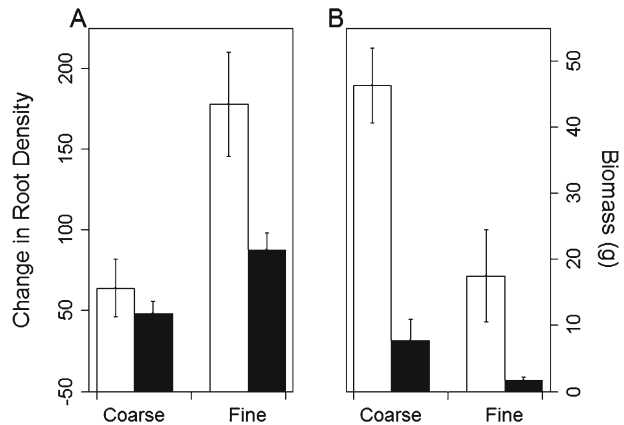
trees ( $4.13 \text{ cm}^2$ ), but neither were statistically different from the pre-treatment baseline (Paired  $t$ -test;  $p_c=0.10$ ;  $p_d=0.48$ ). For apical growth, control trees grew significantly more than drought trees during the experiment by an average of 15 cm ( $t$ -test:  $p=0.04$ ). Control trees grew more basally than drought trees as well, though this was only marginally significant ( $t$ -test:  $p=0.09$ ). Leaf-catch vessels underneath trees recorded no instances of leaf-shedding during drought, which indicates that dynamic changes in total canopy leaf area in response to drought do not play a substantial role in this species. But canopy duration differed significantly between treatments in the experiment. Drought trees shed their canopy an average of 9 days before control trees in the fall ( $t$ -test:  $p=0.002$ ).

Belowground effects of drought on tissue growth were far more striking than aboveground changes in potted trees. Assuming no pre-treatment differences, control trees had higher levels of coarse root growth than drought trees following the experiment relative to baseline trees (Fig. 3). Fine root density was more than 200% higher in control trees than in drought trees at the end of the experiment (Student's  $t$ -test;  $p=0.04$ ) (Fig. 3a). Landscape patterns of standing coarse and fine root density between mature healthy and SAD stands show similar significant differences. SAD-affected areas have coarse and fine root biomass of around 17% ( $p=0.01$ ) and 9% ( $p=0.002$ ), respectively, of healthy areas (Fig. 3b).

#### 4 Discussion

The similar response of potted and mature aspens to seasonal drought reveals that aspen trees experience decreased carbon uptake and decreased growth during moderate drought. Mature forest sites reduced transpiration as drought proceeded with the largest reductions at the

**Fig. 3** (a) Change in coarse and fine root density (mean  $\pm$  SEM; roots/m<sup>2</sup>) between control (*white*) and drought (*black*) potted trees following experimental drought from those of baseline trees. (b) Coarse and fine root biomass (mean  $\pm$  SEM; grams) between healthy (*white*) and SAD-affected (*black*) stands



more stressed site (Figure S1). Tree-ring studies of aspen growth under drought also document large decreases in basal trunk growth during drought years (Hogg et al. 2005). Potted trees significantly curtailed photosynthesis during drought stress and integrated basal and height growth was significantly reduced in drought trees by the end of the growing season.

Because declines in growth are expected to have feedbacks to hydraulic vulnerability and maintenance (McDowell et al. 2011), the observed declines in growth could have important implications for SAD. Aspen trees rely heavily on current and recent 1–3 years' xylem formation to conduct water (Sperry et al. 1991). This suggests that the poor carbon uptake and/or growth in branches and roots in a moderate drought such as the one documented here could lead to a weakened hydraulic capability by affecting xylem formation and/or repair of xylem embolism. This would be especially salient in a multi-year drought, such as the one from 2000 to 2003 that likely induced SAD. Thus, declines in growth observed here and their subsequent consequences may have played an important role in drought-induced SAD. I hypothesize that declines in stem growth and fine root biomass could lead to increased water stress and eventually dieback over longer periods. These areas are in great need of further study.

Tissue NSC concentrations allow an examination of changes during moderate drought and over the growing season. With the exception of roots which accumulated NSCs, few tissues demonstrated a directional trend in NSC concentrations. Increases in branch and leaf starches, however, were observed following monsoonal rain at the end of the drought (gray area in Fig. 2), suggesting recovery in carbon uptake from increased water availability. Increases in NSC reserves are to be expected if growth declines faster than photosynthesis does (McDowell et al. 2011). These changes in growth, photosynthesis, and root NSC reserves have been observed in aspen seedlings in a greenhouse drought experiment (Galvez et al. 2011). Notably, declines in carbon uptake may not necessarily limit growth, as direct water limitations can restrict growth as well (Hsiao 1973).

Modifications in leaf area to limit water loss have been observed in many plant species as a response to drought (Schulze et al. 1987). My results indicate, however, that these changes do not seem to mediate the plastic response of aspens within a season in the drought experiment. I did, however, observe significant decreases in canopy duration, reflected in earlier leaf drop in potted drought trees. Modeling and eddy-covariance studies of boreal aspen forests suggest that changes in canopy duration may be a substantial change during drought, which greatly decreases annual net primary production in these widespread forests (Barr et al. 2007).

The most salient observed changes in carbon dynamics during moderate drought manifested in declines in fine root biomass. Because fine roots are a primary pathway for water uptake (Pinno et al. 2010), low levels of fine root growth during drought could compromise water relations in that year and subsequent years. Hydraulic impairment of aspen roots due to embolism during drought likely occurs and thus may also play a role in determining root density (Anderegg et al. 2011). Because it was not possible to measure the same trees before and after the experiment to avoid damaging root mass beforehand, assessing the precise balance of root growth versus mortality was not possible and instead relied on the assumption that the 8 baseline trees largely represented the other pre-treatment trees. Thus, I suggest caution in interpreting the absolute changes of coarse and fine root density, but their relative differences between treatments are likely robust.

The effects of experimental drought on root density mirrored those of landscape observations in healthy and SAD stands, though no pre-drought baseline was assessed for these stands. This connection suggests that the changes in root density, especially fine root density, could play an important role in landscape levels of forest die-off in this species. Declines in aspen health over multiple seasons or years could be mediated by changes in allocation, tissue function, stress repair or tissue biomass (e.g. healthy fine roots), rather than carbohydrate reserves or catastrophic cavitation expected from current hypotheses.

The results presented here may help inform understanding of carbon cycle responses to drought in these forests, an area relevant to climate science, ecology, biogeochemistry, and plant physiology. In addition to the primary pathway for water and nutrient uptake, fine roots represent 33% of global annual net primary productivity and comprise 10–20% of annual net primary productivity in aspen forests (Jackson et al. 1997; Gower et al. 1997). Trembling aspen is the most widespread tree species in North America (Perala 1990), among one of the most productive forest types in the boreal forest (Gower et al. 1997), and predicted to experience large reductions in suitable climatic conditions with climate change (Rehfeldt et al. 2009). Thus, changes in stem growth, fine root growth, and the decreases in canopy durations discussed here may have substantial effects on aspen forests' carbon uptake, in addition to large estimated carbon losses from widespread mortality (Huang and Anderegg 2012). Furthermore, declines in growth and the differential response of aspen transpiration to soil moisture versus vapor pressure deficit have direct implications for research on hydraulic stress in the recent sudden aspen decline across western North America (Anderegg et al. 2011).

The results presented here elucidate key processes that occur in aspen forests during moderate drought that provide a more integrated assessment of aspen drought response. In particular, decreased carbon uptake, increased carbon allocation to non-structural carbohydrates in roots, and declines in stem and fine root growth illuminated here are notable due to possible physiological consequences that would influence aspen vulnerability to multi-year drought, such as the drought that triggered SAD. Further research is needed to examine these multi-year feedbacks and pathways. Indeed, the below-ground response of forests to drought has substantial physiological effects and carbon cycle ramifications that are largely unstudied and likely important for understanding the future of forests in a changing climate.

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