



Indirect influences of a major drought on leaf litter quality and decomposition in a southwestern stream

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With 4 figures and 1 table

Abstract: Climate models predict that the southwestern United States will experience an increase in drought frequency and intensity with global climate change. We tested the hypothesis that leaf litter produced under natural drought conditions would have an altered litter chemistry profile and affect decomposition rates and macroinvertebrate colonization compared to non-drought conditions. To test this hypothesis we collected leaf litter from *Populus fremontii*, *Alnus oblongifolia*, and *Platanus wrightii* grown during an average precipitation year (2001) and a record drought year (2002) and performed an in-stream decomposition study using both litter types. Three major patterns emerged: 1) Drought conditions significantly altered litter chemistry for mature trees of three species; however, the direction and magnitude of change differed among species and litter chemicals; 2) Leaf litter mass loss was influenced by both differences among species and drought; yet, species effects were more pronounced over time than drought effects; and 3) After 69 days of decomposition, the structure of the macroinvertebrate community was uninfluenced by the drought effect on *A. oblongifolia* or *P. wrightii* litters, but there was a community-wide drought effect on macroinvertebrate communities colonizing *P. fremontii* litter. Many recent studies have explored the influence of drought on stream flow and water temperatures, but these results suggest that litter quality can change under different climatic conditions, but the overall decay of leaf material may not be dramatically altered by droughts. Understanding how forest-stream interactions may be altered by the various influences of climate change will allow for better predictions regarding how long-term disturbances may alter stream ecosystem functioning.

Key words: drought, leaf litter decomposition, *Populus fremontii*, *Alnus oblongifolia*, *Platanus wrightii*.

Introduction

The southwestern United States is expected to experience an increase in the frequency and intensity of drought-like conditions under global climate change scenarios (Cook et al. 2004, Seager et al. 2007, Kerr 2008). A 15-model consensus predicts that this region will experience progressive warming and increased year-to-year variability in precipitation (Differbaugh et al. 2008). The effects of drought and climate change have been well-explored in terrestrial ecosystems (e.g., Allan & Breshears 1998, Hanson & Welt-

zin 2000, Weltzin et al. 2003, Wu et al. 2011); however, fewer studies have examined these disturbances in stream ecosystems (Tank et al. 2010). Those studies that have examined the effects of climate change on stream ecosystems have primarily explored the influence of elevated CO₂ (e.g., Tuchman et al. 2002), altered hydrology (reviewed in Humphries & Baldwin 2003, Palmer et al. 2009), stream intermittency (Corti et al. 2011, Datry et al. 2011, von Schiller et al. 2011), or changes to stream water temperatures (e.g., Durance & Ormerod 2007, Mantua et al. 2010). With increasing pressure on freshwater systems in the

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American Southwest due to multiple stressors (e.g., population growth, hydroelectric power, and climate change) understanding how these systems will respond to large-scale disturbances such as climatic variability and drought will be critical for their future management.

One mechanism by which streams may be indirectly influenced by drought is through changes to adjacent riparian vegetation, especially for stream systems that depend heavily on leaf litter inputs. Changes to leaf tissue chemistry (hereafter referred to as *litter chemistry*) due to water stress could exert strong effects on both ecosystem processes and stream biota. Litter chemistry can affect rates of aquatic decomposition (Webster & Benfield 1986), with leaf litter higher in condensed tannins and lignin correlating negatively with rates of decomposition (Gessner & Chauvet 1994, LeRoy et al. 2007). Leaves with higher concentrations of tannin and lignin deter terrestrial herbivores and tend to persist in litter influencing aquatic organisms (Ostrowsky & Zettler 1986, Whitham et al. 2006). For example, leaf types higher in tannin and lignin support less fungal biomass (Gessner & Chauvet 1994) which may have bottom-up effects on macroinvertebrate consumers.

Leaf litter from trees under drought stress can have altered litter chemical profiles. For example, beech leaves (*Fagus sylvatica*) have higher concentrations of tannins with decreasing soil water (Bussotti et al. 1998). Other species of leaves and needles under water stress (either natural or induced) have decreased concentrations of phosphorus (Peñuelas et al. 2004), increased concentrations of monoterpenes (Kainulainen et al. 1992), and decreased levels of fats, oils, and waxes, and increased nitrogen and non-structural carbohydrates (Runion et al. 1999). The effects of drought, however, are not consistent across geographic regions or tree species (Peñuelas et al. 2004) and the consequences of these litter changes have not yet been examined for the tree species in this system or in coupled terrestrial-aquatic situations like leaf litter decomposition in streams.

Contemporary variability in climate allows for the testing of climate change and drought effects on stream ecosystems. In 2002 the American Southwest experienced a record drought likely due to a protracted cold phase of the El Niño – Southern Oscillation (La Niña) (Hoerling & Kumar 2002). In Arizona, less than 45% of the previous year's precipitation fell during 2002 (USDA 2012). This drought was considered one of the worst in the last 120 years and was primarily centered over Arizona (Quiring & Goodrich 2008).

To determine if a recent major drought altered litter chemistry and subsequent leaf litter decomposition in a southwestern US stream, we compared decomposition rates of leaves naturally grown during non-drought and drought years. We hypothesized that leaf litter from three native riparian tree species would have altered litter chemical profiles as a result of the drought. Specifically, and based on previous studies that examined changes to litter chemistry induced by water stress, we hypothesized that, 1) % phosphorus would decrease and % condensed tannins and nitrogen would increase in leaf litter under drought conditions, 2) due to these litter chemical changes, rates of decomposition would slow due largely to the increase in condensed tannins, and 3) the structure of the macroinvertebrate community would be significantly different between drought and non-drought litter treatments, indirectly influenced by this altered litter chemistry.

Material and methods

Site description

Wet Beaver Creek (34°41'N, 111°41'W) is located in north-central Arizona and flows off the southwestern edge of the Mogollon Rim. It is a moderate-flow stream with average discharge of 340 L s⁻¹ across an 111,375 ha watershed. We chose one representative stream reach (50 m long) within which to place the leaf litter decomposition study. Riparian vegetation includes Fremont cottonwood (*Populus fremontii* S. Wats.), Arizona alder (*Alnus oblongifolia* Torr.), box elder (*Acer negundo* L. var. *arizonicum* Sarg.), Arizona sycamore (*Platanus wrightii* S. Wats), velvet ash (*Fraxinus velutina* Torr.), coyote willow (*Salix exigua* Nutt.), and Goodding's willow (*Salix gooddingii* Ball). Upland vegetation consists of one-seed juniper (*Juniperus monosperma* Engelm. Sarg.) and honey mesquite (*Prosopis glandulosa* Torr.). Geologically, Wet Beaver Creek is located in a sedimentary-dominated landscape with protrusions of volcanic rock of basaltic-origin.

Interannual drought conditions

To describe the interannual variation in precipitation and drought-like conditions in Arizona we used the Palmer Drought Severity Index (PDSI) and the Palmer Hydrological Drought Index (PHDI) (Palmer 1965). PDSI is a meteorological measurement of drought constructed from precipitation, temperature, and soil moisture data. PHDI is a hydrological measurement of drought reflecting moisture inflow (precipitation), moisture outflow (streams) and storage (e.g., groundwater, reservoir levels). These data are available from the National Climatic Data Center (NCDC 2012). First we determined annual PDSI and PHDI by averaging monthly values for each year from 1950–2002 to contextualize the 2002 drought (Fig. 1A and B). Second, we determined PDSI and PHDI for each month between January 2001 and December 2002 to describe the moisture and

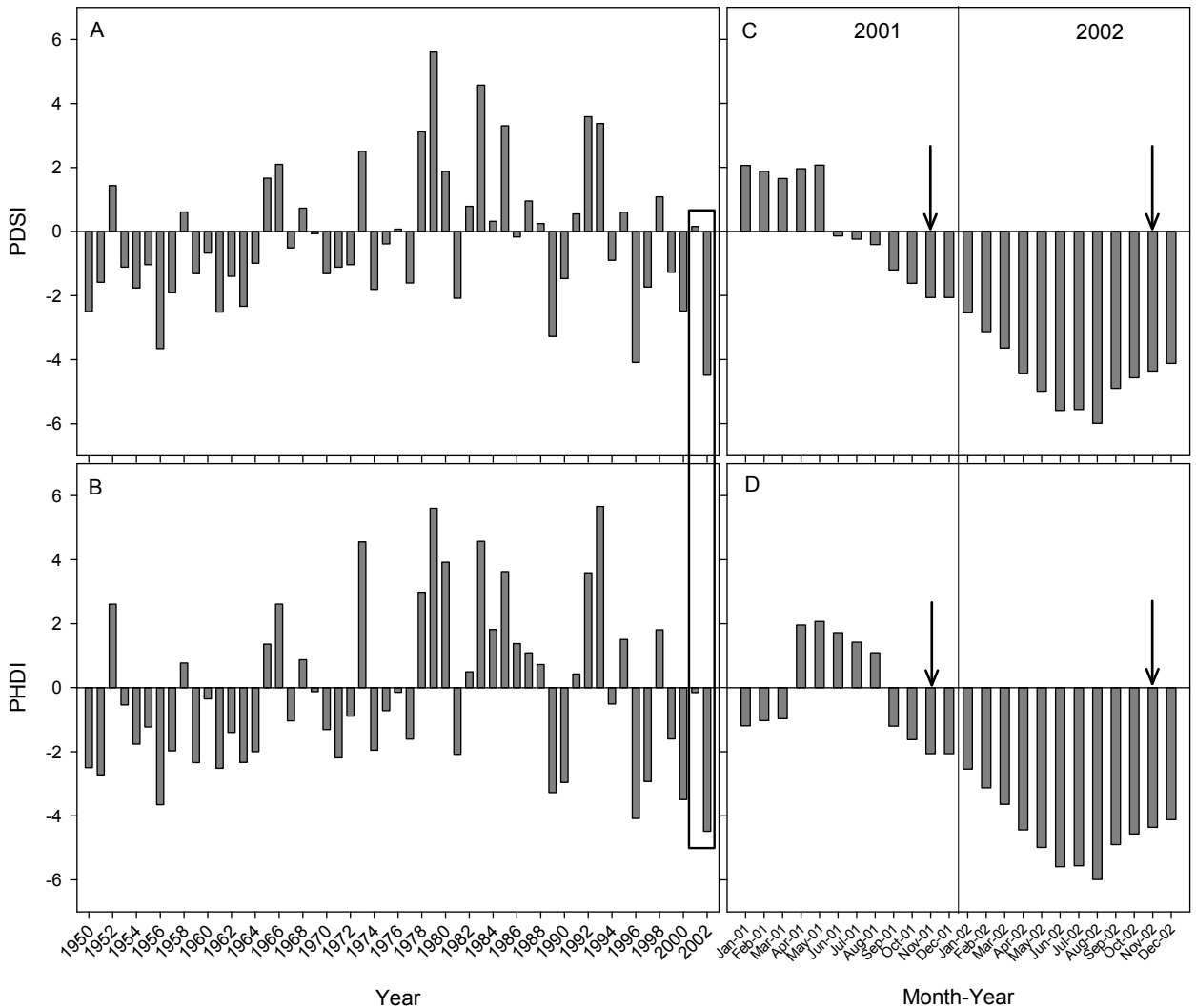


Fig. 1. Palmer Drought Severity Index (PDSI) and Palmer Hydrological Drought Index (PHDI) values for Arizona. Annual (A) PDSI and (B) PHDI for Arizona, 1950–2002; Monthly (C) PDSI and (D) PHDI for Arizona, January 2001 – December 2002. For all figures a value of 0 equals the long-term average condition. Negative values represent drought/dry conditions and positive values represent wet/moist conditions. Extreme values occur around +4 or –4 (Palmer 1965). Rectangle on panels A and B includes study years 2001–2002; arrows on panels C and D represent litter collection periods in both years.

drought conditions facing mature trees at our study site (Fig. 1C and D).

Litter collection and litter chemistry

We collected leaf litter from three dominant riparian species, *P. fremontii*, *A. oblongifolia*, and *P. wrightii*, within 1 or 2 days of natural abscission in hanging tarps strung among a set of trees at Wet Beaver Creek in the fall of both 2001 (non-drought year) and 2002 (drought year). All three species are indeterminate in their growth. Tree species with an indeterminate growth pattern set buds each year, thus we would expect to see the effect of drought within the same year and potentially drought-influenced leaf litter following abscission (Larcher 2003). Tree species that are not indeterminate may not demonstrate drought effects until one or two years following a disturbance such as

drought and were avoided in this study. Additionally, although a greenhouse study would have allowed for more control over drought effects, the use of smaller potted saplings would have limited our ability to generalize drought effects to mature trees capable of providing allochthonous inputs to streams. To collect leaves, multiple tarps were hung under the canopies of multiple mature trees to capture variation among trees of each species (which can be quite high; LeRoy et al. 2007). In this case, all potential drought effects on leaf litter quality were taken into consideration, such as: early leaf drop, altered leaf chemical profiles, reduced resorption, and altered leaf herbivory. Six leaf litter treatments were created to include drought and non-drought litter from each of the three species.

Leaf litter for initial chemical analyses was pooled, air-dried, subsampled, and ground in a Wiley Mill (Thomas Scientific, Swedesboro, NJ, USA) to 425 μm . Subsamples

(25–50 mg) were extracted for condensed tannins with 70% acetone and 10 mM ascorbic acid. We used the butanol-HCl method to determine relative condensed tannin concentrations (Porter et al. 1986), with standards purified from narrowleaf cottonwood following the methods of Hagerman & Butler (1989). We quantified absorbance on a Spectramax-Plus 384 spectrophotometer (Molecular Devices, Sunnyvale, CA, USA). We determined total litter % nitrogen and % phosphorus by modified micro-Kjeldahl digestion (Parkinson & Allen 1975) followed by analysis on a Lachat AE Flow Injection Analyser (Lachat Instruments, Inc., Loveland, CO, USA), using the salicylate and molybdate-ascorbic acid methods, respectively (Lachat Instruments, Inc. 1992). We also estimated % carbon by combustion in a muffle furnace (Barnstead International, Dubuque, Iowa, USA) assuming a 0.5 conversion factor from % organic matter to % carbon (Vogt 1991). All chemical analyses were replicated at least twice.

Litter decomposition

Litter bags were used to standardize the decomposition environment, provide stable substrate for aquatic macroinvertebrates and retain leaf litter (Benfield 2007). Leaves were air-dried and weighed into 4 g quantities and placed into 6.4-mm mesh litterbags. Litterbags were randomly assigned a harvest date and location within the stream. Bags were anchored in the stream along multiple (12) 2-m lengths of steel rebar and wedged into place in active depositional areas. Litterbags were color-coded by harvest date to assist harvesting and avoid disturbing neighboring bags. Litterbags were harvested from the stream after 7, 14, 69 and 84 d with each treatment replicated eight times per harvest date resulting in a total of 192 litterbags. Sampling dates were influenced by river access which was often difficult during high flow events, but the final date was based on a previous study (LeRoy & Marks 2006). Harvested litterbags were placed into individual polyethylene zipper bags and transported on ice to the laboratory.

Litterbags were processed within 24 h of harvesting. Sediment and invertebrates were rinsed from leaves and sieved through 250 μm nets for preservation in 70% ethanol. Remaining leaf material was rinsed with tap water and dried at 70 °C for 3 d. Dry leaf material was weighed and ground in a Wiley Mill to 425 μm . Ground material was combusted at 500 °C in a muffle furnace for 1 h to determine ash-free dry mass (AFDM) remaining fraction.

Aquatic invertebrates

Preserved invertebrate samples from harvest day 69 were further sieved through 1-mm-mesh to remove micro-invertebrates, and sorted under 2 \times magnification. A planned harvest date at 4 weeks was delayed by high flow events and unavoidably extended our invertebrate collection to later stages of decay. Aquatic insects (except some members of Diptera) were identified to genus using Merritt & Cummins (1996) and Wiggins (1996) and other invertebrates were identified to the lowest taxonomic level possible using Thorpe & Covich (2001). Reference specimens are maintained in the LeRoy Aquatic Ecology Laboratory at The Evergreen State College. We identified 35 taxa from a total of 26 families and 13 orders.

Statistical analyses

Differences in initial leaf litter chemistry were analyzed using a two-way analysis of variance (ANOVA) with leaf species, drought and their interaction as fixed factors followed by *post-hoc* comparisons (Tukey's HSD). Leaf litter decomposition was analyzed using two methods: 1) comparisons of decomposition rates (k) using an equality of slopes test in SAS 8.01 (SAS Institute, Inc. 1999–2000) with Hommel's correction for multiple comparisons (Swan & Palmer 2004); and 2) two-way ANOVAs of mass remaining at each harvest date using leaf species, drought and their interaction as fixed factors with *post-hoc* comparisons (Tukey's HSD). Remaining AFDM was ln-transformed for two reasons: 1) to meet normality and equal variance assumptions, and 2) to determine the exponential decomposition rate constants (k) for each treatment (Jenny et al. 1949, Olson 1963, Benfield 2007).

Invertebrate data were analyzed using a variety of community analysis techniques. Specifically, total macroinvertebrate abundance, taxa richness, taxa evenness and Shannon's diversity index (H') values were calculated for each litterbag at day 69. Values were compared among the three leaf species, between drought and non-drought years, and their interaction using two-way ANOVA and *post-hoc* comparisons (Tukey's HSD). To visualize assemblage-wide responses to leaf litter treatments, we used a relativized (to species maximum) non-metric multidimensional scaling (NMDS) ordination method with a Bray-Curtis distance measure in PC-ORD (Version 4.02, MjM Software, Gleneden Beach, OR). Relativizing species abundances to their maxima helps to minimize the overwhelming influences of hyperabundant species. Bray-Curtis (or analogously Sorensen) distance measures have been shown most appropriate for ecological data (Faith et al. 1987). To test for differences among treatments we used a multi-response permutation procedure (MRPP) which is similar to an analysis of variance or analysis of similarity among treatments (PC-ORD).

Results

Litter chemistry

Leaf litter grown during the drought year had altered leaf litter chemistry compared to non-drought litter; however, the direction and magnitude of the changes differed among litter chemicals and tree species leading to significant species, drought and species \times drought interaction effects for all litter chemicals measured (Fig. 2). Specifically, N concentrations increased under drought conditions by 17% for *A. oblongifolia* and 6% for *P. wrightii*, but moderately decreased by 4% for *P. fremontii* (Fig. 2a). Phosphorus concentrations increased slightly (1%) under drought conditions in *P. fremontii*; but, decreased by 3% for *A. oblongifolia* and 49% for *P. wrightii* (Fig. 2b). Finally, condensed tannins were 52% higher under drought conditions in *P. fremontii*, 71% higher in *A. oblongifolia*, but decreased by 50% in *P. wrightii* (Fig. 2c).

Litter decomposition

Decomposition rates ($k \text{ day}^{-1}$) ranged from 0.0157 to 0.0204 for non-drought leaf litter and from 0.0136 to 0.0197 for drought leaf litter of all species (Table 1). Sycamore non-drought litter decomposed at rates significantly slower than either alder or cottonwood (which were not different from one another), and the same pattern was seen for sycamore drought litter which decomposed significantly slower than both alder and cottonwood drought litter. In no case was the decomposition rate for a species under non-drought conditions significantly different from that same species under drought conditions. There were stronger influences of leaf litter species effects on decomposition rates than drought conditions.

Nevertheless, examining patterns of leaf litter mass loss at each harvest date, we can see differential influences of species and drought effects at different stages of decomposition. Early in the decomposition process, significant species effects, significant drought effects and a significant species \times drought interaction emerged (Fig. 3a). After 14 d, species and drought were still significant effects, but the species \times drought interaction was no longer significant (Fig. 3b). Although significant species and drought effects were still present after 69 d in the stream, the patterns were weaker and only alder and sycamore were significantly different from one another (Fig. 3c). Finally, by day 84, all drought effects had disappeared, but strong species differences

Fig. 2. Changes in initial litter chemistry among three species (alder: *Alnus angustifolia*, sycamore: *Platanus wrightii*, and cottonwood: *Populus fremontii*) collected from a non-drought year (2001, gray bars) and a drought year (2002, black bars). Values represent means ($n=2$) \pm 1 SE for litter: **A**) % nitrogen, **B**) % phosphorus, and **C**) % condensed tannin.

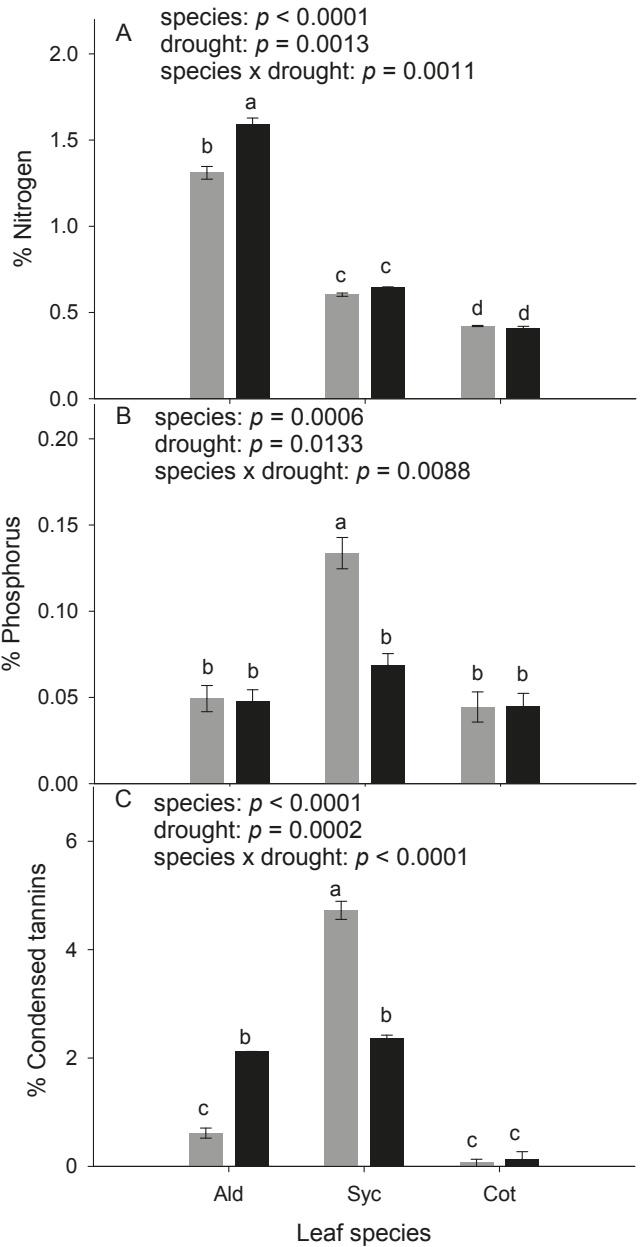


Table 1. Decomposition rate constants ($k \pm 1 \text{ SE}$) for each species by drought treatment combination. Significant differences among treatments are denoted with lower case letters. Regression coefficients (F, degrees of freedom, p -value, and coefficient of determination, R^2) are listed for each treatment.

Treatment	$k \text{ day}^{-1}$	SE	F _(1,37)	p	R^2
Non-drought (2001)					
alder	-0.0204a	0.0008	1109.59	<0.0001	0.9677
sycamore	-0.0157b	0.0008	135.65	<0.0001	0.7811
cottonwood	-0.0195a	0.0008	303.77	<0.0001	0.8914
Drought (2002)					
alder	-0.0195a	0.0008	1497.19	<0.0001	0.9758
sycamore	-0.0136b	0.0008	101.38	<0.0001	0.7274
cottonwood	-0.0183a	0.0008	425.46	<0.0001	0.9180

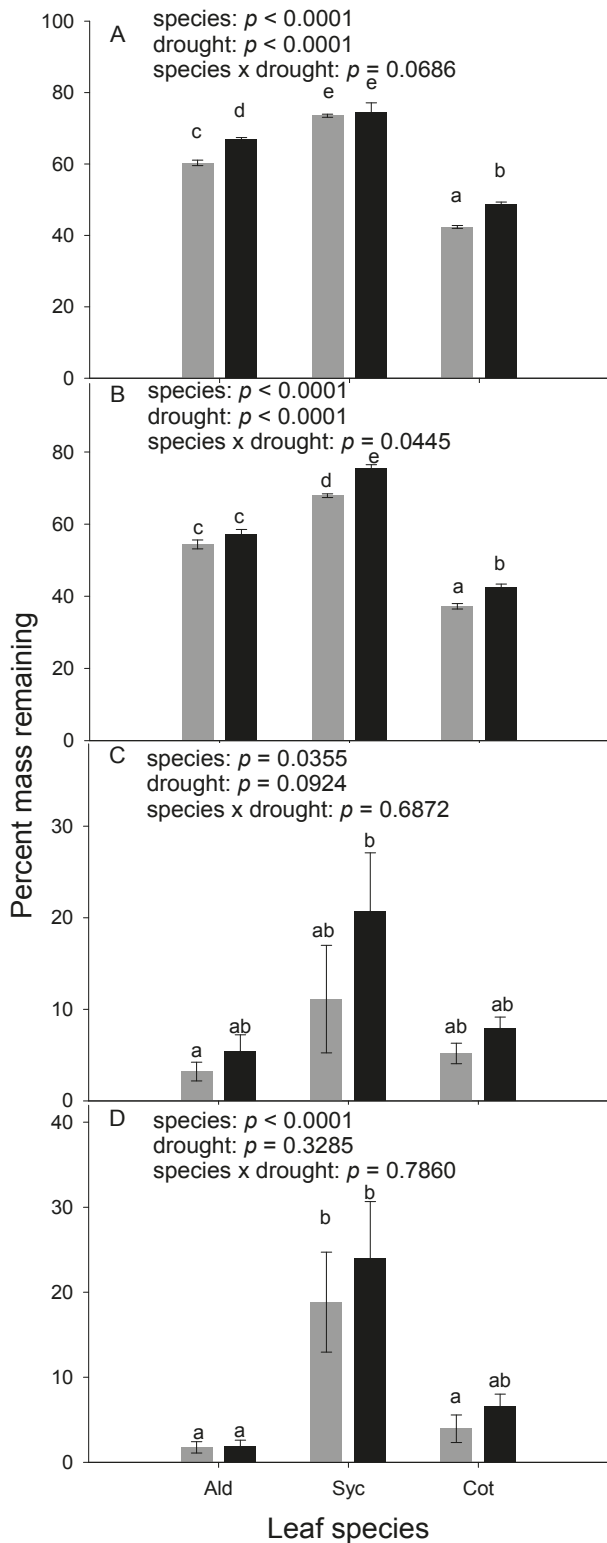


Fig. 3. Percent ash-free dry mass remaining (AFDM) of leaf litter from three different species (alder: *Alnus angustifolia*, sycamore: *Platanus wrightii*, and cottonwood: *Populus fremontii*) collected during a non-drought year (2001, gray bars) and a drought year (2002, black bars). Mean AFDM values ($n=8$) \pm 1 SE are shown for **A**) 7, **B**) 14, **C**) 69, and **D**) 84 days in-stream.

were still present (Fig. 3d) and sycamore had significantly more mass remaining than either alder or cottonwood.

Macroinvertebrate colonization

Wet Beaver Creek is home to a diversity of stream macroinvertebrates and many organisms which belong in the leaf shredder feeding guild (LeRoy & Marks 2006); however, after 69 days we saw only weak patterns in macroinvertebrate community structure among litter species or between drought and non-drought leaf litter. We found no significant differences in metrics of biodiversity among leaf species, between drought treatments or their interaction on macroinvertebrate total abundances, taxa richness, community evenness or Shannon's diversity ($p > 0.05$). Using NMDS ordination and MRPP to distinguish group structure, we found no overall species effect, no drought effect, and no species by drought interaction effect on the community structure of macroinvertebrates; however, a significant drought effect emerged when examining community-wide differences between drought and non-drought leaves for just one species, *P. fremontii* (Fig. 4).

Discussion

Our results show that variability in precipitation resulting from a major drought can indirectly influence stream ecosystems by inducing changes to leaf litter chemistry and subsequent mass loss (especially at early stages of decay) and the colonization of cottonwood litter by macroinvertebrates. As predicted, litter chemistry was significantly altered by drought conditions, although the direction and magnitude of the change varied among species and for particular litter chemicals. Mass loss also differed between drought treatments and among species early in the study; however, the drought effects were lost by the end of the study and leaf species explained more of the variation in mass loss throughout the study.

The variation in litter chemistry response to drought among species with respect to both direction and magnitude is consistent with other studies (Peñuelas et al. 2004, Sardans et al. 2008). The differential responses among species suggest that these riparian trees have different strategies when facing environmental stress. For example, *A. oblongifolia* leaf litter increased in both nitrogen and condensed tannins which are associated with plant defenses. In contrast, *P. wrightii*

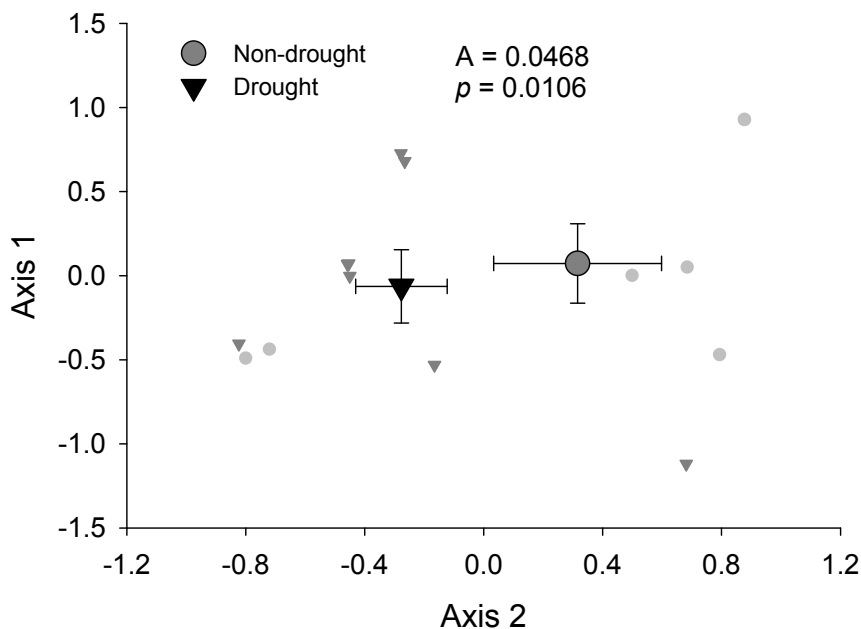


Fig. 4. Non-metric multidimensional scaling ordination showing significant community-wide differences in the macroinvertebrate community colonizing *Populus fremontii* leaf litter collected from non-drought (2001, gray circles) and drought years (2002, black triangles). Centroids are mean nMDS scores with standard error bars.

leaf litter decreased in condensed tannins which may have allowed the trees to use this carbon elsewhere. One important consideration is how the translocation of nutrients by trees prior to leaf abscission is altered due to drought. For example, under drought conditions *Arbutus unedo* reabsorbed more N than other species (Sardans et al. 2008). The decrease in phosphorus in *P. wrightii* observed in this study could be the result of phosphorus re-absorption and storage of the nutrient for future re-growth. In contrast, increased concentrations of foliar phosphorus have been observed under drought conditions in *Quercus ilex*, a dominant Mediterranean species (Sardans & Peñuelas 2007) emphasizing that the response to drought can be highly species-specific. If nutrient resorption and/or increases in foliar concentrations of nutrients are occurring in riparian trees under drought conditions, then in-stream fluxes of carbon, nitrogen and phosphorus may be altered in streams.

The exact mechanism by which drought influences leaf litter chemistry and subsequent decomposition may be one of indirect influence. For example, changes in herbivory can be driven by changes in precipitation and water availability (Maschinski & Whitham 1989, Strauss & Agrawal 1999) and the ability of a tree to tolerate herbivory often correlates with water availability (Maschinski & Whitham 1989). Increased herbivory in turn can promote the production of secondary defensive compounds in-

cluding tannins (Schweitzer et al. 2005). This may explain the drastic increases in tannin concentration for those species that maintain lower tannin concentrations during normal precipitation years (e.g., *P. fremontii*, *A. oblongifolia*). Although we cannot test the influence of indirect versus direct effects in this study we are at least able to account for the combination of various drought effects at a stand level by using the leaf litter of multiple mature trees influenced by intense drought conditions.

Species-specific responses to decreases in precipitation may buffer the effects of drought on stream ecosystems. Although some tree species may reduce the overall recalcitrance of their leaves, other species may balance the effects of this reduction with increased concentrations of recalcitrant compounds. Thus, the net change in leaf litter recalcitrance entering the stream may be zero, mitigating the bottom-up effects on those organisms that respond to leaf litter recalcitrance (e.g. bacteria and fungi). However, this may not be the case for all litter nutrients that enter stream ecosystems during leaf abscission. Drought conditions had little effect on phosphorus concentrations in *A. oblongifolia* or *P. fremontii* whereas *P. wrightii* leaf litter had drastically reduced concentrations of phosphorus under drought conditions. The reduction of foliar phosphorus in a dominant riparian species could exacerbate P-limitation impacting streams that depend on annual pulses of leaf litter-derived phosphorus.

Previous studies have shown similar differences in decomposition among these species and in this same stream system. The previous year, alder and cottonwood leaf litter decomposed at rates similar to the results from this study; however, the previous year, sycamore litter decomposed much slower ($k=0.0075$ compared to the 0.0157 for non-drought and 0.0136 for drought litter) (LeRoy & Marks 2006). Cottonwood litter in this study decomposed at rates two times faster than in a previous study from northern Utah (k ranged from 0.0096 to 0.0111 compared to 0.0195 for non-drought and 0.0183 for drought litter) (LeRoy et al. 2007). Differences in mass loss may be important in structuring the macroinvertebrate communities and help to explain the different communities on cottonwood litter. Although cottonwood leaf litter did increase in tannin concentration under drought conditions, tannins still only comprised a relatively small percentage of the total leaf mass. However, mass loss was higher for the cottonwood drought treatments through time suggesting the possible role of the percentage of leaf biomass remaining in structuring macroinvertebrate communities.

Leaf species effects can be more influential than large-scale environmental effects such as drought. In a recent global meta-analysis, the effects of species on productivity and decomposition were shown to be comparable in strength to the effects of the environment (Hooper et al. 2012). In this study, the species effect was more prominent than the drought effect for almost all variables measured. It is possible that even a major drought, like the one in the American Southwest in 2002–2003 will not overly influence stream ecosystem function through altered allochthonous inputs. Differential responses by riparian tree species to environmental change may shield stream ecosystems from the effects of drought illustrating the importance of conserving biodiversity within riparian ecosystems. Species-level variation also makes it necessary to test the effects of climate change-induced drought within distinct biogeoclimatic regions (e.g. American Southwest, Mediterranean) using dominant species which are likely to have foundation species roles within those ecosystems (Ellison et al. 2005).

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