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Variation in woody plant mortality and dieback from severe drought among soils, plant groups, and species within a northern Arizona ecotone

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Abstract Vegetation change from drought-induced mortality can alter ecosystem community structure, biodiversity, and services. Although drought-induced mortality of woody plants has increased globally with recent warming, influences of soil type, tree and shrub groups, and species are poorly understood. Following the severe 2002 drought in northern Arizona, we surveyed woody plant mortality and canopy dieback of live trees and shrubs at the forest–woodland ecotone on soils derived from three soil parent materials (cinder, flow basalt, sedimentary) that differed in texture and rockiness. Our first of three major findings was that soil parent material had little effect on mortality of both trees and shrubs, yet canopy dieback of trees was influenced by parent material; dieback was highest on the cinder for pinyon pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*). Ponderosa pine (*Pinus ponderosa*) dieback was not sensitive to parent material. Second, shrubs had similar mortality, but greater canopy dieback, than trees. Third, pinyon and ponderosa pines had greater mortality than juniper, yet juniper had greater dieback, reflecting different hydraulic characteristics among these tree species. Our results show that impacts of severe drought on woody plants differed among tree species and tree and shrub groups, and such impacts were widespread over different soils in the southwestern U.S. Increasing frequency of severe drought with climate warming will likely cause similar mortality to trees and shrubs over major soil types at the forest–woodland ecotone in this region, but due to greater mortality of other tree species, tree cover will shift from a mixture of species to dominance by junipers and shrubs. Surviving junipers and shrubs will also likely have diminished leaf area due to canopy dieback.

Keywords Climate change · Water stress · *Juniperus* · *Pinus edulis* · *Pinus ponderosa*

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Introduction

Ecosystem canopy cover is an important property of the landscape as it influences animal habitat, biogeochemical cycles, and other land surface properties such as albedo and potential for erosion (Breshears 2006). Mortality of trees and shrubs can rapidly impact these properties and trigger changes in ecosystem function, including shifting carbon sinks to carbon sources and altering components of evapotranspiration (Breshears and Allen 2002; Newman et al. 2006; Chapin et al. 2008; Montes-Helu et al. 2009). Widespread loss of canopy cover could influence regional fluxes of energy, water, and carbon, potentially altering biosphere–atmosphere feedbacks that influence regional climate (Dominguez et al. 2009).

The recent global increase in drought-induced woody plant mortality has been associated with increasing temperatures (Breshears et al. 2005; Allen et al. 2009b; van Mantgem et al. 2009) that have intensified drought severity, as warmer temperatures increase evapotranspiration and the water-holding capacity of the atmosphere (Dai et al. 2004; Weiss et al. 2009). Recent anomalous climate conditions include a mean global temperature during the last half century greater than any other 50-year period in possibly the last 1,300 years (IPCC 2007). The southwestern U.S., and Arizona in particular, experienced near record warm temperatures and drought during the spring and summer of 2002 (Waple and Lawrimore 2003; Andreadis et al. 2005; Weiss et al. 2009). By August 2002 in northern Arizona, annual precipitation was the lowest instrumentally recorded at 56% below the 1900–2000 average (NOAA National Climatic Data Center 2008). Based on climate reconstruction from tree ring data, 2002 was also the third driest year in over 1,400 years (Salzer and Kipfmueller 2005). Plants in the southwestern U.S. were under severe water stress by the fall of 2002 (Simonin et al. 2006; Gaylord et al. 2007; Breshears et al. 2009) as the Palmer drought severity index (PDSI; Alley 1984; Heim 2002) dropped to -6.3 (Fig. 1), the most extreme value in the last 100 years. Noticeable tree and shrub mortality throughout the southwest followed.

Accelerated plant mortality over the next century, due to drought and induced by climate warming (Hansen et al. 2006; IPCC 2007; Allen et al. 2009a; Kintisch 2009), is predicted to be especially pronounced in mountain forests of the southwestern U.S. (Rehfeldt et al. 2006; Seager et al. 2007). The 2002 drought has been cited as a harbinger of this predicted future scenario in the southwestern U.S. due to the occurrence of an unusually warm, long drought that coincided with widespread mortality of several tree species. Studies of woody plant mortality associated with the 2002 drought in the southwestern U.S. have primarily focused on the amount (Shaw et al. 2005; Breshears et al. 2005) and causes (McDowell et al. 2008; Adams et al. 2009; Breshears et al. 2009; Floyd et al. 2009; Sthultz et al. 2009) of pinyon pine (*Pinus edulis*) mortality, landscape patterns of mortality (Gitlin et al. 2006), and vegetation and community changes caused by higher mortality of pinyon pine than junipers (*Juniperus* spp.) (Mueller et al. 2005). Yet, many potential causal factors and implications of the 2002 severe drought are poorly understood. In this study, we addressed three unresolved questions about this drought.

The first unresolved question is whether impacts of severe drought on woody plants in the southwestern U.S. varied over soil types. Because soil structure and texture influence infiltration, evaporation, and water-holding capacity (Noy-Meir 1973; Brady 1974; Hillel 2004), soil parent material can influence tree survival (Ogle et al. 2000; Moore et al. 2004; Gitlin et al. 2006; Fensham and Fairfax 2007). Previous reports indicate that the southwestern U.S. woodland soils derived from volcanic cinders have rockier, drier, and more nutrient-poor surface horizons than finer textured sedimentary-derived soils (Mopper et al. 1991; Gehring and Whitham 1995; Cobb et al. 1997; Swaty et al. 1998; Selmants and Hart 2008). Yet, studies of tree growth rate suggest surprisingly high resource availability at sites with cinder-derived soil. Radial growth response to eight severe droughts (annual average PDSI < -2.0) between 1950 and 2001, for example, was similar for both pinyon pine and ponderosa pine (*Pinus ponderosa*) on soils derived from cinder, basalt, and sedimentary parent materials (Adams and Kolb 2004). Diameter growth of ponderosa pines in Arizona and New Mexico was greater on soils derived from black cinder compared with red cinder, limestone, and basalt (Colton 1932; Lindsey 1951; Abella and Covington 2006). Following drought in 1996 in northern Arizona, mortality of pinyon pine was unexpectedly greater at a sedimentary than a cinder parent material on flat sites (Ogle et al. 2000). Whether soil water availability to plants during drought is influenced positively by coarse-textured soils via a

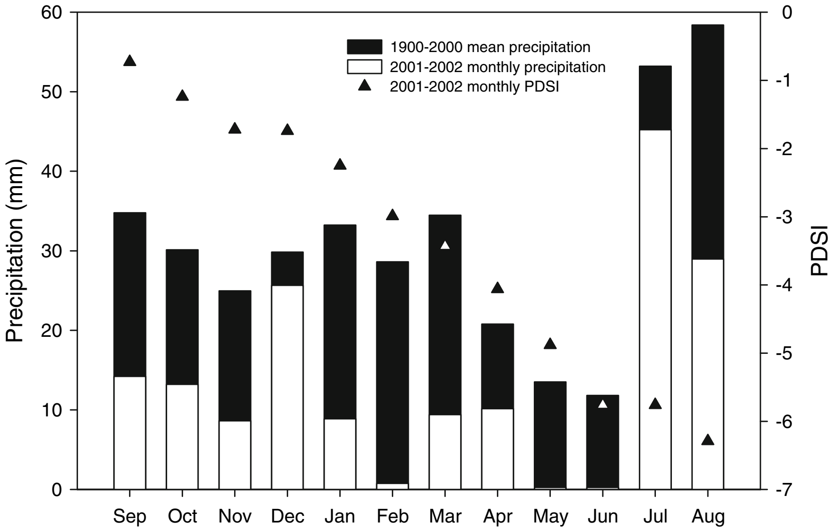

Fig. 1 The 1900–2000 average monthly precipitation (*solid bar*), the Sept 2001–Aug 2002 monthly precipitation (*open bar*) and monthly Palmer drought severity index (PDSI; *triangles*), for northeastern Arizona (climate division 2; NOAA National Climatic Data Center 2008)

mulching effect, or negatively by fine textured soils because of their strong matric potential (Noy-Meir 1973; Brady 1974; Hillel 2004), is uncertain.

The second unresolved question is whether severe drought has similar or different impacts on trees and shrubs. Recent investigations of drought-induced mortality and canopy dieback have focused on a small number of woody plants that dominate or characterize a site (e.g., Breshears et al. 2005, 2009; Mueller et al. 2005; Gitlin et al. 2006) rather than on all woody species. Shrubs may respond differently than co-occurring trees to severe drought. Shrubs often resprout following shoot dieback from disturbance (Davis et al. 2002; Savage and Mast 2005; Bréda et al. 2006), whereas many coniferous trees do not (Barton 2002; Savage and Mast 2005), suggesting greater survival, but also greater canopy dieback, of shrubs than trees during severe drought.

The third unresolved question is whether impacts of severe drought on mortality and canopy dieback of tree species growing in ecotones can be predicted from species' habitat and elevational range. Few studies have intentionally used ecotones to compare impacts of drought among co-occurring tree species. Because ecotonal environmental conditions are the outer ranges of a species' physiological tolerance, drought-induced tree mortality is often greater at ecotones (Allen and Breshears 1998; Loehle 2000; Breshears et al. 2008; Kelly and Goulden 2008; McDowell et al. 2010). Studies of ecotones provide information about inherent species differences in response to environmental changes (Adams and Kolb 2004, 2005), similar to the widely used common-garden approach to evaluating genotypic control of plant performance (Clausen et al. 1940). Earlier comparisons of radial growth response to past droughts (1950–2001) among tree species in ecotonal forests in northern Arizona (Adams and Kolb 2004, 2005) suggest that susceptibility to drought can be predicted from species' habitat and elevational range. Few such comparisons, however, have been made for the more important plant responses of mortality.

Our study addresses the influences of soil type, tree and shrub groups, and species within groups on woody plant condition during the 2002 drought in northern Arizona by comparing mortality and dieback of all woody species in the forest-woodland ecotone among spatially replicated sites with cinder, basalt, and sedimentary soil parent materials. We evaluated three hypotheses: (1) mortality and canopy dieback of live plants would be greater for woody plants at the cinder compared with basalt and sedimentary sites; (2) mortality would be lower for shrubs than trees, but canopy dieback would be greater for shrubs; and (3) mortality and dieback of tree species in the ecotone would be directly associated with species elevational ranges. Specifically for the third hypothesis, because junipers are more drought-tolerant and occur at lower elevation, hotter, and drier sites than ponderosa and pinyon pines (Linton et al. 1998; Pockman and Sperry 2000; Martínez-Vilalta et al. 2004), we expected less effect of drought on mortality and dieback of juniper than for the co-occurring pines. Similarly the elevation range of pinyon pine extends lower than the range of ponderosa pine (Hardin et al. 2001), and thus we expected less mortality and dieback following drought of pinyon pine than for co-occurring ponderosa pine.

Materials and methods

Study sites

Our study area was located in northern Arizona on the Coconino National Forest at elevations ranging from 1,790 to 2,105 m at the ecotone between ponderosa pine-dominated forests and pinyon–juniper-dominated woodlands. We used nine sites located on three soil parent materials ($n = 3$ sites per parent material) that differed in soil texture and percent rock, and represent the major parent materials for the region (Table 1). The sites were established in 2001 by Adams and Kolb (2004) before the onset of the 2002 drought and subsequent tree mortality. Thus, site selection was not biased towards sites with unusual amounts of mortality. The sites included coarse-, moderate-, and fine-textured soils derived from volcanic cinders, flow basalt, and sedimentary (limestone and sandstone) bedrocks, respectively.

Tree ages measured in an earlier study (Adams 2003) suggested that mature ponderosa pines at all study sites established in the early 1900s, while mature pinyon pines established in the early 1900s at the sedimentary parent material and in the late 1800s at the flow basalt and cinder parent materials. These age estimates are consistent with previously reported ages of ponderosa pines (Leiberg et al. 1904; Krauch 1922; Thompson 1940; White 1985), pinyon pines, and Utah junipers (*Juniperus osteosperma*; Sink 2004) in northern Arizona that were similar in diameter to trees in our study. This evidence, along with our visual observations of the sites, strongly suggests little disturbance of the study sites by heavy logging within the last century. None of the sites had signs of recent fire.

Sample design

We sampled three sites (approximately 12 ha each) at each parent material in summer 2004. Within each site, 20 circular plots were established in a 4 × 5 grid, and the location and direction of the initial plot was randomly selected. Plots were 22.4 m in diameter (394 m^2) and

Table 1 Soil characteristics, site names, and locations of the nine study sites

Soil parent material	Subgroup	Surface texture class	Soil depth (cm)	Rock (%)	Site name	Latitude (°N), Longitude (°W)	Elevation[a] (m)
Cinder							
Basaltic cinders	Typic Ustorthent	Coarse sand	>100	75	Painted Desert Vista	35.3986, 111.4334	1,893
Mixed cinders	Vitandric Ustochrept	Loamy coarse sand	>100	70	Haywire Flats	35.3899, 111.4045	1,790
Mixed cinders	Vitandric Ustochrept	Loamy coarse sand	>100	70	Cinder Hills	35.3214, 111.3976	1,924
Flow basalt							
Basalt	Typic Haplustalf	Clay loam	50–100	55	Palatkwapi Trail	34.7640, 111.5997	1,815
Basalt cinders	Typic Argiustoll	Clay loam	50–100	40	Red Mountain	35.5193, 111.8361	2,097
Dacite/andesite	Typic Argiustoll	Coarse sandy loam	>100	50	Route 89 North	35.4003, 111.5726	2,105
Sedimentary							
Limestone	Mollic Eutroboralf	Fine sandy loam	50–100	10	Walnut Canyon West	35.1732, 111.5282	2,049
Sandstone	Typic Haplustalf	Fine sandy loam	50–100	30	Walnut Canyon East	35.1791, 111.4972	2,022
Limestone/sandstone	Mollic Eutroboralf	Fine sandy loam	50–100	10	Cherry Canyon	35.1370, 111.4821	2,050

Soil data is from the US Forest Service Terrestrial Ecosystem Survey of the Coconino National Forest, Arizona (Miller et al. 1995)

[a] No significant differences in elevation among soil parent material means ($P \leq 0.05$ Tukey HSD, one-way ANOVA, rank-transformed)

100 m apart, and the total plot area surveyed within each site was 0.80 ha. Due to the low density of ponderosa pine at some sites, and because our study initially focused on that species, we surveyed one or more additional 1-ha plots adjacent to the other plots until at least 50 ponderosa pines per site were sampled.

Species characteristics and canopy condition

We characterized the woody plant community at each parent material by calculating species richness (S), Shannon diversity index (H) using the relative density (RD) of each species $\left(H = -\sum_{i=species}^{S}(\mathrm{RD}_i) * \ln(\mathrm{RD}_i)\right)$ relative to all woody species, and species evenness (E), which varies between zero and one with one being complete evenness, from Shannon equitability index $\left(E = \frac{H}{\ln(S)}\right)$ (Magurran 2004). We also calculated species composition for trees and shrubs within a parent material as relative density and relative basal area. For both trees and shrubs, relative density was calculated for each species as the total number of individuals of the species divided by the total number of tree or shrub individuals. In addition, relative basal area was calculated for each tree species by parent material. We measured diameter at breast height (DBH; 1.4 m above ground) of each tree within all plots. The diameter of trees <1.4 m tall was measured at stem top; this occurred infrequently and thus these data were combined with DBH data. For trees with multiple stems at breast height, we first calculated basal area at breast height for each stem. Second, we summed basal area over all stems of the tree. Third, we back-calculated a single DBH for the tree from the summed basal area.

We measured canopy condition of all trees and shrubs within plots and classified them into one of three condition classes: (1) healthy live plants with low canopy dieback (Healthy; ≤25% canopy volume recently dead); (2) stressed but alive with high canopy dieback (Stressed; >25% canopy volume recently dead); and (3) recently dead (Dead; recently dead with small diameter twigs and bark present). For trees and shrubs, two observers estimated the percentage of canopy volume containing recently dead branches to assign a condition class. We additionally estimated the percentage of shrub crown volume containing recently dead branches in 10% categories between 10 and 90%, and 5% categories between 0 and 10% and 90 and 100% (Kolb et al. 1992). For each species within a parent material, we calculated the percentage of individuals in each condition class using both site means and data pooled over sites. Trees and shrubs that had clearly died prior to the 2001–2002 drought, which included those that lacked bark or fine twigs, or had fallen to the ground, were not measured.

Statistical analysis

We compared differences in the percentage of trees in each canopy condition (Healthy, Stressed, Dead) among the three tree species common at all sites (ponderosa pine, pinyon pine, and one-seed juniper) and the three soil parent materials with two-way ANOVA on rank-transformed data (Conover and Iman 1981; Potvin and Roff 1993) of site means ($n = 3$ per species per parent material) in order to meet distribution assumptions. We used Tukey HSD ($\alpha = 0.05$) to compare mean differences in ranks among species and parent materials when the main effect *F* test was significant ($P \leq 0.05$). We also tested the significance of the species by soil parent material interaction in the two-way ANOVA. Because rank-transformed data of percent dead trees were not normally distributed due to near absence of dead juniper, we excluded juniper in an additional analysis and compared only the two pine species with two-way ANOVA. We compared differences in the percentage of individuals in each canopy condition class between tree and shrub groups by the same ANOVA approach.

To characterize variation in tree sizes in the study, we used one-way ANOVA to compare DBH among parent materials for each major tree species, and among the three condition classes within a parent material, using site means. One-way ANOVA was used to compare elevation differences among parent material means. We used the statistical package SAS JMP 7.0 for all analyses.

Results

Woody plant characteristics

Differences in plant community structure included lower woody plant species diversity, evenness, and richness at the cinder sites (0.74, 0.30, 12, respectively) than at the flow basalt (2.10, 0.78, 15, respectively) and sedimentary (2.03, 0.72, 17, respectively) sites. Ponderosa and pinyon pines together comprised 85, 56, and 74%, while juniper species comprised 15, 43, and 19%, of basal area at cinder, basalt, and sedimentary sites, respectively (Table 2). Pinyon pine was the most dominant tree in number of individuals at the cinder (79%) and flow basalt (45%) sites, while at the sedimentary sites, ponderosa pine was slightly more

Table 2 Canopy condition and diameter at breast height of all tree species pooled over sites for each soil parent material

Soil parent material and species	Tree condition (%)			Diameter at breast height (cm)				*n*	SC (%) (#, BA)
	Healthy	Stressed	Dead	Healthy	Stressed	Dead	Range		
Cinder									
Juniperus monosperma	52.4	47.6	0.0	21.5 (4.7)	56.0 (6.1)	n/a	6–96	21	5.5, 11.6
Juniperus osteosperma	66.7	33.3	0.0	25.8 (7.8)	33.8 (6.5)	n/a	10–76	12	3.1, 3.8
Pinus edulis	63.5	17.1	19.4	14.5 (0.8)	20.8 (2.6)	23.1 (2.1)	0.3–78	304	79.2, 42.7
Pinus ponderosa	88.0	3.7	8.3	44.8 (2.1)	48.6 (11.6)	54.6 (9.3)	1–153	192[a]	12.2, 41.9
Flow basalt									
Juniperus monosperma	92.1	7.1	0.8	10.8 (0.7)	10.3 (3.0)	12.6 (11.8)	0.3–59	266	20.4, 21.7
Juniperus osteosperma	83.5	16.5	0.0	14.1 (1.0)	31.7 (3.1)	n/a	0.3–63	139	10.6, 21.6
Pinus edulis	79.4	5.3	15.3	8.1 (0.4)	8.8 (1.5)	12.4 (0.8)	0.3–74	583	44.7, 30.5
Pinus ponderosa	75.3	2.2	22.5	18.9 (1.0)	31.2 (13.2)	10.8 (1.4)	0.3–130	404[a]	22.5, 25.3
Quercus gambelii	69.2	30.8	0.0	1.2 (0.3)	11.1 (5.0)	n/a	0.3–26	13	1.0, 0.3
Ulmus pumila	0.0	70.0	30.0	n/a	14.0 (2.3)	7.8 (0.2)	7–25	10	0.8, 0.6
Sedimentary									
Juniperus deppeana	96.7	0.0	3.3	7.8 (2.2)	n/a	4.6 (n/a)	0.5–50	30	2.9, 1.6
Juniperus monosperma	96.7	3.3	0.0	10.8 (1.0)	6.8 (3.2)	n/a	0.3–68	121	11.7, 7.3
Juniperus osteosperma	93.9	6.1	0.0	14.7 (1.6)	11.5 (6.5)	n/a	0.8–61	82	8.0, 9.5
Juniperus scopulorum	100.0	0.0	0.0	15.9 (2.8)	n/a	n/a	0.3–37	15	1.5, 0.9
Pinus edulis	81.5	5.6	12.9	10.6 (0.6)	6.8 (1.4)	14.2 (1.6)	0.5–39	233	22.6, 11.5
Pinus ponderosa	81.5	2.0	16.5	23.3 (1.0)	33.9 (12.6)	25.8 (2.9)	0.8–95	346[a]	29.9, 62.3
Quercus gambelii	36.1	46.1	17.8	7.9 (0.6)	10.0 (0.6)	6.0 (0.7)	0.3–33	241	23.4, 6.9

Trees were grouped into one of three canopy condition classes: alive with low dieback (Healthy; ≤25% of canopy volume recently dead), alive with high dieback (Stressed; >25% of canopy volume recently dead), and recently dead (Dead). For each combination of species and soil parent material, the percentage of trees and the mean (one standard error) diameter in each canopy condition class, the diameter range over all classes, the total number of individuals of each species (*n*), and the percent species composition (*SC*) based on the number of individual trees (#) and basal area (*BA*) are shown

[a] Number of trees sampled in both the circular plots ($n = 47$, 293, and 308 for cinder, flow basalt, and sedimentary, respectively) and the extra 1-ha plots

Table 3 Canopy condition of all shrub species pooled over sites for each soil parent material

Soil parent material	Shrub condition (%)			Dead canopy (%)		*n*	SC (%)
Species	Healthy	Stressed	Dead	Healthy	Stressed		
Cinder							
Brickellia grandiflora	25.0	75.0	0.0	10.0	54.2	8	0.1
Ceratoides lanata	50.0	50.0	0.0	15.0	40.0	4	0.1
Chrysothamnus nauseosus	0.0	68.3	31.7	n/a	68.3	60	1.0
Ephedra viridis	28.9	71.1	0.0	11.4	51.9	38	0.6
Fallugia paradoxa	16.5	74.2	9.3	13.4	56.8	5,435	88.8
Forestiera neomexicana	46.3	53.7	0.0	13.9	38.6	41	0.7
Rhus trilobata	14.1	82.9	3.0	17.5	52.0	363	5.9
Ribes cereum	19.7	73.4	6.9	14.0	54.0	173	2.8
Flow basalt							
Arctostaphylos pungens	71.9	21.9	6.2	8.4	52.4	114	10.0
Berberis fremontii	78.8	20.9	0.3	12.1	39.8	406	35.6
Cercocarpus montanus	25.0	66.7	8.3	11.7	43.8	12	1.1
Chrysothamnus nauseosus	19.9	53.5	26.6	10.2	56.5	297	26.1
Purshia stansburiana	13.5	81.1	5.4	17.5	63.7	37	3.2
Quercus turbinella	69.4	30.6	0.0	10.3	43.1	49	4.3
Rhus trilobata	33.3	66.7	0.0	16.7	60.0	9	0.8
Ribes cereum	0.0	100.0	0.0	n/a	40.0	1	0.1
Tetradymia canescens	33.2	58.4	8.4	12.5	53.0	214	18.8
Sedimentary							
Amelanchier utahensis	0.0	100.0	0.0	n/a	50.0	1	0.1
Berberis fremontii	100.0	0.0	0.0	13.0	n/a	5	0.5
Ceratoides lanata	100.0	0.0	0.0	10.0	n/a	2	0.2
Chamaebatiaria millefolium	26.3	73.7	0.0	13.5	60.9	38	4.0
Chrysothamnus nauseosus	31.5	66.3	2.2	14.2	53.6	270	28.3
Fallugia paradoxa	0.0	100.0	0.0	n/a	80.0	2	0.2
Purshia stansburiana	8.1	63.8	28.1	16.3	67.6	591	62.0
Rhus trilobata	27.3	72.7	0.0	13.3	51.3	11	1.2
Ribes cereum	28.6	71.4	0.0	13.3	47.3	21	2.2
Tetradymia canescens	58.3	41.7	0.0	15.0	32.0	12	1.3

Shrubs were grouped into one of three canopy condition classes: alive with low dieback (Healthy; ≤25% of canopy volume recently dead), alive with high dieback (Stressed; >25% of canopy volume recently dead), and recently dead (Dead). For each combination of species and soil parent material, the percentage of shrubs in each condition class, the mean percentage of recently dead canopy volume for the Healthy and Stressed classes, the total number of individuals of each species (*n*), and the percent species composition (*SC*) based on the number of individual shrubs are shown

common than both pinyon pine and Gambel oak (*Quercus gambelii*) at 30% of the number of individuals and 62% of the total basal area. Ponderosa pine, pinyon pine, one-seed juniper, and Utah juniper occurred at all parent materials. The flow basalt sites also included Gambel oak and the exotic Siberian elm (*Ulmus pumila*), while the sedimentary sites also included Gambel oak, Rocky Mountain juniper (*Juniperus occidentalis*), and alligator juniper (*Juniperus deppeana*).

One or two species dominated shrub composition, especially at the cinder and sedimentary sites (Table 3). Apache plume (*Fallugia paradoxa*) at the cinder sites comprised 89% of the number of individual shrubs, whereas Stansbury cliffrose (*Purshia stansburiana*) and rabbitbrush (*Chrysothamnus nauseosus*) together comprised 90% of shrubs at the sedimentary parent material. Some shrub species were only found at one or two parent materials, and half the shrub species were limited to one parent material. For example, bricklebush (*Brickellia grandiflora*), Mormon tea (*Ephedra viridis*), and stretchberry (*Forestiera neomexicana*) occurred only at the cinder sites; mountain mahogany (*Cercocarpus montanus*), pointleaf manzanita (*Arctostaphylos pungens*), and Sonoran scrub oak (*Quercus turbinella*) occurred only at the flow basalt sites; fernbush (*Chamaebatiara millefolium*) and Utah serviceberry (*Amelanchier utahensis*) occurred only at the sedimentary sites. The most widespread shrub species which occurred on all parent materials were skunkbush (*Rhus trilobata*), rabbitbrush, and wax currant (*Ribes cereum*).

Both ponderosa pine and one-seed juniper had significantly ($P < 0.05$; Tukey HSD) greater average DBH at the cinder sites (51.0 ± 2.2, 38.8 ± 13.5 cm, respectively) than the flow basalt (22.9 ± 7.1, 12.8 ± 3.5 cm, respectively) and sedimentary (25.9 ± 3.3, 12.5 ± 2.2 cm, respectively) sites. Pinyon pine had greater DBH at the cinder (17.4 ± 1.8 cm) than at the flow basalt sites (9.3 ± 1.4 cm), and DBH was intermediate at the sedimentary sites (11.8 ± 1.4 cm). Within a parent material, DBH did not differ significantly among canopy condition classes for any major tree species, except one-seed juniper at the cinder sites where the Stressed trees had a greater DBH than the Healthy trees (56.0 ± 6.1 cm and 21.3 ± 4.7 cm, respectively; Tukey HSD, $P = 0.002$; Table 2).

Condition of trees and shrubs

Healthy was the most common condition for trees. The mean percentage of Healthy trees over all sites was 74% (Table 2). Exceptions to this pattern occurred for Gambel oak at the sedimentary sites and the exotic Siberian elm at the flow basalt sites, where Stressed was the most common condition. The percentage of trees in the Stressed class was high for both one-seed juniper (33%) and Utah juniper (48%) at the cinder sites. Recent tree mortality ranged from 0 to 30% over all species and parent materials (Table 2).

In contrast to trees, Stressed was the most common condition for shrubs. An average of 61% of shrubs were Stressed over all sites, and at least 50% of the canopy volume was recently dead on over two-thirds of the species (Table 3). Healthy shrubs were the exception and included Fremont barberry (*Berberis fremontii*), pointleaf manzanita, and Sonoran scrub oak at the flow basalt sites, and Fremont barberry and winterfat (*Ceratoides lanata*) at the sedimentary sites. Of the 16 shrub species included in our study, only two had mortality greater than 25%: rabbitbrush at the cinder and flow basalt sites, and Stansbury cliffrose at the sedimentary sites.

Percent mortality was similar ($P = 0.51$) for trees (mean ± 1 SE of 12.3 ± 2.4) and shrubs (10.4 ± 3.2; Fig. 2a). Trees, however, had a lower percentage in the Stressed class than shrubs (11.6 ± 1.8 vs 64.4 ± 5.6, respectively; Fig. 2b). Additionally, there was a greater percentage of Healthy trees than Healthy shrubs (76.1 ± 3.0 vs 25.2 ± 6.7, respectively; Fig. 2c). A greater percentage of Healthy trees and shrubs occurred at the flow basalt sites (61.6 ± 12.3) than at the cinder sites (44.2 ± 12.4; $P = 0.044$; Fig. 2c). The percentage of Healthy trees and shrubs was intermediate at the sedimentary parent material (46.2 ± 13.3) and not significantly different from other parent materials.

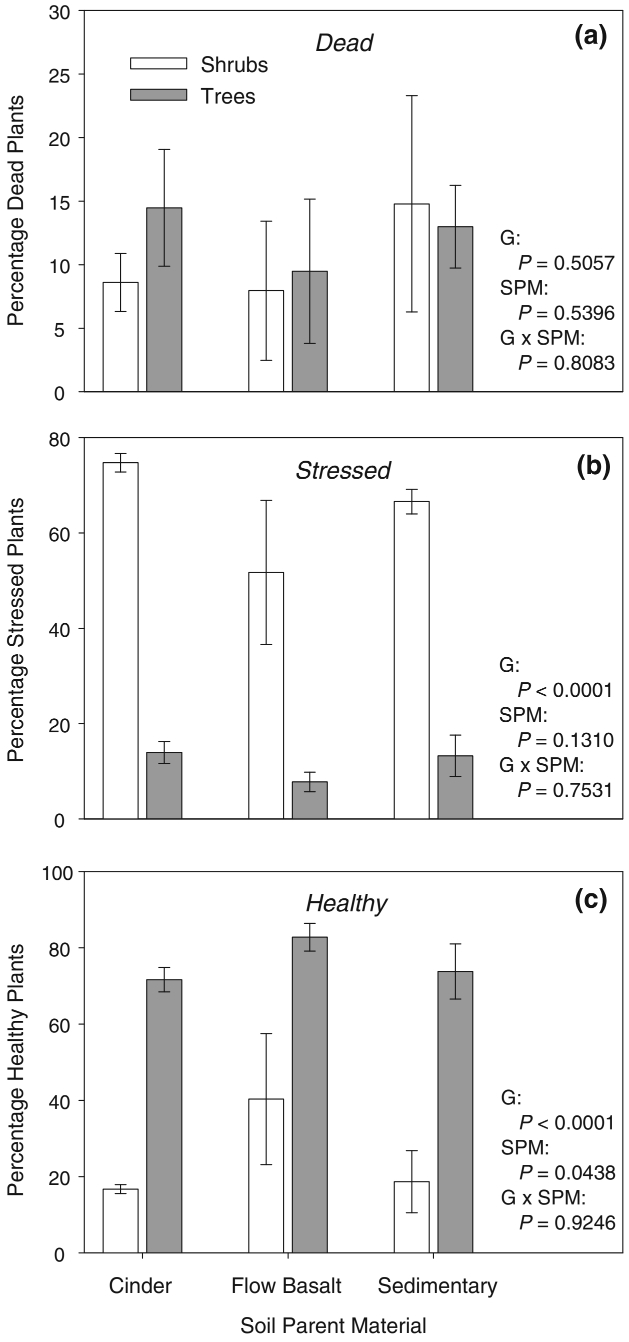

Fig. 2 Mean and 1SE percentage of shrub (*open bar*) and tree (*shaded bar*) groups (*G*) in **a** Dead, **b** Stressed (>25% canopy dieback), and **c** Healthy (≤25% canopy dieback) classes for cinder, flow basalt, and sedimentary soil parent materials (*SPM*). *P* values from ANOVA on site means ($n = 3$ sites for each combination of group and soil parent material) with group, soil parent material, and their interaction are shown

For dominant tree species, mortality was consistently lower at all parent materials for one-seed juniper than ponderosa and pinyon pines ($P < 0.0001$; Fig. 3a). Tree mortality did not differ significantly among parent materials ($P = 0.99$), and the species by soil parent material interaction was not significant ($P = 0.364$). Excluding juniper and comparing only pinyon and ponderosa pines with ANOVA confirmed the absence of a significant difference in mortality between the pine species or among parent materials.

The percentage of Stressed trees was greater for juniper than for both ponderosa and pinyon pines ($P = 0.0199$; Fig. 3b). Moreover, the percentage of Stressed juniper and pinyon pine trees was greater at cinder sites than other sites. In contrast, the percentage of Stressed ponderosa pine was similar over parent materials. Averaged over the three major tree species, the percentage of Stressed trees was greater at cinder compared with sedimentary sites ($P = 0.020$). The species by soil parent material interaction was not significant for the percentage of Stressed trees ($P = 0.287$). In the analysis without the juniper data, the percentage of Stressed trees was greater for pinyon pine than ponderosa pine ($P = 0.013$; Fig. 3b).

The percentage of Healthy trees was influenced by the species by soil parent material interaction ($P = 0.001$; Fig. 3c). The percentage of Healthy junipers was significantly lower at the cinder sites than the other parent materials, whereas parent material did not have a significant effect on the percentage of Healthy ponderosa and pinyon pines. Species differences in the percentage of Healthy trees depended on parent material, with ponderosa pine having a significantly higher percent of Healthy trees than juniper at the cinder sites, and juniper having a significantly higher percent than ponderosa at the sedimentary sites. No differences in the percentage of Healthy trees occurred among species at basalt sites. When the data for juniper was excluded, the percentage of Healthy trees did not differ between pine species ($P = 0.903$), and the species by soil parent material interaction was not significant ($P = 0.326$).

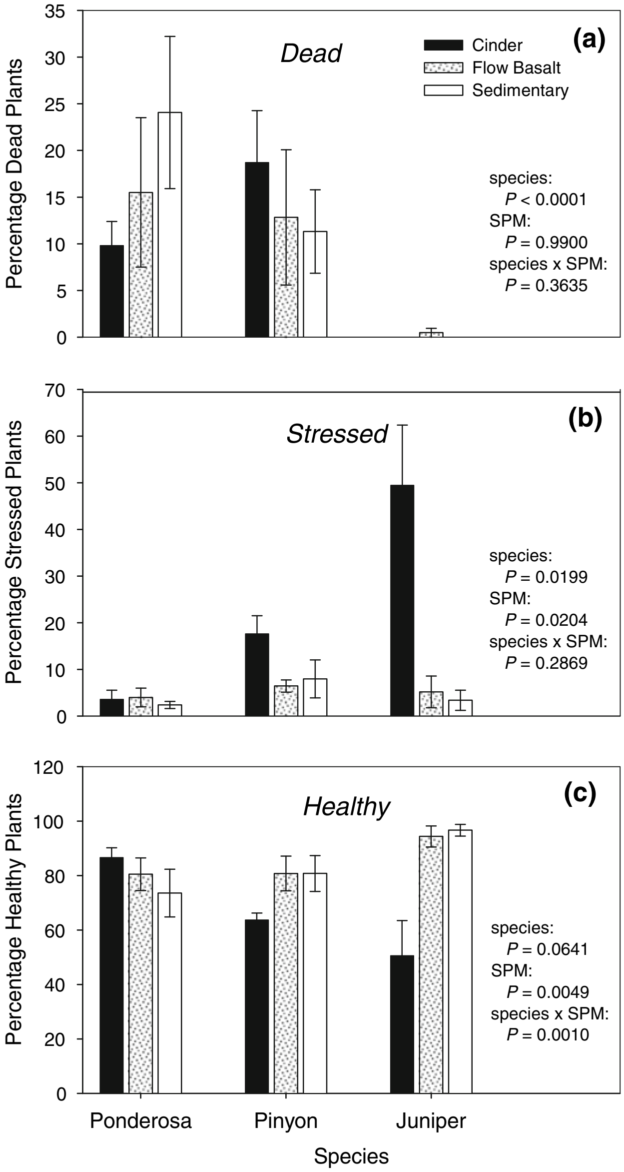

Fig. 3 Mean and 1SE percentage of ponderosa pine (*Pinus ponderosa*), pinyon pine (*Pinus edulis*), and one-seed juniper (*Juniperus monosperma*) in **a** Dead, **b** Stressed (>25% canopy dieback), and **c** Healthy (≤25% canopy dieback) classes at cinder (*solid bar*), flow basalt (*speckled bar*), and sedimentary (*open bar*) soil parent materials (*SPM*). *P* values from ANOVA on site means ($n = 3$ sites for each combination of species and soil parent material) with species, soil parent material, and their interaction are shown

Discussion

Our finding of little difference in mortality among soil parent materials for individual species or groups of trees and shrubs does not support our first hypothesis. While this finding is not entirely consistent with another study (Gitlin et al. 2006), it is consistent with studies that did not find a clear relationship between soil parent material and tree mortality (Ogle et al. 2000; Moore et al. 2004). Gitlin et al. (2006) reported greater mortality of pinyon and ponderosa pines on soils derived from younger red cinder than older black cinder parent materials in the same region as our study but at different sites. No comparisons were made, however, with the older sedimentary or basalt parent materials that we studied where both pine species frequently occur. Our results are more consistent with two other studies. First, bedrock type significantly affected mortality of only three of six conifer species in a northwest U.S. forest, and the effect was not uniform over species (Moore et al. 2004). Second, pinyon pine mortality in the region of our study sites following drought in 1996 did not differ consistently between cinder and sedimentary soil parent materials (Ogle et al. 2000).

Hypothesis one was partially supported by a greater occurrence of Stressed pinyon pine and juniper at the cinder than at other soil parent materials. The lack of such a difference by ponderosa pine and most shrub species indicates that the canopy dieback response to severe drought at the cinder parent material was species-specific. We conclude that severe drought produces more canopy dieback at the cinder than at flow basalt and sedimentary parent materials only for some species of woody plants, but parent material does not strongly influence survival of mature woody plants.

Our results indicate the coarse-textured cinder-derived soils supply more water to established woody plants during severe drought than suggested by previous reports (Mopper et al. 1991; Gehring and Whitham 1995; Cobb et al. 1997; Swaty et al. 1998) that compared soil water content in the upper 30 cm among sites. Larger pores of surface cinders increase infiltration which drives the wetting front deeper into the soil profile compared with the finer-textured soils derived from flow basalt and sedimentary rocks (Brady 1974; Hillel 2004). The cinder soil sites can have deep subsoils (>1.5 m) containing alternating layers of coarse and fine textures (Holzschuh 2004) that promote water retention (Hillel 2004). Surprisingly high water availability to trees at the cinder sites during drought is consistent with our subsequent measurements of predawn xylem water potential (Ψ_{PD}) during drought in 2007 (PDSI = −4.7; Koepke, unpublished), in which we found one-seed juniper to be less water stressed at the cinder ($\Psi_{PD} = -2.0 \pm 0.2$ MPa; mean ± 1 SE) than at the flow basalt (−3.6 ± 0.3 MPa) or sedimentary (−3.2 ± 0.2 MPa) sites. Similar but non-significant Ψ_{PD} patterns occurred for the dominant pine species in 2007.

Our second hypothesis was partially supported by a greater canopy dieback for shrubs than trees; mortality, however, did not differ between groups. Partial canopy dieback during drought appears to be an important survival strategy for shrubs and, similar to previous observations, for shrub-like trees such as juniper species (Johnsen 1962) and Gambel oak (Abella 2008), but not for the pine species in the forest–woodland ecotone of the southwestern U.S. We speculate that most tree species in our study maintained a Healthy canopy condition until reaching a physiological threshold beyond which continued water stress or depleted carbon reserves induced whole-plant mortality. In contrast, shrubs and shrub-like trees likely maintained stomatal conductance during drought to sustain carbon uptake until hydraulic failure from severely negative plant water potential induced branch dieback (e.g., McDowell et al. 2008). By reducing the amount of transpiring leaf area, shoot dieback may increase the root-to-shoot ratio and improve both the water (Rood et al. 2000; Davis et al. 2002; Bréda et al. 2006) and nutrient (Chapin 1980) status of surviving tissues. This strategy is likely more advantageous for shrubs and shrub-like trees because, unlike non-sprouting trees with a single main stem, some of the stems can be sacrificed without causing whole plant mortality, and growth can continue once drought subsides.

Our third hypothesis was partly supported by the finding that juniper, the dominant tree with the lowest elevational range, had the lowest mortality of all tree species. Mortality, however, did not differ between pine species, even though pinyon pine would seem to be more drought tolerant than ponderosa pine based on its lower elevation range (Hardin et al. 2001), lower vulnerability to drought-induced cavitation (Martínez-Vilalta et al. 2004), and lower sensitivity of radial growth to drought (Adams and Kolb 2004). Causes of the unexpectedly high mortality of pinyon pine compared with ponderosa pine at the same ecotonal sites are not known, but may include more pronounced impacts of biotic tree-killing agents such as bark beetles (e.g., Raffa et al. 2008) on pinyon pine (Negrón and Wilson 2003; Floyd et al. 2009) than on ponderosa pine (Negrón et al. 2009) during severe drought.

In contrast to mortality, our results for canopy dieback did not support hypothesis three. Opposite of our prediction, Stressed trees were most prevalent for juniper, intermediate in occurrence for pinyon pine, and least prevalent for ponderosa pine. Canopy dieback during severe drought appears to be a survival mechanism for juniper, and to a lesser extent pinyon pine, but not for ponderosa pine.

Hydraulic mechanisms may underlie our finding of differences in mortality and canopy dieback among tree species. Isohydric species, such as pinyon and ponderosa pines, exhibit strong stomatal control of transpiration during drought to prevent rapid desiccation and relieve xylem tension (e.g., Gaylord et al. 2007; Breshears et al. 2009) due to high sensitivity of the guard cells to changes in soil and rhizosphere water potential, hydraulic conductance, and evaporative demand at the leaf surface (Tardieu and Simonneau 1998; Sperry et al. 2002; Franks et al. 2007; McDowell et al. 2008). Prolonged stomatal closure of isohydric species during drought reduces photosynthesis and may lead to insufficient carbon resources for metabolism and defense against biotic mortality agents (Bréda et al. 2006; McDowell et al. 2008; Adams et al. 2009; Negrón et al. 2009). Alternatively, stomatal conductance of anisohydric species such as juniper is less sensitive to changes in atmospheric or soil water conditions due to a low vulnerability to drought-induced xylem cavitation (Linton et al. 1998; Williams and Jackson 2007; West et al. 2007), and thus such species maintain higher transpiration than isohydric species during drought (Sperry et al. 2002;

Schultz 2003; West et al. 2007). In the upper canopy where xylem tension is greatest, increasing drought duration or intensity can, however, induce xylem cavitation and result in partial canopy dieback in anisohydric species (Johnsen 1962; Rood et al. 2000; Davis et al. 2002; Bréda et al. 2006; West et al. 2007; McDowell et al. 2008), as occurred for juniper on the cinder sites.

Conclusions

Climate models predict a warmer and drier climate throughout the southwestern U.S. in the twenty-first century (Seager et al. 2007; Solomon et al. 2009). Warmer temperatures and increasing frequency of droughts similar to, or more extreme than the 2001–2002 event, should cause major shifts in plant community composition (Allen 2007; Williams and Jackson 2007) in this region via differences in mortality and drought adaptations among woody species. Our results suggest that such vegetation shifts in forest–woodland ecotones in the southwestern U.S. will include similar amounts of mortality of shrub and tree groups, but that overall tree cover will be reduced as the community shifts from a mixture of species to more monotypic stand of junipers due to high pine mortality. Surviving junipers and shrubs will likely have diminished leaf area due to canopy dieback. Moreover, these vegetation changes will occur similarly over major soil types.

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