

Soil water dynamics under low-versus high-ponderosa pine tree density: ecohydrological functioning and restoration implications

Chris B. Zou,^{1,2*} David D. Breshears,³ Brent D. Newman,^{4,5} Bradford P. Wilcox,⁶ Marvin O. Gard⁴ and Paul M. Rich⁷

¹ School of Natural Resources, University of Arizona, Tucson, Arizona 85721-0043, USA

² Now at Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA

³ School of Natural Resources, Institute for the Study of Planet Earth, and Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721-0043, USA

⁴ Earth and Environmental Sciences Division, Los Alamos National Laboratory, Los Alamos, New Mexico 87545, USA

⁵ Now at the Isotope Hydrology Section, International Atomic Energy Agency, PO Box 100, Wagramer Strasse 5, Vienna, A1400, Austria

⁶ Department of Rangeland Ecology and Management, Texas A&M University, College Station, Texas 77841, USA

⁷ Creekside Center for Earth Observation, Menlo Park, CA 94025, USA

ABSTRACT

Soil water dynamics reflect the integrated effects of climate conditions, soil hydrological properties and vegetation at a site. Consequently, changes in tree density can have important ecohydrological implications. Notably, stand density in many semi-arid forests has increased greatly because of fire suppression, such as that in the extensive ponderosa pine (*Pinus ponderosa* Laws.) forests that span much of western USA. Few studies have quantified how soil water content varies in low- versus high-density stands both by depth and years, or the inter-relationships between water content, stand density, and ecohydrological processes. Over a 4-year period, we measured the soil water content throughout the soil profiles in both low-density (250 trees/ha) and high-density (2710 trees/ha) ponderosa pine stands. Our results document significantly greater soil water contents in the low-density stands over a wide range of conditions (wet, dry, winter, summer). We observed substantial differences in water contents at depths greater than are typically measured. Our results also show that differences in monthly average soil water contents between the low- and high-density stands fluctuated between 0.02 and 0.08 m³ m⁻³ depending on the time of year, and reflect a dynamic coupling between infiltration and stand evapotranspiration processes. The difference in soil water availability between low- and high-density stands is substantially amplified when expressed as plant-available water on a per tree, per biomass or per leaf area basis. Our findings highlight important ecohydrological couplings and suggest that restoration and monitoring plans for semi-arid forests could benefit from adopting a more ecohydrological focus that explicitly considers soil water content as a determinant of the ecosystem process. Copyright © 2008 John Wiley & Sons, Ltd.

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INTRODUCTION

Soil water content is a fundamental determinant of many ecological processes, particularly in semi-arid and other water-limited ecosystems (Newman *et al.*, 2006). Soil water content affects vegetation and is also affected by vegetation. The importance of such ecological and hydrological inter-relationships—the realm of ‘ecohydrology’ (Rodríguez-Iturbe and Porporato, 2004; Newman *et al.*, 2006)—is increasingly being recognized as central in predicting and managing ecosystem dynamics. Notably, human activities have altered many ecosystems to the point of changing key structural and functional attributes, associated ecosystem services, and even fundamental ecosystem processes (Eamus *et al.*, 2006). Large-scale restoration efforts are in progress and are

urgently needed across substantial portions of the biosphere (Hobbs and Norton, 1996; Falk, 2006). Effective restoration integrates general ecological theory for site-specific applications, and has evolved from approaches that focused on key structural attributes such as, forest stand density, or the presence of a certain significant plant species, to approaches that consider historical conditions and recent vegetation trajectories (Fule *et al.*, 1997; Mast *et al.*, 1999; Friederichi, 2003). Recently, the focus in restoration has shifted from emphasizing a specific set of conditions, often referred to as ‘reference conditions’, to emphasizing ecosystem processes and how these may change to enhance resilience in the face of environmental disturbances (Allen *et al.*, 2002; Friederichi, 2003; Falk, 2006).

The focus on restoring ecosystem functions is relevant to numerous types of ecosystems, but is particularly critical for semi-arid forests, which are spatially extensive and have developed a high risk for crown fires due to increases in tree density that resulted from fire

* Correspondence to: Chris B. Zou, Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA. E-mail: chriszou1965@gmail.com

suppression (Fule *et al.*, 1997; Covington *et al.*, 2001). Notably, major restoration efforts are in progress or in the process of being considered for substantial portions of the ponderosa pine (*Pinus ponderosa* Laws.) forests that span much of the western USA. Initially, restoration efforts for ponderosa pine forests focused on explicitly mimicking the stand structure at a historical point in time (pre-European settlement), but more recently, such efforts have begun to include a broader array of attributes that relate to ecosystem health and functional integrity, including post-restoration structure, composition and spatial configuration (Allen *et al.*, 2002; Moore *et al.*, 2004; Falk, 2006).

In ponderosa pine ecosystems, most of these structural and functional attributes are driven by soil water content and associated ecohydrological processes (refer Newman *et al.*, 2006 for a related discussion). However, most specific prescription and monitoring plans for forest restoration do not directly consider soil water content (e.g. Allen *et al.*, 2002; Friederichi, 2003). Several studies have evaluated biological responses such as pre-dawn plant water potential as a surrogate to infer soil water conditions associated with stand density treatment in ponderosa pine restoration (Kolb *et al.*, 1998; McDowell *et al.*, 2003; Skov *et al.*, 2004; Wallin *et al.*, 2004; Simonin *et al.*, 2006). Measures of plant water potential are directly relevant in assessing the water status of the measured plant, but do not necessarily reveal the overall soil moisture patterns of the entire soil profile because plant pre-dawn water potential often reflects equilibration with only the wettest soil layer of the plant's rooting zone (Kramer and Boyer, 1995). In addition, there might be a large discrepancy between pre-dawn water potential and soil water potential in the wettest part of the rooting zone (Donovan *et al.*, 2003). Hydraulic redistribution of soil water can further obscure plant-soil relationships (Zou *et al.*, 2005). Direct measurement of soil water content in ponderosa pine forests of contrasting densities are limited to a few studies (Feeney *et al.*, 1998; Stone *et al.*, 1999; Sala *et al.*, 2005; Simonin *et al.*, 2006), some of which reported higher soil water content in low-density stands (Feeney *et al.*, 1998; Stone *et al.*, 1999), and others which reported no differences (Sala *et al.*, 2005) or differences in one year but not in another (Simonin *et al.*, 2006). However, the measurements obtained to date are limited in three key aspects. First, most have focused only on the shallow portion of the soil profile (up to depths of only 30–40 cm), even though soil moisture varies substantially with depth (Wilcox *et al.*, 1997; Brandes and Wilcox, 2000), and ponderosa pine likely use water at depths greater than 40 cm (Tierney and Foxx, 1987; Jackson *et al.*, 1996; Schulze *et al.*, 1996; Newman *et al.*, 2004). Second, these studies have been limited to 1 or 2 years, and mostly to only the growing season, even though there is substantial inter-annual variability in precipitation and associated soil moisture dynamics, including important soil water dynamics outside the growing season. A short observation period, therefore, is insufficient to fully evaluate how soil water content varies

temporally, especially between the winter/spring period when substantial infiltration of snowmelt and early season rains can occur and the summer/fall period when substantial soil moisture depletion by evapotranspiration occurs.

In summary, although soil water dynamics underlie most ecological restoration variables of concern in ponderosa pine forests and other semi-arid ecosystems (Rodriguez-Iturbe and Porporato, 2004), a robust understanding of soil water differences between low- and high-density stands is lacking (Breshears, 2006), particularly with respect to variation inter-annually, seasonally, and as a function of depth. Such variation in soil water dynamics as related to stand density is only implicitly considered currently, but fundamentally underlies the effectiveness of restoration guidelines, specific restoration 'prescriptions', and associated post-restoration monitoring of ecosystem responses (Feeney *et al.*, 1998; Stone *et al.*, 1999; Covington *et al.*, 2001; Fule *et al.*, 2001; Bailey and Covington, 2002; Waltz *et al.*, 2003; Wallin *et al.*, 2004; Skov *et al.*, 2005). To address this issue, our objectives were (1) to compare soil water content in a low- and high-density ponderosa pine forest stand, including spatial variation as a function of depth throughout the soil profile and temporal variation both seasonally (dry season vs wet season) and annually (dry, wet and normal years), and (2) to compare the amount of water available per tree, per unit biomass or per leaf area for the low-versus high-density stands. Our study encompassed the entire soil profile down to the tuff bedrock and spanned a 4-year period that included a relatively wet year, a relatively dry year, and two intermediate years. We discuss the ecohydrological implications of our results, which document substantially more soil water in low-density stands, for future management and restoration of ponderosa pine forests.

METHODS

Site description

The study site was located within the Los Alamos National Laboratory's Environmental Research Park on the Pajarito Plateau of north-central New Mexico, and has been the site of numerous hydrological investigations (Wilcox *et al.*, 1997; Newman *et al.*, 1998; Newman and Robinson, 2005). The site was located on a south-facing hillslope (6%) at an elevation of approximately 2300 m and includes two ponderosa pine stands with contrasting tree densities. The two stands differed in tree density by more than an order of magnitude, with a density of 250 trees ha⁻¹ for the low-density ponderosa pine stand, and of 2710 tree ha⁻¹ for the high-density stands. The high-density stands, a 'doghair thicket', apparently, was naturally regenerated as a result of harvesting in the early 1950s (Lin *et al.*, 1992). The order-of-magnitude difference in stand densities approximates pre- and post-treatment densities of ponderosa pine forests targeted for restoration (Fule *et al.*, 1997; Mast *et al.*, 1999).

The average soil depth at this site was about 100 cm (Newman *et al.*, 1998). A 20–40 cm, sandy loam (loess), A horizon, was present at the top of the soil zone with clay contents that range from 5 to 13%, and sand contents of 35–51%. Below this was a 30–40 cm thick, well-developed, clay Bt horizon, that had 58% clay and 25% sand. A transitional 20–60 cm thick Cr horizon lay between the Bt horizon and the unweathered Bandelier tuff and consisted of 64 to 80% sand and 9 to 27% clay (Newman *et al.*, 2004).

Data collection

Soil water content was measured with a neutron thermalization probe in access tubes that extended through the soil profile and into the underlying tuff bedrock (Gardner, 1986). Soil access tubes were initially installed in the low-density site ($n = 14$; Wilcox *et al.*, 1997; Wilcox and Breshears, 1997). For this study, we installed three additional tubes along a transect in the high-density stands at intervals of ~ 10 m, adjacent to the location described by Lin *et al.* (1992). Neutron probe measurements were obtained at seven soil depths of 10, 25, 40, 55, 70, 85 and 100 cm, and from four bedrock depths of 150, 200, 250, and 300 cm on a weekly basis from January 1995 to August 1998, and converted to volumetric soil water content using a local clay loam calibration (Nyhan *et al.*, 1994). Hemispherical photos were taken 1.0 m above the ground at each neutron access tube position in July 1994 to quantify leaf area index (LAI) of associated densities using the same methods as detailed in Lin *et al.* (1992); see also Zou *et al.* (2007). Water volumetric contents in bedrock beneath low- and high-density stands were tested first using ANOVA, and no significant difference was detected ($P > 0.05$). This allowed us to infer that comparison of any small amount of seepage is possible between the sites (Newman *et al.*, 1998, 2007), and to focus on the soil profile where root interactions should be predominant.

Data analysis and statistics

First, we calculated monthly means of soil water content, averaging across depths, and then averaging across dates within a given month, to evaluate temporal differences between the low- and high-density stands. Next, we evaluated spatial variation along the soil profile using average soil water contents at each of the seven soil depths for March representing the wet season, and for July representing the dry season. Finally, to evaluate the amount of water available on a per tree, per biomass or per leaf area basis for the two stands, we calculated grand means of soil water content that averaged across all depths and all measurement intervals to yield average total water volume (L) retained per hectare. This estimate of average total soil water volume was used to calculate a normalized value of water allocated on a per tree, per unit biomass and per leaf area basis for both stands. Biomass was estimated using allometric relationships developed for the surrounding area (Garcia, 1977). LAI at each

individual neutron access tube position was estimated using canopy analysis software [HemiView 2.1, Delta-T Devices, Cambridge, UK (Rich, 1989, 1990; Rich *et al.*, 1999; Hale and Edwards, 2002) based on hemispherical images acquired in 1994. The mean value of LAI for both stands was then used to calculate a normalized value of water allocated per leaf area. Our LAI estimates are for trees only, which dominates overall site LAI; associated herbaceous and understory shrub LAI values are likely around 0.2 for the low-density stands (McDowell *et al.*, 2007) and negligible for the high-density stands. To test the statistical significance of soil water content between the low- and high-density stands during the experimental period, we used MANOVA Repeated Measures (JMP IN 5.1, SAS Institute, Cary, NC, USA) with 125 repeated measurement dates; soil water content averaged for each access tube was nested under each date as replicates.

RESULTS

Annual precipitation in our study area ranged from 340 mm in 1996, a relatively dry year, to 489 mm in 1997, a relatively wet year, and averaged 421 mm over the 4 years of the study (Figure 1(a)). In the low-density stands, volumetric soil water content averaged over the top 100 cm of the profile for the duration of the study ($29.33 \pm 0.38\%$; $n = 128$) was significantly greater than the average for the high-density stands ($24.29 \pm 0.43\%$; $n = 126$) ($P = 0.022$). Monthly mean volumetric soil water content averaged over the soil profile was consistently higher in the low-density than in the high-density site (Figure 1(b)). Soil water content was greatest following winter snowmelt in March and April (dotted line in Figure 1(b)). Soil water content reached a minimum as early as May in a dry year (1996) and as late as November in a year with a weak monsoon (1995) (black arrows in Figure 1(b)). In a normal year, soil water content reached a minimum in June or July before the onset of the monsoon (1997 and 1998) (black arrows in Figure 1(b)). Differences in soil water content between low- and high-density stands peaked during the winter months, 2–3 months before snowmelt when soil water content was greatest (dotted line in Figure 1(c)). The differences were smallest in, or immediately after the month of snowmelt (April or May, arrows in Figure 1(c)). Differences then increased until they reached a maximum during the winter of the following year (January or February, dotted line in Figure 1(c)).

Soil water content throughout the soil profile (Figure 2) varied by year, by season, and by depth, but for each depth between 25 and 85 cm soil water content was consistently higher in the low-density stands than in the high-density stands; differences in soil water content between the two stands diminished or were non-existent for the shallowest and deepest depths.

The differences in soil water content translated to large differences in the amount of soil water available per tree (Figure 3(b)), per unit of tree biomass (Figure 3(c)), or

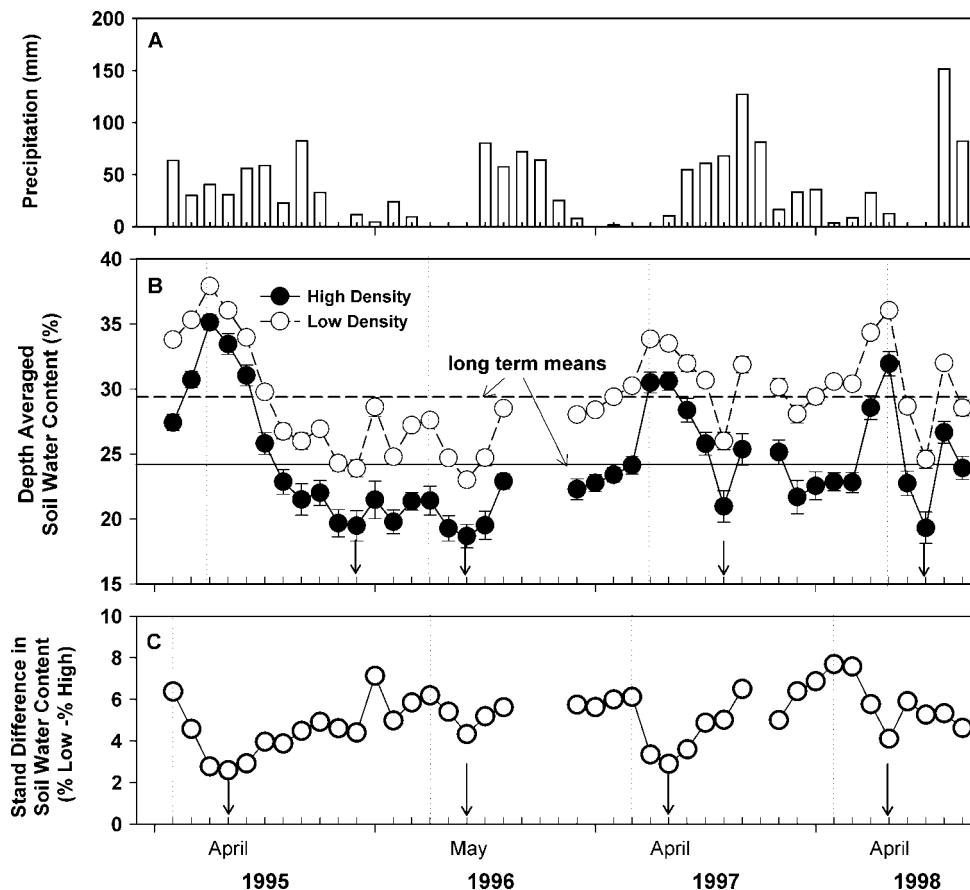


Figure 1. (a) Monthly precipitation (mm); (b) monthly soil volumetric water content (%), maximum soil water content (dotted line), and minimum soil water content (downward arrow) in each year of the study (error bars for soil water content = 1 standard error); (c) Normalized difference between soil water content for low- and high-density stands. Maximum (dotted lines) and minimum (grey downward arrows) values of soil water content differences between low- and high-density stands are indicated for each year.

per leaf area (Figure 3(d)). For the low-density stands, the total soil water volume available per tree was 11 744 l—13 times higher than the 898 l for the high-density stands (Figure 3(b)). For the per unit of biomass (kg), the amount of available soil water in the low-density stands was 24.02 l, whereas that in the high-density stands was only 8.85 l. On a per leaf area basis (m^2), there was 431.47 l water available in the low-density stands, which was approximately three times higher than the 147.98 l in the high-density stands.

DISCUSSION

Our results show that the low-density stands consistently had greater soil water content than the high-density stands (Figure 1). This overall difference varied with depth, season and year, but nonetheless, was consistently evident (Figure 2). The difference in soil water content between low- and high-density stands was not readily apparent at the shallowest or deepest parts of the soil profile, but rather, was greatest through intermediate depths of the profile. Our results, then, are consistent with other studies that did (Feeney *et al.*, 1998; Stone *et al.*, 1999; Simonin *et al.*, 2006) or did not (Sala *et al.*, 2005; Simonin *et al.*, 2006) show differences in soil water content in low- versus high-density stands, given that these

studies only observed relatively shallow depths (upper 30 cm in Feeney *et al.*, 1998; Stone *et al.*, 1999; Simonin *et al.*, 2006; upper 40 cm in Sala *et al.*, 2005). However, our results highlight the importance of evaluating multiple depths to assess site differences in soil water content. Similar differences in soil water availability through evaluating multiple depths have been documented in association with reduction of stand density or canopy coverage in other forest and savanna ecosystems (Stogsdill *et al.*, 1992; Zou *et al.*, 2005). In addition, our results show important differences between wet and dry years that have not been documented in other studies in ponderosa pine forests.

The observed differences in soil water content between low- and high-density stands are likely the net result of several interacting components of the water budget. A previous analysis of soil water data from the low-density site indicated that the soil water dynamics were driven by annual periodicity that seemed related to winter soil water infiltration, followed by depletion through evapotranspiration (Brandes and Wilcox, 2000). Our results show that the winter soil water content increases in the high-density stands are greater than those in the low-density stands, although the high-density stands' water content never reaches the same absolute magnitude as that of the low-density stands. This result seems to be

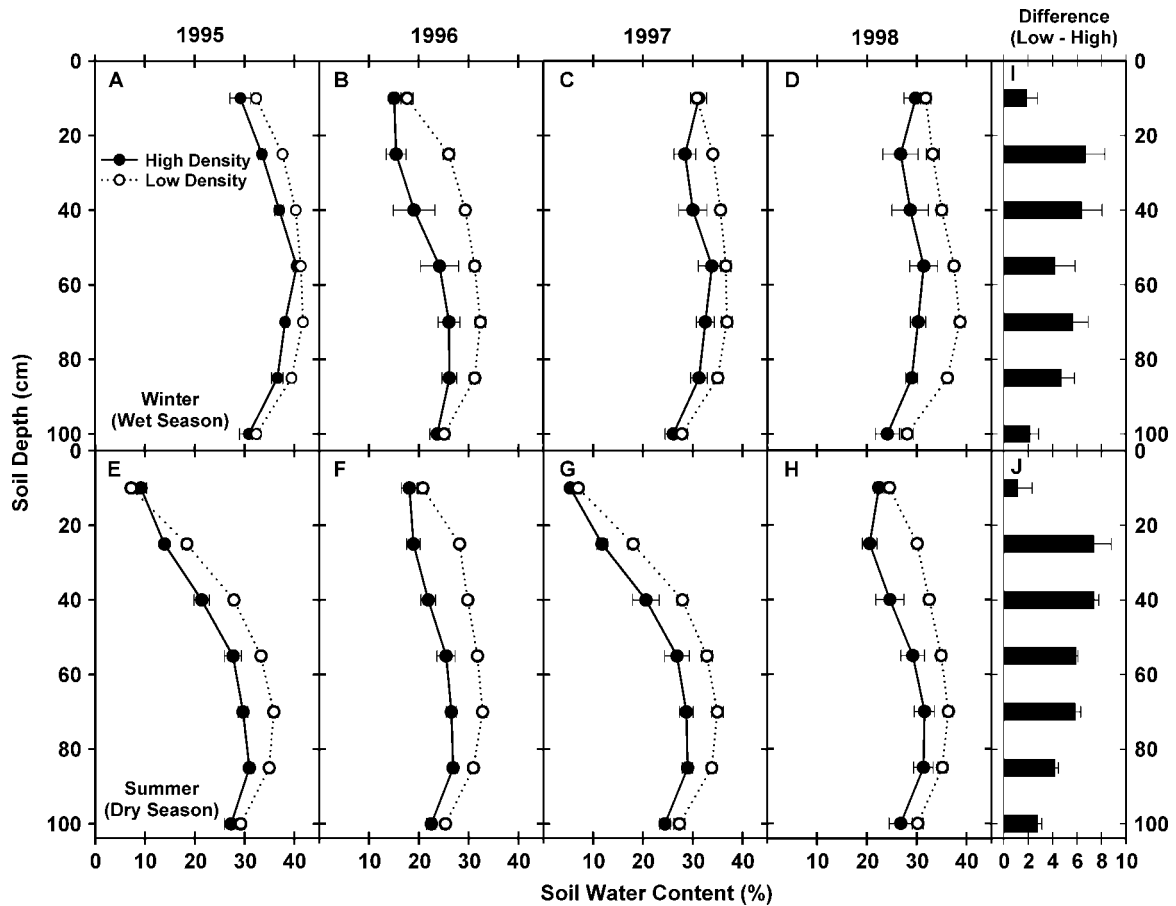


Figure 2. Soil volumetric water content (%) by depth and year for periods following winter snowmelt (March, top row) and before major summer monsoons (July, bottom row). Mean differences during the study period are summarized in the column on the right.

in contrast to the general assumption that infiltration under the high-density stands is less than that of the low-density stands because of greater snow interception associated with higher canopy cover (Storck *et al.*, 2002). It is possible that our results could be attributable to slight differences in soil texture between sites, or could be associated with changes in snowpack melting and stem-flow pattern. In this study, we do not have sufficient data to rule out either of the possibilities, and further study is required to resolve this issue. Nonetheless, the effect of transpiration appears to be greater than such interception effects, given that the soil water content is consistently greater in the low-density stands. More generally, our results highlight the ongoing challenge of interpreting soil water dynamics relative to components of the water budget (e.g. Breshears *et al.*, 1997), despite their basic ecohydrological relevance (Rodriguez-Iturbe and Porporato, 2004).

Our extension of expressing soil water availability to a per tree, per unit biomass or per leaf area basis highlights the degree to which observed differences could be ecologically important. On a per tree basis, individuals in the high-density stands have more than an order-of-magnitude less water available than those in the low-density stands. In addition, soil water seems to be more rapidly depleted in the high-density stands; hence, trees in those stands likely experience longer and more

severe periods of water stress [these differences are not readily apparent in the aggregated data (Figure 3) but are apparent in the time series (Figure 1)]. Importantly, in an ecohydrological context, these relationships may create a feedback that keeps small trees small. In addition, these relationships could create a feedback to fire seasonality, in which higher-density stands become more prone to fire earlier in the year because of the increased fire stress associated with a rapid depletion of soil water, as well as the effects of warmer temperatures (Westerling *et al.*, 2006).

Our results can be applied to test the ability of existing ecosystem models that include water balance to assess their ability to predict abiotic changes with stand density (Running and Coughlan, 1988; Aber and Federer, 1992) as well as to develop site-specific prediction of other physiological and ecosystem attributes (Dye, 2001; Soares and Almeida, 2001; Coops *et al.*, 2005). Our results also document an important ecohydrological link between stand effects, ecosystem attributes, and individual tree water availability. They highlight that ecosystem function and health as measured by soil water dynamics can differ substantially in low- versus high-density stands. In particular, the high-density stands exhibited more rapid and wide-ranging dynamics, as reflected in the greater increases in soil water content following snowmelt, and more rapid depletion of soil

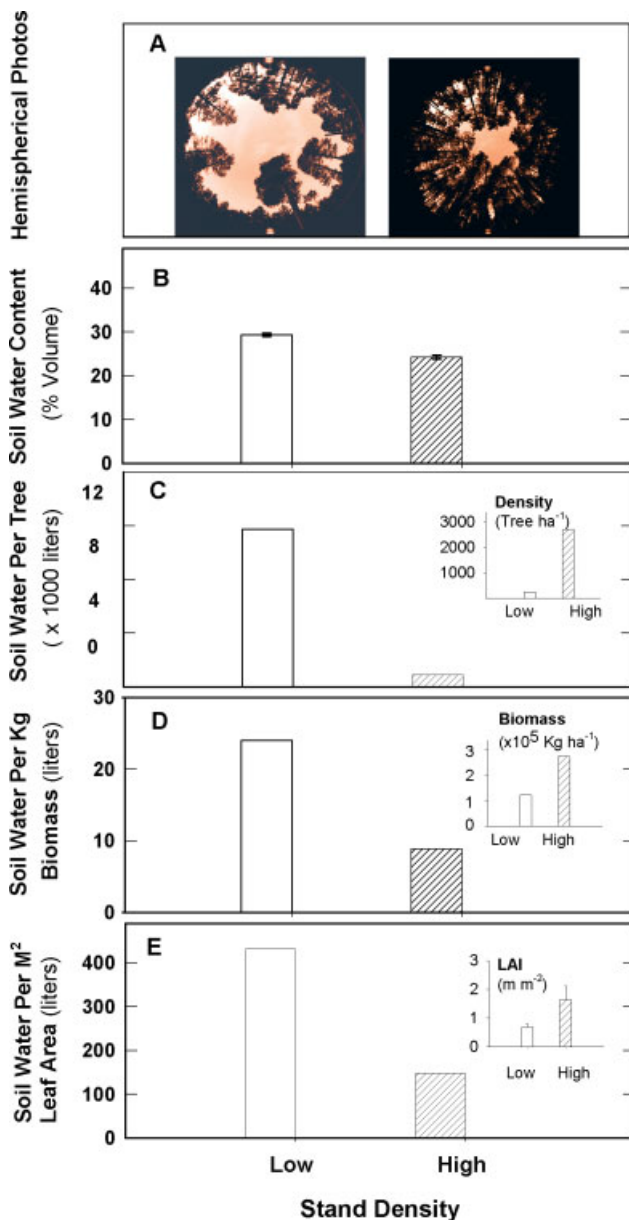


Figure 3. (a) Hemispherical photos associated with low- and high-density stands; (b) Time and depth integrated soil volumetric water content (%) for low- and high-density stands; (c) Mean soil water volume (l) per tree estimated using tree densities (inset) for low- and high-density stands; (d) Mean soil water volume (l) per unit biomass (kg) estimated using tree biomass estimates (inset) for low- and high-density stands; and (e) Mean soil water volume (l) per leaf area (m^2) estimated using LAI (Leaf Area Index) (inset).

water during the growing season. In a restoration context, our results suggest that reducing stand density by an order of magnitude can increase overall soil water content substantially; dramatically increase the amount of water available on a per tree, per biomass or per leaf area basis; and can dampen the dry-down cycle so that remaining trees spend less time in a water-stressed condition. However, reduction of stand density may have a limited effect in improving soil water content under severe and protracted drought conditions (Kolb *et al.*, 2007). In conclusion, our study is notable in documenting a soil water content difference between high- and low-density stands through the whole soil

profile and encompassing inter-annual variability from wet to dry years. Limitations of our study include the fact that only one study site was examined and that our sample size was minimal within the high-density stands. Nonetheless, the differences in soil water content between low- and high-density stands are substantial and highly significant, leading us to hypothesize that similar types of differences probably occur in other ponderosa pine forests. The stand differences were apparently driven in large part by higher transpiration in the high-density stands. A net result of the soil water content dynamics is that trees in high-density stands obtain less water on a per tree, per biomass or per leaf area basis. They spend more time in water-stressed conditions, and this is likely to create a feedback that limits tree growth in high-density stands. Our results have direct implications for forest management and restoration in that they provide ecohydrological insight into ecosystem functioning and can aid in improving restoration practices involving changing ponderosa pine stand density.

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