

RESEARCH ARTICLE

Transpirational Water Loss in Invaded and Restored Semiarid Riparian Forests

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Abstract

The invasive tree, *Tamarix* sp., was introduced to the United States in the 1800s to stabilize stream banks. The riparian ecosystem adjacent to the middle Rio Grande River in central New Mexico consists of mature cottonwood (*Populus fremontii*) gallery forests with a dense *Tamarix* understory. We hypothesized that *Populus* would compensate for reduced competition by increasing its water consumption in restored riparian plots following selective *Tamarix* removal, resulting in similar transpiration (T) among stands. The northern study site included a *Populus* stand invaded by *Tamarix* (INV_N) and a restored *Populus*-only stand (RES_N), as did a southern site (INV_S and RES_S) approximately 80 miles south. At each site, 20 × 20-m plots were established where up to 16 stems were monitored throughout the 2004 growing season using

thermal dissipation sapflow sensors. *Populus* sapflux rates were greater in restored stands, suggesting those trees compensated for understory removal by using more water. Sapflow was scaled to estimate stand-level T based on a quantitative assessment of sapwood basal area (A_{sw}) by species. Although exotic species represented 85 and 91% of the total stems in the invaded stands, it amounted to only 3% (INV_S) and 4% (INV_N) of the total A_{sw} , contributing proportionately less to T compared to *Populus*. Our results indicate that removing *Tamarix* from the *Populus* understory in this riparian forest had a minimal impact on stand water balance. Riparian restoration of the type discussed herein should focus primarily on enhancing riparian health rather than generating water.

Key words: invasive species, *Populus fremontii*, riparian management, *Tamarix*, water resources.

Introduction

Displacement of native riparian vegetation by exotic invaders has degraded ecosystems throughout the Southwestern U.S. (Friedman et al. 2005; Shafroth et al. 2005). Cottonwood gallery riparian forests or “bosque” in this region once supported a wide variety of riparian-adapted species including Fremont cottonwood (*Populus fremontii* S. Watson), Goodding’s willow (*Salix gooddingii* C.R. Ball), and Willow baccharis (*Baccharis salicina* Torr. & A. Gray). These native species are being replaced by non-native invasive species such as saltcedar (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. aphylla* (L.) Karst.), Russian olive (*Elaeagnus angustifolia* L.), and Giant reed (*Arundo donax* L.). *Populus* regeneration has declined in favor of invasive species as a result of anthropogenic disturbances such as flow alterations that reduce suitable regeneration sites (Zamora-Arroyo et al. 2001; Nagler et al. 2005). There is some evidence that *Tamarix* would have established anyway, but at much lower densities and a decreased range (Merritt & Poff 2010). Native plants are well

adapted to regenerate as floodwaters recede (Glenn & Nagler 2005), but they are not as tolerant as *Tamarix* to prolonged drought, salinity, and fire regimes (Vandersande et al. 2001; Glenn & Nagler 2005) now prevalent throughout many western rivers. In some areas, native stands have been completely replaced by exotic species, whereas in others, mature *Populus* trees remain the overstory dominant. When *Tamarix* invades riparian zones, fires become more frequent and intense (Ellis 2001). This can kill native plants typically not fire adapted. For those native plants that do survive, slow post-fire recovery might lead to replacement by non-native vegetation better adapted to reduced flooding and drought (Ellis 2001).

Restoration of the native gallery forests is highly valued by the public (Weber & Stewart 2009). The first step in restoration is the removal of the exotic understory layer; in this case, carried out in the middle Rio Grande to reduce fuel loads and minimize fire risks (Smith et al. 2009). Clearing or thinning unwanted vegetation, particularly invasive species, is also considered a means to reduce evapotranspiration (ET) in riparian stands. *Tamarix* has been removed for this purpose along many miles of western rivers in hopes to recover reduced flows attributed to dense exotic vegetation (Hart et al. 2005). Although such riparian restoration projects typically focus on water salvage, *Tamarix* removal projects should also improve aquatic resources and native species biodiversity (Bateman et al. 2008; Shafroth et al. 2008; Sogge et al. 2008).

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However, in many cases management efforts have not led to increased river flows, even when all riparian vegetation is removed from large sections of a river (Hart et al. 2005). It is unlikely that *Tamarix* can transpire as much water as mentioned in early reports (Owens & Moore 2007) and *Tamarix* has been found to use similar amounts of water as other phreatophytes on a leaf area basis (Sala et al. 1996). That would suggest that the most effective method to alter transpirational losses would be to adjust leaf area. The impact of reducing competition through thinning and the subsequent effect on transpiration has been recognized in forestry for a long time (Stogsdill et al. 1992; Breda et al. 1995). The typical initial response by the remaining trees is increased transpiration rates followed by a decrease to original or even lower rates as regeneration or coppicing occur (Lane & Mackay 2001). In a restoration effort in a Bur oak (*Quercus macrocarpa*) community, the invasive trees (*Ulmus* spp.) were removed, resulting in a 73% increase in the transpiration rates for the *Quercus* species (Asbjornsen et al. 2007). It is critical to understand whether restoration of mature native riparian forests by removing exotic understory, with all the ecological benefits of habitat, diversity, bank stability, and late succession characteristics, has the added benefit of reduced ET.

The objectives of this study are to (1) quantify and compare sap flux rates between *Populus* and *Tamarix* on the Rio Grande in New Mexico and determine their relative contribution to stand transpiration, (2) compare stand-level transpiration (T) in riparian stands with and without invasive *Tamarix* understory following *Tamarix* removal, and (3) evaluate sap flux changes in *Populus*, if any, in response to this restoration technique. We tested if *Populus* compensates to some extent for reduced competition by increasing its water consumption, resulting in similar T among invaded and restored stands.

Methods

Site Descriptions

Mature *Populus* stands within the Rio Grande floodplain were designated for invasive species removal in effort to reduce fuel loads and restore the native ecosystem (Smith et al. 2009). The north area is managed by the Middle Rio Grande Conservancy District and is located just south of Albuquerque, NM (35° 01' 42" N; 106° 40' 14" W), whereas the southern area is within the Bosque del Apache National Wildlife Refuge, located approximately 80 miles to the south (33° 52' 09" N; 106° 50' 35" W). Understory *Tamarix* and *Elaeagnus* were cut at ground level and mulched on site using a Seppi Mulcher (<http://www.seppi.com>). Two pairs of 20 × 20-m sites with and without invasive *Tamarix* understory were established to conduct this study, for a total of four sites. The northern pair of study sites included an invaded stand with a representative density of both native *Populus* overstory and non-native understory (INV_N) and a restored *Populus*-only stand (RES_N). Likewise, a second pair (INV_S and RES_S) was selected at the south site. All sites were located on flat terrain in the active floodplain with very shallow groundwater tables (~2 m

or less), although the southern pair of sites was located on the opposite side of an artificial levee. In addition to *Tamarix*, *Elaeagnus* was also common at the INV_N site, and so it was included in this study for comparative purposes.

Stand Characteristics

Stand characteristics were surveyed to determine the relative dominance of each species and for scaling tree-level transpiration measurements to stand-level estimates. In each site, we measured diameter at breast height (D), bark depth (d_{bark}), and sapwood depth (d_{sw}) by species for all woody plants greater than 10 mm diameter. Sapwood depth was obtained by extracting two 5-mm cores per tree. We verified the distinction between sapwood and heartwood using a dye infusion method where the bottom of the stems were placed in a dye solution for 24 hours and then observed for dye movement in the sapwood. Given that heartwood depth (d_{hw}) equals $D/2 - d_{\text{bark}} - d_{\text{sw}}$, and basal area (A) equals $\pi (D/2)^2$, sapwood areas (A_{sw}) were computed by:

$$A_{\text{sw}} = A - \pi (D/2 - d_{\text{bark}})^2 - \pi (d_{\text{hw}})^2$$

Survey results for A_{sw} were summarized by species and site, per unit ground area, and average per stem.

Sapflow Measurements

At each site, twenty 10-mm thermal dissipation sapflow sensors (Granier 1987) were installed and observed at 30-minute intervals. The final number of sensors by species and site varied because of mechanical failures, and totaled for *Populus* nine, ten, nine, and four at the INV_N, RES_N, INV_S, and RES_S sites, respectively. There were six *Tamarix* sensors at the INV_N site and seven at the INV_S site. Likewise, there were five *Elaeagnus* sensors at the INV_N site. The measurement period extended from late August through early November, 2004.

During periods when heated probes were inoperable, the average difference in temperature between the upper and lower probes was calculated and used to determine background temperature effects (Do & Rocheteau 2002a, 2002b). These values were subtracted from the corresponding site/species data before calculating sap flux. The maximum difference in temperature due to natural gradients did not exceed 1°C, despite the hot climate and relatively open stands, so this correction was relatively minor. Another important consideration for processing sapflow data in these species was the shallow sapwood depth. Because sapwood depths in *Tamarix* and *Elaeagnus* were often less than 10 mm, portions of some of the probes were in nonconducting wood. We followed the methods of Clearwater et al. (1999) to correct for shallow sapwood based on the proportion of probe in nonconducting wood.

In many forest systems, it can be assumed that zero flow occurs nightly in the predawn hours, when vapor pressure deficit (VPD) is near zero and stem capacitance has recovered from the previous day. Zero flow may not occur nightly

in many desert environments, however (Moore et al. 2008). Nights are often dry and warm; low soil moisture may prohibit complete recharging of stem capacitance by the predawn hours. Riparian vegetation, with roots accessing the water table, may consume significant amounts of water at night. Here we explicitly define nighttime as the 11-hour period between 2000 and 0630 hours. Our final calculations of transpiration allow for nonzero flow at night. We defined zero flow as the maximum difference in temperature within a 7-day period.

Sapflow data from each sensor were scaled to stand-level transpiration by multiplying the flux per unit sapwood by the sapwood area per unit ground area. Sapflow was scaled to estimate T based on a quantitative assessment of A_{sw} by species. We then normalized T by values for reference ET of a well watered grass (ET_o) estimated using the modified Penman equation (Sammis et al. 1985; Bawazir 2000) based on 2004 daily meteorological data from the Bosque del Apache (southern) site.

Results

Riparian forest stand densities were 2,925 and 8,525 trees/ha in the invaded sites, and 1,100 and 425 trees/ha in the restored sites. *Populus* densities in the invaded sites were similar to the restored sites (425 and 800 trees ha⁻¹). Despite the much higher number of invasive species individuals (85 and 91% in INV_N and INV_S, respectively), total sapwood basal area of *Populus* greatly exceeded the invasive species (97 and 96% in INV_N and INV_S, respectively). For example, the INV_N site had six times more non-native than native trees (Table 1), yet the total sapwood in *Populus* exceeded *Tamarix* and *Elaeagnus* combined by nearly 11-fold. Likewise, the INV_S site had about 10 times more non-native stems, but nearly three times as much native sapwood area (Table 1). This is because each individual *Populus* stem was so much larger than the other species—see A_{sw} per stem in Table 1. *Populus* sapwood area was similar among invaded and restored sites.

Mean sapflux rates of *Populus* in restored stands were greater than in invaded stands throughout much of the study period (Fig. 1). Mean sapflux for *Populus* in invaded stands peaked at 1,825 kg m⁻² day⁻¹ on September 15, whereas that

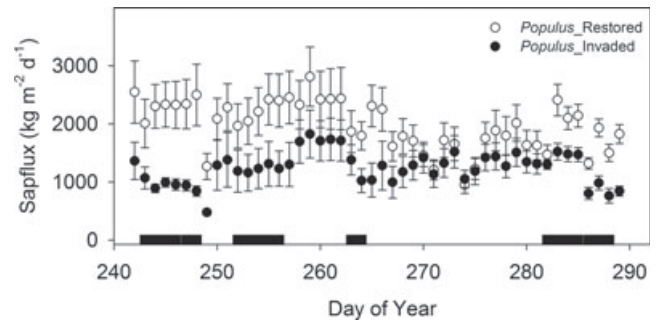


Figure 1. Daily average sapflux rates of *Populus* trees (kg m⁻² d⁻¹) throughout the study period and compared between invaded and restored stands. The black bar at the bottom represents days when the mean values differ among groups ($p < 0.05$).

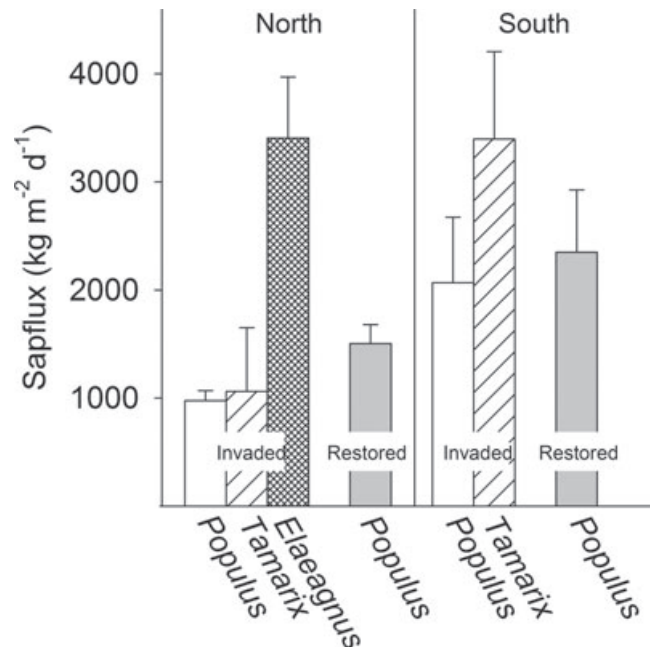


Figure 2. Average sapflux density by species and site. Left to right are *Populus*, *Tamarix*, and *Elaeagnus* at the INV_N site, *Populus* at the RES_N site, *Populus* and *Tamarix* at the INV_S site, and *Populus* at the RES_S site.

Table 1. Results from stand surveys for each 400 m² site, including the ratio of sapwood to ground area, count of stems having more than 10 mm diameter, and average sapwood area per stem in m².

Site ID	Species	$A_{sw} : A_{ground}$ (m ² : m ²)	Stems	A_{sw} per stem
INV _N	<i>Tamarix</i>	0.000169	70	0.00097
	<i>Populus</i>	0.002520	17	0.05929
	<i>Elaeagnus</i>	0.000052	30	0.00069
RES _N	<i>Tamarix</i>	0.000000	0	0.00000
	<i>Populus</i>	0.002262	44	0.02056
INV _S	<i>Tamarix</i>	0.000275	309	0.00036
	<i>Populus</i>	0.000764	32	0.00955
RES _S	<i>Tamarix</i>	0.000000	0	0.00000
	<i>Populus</i>	0.001277	17	0.03005

same rate was exceeded in restored stands on 31 of 48 days. As the growing season progressed, *Populus* sapflux became more similar for the invaded and restored sites (Fig. 1) as temperatures decreased and trees approached winter dormancy.

A comparison of mean sapflux rates among species and sites is given in Fig. 2. Invasive species never had lower flux rates than the native *Populus* at a given site; however, site-specific factors were as important as species-level differences. *Tamarix* at INV_S had higher flux rates than *Tamarix* at INV_N, associated with the lowest A_{sw} of *Populus* (Table 1) and high light conditions. *Elaeagnus*, though uncommon, had very high flux rates as well, even with a very dense overstory canopy. *Tamarix* growing at that same site had very low flux rates. *Populus* at INV_N had lower flux rates than *Populus* at the

other three sites. Fluxes in *Populus* and *Tamarix* were both greater in the south sites compared with the north sites.

Stand-scale T by species, expressed in millimeters of water consumed on a ground area basis, shows that *Populus* in restored stands used more water than *Populus* in invaded stands (Fig. 3a & 3b). *Populus* T in invaded sites, in turn, is greater than *Tamarix* or *Elaeagnus*, although *Tamarix* at the INV_S site was almost as great as *Populus* at that location. Both *Tamarix* and *Elaeagnus* were found to use a tiny fraction of water at the INV_N site (Fig. 3a). Reference evapotranspiration (ET₀) totaled 1,313 mm for the entire year of 2004, and peaked at 10 mm per day in the spring (data not shown). Given our study period spans the later part of the growing season, maximum observed T was only 5.5 mm, which occurred on

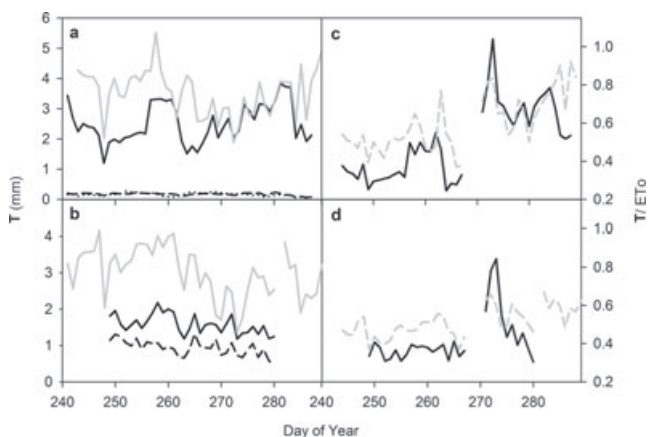


Figure 3. Stand-level transpiration (T) expressed in two ways: (1) on a ground area basis by species and site in the northern (a) and southern (b) area. Gray lines correspond to *Populus* in the restored sites; solid black lines are *Populus* in the invaded sites. Dashed and dotted lines correspond to *Tamarix* and *Elaeagnus*, respectively. (2) The ratio of T to reference evapotranspiration (ET₀) in the northern (c) and southern (d) area. Dashed gray lines correspond to the restored sites; solid black lines correspond to the invaded sites.

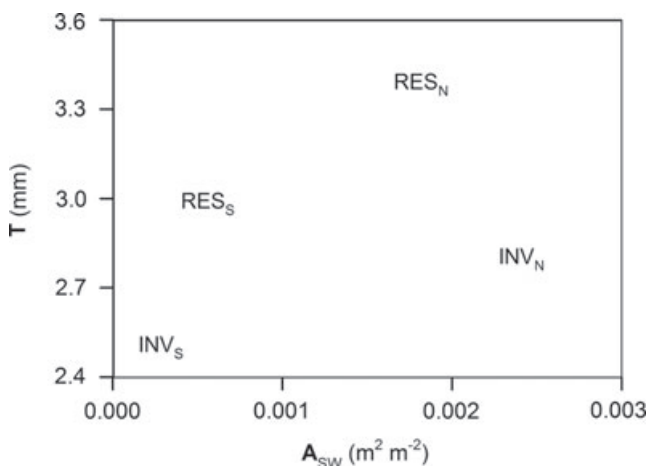


Figure 4. The relationship between stand sapwood area (A_{SW}) and total stand transpiration (T) averaged for all dates shared among sites.

September 14 at RES_N. Throughout much of the study period, T remained well below ET₀ (Fig. 3c & 3d).

Stand-level T varied strongly by A_{SW} (Fig. 4). The two invaded sites, INV_N and INV_S, had the lowest average T . Much of the variation in average T is explained by stand A_{SW} , except for the INV_N site. Despite having the highest A_{SW} , INV_N had relatively low average T because of much lower *Populus* sap flux rates than the other stands (Fig. 2). These trees were much larger and older, which may explain the differences observed.

Discussion

Evapotranspirational water loss at the landscape scale is driven by the balance of energy on the site (Cleverly et al. 2006; Heilman et al. 2009). In arid and semiarid ecosystems, such as the Middle Rio Grande region, over 90% of the total water loss is from the riparian corridor (Cleverly et al. 2006), so there is great interest in managing water loss from riparian zones. At the stand scale energy capture is a function of meteorological conditions, precipitation, and leaf area. Although we did not measure leaf area directly, A_{SW} is a useful surrogate that describes the potential for a site to use water. We found that thinning exotic understory did not result in reduced transpiration for two reasons.

First, understory transpiration was minimal prior to restoration because the A_{SW} of these species was small in comparison with the overstory. The overstory shades the understory, capturing most of the energy and further reducing understory water consumption. Shading apparently reduced sap flux rates in the understory, more so where *Populus* overstory was very dense (INV_N). Due to a greater capacity for light interception, box elder (*Acer negundo* L. var. *interius* [Britt.] Sarg.) was able to out-compete and exclude *Tamarix* from a riparian site (DeWine & Cooper 2010). In our case, *Populus* canopies were dense enough to limit transpirational water loss from *Tamarix* but not dense enough to prevent *Tamarix* invasion.

Second, total leaf area reduction is unlikely to result in a proportional decrease in transpiration at the stand level because of compensatory response. Trees commonly compensate for reduced competition for water, light, and nutrients by increasing growth and water consumption. This is well known in forestry, but we present new evidence of thinning responses in phreatophytes. In our case, *Populus* must have been water-limited, and compensated by increasing water consumption; *Populus* sap flux was significantly greater in restored stands than invaded stands throughout much of the study period. Given that understory *Tamarix* did not compete with *Populus* for light, it follows that interspecific competition for water played a significant role in our observations. Support for this interpretation is found in a conifer thinning experiment where light was manipulated (Morikawa et al. 1986); transpiration per tree increased following thinning even at a constant light level. Another possible explanation for increased *Populus* transpiration is reduced competition for nutrients. Brix and Mitchell (1983) found that thinning and fertilization treatments

in conifers together or individually could increase sapwood area over the long term (5–9 years) and increase the leaf area to sapwood area ratio in the short term. It is possible that both water and nutrients were limiting factors at our study sites. Even old-growth trees can respond positively to thinning (Latham & Tappeiner 2002), but their response might be weaker. The large size, and assumed older age, of the *Populus* trees at INV_N may explain the lower *T* at that site, despite having a slightly higher *A*_{sw} than RES_N.

The idea of water salvage from thinning or removing exotic riparian vegetation is popular in other locations throughout the world. The “Working for Water” program in South Africa, for example, employs thousands of locals to remove invasive species (<http://www.dwaf.gov.za/wfw/>), including in riparian zones (Dye & Jarman 2004) to restore biological diversity and enhance water yield (Le Maitre et al. 2007). In Australia where rising water tables threaten water quality, thinning forests was favored over clearcut methods because it marginally increased stream flow, especially if vegetation reduction was slight (Ruprecht et al. 1991). Similarly, precommercial thinning in Canadian swamps marginally increased water tables compared with clearcut methods, which prevented the need for wetland drainage to combat rising groundwater tables (Jutras et al. 2006).

In the Western U.S., public interests in thinning exotic vegetation as a means to restore riparian ecosystems have been expressed primarily because of public perception that reducing stand densities saves water and reduces fire hazards (Weber & Stewart 2009). Some supporting scientific evidence exists (Shafroth et al. 2005), yet there is conflicting evidence whether or not *Tamarix* removal saves water (Stromberg et al. 2009). Martinet et al. (2009) estimated only a 6–18% reduction in diurnal groundwater amplitude following thinning of *Tamarix* understory even though the understory represented a large proportion of site leaf area index. They concluded that *Populus* overstory transpiration dominated the site water balance. Similarly, Cleverly et al. (2006) found only a 9% reduction in ET following *Tamarix* understory removal.

Additional goals for thinning riparian exotic vegetation, including reduced fire hazard, improved habitat, and enhanced native plant biodiversity, are equally uncertain (Stromberg et al. 2009). For example, it is not known whether thinning *Tamarix* will benefit avian communities (Van Riper et al. 2008), and may even reduce bird diversity (Sogge et al. 2008). Hummingbirds were forced to nest higher in the canopy of thinned stands, putting them at higher risk for predation (Smith et al. 2009). A variety of lizards responded to thinning treatments with mixed results; some species benefited from the open park-like setting (Bateman et al. 2008). Although butterfly diversity is reduced in *Tamarix*-dominated habitats, *Tamarix* removal does not recover butterfly diversity (Nelson & Wydoski 2008). Furthermore, *Tamarix* removal without revegetation (Harms & Hiebert 2006) or restoring historic flow regimes (Nagler et al. 2005) rarely leads to plant diversity recovery. Our results indicate that thinning may not be a viable way to extract water savings, although it still may provide

fire protection. To meet comprehensive restoration goals, managers must carefully plan removal strategies, implement extra measures such as planting native species in many cases, and employ post-restoration adaptive management (Shafroth et al. 2008).

Implications for Practice

- Established techniques exist to quantify transpiration water loss from restored and invaded riparian forests. Inferred differences from stand surveys of density, basal area, or canopy cover may not accurately reflect changes in transpiration.
- Consider that restoration practices that involve thinning *Tamarix* under mature native trees might not result in water savings because of compensatory responses in remaining vegetation.
- Key site factors to evaluate include the relative dominance of *Tamarix* before thinning, whether *Tamarix* is part of the overstory, and post-thinning response by native vegetation.
- Setting additional measures for restoration success besides water savings, including reducing fire hazard, improving habitat, or enhancing native plant biodiversity helps ensure net benefits.

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