Ecohydrological consequences of non-native riparian vegetation in the southwestern United States: A review from an ecophysiological perspective

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[1] Protecting water resources for expanding human enterprise while conserving valued natural habitat is among the greatest challenges of the 21st century. Global change processes such as climate change and intensive land use pose significant threats to water resources, particularly in arid regions where potential evapotranspiration far exceeds annual rainfall. Potentially compounding these shortages is the progressive expansion of non-native plant species in riparian areas along streams, canals and rivers in geographically arid regions. This paper sets out to identify when and where non-native riparian plant species are likely to have the highest potential impact on hydrologic fluxes of arid and semiarid river systems. We develop an ecophysiological framework that focuses on two main criteria: (1) examination of the physiological traits that promote non-native species establishment and persistence across environmental gradients, and (2) assessment of where and to what extent hydrologic fluxes are potentially altered by the establishment of introduced species at varying scales from individual plants, to small river reaches, to entire river basins. We highlight three non-native plant species that currently dominate southwestern United States riparian forests. These include tamarisk (*Tamarix* spp.), Russian olive (*Eleagnus angustifolia*), and Russian knapweed (*Acroptilon repens*). As with other recent reviews, we suspect that in many cases the removal of these, and other non-native species will have little or no impact on either streamflow volume or groundwater levels. However, we identify potential exceptions where the expansion of non-native plant species could have significant impact on ecohydrologic processes associated with southwestern United States river systems. Future research needs are outlined that will ultimately assist land managers and policy makers with restoration and conservation priorities to preserve water resources and valued riparian habitat given limited economic resources.

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1. Introduction

[2] Surface flows along major river corridors serve as the lifeblood of human enterprise and biodiversity in arid regions of the globe. However, intensive urban expansion and agriculture have resulted in a significant over-appropriation of many river systems to the extent that it has become increasingly difficult for water managers to maintain water deliveries while sustaining valued riparian habitats [*Jackson et al.*, 2001]. Compounding these water shortages are projections that climate change over the next century will bring increases in potential evapotranspiration (PET; see Table 1 for list of abbreviations) and an overall reduction in stream discharge [*Seager et al.*, 2007; *McCabe and Wolock*, 2008]. These projections suggest that many regions will face periodic and at times critical water shortages over the 21st century.

[3] Predicted water shortages have resulted in considerable efforts to improve the accounting of hydrologic fluxes within watersheds and river basins. However given that a major component of the water cycle, evapotranspiration (ET), is difficult to quantify at large spatial scales, efforts to define water budgets of complex watersheds can present significant challenges. Complicating water accounting efforts are dramatic changes in riparian vegetation cover along many of these river systems, resulting from the expansion of non-native vegetation [*Le Maitre et al.*, 2002; *Friedman et al.*, 2005]. Invasion of non-native plants may alter water budgets of watersheds and river basins if the invasion results in either larger evapotranspiration fluxes per unit ground area (or river/stream discharge) or if the invasion results in a larger ground area covered by plants that are removing water directly from the stream aquifer.

[4] In this review, we address the simple question: does the conversion of native riparian vegetation to non-native vegetation have a significant impact on ecohydrological processes (i.e., ET fluxes, nutrient cycles, river/stream

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Table 1. List of Abbreviations With Common Units

Abbreviation	Definition	Units
A_l	Leaf area	m^2
A_r	Absorbing root area	m^2
ET	Actual evapotranspiration	mmol d^{-1}
PET	Potential evapotranspiration	mmol d^{-1}
g_s	Leaf stomatal conductance	mol m^{-2} $s^{-1}$$kPa^{-1}$
K	Hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
K_a	Axial root hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
K_l	Lateral root hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
K_{rh}	Rhizosphere hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
K_s	Shoot hydraulic conductivity	mol m^{-1} s^{-1} MPa^{-1}
R	resistivity	MPa s mol^{-1} m^{-1}
vpd	Leaf-to-air vapor pressure deficit	kPa
Ψ	Water potential	MPa
Ψ_l	Leaf water potential	MPa
Ψ_{rh}	Rhizosphere water potential	MPa

discharge) associated with river systems in the arid southwestern United States? If so, can we identify "hot spots" where the hydrologic system is most sensitive to alterations in riparian plant community structure? A number of recent reports have suggested that the potential to increase water savings, defined as either an increase in river discharge or higher groundwater levels, by the removal of non-native riparian vegetation along rivers and streams is at best, limited [*Glenn and Nagler*, 2005; *Shafroth et al.*, 2005, 2010; *Dennison et al.*, 2009; *Nagler et al.*, 2009; *Hultine et al.*, 2010a]. These suggestions are based primarily from research conducted on a dominant invasive riparian tree/shrub species, tamarisk (*Tamarix* spp.) that show that this species typically maintains similar water use rates per unit ground area as native riparian vegetation [*Nagler et al.*, 2009; *Shafroth et al.*, 2010]. However, there are still significant knowledge gaps to the extent that the impact of non-native vegetation on the ecohydrology of many river reaches, watersheds and basins remains unclear. In fact, with the exception of tamarisk, there is currently almost no reported data on ET fluxes from non-native riparian plant species in the southwestern United States (Table 2). The overarching goal of this review is to highlight key knowledge gaps and identify species, river/stream reach attributes (i.e., surface flow volume, floodplain area) and scales that future research should focus on to assess ecohydrological ramifications of non-native species expansion and removal.

[5] Our review will focus primarily on three non-native species that now dominate southwestern United States riparian forests including: tamarisk (*Tamarix* spp.), Russian olive (*Eleagnus angustifolia*), and Russian knapweed (*Acroptilon repens*), all of which are expected to continue spreading unless intensive control practices are implemented [*Duncan et al.*, 2004; *Morrisette et al.*, 2006]. We will also discuss key ecophysiological attributes that underpin water use patterns and plant water relations as a whole. Specifically, we will first review the processes that control the overall transport of water from the soil to the plant and the atmosphere (the Soil-Plant-Atmosphere Continuum, SPAC) and second, compare and contrast these processes

Table 2. Recently Published Evapotranspiration Data for Introduced and Native Riparian Plant Species That Are Currently Widespread in the Southwestern United States[a]

Species	Lifeform	Method	ET mm d^{-1} (m yr^{-1})	Citation
		Introduced Species		
Tamarix spp.	Tree/Shrub	EC	(0.6–1.1)	*Weeks et al.* [1987]
	Tree/Shrub	SF	5.9–16.3	*Sala et al.* [1996]
	Tree/Shrub	BR	0.0–12.5 (0.7–1.4)	*Devitt et al.* [1998]
	Tree/Shrub	EC	1.0–10.0 (1.1–1.2)	*Cleverly et al.* [2002]
	Tree/Shrub	EC	1.0–10.0 (1.1–1.2)	*Dahm et al.* [2002]
	Tree/Shrub	RS	(1.1)	*Allen et al.* [2005]
	Tree/Shrub	EC	6.0–9.0	*Cleverly et al.* [2006]
	Tree/Shrub	RS	4.2–5.0 (1.1–1.4)	*Nagler et al.* [2008]
	Tree/Shrub	RS	5.7–8.5	*Nagler et al.* [2009]
	Tree/Shrub	SF	3.7–9.5	*Nagler et al.* [2009]
	Tree/Shrub	RS	2.7 (0.6)	*Dennison et al.* [2009]
	Tree/Shrub	SF	(0.3)	*Hultine et al.* [2010]
Eleagnus angustifolia	Tree	RS	(1.4)	*Allen et al.* [2005]
Acroptilon repens	Herbaceous perennial	No data	No data	
Arundo donax	Perennial grass/Subshrub	No data	No data	
Centaurea spp.	Herbaceous perennial	No data	No data	
Ulmus pumila	Tree	No data	No data	
Lepidium latiifolium	Herbaceous perennial	No data	No data	
		Native Species		
Populus spp.	Tree	SF	3.1–5.7	*Schaeffer et al.* [2000]
		SF	4.9–9.3	*Pataki et al.* [2005]
		EC	8.0–9.0	*Cleverly et al.* [2006]
		SF	(0.5–1.0)	*Gazal et al.* [2006]
		SF	6.0–12.0	*Nagler et al.* [2007]
Prosopis spp.	Tree	BR	1.6–2.4 (0.4)	*Scott et al.* [2000]
		EC	(0.6–0.7)	*Scott et al.* [2004]
		EC	5.0–6.0	*Scott et al.* [2006]
		SF	8.3	*Nagler et al.* [2009]
Acer negundo	Tree	SF	1.1–7.2	*Hultine et al.* [2007]

[a]BR, Bowen ratio; EC, eddy covariance; RS, remote sensing; SF, sap flux.

between non-native and dominant native plant species. Third, we will review the complex interactions between plant water use and multiple global change processes, including climate, stream management and biological control of non-native plant species. Finally, we will set the stage for future research that we believe will assist land managers and policy makers with setting priorities for restoration and conservation where economic resources may be limited.

2. Review of the Soil-Plant-Atmosphere Continuum (SPAC)

[6] The physical process of water transport through the *SPAC* is driven by pressure (water potential, Ψ) gradients from the soil to the leaves [*Zimmerman*, 1983]. As stomata open, Ψ at the leaf surface (Ψ_l) falls below that of the rhizosphere (Ψ_{rh}). This causes water to flow radially into the fine roots, then axially through larger roots and shoots until finally reaching the leaf surfaces where energy from the sun evaporates the liquid water into the atmosphere (i.e., transpiration). Unfortunately for plants, there is a physical limit of Ψ for which water will flow through the *SPAC*, requiring plants to actively regulate water potential gradients [*Tiree and Sperry*, 1988; *Sperry et al.*, 2002]. During transpiration, stomata on leaf surfaces control the flowrate and the subsequent variation in plant water potential [*Jones and Sutherland*, 1991; *Sperry et al.*, 2002]. Given that stomata act as pressure regulators, factors such as changes in hydraulic conductivity (K) along the soil-leaf pathway, soil moisture, and evaporative demand will inevitably drive changes in stomatal conductance (g_s) and thus transpiration and CO_2 diffusion into the leaf [*Saliendra et al.*, 1995; *Comstock and Mancuccini*, 1998; *Hubbard et al.*, 2001; *Sperry et al.*, 2002]. Therefore, the analysis of soil plant hydraulics can be used to predict patterns of plant water use with respect to the soil and atmosphere, as well as potential differences between species and locations.

[7] Figure 1 illustrates the major transport locations (nodes) along the SPAC of a typical plant. The separate nodes include the rhizosphere, lateral roots, axial roots, shoots (i.e., stems and branches), and leaves. Each node carries a resistivity (R) [the inverse of conductivity (K, defined as the conductance multiplied by the path length)] that varies under a given set of conditions. In theory, plants tend to build a hydraulic transport system so that R of all the nodes remains relatively equal. For example, large water potential gradients within the rhizosphere can at times cause a steep drop in rhizosphere conductivity (K_{rh}) relative to other nodes in the SPAC. Plants may therefore reduce losses in K_{rh} by constructing both higher-absorbing root areas (A_r) and higher root-to-leaf area ratios (A_r:A_l). The resulting rate of flow per unit soil volume (rhizosphere flux density) then decreases thereby reducing water potential gradients in the rhizosphere [*Sperry et al.*, 1998, 2002; *Hacke et al.*, 2000; *Hultine et al.*, 2006]. Physiological changes in fine root activity and subsequent changes in K_l could also offset decreases in K_{rh}.

[8] The hydraulic conductivity of the axial roots (K_a) and shoots (K_s) may also vary, depending on the structure and function of the water transport conduits (xylem). Under conditions where soil water is always highly available (such as in many riparian areas), and/or evaporative demand is low to moderate, plants tend to build xylem conduits with large diameters that can transport water at high rates to the canopy. These conditions allow plants to construct large canopies that produce high transpiration rates per unit ground area. However, larger diameter and more efficient conduits are also more susceptible to drought-induced xylem cavitation, the sudden change from liquid to vapor phase within normally water-filled xylem conduits [*Zimmerman*, 1983; *Tyree and Sperry*, 1989; *Wheeler et al.*, 2005; *Hacke et al.*, 2006]. In other words, there is a physiological tradeoff

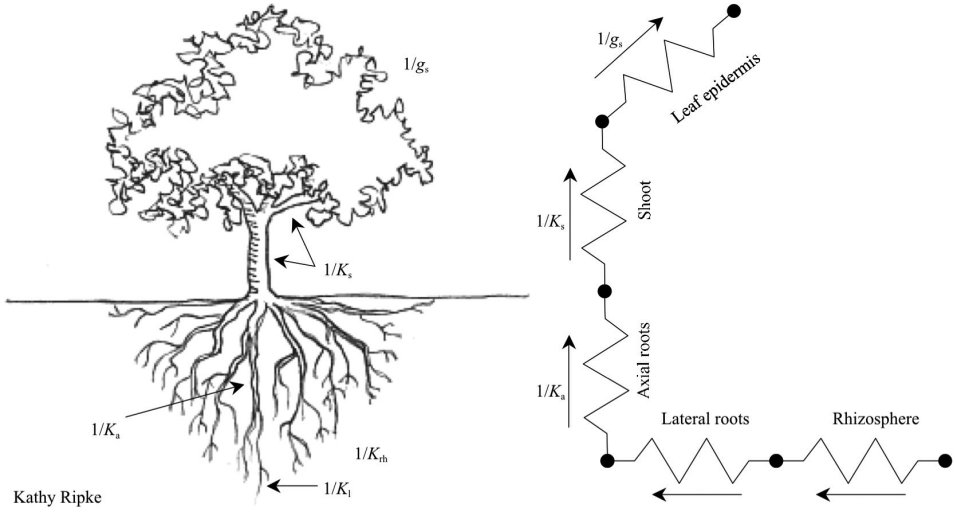

Figure 1. The water transport pathway through the soil plant atmosphere continuum shown as a series of resistivities (R, the inverse of conductivity, K). The individual resisters (i.e., nodes) include the rhizosphere ($1/K_{rh}$), the lateral roots (fine roots and root hairs, $1/K_l$), where water moves in the radial direction from the rhizosphere to the root xylem, the axial roots ($1/K_a$), the shoots ($1/K_s$), and the leaf epidermis ($1/g_s$) where liquid water evaporates from the leaf surface to the atmosphere.

between xylem transport efficiency and xylem cavitation vulnerability. If xylem cavitation occurs throughout the plant, the canopy becomes decoupled from soil water, resulting in significant hydraulic failure, carbon starvation, canopy dieback and in many cases plant mortality [*Sperry et al.*, 1993; *McDowell et al.*, 2008]. Therefore, the physical limitation on water transport generally corresponds with species distribution across water availability gradients [*Pockman and Sperry*, 2000]. In this review, we apply concepts of soil and plant hydraulic limits as the framework for understanding vegetation change, and its consequence on evapotranspiration fluxes in riparian ecosystems.

3. Distribution of Tamarisk and Its Impacts on the Water Cycle

[9] Tamarisk (*Tamarix* spp., also known as saltcedar), native to Eurasia and Africa, was introduced to the western United States more than a century ago [*Robinson*, 1965; *Brock*, 1994]. It has since spread throughout the central and southwest United States, becoming the third most dominant woody plant on the banks of rivers, streams, springs, and ponds in these regions [*Friedman et al.*, 2005]. Tamarisk has previously been cited for having unusually high rates of water use compared to other riparian species. More recent evidence suggests that tamarisk water use per unit ground area is, in fact comparable with that of native riparian vegetation [*Nagler et al.*, 2005; *Owens and Moore*, 2007; *Shafroth et al.*, 2010], and ranges from about 0.3 to 1.4 m yr^{-1} (Table 2). However, tamarisk along many river reaches can establish much larger areas of riparian floodplains than many native riparian tree species. We therefore ask whether 1 m yr^{-1} of water use by native species has the same impact on the water cycle as 1 m yr^{-1} of water use by tamarisk.

[10] In many locations the answer to the above question would appear to be yes. For example, annual water use by tamarisk along the lower Colorado River only equals about 1% of the annual discharge from the river [*Nagler et al.*, 2008, 2009]. Thus, evapotranspiration from adjacent vegetation, regardless of species composition, is unlikely to have a measurable influence on the water budget along this stretch of river (although a savings of 1% could be critical for maintaining downstream water deliveries during drought). Conversely, along many low-order streams, the total vegetation cover is sometimes quite large relative to stream discharge. For example, Annual rates of riparian ET (reported by the Arizona Department of Water Resources and published in the work of *Scott et al.* [2000]) along a lower reach of the San Pedro River, a subwatershed of the lower Colorado River, was 43% of the mean annual river discharge (U.S. Geological Survey (USGS) streamflow data, available at http://waterdata.usgs.gov/az/nwis/uv/?site_no=09471550&PARAmeter_cd=00065,00060). These data clearly demonstrate a larger impact of riparian vegetation on the water budget of this third-order stream compared to adjacent vegetation along the lower Colorado River.

[11] These patterns are further illustrated in the two recent Google Earth images in Figure 2 showing two river confluences in central Utah. The image on the left shows the confluence between the Price River and Green River north of Green River, Utah. The image on the right shows the confluence between the San Rafael River and Green River south of Green River, Utah. Both images reveal a relatively broad riparian floodplain associated with the Price and San Rafael Rivers, both third-order streams with riparian systems comprised almost exclusively of tamarisk (personal observation). On the other hand, vegetation cover along the Green River is much more constrained to the immediate river channel. Mean annual discharge of the Green River at Green River, Utah is 157 m^3 s^{-1}, while mean annual discharge of the Price and San Rafael Rivers is 3.2, and 3.3 m^3 s^{-1}, respectively (USGS streamflow data, available at http://waterdata.usgs.gov/nwis/rt), or about 2% of the mean annual flow of the Green River. The total area covered by riparian vegetation, relative to mean annual discharge along the lower Price and San Rafael Rivers, is more than 2 orders of magnitude greater than the Green River (Table 3). Consequently, riparian ET along these two river systems can also be predicted to be about 2 orders of magnitude higher relative to discharge.

[12] Although these exercises do not provide enough information to assess the impacts of riparian vegetation on basin-wide ET and river discharge, it does illustrate the critical need for riparian ET estimates for an entire stream network. If the discharge of a sufficient number of low-order streams (such as the Price, San Rafael, and San Pedro Rivers) is impacted by the expansion of riparian vegetation cover, then it is possible, or even likely that these changes

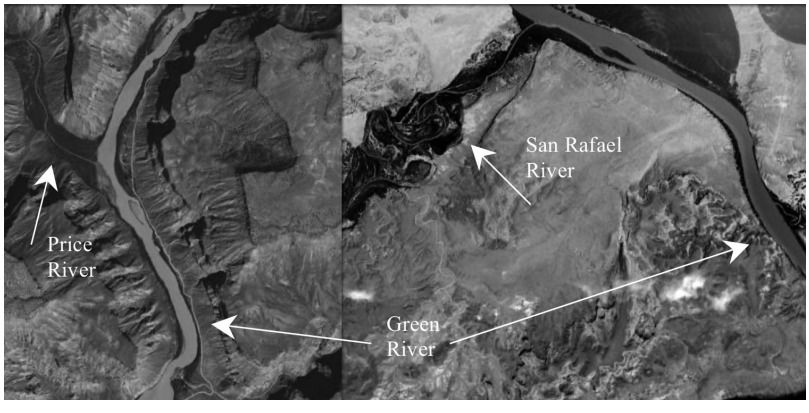

Figure 2. Google Earth images showing (left) the confluence between the Price and Green Rivers and (right) the confluence between the San Rafael and Green Rivers in central Utah.

Table 3. Relationship Between Area Covered by Riparian Vegetation and Mean Annual River Discharge of Four River Reaches in Central Utah[a]

River	Reach Description	Reach Distance (km)	Discharge ($m^3 s^{-1}$)	Riparian Area (h)	Area/Discharge ($h\ m^{-3} s^{-1}$)
Green	The Price River to USGS gauge in Green River, UT	29.9	157	461	0.10
Green	USGS Gauge in Green River, UT to the San Rafael River	42.6	157	336	0.05
Price	USGS Gauge in Woodside, UT to the Green River	43.0	3.19	502	11.7
San Rafael	USGS Gauge neat Utah State Highway 24 to the Green River	61.3	3.27	988	16.1

[a]The Price and San Rafael Rivers are third order streams that flow directly into the larger Green River at confluence points about 70 river km from one another. Relationships between river discharge and riparian area were determined from USGS streamflow data (available at http://waterdata.usgs.gov/nwis/rt), and spatial analysis of recent Google Earth imagery.

in vegetation are having significant impacts on downstream water resources, even if measurements of ET along the Green or Colorado Rivers do not reflect these impacts.

[13] As mentioned above, tamarisk can establish much larger areas of riparian floodplains than many native riparian tree species. The upper floodplain terraces of the upper Colorado River Basin were historically dominated by greasewood (*Sarcobatus vermiculatis*) and rabbitbrush (*Chrysothamnus nauseosus*), species that obtain much lower leaf areas per unit ground area than tamarisk [*Webb et al.*, 2007]. Tamarisk has now replaced greasewood and rabbitbrush along many of these upper terraces such as those along the Price and San Rafael Rivers, effectively increasing the area covered by riparian vegetation. This shift in vegetation cover along low-order streams in the upper Colorado River Basin may have a high accumulative impact on stream discharge of the entire Colorado River Basin. This is because reported ET rates by greasewood/rabbitbrush plant communities only reach 0.14 m yr^{-1} even when depth to groundwater is less than 1 m [*Groeneveld*, 2008]. As reported earlier, tamarisk ET rates range from 0.3 to 1.4 m yr^{-1}. On the flip side, many riparian floodplains in the warm deserts of North America are being encroached, or have been encroached by native mesquite (*Prosopis* spp.). As with tamarisk, mesquite occupies a wider range of microhabitats than either cottonwood or willow, including upper terraces of riparian floodplains. The replacement of mesquite with tamarisk would likely not add to the total riparian vegetation cover or leaf area, and therefore would result in little or no change in riparian ET in warm desert regions.

4. Ecophysiology of Tamarisk With Respect to Ecohydrology

[14] Tamarisk has several physiological advantages over cottonwood, willow and other riparian phreatophytes for tolerating unfavorable soil water conditions including greater rooting depths, and extremely fast root growth compared to cottonwood and willow [*Shafroth et al.*, 2000; *Horton and Clark*, 2001]. Both traits favor access to groundwater where the water table may be too deep and/or too variable to support most native phreatophytic plants species [*Horton and Campbell*, 1974; *Shafroth et al.*, 2000; *Horton et al.*, 2003; *Lite and Stromberg*, 2005].

[15] Another key advantage that tamarisk has over native species is its somewhat unique xylem structure and function that allows it to maintain a higher K_s (and possibly K_a) relative to many native riparian species. Data from southern Arizona show that tamarisk shoots are considerably more resistant to xylem cavitation than co-occurring Fremont cottonwood and Gooding's willow [*Pockman and Sperry*, 2000] (Figure 3). In fact, xylem pressures of −2 megapascals (MPa) would cause complete cavitation in both cottonwood and willow, while tamarisk shoots can retain conductivity at water potentials of −4 MPa or below [*Pockman and Sperry*, 2000] (Figure 3). Not surprisingly, cottonwood and willow in northern Arizona experienced significant canopy dieback when midday water potentials dropped below −2 MPa, while co-occurring tamarisk did not [*Horton et al.*, 2001]. Data from several other studies also show evidence of greater drought tolerance in tamarisk compared to native riparian tree species [*Sala et al.*, 1996; *Smith et al.*, 1998; *Horton et al.*, 2003]. Differences in xylem cavitation resistance and overall greater drought tolerance allows tamarisk to persist in habitats that are not suitable for most other obligate riparian species, in many cases, resulting in riparian tree canopy cover along river reaches that historically supported little or no riparian vegetation.

[16] As discussed earlier, cavitation resistance typically comes with the tradeoff of reduced xylem transport efficiency. However, despite its greater cavitation resistance, mean specific conductivity of tamarisk shoots (defined as the maximum stem hydraulic conductivity divided by the stem cross-sectional area), measured in southern Arizona was 23 and 46% higher than those of Fremont cottonwood and Gooding's willow shoots, respectively [*Pockman and Sperry*, 2000]. Likewise, the mean conduit diameters of

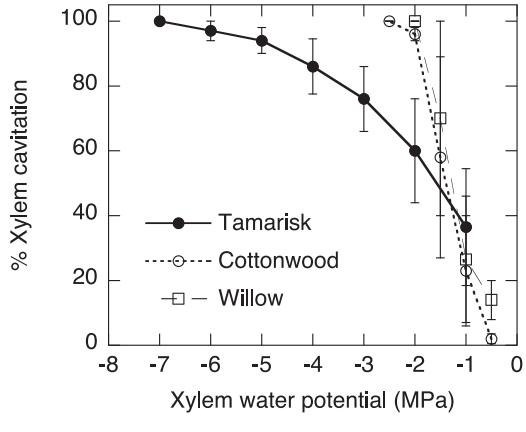

Figure 3. Relationship between xylem water potential and percent xylem cavitation in co-occurring tamarisk, cottonwood and willow trees in southern Arizona. Error bars represent the standard error of the means. The figure was redrawn from data reported by *Pockman and Sperry* [2000].

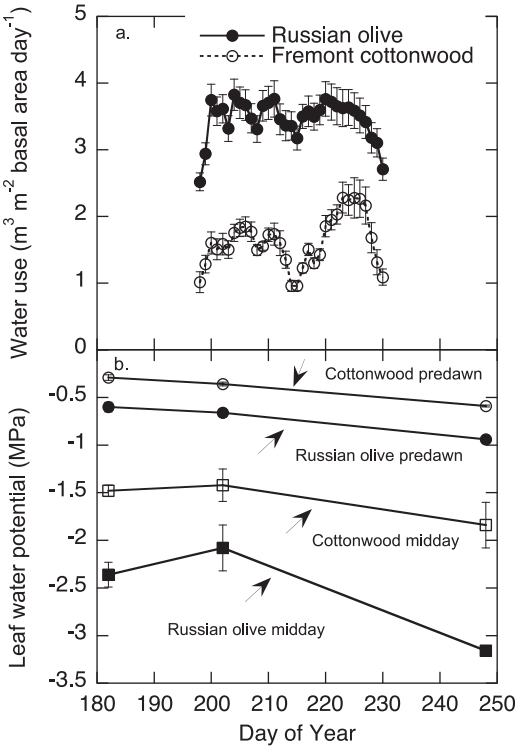

Figure 4. Comparison of plant water relations between co-occurring Russian olive (*Eleagnus angustifolia*) and Fremont cottonwood (*Populus fremontii*) trees during the 2004 growing season in northern Utah. (a) Whole tree water use per unit basal area of Russian olive and Fremont cottonwood trees measured from Day 198 (July 17) to Day 230 (August 18), 2005 (S. Bush, unpublished data, 2005). Data were collected from thermal dissipation sap flow sensors inserted into the stem of 10 trees per species. (b) Predawn and midday xylem water potentials measured on the petioles of Russian olive and Fremont cottonwood trees ($n = 5$ trees per species). Predawn measurements were taken between 0300 and 0400 h and midday measurements were taken between 1200 and 1400 h with a Scholander type pressure chamber. Error bars represent the standard error of the means.

tamarisk shoots were about 30% larger than either cottonwood or willow [*Pockman and Sperry*, 2000]. Consequently, tamarisk shoots likely operate at a higher K_s than either cottonwood or willow regardless of shoot water potential down to about −6 MPa (Figure 4). These observations may have important implications several ecohydrological processes. Tamarisk can maintain a consistently high leaf area to unit shoot area and/or high g_s under a wide range of soil or groundwater conditions. This allows tamarisk to maintain high transpiration rates, high nutrient uptake rates, and maintain a favorable carbon balance across a wide range of environmental gradients. This is not to say that water use by tamarisk does not vary in response to water potential gradients, as several studies have shown that it does [*Sala et al.*, 1996; *Cleverly et al.*, 1997; *Devitt et al.*, 1997a, 1997b; *Nagler et al.*, 2009]. Nevertheless, the dynamic structure and function of tamarisk xylem is an apparent mechanism underpinning its distribution across broad environmental gradients relative to other riparian tree species.

[17] What is less understood with respect to dominant riparian tree species are the belowground components of the SPAC. To our knowledge, there are no data for parameters A_r, A_r:A_l, or root xylem structure and function for either tamarisk or native species. We are therefore left to speculate how these parameters vary among species and over environmental gradients. An important observation is that tamarisk often takes up a higher proportion of water from shallow unsaturated soils than either cottonwood or willow [*Busch et al.*, 1992; *Smith et al.*, 1998]. Its status as a facultative phreatophyte rather than an obligate, such as willow, or semiobligate phreatophyte such as cottonwood [*Snyder and Williams*, 2000] suggests that tamarisk is able to maintain a higher combined K_{rh}, K_l, and K_a in unsaturated soils. If so, in areas where access to groundwater is highly variable, tamarisk would be able to maintain high rates of water uptake and subsequently avoid canopy dieback and mortality.

5. Cascading Impacts of Biological Control on Tamarisk Water Use

[18] Recent releases of the saltcedar leaf beetle (*Diorhabda carinulata* Brullé), a biological control agent from Eurasia, has resulted in the widespread herbivory of tamarisk throughout the western United States [*Dudley*, 2005; *Hultine et al.*, 2010a]. The beetle feeds exclusively on tamarisk leaves, leading to periods of episodic defoliation that last several weeks or longer. Repeated defoliation events (i.e., over several consecutive growing seasons) result in carbon starvation that in turn, reduce leaf production and growth, in some cases leading to tamarisk mortality. In the short term, the impacts of defoliation on tamarisk might be fairly small and confined specifically to periods when the trees/shrubs are defoliated. For example, in the upper Colorado River Basin of southeastern Utah, several weeks of defoliation during two consecutive growing seasons resulted in a 15% reduction in mean annual water use (measured with stem sap flow sensors) by tamarisk [*Hultine et al.*, 2010b]. During both years, canopy leaf area and water use rates rebounded to levels achieved prior to defoliation. Similarly, remote sensing estimates of annual ET from 2000–2007 along a tamarisk dominated river reach showed that ET fluxes were about the same in 2007 (the initial year of widespread defoliation) as the previous 7 years [*Dennison et al.*, 2009].

[19] Detecting the long-term impacts of tamarisk defoliation on ecohydrological processes is more complex, and depend on several ecophysiological factors related to stand productivity and plant water relations. These factors include leaf production, fine root production, leaf phenology, and stomatal control, all of which could have profound impacts on the SPAC and interannual patterns of tamarisk water use at multiple scales.

[20] Repeated defoliation events over several growing seasons should result in plants that are carbon limited. Under these conditions, the size of the nonstructural carbohydrate pool (NSC) decreases [*Hudgeons et al.*, 2007], resulting in a reduced capacity to construct and maintain tissues that have high metabolic costs such as reproductive organs, leaves, and fine roots. An important fundamental question is whether a decrease in either leaf area, or fine root area or both will result in a proportional decrease in

annual plant water use. In many cases transpiration per unit leaf area increases with decreasing leaf area [*Meinzer and Granz*, 1991; *Reich et al.* 1993; *Pataki et al.*, 1998; *Oren et al.*, 1999]. For example, a hurricane-induced 40% reduction in leaf area of a bald cypress stand resulted in only an 18% reduction in transpiration [*Oren et al.*, 1999]. Other studies have found a complete compensation of plant water use in response to a 40% or more reduction in leaf area [*Meinzer and Granz*, 1991; *Pataki et al.*, 1999]. These nonlinear relationships between tree water use and defoliation have been attributed primarily to changes in leaf specific conductivity through the SPAC [*Meinzer and Granz*, 1990; *Meinzer et al.*, 1991], although changes in microclimate around the remaining canopy area may also be a factor. At any rate, data from these studies suggest that water use by tamarisk will likely not decrease proportionally with leaf area unless a threshold is reached that results in a near complete loss in plant function and/or mortality.

6. Distribution of Russian Olive and Its Impacts on the Water Cycle

[21] Russian olive (*Eleagnus angustifolia* L.) was originally introduced to North America in the early 1900s [*Katz and Shafroth*, 2003]. It has since become naturalized in 17 western United States [*Katz and Shafroth*, 2003] and is now the fourth most common riparian tree species in western North America [*Friedman et al.*, 2005]. Relative to tamarisk, there is little data regarding the water relations, water use or impacts of Russian olive (RO) on the ecohydrology of riparian ecosystems. There are two primary challenges that impede studies of Russian olive water use. The first is that RO rarely occurs in monocultures large enough to deploy either micrometeorological approaches such as eddy covariance flux measurements, or remote sensing techniques in order to estimate ET. The second revolves around challenges related to estimating transpiration from sap flow measurements in RO stems. Unlike most riparian woody plants that have diffuse porous wood anatomy, RO has ring-porous wood. The significance of ring porous wood is that sap flow occurs through xylem conduits that are much larger in diameter than in diffuse-porous wood [*Hacke et al.*, 2006; *Bush et al.*, 2008] and concentrated in the outermost growth ring [*Cermák et al.*, 1992; *Tyree and Zimmermann*, 2002]. Unfortunately, most sap flow measurement techniques are engineered to measure uniform flow across a much larger cross-section of the stem than a single growth ring, making water use by ring-porous species such as RO difficult to quantify. Recent lab calibration studies, however, have greatly improved the accuracy of a widely used technique (thermal dissipation method [*Granier*, 1987]) for measuring sap flow on ring-porous stems [*Bush et al.*, 2010]. These improved methods for calculating sap flow will greatly enhance research efforts to quantify RO water use at large spatial and temporal scales and allow for accurate comparison with other dominant riparian species.

[22] Under warm and dry atmospheric conditions (such as those that are typical in the arid west), ring-porous tree species such as RO often express a higher stomatal sensitivity to *vpd* than co-occurring diffuse porous tree species such as cottonwood and willow [*Bush et al.*, 2008]. These differences lead to the prediction that g_s and subsequent leaf-level water loss are typically lower in RO than diffuse-porous riparian tree species. However, recent measurements of stem sap flow using lab-calibration coefficients [*Bush et al.*, 2010] do not support these predictions. Sap-flux-scaled transpiration per unit basal area, measured from mid-July to mid-August, 2004 near Salt Lake City, Utah was on average about two times higher in Russian olive trees than in co-occurring Fremont cottonwood trees (Figure 4a; S. Bush, unpublished data, 2005). Whether these sap flow patterns reflect annual differences in stand water use between RO and other species depends on several factors, including leaf phenology, stand density, leaf area index, etc. To our knowledge there are no published data sets that directly compare the stand structure of RO with other species. One important consideration is that RO is more shade tolerant than other riparian tree species [*Shafroth et al.*, 1995]. This allows RO to sometimes form dense thickets under the canopies of other species such as cottonwood [*Howe and Knopf*, 1991]. Under these conditions RO does not necessarily replace native species but adds to the already existing biomass and leaf area, resulting in potentially higher rates of stand ET. Studies along the Rio Grande in New Mexico show that mixed riparian stands that include RO have higher leaf area indices and annual ET rates than pure stands of either tamarisk or cottonwood [*Dahm et al.*, 2002]. Therefore, the successful establishment of RO should result in mixed riparian tree stands that produce relatively large ET fluxes along many river reaches in the western United States.

7. Ecophysiology of Russian Olive With Respect to the Water Cycle

[23] Russian olive, as with tamarisk, appears to have ecophysiological advantages over many native riparian tree species that allows it to germinate and establish in more marginal soil water conditions. For one, RO has a relatively high salinity tolerance [*Katz and Shafroth*, 2003]. Likewise, RO often occurs on relatively dry terraces of riparian floodplains [*Knopf and Olsen*, 1984; *Johnson et al.*, 1995], suggesting that it is more drought tolerant, and/or maintains a deeper functional root system than species constrained to stream margins and immediate floodplains.

[24] Leaf water potential (Ψ_1) data collected from the same RO and cottonwood trees measured for sap flow (Figure 4a) suggests that RO operates over a wider range of Ψ than cottonwood. Water potential measured in early July, mid-July, and early September was consistently lower (more negative) in RO than in cottonwood (Figure 4b; S. Bush, unpublished data, 2005). In fact, mean midday Ψ_1 of RO stems was consistently at or below the minimum Ψ_1 expected to result in a complete loss of K in cottonwood or willow (see Figure 2). Combined with the fact that flooding or other disturbance processes are not required for germination and establishment, these results may explain why RO, as with tamarisk, often occupies areas of riparian floodplains and terraces that are typically absent of native riparian phreatophytes. Therefore, tamarisk control that is now a primary goal of many land managers could result in an expanding niche for RO unless aggressive restoration practices are undertaken. The expansion of RO could have significant impacts on ecohydrologic processes, particularly in

watersheds that can support large floodplains relative to stream and groundwater discharge.

[25] Unlike almost all other dominant native and non-native riparian plants of the southwestern United States, Russian olive root systems fix nitrogen due to symbiotic actinorhizal associations. In ecosystems that are often limited by lack of nitrogen, such as riparian systems, the proliferation of nitrogen fixing plants can have profound impacts on community structure, productivity and ecohydrology [*Vitousek et al.*, 1987; *Yelenik et al.*, 2004]. Nitrogen fixation by Russian olive trees along the Rio Grande River in New Mexico has been shown to increase available soil N by four times above background levels below native cottonwood stands [*DeCant*, 2008]. Unlike tamarisk stands that often result in areas with high soil salinity, high soil N under RO stands has the potential to facilitate secondary invasion by non-native plant species, especially where RO stands are removed. Many non-native understory plant species that are spreading throughout riparian areas of the southwestern United States leaf out in early spring, before most native riparian plants that are late spring and summer active [*Hultine et al.*, 2010a]. Non-native species, therefore, including perennial pepperweed, Russian thistle and Russian knapweed may benefit from RO removal. Unfortunately, data on the potential impacts these replacement species have on riparian ecohydrology are currently lacking (see Table 2).

8. Distribution of Russian Knapweed and Its Impacts on the Water Cycle

[26] Russian knapweed (*Acroptilon repens* L.) is an herbaceous perennial that was originally introduced to North America from Eurasia in the late 1800s. It now occupies almost 500,000 hectares in 17 western United States and is spreading at an annual rate of 8–14% [*Duncan et al.*, 2004]. Russian knapweed (RK) is often found in abandoned fields, pastures, and open rangeland. In the southwestern United States, RK is primarily located in riparian areas and is quickly spreading along many stream reaches. Russian knapweed reproduces primarily vegetatively: its extensive root systems produce multiple shoots that allow for rapid colonization and survival over large areas. Once established RK tends to form dense monocultures (100 – 300 shoots m^{-1}) [*Maddox et al.*, 1985] with potentially high resource use in areas that were often occupied by native vegetation. Its canopies produce large leaf areas, and its root systems have been reported to reach depths of 5 to 7 m. Taken together, these morphological attributes suggest that RK can have significant impacts on ecohydrology at the plot scale, and at much larger scales if its expansion continues.

[27] To date there is no comprehensive information on either whole plant water relations or the magnitude of water use by Russian knapweed. A significant challenge to measuring water use in RK is that its herbaceous, nonwoody stems limit opportunities for stem sap flow measurements. On the other hand, the relatively short stature (about 1 to 1.5 m tall) of RK plants coupled with its propensity to develop large open monoculture fields are ideal for eddy-covariance or Bowen ratio flux measurements of ET. Other approaches such as leaf, or whole-plant gas exchange measurements with infrared gas analyzers or steady state porometers are useful but are limited in temporal scale since they only provide "snapshots" of ET fluxes.

[28] A fundamental question is whether the replacement of one dominant riparian species with another will alter the ecohydrologic processes of riparian ecosystems. As discussed earlier, control efforts to reduce tamarisk are currently ongoing, and could result in a new niche for secondary invasives such as Russian knapweed. Recent data show that the replacement of tamarisk with RK may result in higher ET rates from riparian areas. Leaf transpiration measurements repeated over a 1 d period in southeastern Utah showed that RK had on average 75% higher transpiration rates per unit leaf area than co-occurring tamarisk trees (Figure 5a; K. Hultine, unpublished data, 2009). When these data were scaled to unit ground area, differences in transpiration increased to 190% (Figure 5b; K. Hultine, unpublished data, 2009) due to RK having a much higher leaf area index than tamarisk: 2.84 m^2 m^{-2} compared to 1.71 m^2 m^{-2}. There are several obvious factors that limit the scope of these data. For one, tamarisk stands typically display higher leaf areas than those reported here [*Nagler et al.*, 2009]. Another important factor is that the two species display different leaf phenologies. Russian knapweed and tamarisk both produce new leaves in southeastern Utah around late April or early May (personal observation). However, RK

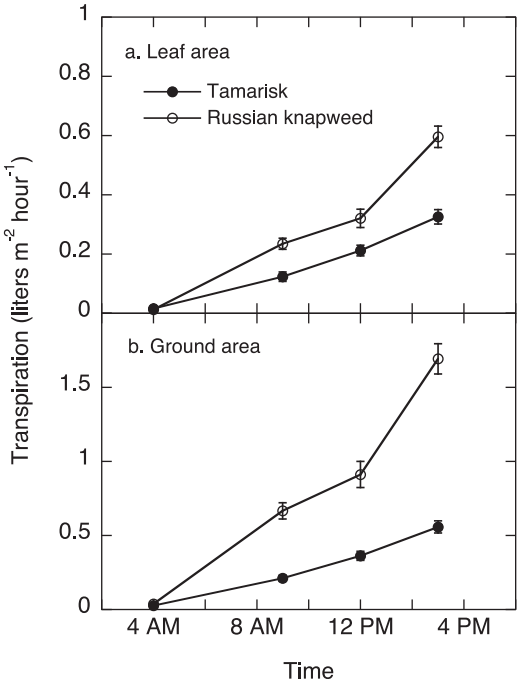

Figure 5. Transpiration by co-occurring tamarisk and Russian knapweed stands (n = six plants per species and per period) along the Dolores River in southeastern Utah. (a) Transpiration per unit leaf area, and (b) transpiration per unit ground area, determined from combined measurements of leaf transpiration and leaf area index (m^2 m^{-2}). Measurements of leaf transpiration were conducted on 19 June 2009 with a Li-Cor 1600, null-balance porometer (Li-Cor Inc., Lincoln, NE). Measurements of leaf area index were conducted with a Li-Cor 2000 leaf area meter (Li-Cor Inc., Lincoln, Nebraska). Error bars represent the standard error of the means.

enters senescence around late September or early October: about four to five weeks earlier than tamarisk. Differences in phenology may offset some of the differences in leaf-level transpiration measured over a 1 d period. On the other hand, defoliation of tamarisk by the saltcedar beetle (see above) is not only having considerable impacts on tamarisk phenology and water use but may also enhance the spread of Russian knapweed and its impacts on regional water cycles.

[29] Another important consideration is whether rates of g_s and subsequent water use by RK are maintained throughout the growing season. When soil moisture is not limiting, g_s in almost all terrestrial plants is inversely correlated with atmospheric vapor pressure deficit (*vpd*) [*Meinzer et al.*, 1997; *Oren et al.*, 1999; *Hultine et al.*, 2008]. Sharp decreases in soil water availability and subsequent decreases in rhizosphere Ψ can decouple the relationship between g_s and *vpd*, especially if the plant is very sensitive to small decreases in water potential (or increases in water potential gradients) within the *SPAC* [*Sperry et al.*, 1998, 2002; *Hultine et al.*, 2010c]. Mean predawn Ψ_1 (an approximation of Ψ_{rh}) of RK plants in mid-June, 2009 was -0.8 MPa (Standard error ± 0.09, $n = 6$ plants), and -2.1 MPa (SE ± 0.14, $n = 6$ plants) in late July, 2009. Despite these differences, the relationship between g_s and *vpd* was similar in late July as it was in mid-June (Figure 6; K. Hultine, unpublished data, 2009). The significance of these data is that RK can maintain high transpiration rates at xylem water potentials that would result in a near complete loss in K_s in many native riparian species (see Figure 4). Thus, it appears that RK can functionally combine high leaf areas and high transpiration rates with a high tolerance for low water potentials relative to other riparian species.

9. Comparison of Leaf N Concentrations Between Native and Non-native Vegetation With Respect to Leaf Gas Exchange and Ecohydrology

[30] The biochemical demand for CO_2 by a given leaf is in part, coupled to leaf stomatal conductance and subsequent water loss [*Katul et al.*, 2003]. The relationship between CO_2 demand and g_s leads to the prediction that plants that maintain relatively high leaf nitrogen concentrations, an analog of leaf photosynthetic capacity, operate with a higher g_s compared to co-occurring plants with lower leaf N concentrations (assuming similar canopy water potential gradients). Nitrogen concentrations of fresh leaves and leaf litter are typically much higher in tamarisk, Russian olive, and Russian knapweed than in co-occurring cottonwood and willow. For example, published data from fresh leaves and leaf litter showed that N concentrations ranged from 23% to 100% higher in tamarisk than co-occurring cottonwood [*Pataki et al.*, 2005; *Folstad Shah and Dahm*, 2008; *Moline and Poff*, 2008]. Nitrogen concentrations in tamarisk leaf litter along two southern California streams was four times higher than willow leaf litter [*Going and Dudley*, 2008]. Leaf N concentrations in Russian olive have been reported to be 93% to 260% higher than leaf N concentrations of co-occurring cottonwood [*Simon and Seastedt*, 1999; *Royer et al.*, 1999; *Tibbetts and Moles*, 2005; *Moline and Poff*, 2008]. Likewise, data collected on the Dolores River near Moab, UT showed that both tamarisk and Russian knapweed maintained higher

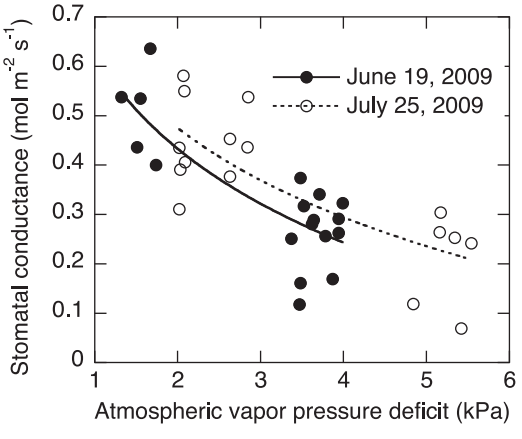

Figure 6. Leaf stomatal conductance of Russian knapweed plants occurring along the Dolores River in southeastern Utah. Measurements were conducted on 19 June 2009, and 25 July 2009 with a Li-Cor 1600, null-balance porometer (Li-Cor Inc., Lincoln, Nebraska).

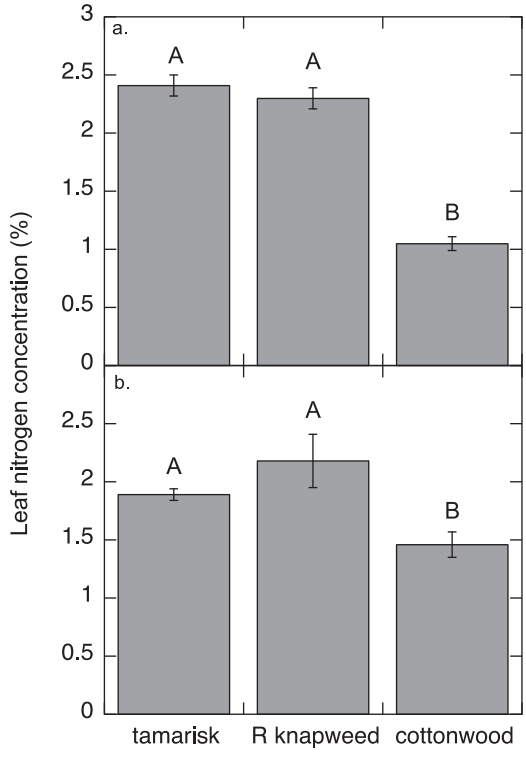

Figure 7. Percent leaf nitrogen concentrations for tamarisk, Russian knapweed, and Fremont cottonwood occurring along the Dolores River in southeastern, Utah. (a) Nitrogen concentrations from leaves collected in September of 2008 from tamarisk ($n = 37$ plants), Russian knapweed ($n = 6$ plants), and Fremont cottonwood ($n = 4$ plants). (b) Nitrogen concentrations from leaves collected in June of 2009 from tamarisk ($n = 39$), Russian knapweed ($n = 7$), and Fremont cottonwood ($n = 4$). Leaf N was measured with an elemental analyzer (Carla Erba, model 118, Milano Italy). Letters above the error bars represent significant differences ($P < 0.1$) between populations.

leaf N concentrations than co-occurring Fremont cottonwood (Figure 7; K. Hultine, unpublished data). In September of 2008, leaf N concentrations were 130% and 120% higher in tamarisk, and Russian knapweed than cottonwood, respectively (Figure 7a). In June of 2009, leaf N was 30% and 50% higher in tamarisk, and Russian knapweed than cottonwood, respectively (Figure 7b).

[31] These data suggest that on a leaf area basis, tamarisk, RO, and RK express higher gas exchange rates than co-occurring cottonwood and willow. Under moist soil water conditions on the Bill Williams River in central Arizona, g_s and net photosynthesis in mature tamarisk trees were about two and three times higher, respectively, than rates expressed by co-occurring cottonwood and willow trees [*Horton et al.*, 2001]. These data suggest that there are large-scale differences in stand-level ET rates between tamarisk and native species, although differences have not been widely reported (see Table 2). Data that directly compares leaf gas exchange of RO and RK with native riparian species are, to our knowledge, lacking but deserves attention, especially in areas where these non-native species are expected to spread in response to widespread tamarisk control.

10. Potential Ecohydrological Impacts of Other Non-native Riparian Plant Species

[32] There are dozens of non-native plant species that have successfully invaded riparian systems of the southwestern United States. Of these, we have identified four (other than tamarisk, RO and RK) that have a high potential impact on riparian ecohydrology at large scales including: giant reed (*Arundo donax*), thistles and knapweeds (*Centaurea* spp.), Siberian elm (*Ulnus pumilla*), and perennial pepperweed (*Lepidium latifolium*) (Table 2). To our knowledge there are no published data that directly compare water relations or water use of any of these species with native riparian vegetation in the southwestern United States. There is some evidence that giant reed can obtain much higher leaf areas and ET rates per unit ground area than co-occurring willow, but may be restricted to lower floodplain terraces due to a relatively shallow root system (T. Dudley, personal communication, 2010). Thistle and knapweed species in the *Centaurea* genus and perennial pepperweed are all known to quickly establish disturbed areas within upper and lower floodplain terraces, but little is known about their maximum rooting depths, xylem structure, or water use rates. Siberian elm is spreading quickly throughout the southwest and is well established in riparian areas in southern Utah, southern Colorado, northern Arizona, and northern New Mexico. This species does establish along upper and lower floodplain terraces and is therefore a considerable threat to secondarily invade areas tamarisk and/or Russian olive have been removed. Evapotranspiration rates in its home range have been reported to far exceed those of co-occurring poplar species but lower than Russian olive [*Khamzina et al.*, 2009]. Data for populations in the southwestern United States remain absent from the literature.

11. Future Research Needs and Management Implications

[33] Severe episodic water shortages are now forecasted for arid regions of the globe including the southwest region of North America [*Jackson et al.*, 2001]. These forecasts are sparking considerable effort to improve the accuracy of water budgets of watersheds and river basins. However, characterizing water budgets of large river basins are extremely challenging, due in part to the complex interactions between vegetation, climate and hydrology [*Shafroth et al.*, 2010]. Changes in vegetation cover and species composition that are inevitable through time and space add to these complex interactions. Thus, efforts to manage scarce water supplies would greatly benefit from a clear analysis of how alterations in vegetation cover impact water cycling processes.

[34] This review identifies the ecophysiological mechanisms that underpin potential alterations in riparian vegetation cover and ecohydrology in the arid southwestern United States. Specifically, our review focused on the conversion of riparian ecosystems from native to non-native vegetation along with the associated impacts these shifts may have on water resources. Our analysis of plant water relations suggests that many non-native plant species have the potential to establish, or at least outperform native vegetation along dryer regions of riparian floodplains. The subsequent increase in vegetation cover will likely increase riparian ET relative to river discharge. Along relatively small river reaches with low mean annual flow rates, these increases in ET have the potential to reduce total basin discharge. Likewise, preliminary data suggests that non-native riparian species such as Russian olive and Russian knapweed produce higher ET fluxes over other dominant species such as tamarisk and cottonwood. Therefore, widespread control of tamarisk could increase riparian ET along many river reaches if these control efforts result in secondary invasion by Russian olive, Russian knapweed, or other non-native species.

[35] Identifying the impacts of non-native riparian plant species on water resources is difficult at best. Although this paper does not address the impacts of every dominant introduced riparian species, or every component of ecohydrology, we believe this review does identify critical areas of research that would enhance the ability for managers, given inevitable limitations in economic resources, to protect water supplies and valued riparian habitat,. Thus, we have identified the following major topics as those we believe deserve high priority for future research.

[36] 1. Research should focus on small watersheds and headwater systems that often support high vegetation cover relative to stream and groundwater discharge. Previous research has shown that ET from vegetation occurring along large first-order stream systems has negligible impacts on stream discharge because the ET flux generated is too low to measurably impact river storage. However, the expansion of non-native vegetation cover along multiple low-order streams could have considerable impact on downstream water discharge into higher order streams, a point that must be taken into account in order to accurately calculate riparian vegetation impacts on basin-wide hydrology.

[37] 2. The expanded use of biological control agents to limit the spread of dominant invasive plants has the potential to result in dramatic changes in species composition, phenology, and subsequent ET fluxes from riparian vegetation. With tamarisk, changes caused by the saltcedar leaf beetle are already ongoing and quickly spreading throughout much of the western United States. Research that

focuses on the ecophysiological responses of tamarisk to repeated defoliation, impacts of defoliation over broad environmental gradients, and cascading impacts of defoliation on population dynamics of riparian ecosystems would greatly improve management efforts to protect water resources, riparian ecosystem function, and ecosystem services as a whole. Potential alteration in germination, phenology, and plant distribution patterns, in response to biological control agents, will be difficult to quantify over large spatial scales by scientists alone. Local management agencies, private land owners, river guides, and the public in general should be encouraged to become "citizen" scientists that document inter-annual changes in phenology and riparian population structure as a whole. Current data clearinghouses, such as the USA National Phenology Network (available at www.usapn.org) would be ideal resource media for downloading and synthesizing ongoing datasets.

[38] 3. Considerable research is needed to address plant-water relations and overall water use of Russian olive, Russian knapweed and other dominant introduced plants species across environmental gradients. Exploratory data suggest that many introduced plant species have the potential to occupy more xeric locations within riparian floodplains and terraces than most native riparian plant species, and may have the potential to use water at higher rates than native vegetation. Management activities such as tamarisk control in the southwestern United States may result in a new niche for secondary introduced plant species. Therefore, a quantitative evaluation of what impacts the expansion of RO and RK in the southwestern United States would have on ET fluxes and subsequent hydrologic cycling would greatly assist land management and water conservation agencies with priorities for controlling the spread of these species, especially where economic resources are limited.

[39] 4. Research that focuses on the below-ground component of the Soil-Plant-Atmosphere-Continuum would greatly enhance process modeling of vegetation impacts on fluvial ecohydrology. Specifically, investigations that describe functional rooting depth, and the structure and function of root xylem across soil water potential gradients would improve efforts to scale ET fluxes from individual plants, to watersheds, to large river basins.

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