FIRE IN A RIPARIAN SHRUB COMMUNITY: POSTBURN WATER RELATIONS IN THE *TAMARIX-SALIX* ASSOCIATION ALONG THE LOWER COLORADO RIVER

David E. Busch
Stanley D. Smith

ABSTRACT

Higher water potentials in recovering burned salt-cedar (Tamarix ramosissima) *relative to unburned plants and the opposite situation in willow* (Salix gooddingii) *provide evidence that postfire water stress is reduced in the former but not the latter. Similarly, diurnal patterns of stomatal conductance in these taxa are consistent with the existence of more vigor in burned salt-cedar than willow. Plots of water potential and transpiration demonstrate that hydraulic efficiencies may contribute to differences in fire recovery.*

INTRODUCTION

Alteration of hydrologic regimes by humans has indirectly impacted communities dominated by woody phreatophytic vegetation along watercourses of the Southwest. The invasion of low-elevation riparian communities throughout western North America by salt-cedar (*Tamarix ramosissima*) may have been aided by the cessation of disturbance from flooding. Moreover, salt-cedar may be both the cause and the beneficiary of a new suite of disturbances, prominent among which is fire.

Alluvial soils are frequently covered by several centimeters of salt-cedar leaf litter to the exclusion of other plants (Haase 1972). Such fuel buildup causes fire with a repetitive frequency of <20 yr in North American desert riparian settings; this has led to the demise of communities dominated by cottonwood (*Populus fremontii*) and willow (*Salix gooddingii*) along the lower Colorado River (Ohmart and others 1977). It is uncertain whether or not fire was important in structuring riparian vegetation communities dominated by cottonwood, willow, or mesquite (*Prosopis* sp.) prior to salt-cedar invasion, but we think that its role was minor. There are few indications that salt-cedar is considered fire-adapted from throughout its native Eurasian range. Provided that fire was historically unimportant, the invasion of salt- cedar with an accompanying propensity for episodic burning has produced a unique disturbance regime in low-elevation southwestern flood plain ecosystems.

The adaptation of salt-cedar to resprout rapidly following fire has been implicated in its rapid colonization of water courses throughout the Southwest (Crins 1989). Roots of salt-cedar are capable of forming adventitious shoots, and stem tissue will sprout vigorously given the proper conditions (Gary and Horton 1965; Wilkinson 1966). Rootstocks of the Salicaceae also are known to sprout vigorously (Fowells 1965). There is evidence for a dependence on groundwater in both willow and salt-cedar based on soil moisture depletion (McQueen and Miller 1972) and water uptake (D. E. Busch, in preparation). Salt-cedar root distribution is well developed in the water table and overlying capillary zone (Gary 1963). Willow (*S. nigra*) groundwater dependence is suggested by inundation tolerance and intolerance of moisture stress (Dionigi and others 1985).

Areas where relict native willow codominates with salt-cedar provide opportunities to study putative competitive factors that may favor the exotic. Similarities in phreatophytic life histories and fire recovery mechanisms led us to hypothesize that postburn water relations may contribute to differential recovery between these taxa.

MATERIALS AND METHODS

Water relations data were collected during the 1989 growing season at two sites in the Arizona flood plain of the Colorado River near Needles, CA (34°50' N., 114°35' W., 150 m elevation). The sites were separated by <2 km and were both 150-200 m from the river. Depth to ground water, as measured with onsite piezometers, averaged (± S.D.) 3.53 ± 0.47 m. The study area was characterized by a tall scrub association dominated by salt-cedar and willow, which form dense thickets with interlocking canopies. Arrowweed (*Tessaria sericea*) was also abundant on these sites. Screwbean (*Prosopis pubescens*) was scattered throughout unburned portions of the flood plain.

Data were collected from single willow and salt-cedar coppices at three sublocations within this vegetation association that showed no sign of recent surface disturbance (controls). The burned site, which had been disturbed by an intense fire in 1986, had no screwbean but was experiencing regrowth of the other three taxa. Resprouting willow and salt-cedar coppices were again selected at three sublocations within the burned area. Mean growing season gravimetric soil moisture in the upper 90 cm of the soil profile was lower for burned sublocations (1.19 ± 0.12 percent) than for control sublocations (3.77 ± 1.24 percent). It is

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David E. Busch is Ecologist, Division of Environment, Bureau of Reclamation, Boulder City, NV 89005. Stanley D. Smith is Associate Professor, Department of Biological Sciences, University of Nevada, Las Vegas, Las Vegas, NV 89154.

uncertain if this condition predated the fire or if the effects of burning or subsequent soil exposure to enhanced evaporative conditions contributed to this difference.

Total water potential (Ψ) was measured twice daily on each plant, before dawn (Ψ_{max}) and at midday (Ψ_{min}). Measurements were made using the pressure chamber technique (Turner 1988) with a PMS Model 1000 pressure chamber apparatus on 10-30 cm terminal branches taken from the midcanopy level. Upon cutting, branches were immediately placed in polyethylene bags and housed on ice and in the dark until pressurization, which was quickly conducted at the site. Stomatal water vapor conductance (*g*) and transpiration (*E*) were measured using a steady-state porometer (Licor LI-1600). Salt-cedar cladophyll morphology necessitated the use of a cylindrical chamber, so this type of cuvette was used for willow as well. Diurnal curves for these parameters were developed from pormeter readings made at 2-hour intervals. For between-site comparative purposes g_{max} was calculated by averaging *g* values from 9 a.m. to 1 p.m. Although willow is amphistomatous, area-specific *g* and *E* data reported here were based on a single projected leaf surface.

Between-site statistical comparisons were made by testing for differences using the Mann-Whitney test for two independent samples (Conover 1990). Test statistics (*U*) and probabilities of a Type I error are presented where results of this nonparametric test were significant ($P < 0.05$). Simple linear regression models were derived to examine the tendency of Ψ to vary with daily increases in *E*.

RESULTS AND DISCUSSION

For both salt-cedar and willow there was a modest tendency for Ψ_{max} to be lower (more negative) during the summer months with recovery demonstrated in autumn (fig. 1). Predawn Ψ showed no significant differences between burned and unburned study sites for either species in either season. The lack of strong site or seasonal differences in Ψ_{max} is consistent with the phreatophytic habit. Apparently the roots of both taxa maintain contact with groundwater or the capillary fringe, and this connection is retained after burning. Predawn Ψ levels for willow over the study's course were lower than those reported for other temperate hardwood species (Abrams 1988), but are not considered stressful for a mesophyte. Salt-cedar Ψ_{max} levels are considerably lower than those reported elsewhere (Anderson 1982), but probably do not indicate water stress for a halophyte that may successfully utilize low osmotic potentials in the water uptake process.

Figure 1 indicates that, for salt-cedar, Ψ_{min} levels on the burn site were not significantly different from those in control coppices. Midday Ψ was significantly ($U = -3.078$, $P < 0.005$) more negative for resprouting burned willow than in controls. On an absolute basis, these are substantially lower Ψ's than have previously been reported for salt-cedar or willow (Abrams 1988; Anderson 1982). However, it is difficult to determine if these levels should be considered stressful in salt-cedar due to its presumed osmotic adjustment adaptations. Although we are pursuing this question with research into phreatophyte tissue water relations, we feel that it is unlikely that salt-cedar experiences water stress on burned sites in view of the lack of significant difference from control plants and the success of its

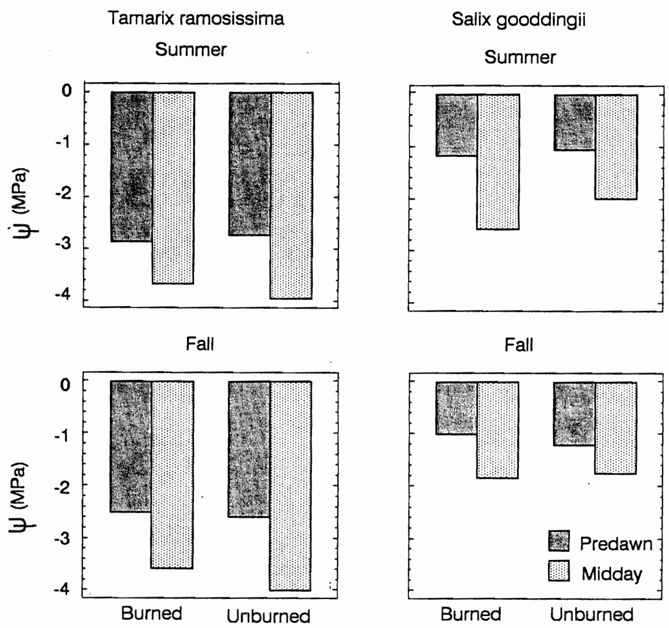

Figure 1—Mean ($n \geq 12$ in all cases) predawn (Ψ_{max}) and midday (Ψ_{min}) water potential in burned and unburned salt-cedar (left) and willow (right) from the lower Colorado River during summer (upper) and autumn (lower) 1989.

recent invasion in the lower Colorado River flood plain. Wilting has been reported for flooded willow at <–1.8 MPa (Dionigi and others 1985). The Ψ_{min} values reached by willow are well below levels thought to reduce photosynthetic capacity and growth in mesophytes (Hsiao 1973). Thus, resprouting willow on burned areas do appear to demonstrate at least transitory water stress.

The short-term water stress shown in burned willow does not appear to induce stomatal closure (fig. 2). While g_{max} on burned and control sites did not differ significantly during the summer, autumn values were significantly higher in plants that had burned ($U = -4.412$, $P < 0.001$). Stomatal conductance patterns for salt-cedar are dissimilar from reports of constant leaf resistance (Anderson 1982) in that a marked late-morning decline was noted in summer (fig. 2). This indicates a degree of stomatal control may be exhibited under mild water stress in this species. Throughout the study's course, salt-cedar g_{max} on burned sites significantly exceeded that on control sites ($U = -4.835$, $P < 0.001$). Beyond confirming our previously stated finding that recovering burned salt-cedar is not water stressed, diurnal stomatal conductance data suggest that rhizosphere water availability is not limiting, and may actually facilitate its reestablishment. Interpretation of the willow results is more problematic, but it is clear that enhanced leaf diffusive conductance did not occur during the summer in burned plants in the manner that it did in salt-cedar.

The relationship between water potential and transpiration offers greater insight into soil moisture limitations than predawn water potential alone (Bates and Hall 1982). To further compare differences in plant water status, the effects of *E* on Ψ were modeled using linear regression (fig. 3). Although a linear model for burned salt-cedar was acceptable, the significance of the regression for controls

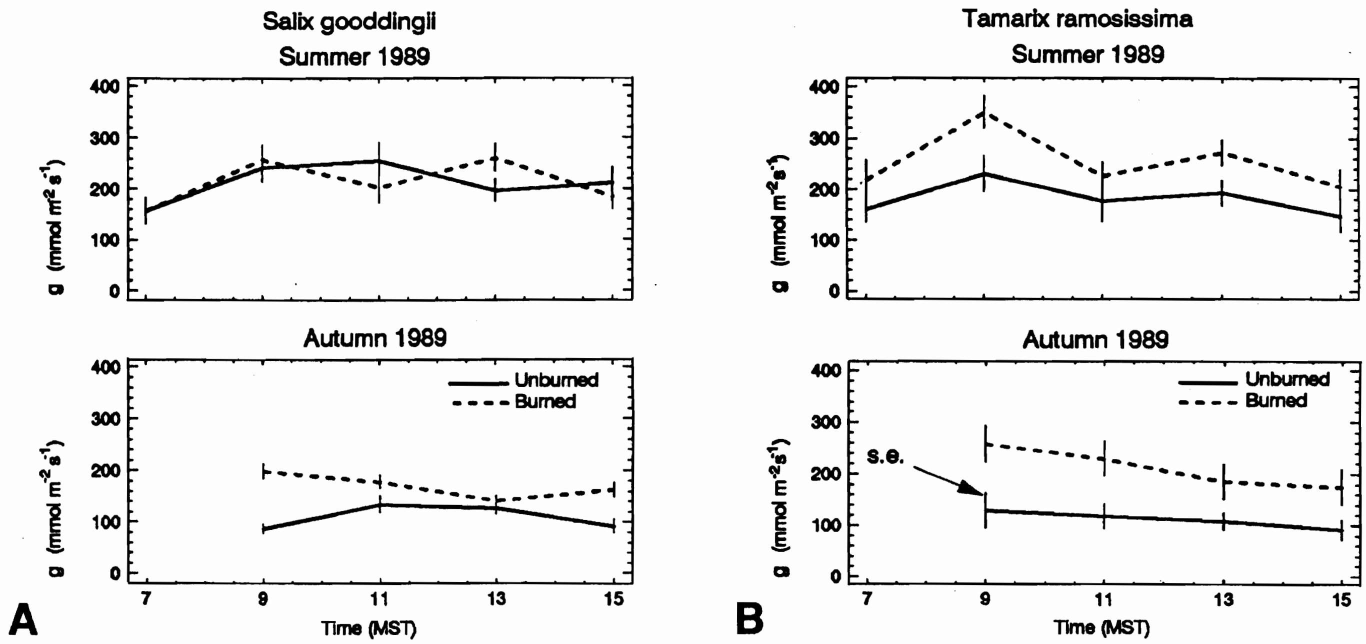

Figure 2—Stomatal conductance (*g*) response curves for willow (A) and salt-cedar (B) from burned and unburned sites in the lower Colorado River flood plain during summer and fall 1989. Each point represents the mean ($n \geq 18$) ± associated standard error.

was low ($r^2 = 0.27, P > 0.05$). Since inferences could not be made for the latter setting and also since interspecific comparisons of porometer-derived E would be meaningless, we elected not to pursue this analysis for salt-cedar. In willow the slope of depression for burned trees was less than that for controls (fig. 3). This is evidence for decreased efficiency of water uptake and transport in the post-fire condition. Lower hydraulic efficiency in burned willow signifies reduced productivity, which is a likely result of diminished effective root:shoot ratio (Bates and Hall 1982).

It has been hypothesized that plant species possessing resprouting mechanisms that are activated by burning might have also developed via natural selection characteristics that enhance the flammability of the communities where they grow (Mutch 1970). We have provided evidence that would support a hypothesis of competitive superiority in water acquisition of burned and resprouting coppices of salt-cedar relative to those of willow. Accumulation of flammable leaf litter beneath salt-cedar appears to contribute to episodic fires, which aid the invasion of this exotic. Is this situation an anomaly in North American communities dominated by this naturalized phreatophyte or does it represent "true" adaptation to fire? This might best be answered by demographic analyses of *Tamarix* associations in Eurasia. Although it resprouts vigorously following fires, our data suggest that willow is hydraulically less efficient than co-occurring salt-cedar. Interactions between these taxa, paired with the impact from fire, would tend to favor the introduced species. Intercorrelated with these factors are other forms of disturbance, which were not discussed here. The complex suite of recently altered environmental factors that has confronted native riparian trees is thus likely to have led to impacts ranging from direct mortality to reduced propagule dissemination and establishment.

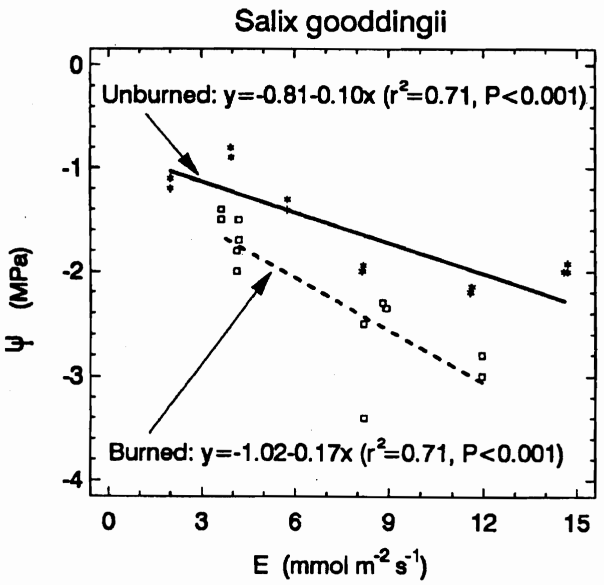

Figure 3—Regressions of water potential (Ψ) on transpiration (*E*) for burned and unburned willow from the lower Colorado River riparian zone during the 1989 growing season.

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