CSIRO PUBLISHING

International Journal of Wildland Fire
http://dx.doi.org/10.1071/WF10089

The effect of leaf beetle herbivory on the fire behaviour of tamarisk (*Tamarix ramosissima* Lebed.)

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Abstract. The non-native tree, *Tamarix* spp. has invaded desert riparian ecosystems in the south-western United States. Fire hazard has increased, as typically fire-resistant native vegetation is replaced by *Tamarix*. The tamarisk leaf beetle, *Diorhabda carinulata* Desbrochers, introduced for biological control, may affect fire behaviour by converting hydrated live *Tamarix* leaves and twigs into desiccated and dead fuels. This potentially increases fire hazard in the short term before native vegetation can be re-established. This study investigates how fire behaviour is altered in *Tamarix* fuels desiccated by *Diorhabda* herbivory at a Great Basin site, and by herbivory simulated by foliar herbicide at a Mojave Desert site. It also evaluates the influence of litter depth on fire intensity. Fire behaviour was measured with a fire intensity index that integrates temperature and duration (degree-minutes above 70°C), and with maximum temperature, duration, flame lengths, rates of spread and vegetation removal. Maximum temperature, flame length and rate of spread were enhanced by foliar desiccation of *Tamarix* at both sites. At only the Mojave site, there was a trend for desiccated trees to burn with greater fire intensity. At both sites, fire behaviour parameters were influenced to a greater degree by litter depth, vegetation density and drier and windier conditions than by foliar desiccation.

Received 3 August 2010, accepted 29 August 2012, published online 9 November 2012

Introduction

Riparian areas have long been considered barriers to the spread of wildfire (Bêche *et al.* 2005; Pettit and Naiman 2007) because the higher foliar moisture and humidity in riparian communities can inhibit fire movement from upland areas (Agee 1988; Dwire and Kauffman 2003). However, natural fires do occur in riparian systems when weather conditions are dry and when fuel loads are sufficient, but because these occurrences are rare few researchers have examined the role of fire in riparian zones (Gregory *et al.* 2003; Pettit and Naiman 2007).

In western North America fire area and frequency have increased in desert riparian areas with the invasion of these systems by tamarisk (*Tamarix* spp.), a tree introduced from Eurasia (Busch 1995*a*). Native gallery forests composed of a mix of cottonwood (*Populus* spp.) and willow (*Salix* spp.) species are being replaced by *Tamarix* that range in distribution from small patches in a vegetation mosaic to dense monocultural stands (Shafroth *et al.* 2005). *Tamarix* monocultures have greater cover, stem density and fine twig density than do stands of native species, thus they increase potential fuel loading (Weisenborn 1996; Lair 2007). This in turn appears to be converting desert riparian areas, historically considered barriers to wildfire, into pathways for wildfire spread (Busch and Smith 1992; Dudley *et al.* 2000). Deeper surface fuels in the *Tamarix* understorey produce more intense fire at the ground level (Bradstock and Auld 1995; Lair and Eberts 2001), which damages or kills native species that resprout poorly following fire (Naiman *et al.* 1993; Ellis 2001). In contrast, *Tamarix* readily resprouts from a fire-resistant root crown (Busch 1995*b*; Ellis 2001). The combination of deep surface fuels and resprouting appears to have created a 10–20-year fire cycle that allows *Tamarix* to dominate riparian zones at the expense of native species (Ohmart and Anderson 1982; Brooks *et al.* 2004).

In addition to increasing wildfire risk, *Tamarix* may deplete groundwater (Pattison *et al.* 2011*a*), increase erosion and alter flooding risk, reduce forage availability for livestock (Brock 1984), salinise the soil (Ladenburger *et al.* 2006) and reduce habitat quality for wildlife (Dudley *et al.* 2000). These effects have led land managers to remove *Tamarix* using treatments such as mechanical clearing, herbicide application, prescribed fire and biological control. Mechanical and herbicidal methods are expensive, temporary and may cause collateral damage in natural areas (Sisneros 1990; Shafroth *et al.* 2005). Prescribed fire reduces biomass, but *Tamarix* readily resprouts, and nutrients released by fire stimulate its regrowth (Ohmart *et al.* 1988; Busch and Smith 1993; Holht *et al.* 2002). Biological control by the beetle *Diorhabda carinulata* (Chrysomelidae) reduces reproductive output and upwards of 60% mortality has been observed in *Tamarix* stands at the original beetle release site outside of Lovelock, NV (Pattison *et al.* 2011*a*), but the remaining dead material is suggested to be highly flammable (Brooks and Minnich 2006).

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Desiccation owing to *Diorhabda* herbivory can increase *Tamarix* flammability both by lowering foliar moisture, and by altering fuel structure. *Diorhabda* consumes the epidermal layer of the stems causing rapid water loss and desiccation of the leaf material and leaving the majority of fuels in place but dead on the stems (Lewis *et al.* 2003; Pattison *et al.* 2011*a*). The resulting fuel structure has high vertical continuity, which has been shown elsewhere to enhance flammability such as following spruce beetle (*Dendroctonus rufipennis*) and mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in coniferous forests, where dead plant material creates dry ladder fuels that are more ignitable and facilitate fire spread into the tree canopy and into adjacent trees (Knight 1987; Bebi *et al.* 2003; Axelson *et al.* 2009). Crown fires are common in *Tamarix* stands during summer months when there is little senesced or dry foliage (Howard *et al.* 1983), and beetle herbivory may further elevate flammability before the dead foliage drops from the plants into the litter layer.

The effects of *Diorhabda* herbivory have been well documented at the tree and stand level, but widespread ecosystem level effects are not yet clear (Hultine *et al.* 2009). Investigation of the relationship between *Diorhabda* herbivory and *Tamarix* flammability is merited given the extent of *Tamarix* invasion in desert riparian ecosystems of western North America and the continuing range expansion of *Diorhabda*. Such an investigation will provide empirical data on an ecosystem level effect (fire) of *Diorhabda* biocontrol.

This study was conducted in two parts to address this issue: (1) we evaluated the effects of *Diorhabda* herbivory on *Tamarix* fire behaviour at a site where *Diorhabda* was already established in the Great Basin and (2) we simulated herbivory using herbicide at a second site in the Mojave where *Diorhabda* were expected to arrive, to anticipate how their establishment may alter fire dynamics. Fire behaviour was measured as flame length, rate of spread, biomass removal and fire intensity. For the purposes of this study, 'fire intensity' refers to an index expressed in degree-minutes (the sum of the area under a temperature–duration curve) above 70°C, the temperature at which most plant tissue dies (Lepeschkin 1938), to infer damage to plant tissues. We hypothesise that fuels desiccated by *Diorhabda* or by simulated herbivory will generate higher maximum temperatures, longer burn durations, higher fire intensity, longer flame lengths and faster rate of spread than will live foliage. We also manipulated the litter layer at both sites to evaluate the effect of accumulated falling leaf litter (as would accumulate with beetle induced leaf mortality) on fire intensity and biomass removal.

Materials and methods

Study sites

The first study site was located in Pershing County in the lower Humboldt River Basin in northern Nevada in an area called the Humboldt Sink (HB; 40°04′17.10″N, 118°32′59.72″W). At the time of the study, *Tamarix ramosissima* infested over 15 000 ha in the Humboldt basin (Sengupta *et al.* 2004). The site was in the Great Basin desert at 1220-m elevation, with warm summer (mean high 32°C) and cold winter (mean high −8°C) temperatures. Average annual precipitation is 14 cm, most of which falls between February and the end of May in the study area. Shallow groundwater is recharged primarily from upper watershed precipitation and snowmelt (Lopes *et al.* 2006). Soils consisted of fine-textured silts and were naturally saline, representing dissolved-salt deposition from upstream transport and termination into the Humboldt Sink.

Dominant vegetation at the site included saltgrass (*Distichlis spicata*), greasewood (*Sarcobatus vermiculatus*) and saltbush (*Atriplex* spp.), as well as non-native forbs (fivehook bassia, *Bassia hyssopifolia*; Russian knapweed, *Acroptilon repens*; tall whitetop, *Lepidium latifolium*; halogeton, *Halogeton glomeratus*) in addition to *T. ramosissima*. *Tamarix* at the site recruited primarily following El Niño flooding in 1982–83 and consisted of trees ranging from 1.6 to 4 m in height with foliage evenly distributed throughout the canopy, covering an average of 44% of the plot area. Non-native plant species comprised the understorey, ranging from 0.25 to 0.75 m in height with an average of 53% cover.

The Pershing County Water District has an ongoing program to eradicate *Tamarix* for water conservation and to regain traditional use as land for dispersed livestock and agricultural production. Local landowners and managers have periodically burned the site to reduce *Tamarix* cover, but with little success. In 2001, the saltcedar leaf beetle (*Diorhabda carinulata*) was released for the biological control of *Tamarix* 6.5 km south-east of the study site (Pattison *et al.* 2011*b*). Two hectares were defoliated by *Diorhabda* in 2002, followed in 2003 by more than 200 ha defoliated, including the study site. At the time of the prescribed fire trials in 2006, *Tamarix* at the study site had experienced three full seasons of herbivory by *Diorhabda*. Extensive dieback (10% mortality and 60–80% desiccation resulting from herbivory by *Diorhabda*) had occurred and the amount of regrowth was variable among trees.

The second site was located in Clark County, Nevada, in Valley of Fire Wash (Valley of Fire; 36°24′06.38″N, 114°23′42.78″W) within Lake Mead National Recreation Area. This Mojave Desert site at 370-m elevation exhibits hot summers (mean high 42°C) and cool winters (mean high 14°C). Average annual precipitation is 11.4 cm, most of which falls during the months of February and March. Moderate to heavy rains provide intermittent flows through the wash causing major channel scouring events, some of which occur in the summer. Soils consist of alluvial deposits of gravel mixed into sand that were deposited when the water levels of Lake Mead receded.

The *Tamarix* stand at the site was contained within steep embankments and consisted of trees with the majority of foliage located in the upper canopy and a poorly developed understorey composed primarily of litter. *Tamarix* ranged from 2 to 5.5 m in height and covered ~95% of the plot area. Although the exact date of *Tamarix* invasion in Valley of Fire Wash is unknown, National Park Service records show widespread recruitment as the shores of Lake Mead receded in the 1960s, and it is likely that *Tamarix* at the site established then. Other vegetation included arrowweed (*Pluchea sericea*), catclaw acacia (*Acacia greggii*) and remnant populations of screwbean mesquite (*Prosopis pubescens*) and Gooding's willow (*S. goodingii*) at the edge of the *Tamarix* monoculture. Although wildfires have been reported in *Tamarix* stands in the Lake Mead area, there is no record of fire in the project area.

Experimental treatments

At the Humboldt site (HB), we evaluated the effect of herbivory (low–high) on fire behaviour with prescribed fires during two seasons (August and October). Fire treatments (August, October, unburned) were randomly assigned to nine 0.5-ha plots, covering a total area of 3 ha. Plots were separated by bulldozed firebreaks, ~6 m in width or approximately twice the height of the vegetation.

At the Valley of Fire site (VoF), we evaluated the effect of herbivory on fire behaviour with a single prescribed fire in September using herbicide treatments to simulate the level of desiccation caused by the initial colonisation of *Diorhabda* at other sites. Foliage treatments (simulated herbivory and control) were randomly assigned to six 30 × 30-m plots, covering 0.54 ha within an overall fire area of 8.1 ha. National Park Service personnel applied 10% glyphosate to the foliage to simulate leaf death by herbivory, followed by the controlled burn 4 weeks later.

Fuel characteristics

Line transects (HB two per plot, VoF one per plot) were used to measure vegetation density. They consisted of set lengths (HB 50 m, VoF 10 m) where at regular intervals (HB 0.5 m, VoF 1 m) the height and species of vegetation within 10 cm of the intercept pole were recorded. To capture the variability of vegetation at Valley of Fire, 18 additional line transects were sampled perpendicular to the stream channel. The abundance, average height and percentage cover of each plant species, and litter depth were measured within quadrats of a set area (HB 0.25 m^2, VoF 1 m^2) placed at regular intervals (HB 10 m, VoF 5 m) along the line transects. Circular plots with a 5-m radius were placed within each treatment plot (HB four per plot, VoF two per plot) to determine *Tamarix* density for biomass estimation. For each tree within the circular plots, maximum height, two maximum canopy diameters and two maximum basal diameters including all stems of each individual tree were measured with metal tapes and calibrated PVC poles. Percentage foliage (green foliage volume per total canopy volume) was visually estimated to the nearest 5% for all trees measured.

Fifteen trees within 20 m of the fire plots were destructively sampled to estimate dry biomass per unit area. Trees were chosen to represent size classes from the smallest to largest trees in the burn plots. Each tree was separated into fuel diameter classes, or timelag classes following Anderson (1982), in which small-diameter fuels desiccate more rapidly; timelag classes were 1 h (<0.625 cm), 10 h (0.625–2.5 cm), 100 h (2.5–7.6 cm) and 1000 h (>7.6 cm). Timelag classes for each tree were weighed with a handheld spring scale. To calculate the biomass per unit area for each 5-m radius circular plot, physical parameters (height, canopy width, % green foliage) were regressed against biomass. Canopy width was the strongest predictor of biomass by non-linear regression at Humboldt, as the trees were round in shape, and canopy was incorporated into the formula $y = 1.010x^{2.863}$ as the x variable ($R^2 = 0.96$, $P = 0.03$). At Valley of Fire, tree shape was irregular, thus a shape index was defined using the following allometric equation:

$$\text{Shape index} = \frac{\text{Average canopy width} \times \text{Average basal width} \times \text{Proportion foliage}}{\text{Canopy ratio}}$$

The formula $y = -0.0002x^2 + 0.1993x + 8.2$ ($R^2 = 0.9384$, $P = 0.009$) derived from quadratic regression was used to calculate biomass using the shape index as the x variable. Canopy ratio was the larger canopy width divided by the smaller canopy width, and indicated the general shape of the trees for which ratios approaching 1 indicated round trees, whereas smaller ratios indicated trees elongated on one axis and truncated on the other. Foliage samples were taken from burn plots preceding the prescribed fires and oven dried at 60°C until dry (4–7 days) to obtain volumetric foliage moisture, which was calculated as:

$$[\text{mass of wet foliage} - \text{mass of dry foliage}] / \text{mass of dry foliage}$$

Trees within treatment plots were marked at the base with numbered steel washers driven into the soil with 30-cm steel nails for monitoring (HB 30 per plot, VoF 21 per plot). We chose trees that were clearly individuals with stems branching from a single base. For each marked tree, maximum height, the average of two maximum canopy diameters, height and species of understorey plants and litter were measured and percentage green *v.* brown (desiccated) foliage and percentage cover of understorey species were visually estimated. At Valley of Fire, herbicide application led to desiccation of 46.8% of the foliage, whereas the control trees showed no desiccation. Because the entire region surrounding the Humboldt site was colonised by *Diorhabda* before the experiment, there were no unaffected trees, so 15 trees with low (mean 42% desiccated foliage) and 15 trees with high (mean 85% desiccated foliage) levels of herbivory were selected.

Fuel manipulation

Litter depth was manipulated beneath selected trees to determine its influence on fire intensity at Humboldt. A subset of monitored trees in each burn plot was assigned to each of the following litter treatments: litter removal, litter addition and unmanipulated control. Litter was collected below *Tamarix* plants adjacent to the burn plots and other nearby infestations. A litter depth of 7.5 cm was chosen to represent maximum litter depth measured in the site area. Trees were selected to investigate the interactive effects of *Diorhabda* herbivory and litter manipulation in a stratified random design: of the 10 trees in each litter treatment, five low and five high herbivory trees were selected.

Prescribed fire treatments

Firebreaks were established at Humboldt to allow for unburned control plots and multiple prescribed fires, which were conducted between 1300 and 1700 hours in August (21, 22 and 24) and October (27, 28 and 29) 2006. At Valley of Fire, a single prescribed fire was conducted on September 26 2008 between 1100 and 1700 hours. Drip torches containing a 1 : 3 gasoline to diesel mixture were used to ignite in a ring around the plots at Humboldt, and flare guns and fuses were used in addition to drip torches at Valley of Fire. Ambient temperature, wind speeds and relative humidity were recorded hourly at each site; at Humboldt data were obtained from the United States Historical

Climatology Network (USHCN) Station at Derby Field Airport located 1.5 km west of the study site, and at Valley of Fire data were collected with a Kestrel 2000 handheld weather meter (Nielsen-Kellerman Co., Birmingham, MI).

Type K nickel–chromium/nickel–aluminium thermocouples and Campbell Scientific CR10X dataloggers (Campbell Scientific, Logan, UT) recorded temperature every 30 s during all prescribed fires to obtain fire temperature over time. To compare temperatures among vegetation layers, thermocouples were placed aboveground in the canopy (HB 1 m, VoF 2 m) within the litter (HB only), at the litter–soil interface near the root crown beneath each monitored tree (HB 30 per plot, VoF nine per plot), and 2 cm below the surface of the mineral soil (HB two per plot) to examine heat penetration. There were an insufficient number of thermocouples to complete the full array at Valley of Fire because all were used in a single prescribed fire, so thermocouples were placed more judiciously among the plots, and were not available for the litter manipulations. Rate of fire spread (m min^{-1}) at Humboldt was calculated using the ignition time of each monitored tree divided by the distance between trees using a map generated by ArcGIS version 9.3 9 (Environmental Systems Research Institute, Inc., Redlands, CA) (HB), and visually estimated at the time of the fire (VoF). Flame lengths were visually estimated during the fires and from video recordings using calibrated poles and other reference objects of known scale.

Statistical analyses

An issue in common with the experimental design of both the Humboldt and Valley of Fire studies, and of fire related studies in general, is that sample units (trees and plots) are by necessity subsamples within burns and are potentially autocorrelated (van Mantgem and Schwilk 2009). Thus the use of inferential statistics to test for treatment effects is potentially problematic because subsamples are not statistically independent by the strictest definition (Hurlbert 1984). However, in ecological studies, the most important aspect is to ensure that the replicate samples are dispersed in a manner appropriate to the hypothesis being tested (Hurlbert 1984). In the setup of these experiments, plots were selected to be representative of the study area, and treatments and subsamples were assigned in a random, or stratified random manner to address these concerns.

All statistical analyses were performed with JMP version 9 using a critical value of 0.05. Proportional data were arcsine square root transformed, and fire intensity index values were natural log transformed to improve normality. Tukey–Kramer Honestly Significant Difference test was used for multiple comparisons of means for significant ANOVA models (Zar 1999). The following analyses are grouped by the level of sampling unit (tree and plot level).

Tree level effects

At Humboldt, four-factor ANOVA models with second degree interactions were used to evaluate the effects of burn treatment (August *v.* October), herbivory level (low *v.* high), litter manipulation (add, control, remove) and thermocouple position (canopy, litter, surface, below) on fire behaviour factors (maximum temperature, duration and fire intensity). At Valley of Fire, two-factor ANOVA models with first degree interactions were used to evaluate the effect of foliar condition (simulated herbivory *v.* control) and thermocouple position (canopy *v.* surface) on fire behaviour factors.

Plot level effects

Two-factor ANOVA models with first degree interactions were used to compare vegetation cover between census timing (pre- *v.* post-fire) and burn treatment (August *v.* October) on vegetation cover at Humboldt, and to compare vegetation cover between census timing (pre- *v.* post-fire) and foliar treatment at Valley of Fire. Foliage moisture was compared between burn season (August *v.* October) and plots at Humboldt, and between foliar treatment and plots at Valley of Fire using two-factor ANOVA with first degree interactions. The effects of plot characteristics (foliar condition, litter depth by plot, tree height by plot, and *Tamarix* and understorey cover) on fire behaviour (rate of spread, flame length, maximum temperature and fire duration) were evaluated using one-factor ANOVA. One-factor ANOVA was used to compare weather conditions between August and October fires at Humboldt.

Results

Site conditions

At Humboldt, weather conditions during the August burn were drier, hotter and windier than during the October burn (Fig. 1, Appendix 1). Wind speeds and relative humidity were generally low at all sites when the burns were conducted. The difference between percentage volumetric foliar moistures in live foliage *v.* foliage desiccated by *Diorhabda* and herbicide at both sites was 10–11%, showing that desiccated foliage was drier than live foliage (Fig. 1, Appendix 1). Vegetation structure was similar across treatment plots within both sites with the exception of tree height: at Humboldt, trees in the autumn burn plots were 11% shorter than those in the summer burn plots, and at Valley of Fire herbicide trees were 13% shorter than control trees (Table 1).

Fire behaviour

Humboldt

At Humboldt, there was no difference in fire intensity (ln degree-minutes above 70°C) between high and low herbivory levels in either summer or autumn burn treatments (Fig. 2, Appendix 2). Fire intensity was instead affected by season and site factors. Fire intensity was 10% greater during the August burn than during the October burn, 28% greater at the ground surface than in the canopy and 12% greater where litter had been added (Figs 3, 4, Appendix 2). Burn duration was 34% longer in the August burn than in the October burn, 88% longer at the surface than in the canopy, 62% longer where litter had been added, 40% longer in high herbivory trees during the August burn only, and there was a strong trend for low herbivory trees to burn 25% longer than high herbivory trees (Appendix 2). Maximum burn temperatures were 19% higher in August than in October, 34% higher at the surface and 70% lower below the soil than in the canopy, and a there was a trend for trees to burn 8% hotter where litter was added (Appendix 2). Interactions occurred when two factors influenced fire intensity, maximum

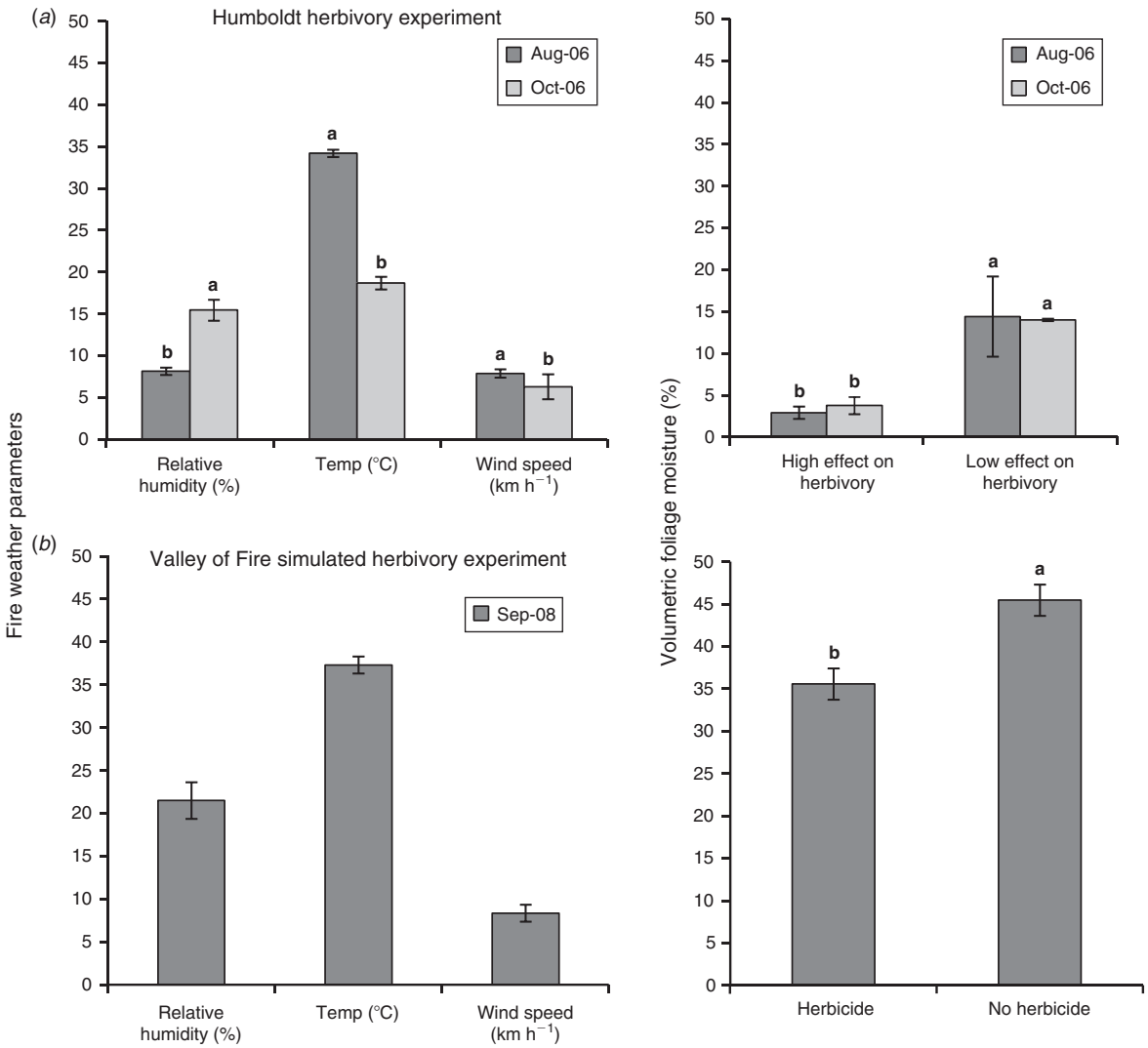

Fig. 1. Fire weather parameters by site and burn timing. Relative humidity, temperature (°C) and wind speed (km h^{-1}) were measured at regular intervals during all prescribed burns (HB, $n = 23$; VoF, $n = 6$). Error bars indicate ± 1 s.e. Multiple comparisons (Tukey HSD) are indicated by bold letters (a, b, etc.) for each parameter. Levels with different superscript letters are significantly different ($P \leq 0.05$).

temperature or duration similarly (i.e. fires burned hottest and longest at the ground surface and when litter was added) and were artefacts of the experimental design (Appendix 2).

The fire spread 38% faster in August than in October, and produced flames that were 60% longer in August than in October. However, the *Tamarix* cover removed was similar across burn seasons: the averages of the two treatments were 44.8% removal of the original *Tamarix* cover and 38% removal of the ground cover (Table 2). *Tamarix* density enhanced fuel consumption (cover reduction) during both burns ($F_{1,8} = 13.37$, $P = 0.0017$, Table 2).

Valley of Fire

At Valley of Fire, flames were 46% longer and the fire spread 47% faster in the simulated herbivory plots than in the control plots (Table 2). The prescribed fire removed 66% of the original *Tamarix* cover and 95% groundcover in both treatments (Table 2). There was a trend for herbicide treated trees to burn with 14% higher intensity than untreated trees (Fig. 2, Table 3). The maximum temperature was 41% higher, and fire duration was 13% longer in the simulated herbivory treatment than in the control treatment (Fig. 2, Table 3). There was no difference in fire intensity, maximum temperature and burn duration between the canopy and ground surface (Fig. 3, Table 3).

Discussion

Maximum temperature and rate of spread were moderately enhanced by herbivory desiccation because dry foliage is more easily ignited. *Diorhabda* consume stem and leaf cuticle, causing water loss from damaged vascular tissues. Initially much of the dry foliage remains intact and is distributed throughout all levels of the vegetation structure. This fuel structure promoted fire behaviour similar to coniferous forests

Table 1. Fuel structure by site

Least square means of fuel structure parameters are reported for each site (±s.e.). *F* ratios and *P* values are reported for 1-factor ANOVA analyses comparing parameters among individual trees and plots between August and October burn treatments at Humboldt, and between simulated herbivory and control treatments at Valley of Fire. Sample sizes varied among measured parameters. *, $P \geq 0.05$

Humboldt		
Tamarix height (m)	Summer 2.5 ± 0.5	$F_{1,178} = 19.37$; $P \leq 0.0001$*
	Autumn 2.8 ± 0.5	
Tamarisk cover (%)	44 ± 5.40	$F_{1,20} = 1.83$; $P = 0.19$
Litter depth (cm)	4.7 ± 0.13	$F_{1,178} = 0.08$; $P = 0.77$
Understorey cover (%)	52.8 ± 3.30	$F_{1,20} = 0.052$; $P = 0.82$
Fuel load (kg ha^{-1})	15 800	N/A
Valley of Fire		
Tamarix height (m)	Herbicide 4.2 ± 0.2	$F_{1,52} = 6.34$; $P = 0.015$*
	Control 4.8 ± 0.2	
Tamarisk cover (%)	$95\% \pm 0.1$	$F_{1,47} = 0.0064$*; $P = 0.94$
Litter depth (cm)	9.1 cm ± 1.0	$F_{1,53} = 1.85$; $P = 0.17$
Ground cover (%)	$88.8\% \pm 0.1$	$F_{1,70} = 0.66$; $P = 0.42$
Fuel load (kg ha^{-1})	212 779	N/A

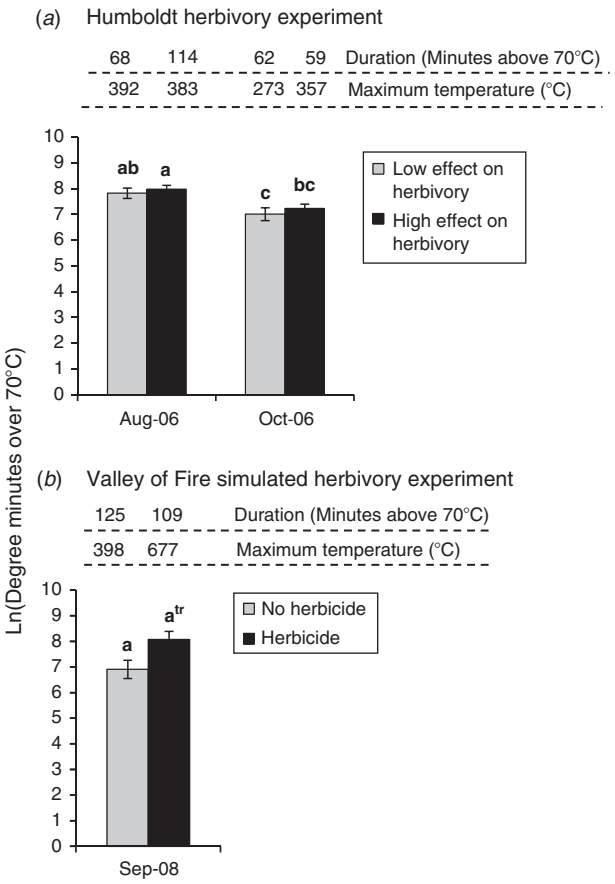

Fig. 2. Fire intensity index *v.* foliage status. At Humboldt, the high herbivory class was defined as Mean 85% desiccation, and the low herbivory class was defined as Mean 42% desiccation. At the Valley of Fire, herbivory desiccation was simulated with herbicide, and the control treatment designated undesiccated foliage (HB, $n = 543$; VoF, $n = 60$). Error bars indicate ±1 s.e. Multiple comparisons (Tukey HSD) are indicated by bold letters (a, b, etc.). Levels with different superscript letters are significantly different ($P \leq 0.05$). Superscript tr indicates a trend.

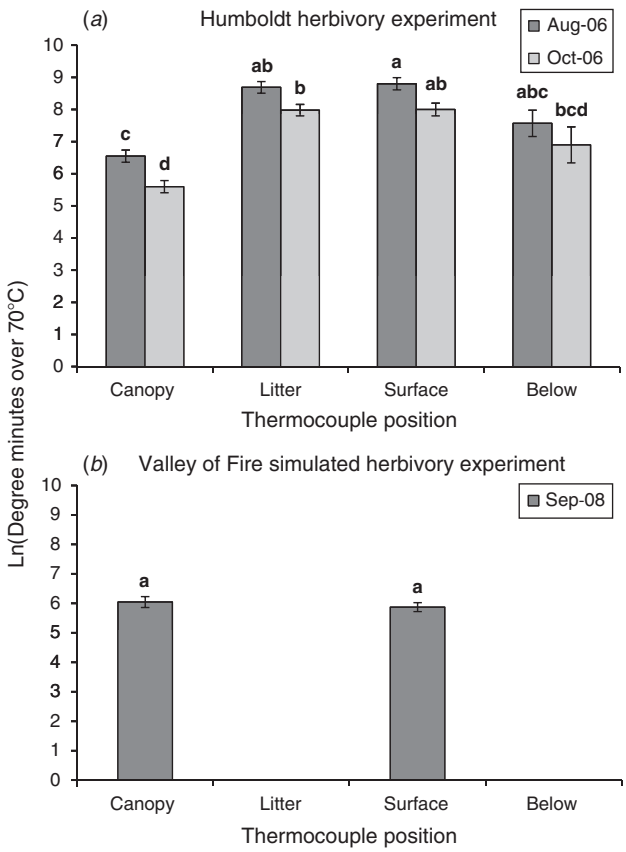

Fig. 3. Thermocouple position by treatment and site, representing fire intensity (index) among different layers of vegetation. Thermocouple position is indicated as canopy (HB and VoF: 1 and 2 m aboveground), litter (HB only: 7.5 cm aboveground within the litter), surface (HB and VoF: at the litter–soil interface) and below (HB and VoF: buried 2 cm below the surface of the mineral soil) and by treatment and thermocouple position. (HB, $n = 543$; VoF, $n = 60$). Error bars indicate ±1 s.e. Multiple comparisons (Tukey HSD) are indicated by bold letters (a, b, etc.). Levels with different superscript letters are significantly different ($P \leq 0.05$).

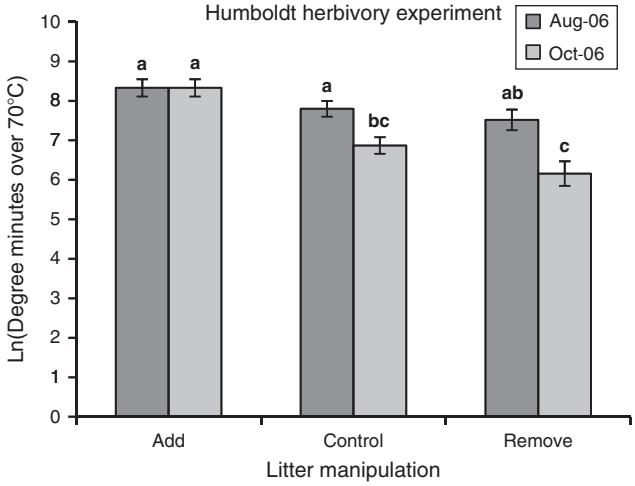

Fig. 4. Fire intensity index in Humboldt summer and autumn burns as a function of litter manipulation. Treatments consist of litter addition (7.5-cm depth), litter removal (bare soil) and an unmanipulated control ($n = 543$). Error bars indicate ±1 s.e. Multiple comparisons (Tukey HSD) are indicated by bold letters (a, b, etc.). Levels with different superscript letters are significantly different ($P \leq 0.05$).

following bark beetle outbreaks where damage to the vascular tissue due to boring also causes foliar desiccation (Knight 1987; Bebi *et al.* 2003). Increased *Tamarix* flammability, even over the short term, could have large-scale effects because more than 600 000 ha of riparian systems in south-western USA have been invaded by *Tamarix* (Everitt 1980; Zavaleta 2000; Gaskin and Schaal 2002) and *Diorhabda* has rapidly spread across lower latitudes in at least nine states, leaving large defoliation zones (Dudley and DeLoach 2004; Dalin *et al.* 2009). However, *Tamarix* is already extremely flammable even in the absence of herbivory, and thus considered a hazardous fuel throughout the south-western states (Racher *et al.* 2003; Dwire *et al.* 2010). The moderate increase in maximum temperature with herbivory desiccation observed in this study suggests that the effects of herbivory are swamped by the innate flammability of *Tamarix.*

Tamarix fire behaviour was influenced by site conditions and vegetation structure to a greater degree than by herbivory desiccation. Fire intensity was enhanced by drier, hotter and windier conditions as was found in previous controlled burns in *Tamarix* conducted during summer months (Howard *et al.* 1983). Because fires are already common during the summer months when *Tamarix* is growing and hydrated, *Diorhabda*

Table 2. Fire behaviour by site, timing and foliage status

Fire behaviour is indicated by rate of spread, flame length and % tamarisk cover reduction. At the Valley of Fire site, both desiccated (herbicide desiccation treatment) and undesiccated (undesiccated control) foliage conditions existed. At the Humboldt site, only desiccated conditions existed (HB, $n = 2546$; VoF, $n = 19$. Values are given ±s.e. *F* ratios and *P* values are reported for 1-factor ANOVA analyses between treatments within a site. *, $P \leq 0.05$

Site	Timing	Foliar status	Rate of spread	Flame length	% *Tamarix* removal	% groundcover removal
Humboldt	Aug-2006	Desiccated	$10.4\ \mathrm{m\,min^{-1}} \pm 1.5$	$6.5\ \mathrm{m} \pm 0.1$	40.0 ± 7.5	40.60 ± 6.1
Humboldt	Oct-2006	Desiccated	$6.5\ \mathrm{m\,min^{-1}} \pm 1.2$	$2.6\ \mathrm{m} \pm 0.0$	49.6 ± 7.5	36.20 ± 6.1
			$F_{1,90} = 4.10$; $P = 0.046$*	$F_{1,2545} = 850.3$; $P < 0.0001$*	$F_{1,10} = 0.68$; $P = 0.43$	$F_{1,10} = 0.27$; $P = 0.61$
Valley of Fire	Sept-2008	Undesiccated	$6.2\ \mathrm{m\,min^{-1}} \pm 2.5$	$19\ \mathrm{m} \pm 4.1$	55.5 ± 4.6	99.50 ± 14.0
Valley of Fire	Sept-2008	Desiccated	$11.7\ \mathrm{m\,min^{-1}} \pm 2.4$	$35\ \mathrm{m} \pm 3.9$	76.7 ± 12.2	90.82 ± 11.1
			$F_{1,18} = 2.51$; $P = 0.13$	$F_{1,18} = 8.2$; $P = 0.01$*	$F_{1,47} = 0.0064$; $P = 0.94$	$F_{1,17} = 0.22$; $P = 0.64$

Table 3. Maximum temperatures, durations and intensities at the Valley of Fire site

2-factor ANOVA model main effects and interaction effects. Main effects include thermocouple position and foliage treatment. Interaction effects are indicated by '×'. *F* ratios and *P* values are reported for main effects and interaction effects where: *, $P \leq 0.05$; superscript tr indicates a trend; $n = 60$. Least squared means (±s.e.) are reported for levels within main effects and interaction effects where superscript letters (a, b, c, etc.) indicate significant differences among levels

		Max temperature (°C)	Duration (min above 70°C)	Intensity (ln degree-minutes above 70°C)
Whole model		$F_{3,59} = 4.40$; $P = 0.007$*	$F_{3,59} = 0.67$; $P = 0.577$	$F_{3,56} = 1.74$; $P = 0.168$
Main effects			Effect levels	
Thermocouple position		$F_{1,59} = 0.52$; $P = 0.473$	$F_{1,59} = 1.80$; $P = 0.185$	$F_{1,56} = 0.94$; $P = 0.336$
	Surface	506.40°C ± 56.09	78.96 ± 36.44	7.17 ± 0.43
	Canopy	569.11°C ± 66.24	154.61 ± 43.04	7.82 ± 0.51
Foliage treatment		$F_{1,59} = 10.31$; $P = 0.002$*	$F_{1,59} = 0.08$; $P = 0.776$	$F_{1,59} = 3.07$; $P = 0.087^{tr}$
	Desiccated	677.10°C ± 60.00[a]	108.72 ± 33.12	8.08 ± 0.39
	Undesiccated	398.42°C ± 75.60[b]	124.85 ± 45.63	6.91 ± 0.54
Interaction effects			Effect levels	
Foliage treatment × Thermocouple position		$F_{1,59} = 0.54$; $P = 0.473$	$F_{1,59} = 0.00$; $P = 0.995$	$F_{1,59} = 0.06$; $P = 0.807$
	Desiccated, canopy	681.41°C ± 68.4[a]	146.73 ± 44.45	8.48 ± 0.53
	Desiccated, surface	672.79°C ± 75.64[a]	70.72 ± 49.14	7.67 ± 0.58
	Undesiccated, canopy	456.81°C ± 113.46[ab]	162.50 ± 73.71	7.15 ± 0.87
	Undesiccated, surface	340.02°C ± 82.86[a]	87.2 ± 53.83	6.67 ± 0.64

desiccation may contribute to a greater number of intense summer fires. Fire intensity was also enhanced by deeper litter and denser vegetation. However, fire intensity is likely to decline with time as repeated *Diorhabda* herbivory eventually reduces the production of fine fuels (Pattison *et al.* 2011*b*). Following an initial defoliation event, regrowth of foliage will occur but at a reduced coverage, and less foliage is produced with each defoliation event (Pattison *et al.* 2011*b*). This suggests that initial defoliation events may pose the greatest fire risk because of the large amount of desiccated leaf and stem material that will hang in the canopy, and that flammability will decrease over time as *Tamarix* plants lose the ability to replace damaged leaves. This is further supported by the strong trend for 25% longer burn durations in the low herbivory trees at Humboldt suggesting that the low herbivory trees had more fuel than did high herbivory trees. Similar reductions in fire intensity have been observed over time with the decay of fine fuels in coniferous forests following bark beetle-induced mortality (Bebi *et al.* 2003; Knight 1987).

The simulated herbivory treatment at Valley of Fire further supports the decline in flammability over time with continued herbivory. Glyphosate was applied to *Tamarix* foliage 1 month before the burn at Valley of Fire to simulate the leaf mortality that would be caused by the establishment of large populations of *Diorhabda.* Glyphosate inhibits the synthesis of aromatic amino acids in the stems, causing rapid leaf dieback and foliar desiccation similar to that caused by *Diorhabda* (Jaworski *et al.* 1984). When *Diorhabda* colonise new areas, entire stands can become rapidly defoliated leaving fine fuels intact (Dudley and Kazmer 2005). Although herbicide cannot truly replicate the effects of a herbivore, glyphosate provided an effective means of desiccating *Tamarix* foliage to replicate an initial *Diorhabda* defoliation event. As with *Diorhabda*, foliar application of glyphosate did not actually kill the plants. However, because there were more fine fuels at Valley of Fire, the comparison was of 0 to 100% herbivory desiccation, whereas the comparison at Humboldt was between medium and high herbivory. Consequently, fire intensity was influenced to a greater degree by foliar status at Valley of Fire. These results support the idea that fire risk is greater immediately following an initial defoliation event than it is after subsequent defoliation events.

Although the sites cannot be compared directly because they were burned at different times, the considerable differences in vegetation structure and fire behaviour observed between them can lend insight into the relative influence of foliar condition and site factors on fire behaviour in *Tamarix*. Greater flame lengths and faster rates of spread were observed at Valley of Fire likely owing to higher fuel continuity (e.g. greater coverage of the ground surface by *Tamarix*) than at Humboldt. Because herbicide was applied only 1 month before the prescribed burn to simulate herbivory desiccation, most fine fuels remained intact and were evenly distributed throughout the canopy. In contrast, *Diorhabda* had defoliated *Tamarix* by 60–80% at Humboldt over several years, leaving only 370 g of fine fuels per square metre before the prescribed burns. Further, although the proportion of the total dry biomass composed of fine fuels was similar between the two sites (HB 24%, VoF 24%), the total biomass of fine fuels at Valley of Fire was 5.7 kg m^{-2}, much greater than at Humboldt (Fig. 5). Additionally, canopy covered only 44% at

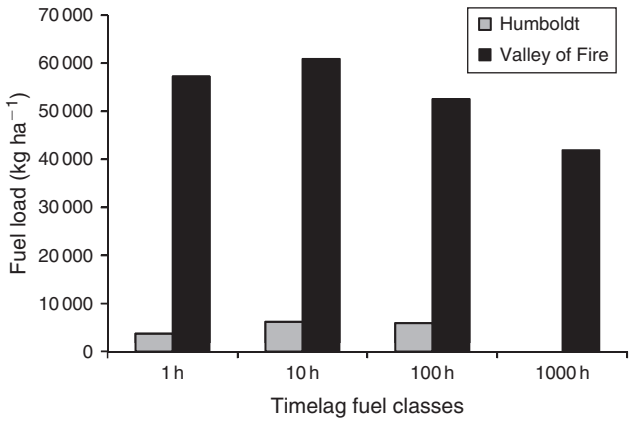

Fig. 5. Fuel load (kg ha^{-1}) by timelag fuel classes at Humboldt and Valley of Fire. Dry biomass was estimated by destructively sampling trees (HB, $n = 15$; VoF, $n = 15$). Samples were separated by timelag fuel classes, and allometric equations were used to extrapolate to the hectare level based on the 5-m radius plots. This method did not allow for error terms.

Humboldt, but covered 95% of the plot area at Valley of Fire. The combination of fine fuels and canopy cover at Valley of Fire created a fuel structure that lead to higher rates of spread and greater flame length. In addition to these factors, trees at Valley of Fire were 2–3 m taller, likely contributing to longer flame lengths than at Humboldt. Larger flame lengths have been shown to be correlated with greater vegetation removal in chaparral, a system with high canopy continuity (Perchemlides *et al.* 2008). In *Tamarix*, however, desiccation increased flame lengths, but not sufficiently to enhance vegetation removal. This shows similar consumability of dense *Tamarix* regardless of foliar condition, and further supports that the effect of herbivory on fire behaviour in *Tamarix* is relatively moderate.

This study shows that *Tamarix* is capable of extreme fire behaviour regardless of foliar condition. Fire behaviour is considered extreme when movement cannot be controlled or predicted, and is commonly indicated by high rates of spread, thermal outputs and flame lengths (Albini 1976; National Wildfire Coordinating Group 2012). However, fire behaviour varies with vegetation structure, topography and weather conditions (Sugihara *et al.* 2006). Fuel models allow prediction and comparison of fire behaviour among systems, and range from simple to complex (Burgan and Rothermel 1984; Finney 1998). Using a 13-fuel model (Anderson 1982) that predicts fire behaviour according to different fuel types (grasslands, shrublands, forests etc.), flame lengths of 5.8 m and a rate of spread of 10.7 m min^{-1} are predicted for dense chaparral vegetation during summer weather conditions with windspeeds of 8 km hr^{-1}. The canopy cover of *Tamarix* at both study sites is similar to the 40–93% observed in chaparral vegetation (Perchemlides *et al.* 2008) and this is reflected by comparable rates of spread observed in this study (10–11 m min^{-1}). However, the flame lengths generated by *Tamarix* were greater than those predicted for chaparral vegetation, and the 3.5-m level that managers generally consider extreme (Caballero *et al.* 2002; Pearce 2007). Chaparral vegetation can produce flame lengths in excess of 30 m under conditions of high wind and slope (Riggan *et al.* 1994), but we observed flame lengths of 35 m in

desiccated *Tamarix* at Valley of Fire during relatively less windy conditions. Surprisingly, the flame lengths we observed in desiccated *Tamarix* were still lower than the 43-m lengths reported in green (undesiccated) *Tamarix* by another study in New Mexico (Racher *et al.* 2001). Such observations suggest that fire behaviour can be extreme in undesiccated as well as desiccated *Tamarix*, and provides further evidence for *Tamarix* invasion increasing fire risk in desert riparian systems.

Riparian zones have long been considered less flammable than upland systems, but fires have become more common with *Tamarix* invasion. Large and intense fires have been reported in native vegetation following drought (Pettit and Naiman 2007), but there are few empirical data on the fire behaviour of native riparian species in the scientific literature with which to compare *Tamarix* fire behaviour. Fire frequency will likely continue to increase with prolonged periods of drought predicted by recent climate change models (Williams and Cooper 2005), and as native riparian species are replaced by the more drought-resistant (Cleverly *et al.* 1997) and fire-resilient *Tamarix* (Ellis 2001). Therefore, a better understanding of the role of fire in riparian systems is needed to effectively manage their ecologically and economically valuable resources over the long term.

In response to the large-scale effects of *Tamarix* invasion on desert riparian ecosystem structure and function, resource managers use biological control, herbicide and other techniques to remove *Tamarix* and ultimately reduce fire risk attributed to its high stem density and deep litter (Harms and Hiebert 2006; Swanson and Gilgert 2009; Conlin 2010). Biological control and herbicide application have been shown to be effective management tools on the Colorado River (Conlin 2010). However, land managers can allocate their resources more efficiently knowing that the early stages of *Diorhabda* establishment and defoliation is when fire risk is moderately elevated, and can focus fire suppression efforts on areas recently colonised by *Diorhabda*. Repeated defoliation could ultimately also result in great mortality of *Tamarix* when fire does occur (G. M. Drus, unpubl. data). Although mechanical removal could be used to quickly reduce fuel loads in high fire risk areas, managers should carefully weigh short-term increases in fire risk with long-term reductions in *Tamarix* biomass due to herbivory. Management plans should also consider the vegetation structure in *Tamarix*-invaded areas, because denser infestations may prove a greater fire risk than those with lower density, even those desiccated by *Diorhabda*. Denser infestations could also become more flammable following *Diorhabda* herbivory, as standing wood could become more ignitable as it dies, and high fuel continuity may facilitate fire spread even when fine fuels have been reduced. Managers also should be aware that areas recently treated with herbicide may exhibit increased flammability due to similarities between herbivory and herbicide. Although herbicide is applied at a much smaller scale than is biocontrol, large expanses of *Tamarix* monocultures are commonly treated; for example 2415 ha on the Pecos river in New Mexico (Barz *et al.* 2009). Ultimately, as *Diorhabda* herbivory or other techniques begin to affect the recovery potential of *Tamarix* at the stand level, fire risk will decline facilitating the reintroduction of less flammable native species either naturally in areas with periodic flooding, or by active restoration practices.

Conclusion

As *Diorhabda* continues to expand its range, herbivory may cause short-term increases in fire risk. Further, herbivory may enhance fire intensity during the summer months when fires are already common in *Tamarix*-dominated riparian areas. However, *Tamarix* fire behaviour in this study was affected to a greater degree by weather conditions, vegetation density and litter depth than by herbivory. Over the longer term, continued *Diorhabda* herbivory will decrease *Tamarix* biomass, thereby ultimately reducing fire intensity and fire risk in *Tamarix*-invaded areas.

Acknowledgements

The authors acknowledge G. Munk, C. Deuser (National Park Service) and Brinkerhoff Ranch for assisting in site selection and burn preparation, and K. Sneider (University of Nevada, Reno) for providing laboratory space and field assistants. Many people provided assistance in the field, but the authors give special thanks to J. TenBrinke, W. Pyle, R. McNeil, M. Taylor, S. Ostoja, the Lake Mead Exotic Plant Management Team (especially D. Coleman, R. Tietjen and B. Points) and the members of the Silver State Hunt Club. We thank the many people who provided constructive comments on this manuscript, especially T. Even, C. D'Antonio, P. Shafroth and several anonymous reviewers. We also thank A. Stewart-Oaten for statistical consultation. This work was supported in part by the Joint Fire Science Program (05-2-1-18), Clark County Multiple Species Habitat Conservation Program (2005-UCSB-552), Luce Environmental Science to Solutions Fellowship and the UC Santa Barbara Graduate Division.

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Appendix 1. Weather conditions and fuel moisture by treatment and site

Least square means of weather parameters are reported for each site (±s.e.). F ratios and P values are reported for 1-factor ANOVA analyses between burn treatments at the Humboldt site, and between live and dead foliage samples at both sites. *, $P \leq 0.05$; superscript tr indicates a trend. Sample sizes differed according to parameter measured

Humboldt	August	October		Valley of Fire	
Relative humidity (%)	8.17 ± 0.44	15.45 ± 1.26	$F_{1,19} = 24.54$; $P \leq 0.001$*	Relative humidity (%)	21.50 ± 2.12
Ambient temperature (°C)	34.20 ± 0.44	18.69 ± 0.77	$F_{1,19} = 308.19$; $P \leq 0.001$*	Ambient temperature (°C)	37.32 ± 0.99
Wind speed (m min^{-1})	8.37 ± 0.97	6.29 ± 1.48	$F_{1,19} = 18.47$; $P = 0.0004$*	Wind speed (m min^{-1})	8.37 ± 0.97
Foliar moisture (%)	8.67 ± 0.97	9.92 ± 2.50	$F_{1,21} = 0.05^{\mathbf{tr}}$; $P = 0.82$	Foliar moisture (%)	41.82 ± 7.17
Live foliage 14.40 ± 4.8				Live foliage 45.50 ± 1.8	
Dead foliage 2.93 ± 0.7				Dead foliage 35.60 ± 1.8	
$F_{1,16} = 5.59$; $P = 0.030$*				$F_{1,35} = 7.39$; $P = 0.009$*	

Appendix 2. Maximum temperatures, durations and intensities at the Humboldt site

4-factor ANOVA model effects and second order interaction effects are reported for maximum temperature, duration and intensity. The main effects include burn treatment, thermocouple position, herbivory level and litter manipulation. Interaction effects are indicated by '×'. F ratios and P values are reported for main effects and interaction effects where: *, $P \leq 0.05$; superscript tr indicates a trend; $n = 477$. Least squared means (±s.e.) are reported for levels within main effects and interaction effects where superscript letters (a, b, c, etc.) indicate significant differences among levels

		Max temperature (°C)	Duration (min above 70°C)	Intensity (ln degree-minutes above 70°C)
Whole model		$F_{24,452} = 7.44$; $P < 0.0001$	$F_{24,452} = 11.85$; $P < 0.0001$	$F_{24,452} = 14.10$; $P < 0.0001$
Main effect		Effect levels		
Burn treatment		$F_{1,452} = 6.45$; $P = 0.0114$*	$F_{1,452} = 6.97$; $P < 0.0086$*	$F_{1,452} = 15.23$; $P = 0.0001$*
	Summer burn	387.69 ± 18.65^{a}	91.30 ± 7.61^{a}	7.90 ± 0.13^{a}
	Autumn burn	315.23 ± 23.62^{b}	60.55 ± 9.64^{b}	7.12 ± 0.17^{b}
Thermocouple position		$F_{3,452} = 31.87$; $P < 0.0001$*	$F_{3,452} = 28.99$; $P < 0.0001$*	$F_{3,452} = 64.16$; $P < 0.0001$*
	Canopy	361.44 ± 19.33^{b}	14.49 ± 7.89^{c}	6.07 ± 0.14^{c}
	Litter	544.87 ± 18.51^{a}	58.57 ± 7.56^{b}	8.33 ± 0.13^{a}
	Surface	334.77 ± 19.90^{b}	116.12 ± 8.12^{a}	8.40 ± 0.14^{a}
	Below	164.76 ± 53.19^{c}	114.52 ± 21.71^{ab}	7.23 ± 0.37^{b}
Herbivory level		$F_{1,452} = 1.76$; $P = 0.1850$	$F_{1,452} = 3.56$; $P = 0.0598^{\mathbf{tr}}$	$F_{1,452} = 0.93$; $P = 0.3356$
	Low	332.50 ± 24.73^{a}	64.93 ± 10.09^{a}	7.41 ± 0.17^{a}
	High	370.42 ± 17.18^{a}	86.93 ± 7.01^{a}	7.61 ± 0.12^{a}
Litter manipulation		$F_{2,452} = 2.45$; $P = 0.0870^{\mathbf{tr}}$	$F_{2,452} = 28.5$; $P < 0.0001$*	$F_{2,452} = 19.1$; $P < 0.0001$*
	Add	390.08 ± 21.99^{a}	134.78 ± 9.00^{a}	8.35 ± 0.15^{a}
	Control	360.56 ± 22.00^{a}	51.69 ± 8.98^{b}	7.33 ± 0.15^{b}
	Remove	303.74 ± 33.47^{a}	41.30 ± 13.66^{b}	6.84 ± 0.24^{b}
Interaction effect		Effect levels		
Burn treatment × Thermocouple position		$F_{3,452} = 1.22$; $P = 0.3013$	$F_{3,452} = 0.99$; $P = 0.3970$	$F_{3,452} = 0.17$; $P = 0.9141$
	Summer burn, canopy	429.43 ± 26.31^{bc}	20.69 ± 10.74^{d}	6.55 ± 0.19^{c}
	Summer burn, litter	588.64 ± 25.59^{a}	70.29 ± 10.45^{bc}	8.69 ± 0.18^{ab}
	Summer burn, surface	388.85 ± 26.65^{bcd}	140.01 ± 10.88^{a}	8.80 ± 0.19^{a}
	Summer burn, below	143.84 ± 58.52^{e}	134.21 ± 23.89^{ab}	7.57 ± 0.41^{abc}
	Autumn burn, canopy	293.44 ± 27.42^{de}	8.30 ± 11.19^{d}	5.60 ± 0.19^{d}
	Autumn burn, litter	501.11 ± 26.01^{ab}	46.84 ± 10.62^{cd}	7.98 ± 0.18^{b}
	Autumn burn, surface	280.69 ± 28.46^{de}	92.22 ± 11.62^{bc}	8.00 ± 0.20^{ab}
	Autumn burn, below	185.67 ± 79.11^{cde}	94.84 ± 32.29^{abcd}	6.90 ± 0.56^{bcd}
Burn treatment × Herbivory level		$F_{1,452} = 4.53$; $P = 0.0338$*	$F_{1,452} = 7.43$; $P = 0.0067$*	$F_{1,452} = 0.03$; $P = 0.8648$
	Summer burn, low	391.90 ± 28.27^{a}	68.19 ± 11.54^{b}	7.82 ± 0.20^{ab}
	Summer burn, high	383.47 ± 21.88^{a}	114.41 ± 8.93^{a}	7.98 ± 0.15^{a}
	Autumn burn, low	273.10 ± 35.05^{b}	61.67 ± 14.31^{b}	7.01 ± 0.25^{c}
	Autumn burn, high	357.36 ± 24.37^{ab}	59.44 ± 9.95^{b}	7.23 ± 0.17^{bc}

(*Continued*)

Appendix 2. (Continued)

	Max temperature (°C)	Duration (min above 70°C)	Intensity (ln degree-minutes above 70°C)
Burn Treatment × Litter manipulation	$F_{2,452} = 6.43$; $P = 0.0018$*	$F_{2,452} = 0.38$; $P = 0.6825$	$F_{2,452} = 7.08$; $P = 0.0009$*
Summer burn, add	378.41 ± 27.23^{a}	147.68 ± 11.11^{a}	8.33 ± 0.22^{a}
Summer burn, control	401.64 ± 28.14^{a}	64.11 ± 11.49^{b}	7.80 ± 0.20^{a}
Summer burn, remove	383.01 ± 36.44^{a}	62.11 ± 14.88^{b}	7.52 ± 0.26^{ab}
Autumn burn, add	401.75 ± 31.23^{a}	121.89 ± 12.75^{a}	8.33 ± 0.22^{a}
Autumn burn, control	319.47 ± 30.53^{ab}	39.27 ± 12.46^{b}	6.87 ± 0.21^{bc}
Autumn burn, remove	224.47 ± 43.73^{b}	20.49 ± 17.85^{b}	6.16 ± 0.31^{c}
Thermocouple position × Herbivory level	$F_{3,452} = 1.07$; $P = 0.3635$	$F_{3,452} = 0.72$; $P = 0.5377$	$F_{3,452} = 0.90$; $P = 0.4390$
Canopy, high	363.67 ± 22.53^{b}	17.13 ± 9.20^{c}	6.26 ± 0.16^{c}
Canopy, low	359.21 ± 31.48^{bc}	11.86 ± 12.85^{c}	5.88 ± 0.22^{c}
Litter, high	562.22 ± 21.77^{a}	67.81 ± 8.89^{b}	8.42 ± 0.15^{a}
Litter, low	527.52 ± 31.13^{a}	49.32 ± 12.30^{bc}	8.24 ± 0.21^{ab}
Surface, high	384.60 ± 22.94^{b}	135.26 ± 9.36^{a}	8.71 ± 0.16^{a}
Surface, low	284.93 ± 32.57^{bc}	96.98 ± 13.30^{ab}	8.09 ± 0.23^{ab}
Below, high	171.17 ± 56.71^{c}	127.51 ± 23.15^{ab}	7.03 ± 0.40^{bc}
Below, low	158.35 ± 81.11^{bc}	101.54 ± 33.11^{abc}	7.44 ± 0.57^{abc}
Thermocouple position × Litter manipulation	$F_{6,452} = 0.48$; $P = 0.8246$	$F_{6,452} = 7.30$; $P < 0.0001$*	$F_{6,452} = 2.05$; $P = 0.0583^{tr}$
Canopy, add	382.14 ± 32.06^{bc}	11.77 ± 13.09^{d}	6.32 ± 0.23^{c}
Canopy, control	353.36 ± 31.83^{bc}	13.43 ± 12.99^{d}	6.04 ± 0.22^{c}
Canopy, remove	348.81 ± 34.09^{bc}	18.27 ± 13.92^{d}	5.86 ± 0.24^{c}
Litter, add	604.72 ± 40.00^{a}	86.54 ± 12.65^{c}	8.99 ± 0.22^{a}
Litter, control	537.68 ± 30.40^{a}	43.40 ± 12.41^{cd}	8.20 ± 0.21^{ab}
Litter, remove	492.22 ± 32.63^{ab}	45.76 ± 13.32^{cd}	7.80 ± 0.23^{b}
Surface, add	380.40 ± 32.10^{bc}	180.86 ± 13.10^{ab}	9.19 ± 0.23^{a}
Surface, control	323.97 ± 31.66^{c}	93.31 ± 12.92^{c}	8.28 ± 0.22^{ab}
Surface, remove	299.93 ± 36.66^{c}	74.19 ± 14.97^{cd}	7.73 ± 0.26^{b}
Below, add	193.06 ± 66.34^{c}	259.96 ± 27.08^{a}	8.92 ± 0.47^{ab}
Below, control	227.21 ± 68.18^{c}	56.63 ± 27.83^{cd}	6.80 ± 0.48^{bc}
Below, remove	74.00 ± 116.40^{c}	26.98 ± 47.51^{bcd}	5.98 ± 0.82^{bc}
Herbivory level × Litter manipulation	$F_{2,452} = 3.35$; $P = 0.0359$*	$F_{2,452} = 3.36$; $P = 0.0358$*	$F_{2,452} = 2.69$; $P = 0.0690^{tr}$
Low, add	339.15 ± 34.43^{ab}	108.77 ± 14.06^{b}	8.05 ± 0.24^{ab}
Low, control	375.44 ± 32.69^{ab}	52.14 ± 13.34^{c}	7.45 ± 0.23^{bc}
Low, remove	282.93 ± 46.38^{b}	33.87 ± 18.93^{c}	6.74 ± 0.33^{c}
High, add	441.02 ± 24.08^{a}	160.79 ± 9.82^{a}	8.65 ± 0.17^{a}
High, control	345.67 ± 26.09^{ab}	51.25 ± 10.65^{c}	7.22 ± 0.18^{bc}
High, remove	324.55 ± 34.21^{b}	48.74 ± 13.97^{c}	6.95 ± 0.24^{c}