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Synergistic interactions between leaf beetle herbivory and fire enhance tamarisk (*Tamarix* spp.) mortality

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HIGHLIGHTS

- We investigated the effect of beetle herbivory and fire on *Tamarix* spp. mortality.
- We quantified fire intensity and a gradient of beetle herbivory.
- Herbivory was measured as proportion of green canopy and percent root crown starch.
- Low root starch and high fire intensity yielded the highest *Tamarix* mortality.
- Disproportionate increases in mortality prediction trace slopes indicate synergism.

GRAPHICAL ABSTRACT

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ABSTRACT

The combined effects of herbivory and fire on plant mortality were investigated using prescribed burns of tamarisk (*Tamarix ramosissima* Lebed) exposed to herbivory by the saltcedar leaf beetle (Chrysomelidae: *Diorhabda carinulata* Desbrocher). *Tamarix* stands in the Humboldt Sink (NV, USA) were divided into three treatments: summer burn (August 2006), fall burn (October 2006) and control (unburned), and litter depth was manipulated to vary fire intensity within burn seasons. A gradient of existing herbivory impact was described with three plant condition metrics prior to fire: reduced proportions of green canopy, percent root crown starch sampled at the height of the growing season (August 2006), and percent root crown starch measured during dormancy (December 2006). August root crown starch concentration and proportion green canopy were strongly correlated, although the proportion green canopy predicted mortality better than August root crown starch. December root crown starch concentration was more depleted in unburned trees and in trees burned during the summer than in fall burn trees. Mortality in summer burned trees was higher than fall burned trees due to higher fire intensity, but December root crown starch available for resprouting in the spring was also lower in summer burned trees. The greatest mortality was observed in trees with the lowest December root crown starch concentration which were exposed to high fire intensity. Disproportionate changes in the slope and curvature of prediction traces as fire intensity and December starch reach reciprocal maximum and minimum levels indicate that beetle herbivory and fire intensity are synergistic.

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1. Introduction

Plants die when their tolerance to environmental stress is exceeded or when disturbance removes so much of them that they cannot regenerate. Both abiotic (weather, water deficit, fire) and biotic (competition, pathogen infections, herbivory) factors can act as stressors for plants. Various stressors may interact (Selye, 1936; Lichtenthaler, 1998) resulting in non-additive responses or synergisms whereby the effect of combined stresses is greater than the sum of the individual stresses (Folt et al., 1999).

Fire is a short-term, high-intensity disturbance event that can have long-term consequences because it damages and removes plant tissues. The removal of photosynthetic tissue forces plants with resprouting capabilities to compensate by allocating non-structural carbohydrates (sucrose, fructose, and starch) from storage organs to replace lost or damaged tissues (Turgeon, 1991; Cannell and Dewar, 1994). Many woody plants recover from fire by resprouting from apical meristems in lignotubers or fire resistant root crowns (Bond and Midgley, 2001). This draws upon stored carbohydrates making resprouting a metabolically demanding process (Verdaguer and Ojeda, 2002).

Biotic factors such as herbivory also influence plant performance and can induce plant stress responses. Insect herbivory removes photosynthetic tissue altering plant morphology and physiology, reducing resource acquisition rates and carbohydrate and nutrient storage (Trumble et al., 1993; Baldwin, 1994; Karban and Baldwin, 1997). In response to herbivory, regrowth and the production of defensive compounds can be metabolically costly (Baldwin, 1994). With repeated bouts of herbivory, carbohydrate demand to replace lost or damaged tissues and to maintain metabolism can exceed supply, resulting eventually in mortality as a consequence of cumulative carbon starvation (McDowell et al., 2008; Bean et al., 2013). Mortality can also occur before carbohydrate stores are exhausted because plants no longer have access to them, such as during drought where phloem transport is inhibited by low turgor pressure and xylem cavitation (McDowell, 2011). Thus the sensitivity of plants to stress can be a function of resource storage as well as resource access.

Although individual stresses can cause mortality over time, the impacts of two or more stresses can increase likelihood of mortality (Sih et al., 1998; Alexieva et al., 2003). For example damage to water hyacinth (*Eichhornia crassipes*) by the burrowing weevil (*Neochetina* spp.) has been shown to facilitate access into plant tissues by secondary microbial infections (Charudattan, 1986). Insect damage has also been shown to amplify the effects of fire in conifer forests following bark-beetle outbreaks which cause desiccation of foliar tissues which increases fire intensity and reduces post-fire recovery (Brown, 1975; Knight, 1987; Bebi et al., 2003). Consequently, these interactions increase the probability of individual mortality, and thus enhance population mortality.

The invasion and management of tamarisk (*Tamarix ramosissima* Lebed), a non-native tree from Eurasia, provides a context for investigating how multiple stress factors may interact to influence plant mortality. *Tamarix* spp. dominate desert river (riparian) areas across the southwestern United States forming dense stands that can increase the threat of flooding and erosion, increase fire risk, deplete groundwater and cause other landscape-level effects (Shafroth et al., 2005). Mechanical and chemical treatments to reduce *Tamarix* abundance are common yet expensive, temporary, and cause collateral damage to riparian habitat by altering vegetation structure, disturbing soils, promoting secondary plant invasion, and contaminating riparian areas (Shafroth et al., 2005). Prescribed fire can be an efficient means for reducing aboveground *Tamarix* biomass because the monocultures of fine-textured foliage and the accumulation of understory litter and debris readily carry high intensity fires (Drus et al., 2012). However, fire rarely leads to mortality because *Tamarix* spp. regenerate rapidly from a root crown protected belowground from fire (Racher and Mitchell, 2009). Fire itself is a variable disturbance agent in that its effects on plants vary with condition of the plants (moisture, stress), and climate factors influencing fire intensity. In addition, fire intensity can vary as a function of litter accumulation (Drus et al., 2012) which in turn can influence the severity of damage to the root crown. Seasonal timing of fire will affect plant condition as well as intensity achieved due to weather conditions.

In 2001, the northern tamarisk leaf beetle (Chrysomelidae: *Diorhabda carinulata* Desbrocher, hereafter *D. carinulata*) was released in the United States for the biological control of *Tamarix* spp. (DeLoach et al., 2003). *D. carinulata* feeds on the epidermis of *Tamarix* stems and leaves causing them to desiccate (Lewis et al., 2003). Much of the foliar material is left intact and is termed defoliation when the foliage turns brown and dies (Lewis et al., 2003; Pattison et al., 2011a). This herbivory has been demonstrated to alter *Tamarix* physiology including water relations (Pattison et al., 2011a), reduce *Tamarix* growth, and eventually results in tree mortality as carbohydrate stores, particularly starch, are depleted (Hudgeons et al. 2007; Pattison et al., 2011a,b; Bean et al., 2013). Mortality from herbivory alone is a slow process because *Tamarix* can compensate for herbivore damage via foliage re-growth between *D. carinulata* cohorts, and can partially recover carbohydrate stores (Bean et al., 2013). However, the reduction in carbohydrate stores may enhance the susceptibility of *Tamarix* spp. to additional stresses such as fire. Thus although *D. carinulata* does not directly kill many *Tamarix* trees during initial years of beetle feeding, plants stressed by herbivory may become more controllable with fire than those not affected by herbivory.

The central question addressed by this study is: does *D. carinulata* herbivory enhance post-fire mortality in *Tamarix* spp.? The following hypotheses were tested: (1) Root crown starch will be the strongest predictor of post-fire recovery in the following spring and summer. (2) High fire intensity as a result of either season of fire or litter manipulation will cause greater tissue damage and subsequent mortality than lower fire intensity (3). The greatest mortality will occur in *Tamarix* exposed to both high fire intensity and high levels of pre-fire herbivore damage, and we suspect that the interaction is non-additive.

2. Materials and methods

In this study, we used prescribed burning in stands of tamarisk (*T. ramosissima* × *chinensis* hybrids, hereafter *Tamarix*) exposed to *D. carinulata* beetle herbivory to evaluate the combined effects of herbivory and fire damage on *Tamarix* mortality. Because there were no trees without at least some herbivore damage, we used variation in herbivore damage, indicated by variation in the proportion of canopy of individual trees showing re-growth (green tissue) and by variation in root crown starch, to evaluate herbivory effects. Root crown starch was measured prior to fire as part of our description of plant condition, and was measured following fire during dormancy to quantify the amount of carbohydrate storage available for regrowth in the following spring. Variation in fire intensity occurred as a result of burning during summer (hot and drier) versus autumn (cooler) and by active manipulation of litter depth.

2.1. Study site

The study site is in the Great Basin, USA at 1220 m elevation in the lower Humboldt River basin, in Pershing County, northern Nevada (40.07°N, 118.5°W). The site experiences warm summer (mean high 32 °C) and cold winter (mean high 8 °C) temperatures, and the average annual precipitation is 14 cm, most of which falls between February and late May (NOAA, 2011). Shallow groundwater (⩽5 m) is recharged primarily through upper watershed precipitation and snowmelt (Lopes et al., 2006; Pattison et al., 2011a). Soils are saline, fine-textured silts deposited into the Humboldt Sink terminal basin via drainage from much of northern Nevada (Nash, 2005). Dense stands of *Tamarix* occupy over 15,000 hectares in the Humboldt basin (Sengupta et al., 2004). The *Tamarix* at the site were most likely *T. ramosissima* × *chinensis* hybrids, as hybrids comprise the vast majority of *Tamarix* infestations in western North America (Gaskin and Kazmer, 2009).

The study site is located 8.5 km north of the Humboldt River in a saline floodplain adjacent to agricultural fields. *Tamarix* forms a nearly continuous monoculture 2–4 m in height with an understory of non-native forbs (fivehook bassia – *Bassia hyssopifolia*, Russian knapweed – *Acroptilon repens,* tall whitetop – *Lepidium latifolium,* and halogeton – *Halogeton glomeratus*). Native alkaline scrub vegetation in the vicinity of the site includes saltgrass (*Distichlis spicata*), greasewood (*Sarcobatus vermiculatus*), and saltbush (*Atriplex* spp.).

The Pershing County Water District has a goal of eradicating *Tamarix* for water conservation and to regain traditional land uses for the region. Local landowners and managers periodically burn *Tamarix* to reduce its cover, although this approach has not decreased *Tamarix* cover beyond the immediate post-fire year (C. Clinger and G. Munk personal communication June 2006). In 2001, *Diorhabda* was released 6.5 km southeast of the study site. By 2003 it had spread to defoliate ca. 200 hectares, including the study site (Dudley, 2005). At the time of the experimental fire treatments (2006), *Tamarix* individuals at the study site had experienced *Diorhabda* herbivory over 3 growing seasons resulting in 60–80% canopy dieback (Pattison et al., 2011b) and in 10% mortality.

2.2. Experimental design

The combined effects of herbivory and fire on *Tamarix* mortality were evaluated as part of experimental burns conducted for a concurrent study of fire behavior in summer versus fall seasons (Drus et al., 2012). Summer burn, fall burn and unburned (control) treatments were replicated among three blocks across the project area, covering a total of 4.5 hectares. Within each block, three 0.5 ha plots were randomly assigned to each treatment (summer, fall, unburned). Prescribed burns were carried out by U.S. Geological Survey (USGS) personnel using drip torches and backing fires. Details are explained by Drus et al. (2012).

2.3. Herbivory, plant condition and mortality

To evaluate the relationship between herbivory and post-fire mortality, we exploited existing variation in regrowth of *Tamarix* trees in response to defoliation following several seasons of *D. carinulata* herbivory. Variation in regrowth may be due to genetic variation or to subtle environmental variation (e.g. access to water) that affects the tree's ability to regrow. In either case its existence allows us to evaluate whether more vigorous trees (more regrowth) are more or less susceptible to fire. We estimated the impact of herbivory in two ways: (1) by evaluating canopy reduction by herbivory and (2) via measures of root crown carbohydrate storage before fire.

Thirty trees per plot were equally separated into two categories based on the proportion of the canopy that was green, which represented the trees' ability to re-grow following herbivory. Proportion green canopy was estimated visually by two different investigators (TD, GD) and were within 5% of one another. Values were obtained by dividing the live canopy volume by the total canopy volume. In each plot, 15 high green canopy (58 + 0.8%) and 15 low green canopy (15 + 0.6%) trees were selected (90 trees per treatment, 270 total) in a stratified random design. Values ranged from 5% to 95%. Although we categorized the trees into high and low canopy removal, the actual% canopy that was green was recorded for each tree.

Root crown starch content appears to decrease in *Tamarix* in response to *D. carinulata* herbivory (Hudgeons et al., 2007) and thus can be used as an index of herbivore stress. Tissue was extracted from the root crowns of ten of the thirty trees (five high regrowth, and five low regrowth) per plot. The tree root crown was exposed by digging. A cordless drill and a 3/4″ (20 mm) wood boring bit were employed to drill 10 mm into the crown tissue. Prior to collecting crown tissue, the bark layer was removed from the point of sampling using the cordless drill and bit. The shavings were collected in foil and placed on dry ice. Once back in the laboratory, the samples were dried at 100 °C for one hour and then at 65 °C for two days. Subsequently, the samples were ground on a Wiley mill using a 40 mesh (0.5 mm) screen, and were stored in the dark at room temperature. Percent starch was then determined using an enzymatic extraction technique. Water soluble sugars were separated from starch using an ethanol extraction. Starch was then digested into glucose by Amyloglucosidase and converted into NADPH (stoichiometric to glucose) and measured by means of light absorbance at 340 nm using a Spectronic 601 Spectrophotometer (Milton-Roy, Ivyland, PA). Starch concentration was then calculated as the percent of sample dry weight (Hudgeons et al., 2007).

Starch samples were carried out across litter manipulation trees (see Section 2.4) in a stratified random manner such that an equal number of addition, removal and control trees were sampled for each regrowth class within each burn treatment. Samples were collected in August 2006 during the peak of the growing season, and in December 2006 during dormancy. The former is indicative of the degree to which herbivory might have reduced plant performance while the latter indicates starch available for recovery in the spring and summer following the prescribed burns. It should thus be a predictor of regrowth ability or probability of mortality. It is a third measure of plant condition, although influenced by both herbivory and fire.

Prior to the prescribed fires, trees that had died from either *D. carinulata* herbivory or other causes were tallied across plots as a baseline for mortality and subtracted from the total number of trees to monitor. Following the prescribed fires, tree mortality was monitored monthly during growth periods (April–November 2007) for a year following the prescribed burns. Resprouting (presence or absence) was recorded for each monitored tree, and two 50 m long by 2 m wide transects were established in each plot to record the number of unmonitored trees resprouting vs. not resprouting to estimate burning-induced plot-level mortality. Trees that initially produced fresh post-fire sprouts which then died, and trees that failed to produce resprouts one-year post-fire were classified as dead and were confirmed dead by follow-up censuses in 2009 and 2013.

2.4. Fire intensity index

A fire intensity index was generated to evaluate the importance of the exposure of the root crown to heat (Drus et al., 2012). The index integrates burn duration and maximum temperature in units of Degree-Minutes above 70 °C, a temperature lethal to most plant tissues (Lepeschkin, 1938). Type K Nickel–Chromium/Nickel–Aluminum thermocouples were placed at the root crown of each tagged tree and CR10X dataloggers (Campbell Scientific, USA) recorded temperature at 30 s intervals during experimental burns to obtain temperature over time, and to calculate fire intensity. Litter depth was manipulated to influence fire intensity in the vicinity of the root crown (10 trees per plot, 30 trees per burn treatment), as deeper litter has been shown to increase fire intensity (Van Wagtendonk, 2006). The goal was to create high and low fire intensity root crown areas to evaluate how fire intensity interacted with herbivory. Treatments included the addition of litter 7.5 cm deep within 25 cm of the tree base to enhance fire intensity, the removal of litter extending at least 25 cm from the tree base to reduce fire intensity, and no litter manipulation as a control (mean depth 4.67 cm). A litter depth of 7.5 cm was used because it is within the high range of natural litter depth observed in other *Tamarix* infestations in the Humboldt basin. Drus et al. (2012) found clear relationships between litter manipulations and fire intensity at this site, thus analyses in the present study emphasize the fire intensity index as a continuous variable in lieu of litter manipulation treatment categories.

2.5. Statistical Analyses

JMP© version 9.0 (SAS Corporation) was used for statistical analysis and a *p*-value of <0.05 was used as a detection of significance although any values between 0.05 and 0.10 are reported as trends. Tukey HSD (honestly significantly different test) was used for multiple comparisons. Burning-induced plot-level mortality (proportion of total live vs. dead trees in a plot excluding monitored trees), was compared across treatments (summer, fall and unburned control) using 1-factor ANOVA. Relationships between the percent live *Tamarix* canopy following several seasons of *D. carinulata* beetle herbivory and the percent root crown starch sampled in August vs. December 2006 were compared to relationships between proportion green canopy and percent root crown starch (December 2006) for the summer burn, fall burn and unburned control using 2-factor ANCOVA. To address sample size issues created by thermocouple failures (7 Fall, 5 Summer) at trees sampled for starch, missing intensity values were interpolated using parameter estimates derived from a 3-factor ANCOVA model which evaluated fire intensity by burn season, litter manipulations, proportion green canopy, and their second-order interactions ($F_{11,141} = 4.29$, $P < 0.0001$, Appendix 1).

GLM (binomial distribution, logit link function) models were used to investigate seasonal trends in mortality as a function of plant condition metrics (proportion green canopy, August starch and December starch) and fire intensity. The corrected Akaike Information Criteria (AICc) was used as a means of comparing the three plant condition metrics across GLM's with all other factors held constant in the model structure. Two-factor ANOVA models were used to compare plant condition metrics and fire intensity between live and dead plants, by season, and their interaction. General Linear Models (GLM: binomial distribution, logit link function) were used to estimate the probability of mortality associated with plant condition metrics (proportion green canopy, August starch, and December starch) and fire

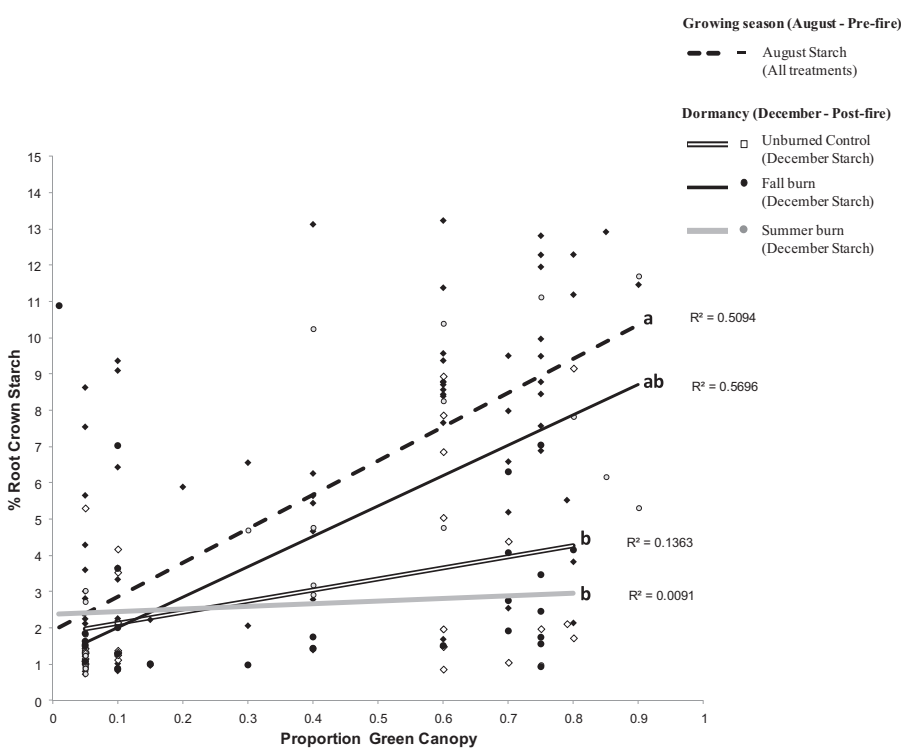

Fig. 1. Comparison of root crown carbohydrate samples taken at the height of the growing season (August 2006) prior to the experimental fires (dashed line) with samples taken during dormancy (December 2006) from trees burned in the summer (August 2006) and fall (October 2006), and from trees in the unburned control plots. The figure was generated using Analysis of Covariance. To confirm that trees exceeding 0.8 green canopy were not driving the positive relationships shown for pre-fire (August) starch, and post-fire (December) starch in fall burn trees, these high canopy trees were excluded in supplementary analyses. Slopes did not change when high canopy trees were removed. Letters (a and b) indicate significant differences between groups.

intensity by season (summer, fall), and full factorial interactions. Significant interactions between fire intensity and plant condition metrics on *Tamarix* mortality were investigated using the GLM Profiler in JMP. Profiling is a method where one variable at a time is changed while the others are held constant providing a means to observe the effect of a single variable on the response variable in a prediction trace, which is a graphical depiction of this relationship (SAS Institute Inc., 2010). Significant interactions are indicated when the prediction traces shift their slope and curvature as values of other terms are changed, but if there are no interaction effects, the traces only change in height, not slope or shape (SAS Institute Inc., 2010).

3. Results

Prior to fire, there was a strong correlation between% starch and proportion of canopy green with a slope that was higher than the post-fire/December measurements for the summer burn and unburned control trees ($F_{7,172} = 1.14$, $P < 0.0001$, Fig. 1). The slope of this relationship changed dramatically with summer fire or with continued herbivory in the absence of fire (unburned control) (Fig. 1). The summer burn and unburned control trees exhibited lower slopes for this relationship than the fall burn trees (Fig. 1). Unburned control plants were also depleted of starch by December, but the fire appeared to stimulate starch accumulation in the root crown compared to the unburned control trees and the summer burn trees (Fig. 1).

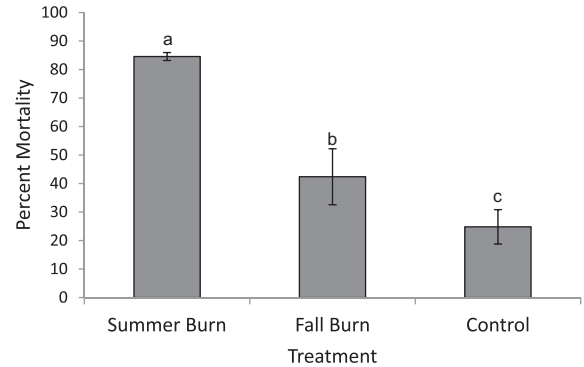

Fig. 2. Plot-level mortality by treatment: summer and fall burn mortality was due to both fire and herbivory, while the unburned control mortality was due to herbivory alone. Letters (a, b, and c) indicate significant differences between treatments. $n = 18$ transects.

Tree mortality was strongly affected by burning and by season of burn (Fig. 2). Fire intensity (Ln Degree-Minutes above 70 °C) was 10% higher in summer burn than in the fall burn ($F_{1,452} = 15.23$, $P = 0.0001$; Drus et al., 2012). Plot-level tree mortality was 42% greater for the summer than the fall burn (summer = 84%, fall = 42%), and 59% greater than the unburned control treatment (=25%; $F_{2,8} = 8.22$, $P = 0.02$, Fig. 2). Burn season interacted with litter manipulation such that litter manipulation contributed to mortality in the fall burn when intensity was lower

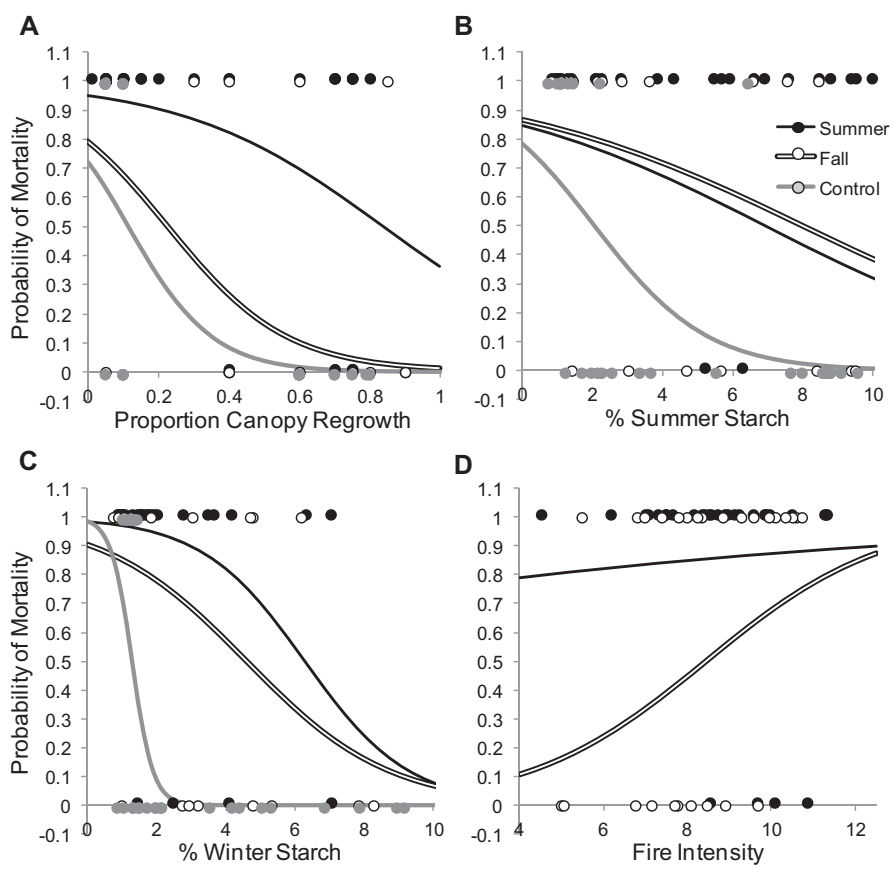

Fig. 3. Cumulative probability curves of *Tamarix* mortality in summer burn, fall burn and unburned control trees associated with (A) proportion green canopy, (B)% Summer (August) starch, (C)% Winter (December) starch, and (D) Fire intensity (Ln Degree-Minutes above 70 °C). Cumulative probability curves were generated using logistic expressions derived from within-season general linear models (binomial distribution, logit link function). Model details are provided in Table 2.

Table 1
Model-fit parameters and logistic expressions from general linear model analyses (binomial distribution, logit link function) of *Tamarix* mortality in summer burn, fall burn and unburned control trees associated with (a) proportion proportion green canopy, (b) % August starch, (c) % December) starch and (d) Fire intensity (Ln Degree-Minutes above 70 °C). Logistic expressions derived from these analyses were used to generate cumulative probability curves in Fig. 3.

Season/ treatment	(a) Proportion Proportion green canopy	(b) % Summer starch	(c) % December starch	(d) Fire intensity (Ln Degree-Minutes Above 70 °C)
Summer				
Equation	=1 + exp (2.95 + −3.51* Proportion green canopy)	=1 + exp(1.70 + −0.24* Summer starch)	=1 + exp(1.31 + −0.29* December starch	=1 + exp (0.92 + 0.10* intensity)
Model Fit	χ^2 = 1, DF = 1, $P > \chi^2$ = 0.0029, AICc = 76.37	χ^2 = 17.45, DF = 1, $P > \chi^2 < 0.0001$, AICc = 104.73	χ^2 = 12.62, DF = 1, $P > \chi^2$ = 0.0004, AICc = 107.75	χ^2 = 0.16, DF = 1, $P > \chi^2$ = 0.68, AICc = 62.03
Fall				
Equation	=1 + exp (1.34 + −5.89* Proportion green canopy)	=1 + exp(1.85 + −0.23* Summer starch)	=1 + exp(1.91 + −0.36* December starch)	=1 + exp (−3.98 + 0.47* intensity)
Model fit	χ^2 = 26.34, DF = 1, $P > \chi^2 < 0.0001$, AICc = 101.85	χ^2 = 6.35, DF = 1, $P > \chi^2$ = 0.012, AICc = 35.65	χ^2 = 8.39, DF = 1, $P > \chi^2$ = 0.0038, AICc = 33.6	χ^2 = 11.49, DF = 1, $P > \chi^2$ = 0.0007, AICc = 89.67
Unburned control				
Equation	=1 + exp(0.96 + −8.37* Proportion green canopy)	=1 + exp(−1.28 + −0.62* Summer starch)	=1 + exp(−4.32 + −3.318* December starch)	
Model Fit	χ^2 = 21.7, DF = 1, $P > \chi^2 < 0.0001$, AICc = 84.74	χ^2 = 12.75, DF = 1, $P > \chi^2$ = 0.0004, AICc = 28.38	χ^2 = 12.09, DF = 1, $P > \chi^2$ = 0.0005 AICc = 25.89	

overall but it did not contribute to mortality in the summer burn ($F_{2,452}$ = 7.08, P = 0.0009; Drus et al., 2012, Appendix 2).

The probability of tree mortality increased with herbivory impact within summer and fall burns and the unburned control treatment whether measured as lower proportion of green canopy (Fig. 3A, Table 1), reduced% August starch (Fig. 3B, Table 1), or reduced% December starch (Fig. 3C, Table 1). On average, live trees had higher proportion green canopy (Fig. 4A), higher% August starch (Fig. 4A), and lower fire intensity (Fig. 4D). However, these relationships were weaker for summer burn trees in the% green canopy (Fig. 3A) and fire intensity metrics (Fig. 4D), and for summer burn and unburned control trees in the% December starch metric (Fig. 3C). The canopy greenness metric was the best predictor of tree mortality because it strongly predicted mortality across all burning treatments without any significant interactions (Table 2). However, the influence of individual factors and their interactions differed among the various measures of plant condition (Table 2). December starch concentration interacted with fire intensity such that fire intensity had a greater affect on mortality when starch concentration was high, but the effect of starch on mortality was greater than fire intensity at low starch concentrations (Table 2, Fig. 5).

At high December starch concentrations and low-medium fire intensity (Fig. 5a and b), the shape of the relationships of starch and fire intensity to mortality were similar: as stress levels increase, both show a sharp increase in the probability of mortality (χ^2 = 26.7, DF = 7, $P > \chi^2$ = 0.0004*, AICc = 58.54: Table 2). However, when high fire intensity is reached (Fig. 5c), the relationship between December starch and mortality flattens out. The same relationship is seen for medium December starch levels (Fig 5d–f). However, at low December starch levels, both curves begin to flatten. At low and medium fire intensity (Fig 5g and h), the December starch curve is sharper than the intensity curve. At high fire intensity and low starch levels (Fig. 5i), both factors display almost maximum mortality at all levels.

4. Discussion

Most empirical studies of plant stress responses have investigated the effect of a single stress on plant performance in controlled conditions (Levitt, 1980; Vouk et al., 1987). Yet plants are exposed to multiple stresses simultaneously, which can vary in type and magnitude, and commonly interact (Baldwin and Preston, 1999; Alexieva et al., 2003). Studies of multiple stresses have produced mixed outcomes with both antagonism (interaction decreases stress response) and synergism (interaction increases stress response) common in the same system (Schindler, 1987; Hatcher, 1995; Hay, 1996; Sih et al., 1998; Alexieva et al., 2003). This study describes a synergism where beetle herbivory occurred before fire and enhanced the vulnerability of *Tamarix* to fire by decreasing starch storage in the root crown.

4.1. Root crown starch available for post-fire recovery is affected by beetle herbivory and seasonality

Hudgeons et al. (2007) documented that root crown starch declines with repeated herbivory by *D. carinulata*. Cumulative depletion of stored metabolites with inadequate post-defoliate compensatory regrowth increases *Tamarix* mortality, as carbohydrates are reduced to levels at which energy stores are no longer available to replace leaf material consumed by herbivores or to maintain growth and vigor (Hultine and Dudley, 2013). In the present study, strong relationships between root crown starch content measured at the height of the summer growing season (August) and proportion of green canopy demonstrate the lowered ability

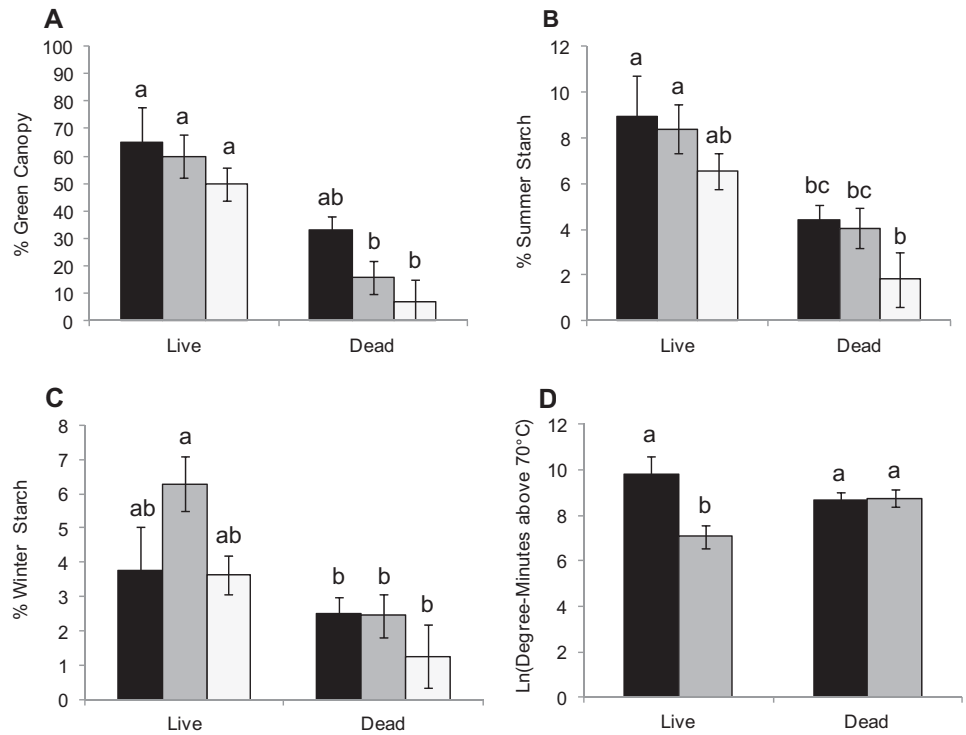

Fig. 4. (A) Average percent green canopy in live and dead trees in the summer burn, fall burn and unburned control treatments. $N = 86$ trees ($F_{5,83} = 8.45$, $P < 0.0001^*$). (B) Average percent root crown starch in live and dead trees measured in August 2006 in the summer burn, fall burn and unburned control treatments. $N = 87$ trees ($F_{5,81} = 5.39$, $P = 0.0002^*$). (C) Average percent root crown starch in live and dead trees measured in December 2006 the summer burn, fall burn and unburned control treatments. $N = 86$ trees, $F_{5,80} = 4.79$, $P = 0.0007^*$). (D) Average fire intensity (Ln Degree-Minutes above 70 °C) live and dead trees measured in the summer and fall burn treatments. $N = 59$ trees ($F_{3,55} = 3.94$, $P = 0.0128^*$). Letters (a and b) indicate significant differences among treatments. Error bars indicate +standard error.

Table 2
General linear model analyses (binomial distribution, logit link function) used to estimate the probability of *Tamarix* mortality by season, fire intensity and each of three plant condition metrics (a) proportion green canopy, (b)% August starch, and (c)% December starch.

Plant condition metric (a–c):	(a) Proportion Green canopy (pre-fire)	b)% August (pre-fire) starch	c)% December (post-fire) starch
Whole Model	$\chi^2 = 33.7$, DF = 7, $P > \chi^2 < 0.0001^*$, AICc = 52.06	$\chi^2 = 28.16$, DF = 7, $P > \chi^2 = 0.0002^*$, AICc = 56.54	$^2 = 26.7$, DF = 7, $P > \chi^2 = 0.0004^*$, AICc = 58.54
Main Effects			
Season	$\chi^2 = 7.78$, DF = 1, $P > \chi^2 = 0.0053^*$	$\chi^2 = 6.35$, DF = 1, $P > \chi^2 = 0.0117^*$	$\chi^2 = 2.39$, DF = 1, $P > \chi^2 = 0.1222$
Intensity	$\chi^2 = 0.36$, DF = 1, $P > \chi^2 = 0.5434$	$\chi^2 = 1.53$, DF = 1, $P > \chi^2 = 0.2167$	$\chi^2 = 0.06$, DF = 1, $P > \chi^2 = 0.8016$
Plant condition metric	$\chi^2 = 5.76$, DF = 1, $P > \chi^2 = 0.0164^*$	$\chi^2 = 5.91$, DF = 1, $P > \chi^2 = 0.0151^*$	$\chi^2 = 8.18$, DF = 1, $P > \chi^2 = 0.0042^*$
Interaction effects			
Season*intensity	$\chi^2 = 6.14$, DF = 1, $P > \chi^2 = 0.0132^*$	$\chi^2 = 5.58$, DF = 1, $P > \chi^2 = 0.0182^*$	$\chi^2 = 2.59$, DF = 1, $P > \chi^2 = 0.1075$
Season*plant condition Metric	$\chi^2 < 0.01$, DF = 1, $P > \chi^2 = 0.9204$	$\chi^2 = 0.92$, DF = 1, $P > \chi^2 = 0.3386$	$\chi^2 = 0.56$, DF = 1, $P > \chi^2 = 0.4536$
Intensity*plant	$\chi^2 = 0.25$, DF = 1, $P > \chi^2 = 0.6137$	$\chi^2 = 0.11$, DF = 1, $P > \chi^2 = 0.7351$	$\chi^2 = 6.87$, DF = 1, $P > \chi^2 = 0.0087^*$
Condition metric			
Season*intensity*plant Condition metric*	$\chi^2 = 0.27$, DF = 1, $P > \chi^2 = 0.6004$	$\chi^2 = 0.28$, DF = 1, $P > \chi^2 = 0.5967$	$\chi^2 = 0.24$, DF = 1, $P > \chi^2 = 0.6216$

of *Tamarix* to replace foliar tissues when metabolite stores have been reduced by herbivory.

High carbohydrate demand is associated with foliage production in woody species even in the absence of herbivory because high respiratory costs are incurred to maintain photosynthetic tissue, and these costs vary considerably depending on the seasonal demands of the plant (McLaughlin and McConathy, 1979). *Tamarix* and other deciduous species allocate photosynthate to foliage production during the height of the growing season (July–August) resulting in depletion of root carbohydrates, whereas photosynthate is translocated to the roots in preparation for dormancy (October–November) resulting in higher root carbohydrate stores (Cords and Badiel, 1964; Mooney, 1972).

At the same site, other investigators have measured higher August starch concentrations in the absence of herbivory than those measured in *Tamarix* exposed to *D. carinulata* herbivory in

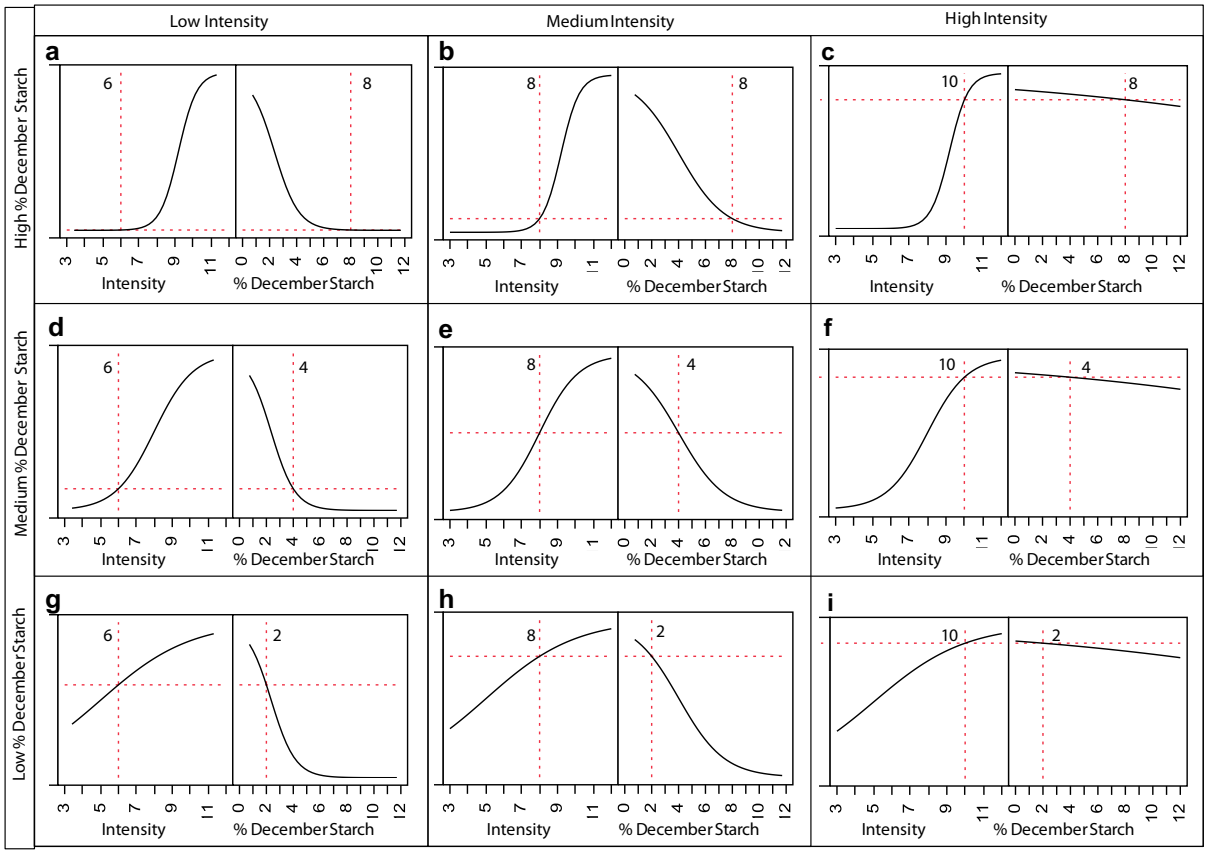

Fig. 5. Profiler traces of fire intensity and% December starch characterizing the nature of their interaction. Profile traces show predicted mortality (*y*-axis) as one variable (i.e. fire intensity) is changed while the other (i.e.% December starch) is held constant. The vertical dotted lines show the value on the *x*-axis of each variable. For both fire intensity and starch, low, medium and high values were chosen using Fig. 4 as a reference to ensure that the values were representative of those observed during the study. The rows indicate decreasing values of December starch from top to bottom which correspond to increasing metabolic stress, and the columns indicate increasing values of fire intensity. Thus, part **a** shows High December Starch and Low Intensity (representing the lowest combined stresses), **b** shows High December Starch and Medium intensity, **c** shows High December Starch and Low intensity, **d** shows Medium December Starch and Low Intensity, **e** shows Medium December Starch and Medium Intensity, **f** shows Medium December Starch and Low intensity, **g** shows Low December Starch and Low Intensity, **h** shows Low December Starch and Medium Intensity, and **i** shows Low December Starch and High Intensity (representing the highest combined stresses). Changes in the height and the slope of the lines indicate an interaction, and the magnitude of these changes indicates the strength of the interaction.

this study (Tomanek and Ziegler, 1960; Bartley and Otto, 1961; Cords and Badiel, 1964). This is likely because the *Tamarix* at our study site had experienced at least two defoliation events prior to the fire, and subsequent foliage replacement likely reduced starch concentrations before the samples were taken. Further, the starch content measured during dormancy in this study was not greater than the starch content measured during the height of the growing season as commonly observed in *Tamarix* and in many woody plants (Bartley and Otto, 1961; Chapin et al., 1990). Instead, the December starch concentrations, regardless of treatment (summer burn, fall burn or control), were lower than those of trees taken pre-fire, during the height of the growing season in August. Repeated herbivory by *D. carinulata* can account for the observed decline in starch content during dormancy as the metabolic demand for foliar replacement reduced starch concentrations in the root crown (Hudgeons et al., 2007).

4.2. Tamarix mortality increases with fire intensity

The present study also demonstrates that *Tamarix* mortality increases as a function of fire intensity. In *Tamarix* monocultures, litter accumulation and weedy understory plants contribute to fuel loads that produce high fire intensities (Bradstock and Auld, 1995). Previously published work on this system (Drus et al., 2012) found that fire intensity was positively related to litter depth, as denser and deeper fuels promoted smoldering, thereby sustaining high temperatures over longer periods of time which enhanced mortality. Higher fire intensity was measured during the summer burn than the fall burn most likely because fire intensity is enhanced by drier fuels, higher ambient temperature and lower relative humidity (van Wagtendonk, 2006). Consequently, greater *Tamarix* tissue damage and mortality occurred in trees burned during the summer than trees burned during the fall, a result in accord with Howard et al. (1983) who observed greater mortality in stands of *Tamarix* on the lower Colorado Plateau following fire in the summer versus fall, winter and spring months. Greater fire intensity has been shown to reduce resprouting in other systems, such as chaparral, when root-crown tissues are exposed to lethal temperatures and apical meristems are permanently damaged (Keeley, 2006; Hood et al., 2008).

4.3. Root crown starch available for post-fire recovery is affected by fire intensity and seasonality

The significant interaction between December starch content and fire intensity suggests that the ability of *Tamarix* to use carbohydrates following fire is affected by fire intensity. In the December root crown samples, starch content was lower in the

summer burn trees than in the fall burn or the unburned control trees. It is possible that intense fire damage to the bark and vascular system of the summer burn trees could have inhibited carbohydrate allocation and access. *Tamarix* with ample carbohydrate stores that failed to resprout following fire suggested inhibited access to carbohydrates. However, the fact that root crown starch content was higher in the fall burn trees than in the unburned control trees proves more difficult to explain. It is possible that the removal of foliage forced the fall burn trees into an early dormancy where they retained pre-fire carbohydrate stores, while the carbohydrate stores of the unburned control trees were further depleted by herbivory before going into dormancy.

The higher mortality observed in the summer burn trees can also be attributed to seasonal starch fluctuations. At the time of the summer burn, metabolites were being allocated to growth, and the carbon demand to replace tissues reduced the allocation of metabolites to the root crown prior to dormancy. Conversely, lower mortality was observed in trees burned during the fall likely because the trees were beginning to translocate metabolites to the root crown in preparation for dormancy, thus providing ample resources for recovery.

Further evidence to support the importance of available carbohydrate stores to recovery was provided by an unanticipated fire in a repeatedly defoliated *Tamarix* monoculture 6 km from our experimental site in March 2007, when plants were still dormant. This fire initially reduced the cover of *Tamarix* by 90%, but there was 100% recovery within 3 months, suggesting that trees are less susceptible to mortality when carbohydrates are stored belowground during dormancy (Drus Unpublished data). Therefore, the effect of burn timing on *Tamarix* mortality is related to metabolic storage and phenology because carbohydrate stores fluctuate seasonally. Ultimately, it is important to note that root crown starch does not represent the total storage in the root system and other unmeasured stores may be contributing to the observed patterns.

4.4. The effect of herbivory and fire intensity on Tamarix mortality is synergistic

Fire-induced *Tamarix* mortality is ultimately a function of fire damage to tissues, carbohydrate stores available for recovery and the interaction between those factors. As predicted, the greatest mortality was measured in *Tamarix* exposed to high fire intensity and high levels of pre-fire herbivore damage. *Tamarix* mortality was particularly enhanced by low starch levels, as even *Tamarix* exposed to less-damaging lower intensity fires lacked the resources to recover. Factor profiling showed that the effect of herbivory on mortality increased with fire intensity, and the effect of fire intensity on mortality increased with herbivory impact. As both stress factors increased, their effect on *Tamarix* mortality became disproportionate. When a particular risk factor increases in magnitude as other risk factors shift from absent to present or low to high in logistic analyses, a synergism is indicated (Gustafson et al., 2005). Thus, herbivory and fire intensity have a synergistic effect on *Tamarix* mortality.

5. Conclusion

The results of this study show that a coupled management strategy of *D. carinulata* herbivory and prescribed fire may be more effective than either strategy employed separately. Burn timing is a critical component to incorporate into any *Tamarix* management strategy involving prescribed fire, as the outcome is dependent upon a delicate balance between exposing *Tamarix* root-crown tissues to lethal temperatures and burning when starch reserves are lowest to reduce the ability of surviving plants to resprout. Physiological stress resulting from *D. carinulata* herbivory is integral to enhancing the post-fire mortality of *Tamarix*, but it is difficult to quantify and/or predict. The graphical relationships presented in this study can provide valuable insight into predicting the outcomes of multiple interacting stressors and can be used by land managers as a valuable tool to facilitate more effective and less costly *Tamarix* management. However, biological control by *D. carinulata carinulata* is now restricted because nest failures of the endangered southwestern willow flycatcher (*Empidonax trailii extimus*) have been attributed to foliar desiccation, but *D. carinulata* continues to expand its range because *Tamarix* is widespread (USDA, 2010). The effects of *D. carinulata* herbivory have been well documented at the tree and stand level, but widespread ecosystem level impacts are not yet clear (Hultine et al., 2009).

In the American Southwest, the shift in riparian community composition from cottonwood-willow gallery forests to *Tamarix* monocultures is proving a difficult trajectory to alter given the complexity of the physical and physiological factors promoting the establishment and dominance of *Tamarix*. Changes in hydrology associated with river regulation and the consequent alteration of disturbance regimes, especially increased fire and flooding risk, promote *Tamarix* establishment and propagation, and are likely to persist over the long-term. However, synergisms between *D. carinulata* herbivory and fire have the potential to reduce *Tamarix* dominance at large spatial scales which can provide opportunities to restore diversity and wildlife habitat in riparian systems degraded by *Tamarix.*

6. Author Contributions

G.M.D., T.L.D., M.L.B. and C.M.D. conceived and designed the experiments. G.M.D. and J.R.M. performed the experiments. J.R.M. calculated the fire intensity index. G.M.D. performed carbohydrate assays. G.M.D. and T.J.E. conceived and executed the general linear model analyses. G.M.D. wrote the manuscript; other authors provided editorial advice.

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Appendix 1

JMP script of the three-factor Analysis of Covariance model used to interpolate missing fire intensity values (5 Summer, 7 Fall) for general linear model analysis.

```
8.74825585588632
+ Match(Season)
    "Fall"   ⇒ -0.3954125538631
    "Summer" ⇒ 0.39541255386306
    else     ⇒ .
+ Match(Litter Manipulation)
    "Add"    ⇒ 0.48284642946203
    "Control" ⇒ 0.07179913105876
    "Remove" ⇒ -0.5546455605208
    else     ⇒ .
+ -0.9787976075374 * Canopy Regrowth
+ Match(Season)
    "Fall"   ⇒ Match(Litter Manipulation)
                 "Add"    ⇒ 0.45500487207948
                 "Control" ⇒ 0.07608888582127
                 "Remove" ⇒ -0.5310937579007
                 else     ⇒ .
    "Summer" ⇒ Match(Litter Manipulation)
                 "Add"    ⇒ -0.4550048720795
                 "Control" ⇒ -0.0760888858213
                 "Remove" ⇒ 0.53109375790075
                 else     ⇒ .
    else     ⇒ .
+ Match(Season)
    "Fall"   ⇒ (Canopy Regrowth - 0.35440677966102) * -0.8317032175162
    "Summer" ⇒ (Canopy Regrowth - 0.35440677966102) * 0.83170321751617
    else     ⇒ .
+ Match(Litter Manipulation)
    "Add"    ⇒ (Canopy Regrowth - 0.35440677966102) * -1.8566237932201
    "Control" ⇒ (Canopy Regrowth - 0.35440677966102) * 0.84427286481044
    "Remove" ⇒ (Canopy Regrowth - 0.35440677966102) * 1.01235092840971
    else     ⇒ .
+ Match(Season)
    "Fall"   ⇒ Match(Litter Manipulation)
                 "Add"    ⇒ (Canopy Regrowth - 0.35440677966102) * 1.68809068704681
                 "Control" ⇒ (Canopy Regrowth - 0.35440677966102) * -0.0335686906132
                 "Remove" ⇒ (Canopy Regrowth - 0.35440677966102) * -1.6545219964336
                 else     ⇒ .
    "Summer" ⇒ Match(Litter Manipulation)
                 "Add"    ⇒ (Canopy Regrowth - 0.35440677966102) * -1.6880906870468
                 "Control" ⇒ (Canopy Regrowth - 0.35440677966102) * 0.03356869061323
                 "Remove" ⇒ (Canopy Regrowth - 0.35440677966102) * 1.65452199643358
                 else     ⇒ .
    else     ⇒ .
```

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

4-Factor ANOVA model effects and 2nd 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 'x'. F-ratios and *P*-values are reported for main effects and interaction effects where *indicates $P < 0.05$ and tr indicates a trend. $N = 477$. Least squared means and ±standard error are reported for levels within main effects and interaction effects where letters (a, b, c etc.) indicate significant differences among levels.

		Max temp (°C)	Duration (minutes 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 ± 18.65a	91.30 ± 7.61a	7.90 ± 0.13a
	Fall burn	315.23 ± 23.62b	60.55 ± 9.64b	7.12 ± 0.17b
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 ± 19.33b	14.49 ± 7.89c	6.07 ± 0.14c
	Litter	544.87 ± 18.51a	58.57 ± 7.56b	8.33 ± 0.13a
	Surface	334.77 ± 19.90b	116.12 ± 8.12a	8.40 ± 0.14a
	Below	164.76 ± 53.19c	114.52 ± 21.71ab	7.23 ± 0.37b
Herbivory level		$F_{1,452}$ = 1.76, P = 0.1850	$F_{1,452}$ = 3.56, P = 0.0598^{tr}	$F_{1,452}$ = 0.93, P = 0.3356
	Low	332.50 ± 24.73a	64.93 ± 10.09a	7.41 ± 0.17a
	High	370.42 ± 17.18a	86.93 ± 7.01a	7.61 ± 0.12a
Litter manipulation		$F_{2,452}$ = 2.45, P = 0.0870^{tr}	$F_{2,452}$ = 28.5, P < 0.0001*	$F_{2,452}$ = 19.1, P < 0.0001*
	Add	390.08 ± 21.99a	134.78 ± 9.00a	8.35 ± 0.15a
	Control	360.56 ± 22.00a	51.69 ± 8.98b	7.33 ± 0.15b
	Remove	303.74 ± 33.47a	41.30 ± 13.66b	6.84 ± 0.24b
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 ± 26.31bc	20.69 ± 10.74d	6.55 ± 0.19c
	Summer burn, Litter	588.64 ± 25.59a	70.29 ± 10.45bc	8.69 ± 0.18ab
	Summer burn, Surface	388.85 ± 26.65bcd	140.01 ± 10.88a	8.80 ± 0.19a
	Summer burn, Below	143.84 ± 58.52e	134.21 ± 23.89ab	7.57 ± 0.41abc
	Fall burn, Canopy	293.44 ± 27.42de	8.30 ± 11.19d	5.60 ± 0.19d
	Fall burn, Litter	501.11 ± 26.01ab	46.84 ± 10.62cd	7.98 ± 0.18b
	Fall burn, Surface	280.69 ± 28.46de	92.22 ± 11.62bc	8.00 ± 0.20ab
	Fall burn, Below	185.67 ± 79.11cde	94.84 ± 32.29abcd	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 ± 28.27a	68.19 ± 11.54b	7.82 ± 0.20ab
	Summer burn, High	383.47 ± 21.88a	114.41 ± 8.93a	7.98 ± 0.15a
	Fall burn, Low	273.10 ± 35.05b	61.67 ± 14.31b	7.01 ± 0.25c
	Fall burn, High	357.36 ± 24.37ab	59.44 ± 9.95b	7.23 ± 0.17bc
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 ± 27.23a	147.68 ± 11.11a	8.33 0.22a
	Summer burn, Control	401.64 ± 28.14a	64.11 ± 11.49b	7.80 0.20a
	Summer burn, Remove	383.01 ± 36.44a	62.11 ± 14.88b	7.52 0.26ab
	Fall burn, Add	401.75 ± 31.23a	121.89 ± 12.75a	8.33 0.22a
	Fall burn, Control	319.47 ± 30.53ab	39.27 ± 12.46b	6.87 0.21bc
	Fall burn, Remove	224.47 ± 43.73b	20.49 ± 17.85b	6.16 0.31c
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 ± 22.53b	17.13 ± 9.20c	6.26 ± 0.16c
	Canopy, Low	359.21 ± 31.48bc	11.86 ± 12.85c	5.88 ± 0.22c
	Litter, High	562.22 ± 21.77a	67.81 ± 8.89b	8.42 ± 0.15a
	Litter, Low	527.52 ± 31.13a	49.32 ± 12.30bc	8.24 ± 0.21ab
	Surface, High	384.60 ± 22.94b	135.26 ± 9.36a	8.71 ± 0.16a
	Surface, Low	284.93 ± 32.57bc	96.98 ± 13.30ab	8.09 ± 0.23ab
	Below, High	171.17 ± 56.71c	127.51 ± 23.15ab	7.03 ± 0.40bc
	Below, Low	158.35 ± 81.11bc	101.54 ± 33.11abc	7.44 ± 0.57abc
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 ± 32.06bc	11.77 ± 13.09d	6.32 ± 0.23c
	Canopy, Control	353.36 ± 31.83bc	13.43 ± 12.99d	6.04 ± 0.22c
	Canopy, Remove	348.81 ± 34.09bc	18.27 ± 13.92d	5.86 ± 0.24c
	Litter, Add	604.72 ± 40.00a	86.54 ± 12.65c	8.99 ± 0.22a
	Litter, Control	537.68 ± 30.40a	43.40 ± 12.41cd	8.20 ± 0.21ab
	Litter, Remove	492.22 ± 32.63ab	45.76 ± 13.32cd	7.80 ± 0.23b
	Surface, Add	380.40 ± 32.10bc	180.86 ± 13.10ab	9.19 ± 0.23a
	Surface, Control	323.97 ± 31.66c	93.31 ± 12.92c	8.28 ± 0.22ab
	Surface, Remove	299.93 ± 36.66c	74.19 ± 14.97cd	7.73 ± 0.26b
	Below, Add	193.06 ± 66.34c	259.96 ± 27.08a	8.92 ± 0.47ab
	Below, Control	227.21 ± 68.18c	56.63 ± 27.83cd	6.80 ± 0.48bc
	Below, Remove	74.00 ± 116.40c	26.98 ± 47.51bcd	5.98 ± 0.82bc
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 ± 34.43ab	108.77 ± 14.06b	8.05 ± 0.24ab
	Low, Control	375.44 ± 32.69ab	52.14 ± 13.34c	7.45 ± 0.23bc
	Low, Remove	282.93 ± 46.38b	33.87 ± 18.93c	6.74 ± 0.33c
	High, Add	441.02 ± 24.08a	160.79 ± 9.82a	8.65 ± 0.17a
	High Control	345.67 ± 26.09ab	51.25 ± 10.65c	7.22 ± 0.18bc
	High, Remove	324.55 ± 34.21b	48.74 ± 13.97c	6.95 ± 0.24c

Gail Drus Ph.D. Permission has been granted by the author to reproduce appendix 2.

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