



## 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.

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