

Herbivory-induced mortality increases with radial growth in an invasive riparian phreatophyte

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- **Background and Aims** Under equal conditions, plants that allocate a larger proportion of resources to growth must do so at the expense of investing fewer resources to storage. The critical balance between growth and storage leads to the hypothesis that in high-resource environments, plants that express high growth rates are more susceptible to episodic disturbance than plants that express lower growth rates.
- **Methods** This hypothesis was tested by measuring the radial growth, basal area increment (BAI) and carbon isotope ratios ($\delta^{13}\text{C}$) in tree-ring α -cellulose of 62 mature tamarisk trees (*Tamarix* spp.) occurring at three sites in the western USA ($n = 31$ live and 31 killed trees across all sites, respectively). All of the trees had been subjected to periods of complete foliage loss by episodic herbivory over three or more consecutive growing seasons by the tamarisk leaf beetle (*Diorhabda carinulata*), resulting in approx. 50 % mortality at each site.
- **Key Results** Mean annual BAI (measured from annual ring widths) in the 10 years prior to the onset of herbivory was on average 45 % higher in killed trees compared with live trees ($P < 0.0001$). Killed trees that had higher growth rates also expressed higher (less negative) $\delta^{13}\text{C}$ ratios compared with live trees. In fact, at one site near Moab, UT, the mean annual BAI was 100 % higher in killed trees despite having about a 0.5 ‰ higher $\delta^{13}\text{C}$ relative to live trees ($P = 0.0008$). Patterns of $\delta^{13}\text{C}$ suggest that the intrinsic water-use efficiency was higher in killed than surviving trees, possibly as a consequence of lower whole-canopy stomatal conductance relative to live trees.
- **Conclusions** The results show that a likely trade-off occurs between radial growth and survival from foliage herbivory in *Tamarix* spp. that currently dominates riparian areas throughout the western USA and northern Mexico. Thus, herbivory by *D. carinulata* may reduce the overall net primary productivity of surviving *Tamarix* trees and may result in a reduction in genetic variability in this dominant invasive tree species if these allocation patterns are adaptive.

Key words: Plant mortality, tree ring growth, tree-ring $\delta^{13}\text{C}$, *Tamarix*, *Diorhabda carinulata*, riparian ecosystems.

INTRODUCTION

Plants in most terrestrial environments face the difficulty of maximizing growth while simultaneously defending against potential biotic mortality from disease and herbivory. This inevitable trade-off requires plants to balance the allocation of resources such as photosynthates (i.e. sugar and starch reserves) and mineral nutrients to growth, reproduction, defence (i.e. secondary metabolites) or internal storage (Bloom *et al.*, 1985; Chapin *et al.*, 1990; Ayres, 1993). If all else is equal, plants that allocate a larger proportion of resources to growth must do so at the cost of allocating fewer resources to other areas such as storage. For perennial plants such as trees and woody shrubs, maintaining relatively large storage pools is not only necessary to facilitate the seasonal growth of new tissues, but also provides critical resources to maintain functional metabolism and/or replace tissues after a catastrophic event such as fire or intense herbivory (Chapin *et al.*, 1990). Therefore, plants that are well

adapted to episodic disturbance often ‘bank’ internal resources within complex storage organs, or recycle materials from expendable tissues with high turnover rates (i.e. leaves and fine roots).

For woody plants, susceptibility to disturbance-induced mortality is often reflected in radial stem growth patterns prior to disturbance events. Two general growth patterns have emerged or been proposed as indicators of mortality. The first is that surviving plants maintain higher growth rates than co-occurring plants that failed to survive. In such cases, mortality is usually facilitated by episodic drought, or drought in combination with other disturbance events such as pathogen infections, insect outbreaks or fire (Pederson, 1998; Cherubini *et al.*, 2002; Bigler *et al.* 2004, 2006, 2007; Antos *et al.*, 2008). Mortality is generally attributed to chronic stress caused by resource limitation relative to surviving plants. The second pattern is one in which surviving plants express a lower inter-annual variability in radial growth than non-surviving plants (even if the mean growth rate between

populations is similar). These growth patterns are typically associated with drought–inter-drought cycles, whereby surviving plants express a lower sensitivity to these cycles (Ogle *et al.*, 2000; Ruel and Whitham, 2002; Suarez *et al.*, 2004; Bigler and Veblen, 2009; McDowell *et al.*, 2010; Levanic *et al.*, 2011). A key factor that relates plant growth and mortality to drought–inter-drought cycles is the interaction between stomatal function and xylem structure and function. This is because woody plants face the inevitable trade-off between water-transport efficiency (a key determinate for fast growth) and avoidance of catastrophic xylem cavitation (Tyree and Sperry, 1989; Wheeler *et al.*, 2005; Hacke *et al.*, 2006). In other words, plants that grow fast tend to be less resilient to catastrophic xylem cavitation and subsequent mortality. Differences in growth between killed and surviving trees have been attributed to differences in stomatal regulation such that killed trees were unable to adequately minimize runaway xylem cavitation during drought (McDowell *et al.*, 2008; 2010; Levanic *et al.*, 2011).

On the other hand, direct mortality from insect or pathogen outbreaks, or outbreaks in combination with drought, may be largely a function of resource allocation rather than stomatal regulation. This pattern may be particularly relevant for plants that evolved in high disturbance environments. Under such circumstances, plants that allocate proportionately greater resources towards growth would have fewer reserves in storage pools to draw on during disturbance, and are thus more likely to experience mortality. Regardless of the mechanism, it is unclear whether high radial growth rates are a key determinant of population-level sensitivity to episodic disturbance across a broad range of woody taxa.

Riparian woodlands in the arid regions of North America are highly productive ecosystems with significantly greater plant and animal diversity compared with surrounding landscapes. Likewise, species of riparian systems typically evolved under intense pressure from episodic disturbance caused by frequent flooding, large crown fires and widespread insect herbivory. Adding to the complexity of these systems is a dramatic shift in vegetation cover over the last several decades from native riparian forests to shrublands dominated by the Eurasian tree/shrub tamarisk (*Tamarix* spp.). Several *Tamarix* species (also known as saltcedar) were introduced to North America in the early to mid-1800s, and two species, *T. chinensis* and *T. ramosissima*, along with their

hybrids, *T. chinensis* × *T. ramosissima*, have become widely established throughout the western USA and parts of northern Mexico (Gaskin and Schaal, 2002; Friedman *et al.*, 2005).

Although the implications of *Tamarix* on the structure and function of riparian ecosystems have been widely debated, its proliferation along streams and rivers in the western USA has resulted in intensive eradication programmes throughout the region. The most successful, but controversial, approach has been the release of a biological control agent from Eurasia, the tamarisk leaf beetle, *Diorhabda carinulata* (Dudley 2005; Hultine *et al.*, 2010a). The beetle feeds exclusively on *Tamarix* foliage, resulting in periods of complete defoliation that lasts for several weeks (Fig. 1; Dudley, 2005; Hultine *et al.*, 2010b; Pattison *et al.*, 2011). Beetle infestations typically result in one to three defoliation events per year. These episodic defoliation events inevitably reduce carbon storage and, in turn, reduce leaf production and growth, and in some cases lead to *Tamarix* mortality (Hudgeons *et al.*, 2007). The actual rate of mortality, however, can be highly variable across the landscape. Repeated years of defoliation can result from anywhere between 0 % and 100 % mortality (K. R. Hultine, pers. obs.), with mortality rates of 20–40 % being common after 3–5 years (Dudley and Bean, 2012). The wide range in mortality within individual populations provides a unique opportunity to explore the interactions between episodic disturbance, growth and mortality of a dominant woody plant species.

We assessed potential trade-offs between growth and resource storage by comparing radial growth and $\delta^{13}\text{C}$ in tree-ring cellulose of killed versus surviving *Tamarix* during years prior to the onset of episodic herbivory by the *Tamarix* leaf beetle. This plant–herbivore interaction was ideal for investigating allocation trade-offs between growth and storage, because *Tamarix* defence strategies are insufficient to avoid complete canopy herbivory by *D. carinulata* (Fig. 1). Two related hypotheses were tested: (1) surviving trees would express lower radial growth rates than co-occurring killed trees in years prior to the onset of defoliation; and (2) surviving trees express a lower sensitivity to environmental variables, including the regional Palmer Drought Severity Index (PDSI) and volumetric river flow (an analogue for soil water availability) compared with co-occurring killed trees. The expectation is that higher rates of growth occur at the direct expense of storage of photosynthates and nutrients, thereby



FIG. 1. Photographs showing a *Tamarix* stand near Moab, UT before and after defoliation by *D. Carinulata*. The photos were taken 2 weeks apart in July 2007.

reducing the reserve capacity to construct new foliage after several repeated defoliation events. Under this scenario, trade-offs between growth and survival would not be related to differences in available resources or leaf-level gas exchange (i.e. stomatal conductance and photosynthesis) between live and killed trees. Therefore, we also predicted that $\delta^{13}\text{C}$ during years prior to defoliation would be similar between live and killed trees. Results from this study shed light on the mechanistic relationships between intensive herbivory pressures, net primary productivity and population dynamics of woody riparian plant species. Likewise, this study improves the ability for riparian ecologists and managers to forecast patterns of *Tamarix* mortality in response to defoliation by *D. carinulata*.

MATERIALS AND METHODS

Research sites

Research was conducted at three sites in the western USA where all the trees in dense *Tamarix* stands had experienced multiple years of episodic defoliation by *Diorhabda carinulata*, as verified by intensive monitoring programmes (Pattison *et al.*, 2011; Grand County, UT Weed Control Office, pers. comm.). Approximately 50 % mortality caused by repeated defoliation events was observed at each site. The first site (labelled Moab hereafter) was located along the Colorado River in south-eastern Utah, USA approx. 15 km upriver from the town of Moab, UT (38°38'57.72"N, 109°30'20.41"W, 1220 m a.s.l.). The riparian area along this stretch of river was comprised almost exclusively of *Tamarix chinensis*, *T. ramosissima* and their hybrids (*T. chinensis* × *T. ramosissima*) intermixed with a sparse understorey of herbaceous perennial and seasonal annual plants. In 2004 the Grand County, Utah Weed Control Office released several thousand *D. carinulata* at locations along the Colorado River, including a release location about 12 km downstream from the Moab site. Initially the beetle had little impact on *Tamarix* as defoliation was localized to the original release sites. However, beginning in 2007, the beetle began to spread rapidly up and down the Colorado River, and by 2009 over 1000-river km were affected by the beetle (Hultine *et al.* 2010a; Meng *et al.*, 2012). *Tamarix* trees at the 'Moab' site were initially defoliated in mid-summer of 2007 with complete stand defoliation occurring at least once during each subsequent growing season (T. Higgs, Grand County Weed Control Supervisor, pers. comm.), resulting in about 50 % mortality of *Tamarix* trees by 2010.

The other two sites were in the terminal basin of the Humboldt River (Humboldt Sink) in north-western Nevada, approx. 6 km south-east of Lovelock, NV. Soils in the Humboldt Sink are naturally saline and comprise fine-textured silts (Nash, 2005). One site (called Army Drain hereafter) was adjacent to a perennially flowing irrigation canal (40°05'00.97"N, 118°34'41.97"W, 1190 m a.s.l.), and the other (called Allen's Patch hereafter) was located in a pasture approx. 1 km from Army Drain (40°05'03.75"N, 118°32'44.54"W 1195 m a.s.l.). These sites were composed almost exclusively of hybrid *Tamarix* trees (*T. chinensis* × *T. ramosissima*) with an understorey characterized by saltgrass (*Distichlis spicata*) and various native and non-native forbs.

Diorhabda carinulata beetles were released in late spring of 2001 at a single location at the Humboldt Sink, approx. 8 km from the study sites. *Tamarix* trees were initially defoliated during the 2004 growing season at both sites, with complete defoliation (>90 %) of all trees being reported during the 2004 and 2005 growing seasons (Pattison *et al.*, 2011). Complete to nearly complete defoliation of all trees has occurred during subsequent years, resulting in approx. 50 % mortality by 2011 (T. L. Dudley, unpubl. res.) and over 80 % mortality at other nearby locations (Bean *et al.*, 2012).

Dendrochronological analysis

Surviving and recently killed *Tamarix* trees were selected for study based on their diameters at approx. 1.5 m above the base of the tree, and their hydrologic relationship to water bodies (i.e. distance to and height above open water) such as the Colorado River at the Moab site and the irrigation canal at the Army Drain site. At the Moab site, stem cross-sections were collected from ten live and ten recently killed trees with a chainsaw in July 2010. The stems of the live trees ranged in diameter from 9.8 to 13.4 cm (mean = 11.6 cm), with an age range prior to the first year of defoliation in 2007 from 11 to 36 years (mean = 19.9 years), and the stems of the killed trees ranged in diameter from 11.4 to 16.7 (mean = 13.8 cm), and age from 17 to 28 years (mean = 23.4 years). At Army Drain, stem cross-sections were collected from six live and six killed trees with a chainsaw in November 2011. The live trees ranged in diameter from 9.2 to 12.6 cm (mean = 10.5 cm) with an age range prior to the first year of defoliation in 2004 from 24–45 years (mean = 34.5 years), and killed trees ranged in diameter from 7.8 to 13.5 cm (mean = 10.8 cm) and age from 25 to 36 years (mean = 30.7 years). At Allen's Patch, stem cross-sections were collected from 15 live and 15 killed trees in November 2011. The live tree stems ranged in diameter from 6.5 to 12.7 cm (mean = 9.5 cm) with an age range prior to the first year of defoliation in 2004 from 12 to 16 years (mean = 14.0 years), and killed tree stems ranged in diameter from 5.7 to 12.5 cm (mean = 8.6 cm) and age from 13 to 18 years (mean = 14.9 years).

The cross-sections were transported to the laboratory and sanded using progressively finer-grained sandpaper to enhance the visibility of individual growth rings. The sanded cross-sections were scanned with a high-resolution computer scanner, and ring widths were measured using public domain NIH image program software (<http://rsb.info.nih.gov/nih-image/>). Whole-wood ring widths were analysed by first measuring a single randomly selected radius from the centre of the cross-section to the edge. A second radius was measured from the centre at a 45° angle from the first radius, and a third and fourth radius were measured at 45° angles from the previous radius. Mean ring widths were then determined for each year from the measurements of the four radii. False rings and missing rings were determined by cross checking the ring widths with other stem cross-sections, and by comparing with local and regional environmental data. To assess volume growth rates per year, mean ring-width values were converted to basal area increment [annual rate of

circumferential growth (BAI $\text{mm}^2 \text{year}^{-1}$] using tree-specific circumference growth and assuming concentric circularity.

To account for the various age classes among sites, and to minimize the impact of juvenile effects, tree-ring measurements were conducted over periods of variable length. For Moab, the most recent 15 years before defoliation by the beetle were analysed (1992–2006), for Army Drain we analysed the most recent 20 years before defoliation (1984–2003), and for Allen's Patch, we analysed the most recent 10 years prior to defoliation (1994–2003).

Carbon isotope analysis

Leaf carbon isotope ratios were measured ($\delta^{13}\text{C}$, ‰) to assess the relative balance between the supply of CO_2 via leaf conductance and the demand for CO_2 by photosynthetic enzymes. Specifically, decreases in stomatal conductance and/or increases in photosynthetic capacity (from increased leaf N content) will result in reduced fractionation against ^{13}C and less negative values of leaf $\delta^{13}\text{C}$ (Ehleringer, 1991). Carbon isotope ratios in tree-ring α -cellulose were analysed on a subset of trees ($n = 6$ live and 6 killed trees per site), and a subset of years ($n = 6$ years per tree). For trees from each site, we chose to analyse $\delta^{13}\text{C}$ from growth rings formed during the wettest and driest periods prior to defoliation. We defined these periods as the wettest and driest 3-year periods, based on regional Palmer Drought Severity Indices (see below). For Moab, the wettest period was 1997–1999, and the driest period was 2002–2004. For Army Drain and Allen's Patch, the wettest period was 1996–1998, and the driest period was 2001–2003. Samples for stable isotope analysis were removed from portions of stem cross-sections that were sanded to avoid contamination. Individual tree rings, including earlywood and latewood were separated using a razor blade. Wood from the individual rings was ground into coarse powder (20 mesh) with a Wiley mill (Thomas Scientific, Swedesboro, NJ, USA). The ground samples were placed in tissue digestion bags and sealed. α -Cellulose was extracted from the bagged wood samples as described by Leavitt and Danzer (1993). The extracted cellulose samples were weighed to 200 μg and loaded into tin capsules, then analysed on a continuous-flow-gas-ratio mass spectrometer (Finnigan Delta PlusXL, ThermoFisher Scientific, Waltham, MA, USA) coupled to an elemental analyser (Costech Technologies, Valencia, CA, USA) at the Environmental Isotope Laboratory at the University of Arizona. Carbon isotope ratios were expressed in δ (delta) notation in reference to the PDB standard (Pee Dee Belemnite, SC, USA). The instrument error (twice the standard deviation) associated with each measurement was ± 0.1 ‰.

Environmental data

Ring widths at all sites were compared with the mean water year (October to September) regional PDSI. PDSI data were available from the NOAA climate data website using data for Utah Climate Region 7 (<http://wlf.ncdc.noaa.gov/temp-and-precip/time-series/index.php?parameter=pdsi&month=1&year=2008&filter=1&state=42&div=7>) and Nevada Climate Region 1 (<http://www.ncdc.noaa.gov/temp-and-precip/time-series/index.php?parameter=pdsi&month=12&year=2009&filter=1&state=26&div=1>). In addition, we compared the Moab tree-ring data with the mean annual flow (F_r) of the Colorado River. Flow data were from a gauge located on the Colorado River near Cisco, UT (http://waterdata.usgs.gov/ut/nwis/uv/?site_no=09180500&PARAMeter_cd=00065,00060,72020,00010,00095,00300,63680) from the US Geological Survey stream gauge network.

series/index.php?parameter=pdsi&month=12&year=2009 & filter=1&state=26&div=1). In addition, we compared the Moab tree-ring data with the mean annual flow (F_r) of the Colorado River. Flow data were from a gauge located on the Colorado River near Cisco, UT (http://waterdata.usgs.gov/ut/nwis/uv/?site_no=09180500&PARAMeter_cd=00065,00060,72020,00010,00095,00300,63680) from the US Geological Survey stream gauge network.

Statistics

To compare radial growth with environmental variables, PDSI and F_r , ring widths were plotted over time and detrended using linear regression and by dividing residuals by predicted values to create a ring-width index (RWI) for each annual ring (Fritts, 1976; Fritts and Swetnam, 1989). The standardized indices from each tree were then averaged to create a mean chronology within each age group.

Mean annual differences in BAI and $\delta^{13}\text{C}$ between live trees and killed trees were tested over time (years) using analysis of covariance, where tree condition (i.e. live or killed), year and tree condition \times year were independent variables. Relationships between radial growth, RWI and $\delta^{13}\text{C}$ with environmental variables F_r and PDSI were tested using analysis of variance after verifying linearity. Radial growth, RWI and $\delta^{13}\text{C}$ relationships with PDSI, F_r and tree condition (i.e. live or killed) were tested using analysis of covariance, where F_r , PDSI, tree condition, $F_r \times$ tree condition, and PDSI \times tree condition were used as independent variables. Differences in $\delta^{13}\text{C}$ between live and killed trees were compared with a Student's *t*-test. Differences in $\delta^{13}\text{C}$ among sites were compared with a Tukey–Kramer *post hoc* test. Relationships between radial growth and $\delta^{13}\text{C}$ were tested using analysis of variance after testing for linearity. Where relationships between $\delta^{13}\text{C}$ and PDSI were non-linear, we normalized PDSI (PDSI_n) to eliminate negative values by adding the integer of the most negative mean annual PDSI year (i.e. most-intense drought year) to all mean annual PDSI values within the measurement interval. This allowed the PDSI data to be log transformed. JMP 8.0 (SAS Institute, Cary, NC, USA) was used for all statistical analysis, with $P \leq 0.1$ as the significance level of acceptance.

RESULTS

The primary outcome of this study was the comparison of radial growth patterns between co-occurring live and killed trees. Therefore, raw ring widths [i.e. radial growth (RG)] are presented along with ring-width indices that are commonly reported in tree-ring studies. Mean annual RG of all trees (i.e. live and killed trees pooled) were similar between Moab ($2.27 \pm 0.16 \text{ mm year}^{-1}$) and Allen's Patch ($2.26 \pm 0.12 \text{ mm year}^{-1}$), whereas the mean annual RG of the older trees at Army Drain was much smaller ($1.00 \pm 0.16 \text{ mm}$). Basal area increment (BAI) of live and killed trees, measured from whole-wood growth, yielded very different patterns among sites. At Moab, annual BAI during years prior to herbivory (1992–2006) was on average 100 % greater in killed trees than in living trees ($P < 0.0001$; Table 1 and Fig. 2A). Mean annual BAI differed, with $265 \pm 42.3 \text{ mm}^2 \text{ year}^{-1}$ in

TABLE 1. Analysis of covariance of basal area increment and $\delta^{13}\text{C}$ against year prior to episodic herbivory of *Tamarix* by the *Tamarix* leaf beetle and tree condition (i.e. live or killed) of tamarisk trees occurring at three sites in the western USA. Values of $P < 0.1$ are highlighted in bold

	Basal area increment (mm^2)		$\delta^{13}\text{C}$ (‰)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Moab				
Year	227	< 0.0001	3.75	0.0888
Tree condition	238	< 0.0001	27.8	0.0008
Year \times tree condition	6.17	0.0197	5.16	0.0528
Army Drain				
Year	0.02	0.88	0.04	0.84
Tree condition	18.4	< 0.0001	7.81	0.0234
Year \times tree condition	0.16	0.69	0.00	0.96
Allen's Patch				
Year	97.5	< 0.0001	0.27	0.62
Tree condition	2.11	0.17	0.00	1.00
Year \times tree condition	0.01	0.91	0.14	0.72
All sites				
Year	NA	NA		
Tree condition	1403	< 0.0001		
Year \times tree condition	32.2	< 0.0001		

live trees to 530 ± 66.3 $\text{mm}^2 \text{year}^{-1}$ in killed trees. There was also a significant interaction between tree condition (i.e. live vs. killed) and year ($P = 0.0197$; Table 1), such that the differences in BAI between live and killed trees increased through time (Fig. 2A).

Mean annual BAI of trees killed at Army Drain was 43 % higher in years prior to the onset of herbivory (1984–2003) than co-occurring trees that survived, with 169 ± 31.9 $\text{mm}^2 \text{year}^{-1}$ in live trees to 241 ± 63.7 $\text{mm}^2 \text{year}^{-1}$ in killed trees ($P < 0.0001$; Table 2 and Fig. 2B). Unlike the Moab site, there was no interaction between tree condition and year ($P = 0.69$; Table 1), suggesting the differences in growth between live and killed trees remained constant through time (Fig. 2B). Trees at Allen's Patch did not differ significantly in mean annual BAI in years prior to herbivory (1994–2003) ($P = 0.17$; Table 1 and Fig. 2C). Mean annual BAI was 296 ± 39.2 $\text{mm}^2 \text{year}^{-1}$ vs. 323 ± 41.8 $\text{mm}^2 \text{year}^{-1}$ in live and killed trees, respectively.

To compare the mean annual BAI of live and killed trees across all sites, we analysed the relative BAI of all live and killed trees over the most recent 10 years prior to the onset of herbivory at each site. For Moab, this included BAI from 1997 to 2006, and from Army Drain and Allen's Patch, this included BAI from 1994 to 2003. Mean annual BAI across all sites was on average 45 % higher in killed trees compared with live trees ($P < 0.0001$; Table 1 and Fig. 2D). There was also a significant interaction between tree condition and year before the onset of herbivory ($P < 0.0001$), such that the differences in BAI between live and killed trees decreased through time (Table 1 and Fig. 2D).

Ring width indices (RWI), pooled across all sites, were correlated with mean annual PDSI (an analogue of inter-annual drought–inter-drought cycles) in both live ($F = 15.9$, $P = 0.0003$, $R^2 = 0.27$, $\text{RWI} = 0.034 + 0.042 \times \text{PDSI}$) and killed trees ($F = 15.4$, $P = 0.0003$, $R^2 = 0.26$, $\text{RWI} = 0.043 +$

$0.051 \times \text{PDSI}$) (Fig. 3). Despite clear differences in mean annual growth (Fig. 2), the relationship between RWI and PDSI was similar between live and killed trees ($F = 0.00$, $P = 0.99$; Fig. 3). However, an analysis of RG from each site separately showed divergent patterns between live and killed trees. At Moab, the relationship between RG and PDSI was strongly related to tree condition ($P < 0.0001$; Table 2 and Fig. 4A), although there was no interaction between PDSI and tree condition ($P = 0.26$; Table 2). Mean annual RG in killed trees was marginally correlated with PDSI ($F = 4.46$, $P = 0.0547$, $R^2 = 0.26$, $\text{RG} = 2.62 + 0.07 \times \text{PDSI}$), whereas RG in live trees showed no such relationship with PDSI ($F = 0.62$, $P = 0.44$, $R^2 = 0.05$) (Fig. 4A). At Army Drain, the relationship between RG and PDSI was moderately well correlated with tree condition ($P = 0.0014$; Table 2 and Fig. 4B), with no temporal interaction between tree condition and PDSI ($P = 0.29$; Table 2). Mean annual RG was moderately correlated with PDSI in both live ($F = 12.7$, $P = 0.0022$, $R^2 = 0.41$, $\text{RG} = 0.93 + 0.05 \times \text{PDSI}$) and killed trees ($F = 20.3$, $P = 0.0003$, $R^2 = 0.53$, $\text{RG} = 1.22 + 0.08 \times \text{PDSI}$). Unlike the other two sites, tree condition at Allen's Patch did not affect the relationship between RG and PDSI ($P = 0.90$; Table 2 and Fig. 4C). Likewise, there was virtually no interaction between tree condition and PDSI ($P = 1.00$; Table 2). Mean annual RG in live trees was marginally correlated with PDSI ($F = 5.02$, $P = 0.0554$, $R^2 = 0.39$, $\text{RG} = 2.30 + 0.05 \times \text{PDSI}$), whereas RG in killed trees showed no relationship with PDSI ($F = 3.02$, $P = 0.12$, $R^2 = 0.27$).

At Moab, the close proximity of the trees to the Colorado River allowed us to investigate the relationship between RG and mean annual river discharge (F_r , $\text{m}^3 \text{s}^{-1}$). The relationship between RG and F_r was highly dependent on tree condition ($P < 0.0001$; Table 2 and Fig. 5). Likewise, there was a weak interaction between tree condition and F_r ($P = 0.0478$; Table 2), such that differences in growth between live and killed trees increased with F_r (Fig. 5). Mean annual RG in killed trees was moderately well correlated with F_r ($F = 13.39$, $P = 0.0029$, $R^2 = 0.51$, $\text{RG} = 2.024 + 0.003 \times F_r$), whereas RG in live trees showed no relationship with F_r ($F = 0.57$, $P = 0.46$, $R^2 = 0.04$).

In general, measurements of $\delta^{13}\text{C}$ in tree-ring α -cellulose paralleled patterns of BAI at the three sites. Moab yielded a fairly robust difference in $\delta^{13}\text{C}$ between live and killed trees ($P = 0.0008$; Table 1 and Fig. 6A); mean $\delta^{13}\text{C}$ averaged across all years was -26.1 ± 0.1 ‰, and -25.6 ± 0.2 ‰ in live and killed trees, respectively. There was a weak, but significant interaction between year and tree condition ($P = 0.0528$; Table 1) due to a generally larger difference in $\delta^{13}\text{C}$ during the driest set of years (i.e. 2002–2004) (Fig. 6A). There was also a modest difference in $\delta^{13}\text{C}$ detected between live and killed trees at Army Drain ($P = 0.0234$; Table 1 and Fig. 6B); mean $\delta^{13}\text{C}$ averaged across all years was -26.1 ± 0.4 ‰, and -25.8 ± 0.3 ‰ in live and killed trees, respectively. Unlike at Moab, there was no interaction between year and tree condition ($P = 0.96$; Fig. 6B). As with BAI measurements, there were no detectable differences in $\delta^{13}\text{C}$ between live and killed trees at Allen's Patch ($P = 1.00$; Table 1 and Fig. 6C). Mean annual $\delta^{13}\text{C}$ was -23.9 ± 0.2 ‰, and -23.9 ± 0.3 ‰ for live and killed trees,

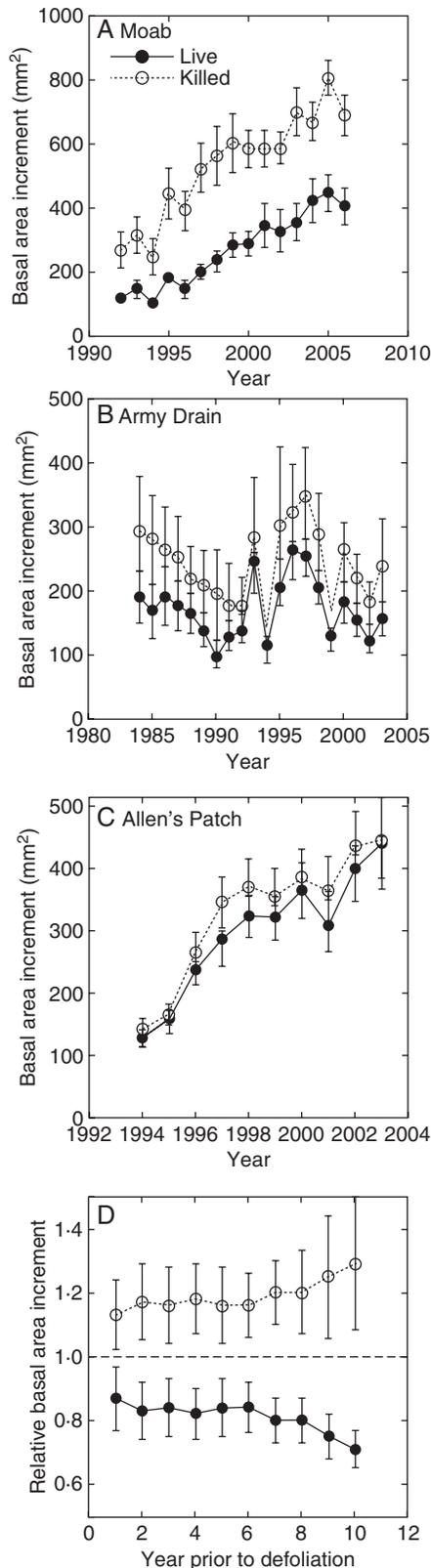


FIG. 2. Mean annual basal area increment (mm^2) during years prior to the onset of episodic herbivory of live and recently killed *Tamarix* trees occurring in the western USA. (A) Annual BAI from 1992 to 2006 of live ($n = 10$) and killed trees ($n = 10$) occurring along the Colorado River near Moab, UT. (B) Annual BAI from 1984 to 2003 of live ($n = 6$) and killed ($n = 6$) trees

TABLE 2. Analysis of Covariance (ANCOVA) of ring width and carbon isotope ratios ($\delta^{13}\text{C}$) of wood α -cellulose against annual PDSI, annual river flow (Moab site only), tree condition (i.e. live vs. killed) of *Tamarix* trees occurring at three sites in the western USA. Values of $P < 0.05$ are highlighted in bold

	Radial growth (mm)		$\delta^{13}\text{C}$ (‰)	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Moab				
PDSI	4.58	0.0418	8.66	0.0186
Tree condition	46.3	< 0.0001	39.1	0.0002
PDSI \times tree condition	1.34	0.26	7.12	0.0284
River flow	9.83	0.0042	7.10	0.0286
Tree condition	58.2	< 0.0001	37.5	0.0003
$F_r \times$ tree condition	4.32	0.0478	7.74	0.0239
Army Drain				
PDSI	32.7	< 0.0001	0.13	0.73
Tree condition	11.9	0.0014	7.91	0.0228
PDSI \times tree condition	1.50	0.29	0.02	0.89
Allen's Patch				
PDSI	7.55	0.0143	0.65	0.22
Tree condition	0.02	0.90	0.00	1.00
PDSI \times tree condition	0.00	1.00	0.02	0.90

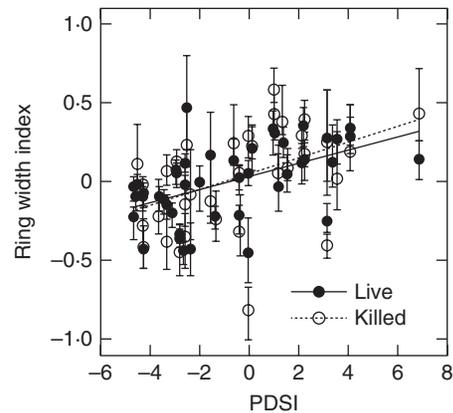


FIG. 3. Mean ring width index of all sample live ($n = 31$) and recently killed ($n = 31$) *Tamarix* trees occurring in the western USA in relation to the regional Palmer Drought Severity Index (PDSI). Error bars represent \pm s.e.m.

respectively. Not surprisingly given the similar $\delta^{13}\text{C}$ values, there was no interaction between year and tree condition at Allen's Patch ($P = 0.72$; Table 1 and Fig. 6C). Mean $\delta^{13}\text{C}$ of all trees was similar between Moab and Army Drain ($P = 0.93$, Tukey–Kramer *post hoc* comparison of means; Fig. 6C inset). Conversely, $\delta^{13}\text{C}$ at Allen's Patch was approx. 2 ‰ higher (less negative) than the other two sites ($P < 0.0001$, Tukey–Kramer *post hoc* comparison of means; Fig. 6C inset).

As with RG, the relationship between $\delta^{13}\text{C}$ and PDSI differed among sites. At Moab, the relationship between $\delta^{13}\text{C}$ and PDSI was correlated with tree condition ($P = 0.002$;

occurring at Army Drain near Lovelock, NV. (C) Annual BAI from 1994 to 2003 of live ($n = 15$) and killed ($n = 15$) trees occurring at Allen's Patch near Lovelock, NV. (D) Relative BAI of live and killed trees measured across all sites during the most recent 10 years prior to the onset of episodic herbivory. Error bars represent \pm s.e.m.

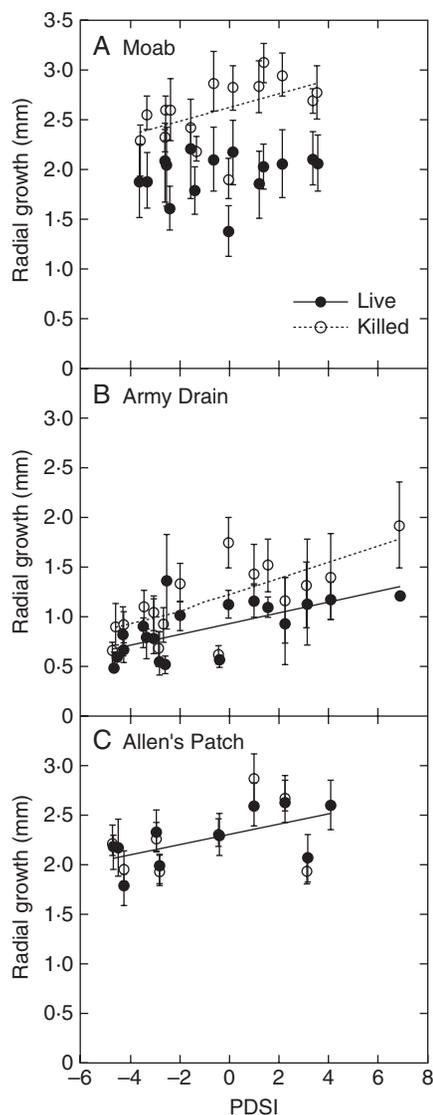


FIG. 4. Mean annual radial growth (mm) in relation to the mean annual Palmer Drought Severity Index (PDSI) during years prior to the onset of episodic herbivory of live and recently killed *Tamarix* trees occurring in the western USA. (A) Annual ring width in relation to the PDSI from 1992 to 2006 of live ($n = 10$) and killed trees ($n = 10$) occurring along the Colorado River near Moab, UT. (B) Annual ring width in relation to the PDSI from 1984 to 2003 of live ($n = 6$) and killed ($n = 6$) trees occurring at Army Drain near Lovelock, NV. (C) Annual ring width against PDSI from 1994–2003 of live ($n = 15$) and killed ($n = 15$) trees occurring at Allen's Patch near Lovelock, NV. Error bars represent \pm s.e.m.

Table 2 and Fig. 7A). There was also a weak interaction detected between PDSI and tree condition ($P = 0.0284$; Table 2) due to killed trees having higher (less negative) $\delta^{13}\text{C}$ during dry years (Fig. 7A). Mean annual $\delta^{13}\text{C}$ of killed trees was reasonably well correlated with PDSI (normalized to eliminate negative values; PDSI_n) [$F = 27.5$, $P = 0.0063$, $R^2 = 0.89$, $\delta^{13}\text{C} = -25.5 - 0.5 \times \log(\text{PDSI}_n)$], whereas $\delta^{13}\text{C}$ of live trees showed no relationship with PDSI ($F = 0.47$, $P = 0.53$, $R^2 = 0.10$) (Fig. 7A). Neither Army Drain nor Allen's Patch yielded significant relationships between $\delta^{13}\text{C}$ and PDSI (Table 2).

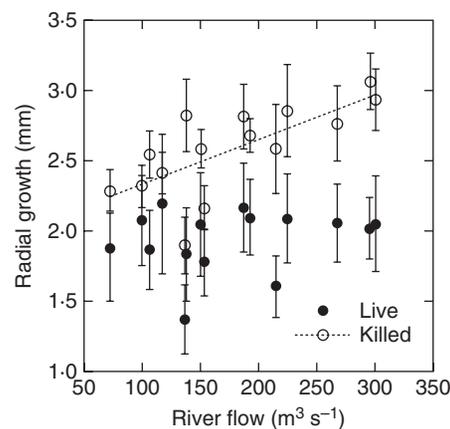


FIG. 5. Mean annual radial growth (mm) in relation to mean annual river flow ($\text{m}^3 \text{s}^{-1}$) during years prior to the onset of episodic herbivory of live ($n = 10$) and recently killed ($n = 10$) *Tamarix* trees occurring along the Colorado River near Moab, UT. Error bars represent \pm s.e.m.

The $\delta^{13}\text{C}$ in the Moab trees was inversely related to river flow ($P = 0.0286$; Table 2), although the relationship between $\delta^{13}\text{C}$ and F_r depended on tree condition ($P = 0.003$; Table 2 and Fig. 7B). As with PDSI, there was a weak interaction between F_r and tree condition ($P = 0.0239$; Table 2), as $\delta^{13}\text{C}$ was considerably higher (less negative) in killed trees during years of low mean annual flow (Fig. 7B), indicating lower stomatal conductance during dry years. Mean annual $\delta^{13}\text{C}$ of killed trees was well correlated with F_r [$F = 47.8$, $P = 0.0019$, $R^2 = 0.93$, $\delta^{13}\text{C} = -23.3 - 1.1 \times \log(F_r)$], whereas $\delta^{13}\text{C}$ of live trees showed no relationship with F_r ($F = 0.05$, $P = 0.84$, $R^2 = 0.01$) (Fig. 7B).

DISCUSSION

In many ways, the results from the present study are counter-intuitive, in that mortality caused by repeated defoliation generally corresponded with higher rates of growth compared with trees that survived defoliation. Accelerated growth often reflects higher resource availability, greater fitness, and enhanced resistance to mortality from physical damage. Greater mortality might be expected in slower-growing trees as a consequence of chronic or episodic resource limitation and subsequent lowered capacity to tolerate environmental stresses (Manion, 1991; Fine *et al.*, 2004), such as from drought, fire, insect outbreaks, etc. In the present study, trees that succumbed to repeated herbivory did, in fact, express a slightly less-negative mean annual $\delta^{13}\text{C}$ at two of the three sites (about 0.5 ‰ and 0.3 ‰ at Moab and Army Drain, respectively), suggesting that there may have been small micro-site differences in water availability, and subsequent canopy stomatal conductance between live and killed trees at these sites. Nevertheless, the spatial distribution of resources within alluvial floodplains, such as those studied here, are relatively uniform compared with many other ecosystems. The spatial smoothing of resource availability means that co-occurring plants do not necessarily have a predisposed advantage over one another. Therefore, the survival of individual *Tamarix* trees following episodic herbivory may result from

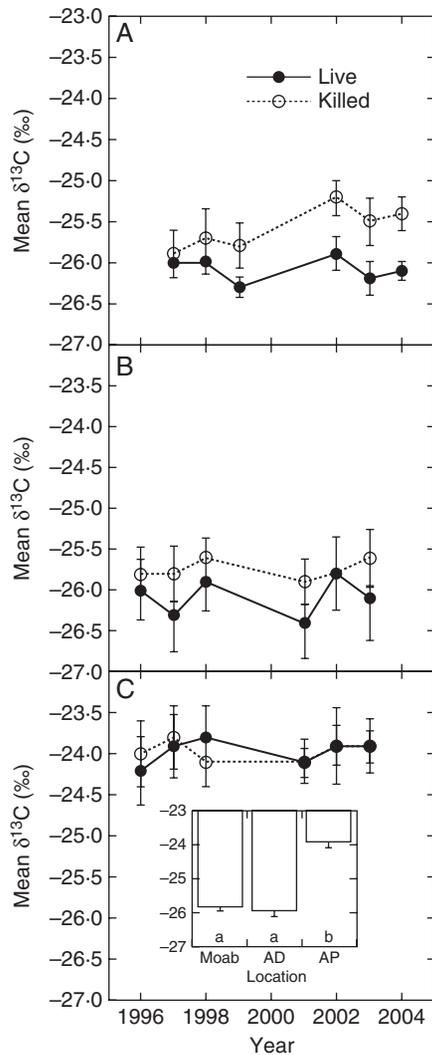


FIG. 6. Mean annual tree-ring cellulose $\delta^{13}\text{C}$ (‰) during years prior to the onset of episodic herbivory of live and recently killed *Tamarix* trees occurring in the western USA. (A) Mean annual $\delta^{13}\text{C}$ of live ($n = 6$) and killed trees ($n = 6$) occurring along the Colorado River near Moab, UT. (B) Mean annual $\delta^{13}\text{C}$ of live ($n = 6$) and killed ($n = 6$) trees occurring at Army Drain near Lovelock, NV. (C) Mean annual $\delta^{13}\text{C}$ of live ($n = 6$) and killed ($n = 6$) trees occurring at Allen's Patch near Lovelock, NV. Inset: mean annual tree-ring cellulose $\delta^{13}\text{C}$ of live ($n = 6$) and recently killed ($n = 6$) trees during recent years ($n = 6$ years) prior to the onset of episodic herbivory of *Tamarix* trees occurring at three sites in the western USA. Different letters represent differences ($P < 0.1$) among sites. Error bars represent \pm s.e.m.

prior selection, whereby resources are allocated for storage and defence at the expense of greater tissue structure and synthesis. If so, patterns of survival and mortality likely reflect trade-offs between allocation strategies to maximize growth versus survival capacity in the face of episodic disturbance.

Non-structural carbohydrate (NSC) pools play a critical role in plant survival following episodic disturbance (Bloom *et al.*, 1985; Chapin *et al.*, 1990). Nevertheless, the internal storage of NSCs in woody plants has traditionally been viewed as a passive process, where storage pools accumulate only when the supply of carbon via photosynthesis is greater than the demand for growth and metabolism (Körner, 2003).

However, recent evidence suggests that NSC storage is often a highly regulated process (Hoch *et al.*, 2003; Sala *et al.*, 2012). For example, NSC concentrations in branch sapwood of mature deciduous trees can remain fairly constant over a calendar year despite large seasonal fluctuations in demand (Hoch *et al.*, 2003), suggesting that trees continue to allocate carbon to storage pools during the growing season when carbon demand for growth and metabolism are high (Sala *et al.*, 2012). This apparent active regulation of carbon allocation may be co-ordinated by a complex genetic linkage between photosynthesis, growth and storage (Smith and Stitt, 2007). If so, carbon allocation strategies may be highly variable within and among plant populations, depending on selective pressures from competition, resource limitation and disturbance.

Many *Tamarix* species have evolved under intense pressure from herbivory. In its home range, *Tamarix* is attacked by >320 species of insects and mites from 88 genera (Kovalev, 1995). This plant–insect co-evolution has likely resulted in a diverse set of strategies that can be drawn upon if needed to compensate for tissues damaged by herbivory (Bloom *et al.*, 1985). With *Tamarix* in North America, defence mechanisms are inadequate to prevent complete defoliation by *D. carinulata* (Dudley, 2005; Hultine *et al.*, 2010b; Pattison *et al.*, 2011). Therefore, its survival depends on the ability to produce new foliage after each defoliation event. Otherwise, individual *Tamarix* plants will become carbon-starved and unable to maintain a minimum level of metabolic activity for survival. Repeated *Tamarix* defoliation by *D. carinulata*, over a 3-year period in north-western Nevada, resulted in a 75 % decrease in NSC concentrations that resulted in measurable reductions in total leaf area (Hudgeons *et al.*, 2007) and plant water use (Pattison *et al.*, 2011). Despite these sharp declines, most *Tamarix* trees survived even after several years of defoliation (Dudley *et al.*, 2006). As with the present study, patterns of mortality and survival may have reflected differences in metabolite storage prior to the onset of defoliation, although further research is needed to support this hypothesis.

Killed trees that expressed higher radial growth rates also expressed higher (less negative) $\delta^{13}\text{C}$ in tree-ring cellulose, although mean annual differences in $\delta^{13}\text{C}$ between live and killed trees were relatively small (Fig. 6A, B). The ratio of $\delta^{13}\text{C}$ in the tissues of C_3 plants reflects the balance between the supply of CO_2 into the leaf (i.e. stomatal conductance) and the demand for CO_2 by photosynthetic enzymes. Therefore, differences in $\delta^{13}\text{C}$ between live and killed trees could reflect a higher photosynthetic capacity in killed trees, a lower stomatal conductance in killed trees or both. A higher photosynthetic capacity could explain the higher growth rates in killed trees, although this would not explain why higher growth rates were correlated with mortality. Plant canopies with high photosynthetic capacities typically have high leaf nitrogen concentrations, because the large majority of leaf N is present in either the chloroplasts or photosynthetic enzymes (primarily RUBISCO in C_3 plants) (Evans and Seemann, 1989). Leaves that are high in N are generally more palatable to herbivores (Feeny, 1970; Knepp *et al.*, 2005). However, in the present study, *D. carinulata* consumed virtually all of the foliage in *Tamarix* canopies during the first

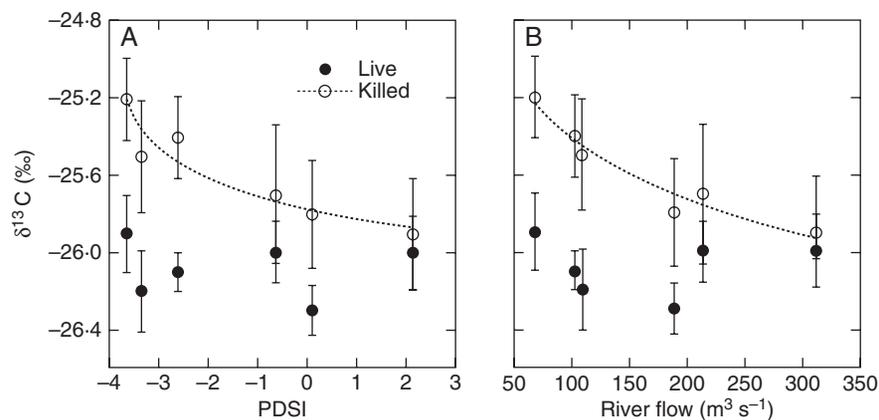


FIG. 7. Mean annual tree-ring cellulose $\delta^{13}\text{C}$ (‰) in relation to (A) mean annual Palmer Drought Severity Index (PDSI) and (B) mean annual river flow of live ($n = 6$ trees) and recently killed ($n = 6$ trees) during recent years ($n = 6$ years) prior to the onset of episodic herbivory of *Tamarix* trees occurring along the Colorado River near Moab, UT. Error bars represent \pm s.e.m.

several years following its initial arrival (Pattison *et al.*, 2011). Given that live and killed trees were subjected to similar defoliation pressures, there is no apparent link between cellulose $\delta^{13}\text{C}$, photosynthetic capacity and survival from episodic herbivory in the *Tamarix* stands that we investigated.

Alternatively, differences in $\delta^{13}\text{C}$ between live and killed trees may have been related to differences in stomatal conductance. As discussed earlier, the two sites (Moab and Army Drain) that showed significant disparities in mean annual RG, and BAI between live and killed trees also expressed somewhat higher $\delta^{13}\text{C}$ ratios in cellulose. In fact, at Moab, BAI was 100 % higher in killed trees relative to live trees despite having about a 0.5 ‰ higher mean annual $\delta^{13}\text{C}$. At this site, $\delta^{13}\text{C}$ in killed trees was inversely correlated with river flow and PDSI, while surviving trees expressed no relationship with climate (Fig. 7). Although we cannot rule out the possibility that photosynthetic capacity increased in killed trees with aridity, it seems far more likely that stomatal conductance decreased with aridity. Therefore, these patterns suggest that despite potentially having a somewhat lower canopy stomatal conductance (especially during drier years), radial growth remained significantly higher in killed trees.

Conversely, the live trees at Allen's Patch had similar BAI and $\delta^{13}\text{C}$ as the killed trees. These trees also expressed a 2 ‰ higher mean annual $\delta^{13}\text{C}$ compared with the other sites – a relatively large difference that likely reflects either a lower water table and/or higher soil salinity relative to the other two sites. Although we have no way of knowing for sure, it is plausible that higher relative moisture stress played a role in the different patterns displayed at Allen's Patch relative to the other sites that showed measurable differences in growth between live and killed trees.

As hypothesized, radial growth of killed *Tamarix* trees was generally more sensitive to inter-annual variation in climate than that of surviving trees (although differences in ring-width indices were undetectable; Fig. 3). In fact, radial growth of live trees at Moab showed no relationship with either PDSI or river discharge, while radial growth of killed trees was correlated to both variables. A reasonable explanation for the complacent growth in surviving trees is that they had a more favourable water balance, as evidenced by the lower mean annual $\delta^{13}\text{C}$

(particularly during dry years) relative to killed trees. This explanation would be supported if the killed trees had a significantly lower growth rate during low-flow years compared with live trees, a common pattern during drought in upland ecosystems (Ogle *et al.*, 2000; Ruel and Whitham, 2002; McDowell *et al.*, 2010). Instead, radial growth of killed trees was much higher during wet years, and remained somewhat higher during drought relative to live trees. Therefore, a more plausible explanation is that live trees preferentially maximize internal storage pools rather than maximize growth during periods when resources are readily available. If so, the combination of extended periods of drought that are predicted to occur at higher frequencies in the south-western USA, and repeated herbivory by the *D. carinulata* can be expected to deplete internal resource pools and cause widespread *Tamarix* mortality. In other words, the synergistic effects of drought and defoliation are likely to reduce the relative dominance of *Tamarix* populations over the long term, even those that are well adapted to episodic disturbance.

Results from this study show evidence of a trade-off between radial growth and survival in response to foliage herbivory in an invasive phreatophyte that currently dominates riparian areas throughout the western USA and northern Mexico. Although further work is needed to explore the potential mechanisms (e.g. carbon allocation, nitrogen resorption/availability and plant hydraulics) that underpin the apparent trade-offs between growth and survival, these data expand on previous dendrochronology studies of woody-plant mortality and shed light on the theoretical relationships between intensive herbivory pressures, net primary productivity and population dynamics of woody riparian plant species. Likewise, this study improves the ability to forecast patterns of *Tamarix* mortality in response to episodic defoliation by the *D. carinulata* that will assist future restoration efforts.

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