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Early impacts of biological control on canopy cover and water use of the invasive saltcedar tree (*Tamarix* spp.) in western Nevada, USA

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Abstract The success of biological control programs is rarely assessed beyond population level impacts on the target organism. The question of whether a biological control agent can either partially or completely restore ecosystem services independent of population level control is therefore still open to discussion. Using observational and experimental approaches, we investigated the ability of the saltcedar leaf beetle [*Diorhabda carinulata* (Brullé) (Coleoptera: Chrysomelidae)] to reduce the water use of saltcedar trees (*Tamarix ramosissima* Ledeb.) in two sites (Humboldt and Walker Rivers) in Nevada, USA. At these sites *D. carinulata* defoliated the majority of trees within 25 and 9 km, respectively, of the release location within 3 years. At the Humboldt site, *D. carinulata* reduced the canopy cover of trees adjacent to the release location by >90%. At a location 4 km away during the first year of defoliation, *D. carinulata* reduced peak (August) stem water use by 50−70% and stand transpiration (July to late September) by 75% ($P = 0.052$). There was, however, no reduction in stem water use and stand transpiration during the second year of defoliation due to reduced beetle abundances at that location. At the Walker site, we measured stand evapotranspiration (ET) in the center of a large saltcedar stand and found that ET was highest immediately prior to *D. carinulata* arrival, dropped dramatically with defoliation, and remained low through the subsequent 2 years of the study. In contrast, near the perimeter of the stand, *D. carinulata* did not reduce sap flow, partly because of low rates of defoliation but also because of increased water use per unit leaf area in response to defoliation. Taken together, our results provide evidence that in the early stages of population expansion *D. carinulata* can lead to substantial declines in saltcedar water use. The extent of these declines varies spatially and temporally and is dependent on saltcedar compensatory responses along with *D. carinulata* population dynamics and patterns of dispersal.

Keywords Defoliation · Evapotranspiration · Herbivory · Sap flow

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Introduction

The invasion of ecosystems by introduced species has widespread implications for the conservation of native biodiversity and ecosystem functions, leading to many efforts to reduce their abundances and impacts. As an

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alternative to conventional mechanical and chemical control treatments, biological methods of invasive plant control involving the introduction of specialist natural enemies may provide a cost-effective and environmentally benign approach for reducing the spread and impacts of invasive plants (Moran et al. 2005). The actual ecological outcomes of biological control on communities and ecosystems, however, are often not well studied and measures of 'success' are poorly defined (Denslow and D'Antonio 2005; Thomas and Reid 2007; Carson et al. 2008; Morin et al. 2009). For example, success is often defined as the ability to control a target invasive species (Thomas and Reid 2007), yet rarely have studies evaluated whether ecosystem services were improved with either complete or partial control (see Denslow and D'Antonio 2005 for a review). The most robust insights in this regard come from manipulative field studies (with and without agents) carried out at multiple sites. However, such studies are rare because of the difficulty in implementing them (Carson et al. 2008; Morin et al. 2009).

In this study we used observational and manipulative approaches to examine the impacts of the foliage feeding saltcedar leaf beetle *Diorhabda carinulata* (Brullé) (Coleoptera: Chrysomelidae) on the water use of invasive saltcedar (*Tamarix ramosissima* Ledeb., *T. chinensis* Lour., *T. gallica* L. and hybrids). Saltcedar is a deciduous small tree native to Eurasia and Africa that has invaded over a million hectares of riparian and wetland habitats throughout western North America, Argentina, Australia and South Africa with suites of impacts on native biodiversity and water use (Glenn and Nagler 2005; Shafroth et al. 2005). *Tamarix* spp. is considered to use large amounts of groundwater via transpiration, and while it is comparable in water use to native riparian plants on a leaf-area basis, its high leaf area and occupation of broad floodplain expanses contribute to water resource depletion (Sala et al. 1996; Dahm et al. 2002; Shafroth et al. 2005). Because water is a scarce and valued resource for humans throughout most of saltcedar's adventive range, reduction of its water use has been an important incentive for implementing control measures.

Diorhabda carinulata has been recently introduced into sites throughout the western USA to assist in saltcedar control (Lewis et al. 2003; Hultine et al. 2010a). To date, the results of preliminary studies of the beetle's impact on saltcedar water use have been equivocal (Dennison et al. 2009; Hultine et al. 2010b). Dennison et al. (2009) found that during the first year of defoliation saltcedar stem sap flow declined by >65% during peak defoliation and remained low for the duration of the season, but estimated annual evapotranspiration (ET) derived from remotely sensed data during this year for this site was not lower than that in previous years without *D. carinulata*. Hultine et al. (2010b) found that defoliation by beetles reduced sap flow by 16%, but these estimates were based on modeled rather than actual measures of non-impacted sap flow.

Overall few examples exist of the impacts of insect herbivory on water use at the whole tree or stand level (Cunningham et al. 2009; Schäfer et al. 2010). Psyllid herbivory resulted in tree leaf necrosis levels of 38% and a 25−50% reduction in tree sap flow in the tree *Eucalyptus blakelyi* (Cunningham et al. 2009). Schäfer et al. 2010) document that an outbreak of gypsy moths (*Lymantria dispar*), reduced tree sap flow by >80%, but effects were temporary due to tree refoliation.

In the study reported here, we examined the impacts of *D. carinulata* on saltcedar water use in two sites in western Nevada, USA, during the first years of *D. carinulata* establishment. Because water use in saltcedar stands is correlated with canopy cover (Dahm et al. 2002), we examined how *D. carinulata* defoliation affected saltcedar canopy cover while simultaneously measuring stem sap flow at targeted sites. We also used a manipulative approach to reduce beetle herbivory and compared water use between defoliated and 'protected' trees. Finally, we measured *D. carinulata* impacts on water use with Bowen ratio measures of stand ET.

Materials and methods

Study sites

Diorhabda carinulata was released at single locations in saltcedar stands on the lower reaches of the Humboldt and Walker Rivers in central Nevada, USA, in the late spring of 2001. The Humboldt River (hereafter the Humboldt site) and Walker River (hereafter the Walker site) sites are characterized by fine, saline silt soils from fluvial deposits within active and remnant, moderately incised river channels. The understory of both sites is characterized by saltgrass (*Distichlis spicata*) and various halophytic native and non-native forbs. Annual precipitation is 14 and 12 cm at the Humboldt site and Walker site, respectively.

Diorhabda carinulata overwinters in the adult stage under the litter of saltcedar and emerges in late April to early May (Lewis et al. 2003). Both larvae and adults feed on saltcedar foliage, resulting in dessication of the foliage and its eventual loss from trees. Adults typically move in large aggregations that appear to be directed towards available foliage (Lewis et al. 2003). As a result, trees are typically impacted by a single major defoliation event during a season followed by lesser amounts of defoliation by subsequent insect cohorts later in the season. Trees typically produce new foliage after defoliation within several weeks.

The dispersal of *D. carinulata*, as determined from ground surveys conducted at intervals of 1–4 weeks throughout stands and by survey flights conducted once or twice per growing season from 2002 until 2005, showed an expanding pattern of defoliation within and across seasons. At the Humboldt site we worked in three areas of defoliation. The Humboldt 2002 Defoliated Area (H2002DA) included the release site and the 2-ha area subsequently defoliated in 2002. The H2003DA consisted of trees outside of the H2002DA that were first defoliated in 2003. This area comprised approximately 200 ha and extended 2 km away from release site. The H2004DA consisted of trees beyond the other areas that were first defoliated in 2004. By 2004 *D. carinulata* had defoliated trees up to 25 km away from the release site in addition to previously defoliated areas, for a total defoliated area in that year of approximately 1,800 ha (Geraci 2006). Our study locations in the H2004DA occurred within 6 km of the release site. In 2005 *D. carinulata* fed to varying extents on trees in all previously impacted areas. The total extent of defoliation exceeded 8,100 ha within 3 years (Geraci 2006).

At the Walker site *D. carinulata* established in September, 2003 when they were detected on 10−20 trees near the release site. In 2004 *D. carinulata* had spread and defoliated most of the trees within approximately 2.5 km from the release site. In 2005 *D. carinulata* had continued to spread and had defoliated the entire southern extent of the Walker riparian area up to 9 km away from release site; this area is referred to in this study as the Walker 2005 Defoliated Area (W2005DA). Two locations were established within the W2005DA, both approximately 5 km south of the release site. One, referred to here as the Walker perimeter location, was 1.8 km from the Walker River, near the edge of a stand in an area of sparsely distributed saltcedar cover. The other location, referred to here as the Walker tower location, was 100 m from the Walker River, in an area of dense saltcedar. This latter location was within 250 m of a Bowen ratio tower established to measure the impacts of *D. carinulata* on stand ET (see below).

Canopy cover

At the Humboldt site, randomly selected trees were monitored within single locations (radius 100 m) in the H2002DA and H2003DA from 2003 to 2005 and in the H2004DA from 2004 to 2005. Trees at the tower location of the Walker site were monitored in 2005. Except for the H2002DA, the selection of monitoring locations occurred prior to *D. carinulata* arrival and was based on accessibility and similarity to the surrounding stand. At the Humboldt site, the same trees within each location were monitored over consecutive years, with additional trees being added in successive years. Trees at the Humboldt site were monitored from early June to October every 2 weeks in 2003 and 2004 and monthly in 2005. At the Walker tower location, 15 trees were monitored monthly from early June to October 2005; these trees were not monitored in August, 2005.

At both the Humboldt and Walker sites, pairs of trees with and without *D. carinulata* were established to provide controlled comparisons of *D. carinulata* impacts on canopy cover. Eight pairs of trees were established in May 2004 at the H2004DA and ten pairs were established in May 2005 at the Walker perimeter location. Trees in each pair were within 4−10 m of each other and were similar in size and canopy cover. One member of each pair was randomly selected to be sprayed with the commercial insecticide 4F carbaryl (trade name SEVIN; Bayer Crop Science, Research Triangle Park, NC) to reduce defoliation. Trees were sprayed as often as necessary (3−5 times/year) to minimize *D. carinulata* defoliation. Experimental trees were monitored at similar intervals as observational trees at each site.

Visual estimates of live canopy cover of individual trees rather than light extinction-based measures were used to quantify the impacts of *D. carinulata* on canopy cover because feeding by adults and larvae does not immediately reduce canopy cover. Rather, it leads to the desiccation of foliage, which typically remains on trees for several weeks. Light extinction measures do not distinguish foliage coloration so attached desiccated foliage cannot be differentiated from healthier tissue. Canopy cover of a tree at each sampling date was determined by multiplying a visual estimate of the percentage of each tree's canopy volume with foliage by a visual estimate of the percentage of that foliage that was characterized as green (undamaged). Estimates of canopy volume with foliage and the percentage of that foliage that was green were made based on comparisons with sprayed or non-defoliated trees. Independent assessments of the canopy cover of each tree were determined by two observers, and the average of these estimates was used. The same observers performed all estimates of canopy cover and were trained to ensure consistency. Average percentage canopy with green foliage (hereafter, canopy cover) was determined for each tree by averaging across all of the monitoring dates from June to October within 1 year. The estimates of canopy cover were not intended to provide an assessment of the leaf area of individual trees or the leaf area index of the stand; rather, they were intended as a measure of the impacts of *D. carinulata* on canopy cover relative to non-defoliated trees. At the same time, trees were monitored for canopy cover, and estimates of the number of *D. carinulata* in each life history stage were also obtained.

Stem water use

Stem water use was measured with the stem-heat-balance method (Baker and van Bavel 1987) using a Flow32 sap-flow system (Dynamax, Houston, TX). A similar system has been used for this species in southern Nevada (Sala et al. 1996). Beetle counts on similar-sized gauged and ungauged branches on the same tree revealed that gauges did not affect *D. carinulata* establishment (Pattison et al. 2010). Values of daily potential evapotranspiration (PET) were made concurrently with stem sap flow (see below). A single stem from each tree was selected based on the size of available stem gauges (2.0−3.0 cm) and the absence of lateral stems on the stem for a length of 30 cm. Gauges were placed on stems for 2−5 full days and daily water use (DWU) for each stem was determined by summing hourly water use (in grams per hour) over a complete day. Daily water use per sapwood area (SA) or per leaf area (LA) normalized by daily PET (DWU SA^{-1} PET^{-1} or DWU LA^{-1} PET^{-1}) for each gauge was determined by averaging across the number of days that gauges were on stems ($n = 2-5$).

Non-desiccated foliage of each stem was harvested immediately after sap flow measurements, placed in plastic bags in coolers and refrigerated until leaf area measurements could be made (within 1 week of harvesting). Because of the large amount of foliage per stem, a sub-sample of foliage was randomly selected from each branch and measured on a LI-3100 leaf area meter (LI-COR, Lincoln, NE). This sub-sample and the remaining leaves were dried at 55°C (3−4 days). Stem leaf area (one sided) was determined by multiplying the leaf area specific weight of the sub-sample by the total weight. Stem leaf area per stem area (LA SA^{-1}) was calculated to provide insights into impacts of *D. carinulata* on leaf area.

Gauges were insulated from solar radiation through the use of insulating shields. The sheath thermal conductance of branches (K_{sh}; see Baker and van Bavel 1987) was determined from the lowest nighttime measurements when flow was considered to be negligible. These values were compared to those of severed branches with gauges and found to be similar (Pattison et al. 2010). Moore et al. (2008), working with *Tamarix chinesis* in New Mexico, found no detectable sap flow at vapor pressure deficits (VPD) of <1 kPa, an event that occurred at least once each night. As the minimum daily VPD in our study was always <1 kPa (Pattison et al. 2010), our choice of the lowest nightly flows to calculate K_{sh} likely reduced errors associated with non-zero flows.

Measurements of PET were made using Penman–van Bavel ETP software (Dynamax, Houston, TX) based on inputs of global shortwave radiation, air temperature, relative humidity and wind velocity from a Dynamet weather station (Dynamax, Houston, TX). The station was placed in a >100-m diameter open area, 400 m from the sap flow station.

Sap flow measurements were taken on different randomly selected trees in the H2004DA location at the Humboldt site and at the Walker perimeter location. Sap flow measurements in the H2004DA were performed at two locations. At one location closer to the release site, measurements were made in August 2004 ($n = 7$ trees) and August 2005 ($n = 7$ trees). These trees experienced major defoliation events in June 2004 and 2005 with minimal defoliation at other times. At another location in the H2004DA (approx. 6 km from the release site), sap flow was measured in August 2004 on ($n = 13$) trees that *D. carinulata* had not yet defoliated. These trees were defoliated soon after measurements had been made and were not re-measured but used to provide an index of sap flow of non-defoliated trees.

At the Walker perimeter location, 12 trees were randomly selected at the beginning of the 2005 growing season, prior to the arrival of *D. carinulata*, to be sprayed with insecticide for use in our study as non-defoliated trees. Measurements of non-defoliated trees consisted of unsprayed trees measured prior to *D. carinulata* arrival in mid June ($n = 8$) and sprayed trees after *D. carinulata* arrival in July ($n = 4$), August ($n = 4$) and September ($n = 4$) 2005. The measurements of defoliated trees were performed in late June (when the beetles first arrived; $n = 8$), July ($n = 4$), August ($n = 8$) and September ($n = 3$) 2005.

At the Humboldt site, repeated sap flow measurements were performed on four randomly selected pairs of the eight experimental pairs of trees at the H2004DA to provide insights into the impacts of *D. carinulata* on stem sap flow before, during and after defoliation. Paired measurements were made on the same stems seven times in 2004, starting in May prior *D. carinulata* arrival in June and continuing until 29 September 2004. The measurements were made on the same stems in late July and mid-September, 2005. All stems were 2.4−2.7 cm in diameter and were on similar locations on trees. The sapwood area of these trees was determined from regressions of stem diameter to sapwood area.

Stand transpiration

In order to scale up stem level water use to stand level transpiration at the H2004DA, the sapwood area per hectare of saltcedar trees was measured in June 2004 in three 5 × 5-m plots randomly located within the H2004DA location. The diameter of all live saltcedar stems >1 cm at a height of 20 cm above the ground was measured. The values of stem sapwood area were determined from

regressions of sapwood area to stem area from destructive harvests of stems. The stand transpiration of trees with and without *D. carinulata* was calculated by multiplying the DWU SA^{-1} of each of the four pairs of trees by sapwood area per hectare for each of the seven measurement dates in 2004. Stand transpiration between 8 May and 29 September 2004 was then determined by calculating the area under the respective curves (SigmaPlot 8.0; SPSS, Chicago, IL) of stand transpiration of insecticide-treated and *D. carinulata*-exposed trees across these seven measurement dates.

Stand evapotranspiration

The impact of *D. carinulata* defoliation on ET in the center of the Walker River site was measured using the Bowen-ratio energy budget method, which incorporates the ratio of sensible to latent heat losses above a canopy to estimate evaporation (Bowen 1926). Micro-meteorologic data were measured from a tower constructed on 23 March 2005 prior to beetle arrival in mid-May 2005 (see Laczniak et al. 1999 for details on tower instrumentation). The tower was placed in a dense monotypic stand of saltcedar (2 m tall) in a location that had an adequate fetch between sensors and the edge of saltcedar stand. Data were recorded at 20-min intervals. Temperature and relative humidity were measured at 3.0 and 4.0 m above ground, respectively. These sensors were mounted on an automated exchange mechanism that exchanged sensor positions every 10 min in order to minimize bias between the sensors. Net radiation was recorded at 4.0 m above the ground. Wind speed was measured using a three rotor cup anemometer at a height of 3.5 m. Volumetric water content was measured with probes at 2 and 6 cm below the ground surface. Soil heat flux was measured at 6 cm below the ground surface using the average values of two soil heat flow transducers. Soil temperature was measured using two thermocouples placed at depths of 2 and 4 cm, respectively, below the ground surface. Bulk precipitation was measured three times during the summer field season with a rain gauge installed on 10 May 2005, with refrigerant oil added to prevent freezing and evaporation between site visits. Daily ET was not computed if >10% of the day's 20-min data set was missing. PET at the tower was computed based on global shortwave radiation, air temperature, relative humidity and wind velocity data, using the equations of Penman (1948) with a wind function as modified by Jensen (1974).

Measurements of *D. carinulata* abundance and the percentage of canopy with green foliage at the tower monitoring location (250 m from the tower site) provided an index of *D. carinulata* activity and canopy cover near the ET site. An electric tape was used to measure depth to ground water below the tower; this measurement was made eight times (between 10 May 2005 and 27 September 2005) during the 2005 growing season and five times (between 13 June 2006 and 18 October 2006) during the 2006 growing season. Stream flow data of the Walker River were taken from the U.S. Geological Survey (USGS) stream gauge (10302002) located at approximately 10 km upstream of the tower site.

Data analysis

All statistical comparisons were made between trees within either the Humboldt or Walker sites. Differences in canopy cover across years within the three different areas (H2002DA, H2003DA and H2004DA) at the Humboldt site were determined using repeated measures analysis of variance (ANOVA) with adjusted Tukey tests for post-hoc comparisons of least squares means (proc Mixed, SAS software 2002; SAS Institute, Cary, NC). The difference in canopy cover of the eight pairs of trees at the H2004DA at the Humboldt site in 2004 and 2005 was tested with repeated measures ANOVA (proc Mixed, SAS) with separate tests of simple effects of defoliation in 2004 and 2005. The canopy cover of the ten pairs of trees at the Walker perimeter location in 2005 was compared using ANOVA (proc GLM, SAS).

The number of major defoliations (0−2) was included as a factor in the one-way ANOVAs (proc GLM, SAS) performed to examine differences in DWU SA^{-1} PET^{-1}, DWU LA^{-1} PET^{-1} and LA SA^{-1} at the Humboldt site across measurements in August. Adjusted Tukey tests for post-hoc comparisons of least squares means were used to identify differences.

The repeated measurements of DWU SA^{-1} PET^{-1} in 2004 and 2005 of the paired trees at the H2004DA were compared with separate (one for 2004 and one for 2005) repeated measures ANOVAs (proc MIXED, SAS). A two-way (with and without defoliation and month) ANOVA (proc GLM, SAS) was used to test for differences in DWU SA^{-1} PET^{-1} DWU LA^{-1} PET^{-1} and LA SA^{-1} of trees at the Walker site. Analysis of covariance (ANCOVA) (SPSS 2003) was used to test for a significant interaction term for DWU/PET and the covariate LA of all trees measured at the 2005DA at the Walker site.

Data for stand transpiration (DWU ha^{-1}) for insecticide-treated ($n = 4$) and *D. carinulata*-exposed ($n = 4$) trees in 2004 lacked homogeneity of variance despite transformation. As a result, Mann–Whitney U tests were used to determine significant ($P < 0.05$) differences.

In all ANOVA analyses, type III sums of squares and least squares means were used to determine levels of significance because of missing data. We tested the residuals from all analyses for normality and homogeneity of variance. Levels of significance were determined at $P < 0.05$

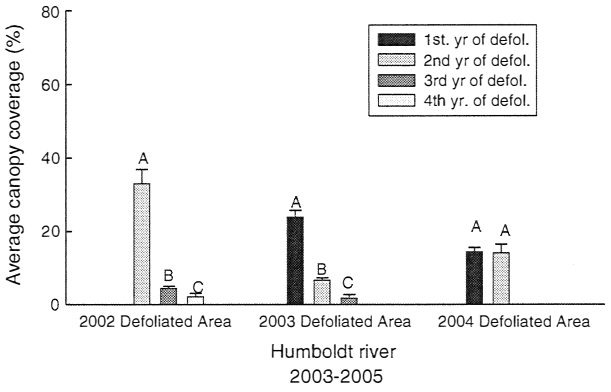

Fig. 1 Average percentage of canopy with green foliage for trees in three defoliated areas at the Humboldt River site. Defoliated areas refer to the year when *Diorhabda carinulata* first defoliated trees in that area. *Different shading of bars* indicates the number of years that trees had been defoliated. *Bars* Means of 5–54 trees [±1 standard error (SE) of the mean]. Values represent the yearly average of approximately bimonthly measurements from June to October. *Bars with the same letters* are not significantly different ($P < 0.05$) from each other within an area. Trees in the 2002 defoliated area include the release site and were first monitored for canopy cover in 2003; hence there is no black bar for that site

with adjustments (Tukey) made to alpha levels for multiple comparisons. The software program SAS ver. 9.1 was used for all statistical analyses (SAS 2002).

Results

Canopy cover

Canopy cover of trees in the H2002DA ($F_{2,23} = 223.8$, $P < 0.0001$) and the H2003DA ($F_{2,86} = 155.18$, $P < 0.0001$) decreased with increasing defoliation events (Fig. 1). The reduction in canopy cover in the H2002DA from the second (33.0%) to the fourth year (2.1%) was 93% ($T_{2,23} = 20.97$, $P < 0.001$). The canopy cover of trees in the H2003DA decreased from 24% in the first year of defoliation to 1.8% in the third year of defoliation—a reduction of 92.5% ($T_{2,86} = 17.31$, $P < 0.0001$). There was no difference in the canopy cover of trees in the H2004DA between the first and second years ($F_{1,34} = 0.00$, $P = 0.969$) (Fig. 1).

Among the eight paired trees at the H2004DA in 2004 and 2005 there was a significant year-by-defoliation interaction ($F_{1,10} = 8.63$; $P = 0.0148$) for canopy cover. Within 2004, *D. carinulata* reduced the seasonal canopy cover of exposed trees (19.5 ± 1.5%) relative to paired insecticide-treated trees (57.8 ± 2.3%) by 66% ($F_{1,10} = 13.76$, $P < 0.001$). In 2005, *D. carinulata* had reduced the seasonal canopy cover of *D. carinulata*-exposed trees (29.6 ± 4.9%) relative to insecticide-treated trees (55.9 ± 1.8%) by 47% ($F_{1,10} = 9.71$, $P = 0.011$) (Fig. 2a). Among the paired trees at the Walker site, *D. carinulata*-exposed trees (36.4 ± 2.0%) had a 28% ($F_{1,18} = 11.60$; $P = 0.0031$) reduction in seasonal canopy cover relative to the paired insecticide-treated trees (50.7 ± 3.7%) in 2005 (the only year measured).

Tests involving spraying insecticide on ten pairs (with and without insecticide) of non-defoliated saltcedar trees indicated that insecticide did not alter foliage coloration, canopy cover or stem sap flow rates (Pattison et al. 2010). However, while spraying was effective in removing larvae and adult *D. carinulata* present on the tree, it did not prevent new adults from arriving and feeding on sprayed trees. Consequently, sprayed trees were defoliated to varying degrees (<10% of canopy). Consequently, these

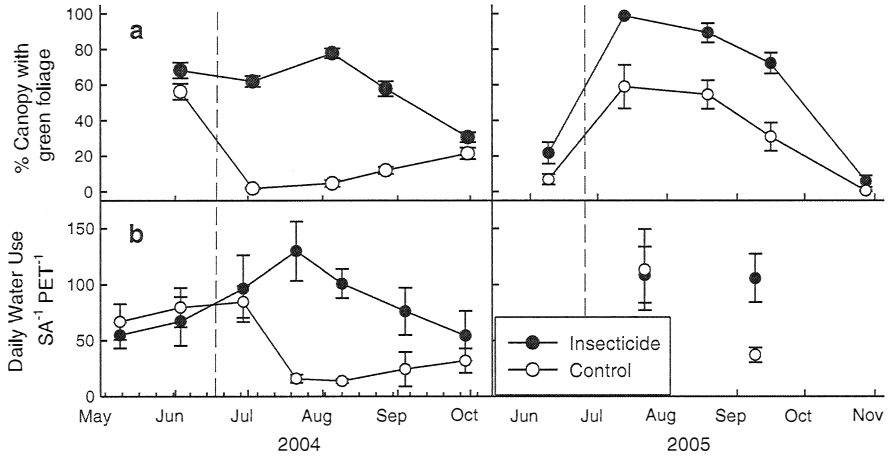

Fig. 2 **a** The percentage of canopy with green foliage for $n = 8$ pairs of insecticide-treated and *D. carinulata*-exposed trees at the H2004DA location of the Humboldt site in 2004 and 2005. **b** The daily water use (DWU; g day^{-1}) per sapwood area (*SA*; cm^2) per daily potential evapotranspiration (*PET*; mm day^{-1}) in 2004 and 2005 of stems on $n = 4$ of the eight pairs of trees monitored for canopy cover. *Dashed line* Arrival of *D. carinulata*. *D. carinulata* first occurred in the area in 2004, *symbols* means of $n = 4$ trees ± 1 SE

results are conservative and underestimate the impacts of *D. carinulata* on saltcedar.

Stem water use

There was a significant and strong effect of defoliation on DWU SA^{-1} PET^{-1} ($F_{2,27} = 20.63$, $P = <0.001$) (Fig. 3a). The DWU SA^{-1} PET^{-1} of non-defoliated trees in August 2004 for trees in the H2004DA was 121.4 ± 10.0. Based on this value, *D. carinulata* reduced the August values of DWU SA^{-1} PET^{-1} of trees in the H2004DA in 2004 (32.5 ± 6.9) by 73%. The reduction in DWU SA^{-1} PET^{-1} in the H2002DA in both years and in the H2003DA in 2005, while not measured, was likely to be substantial as the live canopy cover of these trees was less than 5%. The reduction in the H2004DA was not sustained as there was not a significant difference between non-defoliated trees and the values of DWU SA^{-1} PET^{-1} of defoliated trees when measured in 2005 (Fig. 3a). Likewise, there was no reduction in leaf area/stem area of defoliated trees that year (Fig. 3c).

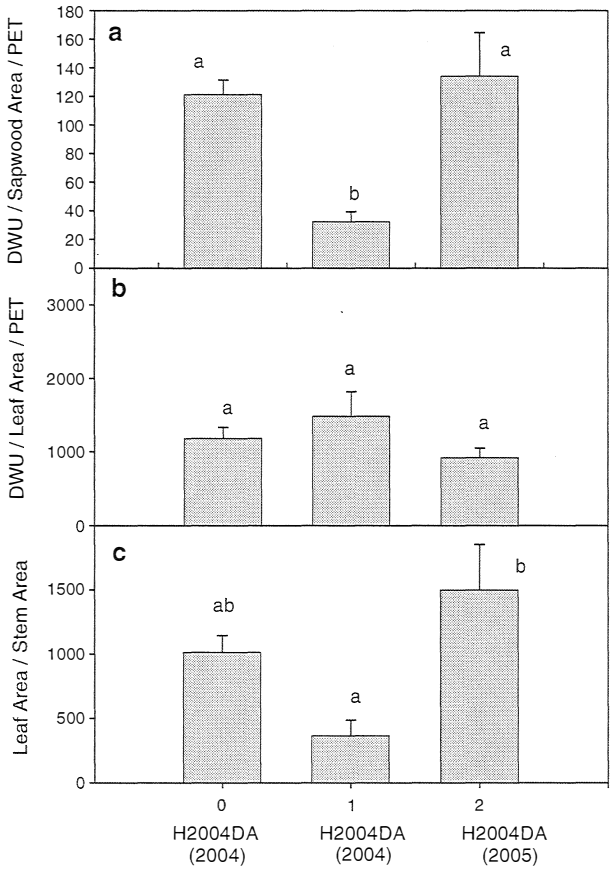

Fig. 3 Values of single stems on randomly selected trees at the Humboldt River site for: **a** daily water use (*DWU*; g day^{-1}) per sapwood area (SA; cm^2) per daily potential evapotranspiration (*PET*; mm day^{-1}), **b** DWU (g day^{-1}) per unit leaf area (m^2) per daily PET, **c** the ratio of leaf area to stem area for measurements made in August. *Numbers on the x-axis* Number of major defoliation events trees experienced prior to measurement. *Symbols* Means ± 1 SE of $n = 3–8$ stems on different trees. *Different letters* represent significant ($P < 0.05$) differences in comparisons across levels of defoliation. *HD2004DA* Humboldt Defoliated Area 2004 (see text for description)

Repeated measures analysis of the paired trees at the Humboldt site indicated that from 21 July to 29 September 2004, there was a significant difference in the DWU SA^{-1} PET^{-1} of trees with *D. carinulata* relative to their insecticide-treated counterparts across time after *D. carinulata* arrival. Insecticide-treated trees had an average DWU SA^{-1} PET^{-1} of 90.2 (±16.2) while *D. carinulata* exposed trees had an average of 21.4 (±4.1)—a reduction of 76% ($F_{1,4} = 15.84$, $P = 0.012$). However, there was no difference in the DWU SA^{-1} PET^{-1} of trees with *D. carinulata* relative to their insecticide-treated counterparts across the two measurements made in 2005 ($F_{1,5} = 1.154$, $P = 0.331$) (Fig. 2b). There was a delay in the reduction in stem water use relative to canopy cover (Fig. 2a, b) such that trees that had been defoliated continued to transpire for a short period even though their canopy cover had been reduced.

Defoliation did not have a significant effect ($F_{1,35} = 1.57$, $P = 0.2191$) on DWU SA^{-1} PET^{-1} among trees at the Walker perimeter location (Fig. 4a). Date ($F_{3,35} = 4.82$, $P = 0.0065$), but not a date-by-defoliation interaction ($F_{3,35} = 1.67$, $P = 0.192$), did have a significant effect on these trees.

Leaf water use

Defoliation did not have a significant effect ($F_{2,18} = 1.61$, $P = 0.2283$) on leaf level water use (DWU LA^{-1} PET^{-1}; Fig. 3b) at the Humboldt site. At the perimeter location of the Walker site, *D. carinulata* defoliation significantly increased DWU LA^{-1} PET^{-1} ($F_{1,29} = 4.65$, $P = 0.0396$) (Fig. 4b), but there was no effect of date ($F_{3,29} = 1.38$, $P = 0.2689$) or date-by-defoliation interaction ($F_{3,29} = 0.93$, $P = 0.4384$). The interaction term for the ANCOVA of DWU PET^{-1} with the leaf area of trees with and without *D. carinulata* at the perimeter location was significant ($F_{1,29} = 39.25$, $P < 0.001$), indicating that while the canopy cover of trees was reduced by herbivory, remaining foliage on *D. carinulata*-exposed trees had greater water transpiration per unit leaf area.

Leaf area per stem area

Defoliation did not significantly reduce the LA SA^{-1} of stems used for sap flow measures, but there was a significant increase from the first to the second year of defoliation ($F_{2,18} = 6.21$, $P = 0.0089$) at the Humboldt site (Fig. 3c).

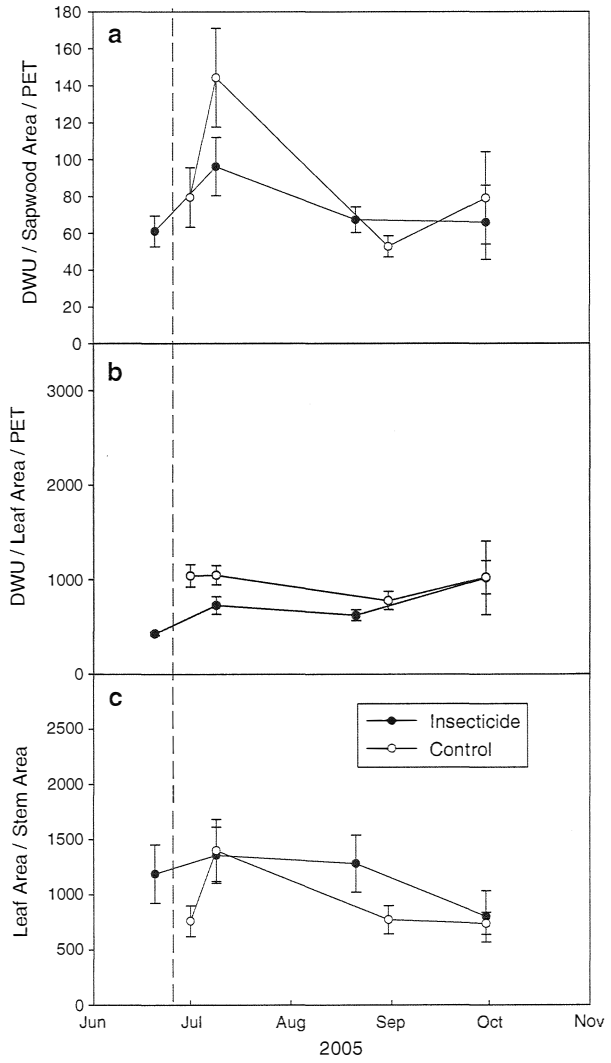

Fig. 4 Values of single stems on randomly selected trees at a location near the perimeter of the Walker River site for: **a** daily water use (*DWU*; g day^{-1}) per sapwood area (SA; cm^2) per daily potential evapotranspiration (*PET*; mm day^{-1}), **b** DWU (g day^{-1}) per unit leaf area (m^2) per daily PET, **c** the ratio of leaf area to stem area. *Symbols* Means of $n = 4-8 \pm 1$ SE single stems on different trees. *Dashed line* Arrival of *D. carinulata* for the first time

Defoliation did not significantly ($F_{1,29} = 2.35$, $P = 0.1364$) reduce the LA SA^{-1} of stems used in the sap flow measurements (Fig. 4c) at the Walker site. For trees at this site, date had a marginally significant effect on LA SA^{-1} ($F_{3,29} = 2.58$, $P = 0.0728$), but date-by-defoliation did not ($F_{3,29} = 0.82$, $P = 0.4946$).

Stand transpiration

The average sapwood basal area at the H2004DA location was 39.7 m^2 ha^{-1} (±10.15). Based on this value insecticide-treated and *D. carinulata*-exposed trees transpired 499 (±84) and 263 (±14) mm, respectively, from May 8 to September 28, 2004, resulting in a reduction of 236 mm or 47% ($U = 25.0$, $P = 0.0606$). When the DWU ha^{-1} was compared post-*D. carinulata* arrival, i.e., from 23 July to 28 September 2004, the reduction was 75% ($U = 22.0$, $P = 0.0518$).

Stand evapotranspiration

Evapotranspiration at the Walker River tower site from 24 March to 31 December 2005 was 273 mm. The annual ET for 2006 was 256 mm. Daily ET was estimated for those days on which insufficient data were available, by linear interpolation between observed data on either side of the missing data (Fig. 5a). There were 24 and 48 days of missing data for which daily ET was estimated in 2005 and 2006, respectively. There were also 18 days in December 2006 for which we did not attempt to estimate daily ET. The average daily ET from May 1 to September 30 was 1.27 (±0.04) and 0.83 (±0.03) mm day^{-1} for 2005 and 2006, respectively. Daily ET was highest from mid-May to late June, 2005 and was less for the remainder of the growing season (Fig. 5a). This decrease coincides with *D. carinulata* defoliation at the nearby tower location monitoring site. Adult *D. carinulata* first arrived on these trees in mid-May 2005. However, adult activity at this time consisted primarily of mating; little feeding occurred. On May 31, 2005 there were an average of 38.0 adults (±4.9) and 535 eggs (±143.6) per tree, but there were no larvae at the Walker tower location. On June 28, 2005 there were no adults or eggs found on trees and an average of 466.7 (±52.2) larvae per tree. The percentage canopy with green foliage of these trees decreased from 83% at the end of May to 3.7% by the end of July. During the entire period of monitoring, the depth to ground water remained shallow (<2 m), and stream flows were similar between years (Fig. 5b).

Discussion

The success of plant biological control efforts is often gauged by population level impacts, such as a dramatic reduction in stem density or areal coverage of the invader (Thomas and Reid 2007; Morin et al. 2009). Rarely does biocontrol monitoring entail quantification of changes in non-target species or altered ecosystem functioning due to the control agent's actions. Furthermore, few studies use robust methodologies including working in multiple sites and with experimental manipulation of agent abundance. In this study we provide evidence that in the early stages of release and agent establishment, the beetle *D. carinulata* can reduce target plant cover and water use across a large

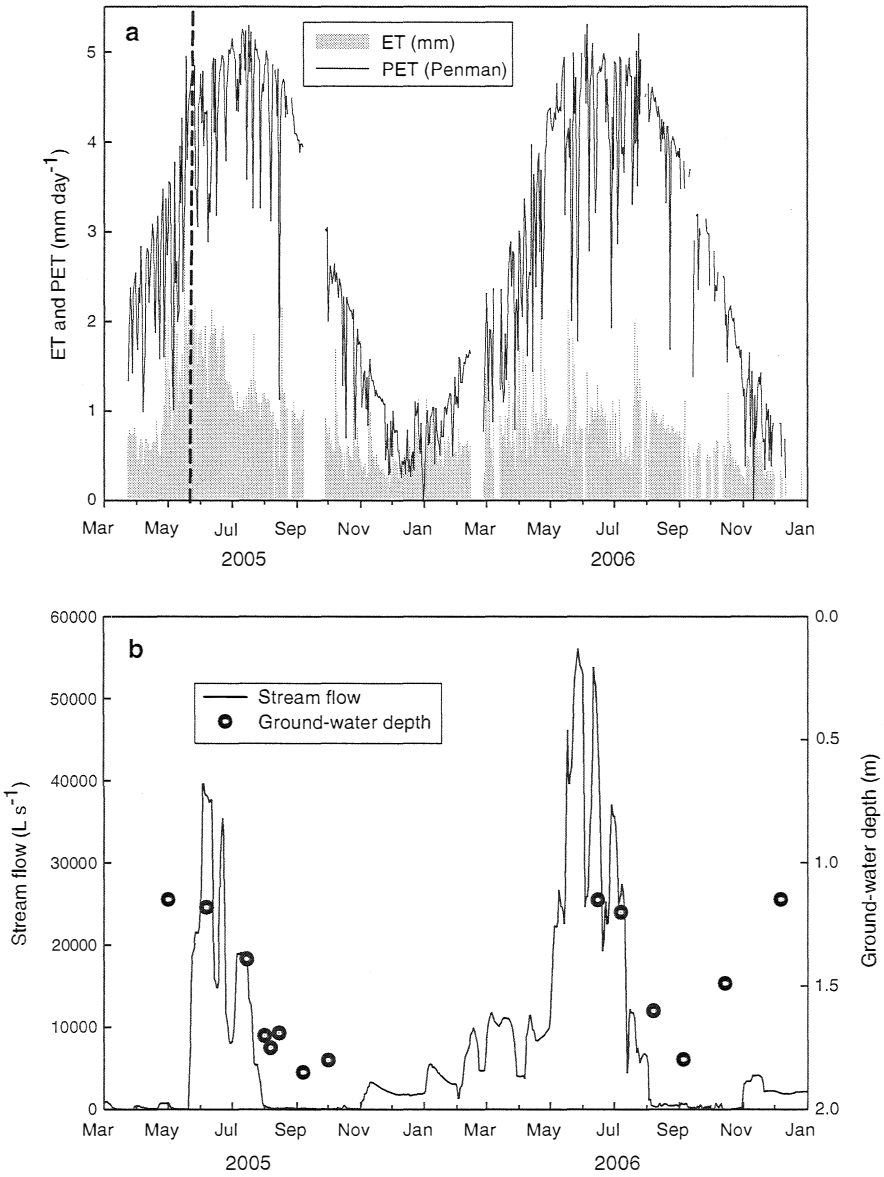

Fig. 5 **a** Daily evapotranspiration (*ET*) and potential evapotranspiration (*PET*) (mm day^{-1}) of a dense monotypic stand of saltcedar (*Tamarix* spp.) near the Walker river at the Walker River site. *Vertical dashed line* First arrival of *D. carinulata* to the ET tower, *dashed line* Arrival of *D. carinulata* to the stand for first time. **b** Walker River stream flow at the nearby USGS Gauging Site (site ID: 10302002) and depth to ground water at the Walker River ET tower site

spatial scale. The extent of these reductions greatly varied both spatially and temporally and was dependent largely on *D. carinulata* abundance.

Defoliation and stem water use

At the Humboldt site *D. carinulata* impacts on canopy cover were greatest closest to the release site (Fig. 1) where by the second and third years after release, defoliation had reduced the canopy of trees to less than 5% of their original cover. However, farther (4 km) away from the release site (H2004DA), the impacts on canopy cover were substantially less and also inconsistent across years (Fig. 1). For example, canopy cover of *D. carinulata*-exposed trees in the paired tree experiment at the H2004DA increased between the first and second years of defoliation (Fig. 2a), a likely consequence of the decreased abundance of *D. carinulata* in 2005 compared to 2004. The average number of larvae per *D. carinulata*-exposed tree of these paired trees declined between 2004 (276.6 ± 91.6) and 2005 (12.9 ± 2.4). The largest reductions in stem water use at the Humboldt site clearly also occurred on trees closest to the release site in the H2002DA and H2003DA (Fig. 3a), but the lack of foliage on these trees made it impossible to quantify water use reductions for these heavily defoliated trees because we lacked pre-defoliation measurements. As there were no increases in water use per unit leaf area at the Humboldt site, the sustained and dramatic reductions (up to 95%) in canopy cover of the vast majority trees in the H2002DA and H2003DA areas are likely to

reflect similar reductions in sap flow for this area. However, for lightly defoliated trees, such as those at the perimeter location of the Walker site, refoliation and increases in water use per unit leaf area did occur. Here, the lack of a decrease in DWU SA^{-1} PET^{-1} is likely a function of both increased leaf level water use in response to initial defoliation (Fig. 4b) and less defoliation—as evidenced by the non-significant effects of *D. carinulata* on LA/SA (Fig. 4c). The mean number of larvae per tree across monitoring dates in 2005 for *D. carinulata*-exposed trees at this perimeter location was substantially less than that for trees at the tower location within the main saltcedar stand (12.9 ± 2.8 vs. 114 ± 13.8, respectively).

The long-term consequences of insect defoliation are poorly understood. Schäfer et al (2010) found that defoliated trees of *Pinus* spp. and *Quercus* spp. had an extended growing season and therefore were able to partially compensate for short-term reductions in sap flow of >80% in response to an outbreak of insect defoliation. The reductions in tree sap flow seen by Cunningham et al. (2009) of 25−50% from insect-induced leaf necrosis in *Eucalyptus* occurred on trees that had experienced an outbreak of insect herbivory in the previous year, suggesting that repeated defoliation can limit a tree's compensatory responses. Experimental manual defoliation decreased the ability of a facultative phreatophyte, velvet mesquite (*Prosopis velutina*), which often co-occurs with saltcedar, to access deeper sources of water in Arizona (Synder and Williams 2003). It is possible that in saltcedar, the long-term consequence of defoliation is a reduced access to deeper sources of water.

An unexpected finding of this study is that the stems continued to transpire for a short period after defoliation (Fig. 2a, b). This has potential consequences for the maintenance of favorable water relations: defoliation may limit the ability of saltcedar to regulate water loss in response to water stress, an important component of this species' success in arid environments (Cleverly et al. 1997; Horton et al. 2001). Furthermore, this result may complicate estimates of ET derived from remote sensing (Dennison et al. 2009).

Stand transpiration

The reduction in stand transpiration of 173 mm ($U = 22.0$, $P = 0.0518$) between 23 July and 29 September 2004, when scaled up to the size of the H2004DA of 1800 ha (Geraci 2006), suggests that *D. carinulata* decreased transpiration during this period for this area alone by up to 3.11×10^6 m^3 (2,500 acre-feet). This estimate does not account for the heterogeneity of the impacts. For example, reductions in transpiration may have been lower at the edges of this stand, as seen at the Walker site. However, reductions in transpiration on a per-hectare basis in areas where there was too little foliage for measurement with sap flow gauges (e.g., H2002DA and the H2003DA in 2005) were certainly larger than those for the H2004DA. Furthermore, this estimate does not take into account defoliation that occurred well beyond the extent of the H2004DA. Hultine et al. (2010b) estimated annual stand level reductions in transpiration during the second and third years of defoliation from *D. carinulata* at a site in Utah to be 44 mm $year^{-1}$. These estimates were based on modeled estimates of non-defoliated sap flow and did not account for first-year impacts of *D. carinulata*. In our study, first-year reductions in sap flow were substantially greater than those in the second year of defoliation (Fig. 3a).

Evapotranspiration

The spread (3-year dispersal distance: 9 km) of *D. carinulata* was faster than expected; consequently, we were unable to obtain measures of ET at the Walker site prior to defoliation. The lack of a control year makes estimating the reduction in ET due to beetle activities difficult. However, several lines of evidence suggest that *D. carinulata* substantially reduced ET.

Firstly, Allander et al. (2009), using Landsat imagery, compared the peak season Modified Soil-Adjusted Soil Vegetation Index (MSAVI) of the footprint of the ET tower in 2005 and 2006 to that of 2000—prior to the release of *D. carinulata*—and found that the MSAVI in 2005 and 2006 was 35 and 39% lower, respectively, than that in 2000. The average precipitation in 2000, 2005 and 2006 was 85, 124 and 166 mm, respectively. These authors then used the relationship between MSAVI and measured the ET using data from a range of plant communities in the Walker River basin collected from 2005 through to 2007 to estimate the ET of the tower footprint in 2000 based on the value of MSAVI in 2000. The estimated ET of the tower footprint for 2000 was 518 mm per year as compared to the estimated values of 297 and 269 mm per year in 2005 and 2006, respectively—a 42–48% reduction in ET.

Secondly, peak daily ET occurred immediately prior to *D. carinulata* arrival in 2005 and was relatively low. In other saltcedar-dominated communities in the southwestern USA, daily ET peaked later in the season. For example, on the Virgin River of southern Nevada (Devitt et al. 1998) and the Lower Colorado River of southern Arizona (Nagler et al. 2005), daily ET peaked in June–July. On the Middle Rio Grande (Cleverly et al. 2002; Nagler et al. 2005) and San Pedro Rivers (Nagler et al. 2005), daily ET peaked in July, August and September. Data from sap flow rates on trees without *D. carinulata* at the Humboldt (Fig. 2b) and Walker sites (Fig. 4b) suggest that the ET of non-defoliated stands were likely to have peaked in late and early July, respectively.

Cleverly et al. (2002), working in a similar xeroriparian site dominated by saltcedar and saltgrass, observed peak mid-summer daily values of 4–6 mm day^{-1}and an annual ET of 740 mm. Peak ET from the Walker site with *D. carinulata* was only 2 mm day^{-1}, and this occurred immediately prior to *D. carinulata* arrival (Fig. 5a). The ET values were at or below 1 mm day^{-1} in mid-August (Fig. 5a). Values of ET from 24 March to 31 December 2005 and those for all of 2006 for the Walker site were 273 and 256 mm, respectively. Nagler et al. (2005) found that the ratio of mean annual ET of saltcedar to PET was 0.5 across a series of sites in the southwestern USA; in comparison, the ratio for 2006 at the Walker site was 0.22 (28% lower).

There was no evidence to suggest that other conditions (e.g., drought) contributed to the rapid midseason decline in canopy cover and ET. In actuality, stream flows and ground water levels were substantially higher than past levels for both 2005 and 2006 (Fig. 5b). Average monthly flows for the Walker River from 2000 to 2004 (pre-beetle) for June and for July were 0.193×10^3 ($\pm 0.153 \times 10^3$) and 0.0205×10^3 ($\pm 0.015 \times 10^3$) L s^{-1}, respectively. By contrast, average stream flows for 2005 and 2006 for June and July were 30.0×10^3 ($\pm 4.3 \times 10^3$) and 13.6×10^3 ($\pm 2.0 \times 10^3$) L s^{-1}, respectively (United States Geological Survey 2008).

Conclusions

During the early stage of establishment of *D. carinulata*, its feeding can reduce saltcedar live canopy cover and subsequent water use across large scales. This agent has also been shown to decrease stem growth (Pattison et al. 2010) and the carbohydrate storage capacity of trees at the Humboldt River site (Hudgeons et al. 2007). Collectively, these impacts may decrease the ability of trees to withstand events such as drought and fire (Brooks et al. 2008), although large-scale eradication of saltcedar at this point appears unlikely. Further research is needed to understand how the introduction of *Diorhabda* spp. will impact water use over the long term and in communities with inherently higher rates of ET than those found in this study. Without sustained, long-term reductions in saltcedar canopy cover, the reductions in water use seen in this study are likely to be short lived (Cleverly et al. 2006). Furthermore, the extent to which reductions in saltcedar water use might lead to overall reductions in ecosystem ET and increase water availability for other uses is uncertain and requires further investigation. For example, the removal of mesquite (*Prosopis glandulosa*) from rangelands did not result in a reduction in community ET because of an associated increase in both herbaceous biomass and transpiration (Dugas and Mayeux 1991). However, in this case the increase in herbaceous biomass was considered to be a beneficial result to livestock. The dominant understory species at both of the study sites and that which is likely to increase as a result of a reduction of saltcedar canopy cover is saltgrass. This species has a relatively low annual ET of 0.4 m year^{-1} (Shafroth et al. 2005). Increases in saltgrass in association with decreases in saltcedar are likely to result in reduced ecosystem water use over the long-term at both of these sites.

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