

# Multiple year effects of a biological control agent (*Diorhabda carinulata*) on *Tamarix* (saltcedar) ecosystem exchanges of carbon dioxide and water

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## ARTICLE INFO

### Article history:

Received 30 June 2011

Received in revised form 17 February 2012

Accepted 6 March 2012

### Keywords:

Evapotranspiration

Biological control

Invasive weeds

Remote sensing

Eddy covariance

Ecohydrology

Riparian

## ABSTRACT

Biological control of *Tamarix* spp. (saltcedar) with *Diorhabda carinulata* (the northern tamarisk beetle) is currently underway in several western states U.S.A. through historical releases and the natural migration of this insect. Given the widespread dispersal of this biological control agent and its many unknown consequences, this study examines a variety of ecohydrological effects of the beetle on a *Tamarix* invaded ecosystem in the Great Basin Desert, Nevada. Nearly four years of ecosystem carbon dioxide (CO<sub>2</sub>) and evapotranspiration (ET) fluxes, measured with an eddy covariance system, are examined in relation to normalized difference vegetation index (NDVI) from Landsat imagery and on the ground measures of leaf area index (LAI) with a light attenuation instrument. We predicted that successive years of beetle herbivory should result in a trajectory of reduced ET and reduced CO<sub>2</sub> uptake. We found that three and a half years of beetle herbivory and the resulting defoliation events produced short-term decreases in ET and C uptake. However, total ET and C fluxes over multiple growing seasons were not affected in a clear directional trajectory of reduced ET loss and reduced CO<sub>2</sub> uptake, perhaps due to variability in beetle density. LAI and NDVI were fairly well correlated with each other and NDVI was correlated with ET during the summer months, indicating that these measures are useful for detecting beetle damage to the canopy.

Published by Elsevier B.V.

## 1. Introduction

*Tamarix* L. (*Tamarix ramosissima* Ledeb., and *T. chinensis* Lour.) and their hybrids (Gaskin and Schaal, 2002), hereafter referred to as *Tamarix*, is a long-lived, exotic, deciduous, scale-like leaved tree that can produce ca. half a million seeds per year and vigorously re-sprouts from the root crown following disturbance (Di Tomaso, 1998). *Tamarix* (saltcedar) is an aggressive invader of riparian areas in the western United States, and traditional control methods have proven costly or ineffective (Carruthers et al., 2008). Therefore insect biological control efforts were pursued to control this species. Assessments of the efficacy of biological control efforts have rarely considered ecosystem level effects such as carbon, water and nutrient cycling (Denslow and Dantonio, 2005). More often the success of these efforts is measured in metrics such as ability of the control agent to reduce target populations. However, plant mortality can take many years to detect, especially if: (1) the species are long-lived woody plants, (2) they are profligate seed producers, and/or (3) can re-sprout from belowground storage

organs. Therefore, more immediate indicators of other ecosystem processes are needed.

Reductions in carbon dioxide (CO<sub>2</sub>) uptake or changes in evapotranspiration (ET) are indicative of the physiological status of plants. Therefore these stand-level measures can be useful to determine if biological control efforts show promise in achieving their intended outcomes of reducing the presence of target invasive species by negatively impacting plant physiological status. The objective of this study was to determine how herbivory of a biological control agent, the northern tamarisk beetle (*Diorhabda carinulata* (Desbrochers, 1870), previously classified as *Diorhabda elongata deserticola* (Chen, 1961) (Tracy and Robbins, 2009)) affected indicators of plant physiological status. Specifically, we were interested in examining changes in ecosystem carbon dioxide and water use of a *Tamarix* invaded area on the lower Truckee River in western Nevada over multiple years since the beetle arrived.

Feeding by *D. carinulata* is followed by discoloration and desiccation of the remaining leaves, producing a “defoliation event”. Irreversible desiccation from herbivory-induced leaf wounding reduces the plant’s ability to regulate water loss and induces premature senescence and leaf drop (Snyder et al., 2010). Severe defoliation results in a more open canopy (Dennison et al., 2009), which can alter understory microclimate and soil

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conditions. Regrowth of leaves generally occurs after initial defoliation, and a second defoliation event may occur. Therefore in addition to changes in transpiration, higher soil evaporation may result from greater exposure to solar radiation during defoliation. If successive years of herbivory and defoliation produce carbon limited trees with reduced canopy vigor and increased mortality, the effects on soil evaporation and tree transpiration may be amplified. In many sites where *Tamarix* is the canopy dominant, invasive herbaceous understory species may increase, and proliferate with higher light availability (Hultine et al., 2010a).

A primary justification for controlling *Tamarix* has been the potential for water savings. Water savings would be a net decrease in evapotranspiration (ET), which could result from reductions in photosynthetically active plant biomass or changes in plant community composition. This concept of removing or reducing invasive exotic and native encroaching woody species to achieve water savings, especially in riparian areas, has recently been increasingly questioned in semi-arid and arid regions (Cavaleri and Sack, 2010; Hultine et al., 2010a; Huxman et al., 2005; Nagler et al., 2010; Wilcox and Huang, 2010; Wilcox et al., 2006). There is increasing evidence that *Tamarix* stands do not necessarily use more water than native cottonwood and willow stands (Dahm et al., 2002; Nagler et al., 2005b, 2008; Shafroth et al., 2005), as *Tamarix* stands have highly variable water use (Nagler et al., 2010; Owens and Moore, 2007).

This study followed the effects of successive years of beetle herbivory on ecosystem water and carbon fluxes following the arrival of the beetle at the lower Truckee River study site in 2007 after widespread release in several western states in 2001. In this study we were unable to directly assess the magnitude of change in overall ET and C fluxes that may have occurred due to the presence of the beetles because of the rapid and unexpected arrival of the beetles that precluded the collection of baseline data in this drainage. Therefore, we examined if beetle herbivory produced quantifiable effects on carbon dioxide and ET fluxes and whether these effects were greater with successive years of herbivory. Successive years of beetle herbivory that showed a trajectory of decreased carbon uptake and ET would be indicative of severely impaired plant status that could produce significant mortality in the long-term. We hypothesized that: (1) beetle herbivory would decrease ET due to the reduction in canopy leaf area, (2) that as ET fluxes decreased, net carbon uptake would decrease and make this ecosystem more of a carbon source to the atmosphere, and (3) that these two effects would be more pronounced with successive years of beetle herbivory. Additionally, we determined how remotely sensed imagery could be used to detect defoliation and its effects on ecosystem water use.

## 2. Methods

### 2.1. Site description

The study site is located along the lower Truckee River in the Great Basin Desert near Pyramid Lake, approximately 50 km NE of Reno, Nevada, USA (39°51'N, 119°24'W; Elevation 1175 m). Average annual precipitation is 173 mm of which 70% falls during October through April; average maximum daily temperature is 33.6 °C in July, and average minimum daily temperature is –6.6 °C in January (based on 48 years of record at Nixon, NV, 4 km away; Western Regional Climate Center, Desert Research Institute). Lower floodplain soils are gravelly sands, classified as beaches (Soil Survey Staff, NRCS). The riparian area along the river terminus before it flows into Pyramid Lake is dominated by *Tamarix* (average canopy height of ca. 3.5 m), with remnant populations of native Fremont cottonwood (*Populus fremontii* S. Watson) and Coyote willow (*Salix*

*exigua* Nutt.) and scattered, large individuals of exotic Russian olive (*Elaeagnus angustifolia*). The site has some areas of bare ground and the understory vegetation is comprised primarily of rushes, perennial and clasping pepperweed (*Lepidium latifolium* and *Lepidium perfoliatum*), cheatgrass (*Bromus tectorum*), and salt grass (*Distichlis spicata* var. *stricta*). Beetles were released in 2001 in the Humboldt drainage ca. 80 km from the site and migrated to the Truckee drainage. In 2006 beetles were observed in very low densities a few kilometers from the site.

### 2.2. Environmental measurements

In July 2007 a micrometeorological tower was installed on the primary floodplain terrace in a fairly contiguous stand of *Tamarix* ~200 m wide and running for ~500 m along the river, which flows southeast to the northwest. Tower measurements began on July 17th, 2007. Temperature and relative humidity (HMP35D, Vaisala, Helsinki, Finland) were monitored at 4 m height, as was above-canopy net radiation, measured with a net radiometer (Model NR-LITE, Kipp & Sonen, Delft, the Netherlands) and incoming photosynthetically active radiation (PAR; LI-190, LI-COR, Lincoln NE) sensors attached to a horizontal boom extended 2 m from the tower. Ground heat flux was measured with four soil heat flux plates (TP01, Hukseflux, Delft, the Netherlands) installed 0.08 m below the soil surface. Four water content probes at 0.025 and 0.057 m below the soil surface measured soil moisture in the upper 0.08 m of soil (Model CS616, Campbell Scientific, Inc., Logan, UT). Average ground heat flux (G) was calculated from measurements of the rate of soil temperature change above the heat flux plates (at 0.02 and 0.06 m), bulk density, and soil water content data to estimate soil specific heat and soil heat flux at the surface. Precipitation was measured with a tipping bucket rain gage, fitted with a snow adapter (Model TE525, Texas Electronics, Dallas, TX). A piezometer with a continuously recording pressure transducer was installed to determine depth to groundwater ca. 10 m from the tower.

### 2.3. Eddy covariance measurements

Ecosystem evapotranspiration (ET) and carbon dioxide flux ( $F_C$ ) were quantified using the eddy covariance technique. An open-path infrared gas analyzer (LI-7500, LI-COR, Lincoln, NE) and a 3-dimensional, sonic anemometer (Model CSAT-3; Campbell Scientific, Logan, UT) were mounted at 4.9 m height to measure the three wind velocity vectors, sonic temperature, and water and carbon dioxide densities at 10 Hz. Every two to three months, IRGAs were zero- and span-calibrated using a CO<sub>2</sub>/H<sub>2</sub>O – free gas, a standard CO<sub>2</sub> concentration ([CO<sub>2</sub>]) gas and a dew point generator. Covariances were calculated by filtering spikes and using a 30-min block average, and a two-dimensional coordinate rotation and density corrections were applied to calculate fluxes (Webb et al., 1980). We calculated the net ecosystem exchange of CO<sub>2</sub> (NEE) by adding  $F_C$  and the 30-min CO<sub>2</sub> storage in the canopy ( $\Delta S$ ), estimated by using the change in [CO<sub>2</sub>] at the top of the tower multiplied by the measurement height as profile measurements were not made.

Flux data were filtered for spikes, instrument malfunctions, and poor quality (ca. 5.0% of ET and 5.9% of NEE data). The filtering criteria were: rain events, out-of-range signals, and spikes with the standard deviation of [CO<sub>2</sub>] and [H<sub>2</sub>O]. We applied a friction velocity ( $u^*$ ) filter to omit NEE fluxes when turbulence was insufficient for representative flux measurements (Malhi et al., 1998). The  $u^*$  threshold was identified by evaluating the average nighttime CO<sub>2</sub> flux over increasing  $u^*$  bins for 90-day growing and non-growing season periods. The  $u^*$  threshold was identified as the point where averaging resulted in no further changes in flux estimation (Scott et al., 2006), with a 0.25 m s<sup>-1</sup> value chosen as an average. Daily average ET values were calculated by first filling the gaps in the

30 min data using 14-day look-up tables of ET and incoming PAR averaged over 100  $\mu\text{mol m}^{-2} \text{s}^{-1}$  intervals (Falge et al., 2001). There were no large continuous gaps in the flux data with the exception of one 22 day period beginning on October 1st, 2008, which was not gap-filled.

NEE was partitioned into ecosystem photosynthesis (GEP) and ecosystem respiration ( $R$ ). 30-min average  $R$  was determined by fitting an exponential function to air temperature and nighttime NEE data over a moving  $\sim 5$ -day window (Reichstein et al., 2005). The window size varied to ensure that data from pre-rainstorm (dry) periods were not grouped with data following storms. This model was used to fill missing nighttime NEE data and estimate daytime  $R$ . Missing daytime NEE values were filled by fitting a 2nd order polynomial to the response of NEE to PAR over a 15-day moving window (Gilmanov et al., 2007), and GEP was determined as  $\text{GEP} = R - \text{NEE}$ . We used the standard sign convention for NEE with  $\text{NEE} > 0$  indicating a net loss of  $\text{CO}_2$  to the atmosphere (source) and  $\text{NEE} < 0$  indicating ecosystem  $\text{CO}_2$  uptake (sink).  $R$  and GEP are always positive.

Dominant wind directions over the study were from the west and east, with stronger westerly daytime winds. Nighttime wind distribution was equal between west and east. The tower was positioned such that the minimum upwind fetch for *Tamarix* cover was  $\sim 100$  m, which was SW and NE from the tower. In the dominant wind directions, *Tamarix* fetch was about 130 m. Flux footprints were modeled following (Kljun et al., 2004). To obtain the dynamically varying inputs for the model, we randomly sampled ( $n = 10,000$ ) coupled 30 min values of friction velocity, Monin–Obukov length scale, and the standard deviation of the vertical wind speed and randomly varied unknown boundary layer heights from 50 to 2000 m. This revealed that average daytime peak scalar flux source was located at  $49 \pm 5$  ( $\pm$  one standard deviation) m upwind from the tower. The average along-wind extent of the 80% cross-wind integrated flux footprint was  $108 \pm 10$  m upwind of the tower measurements. Based on this, we assumed measured fluxes were determined by the *Tamarix* stand. For additional verification we filtered out fluxes for higher wind speeds (e.g., excluding measurements with winds greater than 2 and 3  $\text{m s}^{-1}$ ) when we expected that the fluxes might be more influenced by non-*Tamarix* cover. We found that the magnitude and relationship between the different years of fluxes (examined below) changed little with this filtering (data not shown).

#### 2.4. Understory vegetation and beetle density

Leaf area index (LAI) was measured about every three weeks during the 2008–2010 growing seasons with a LI-191 line quantum sensor (LI-COR, Inc., Lincoln, NE) at 1 m above the ground. LAI surveys were made between 11:00 am and 1:00 pm on nine stratified fixed transects within the tower's upwind NW fetch. Three sets of three transects started at 20, 150 and 280 m from the tower, consisting of three parallel 100 m transects separated by 30 m. Transect start and end points were marked, and 5 m intervals were paced off, giving 20 points for each transect and 180 points total. Open areas points were not included in the site average. Care was taken to ensure similar locations were sampled. PAR was converted to LAI following (Welles and Cohen, 1996) using an extinction coefficient of 0.34 from another *Tamarix*-invaded riparian stand (Nagler, 2004). LAI estimates done during leafless periods still include the interception of light from leafless branches. Understory vegetation cover was characterized in June of 2009 and 2010. Point intercepts were made every 2 m along nine 100 m transects (Herrick et al., 2005) roughly corresponding to the LAI transects. In 2009 and 2010 the growing season density of adult beetles and larvae was measured. One hundred trees along the LAI transects were selected, a branch was randomly selected, and the number of beetles and

larvae counted along the length of the branch; insect density was standardized by dividing by the length of the branch in cm.

#### 2.5. Remote sensing

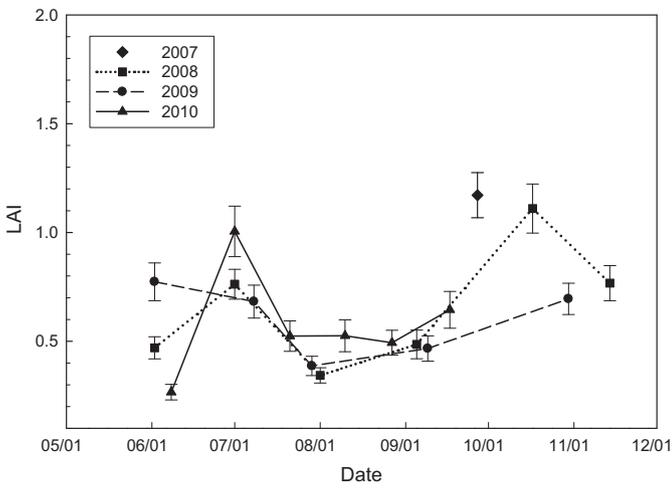
Landsat 5 Thematic Mapper (TM) images were acquired between May and October from 2003 to 2010 from the U.S. Geological Survey's Earth Explorer website. TM images were in level 1T format with improved radiometric correction and terrain-corrected, geometric rectification to the Universal Transverse Mercator (UTM) projection (zone 11), with 30 m spatial resolution using cubic convolution resampling. The TM image from June 12, 2007 was converted to radiance based on the provided meta-data, then atmospherically corrected and converted to reflectance with FLAASH (Fast Line-of-sight Atmospheric Analysis of Spectral Hypocubes, Adler-Golden et al., 1999) using a rural mid-latitude model atmosphere and K-T correction for aerosol scattering based on TM bands 7 and 3 (Kaufman et al., 1997). Vegetation-free bright and dark calibration targets were identified, and all other images were normalized to the corrected image using empirical line correction (Roberts et al., 1985). Images with clouds or haze over the calibration targets or study area were discarded, resulting in 60 TM images that had an average spacing of 20 days through each growing season. Gaps in the TM time series were filled using Enhanced Thematic Mapper (ETM) images from the Landsat 7 satellite. These could not be used as the primary data source as its scan line corrector mirror failed in 2003 and subsequent images have numerous, striped data drop-outs. Four ETM images were added to the time series, as many cloud-free ETM scenes had missing data over the site or calibration targets.

Normalized difference vegetation index (NDVI (Holben and Justice, 1981)) was calculated for all TM and ETM images. NDVI is a ratio of red and near infrared (NIR) light wavelengths in the form:  $(\text{NIR} - \text{red})/(\text{NIR} + \text{red})$ , and contrasts the absorption of red light by chlorophyll versus the reflection of NIR due multiple scattering within leaves. Changes in image brightness due to topographic shadows are cancelled out by the ratio, assuming proper atmospheric correction (Crippen, 1988). UTM corner coordinates were calculated for a 600 by 190 m rectangle corresponding to the *Tamarix* stand and mean NDVI was calculated for each image. NDVI values were linearly interpolated to match dates when LAI was measured. Correlations between NDVI and daily ET were made using five-day average ET values (2 days prior, the day of, and two days after image acquisition).

### 3. Results

#### 3.1. Stand phenology, LAI, and beetle chronology

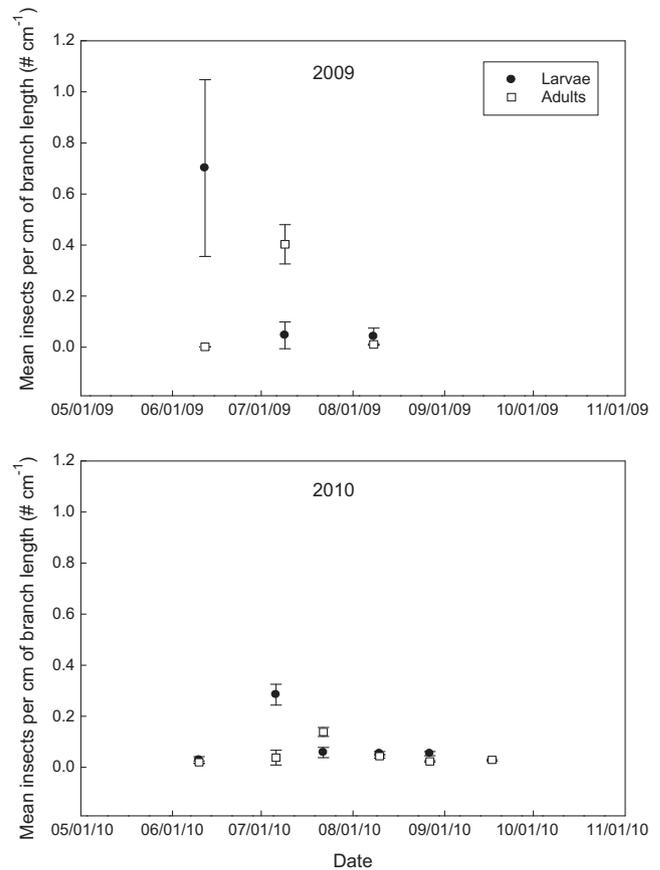
After installation of instrumentation in July 2007, the first small patch of defoliation (0.28 ha) occurred in August directly in front of the tower in the upwind direction, and refoliated by the first week of September. Natural senescence occurred in November. In 2008, trees fully leafed out in June, as reflected in LAI in early July (Fig. 1), followed by a large-scale outbreak and complete defoliation of the entire site (Fig. 1). Trees refoliated the third week of August. A second generation of beetles desiccated or removed 40–60% of the regrowth by late September (personal observation). However, there was another period of leaf regrowth in October. Natural senescence occurred in early November. In 2009, trees fully leafed out by early to mid June (Figs. 1 and 2) when beetle density was highest (Fig. 3) resulting in nearly complete desiccation of the canopy during July (Figs. 1 and 2). By mid-August trees had partially refoliated; though beetles were still present, there was no subsequent large-scale



**Fig. 1.** Leaf Area Index (LAI) measured with quantum line sensor throughout several growing seasons.



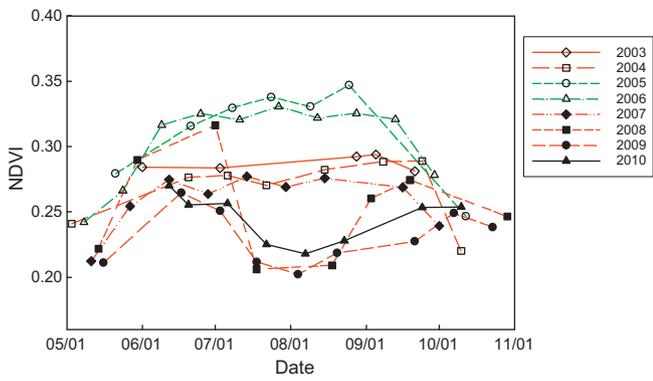
**Fig. 2.** Photo illustrating full leaf out and the maximum green canopy on June 17th, 2009 and a large scale beetle induced discoloration of the canopy, July 29th, 2009. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



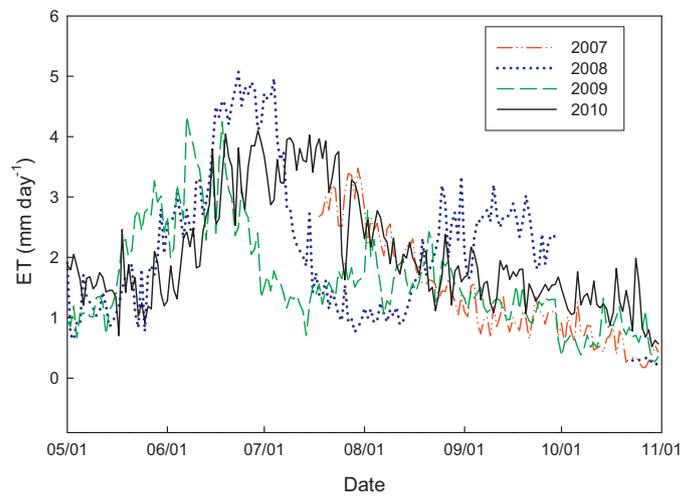
**Fig. 3.** Beetle density measured in 2009 and 2010 at the Truckee River field site.

defoliation event. A second flush of re-growth occurred in mid-September and few beetles and larvae were observed at this time. By October 26th natural senescence had begun after an early freeze event. In 2010, trees started to leaf out in May, but a late freeze (May 6th) damaged foliage and delayed full leaf out until July (Fig. 1). Beetle density peaked in July instead of June (Fig. 3) and foliage was brown in August. Tree green up and defoliation events seemed to be more variable and less extreme, and peak beetle density in 2010 was less than half of peak beetle density in 2009, hovering near 0 for most of the growing season (Fig. 3). Natural senescence occurred in early November.

Generally, NDVI increased from May through June, synchronous with canopy leaf out, and decreased from mid September through October, coinciding with lower fall temperatures and natural senescence (Fig. 4). NDVI trajectories for 2005 and 2006 were much higher than 2003 and 2004. The Palmer Drought Severity Index (PDSI), using climate data for Washoe County, Nevada (National Climatic Data Center), indicated 2003–2004 had extreme drought conditions ( $\text{PDSI} \leq -4$ ), while compared to mid-range to moderately moist PDSI in 2005–2006 ( $-1.99 < \text{PDSI} < 2.99$ ). Extreme drought occurred across Washoe county PDSI from 2007 to 2009 ( $\text{PDSI} \leq -4$ ), and severe drought in 2010 ( $-4 < \text{PDSI} < -3$ ). While there were not clear reductions in NDVI during the beetle arrival in 2007 (which only visibly impacted a small portion of the fetch), subsequent years showed a strong NDVI signal reflecting beetle defoliation of *Tamarix* beginning in July, 2008 (Fig. 4). NDVI was not well correlated with all measured values of LAI ( $N = 20$ ,  $r^2 = 0.15$ ,  $p = 0.09$ ), but when three outlying points were excluded the relationship improved substantially ( $N = 17$ ,  $r^2 = 0.64$ ,  $p < 0.0001$ ). The three points we removed occurred in June and early July and were characterized by higher NDVI relative to LAI. We suspect these early season NDVI values were capturing understory greenness



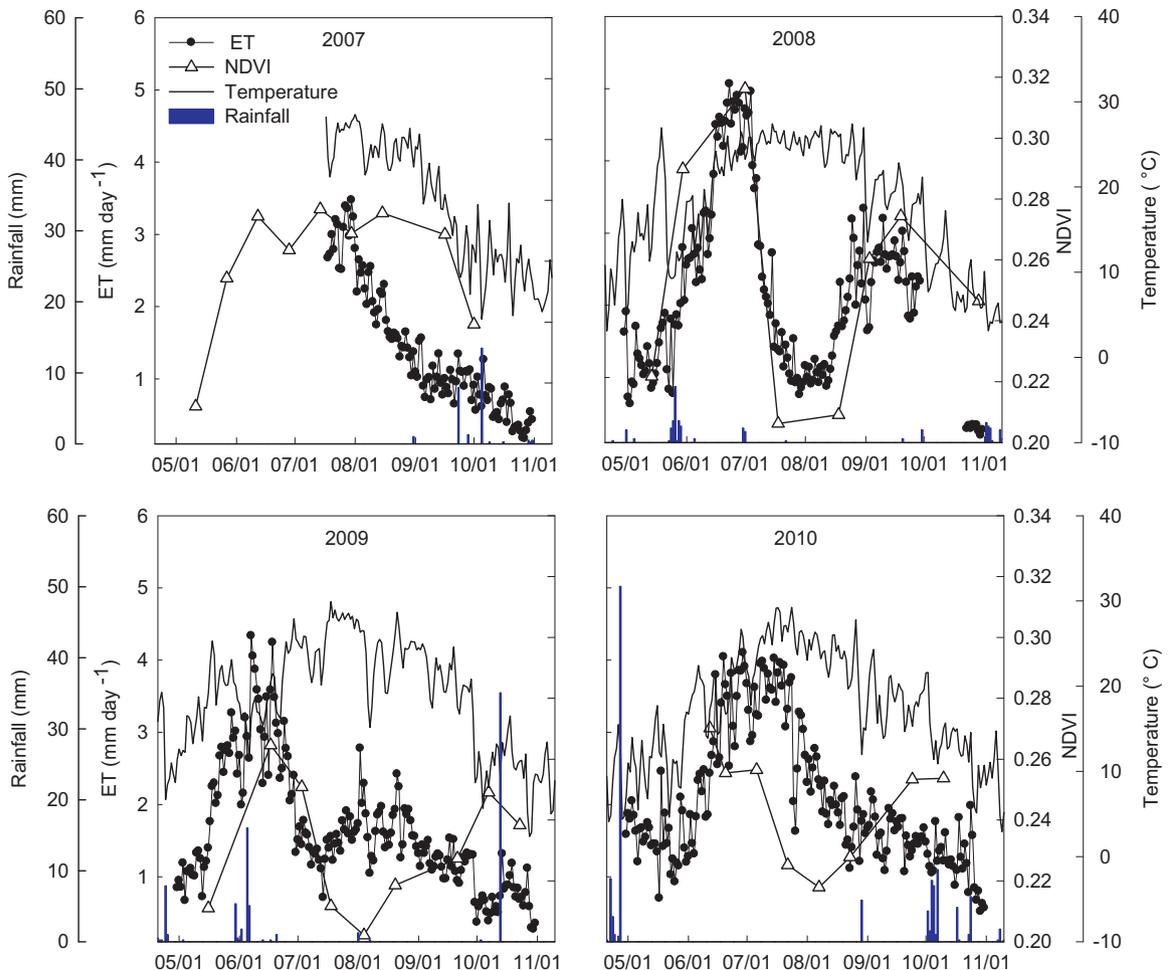
**Fig. 4.** NDVI for eight years. Open symbols are years before the eddy covariance tower was installed and closed symbols are years when the tower was installed. 2007 was the first year beetles were at the site and the defoliated area was minimal (7% of the fetch). 2008–2010 were years with significant beetle defoliation events. Green lines indicate moderately moist years (2005 and 2006), black lines indicate severe drought years (2010), and red lines indicate extreme drought (2003, 2004, 2007–2009) according to the Palmer Drought Severity Index. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)



**Fig. 5.** Evapotranspiration (ET) measured since end of July 2007, and from May 1 (when available) to November 1st.

that was not measured by LAI because LAI measurements were made above the understory vegetation. Additionally, when only points occurring after July 7th were retained (a time when understory vegetation is senescent) and one hazy day was removed the relationship improved ( $N = 12$ ,  $r^2 = 0.85$ ,  $p < 0.0001$ ).

Mean understory canopy cover differed significantly between the two years it was measured (Student's  $t$ -test,  $p = 0.0003$ ). Canopy cover was 46% in 2009 and increased to 82% in 2010 as a result of a nine-fold increase in cheatgrass (data not shown). Precipitation totals for the water years 2008, 2009 and 2010 were 100, 117 and 217 mm, respectively. Additionally, an exotic mustard



**Fig. 6.** Evapotranspiration (ET), NDVI, average temperature and daily rainfall over four growing seasons.

(different than perennial pepperweed) was encountered 38 times in 2010 and only once in 2009. The perennial pepperweed decreased in 2010 as did the presence of saltgrass. Understory cover of native species was 41% of the total cover in 2009, but decreased to 11% in 2010.

### 3.2. Ecosystem-scale processes

As mentioned above, a small patch was defoliated in August 2007 directly upwind from the tower. ET was clearly reduced by  $\sim 2 \text{ mm day}^{-1}$  from July to September (Fig. 5). Though this decline may be due to fall leaf senescence, August temperatures were warm (Fig. 6), and solar radiation was high. Thus, it appears more likely that this decline was due to the defoliation event. Yet, NDVI averaged over a larger area showed little decline (Fig. 6), likely due to the location of this defoliated patch and the smaller source area of the ET fluxes (typical peak footprint function was only at about 50 m). Evapotranspiration showed pronounced periods of reduced ET in 2008 and 2009 (Fig. 5). These periods were detected in NDVI (Fig. 6) and LAI (Fig. 1). In the first year of large-scale beetle outbreak (2008) there was a pronounced double peak in both NDVI and ET that corresponded to a strong regrowth response (Fig. 6). In 2009, ET and NDVI declined in response to beetle defoliation. However, the partial recovery in ET was somewhat asynchronous with NDVI and LAI (Figs. 2 and 6). This was likely due to full regrowth of leaves reaching the completion in the fall, which is a period where ET appears to become decoupled from NDVI which may be a function of reduced atmospheric demand (lower available energy and decreased vapor pressure deficit) or the onset of tree dormancy which would limit ET losses. Beetle density in 2010 was significantly lower than the prior two years (Fig. 3), and there was a more gradual drop-off in mid-summer ET (rather than a sharp dip) during periods when partial defoliation was observed (Fig. 5). Also, NDVI and LAI both showed a less dramatic defoliation effect and appeared to reflect the patterns in ET (Fig. 6), and there were greater ET losses later into the fall relative to other years (Fig. 5). Plots of daily rainfall and ET indicated that ET in this system is not strongly affected by growing season rainfall (Fig. 6).

Overall, NDVI was not well correlated with 5-day average ET rates during the time of the Landsat acquisition. When all May 1 to November 1 data was used, the correlation coefficient was  $r^2 = 0.18$ ,  $p < 0.02$ . However, using peak growing season data (June 1 to September 1) the relationship improved ( $r^2 = 0.48$ ,  $p < 0.003$ ), likely due to the apparent decoupling of ET from green leaf area in the fall.

To rule out if peak growing season declines in ET were attributable to declining groundwater, we plotted groundwater depth versus ET rates (only 2008 is shown as an example, Fig. 7). In 2008, ET increased even though depth to groundwater increased and there was no significant rainfall in August and September (Fig. 6). While regressions between groundwater depth and ET were significant in 2008 and 2009, the total variance explained was low ( $r^2 < 0.17$ ;  $p < 0.0001$ ). In 2010 this relationship was not significant ( $r^2 = 0.02$ ;  $p = 0.12$ ). Also, wounding from beetle herbivory increased nighttime ET (Fig. 7). The percent of nighttime ET during the ET peak, at the onset of defoliation and during the second ET peak, was 23%, 28% and 13%, respectively.

Net ecosystem carbon dioxide exchange (NEE) followed patterns in ET with peaks in ET corresponding to increased net carbon uptake (Fig. 8a). During periods of leaf desiccation and defoliation the ecosystem switched from being a sink to a source of carbon to the atmosphere ( $\text{NEE} > 0$ ). In 2010, the ecosystem was a carbon sink early in the season, essentially carbon neutral during the beetle herbivory, and then gained carbon again in September after beetle herbivory (Fig. 8a). This switching between a source and sink was even more apparent in cumulative NEE patterns (Fig. 8b). In 2008

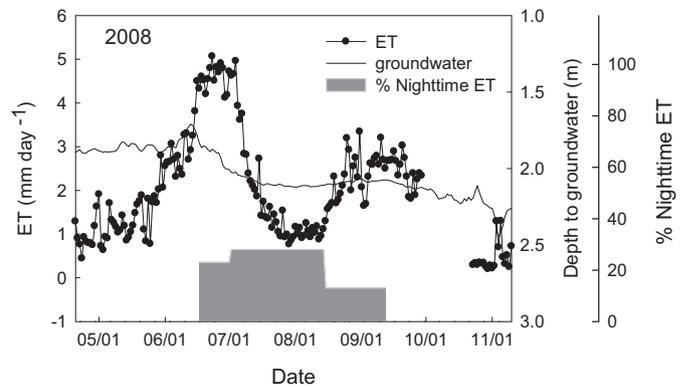


Fig. 7. The depth to groundwater and daily total evapotranspiration (ET) for the 2008 growing season and the percent of total daily ET that occurred at nighttime for the weeks prior to, during, and after the major defoliation event.

and 2009, defoliation events produced a change in the sign of the slope reflecting the switch to a carbon source around the first of July. However in 2010, defoliation resulted only in a flattening of the cumulative curve (carbon neutral).

The growing seasons of 2008 and 2010 had approximately equal C uptake, while 2009 had significantly less C uptake and was a C source. In terms of cumulative gross ecosystem production of  $\text{CO}_2$

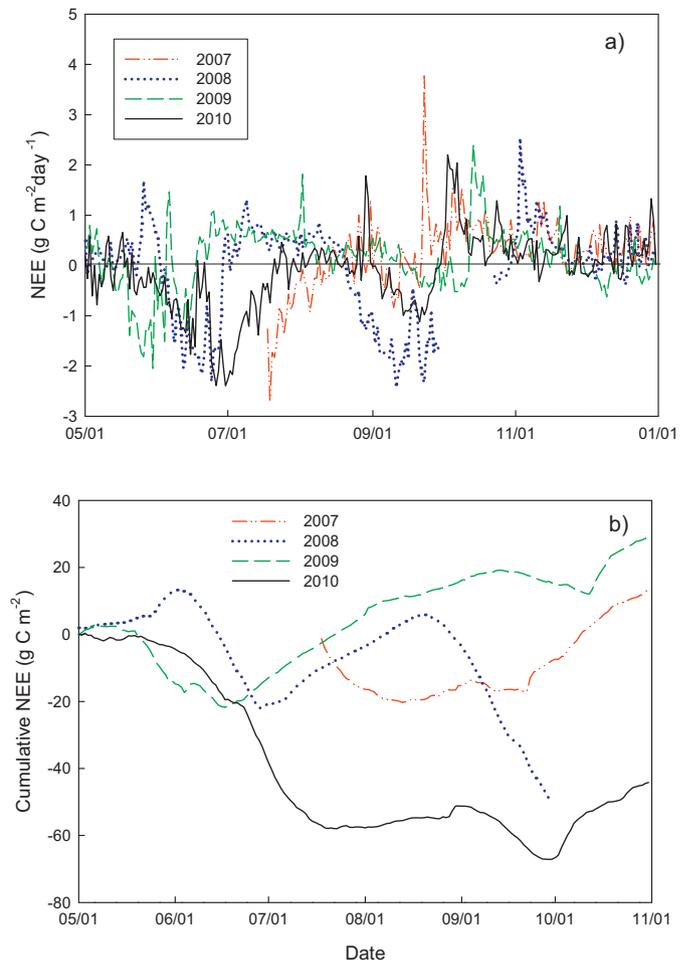
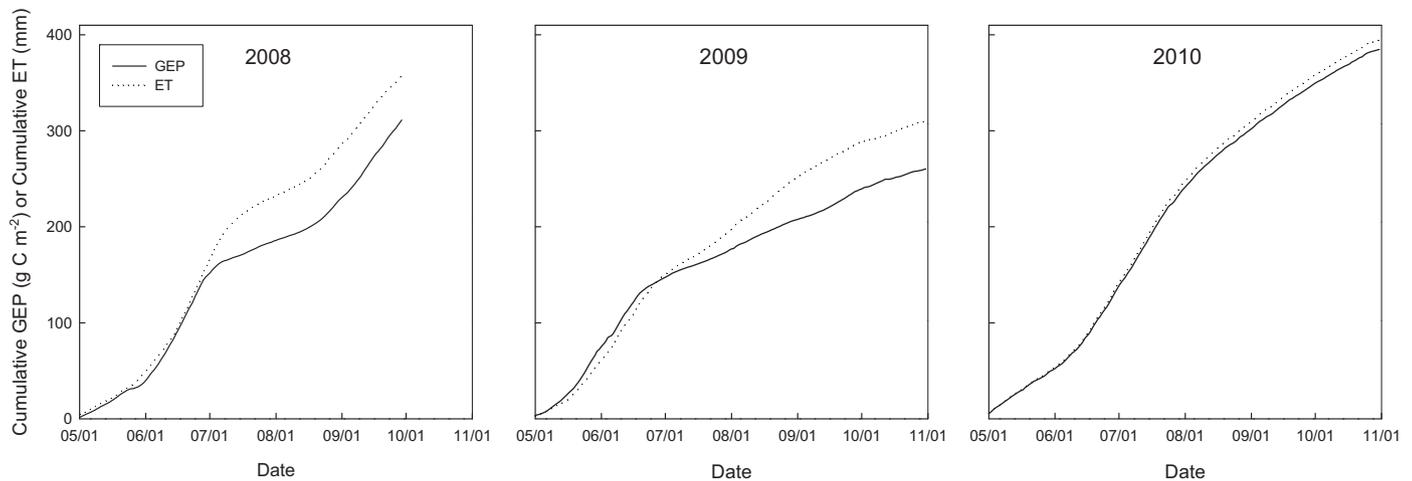


Fig. 8. Net ecosystem exchange of carbon dioxide (NEE) from 2007 to 2010 on panel (a) daily basis and panel (b) cumulative throughout the growing season. Negative NEE flux indicates a net uptake of carbon dioxide by the ecosystem. Cumulative NEE ends on October 1st in 2008 due to 22 days of missing data from equipment malfunction.



**Fig. 9.** Cumulative gross ecosystem production of carbon dioxide (GEP) and cumulative evapotranspiration (ET) throughout the 2008–2010 growing seasons. Cumulative GEP and ET ends on October 1st in 2008 due to 22 days of missing data from equipment malfunction.

(GEP, i.e., photosynthesis) and ET, 2010 had the greatest GEP and ET loss whereas the other years there was a greater decoupling of GEP from ET (Fig. 9). This decoupling or separation between the magnitude of GEP and ET fluxes in 2008 and 2009 coincided with periods of severe defoliation. After these events and refoliation, the slope of the GEP and ET lines became parallel again.

#### 4. Discussion

Our hypotheses that ET would decrease and NEE increase due to the defoliation events were clearly supported, but we did not find a declining trajectory of ET loss and carbon dioxide uptake with successive years of beetle herbivory and defoliation (Figs. 8 and 9). Cumulative NEE for 2009 did show a strong change from 2008 with the ecosystem changing from a C-sink to a C-source. However, cumulative ecosystem exchange in the 2010 growing season was similar to 2008 (Figs. 8 and 9). This may be a result of the lower beetle density found in 2010 relative to 2009, which may have reduced herbivory pressure, though there were still periods with very reduced canopy coverage due to beetle herbivory. However, even though the cumulative effect on NEE was similar in 2008 and 2010 the seasonal pattern was very different with outbreak beetle conditions in 2008 producing large transient changes in carbon uptake or release (Fig. 8). Some of the release of carbon dioxide in 2009 may have been from increased rates of litter decomposition. Northern tamarisk beetle herbivory can produce higher quality, rapidly decomposing litter (Uselman et al., 2011a,b) and increased litter production rates (Uselman et al., 2011a).

There were distinct periods in all three years when beetle damage and leaf desiccation reduced ET and decreased C uptake, supporting hypotheses 1 and 2, that defoliation would impact these fluxes. However, these periods were usually of short duration (2–4 weeks) and did not produce a definitive long-lasting impact on stand water loss and carbon uptake relative to other years with beetle herbivory (Figs. 5 and 6). Similarly, Dennison et al. (2009) found that ET predicted from MODIS EVI data and calibrated with scaled-up sap flow data showed that similar decreases in ET from beetle herbivory had little effect on annual ET. However, in our study *Tamarix* was only subject to large-scale beetle outbreak breaks for three growing seasons, which may not be long enough to induce strong carbon limitation in these trees (but see Hudgeons et al., 2007).

Although there was a doubling of understory vegetation in 2010, it is doubtful that this was mainly responsible for the increased C uptake and ET loss, because most of this increase was in cheatgrass which senesced by the end of June. The close coupling between ET and GEP in this ecosystem, except in periods of severe herbivory (Fig. 9), indicates that the ET is largely dominated by *Tamarix* transpiration, not soil evaporation. The lack of relationship between summer rainfall and ET (Fig. 6) indicate that *Tamarix*, which is deeply rooted and able to use groundwater, is the dominant contributor to ET, not shallow rooted grasses and forbs. However, our field observations of plant vigor in 2010 indicated the plants were showing visible signs of canopy damage, and NDVI patterns show reduced greenness (Fig. 4), yet on the whole *Tamarix* performed better than previous years. This suggests there may have been some compensatory photosynthetic response by the remaining leaf tissue (Nowak and Caldwell, 1984). Greater transpiration per unit leaf area in response to beetle herbivory was observed along the Walker River, NV, but did not occur along the Humboldt River, NV (Pattison et al., 2011b). Additionally, no differences were observed in leaf-level gas exchange on paired trees with and without beetles (Pattison et al., 2011a). Thus, it seems more plausible that the warmer fall growing season and decline in beetle density allowed *Tamarix* to perform efficiently.

The lack of baseline ecosystem level ET and CO<sub>2</sub> flux data or tree level transpiration (*T*) is not unique to this study (Hultine et al., 2010b; Pattison et al., 2011b). Beetles were released in the Great Basin in 2001, but there was a paucity of ecosystem level studies in this region until recently. This highlights the need to establish multiple years of baseline data in areas where the beetles are predicted to migrate. Several methods have been employed to overcome the lack of baseline data. One study used an experimental approach with insecticide to control beetles on pairs of trees with and without beetles that were instrumented for sap flux (Pattison et al., 2011b). Their results differed depending on sites and between years with differences in sap flux rates varying between 0 and 75%. Hultine et al. (2010b) used sap flux data from 41 days before *Tamarix* trees visibly defoliated and beetles were observed at the site, to model the decline in ET based on a relationship with vapor pressure deficit. They found that beetle defoliation, one and two years after the initial beetle outbreak along the Dolores River in Utah, reduced overall transpiration as measured by sap flux density, by 16% for a period of a few weeks. Furthermore, after defoliation there was no

reduction in leaf area regrowth or sap flux. The beetles produced a transient response that moderately reduced stand-level water loss.

Studies, including this one, have found an initial transient increase in water loss from beetle damage both during the day and night. Hultine et al. (2010b) found that during the initial stages of defoliation, large increases in sapflux were observed especially at night, when transpiration increased three-fold. A greenhouse study (Snyder et al., 2010) found daytime leaf-level stomatal conductance increased two-fold and nighttime stomatal conductance increased five-fold during a 14 day period when leaves were extremely damaged due to beetle herbivory, but before leaves visibly turned brown and desiccated. This water loss was attributed to damage of leaf tissue that renders plants unable to control water loss through stomata. Pattison et al. (2011b) found stems continue to lose water after defoliation. In this study we found an increase in the contribution of nighttime ET to daily ET during a defoliation event (Fig. 7). Additionally, ET rates remained relatively higher than GEP rates during defoliation events (Fig. 9). Thus, reduced daytime canopy-driven transpiration loss may be partially offset by the transient increase in water loss through damaged plant tissues (Snyder et al., 2010).

Total yearly ET loss from this *Tamarix* dominated ecosystem was between 0.4 and 0.5 m. In a recent review using data from flux towers, MODIS EVI and sap flow, *Tamarix* ET was estimated to be between 0.6 and 1.3  $\text{m yr}^{-1}$  (Nagler et al., 2010). Our results show even less total water use, which is likely attributable to the lower temperatures and lower summer rainfall in the Great Basin compared to hot deserts with summer monsoons, and may in part be due to the activity of the beetle at this site. Our estimates are more than the 0.26  $\text{m yr}^{-1}$  reported by Pattison et al. (2011b) at the beetle infested Walker River site, with a similar climate to our site. In the current study, the correlation between NDVI and ET, especially during the height of the growing season was relatively strong ( $r^2 = 0.47$ ) and in the range of other studies looking at the correlation between ET and remotely sensed vegetation indices (Nagler et al., 2005a,b; Scott et al., 2008). Though it appears that ET becomes decoupled from NDVI in the fall perhaps due to shorter day length and lower temperatures that limit ET losses and induce leaf senescence. The ability of Landsat data to detect defoliation events appears useful for this narrow riparian ecosystem. Ground-based measures of LAI were well correlated to NDVI ( $r^2 = 0.64$ ) during the height of the growing season indicating Landsat NDVI can detect defoliation. Similarly, Dennison et al. (2009) using remotely sensed NDVI and enhanced vegetation index (EVI) data from high resolution ASTER data and low resolution MODIS data found beetle induced defoliation of *Tamarix* was detected by both types of imagery along the Dolores River in Utah.

In summary, we found there was a tight coupling of *Tamarix* to ecosystem-level fluxes of carbon dioxide uptake and water use, except during periods of substantial leaf damage due to beetle herbivory that leads to premature senescence. *Tamarix* response to beetle herbivory produced short-term decreases in ET and carbon uptake. However, these responses were transient as *Tamarix* was able to refoliate, likely due to its access to groundwater at this site and because extensive beetle herbivory is a relatively recent (three year) phenomenon at this site. Therefore, the cumulative growing season totals for ET and NEE did not indicate any trend. This pattern is likely in part due to fluctuations in beetle density that reduced herbivore pressure in 2010. The net outcome on ET and NEE depends on the amount of initial damage to the canopy, time to regrowth, and degree of canopy recovery. It remains to be seen if future beetle herbivory might permanently alter water and carbon fluxes from *Tamarix* ecosystems.

## Acknowledgements

We thank the Pyramid Lake Paiute Tribe for access to their lands. We also wish to thank the following USDA-ARS staff and University Nevada Reno students: Timothy Jones, Amira Dittrich, Mike Schmeiske, Sarah Thompson, Michelle Newell and Shannon Swim for valuable field and laboratory assistance. We thank Shauna Uselman, Erik Hamerlynck and two anonymous reviewers for valuable comments on earlier versions of this manuscript. USDA is an equal opportunity employer.

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