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Regional scale impacts of *Tamarix* leaf beetles (*Diorhabda carinulata*) on the water availability of western U.S. rivers as determined by multi-scale remote sensing methods☆

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ABSTRACT

Tamarix leaf beetles (*Diorhabda carinulata*) have been widely released on western U.S. rivers to control introduced shrubs in the genus *Tamarix*. Part of the motivation to control *Tamarix* is to salvage water for human use. Information is needed on the impact of beetles on *Tamarix* seasonal leaf production and subsequent water use over wide areas and multiple cycles of annual defoliation. Here we combine ground data with high resolution phenocam imagery and moderate resolution (Landsat) and coarser resolution (MODIS) satellite imagery to test the effects of beetles on *Tamarix* evapotranspiration (ET) and leaf phenology at sites on six western rivers. Satellite imagery covered the period 2000 to 2010 which encompassed years before and after beetle release at each study site. Phenocam images showed that beetles reduced green leaf cover of individual canopies by about 30% during a 6–8 week period in summer, but plants produced new leaves after beetles became dormant in August, and over three years no net reduction in peak summer leaf production was noted. ET was estimated by vegetation index methods, and both Landsat and MODIS analyses showed that beetles reduced ET markedly in the first year of defoliation, but ET recovered in subsequent years. Over all six sites, ET decreased by 14% to 15% by Landsat and MODIS estimates, respectively. However, results were variable among sites, ranging from no apparent effect on ET to substantial reduction in ET. Baseline ET rates before defoliation were low, 394 mm yr^{-1} by Landsat and 314 mm yr^{-1} by MODIS estimates (20–25% of potential ET), further constraining the amount of water that could be salvaged. Beetle–*Tamarix* interactions are in their early stage of development on this continent and it is too soon to predict the eventual extent to which *Tamarix* populations will be reduced. The utility of remote sensing methods for monitoring defoliation was constrained by the small area covered by each phenocam image, the low temporal resolution of Landsat, and the low spatial resolution of MODIS imagery. Even combined image sets did not adequately reveal the details of the defoliation process, and remote sensing data should be combined with ground observations to develop operational monitoring protocols.

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1. Introduction

1.1. Use of remote sensing to monitor forest defoliation by insects

Insect infestations can cause wide-spread damage to forest ecosystems, and deleterious effects can be compounded if plants are under heat or water stress, raising the possibility that insect damage could increase as regional climates become warm and drier (Dale et al., 2001). Remote sensing offers the possibility of monitoring insect damage over spatial and temporal time scales that are difficult to achieve with ground surveys. Wulder et al. (2006) pointed out that forest management agencies require information at several scales of measurement, so no single remote sensing approach is adequate. For example, Eklundh et al. (2009) tested a method for mapping Scots pine defoliation by the pine sawfly in Norway, using coarse-resolution 16-day composite imagery from the Moderate Resolution Imaging Spectrometer (MODIS) sensors on the Terra satellite. Normalized Difference Vegetation Index (NDVI) values were useful in detecting areas of defoliation within the forest, but only

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weak relations were found between the degree of damage and MODIS change parameters. They concluded that MODIS could be used to detect damaged forest areas but that high-resolution imagery or fieldwork would be needed to estimate the intensity of the infestation.

Medium-resolution Landsat imagery has also been used to detect insect damage. Healy et al. (2005) combined six Landsat bands into a three-parameter Forest Disturbance Index (FDI), using a tasseled cap transformation in which brightness, greenness and wetness were evaluated by different band combinations. Areas of forest clearing were characterized by high brightness and low greenness and wetness values. Eshleman et al. (2009) tested the ability of the FDI to detect gypsy moth damage to an Appalachian oak forest, using stream nitrogen levels as a proxy for defoliation, because nitrogen is released from damaged leaves into the watershed. The FDI was able to predict both the overall intensity and extent of forest damage; however, nearly-complete defoliation was needed for the FDI to detect damage at the stand level (Healy et al., 2005).

High-resolution hyper-spectral imagery has also been used to detect insect damage. Leckie et al. (2005) developed an automated procedure for detecting forest defoliation by the jack pine beetle using airborne, 2.5 m resolution hyper-spectral imagery from the Multi-spectral Electro-optical Imaging Sensor. Information from six visible bands and one near infrared (NIR) band were combined to detect canopy discoloration due to beetle damage. Insect damage was detected with an overall accuracy of 84% in stands with damage levels ranging from light to heavy. Martin et al. (2008) used foliar nitrogen levels as a proxy for forest damage in 137 forested plots in North America, South America and Australia. Most plant nitrogen is contained in pigments and enzymes in leaf chloroplasts, and defoliation results in a marked drop in both canopy nitrogen and chlorophyll, which can be detected spectrally. Imagery from the Airborne Visible/Infrared Imaging Spectrometer accurately predicted canopy nitrogen levels measured by ground sampling. The results were valid regardless of the source of forest damage. However, high-resolution, hyper-spectral imagery is not currently available for routine forest monitoring.

Given that insect dynamics are highly variable across scales we present a study which uses a multi-platform approach to monitor the impacts of leaf beetles (*Diorhabda carinulata* and related species) deliberately released on western U.S. rivers to control *Tamarix* spp. (e.g., saltcedar). The beetles have spread more rapidly than anticipated, raising new management issues in already stressed western riparian corridors (Hultine et al., 2010a,b). Among these are the effects of *Tamarix* defoliation on riparian evapotranspiration (ET), the sum of evaporation and plant transpiration from the surface to the atmosphere. The prospect of water salvage was a prime motivation for introducing the beetles (e.g., Pattison et al., 2011). Developing ground-validated remote sensing tools for monitoring the effects of beetles on riparian ET was the primary goal of this study.

1.2. Background of *Tamarix*/beetle interaction on western rivers

Tamarix spp. are salt-tolerant shrubs or small trees introduced to the U.S. in the 1800s (Chew, 2009). They have minute, scale-like leaves attached to terminal stems that resemble conifer needles. Leaves are deciduous, produced in spring and shed in fall. *Tamarix* escaped cultivation, and by 1900, they were widely established in several western states. Today, naturalized stands of *Tamarix* cover several hundred thousand hectares of mainly riparian habitat in North America, stretching from northern Mexico to Montana and from Kansas to California (Nagler et al., 2010a).

Starting in the 1950s, *Tamarix* began to be perceived as a problem (Chew, 2009). The most commonly stated reasons for *Tamarix* control are that it uses large amounts of water, out-competes native trees, and provides poor wildlife habitat (reviewed in DeLoach et al., 2000; Di Tomaso, 1998; Zavaleta, 2000). Local, state, and federal agencies have undertaken efforts to eradicate *Tamarix* and restore riparian habitats to pre-invasion status (O'Meara et al., 2010). However, the rationale for *Tamarix* control has been challenged by findings that *Tamarix* actually uses the same or less water than native riparian plants (Nagler et al., 2005a,b; 2009a; 2010b), competes with native species mainly when river systems are disturbed (Stromberg et al., 2007), and provides habitat for native wildlife species, including threatened and endangered birds (Sogge et al., 2008; van Riper et al., 2008). Hence, the role of *Tamarix* spp, in riparian degradation, once considered to be a major concern throughout its range, is now being reevaluated (Stromberg et al., 2009; Shafroth et al., 2010).

In the meantime, *Tamarix* leaf beetles from Eurasia (Tracy & Robbins, 2009) have been widely released throughout the western U.S. as biological control agents for *Tamarix* (DeLoach et al., 2000, 2003, 2004; DeLoach & Carruthers, 2004; Moran et al., 2009; Tracy & Robbins, 2009; O'Meara et al., 2010). Since the initial releases in 2001 beetle populations have expanded and moved through a number of river systems in the intermountain west where they periodically defoliate *Tamarix* over a vast area (O'Meara et al., 2010; Pattison et al., 2011). Similar to other defoliating insects such as the willow sawfly (Doody & Benyon, 2010), the *Tamarix* leaf beetle is active for only a few weeks in the summer. The timing of defoliation is linked to the seasonal timing of reproductive activity and dispersal which is in turn linked to beetle physiology and behavior (Bean et al., 2007a, b). Defoliation can occur as early as June and as late as August at different sites, or at the same site in different years. At most sites defoliation lasts 6–8 weeks. After defoliation, the beetles enter a dormant stage and shrubs grow new leaves in late summer or in spring of the following year.

The presence of leaf beetles in *Tamarix*-dominated river systems raises a number of new management issues (Nelson & Wydoski, 2008; Hultine et al., 2010a,b; O'Meara et al., 2010). Before field data were available it was suggested that *Tamarix* plants could weaken after two to three years and several cycles of defoliation, resulting in mortality rates of 75–85% (Quimby et al., 2003; DeLoach & Carruthers, 2004). In support of this hypothesis, Hudgeons et al. (2007) showed that successive cycles of defoliation led to a decrease in stored carbohydrates which could weaken the plants. Apparent tree death has been noted at several sites (author's personal observations), and mortality is high at one of the original release sites near Lovelock, Nevada (Dudley et al., 2006; Pattison et al., 2011). Preliminary evidence, however, suggests that *Tamarix* shrubs re-sprout with nearly equal vigor each year at some locations despite infestation with leaf beetles (Hultine et al. (2010a,b)). At this point it appears that beetle impacts and *Tamarix* mortality vary with the ecological setting.

Hultine et al. (2010a,b), working on the Lower Dolores River in Utah, measured transpiration of infested *Tamarix* stands by sap flux sensors, and reported that annual water use was reduced by only 15% due to the short period over which defoliation occurred. Over three years of defoliation, shrubs refoliated with equal vigor each spring. Base rates of ET were only 200 mm yr^{-1}, much lower than had been assumed in early estimates of water salvage potential; hence, the study suggests that actual water salvage might be very low. By contrast, Pattison et al. (2011) found more substantial reductions in water use at beetle release sites on the Humbolt and Walker Rivers. However, it is difficult to generalize from a few sites to the regional level at which information is needed by resource managers.

1.3. Objectives of the study

Developing ground-validated remote sensing tools for monitoring the effects of beetles on riparian ET is the primary goal of this study.

Two key questions are addressed: 1) how do leaf beetles affect the phenology of *Tamarix* leaf development over multiple years of infestation; and 2) what magnitude of water salvage can be expected in infested river systems. We determine the effects of beetles on the phenology and ET of *Tamarix* stands at beetle release sites on six river systems. Networked multiband digital cameras (phenocams) (Richardson et al., 2007) deployed over individual shrubs document the phenology of defoliation with high temporal and spatial resolution but over a very limited sample of shrubs. Landsat TM and MODIS satellite images are used to quantify the effects of defoliation on riparian ET from 2000 to 2010 at all sites, and ET measured in years before beetle release and years after release was subjected to an Analysis of Variance (ANOVA) to test the hypothesis that beetles reduce riparian ET. Study sites were selected where ground observations were available to correlate with remote sensing data, and all were sites where extensive defoliation has been documented since beetles were first released. Therefore, this study describes the range of impacts that can be expected at successful release sites during the early stages of leaf beetle–*Tamarix* interactions (the first 5–8 years after infestation) within the study area.

1.4. Remote sensing methods for estimating ET

Numerous remote sensing methods for estimating ET have been developed (reviewed in Glenn et al., 2007; Kalma et al., 2008). These can be based on thermal band measurements, which estimate sensible heat flux then calculate the latent heat of evaporation due to ET as a residual in the surface energy balance equation (Kalma et al., 2008), or on vegetation indices, which estimate the amount of green leaf area available to carry out ET over a landscape (Glenn et al., 2008, 2010), or on combinations of the two approaches, such as the dual-source model which divides the landscape into vegetated and unvegetated areas with vegetation indices, then estimates evaporation from each component with different algorithms (Kustas & Anderson, 2009).

This study used two similar methods derived from the crop coefficient method for estimating ET (Allen et al., 1998), in which ET is calculated by multiplying potential ET (ET_0), determined from meteorological data, by a crop-specific crop coefficient (K_c), which is usually less than 1.0:

$$ET = K_c ET_0. \quad (1)$$

ET_0 is calculated by several methods, and is a measure of the amount of ET that can occur from a fully-transpiring plant canopy under a given set of meteorological conditions. In the remote sensing methods, the static crop coefficient is replaced by a vegetation index that is scaled between 0 (representing bare soil) and 1.0 (representing fully transpiring vegetation). We used methods developed for western U.S. phreatophyte communities by Groeneveld et al. (2007) for Landsat and by Nagler et al. (2009a) for MODIS. The methods are especially well suited for arid-zone phreatophytes, which are deep-rooted plants that obtain water from a permanent groundwater supply, because the surface soil is normally dry, and ET is dominated by plant transpiration, which is highly correlated with green leaf area as measured by vegetation indices (Nagler et al., 2005a, 2005b).

2. Methods

2.1. Study sites: locations and history of defoliation

Six sites on the Lower Dolores River, Middle–Upper Dolores River, Humbolt River, Walker River, Upper Colorado River and Bighorn River (Fig. 1, Table 1) were selected based on high levels of initial defoliation observed at these release sites (DeLoach et al., 2004; Pattison et al., 2011). The individual site descriptions are as follows.

2.1.1. Dolores River sites

Leaf beetles were released on the Lower Dolores River, Utah, near the confluence with the Colorado River in 2004 and 2006. Ground surveys have been conducted at the University of Utah's Rio Mesa Research Station from 2006 to the present, and extensive seasonal defoliation was noted from 2007 onward (Fig. 2A) (Dennison et al., 2009; Hultine et al., 2010a,b). The beetles migrated upstream, and defoliation was noted at sites on the Middle and Upper Dolores River in 2007. Defoliation was measured in ground surveys conducted in 2008–2010 and results are reported here. The Lower Dolores River site was dominated by *Tamarix* on the river terraces but with *Salix exigua* (willows) and *Populus deltoides* (cottonwood) trees growing along the active river channel. Middle and Upper Dolores River had a more diverse flora, supporting *Alnus tnuifolia* (alder), *Populis tremuloides* (aspen), *Juniperus* spp. (junipers), *Forestiera pubescens* (desert olive), and *Quercus gambelii* (Gambels oak) in addition to *Tamarix*, cottonwood and willows. The Bedrock, Slickrock and Egnar sites listed in Table 1 are close together (see Fig. 1) and have similar vegetation and were combined into a single site called the Middle–Upper Dolores River Site in the analyses.

2.1.2. Humbolt River site

Beetles were released on the Humbolt River near the town of Lovelock, Nevada in June, 2001 in a dense stand of *Tamarix*. No defoliation was seen in 2001 but about 1 ha was seen in August of 2002. At the end of July, 2003, beetles had defoliated a large area (200 ha or more) extending out from the release site in all directions. In 2004 beetles defoliated the release site area by about July 1 and total *Tamarix* green biomass had declined by at least 80% around the release area. In September, 2004, there was little green biomass in the *Tamarix* stands for several hundred meters out from the release site. At the release site *Tamarix* biomass remained low, and beetle numbers were also low throughout 2005. *Tamarix* mortality at the monitoring site was 40% (Dudley et al., 2006). In the winter of 2005–2006 flooding submerged the release site for several months. When the water subsided there was a flush of growth from herbaceous weeds while mortality in *Tamarix* reached 60%. In 2007 beetles continued to be present, *Tamarix* green biomass was low and mortality reached 70% (Pattison et al., 2011) (Fig. 2B).

2.1.3. Walker River site

Beetles were released into a sparse stand (ca. 50% cover) of *Tamarix* on the Walker River near Hawthorne, Nevada, in 2001 but

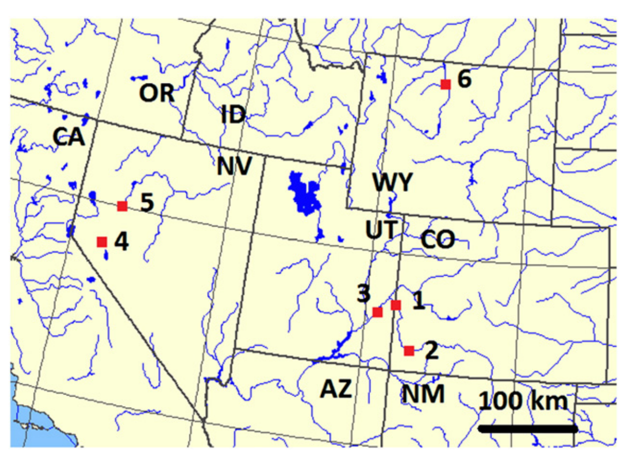

Fig. 1. Locator map for river systems in the study. Numbered sites are: 1) Lower Dolores River; 2) Middle–Upper Dolores River; 3) Upper Colorado River; 4) Walker River; 5) Humbolt River; and 6) Big Horn River.

Table 1
Locations of study sites and pixels used in MODIS ET analyses of beetle-infested Tamarisk sites in the western US. Some pixels contained adjacent mostly-bare areas of soil in addition to riparian vegetation; three pixels had some water in the scene in addition to soil and vegetation.

Site number	Site name/river	Pixel locations	% riparian in pixel	Comments
1	Lower Dolores River, UT (Entrada Ranch and near confluence of Colorado R.)	38.7959, −109.1912 38.7962, −109.1200 38.7946, −109.1859 38.8067, −109.2674	77.8 87.5 (4.6% water) 94.6 (15.8% water) 100	Beetles released 2005, 2006; extensive defoliation noted in 2007.
2	Middle–Upper Dolores River, CO (sites near Bedrock)	38.0710, −108.8931 38.3313, −118.8586 38.3093, −118.8872	32.0 100 42.9	Beetles released 2005, 2006; extensive defoliation noted in 2007.
2	Middle–Upper Dolores River, CO (sites near Slickrock)	38.0309, −108.8688 38.0459, −108.8120 38.0317, −108.8374 38.0328, −108.8864	33.7 33.0 31.7 33.6	Beetles released 2005, 2006; extensive defoliation noted in 2007.
2	Middle–Upper Dolores River, CO (site near Egnar)	37.8529, −108.9425	100	Beetles released 2005, 2006; extensive defoliation noted in 2007.
3	Lower Colorado River, near Williams Bottom, UT	38.5363, −109.6040	100 (13.8% water)	Beetles released in 2004 and again 2005. Extensive defoliation noted at location of pixel in 2006, 2007.
4	Walker River, near Hawthorne, NV	38.8928, −118.7816	100	Beetles released in 2001 with modest defoliation (1 ha) seen in 2003 and large scale defoliation seen in 2004 and continued defoliations noted in 2005–2008.
5	Humbolt River, near Lovelock, NV	40.0092, −118.5313 40.0112, −118.5279 40.0152, −118.5284	100 100 100	Beetles released 2001. Defoliation began in 2002, extended over 200 ha by 2003. Flooding produced weeds in 2005–2006. In 2007 beetles continued to be present, tamarisk mortality reached 70%.
6	Bighorn River, near Lovell, WY	44.8827, −108.2041	100	Beetles released 2001. Spotty defoliation in 2003. Nearly complete defoliation of 200 ha by 2004. Defoliation spotty by 2007–2008 at release site but more extensive along 51 km of the Bighorn River.

defoliation lagged about one year behind those seen in Lovelock with modest defoliation (1 ha) seen in 2003 and large scale defoliation seen in 2004 and continued defoliations noted in 2005–2008. From 2004 onward, trees showed reduced green biomass. In the spring of 2004 *Tamarix* initially developed leaves but beetles defoliated almost the entire monitoring site by June 24, and caused extensive mortality through 2007 (Fig. 2C).

2.1.4. Upper Colorado River site

Beetles were released into a dense stand on a sandbar near Williams Bottom site on the Upper Colorado River in 2004 on August 3 and August 18. They were released again in July, 2005 and by September, 2005 approximately 0.1 ha of *Tamarix* had been defoliated around the release site. Regrowth was seen by October 15, 2005. In 2006 defoliation started in June and covered an extensive area on the river. Cycles of defoliation hit this area throughout 2007 and 2008 (Fig. 2D).

2.1.5. Big Horn River site

Beetles were released in a dense stand of *Tamarix* near Lovell, Wyoming on the Big Horn River in 2001. Ten ha of spotty defoliation were seen in September, 2003. By September, 2004 all *Tamarix* around the release site was defoliated (ca. 200 ha). In spring, 2005, flooding covered some of the previously defoliated areas but by fall, 2005, the area around the release site was again defoliated, and *Tamarix* biomass continued to decline. *Tamarix* was again defoliated by the fall of 2006 at the release site and more extensively along 51 km of the Big Horn River (personal communication, D. Kazmer, USDA ARS, Sydney, MT). Defoliation was patchy in 2007–2008, and *Tamarix* biomass was low at release site as a result of defoliation cycles.

2.2. Phenocam measurements of defoliation on the Lower Dolores River

Down-looking multi-band and visible band cameras (phenocams) collected data over three seasons of *Tamarix* defoliation (2008–2010) at the Lower Dolores River site. Phenocams have been successfully deployed in other ecosystems to monitor seasonal vegetation changes via the Normalized Difference Vegetation Index (NDVI) or other band combinations sensitive to green foliage density (Richardson et al., 2007). Two 10 m towers were installed over two *Tamarix* stands (called Gauge and Orchard) at the Rio Mesa Research Station. Each tower was equipped with one multi-band and one visible-band camera trained on different *Tamarix* canopies immediately beneath the towers. Multi-band cameras (Tetracam Model ADC Sentry, Tetracam, Inc., Chatsworth, CA) had red, green and NIR sensors and collected 3.1 megapixels per image over an image area of approximately 1 m^2. Data was collected at 15 minute intervals and transmitted via a wireless telemetry system to the Rio Mesa website (http://entradadata.biology.utah.edu). Red and NIR data collected between 1000 and 1400 hours were used to calculate mean daily NDVI values. Sensors were not inter-calibrated and red and NIR digital number (DN) values and consequently NDVI varied considerably between the two cameras and NDVIs were negative in some cases. To produce a temporal dataset responsive to changes in *Tamarix* canopy condition, NDVI was calculated, averaged, and scaled using the following steps:

(1) DN values of reflected light in the red and NIR bands were used to calculate NDVI:

$$\mathrm{NDVI} = (\mathrm{NIR{-}Red})/(\mathrm{NIR} + \mathrm{Red}) \tag{2}$$

(2) A seven-day running average of all pixels within a subset area of the camera field of view (ca. 1 m^2) was calculated.
(3) Values for each camera were scaled between 0 and 1.0 using NDVI_{max} and NDVI_{min} values at each tower site over the three years of data collection:

$$\mathrm{NDVI}^*_{PC} = 1{-}(\mathrm{NDVI}_{max}{-}\mathrm{NDVI})/(\mathrm{NDVI}_{max}{-}\mathrm{NDVI}_{min}) \tag{3}$$

where NDVI^*_{PC} is scaled phenocam NDVI. This transformation allowed comparison of the relative amount of defoliation at each site but did not allow comparisons of the actual amount of foliage at each site due to differences between cameras.

Visible-band digital cameras (NetCam SC-Multi-Megapixel Hybrid IP Camera, StarDot Technologies, Buena Park, CA) acquired 5 megapixels per image over a 1 m^2 field of view. Images acquired in early afternoon (13:45 local time) were used for analyses. From the daily images, a subset of dates that captured the onset and extent of leaf greening in spring, defoliation in summer, regrowth of leaves in late

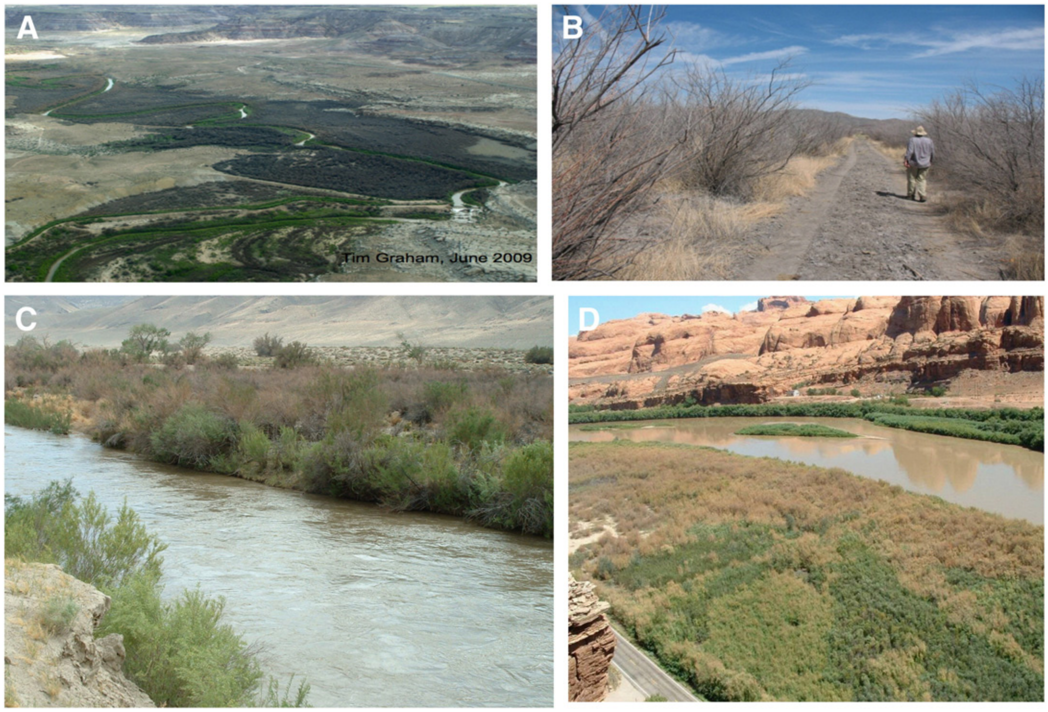

Fig. 2. Photographs showing effects of leaf beetles on *Tamarix* stands at the Lower Dolores River site in 2009 (A); the Humbolt River site in 2007 (B); the Walker River site in 2006 (C); and the Upper Colorado River site in 2007 (D).

summer, and senescence of leaves in fall was selected for analysis. *Tamarix* has minute, scale-like leaves attached to needle-like terminal stems. During defoliation, beetles eat the mesophyll cells of the leaves but leave the dead leaf remains and the terminal stems intact. Visually, leaves (needles) turn from green to brown during defoliation but remain on the plant. Individual green or brown leaves were easily visible on the images and were quantified by placing a 200 point grid over the image in Adobe Photoshop 8.0 (Adobe Systems, Inc., San Jose, California) then scoring the fraction of grid intersections that covered green leaf material.

Results were quantified as the percent of annual green leaf cover or $NDVI^*_{PC}$ lost due to defoliation for each year at each camera station. Time-series of visible-band and $NDVI^*_{PC}$ results used to make these calculations are in Fig. 3A, B, C and D, respectively. All four cameras captured at least a portion of the initial greening of canopies which started on about April 1 each year and reached a maximum value by mid-June. This was followed by a rapid loss of nearly all green leaves during the defoliation period, and a subsequent production of new green leaves in August and September. Plants then dropped their leaves and entered winter dormancy in early October. The extent of defoliation was estimated by projecting each curve in Fig. 3 over a complete growing season (April 1 to October 15), then inferring what the shape of the seasonal curve would have been in the absence of defoliation, by assuming that peak green cover had been reached before beetles were active, as documented by at this site. The "missing" portion of the curves due to defoliation (gray wedges in Fig. 3) was then estimated on paper printouts of plots, by weighing cut-out sections of the curves on an analytical balance, following a method used to determine the area of irregular shapes (e.g., Patil & Bohde, 2001). For each curve, the weight of the lost-production cut-out (gray wedges in Fig. 3) was divided by the weight of the cut-out representing the total area under the curve, times 100 to obtain % reduction.

Estimates of percent reduction in green cover and $NDVI^*_{PC}$ due to defoliation were analyzed by a three-way ANOVA, in which Site (Gauge or Orchard), Method (visual or $NDVI^*_{PC}$), and Year (2008–2010) were categorical variables and % Reduction was the dependent variable.

2.3. Ground estimates of defoliation on the Middle–Upper Dolores River site

Fixed survey sites on the Middle and Upper Dolores River, selected as representative of riparian vegetation in the area and for accessibility (Table 1), were scored in surveys conducted at approximately monthly intervals over the growing season, starting in September, 2008 and extending to June, 2010. At each site the percent of green and brown leaf cover was estimated on 100 separate *Tamarix* shrubs selected by the nearest-neighbor method (Bonham, 1989). Cover was estimated visually in 5% increments. These ground estimates of defoliation were then compared to remote sensing estimates of ET reductions.

2.4. Landsat TM methods for estimating NDVI and ET

For each of the six beetle release sites, we obtained one annual summer Landsat 5 image for each year from 2000 to 2009, and two images per site for 2010 (Table 2). Images with no cloud cover over the sites of interest acquired from June 15 to August 15 were selected. The two images in 2010 represented early season (June) and late season (August) to see if the chronology of defoliation could be discerned within a season by Landsat imagery. Level 1 T processed images referenced to fixed ground points were obtained from the United States Geological Survey Earth Explorer web site (http://edcsns17.cr.usgs.gov/NewEarthExplorer/).

Methods for processing band data, converting NDVI values to scaled values ($NDVI^*_{TM}$) and calculating ET followed methods developed to estimate annual ET by western U.S. phreatophye communities, including *Tamarix* sites, from single summer Landsat images (Baugh & Groeneveld, 2006; Groeneveld & Baugh, 2007; Groeneveld et al., 2007). DN values were converted to apparent at-satellite reflectance values using data in the header files and equations and tabular

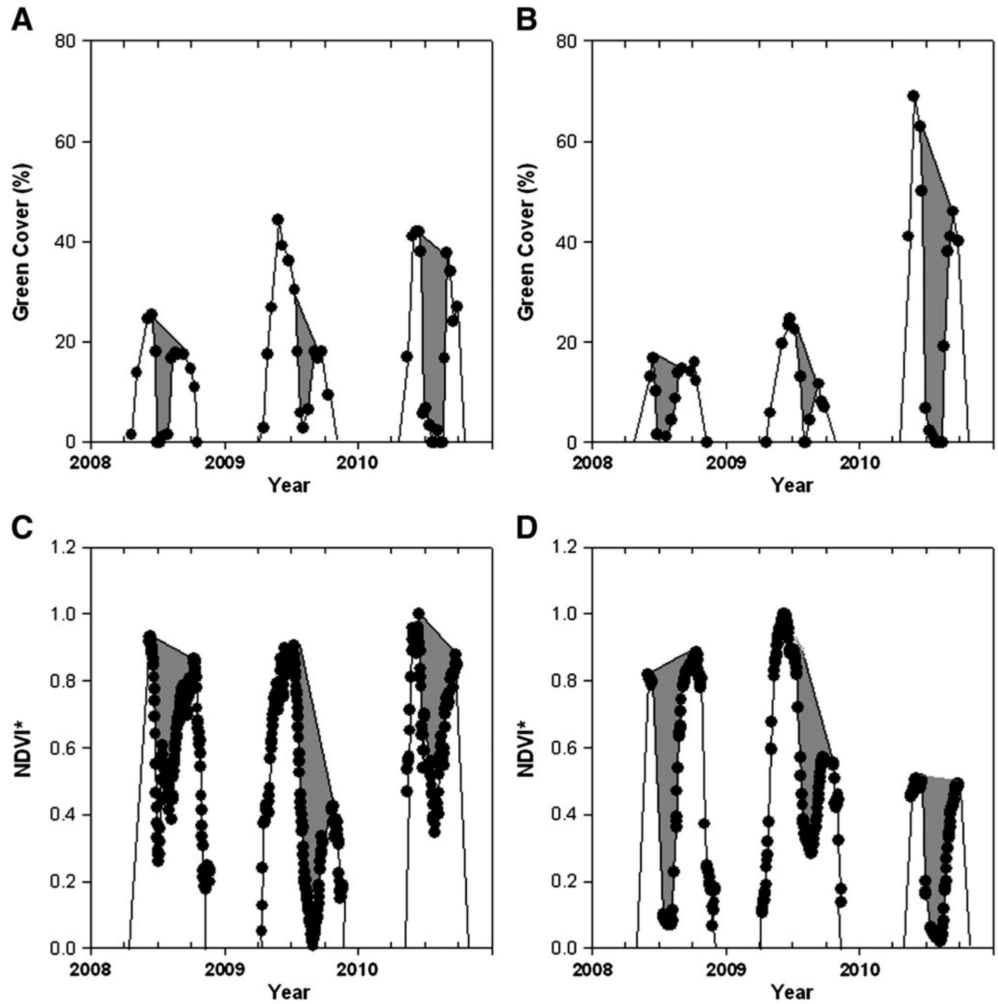

Fig. 3. Visual count of green leaf percent cover determined on visible-band phenocans over three years at Gauge (A) and Orchard (B) sites on the Lower Dolores River, and $NDVI^*_{PC}$ images (C, D) from multiband phenocams at the same sites over the same time period. Digital number NDVI values for each camera were scaled between 0 (lowest NDVI value) and 1.0 (highest NDVI value) to normalize values among cameras. Gray wedges show estimated lost leaf cover or $NDVI^*_{PC}$ due to defoliation by beetles.

information in the Landsat 7 Science Handbook (Irish, 1999). NDVI values were then scaled ($NDVI^*_{TM}$) between bare soil ($NDVI_{Soil}$) and maximum vegetation response ($NDVI_{Max}$) on each image using the relationship:

$$NDVI^*_{TM} = 1–(NDVI_{Max}–NDVI)/(NDVI_{Max}–NDVI_{Soil}) \tag{4}$$

where $NDVI_{Max}$ was the highest NDVI value on the image determined from a display of the pixel statistics in ERDAS Imagine (ERDAS, Inc., Norcross, GA); and $NDVI_{Soil}$ was the NDVI of an area (1–2 ha) of dry lake bed or rock outcrop that was apparently unvegetated and stable year to year. This bare-soil (or rock) area was selected on the Year 2000 image for each image series and the same area was re-sampled on subsequent images to evaluate the variability in the

Table 2
Landsat images used to estimate ET. Path/row 36 33 was used for Upper Colorado River, Lower Dolores and Middle–Upper Dolores sites; path/row 42 33 was used for the Walker River site; path/row 42 32 was used for the Humbolt River site; and path/row 36 29 was used for the Big Horn River site. Table gives the day and year of image acquisition and $NDVI_{Soil}$ and $NDVI_{Max}$ for each image. Bottom row gives the mean $NDVI_{Soil}$ and $NDVI_{Max}$ for each time series and the% coefficient of variation (standard deviation/mean × 100).

Path/row	36 33 DOY	$NDVI_{Soil}$	$NDVI_{Max}$	42 33 DOY	$NDVI_{Soil}$	$NDVI_{Max}$	42 32 DOY	$NDVI_{Soil}$	$NDVI_{Max}$	36 29 DOY	$NDVI_{Soil}$	$NDVI_{Max}$
2000	159	0.121	0.917	169	0.121	0.930	201	0.141	0.995	207	0.139	0.923
2001	159	0.133	0.919	169	0.121	0.936	171	0.156	0.914	209	0.121	0.919
2002	196	0.119	0.832	174	0.118	0.915	174	0.087	0.914	228	0.118	0.929
2003	209	0.137	0.924	161	0.164	0.977	177	0.154	0.916	183	0.122	0.914
2004	164	0.137	0.919	154	0.162	0.870	196	0.156	0.906	118	0.112	0.943
2005	172	0.119	0.988	166	0.162	0.929	198	0.082	0.911	204	0.157	0.975
2006	175	0.127	0.923	169	0.152	0.933	201	0.095	0.915	175	0.141	0.924
2007	178	0.152	0.920	172	0.158	0.929	204	0.128	0.858	162	0.160	0.922
2008	229	0.141	0.900	175	0.159	0.868	175	0.092	0.919	175	0.158	0.940
2009	231	0.135	0.931	177	0.162	0.865	177	0.159	0.858	234	0.128	0.988
2010	170	0.144	0.940	164	0.177	0.927	159	0.160	0.935	186	0.141	0.924
2010	218	0.130	0.925	212	0.159	0.931	223	0.139	0.934	234	0.128	0.988
Mean (CV%)		0.134 (7.90)	0.920 (4.18)		0.157 (10.2)	0.914 (3.94)		0.125 (26.2)	0.907 (3.00)		0.137 (12.8)	0.945 (3.00)

NDVI of the same scene across images in a time series. $NDVI_{Max}$ and $NDVI_{Soil}$ values for each image are in Table 2. In a test of the value of scaling NDVI for each image, Baugh and Groeneveld (2006) compared $NDVI^*_{TM}$ with unscaled NDVI for its correlation with annual precipitation at 15 moisture flux tower sites in phreatophyte communities from 1986 to 2002. Foliage density as determined by NDVI in desert plant communities is expected to be correlated with annual rainfall. The coefficient of determination (R^2) between NDVI and precipitation was 0.37, compared to 0.77 for precipitation and $NDVI^*_{TM}$, and $NDVI^*_{TM}$ was better correlated with precipitation than any of 13 other VIs tested in the same study. They concluded that $NDVI^*_{TM}$ corrected for both atmospheric and soil-induced effects in an image series, and eliminated the need to correct for these two effects separately in this application. Hence, we followed their protocol in this study, but we did not independently test its efficacy compared to other methods of image-based atmospheric correction.

Following Groeneveld et al. (2007), ET was calculated as:

$$ET = NDVI^*_{TM}(ET_0) \tag{5}$$

where ET_0 is potential ET from a fully transpiring plant canopy determined from meteorological data. Eq. (5) is based on the assumption that ET should be 0 at $NDVI_{Soil}$ because surface soils are normally dry in arid and semi-arid phreatophyte communities, while it should be equal to ET_0 for a fully transpiring crop at $NDVI_{max}$. Groeneveld et al. (2007) reported an R^2 of 0.94 for ET determined from single summer Landsat images and annual ET measured at 15 moisture flux tower sites set in western U.S. phreatophyte communities.

In this study, ET_0 was calculated by the Blaney–Criddle formula (Brouwer & Heibloem, 1986).

$$ET_0 = p(0.46\ T_{mean} + 8) \tag{6}$$

where p is day light hours determined from a table by month and latitude and T_{mean} is mean monthly air temperature, obtained from NOAA Cooperative Reporting Stations near each site (http://lwf.ncdc.noaa.gov/oa/climate/climatedata.html). ET_0 for sites on the Dolores and Colorado River were calculated from Moab, UT data; the site on the Humbolt River was calculated from Lovelock, NV data; the site on the Walker River was calculated from Hawthorne, NV data; and the site on the Big Horn River was calculated from Lovell, WY data.

To determine the effects of defoliation on ET at each site, an Area of Interest (AOI) file was prepared in ERDAS that encompassed the area of maximum defoliation reported from ground surveys at each site (Fig. 4), and the same AOI file was used to extract $NDVI^*_{TM}$ values for each Landsat image from 2000 to 2010 and used to calculate annual ET by Eqs. (5) and (6). Annual ET values were divided into two groups representing years before and after widespread defoliation was noted at each site. Data were subjected to two-way ANOVA in which ET was the dependent variable and Site and Before/After defoliation were the categorical variables (Stevens, 1996). ET values for individual years before or after defoliation were treated as replicates in the ANOVA.

2.5. MODIS methods for estimation of Enhanced Vegetation Index (EVI) and ET

MODIS Enhanced Vegetation Index (EVI) MOD13Q1 data were acquired from the Oak Ridge National Laboratory DAAC site (ORNL, 2010). EVI is calculated from red, blue and NIR bands as described in Huete et al. (2002):

$$EVI = G(rNIR - rRed)/(rNIR + C_1 xrRed + C_2 xrBlue + L) \tag{7}$$

where C_1 and C_2 are coefficients designed to correct for aerosol resistance, which use the blue band to correct for aerosol influences in the red band. C_1 and C_2 have been set at −6 and 7.5, while G is a gain factor (set at 2.5) and L is a canopy background adjustment (set at 1.0) (Huete et al., 2002). Pixel resolution is 250 m and each image is a composite of 3–5 cloud-free images during each 16 day collection period. Pixel footprints were projected on high-resolution images using the Google Earth to ensure it encompassed the beetle release site. In a few cases the only available MODIS pixels were wider than the riparian corridor and contained areas of adjacent uplands, which were sparsely vegetated. For those pixels, the approximate percentage of riparian habitat was estimated visually (see Table 1). These estimates are only approximations, as the center point of the pixels is somewhat indeterminate (Tan et al., 2006) and the area covered by each pixel is variable, depending on view angle (ORNL DAAC, 2010).

Numerous MODIS pixels were obtained for sites on the Dolores River, because widespread defoliation was documented along the river system in both Utah and Colorado. On the other hand fewer pixels, centered around the leaf beetle release sites, were acquired for the other sites, as the extent of defoliation away from the release site was not as well documented (Table 1). Data sets extended from DOY 49, 2000, to DOY 353, 2009. Similar to phenocam $NDVI^*_{PC}$ and Landsat $NDVI^*_{TM}$ values, EVI values were stretched between 0 (bare) and 1.0 (full riparian vegetation cover) by the equation:

$$EVI^* = 1-(0.542-EVI)/(0.542-0.091) \tag{8}$$

where EVI* is scaled EVI, and 0.542 and 0.091 are maximum and minimum EVI values from a large data set of riparian values in the western U.S. (Nagler et al., 2005a, 2005b).

EVI* values were transformed to estimates of ET (mm d^{-1}) by the equation:

$$ET = 1.22\ EVI^*(ET_0). \tag{9}$$

Eq. (9) was developed by regressing measurements of riparian and crop ET on the Lower Colorado River (measured by sap flux, moisture flux tower, and soil water depletion methods) with meteorological and remote sensing data, and it has a Root Mean Square Error of about 20% of the mean value (Nagler et al., 2009b).

For sites where the pixels contained adjacent upland as well as riparian habitat, calculated ET values were adjusted using EVI* values for adjacent upland areas to calculate upland ET.

Riparian ET was then calculated as:

$$ET_{riparian} = \left(ET_{total\ pixel} - ET_{upland} \times f_{upland}\right) \Big/ f_{riparian} \tag{10}$$

where $f_{riparian}$ and f_{upland} are the fraction of the pixel covered by riparian and upland vegetation as shown in Table 1. Three pixels had a small amount of water in the scene (Table 1) but ET values were not corrected for open water evaporation or the effect that presence of water would have on EVI values.

As with Landsat data, mean annual ET values for the years 2000–2009 at each site were divided into two groups: years before widearea defoliation was noted, and years after defoliation was noted. Data for mean values across pixels at each site were then subjected to two-way analysis of variance (ANOVA) (Stevens, 1996) with Site and Before/After defoliation as categorical variables. Sites were defined as the six river systems for which pixels were collected. Individual pixels represented non-overlapping and non-adjacent sample points within each site. Variances in pixel values within each of the six sites showed no significant departure from normality by the

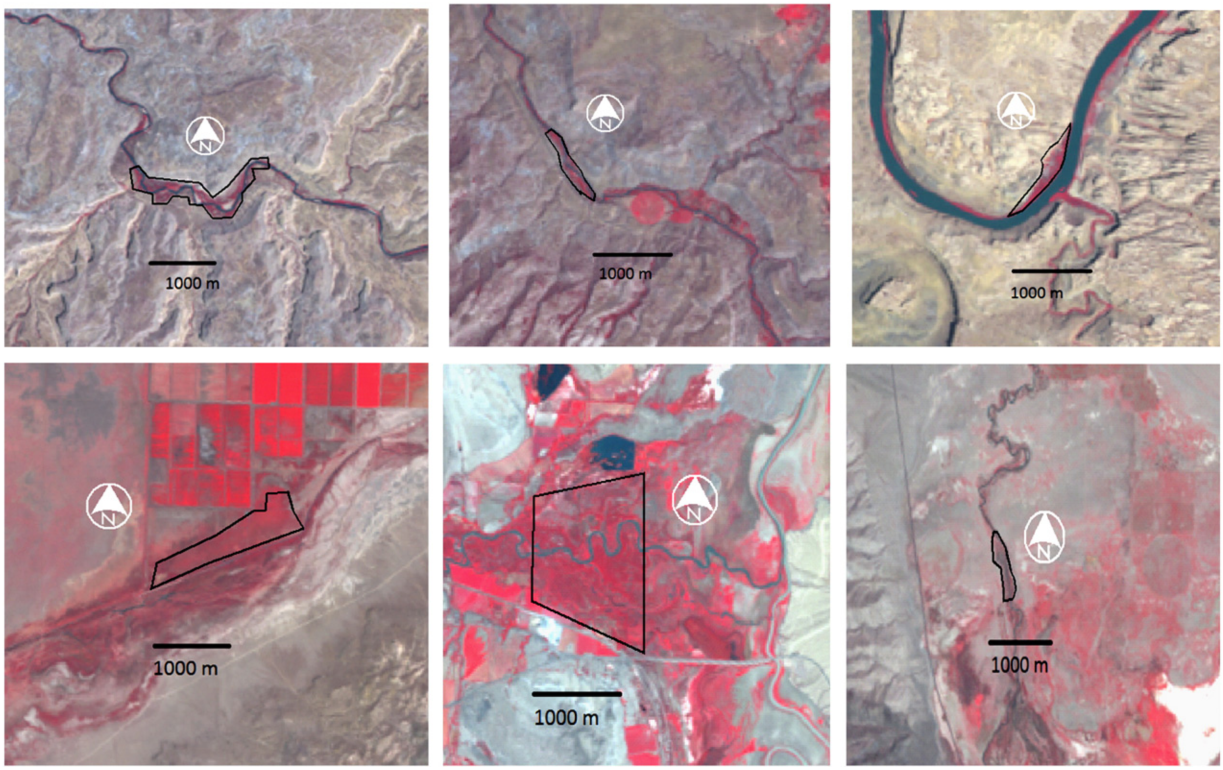

Fig. 4. Beetle release sites and areas of initial damage delineated on Landsat TM 5 images on six river systems. Top row, left to right: Lower Dolores River, Middle–Upper Dolores River, Upper Colorado River. Bottom row, left to right: Humbolt River, Big Horn River, Walker River.

Shapiro–Wilk's test ($p>0.05$), so they were treated as replicates samples of ground conditions within each site.

2.6. Test of ET estimates

Remote sensing estimates of ET are subject to several sources of error and uncertainty and should be compared to other, independent, measurements of ET whenever possible (Glenn et al., 2008). The MODIS-based method used in this study is subject to error due to the large pixel size which does not necessarily re-sample the same footprint area at each satellite overpass (Tan et al., 2006), while the Landsat 5 method provides only a single, snap-shot estimate of ET that must be extrapolated to an annual ET rate by assuming that it is representative of the entire growing season. Furthermore, all VI-based methods are based on the assumption that stomatal conductance can be treated as a constant at daily time steps (Glenn et al., 2007), whereas stress effects can differentially affect stomatal conductance of stands of *Tamarix* growing at the same location (Nagler et al., 2009a, 2009b). Finally, remote sensing methods for ET are only as accurate as the ground methods by which they are calibrated or validated, and ground methods are subject to errors ranging from 10 to 30% (Glenn et al., 2007; Allen et al., 2011).

In this study, we compared MODIS and Landsat ET values with independent results obtained by sap flux sensors in 2004 at the Humbolt River site (Pattison et al., 2011). In that study, transpiration by individual plants was monitored from May 8 to September 29 at approximately monthly intervals during a period of intense defoliation. Pattison et al. (2011) reported that transpiration on a stand area basis averaged 1.85 mm d^{-1} over the study, and they plotted transpiration normalized to ET_0 on a monthly basis. We re-plotted those data in units of ET in mm d^{-1} to compare with ET values for the time period calculated by Eq. (5) (Landsat) and Eq. (9) (MODIS).

3. Results

3.1. Phenology of defoliation on the Dolores River

Estimates of lost leaf production from visible-band and NDVI camera were similar across years and sites: 32.0% and 30.8% per season, respectively ($F=0.05$, $p=0.838$, $df=1,10$) (Table 3). Gauge and Orchard canopies produced similar results: 29.7% and 33.1%, respectively ($F=0.39$, $p=0.548$, $df=1,10$). Reduced productivity was significantly higher in 2010 (40.9%) than in 2008 and 2009 (26.6%) ($F=8.29$, $p=0.009$, $df=2,9$). However, no reduction in peak green cover or NDVI was noted at either tower site over the three study years (Fig. 3).

Similar patterns of defoliation followed by regeneration of new leaves each season were noted at the Middle–Upper Dolores River site (Fig. 5). The 2008 DOY 252 survey showed that shrubs had re-greened following early season defoliation by beetles; shrubs were still dormant in 2009 DOY 96–97 but had equal amounts of brown and green leaves from DOY 172–188 during defoliation; they then recovered by DOY 252 and had >70% leaf cover the following year (2010 DOY 181).

3.3. Impact of the leaf beetles based on Landsat ET estimates

The coefficient of variation (CV) for $NDVI_{Max}$ was low among image series, ranging from 3.0 to 4.2%, while the CV for $NDVI_{Soil}$ was higher (7.9–26.0%). The use of NDVI* rather than NDVI is designed to minimize soil effects on ET estimates (Baugh & Groeneveld, 2006). Landsat-based ET estimates are in Fig. 6. ET rates tended to be variable year-to-year and differed markedly among sites. The lowest ET rates were at the Lower Dolores River site (100–350 mm yr^{-1}), while rates were as high as 600–800 mm yr^{-1} at the Humbolt River and Big Horn River sites. All sites except for the Middle–Upper Dolores River site showed a marked reduction in ET during the first year of active defoliation (arrows in Fig. 6), The Middle–Upper

Table 3
Estimated reduction in green leaf cover and NDVI*$_{PC}$ due to *Tamarix* leaf beetle activity at two sites on the Lower Dolores River monitored visible-band and NDVI-phenocams.

Year	Gauge site visible-band camera % green cover reduction	Orchard site visible-band camera % green cover reduction	Gauge site NDVI camera % NDVI*$_{PC}$ reduction	Orchard site NDVI camera % NDVI*$_{PC}$ reduction
2008	27.2	33.3	23.4	31.9
2009	20.9	24.1	32.1	20.1
2010	44.4	41.8	30.2	47.1
Mean	30.8 (7.2)	33.1 (5.2)	28.6 (2.7)	33.0 (8.0)

Dolores River site had a mixed riparian community whereas the other sites were dominated by *Tamarix*. All sites showed at least a partial recovery in subsequent years, and at the Humbolt River site the highest ET rates over the decade were in post-release years. Early and late season images acquired in 2010 showed lower early season ET compared to late season ET at the Humbolt and Big Horn River sites, possibly due to beetle effects, but early and late season images were similar at the other sites.

When sites were analyzed individually, only the Upper Colorado River site had a significant ($p = 0.002$) decrease in ET after beetle release (Table 4). However, a two-way ANOVA showed that ET was significantly different among sites ($p < 0.001$) and was higher before beetles release than after ($p = 0.024$) across sites. The interaction term (Site x Before/After) was not significant ($p = 0.331$). Annual ET was 394 mm yr^{-1} before beetle release and 335 mm yr^{-1} after release, 15% lower. The results are consistent with concurrent ground observations at the Lower Dolores River site and the Middle–Upper Dolores site, which showed that defoliation was relatively brief each year and did not affect all plants.

3.3. Impact of leaf beetles based on MODIS ET estimates

MODIS-based ET estimates are in Figs. 7 and 8. Results were similar in magnitude and direction to those from Landsat estimates. Baseline ET values varied widely over sites, from peak summer rates of just 2 mm d^{-1} on the Middle–Upper Dolores River site, to 6–8 mm d^{-1} at the Humbolt River site, where peak *Tamarix* ET was equal to ET$_0$ in some years. ANOVA results (Table 5) were significant by both Site ($p < 0.001$) and Before/After defoliation ($p = 0.031$), but the interaction term was also significant ($p = 0.03$). Hence, a one-way ANOVA with Before/After defoliation as the categorical variable was also conducted for each site. ET was significantly lower at the Upper Colorado River, Walker River and Humbolt River sites in years after defoliation, but differences were not significant ($p > 0.05$) at Dolores River or Big Horn River sites. Over all sites, mean annual ET was 314 mm yr^{-1} before beetle infestation (about 23% of ET$_0$), and 269 mm yr^{-1} after infestation, a 14% reduction. MODIS ET estimates were 15% lower than Landsat ET estimates across sites and years.

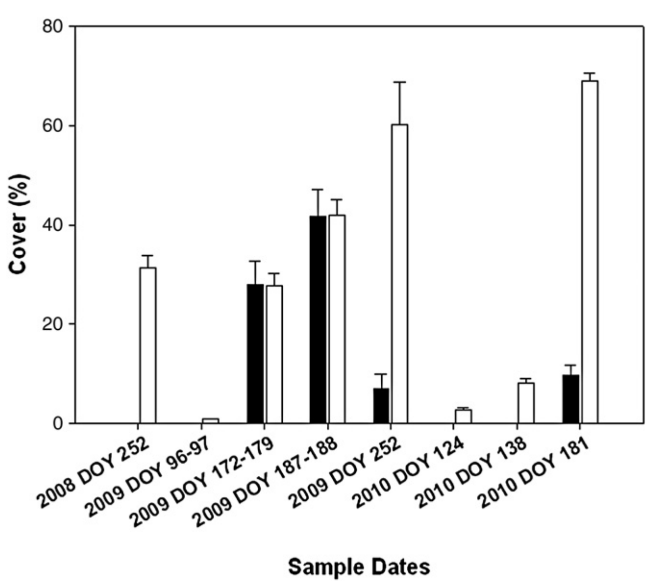

Fig. 5. Visual field estimates of percent green (white bars) and brown (black bars) leaf cover estimated for *Tamarix* shrubs at eight sites along the Middle–Upper Dolores River. Error bars are standard errors of 100 shrubs at each site.

3.4. Test of methods: comparison of ET estimates at the Humbolt River site

MODIS ET and Landsat ET estimates for 2002 and 2004 at the Humbolt River site were compared with sap flux ET estimates conducted by Pattison et al. (2011) in 2004 (Fig. 9). In 2002, before widespread defoliation, MODIS ET increased steadily over the early season, reaching 5.5 mm d^{-1} by DOY 230 (August 18). The trend began the same in 2004, but ET decreased after DOY 170 (June 19) due to defoliation of leaves by beetles. Point estimates of ET by Landsat images on DOY 174 (June 23), 2002, and DOY 196 (July 15), 2004, fell on the same trend line as MODIS ET estimates. Sap flux ET measurements made on four plants per measurement period showed a more rapid greening of plants in spring than MODIS estimates, but estimates were similar from DOY 185–280 (July 4–October 7), showing a marked reduction in ET due to beetle effects.

4. Discussion

4.1. Impacts of beetles on Tamarix stands

A common pattern of beetle effects was seen across the sites in this study. After an acclimation period of one to several years, beetles engaged in wide-spread defoliation at each site, followed by a recovery in green leaf cover and ET in subsequent years. Ground studies at the Lower and Middle–Upper Dolores River sites showed that beetles remained active in post-release years, but overall site ET was not markedly reduced because beetle damage was patchy and temporary, with shrubs re-greening in late summer following the annual period of defoliation. The phenocam results at the Lower Dolores River site showed that beetles reduced annual leaf cover by about 30% for individual canopies. However, because not all *Tamarix* canopies are affected and because plants other than *Tamarix* grow in the riparian zones, actual reductions in leaf cover and ET were on the order of 14–15% across sites as determined by MODIS and Landsat imagery, respectively. Phenocam results at the Lower Dolores site and field survey results at the Middle–Upper Dolores site confirm that plants can regreen each year despite multiple years of beetle damage.

Tamarix spp. and *Diorhabda* spp. coevolved in Eurasia, hence it is logical to conclude that they will eventually develop stable equilibrium conditions in the western U.S. At present it is not possible to predict the eventual equilibrium state, or how higher trophic levels and avian habitat value will be impacted. Beetle numbers might ultimately be controlled by insect-eating predators, a process that has not yet been studied on these river systems.

Annual recovery of *Tamarix* following seasonal defoliation might not continue indefinitely. Due to lack of overbank flooding, recruitment of new *Tamarix* plants and replacement vegetation is often low (Nagler et al., 2010a). Even a low rate of mortality of shrubs from beetle damage might eventually reduce vegetation cover along these rivers, and active restoration might become necessary. Hence, close monitoring of leaf beetle–*Tamarix* interactions using both ground and remote sensing methods will be needed for the foreseeable future, because restoration and mitigation measures might be necessary to

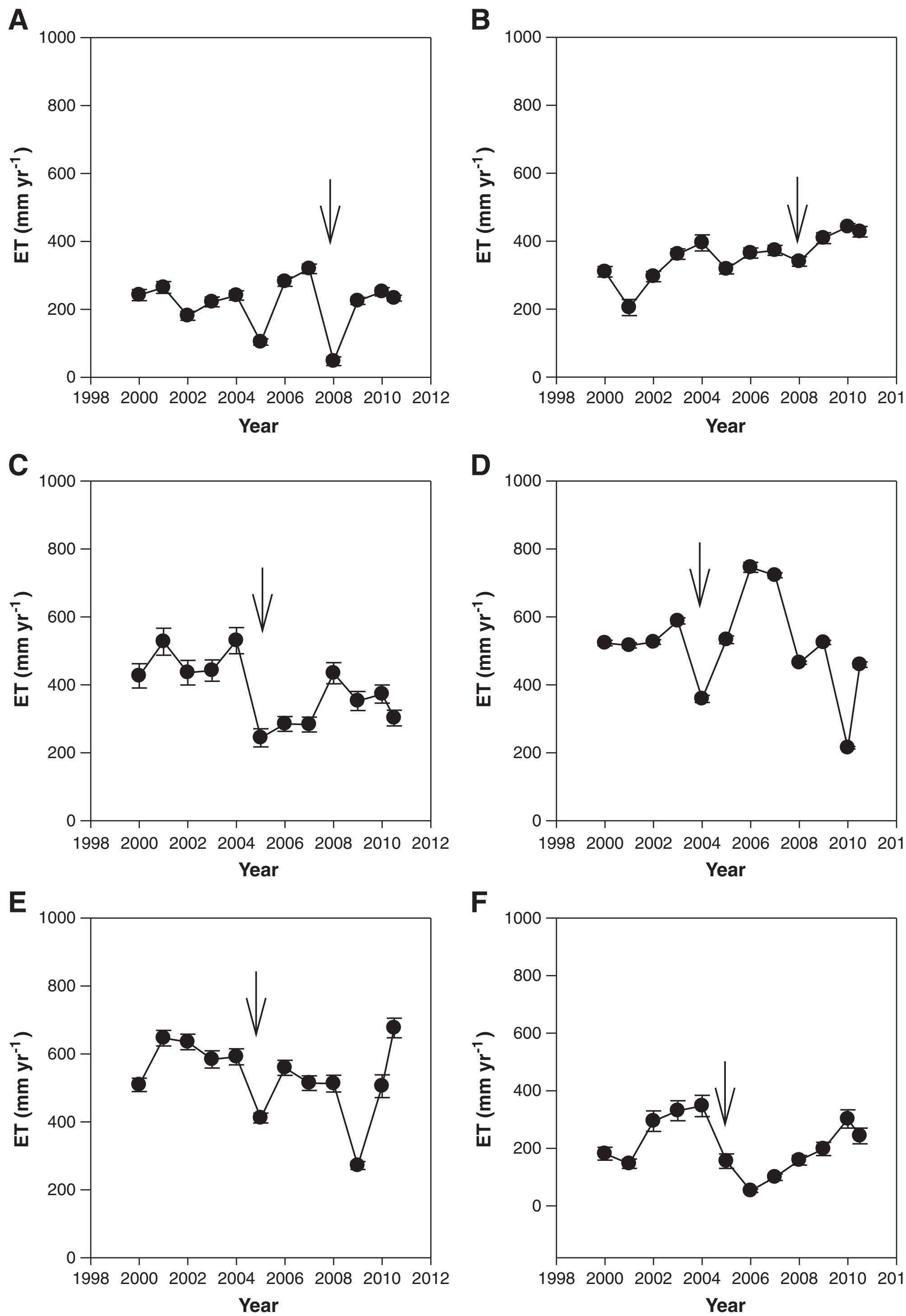

Fig. 6. Landsat TM 5 ET estimates for beetle release sites on each river. Arrow shows the first year widespread defoliation that was noted in field surveys. Error bars are 95% confidence intervals.

preserve (or improve) riparian habitat values under the new conditions that exist on western rivers.

4.2. Comparison of ET results with other ET studies

The MODIS and Landsat ET estimates are not direct measurements of plant water use; rather they are empirical estimates based on the correlation between green leaf density measured by EVI* and NDVI* and potential water use based on ET_0 (Glenn et al., 2010; Groeneveld et al., 2007; Kalma et al., 2008). This approach to estimate ET is appropriate for quantifying the potential impacts of leaf beetles on riparian water budgets, because they are based on the reduction in leaf area that can be attributed to beetles, as measured by vegetation indices. The disparity between Landsat and MODIS estimates of ET across sites (15% difference) was within the range of errors and uncertainties typically encountered in cross-comparisons of remote sensing and ground methods for estimating ET over wide areas in other studies (e.g., Kalma et al., 2008). The two methods used similar algorithms based on ET_0, but different satellite sensors and different sets of ground data for calibration. The ET

Table 4
Means, standard errors (in parentheses), and ANOVA statistics for ET measured each year by Landsat imagery in *Tamarix* stands before and after beetle infestation (2000–2010) on western U.S. river systems.

Site	ET before mm yr^{-1}	ET after mm yr^{-1}	F	p	df
Lower Dolores	232 (17)	149 (102)	1.69	0.23	1,10
Middle–Upper Dolores	328 (21)	370 (39)	1.10	0.32	1,10
Upper Colorado	472 (23)	325 (25)	17.6	0.002	1,10
Bighorn	551 (24)	484 (117)	0.81	0.39	1,10
Humbolt	538 (17)	503 (62)	0.15	0.70	1,10
Walker	242 (37)	176 (37)	1.60	0.24	1,10
Mean	394 (59)	335 (61)			
Two-way ANOVA					
Before/after			5.37	0.024	1,59
Site			20.0	<0.001	5,59
Interaction			1.18	0.331	5,59

estimates were also similar to those made on individual plants by Pattison et al. (2011) in 2004 at the Humbolt River site. The earlier spring onset of ET observed in the sap flux results compared to the MODIS results was due to the fact that plants that already had green leaves were chosen for early-season sap flux measurements in the Pattison et al. (2011) study, whereas the satellite data included both green and non-green canopies.

The Pattison et al. (2011) study projected ET values of 518 mm yr^{-1} pre-release (based on NDVI data) and 269–296 mm yr^{-1} for 2004 and 2005 (based on sap flux data) at the Humbolt River site, for an estimated ET reduction of 45%. Our annual estimates for 2002 (before defoliation) and 2004 (during defoliation) by MODIS were 437 mm yr^{-1} and 234 mm yr^{-1}, respectively, for a 46% reduction. Given the difference in methods and sampling strategies, satellite and ground methods give convincingly similar estimates of the magnitude of ET and the effect of beetles at this site. Our estimate of ET for

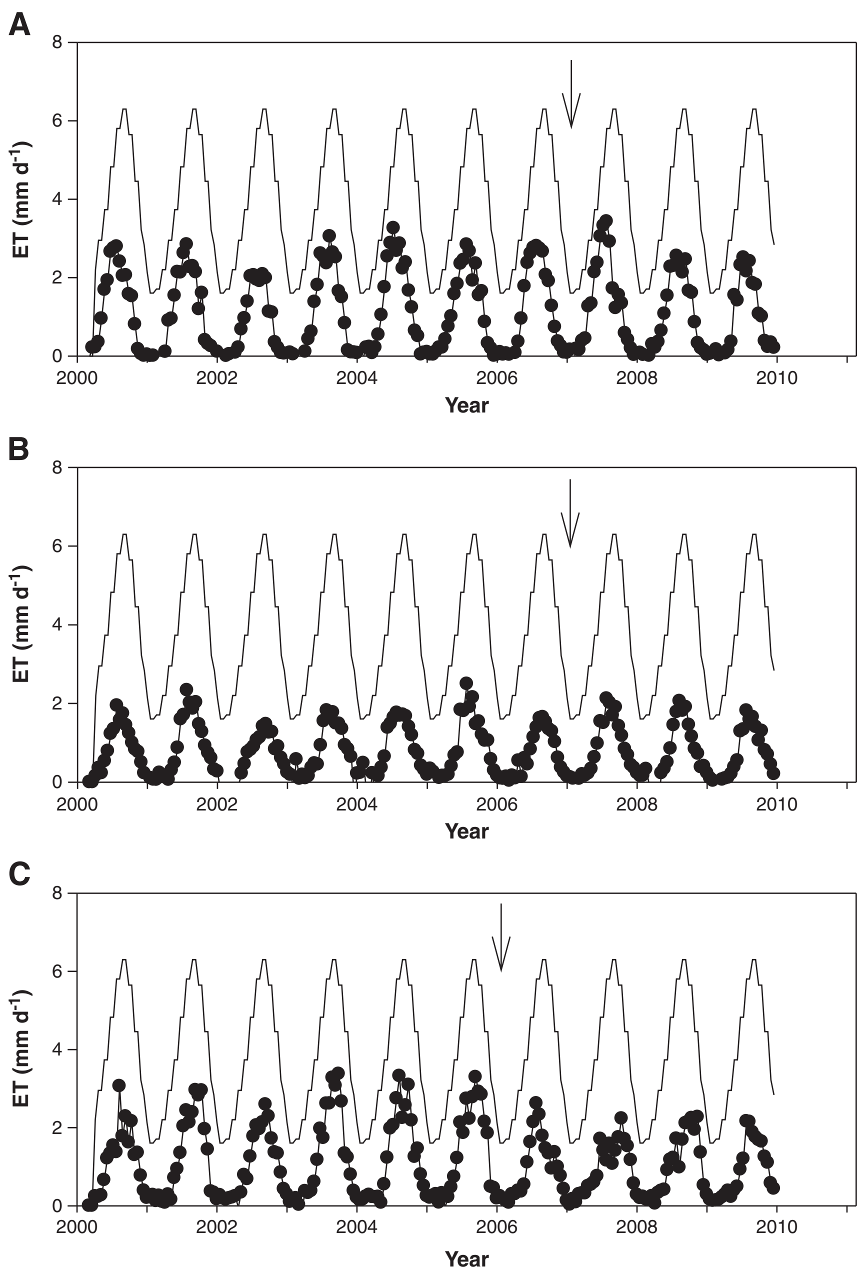

Fig. 7. MODIS ET estimates for beetle release sites on the Lower Dolores River (A), the Middle–Upper Dolores River (B) and the Upper Colorado River (C). Arrows show the first year widespread defoliation that was noted in field surveys. Solid line without symbols shows ET_0 at each site.

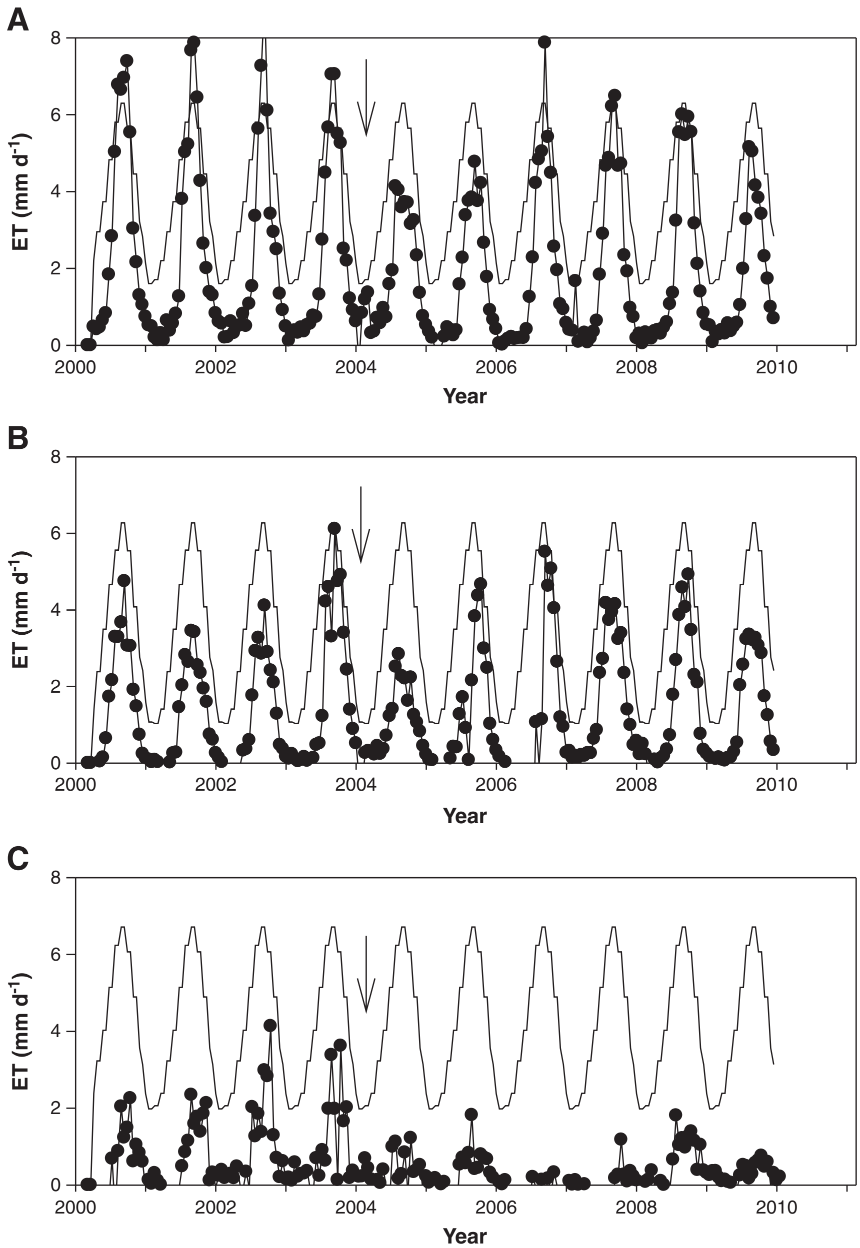

Fig. 8. MODIS ET estimates for beetle release sites on the Humbolt River (A), the Big Horn Riverr (B) and the Walker River (C). Arrows show the first year widespread defoliation that was noted in field surveys. Solid line without symbols shows ET_0 at each site.

Table 5
Means, standard errors (in parentheses), and ANOVA statistics for ET measured each year by MODIS imagery in *Tamarix* stands before and after beetle infestation (2000–2009) on western U.S. river systems.

Site	ET before mm yr^{-1}	ET after mm yr^{-1}	F	p	df
Lower Dolores	270 (12)	251 (11)	0.702	0.406	1,48
Middle–Upper Dolores	224 (15)	232 (23)	0.203	0.653	1,88
Upper Colorado	349 (12)	275 (9)	10.8	0.001	1,8
Walker	169 (20)	109 (13)	7.04	0.029	1,8
Humbolt	587 (30)	466 (19)	11.4	0.002	1,28
Bighorn	282 (23)	275 (35)	0.041	0.846	1,8
Mean	314 (60)	269 (47)			
Two-way ANOVA					
Before/after			4.73	0.031	1,188
Site			66.5	<0.001	5,188
Interaction			2.54	0.030	5,188

2009–2010 at the Lower Dolores River site was 250 mm yr^{-1} by MODIS, similar to the 200 m yr^{-1} estimate determined from sap flux data at the same site during that period (Hultine et al. (2010a,b)).

The results of our study also support other research (e.g., Dennison et al., 2009) which has shown that water salvage due to defoliation of *Tamarix* by leaf beetles might be lower than previously expected. Defoliation reduced annual ET by only 14–15% on average, although it was higher at some sites than at others. The opportunities for regional water salvage were also constrained by the low baseline value for ET at most sites, which averaged only 200–400 mm yr^{-1} across river systems or 15–25% of ET_0 (ca. 1500 mm yr^{-1} across sites). Early projections of large water savings were based on assumed high rates of annual ET by *Tamarix* (e.g., Zavaleta, 2000) but these have not been supported by recent ET measurements (reviewed in Nagler et al., 2010b).

ET rates on these upper basin streams and rivers were lower than have been reported for lower-elevation sites in the southwestern U.S.

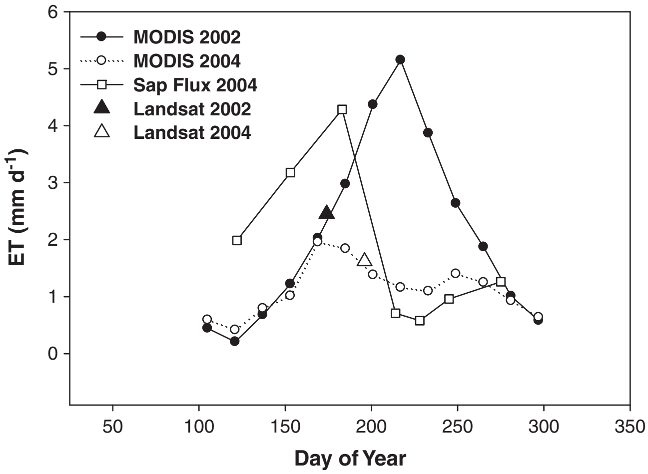

Fig. 9. Comparison of ET estimates for the Humbolt River site by MODIS and Landsat in 2002 and 2004, and by sap flux sensors in 2004 as reported in Pattison et al. (2011).

(Murray et al., 2009; Halter & Hart, 2009). These ET rates are at the low end of rates recorded for other riparian species (Nagler et al., 2005a, 2005b, 2009a, 2009b, 2010b); hence, any replacement vegetation would further reduce the small amount of water salvage that could occur due to leaf beetle activity.

4.3. Utility of remote sensing methods for monitoring Tamarix/beetle interactions

No single remote sensing tool was sufficient for monitoring beetle effects. Phenocams provided detailed canopy-level observations at a daily time step, and were able to capture the defoliation and recovery periods each year. However, it would be expensive to deploy enough cameras to characterize the defoliation process over a wide area. Furthermore, digital-number NDVI values differed among cameras because red and NIR bands were not intercalibrated, and visual interpretation of images actually provided more information than NDVI*$_{PC}$ plots, because the results were in physiologically meaningful units (% green cover) rather than relative units (NDVI*$_{PC}$). Landsat had adequate resolution to detect stand-level insect damage, but it was difficult to obtain enough imagery to plot seasonal changes in leaf phenology due to the 16-day return time of the satellite. MODIS gave similar results to Landsat and provided better temporal coverage, and it was able to track the time course of beetle damage over a season when insect damage was heavy (Fig. 9), but the coarse resolution made it impossible to detect the spatial distribution of defoliation within a site. Furthermore, some riparian areas, such as sites on the Dolores River sites, were narrower than the resolution of a MODIS pixel, and contained water as well as vegetation in the pixel area, introducing a source of error into the analyses. Neither Landsat nor MODIS was able to reliably detect the light levels of damage that characterized most of the sites after the first year of defoliation.

Tan et al. (2006) cautioned against relying on single-pixel MODIS analyses to build a record of remote sensing observations over time, as we used in this study. They pointed out that the average overlap of the footprint area of a MODIS pixel between sampling dates was only 30%, and recommended using larger arrays of pixels to minimize gridding errors. However, the narrow, irregular shape of some of the riparian zones in this study precluded the use of a wide pixel array. Kim (2006) correlated pixel arrays from MODIS (250 m resolution) and from the Airborne Visible/Infrared Imaging Spectrometer (4 m resolution) with ET measured at moisture flux towers at riparian and upland sites in southeastern Arizona. Pixel arrays with footprint areas ranging from 144 m^2 to 921,600 m^2 were tested. Best results were obtained with arrays of 5600 m^2 (approximately one MODIS pixel) and 22,400 m^2 (4 MODIS pixels), at all sites. Nagler et al. (2005a, 2005b) correlated single MODIS EVI pixels with flux tower ET to develop algorithms for ET three western rivers, with $r^2 = 0.76$ across sites and river systems. However, some of the river reaches in the present study were narrower than those measured in Nagler et al. (2005a, 2005b), and some error was undoubtedly introduced by the incongruitous between MODIS pixels and the width of some of the riparian corridors.

We conclude that by combining different remote sensing tools it is possible to obtain an overview of *Tamarix*/beetle interactions on western U.S. rivers. However, as with other studies that used remote sensing to assess insect damage in forests (e.g. Eklundh et al., 2009), we were not able to monitor the details of defoliation at any given site even with a combined approach. Beetle damage so far is patchy and temporary in most stands, making it difficult to correlate remote sensing data with beetle effects on ET or leaf phenology. Remote sensing data should be combined with ground observations to develop operational monitoring protocols.

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