

# Saltcedar (*Tamarix ramosissima*) invasion alters organic matter dynamics in a desert stream

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## SUMMARY

1. We investigated the impacts of saltcedar invasion on organic matter dynamics in a spring-fed stream (Jackrabbit Spring) in the Mojave Desert of southern Nevada, U.S.A., by experimentally manipulating saltcedar abundance.
2. Saltcedar heavily shaded Jackrabbit Spring and shifted the dominant organic matter inputs from autochthonous production that was available throughout the year to allochthonous saltcedar leaf litter that was strongly pulsed in the autumn. Specifically, reaches dominated by saltcedar had allochthonous litter inputs of 299 g ash free dry mass (AFDM) m<sup>-2</sup> year<sup>-1</sup>, macrophyte production of 15 g AFDM m<sup>-2</sup> year<sup>-1</sup> and algal production of 400 g AFDM m<sup>-2</sup> year<sup>-1</sup>, while reaches dominated by native riparian vegetation or where saltcedar had been experimentally removed had allochthonous litter inputs of 7–34 g AFDM m<sup>-2</sup> year<sup>-1</sup>, macrophyte production of 118–425 g AFDM m<sup>-2</sup> year<sup>-1</sup> and algal production of 640–900 g AFDM m<sup>-2</sup> year<sup>-1</sup>.
3. A leaf litter breakdown study indicated that saltcedar also altered decomposition in Jackrabbit Spring, mainly through its influence on litter quality rather than by altering the environment for decomposition. Decomposition rates for saltcedar were lower than for ash (*Fraxinus velutina*), the dominant native allochthonous litter type, but faster than for bulrush (*Scirpus americanus*), the dominant macrophyte in this system.

*Keywords:* allochthonous, autochthonous, desert stream, decomposition, *Tamarix*

## Introduction

Although anthropogenic biological invasions are one of the most pervasive features of global change (Allan & Flecker, 1993; Lodge, 1993; Vitousek *et al.*, 1996), how such invasions impact biological communities and ecosystem processes is often poorly understood. The effective management and restoration of invaded habitat requires such understanding, however.

Saltcedar [*Tamarix ramosissima* (Ledeb)], a tree native to Eurasia, was brought to North America in the mid-1800s by nurseries for use as an ornamental and to prevent erosion in arid regions. Saltcedar was

first collected in the wild in Texas in 1877 (Everitt, 1980; Brotherson & Winkel, 1986). Although the spread of saltcedar was initially slow, its range expanded rapidly during the 1930s (Everitt, 1980). It is currently the dominant tree along many rivers of the western United States, covering over 600 000 ha of this habitat (DiTomaso, 1998). In addition to its geographically broad distribution, saltcedar spans a large range of altitudes, from below sea level in California to above 2000 m in Colorado (Everitt, 1980).

Much of the previous research on saltcedar has focused on its water use relative to native plant species (Van Hylckama, 1970; Everitt, 1980; Busch & Smith, 1995; Sala, Smith & Devitt, 1996), its displacement of native vegetation (Robinson, 1965; Everitt, 1980; Busch & Smith, 1995) and the use of saltcedar by native terrestrial fauna (Hunter, Ohmart & Anderson, 1988; Ellis, 1995; Manning, Cashore &

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Szewczak, 1996). Virtually no published research has addressed the impacts of saltcedar on the aquatic environment.

Ecosystem dynamics of running waters, particularly small streams, are tightly linked to their riparian vegetation which determines the nature, timing and quality of organic matter inputs into streams (Hynes, 1975; Vannote *et al.*, 1980; Naiman & Decamps, 1997; Wallace *et al.*, 1997, 1999). Thus, the widespread invasion of saltcedar along streams of the southwestern United States has probably altered the food webs of these aquatic systems. Our objective was to determine whether saltcedar invasion alters the nature, timing and quality of organic inputs that serve as the base of the aquatic food web in a desert spring-fed stream of the southwestern United States.

Along a single stream we quantified organic matter inputs for sites where the riparian zone was characterised by different types of vegetation: sites that were dominated by saltcedar, sites where saltcedar was experimentally removed and sites that were dominated by intact native vegetation. Breakdown of saltcedar litter was also compared with that of the dominant native riparian species and related to initial litter chemistry. We also determined whether saltcedar is altering the environment for decomposition in this stream.

## Methods

### Research site

This work was conducted in Jackrabbit Spring (36°23.379'N, 116°16.278'W) at Ash Meadows National Wildlife Refuge. Ash Meadows is a desert wetland comprising a dozen springs and over twenty seeps that is located about 20 km east of Death Valley in the Mojave Desert of Nevada. The aquatic habitats of Ash Meadows support numerous threatened and endangered species including the Ash Meadows speckled dace [*Rhinichthys osculus nevadensis* (Girard)] and the Ash Meadows pupfish [*Cyprinodon nevadensis mionectes* (Miller)] (Soltz & Naiman, 1978).

Jackrabbit Spring supports both invasive saltcedar and native riparian vegetation, providing a reference for determining the impact of saltcedar. Furthermore, Jackrabbit Spring is sufficiently small to enable an ecosystem-scale manipulation of saltcedar abundance (see Experimental design).

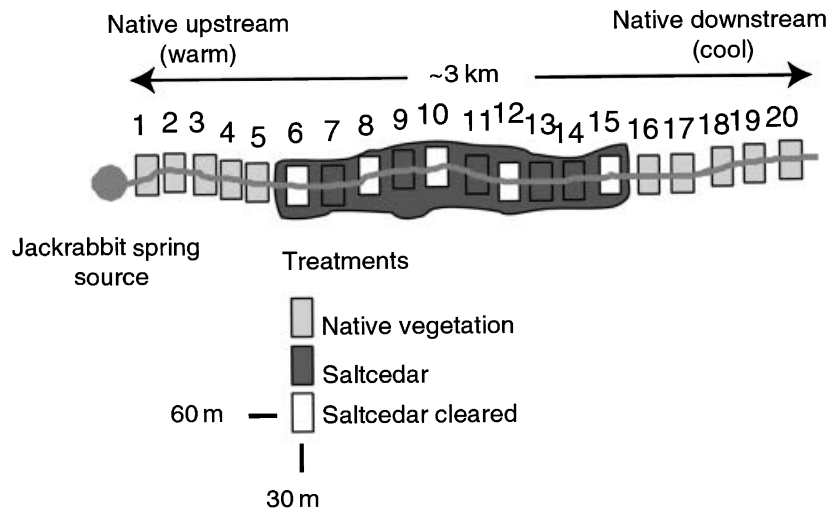
### Stream description

Jackrabbit Spring has an approximately constant discharge of 47 L s<sup>-1</sup> at a temperature of 28 °C. There is a strong downstream temperature gradient, the magnitude of which varies seasonally (Kennedy, 2002). For example, mean daily temperature upstream is 27.8 °C in January and 28.0 °C in June (daily range <1 °C) while average daily temperature downstream is 15.9 °C in January and 22.8 °C in June (daily range between 5–10 °C, depending on season). The limestone geology of the Ash Meadows groundwater basin results in high conductivity (770–790 µS cm<sup>-1</sup>) and high pH (approximately 7.6–8.3; Kennedy, 2002). Nitrate concentration in Jackrabbit Spring declines steadily from up to downstream (from 11.23 to 7.02 µM) and soluble reactive phosphate concentration is extremely low (<0.05 µM, below analytical detection-limit) throughout the stream and during all seasons (Kennedy, 2002).

Native vegetation plots have dense concentrations of bulrush [*Scirpus americanus* (Pers.)] emerging from the stream and along the stream margin. Scattered ash [*Fraxinus velutina* (Torrey)] and mesquite [*Prosopis pubescens* (Benth.)] trees lead to an open canopy above the stream at these sites. In contrast, bulrushes are rare at saltcedar sites where the canopy is closed.

### Experimental design

Twenty 30 × 60 m research plots were established in June 1998 along the creek that is fed by Jackrabbit Spring (Fig. 1). The five furthest upstream and five furthest downstream plots were located in native riparian vegetation while the ten middle plots were located in the saltcedar reach. The minimum distance between plots in the saltcedar reach was 20 m while native vegetation plots were at least 30 m apart. In the winter of 1999 saltcedar was removed from five of the 10 plots dominated by saltcedar using the 'cut-stump' method (Reinartz, 1997): saltcedar trees were cut at the base using a chainsaw, dragged off the plot and stumps were sprayed with Garlon IV® herbicide (Dow Agro Sciences, Indianapolis, IN, U.S.A.) within 10 min of cutting. Clearing treatments were maintained by spraying re-sprouting saltcedar with herbicide at least twice per year. In order to control for the known downstream gradient in temperature we paired each saltcedar plot with an adjacent cleared



**Fig. 1** Schematic of Jackrabbit Springs study site. Plot numbers are listed above each plot. Schematic is not to scale; the minimum distance between cleared and saltcedar plots is 20 m while the minimum distance between native vegetation plots is 30 m.

plot. We randomly selected the upstream plot of each pair as the one to clear. However, saltcedar stands in plots 12–14 were extremely large and limited resources and time made clearing them impractical, as dictated by our experimental design. Therefore, we cleared the downstream plot of the final pairing, i.e. plot 15 rather than 14. Prior to clearing the saltcedar, there were no differences in canopy cover or herbaceous vegetation in the stream reaches used for saltcedar and cleared saltcedar treatments (unpublished data). Thus, differences between these sites are assumed to be due to treatment effects. This study design yields four riparian vegetation types (native-upstream, native-downstream, saltcedar, cleared) with five replicates of each type. Clearing native vegetation was not possible because of the two endangered fish present in Jackrabbit Spring; we were only permitted to remove exotics.

#### *Photosynthetically active radiation*

To determine if the dense canopy of saltcedar might be shading Jackrabbit Spring more than native or cleared vegetation, Hobo® Light Intensity Loggers (Onset Corp., Bourne, MA, U.S.A.) were used at the benthos within each reach. Light meters were sealed inside Petri dishes using silicone aquarium sealant and placed in each plot for 24 h adjacent to the tiles used for net chlorophyll production (described below). A Li-Cor® Model Li 250 Light Intensity Meter (Lincoln, NE, U.S.A.) that measures Photosynthetically Active Radiation ( $\text{PAR} - \mu\text{mol m}^{-2} \text{s}^{-1}$ ) was used to convert the values of lumens  $\text{m}^{-2} \text{s}^{-1}$  recorded by

Hobo® loggers to PAR (non-linear regression,  $r^2 = 0.91$ ). Data used in analyses were the 24 h average PAR reading for each plot.

#### *Allochthonous inputs*

To quantify allochthonous inputs we secured four plastic tubs ( $0.40 \times 0.84 \text{ m}$ ,  $0.338 \text{ m}^2$  sampling area) adjacent to the stream in each plot to catch vertically falling litter (Minshall, 1996). Tubs were placed adjacent to both banks of the stream at a distance of 10 and 20 m from the upstream edge of each plot. A 5 cm diameter hole was drilled into the centre of each tub to allow water to drain.

We quantified lateral inputs using four nets that were placed next to each direct litter trap. Nets were constructed of a  $50 \times 25 \text{ cm}$  plywood base, with the long axis parallel to the stream. A  $100 \times 50 \text{ cm}$  piece of nylon window screening with a mesh size of 1 mm was secured to rebar posts at the stream side of the base forming a net with a 50 cm wide base and a height of 25 cm. Litter traps were set up on 17–19 October 1999 and the accumulated litter was collected on 6 November and 10 December 1999 and 5 January, 30 March and 20 June 2000.

#### *Autochthonous production*

Emergent macrophytes, mainly bulrush, with above ground ramets that senescent annually were extremely dense along reaches with native vegetation and are probably a major source of autochthonous organic matter. Macrophyte inputs were quantified with a

single harvest at maximum biomass of emergent plants along 0.5 m of stream length across each of two sampling transects within each plot (Wetzel & Howe, 1999). We harvested only the submerged portions of macrophytes to provide a conservative estimate of the amount of bulrush organic matter that was available for decomposition at each site. Harvesting was carried out on 10–13 December 1999 and 24 January 2002.

We used chlorophyll *a* accumulation on tiles as a proxy for algal production (Lamberti & Feminella, 1996). Chlorophyll production was measured by placing one clay tile (7.6 × 7.6 cm) into each plot on a platform that excluded invertebrate grazers (Lamberti & Feminella, 1996). Production was measured in November to December 1999 (38-day incubation), June 2000 (14 days), in April (15 days), July (12 days) and October 2001 (15 days), and January 2002 (16 days). After incubating in the stream, tiles were collected, placed into individual plastic bags and refrigerated at 4 °C. The tiles were processed within 24 h of collection by brushing the top surface of the tile with a nylon toothbrush and then rinsing the tile and the toothbrush. The slurry was then filtered onto precombusted 4.7 cm Whatman® GF/C filters (Whatman PLC, Kent, U.K.) using a hand vacuum pump and vacuum not exceeding 30 cm Hg. Filters were placed into individual 5 cm Petri dishes were covered in aluminium foil to exclude light and frozen until analysis for chlorophyll *a*, which occurred within 3 months of collection. Chlorophyll was extracted from the filters for 24 h in the dark at 4 °C in a solution of 90% acetone. The test tubes containing the filter and acetone were vigorously shaken at least three times during the extraction period. Chlorophyll *a* content was then measured on a Turner Designs® 10-AU fluorometer (Sunnyvale, CA, U.S.A.). Daily algal production was estimated as chlorophyll *a* accumulation, divided by the surface area of tiles and the incubation period. Analysis of covariance (ANCOVA) was used to determine the effects of riparian vegetation type on algal production and adjust for the downstream temperature gradient.

#### *Leaf breakdown*

Five grams of air-dried saltcedar, ash or bulrush litter were placed in 15 × 15 cm litterbags construc-

ted of fibreglass window screening with a mesh size of 1 mm. Saltcedar and ash leaves were pulled from trees after senescence but prior to abscission. Bulrush litter was obtained by clipping the emergent tops of senescent ramets. Seven bags of each litter type were placed in each of the 20 plots on 2 November 1999. Within each plot, litterbags (one per litter type) were connected in strings of three and fastened to the stream bottom using survey flags. The order of litter types on these strings was randomised. One string was collected from each plot after 1, 3, 7, 14, 33, 60 and 144 days in the stream. An additional set of five bags of each litter type were strung together and carried into the field but never placed in the stream to quantify mass loss from handling and to develop air-dried to oven-dried mass conversions. Upon collection, litterbags were placed into individual plastic bags, stored at 4 °C and processed within 24 h by placing litter in a 250 µm sieve and gently rinsing the litter of debris. Leaf litter was dried (65 °C) and weighed. Subsamples (1 g) of ground litter from each bag were combusted at 550 °C for determination of ash free dry mass (AFDM).

To adjust for the known downstream gradient in water temperature, degree-days were used as the predictor of AFDM remaining (Benfield, 1996). Onset® Optic temperature data loggers (Onset Corp., Bourne, MA, U.S.A.) in plots 2, 8, 10, 16 and 20 recorded water temperature to within 0.1 °C every hour for the duration of the experiment. To estimate the temperature at sites without data loggers, we collected temperature profiles of the stream by measuring the temperature at all 20 plots, starting at the upstream end, at 6 am, noon and 6 pm on three different days. These profiles were used to develop regressions for calculating the temperature at plots lacking data loggers based on the temperature at the closest upstream and downstream sites with data loggers. Degree-days were calculated by summing the average daily water temperature at each site over each incubation period (Benfield, 1996).

Decay constants (*k*) were calculated for each litter type at each of the 20 plots assuming simple negative exponential decay (Olson, 1963):

$$\ln M_t/M_0 = -kt$$

where  $M_t$  is the litter mass at time  $t$  and  $M_0$  is the initial litter mass. The effects of both riparian veget-

ation and litter types on decay constants were compared using two-way ANOVA.

There is a positive relationship between leaf decay rates and invertebrate feeding preferences (Webster & Benfield, 1986). Therefore, we used differences in decay rates among litter types to make inferences about the relative 'quality' of litter types as a food resource for aquatic consumers. That is, we assumed that leaf litter with a faster decay rate was a better 'quality' food resource than leaf litter with a slower decay rate.

Initial samples of litter were analysed for carbon fractions (Ryan, Melillo & Ricca, 1990) at the Center for Water and the Environment (National Resources Research Institute, University of Minnesota, Duluth, MN, U.S.A.). Fractions measured included water solubles (WS: amino acids, simple sugars, soluble phenolics), acid-solubles (AS: cellulose, hemicellulose, starch, polypeptides, nucleic acids), lignin, WS polyphenols as tannin, WS polysaccharides as percent glucose equivalents and AS polysaccharides as percent glucose equivalents. Initial samples of litter were also analysed for elemental composition (silica, magnesium and sodium) using Inductively Coupled Plasma-Mass Spectrometry at the Research Analytical Laboratory (University of Minnesota, Twin Cities, MN, U.S.A.). Percent nitrogen for all litter samples used in the experiment were determined on a Carbon-Hydrogen-Nitrogen (CHN) auto-analyser (Carlo Erba Instruments, Milan, Italy). The percentage nitrogen remaining was determined by multiplying the percent nitrogen for a sample by the initial sample mass.

## Results

### *Photosynthetically active radiation*

Average daily PAR values for saltcedar sites were lower than PAR values at all other riparian vegetation types, at all times measured except for native-upstream sites in January 2002 (Fig. 2). However, the only significant pairwise difference in light was among cleared and saltcedar sites in June 2000 (Tukey's HSD,  $P < 0.05$ ). Saltcedar sites were the only riparian vegetation type where average PAR values were actually higher in January ( $12.9 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) than in October ( $8.0 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

### *Allochthonous inputs*

Allochthonous litter inputs at saltcedar sites were an order of magnitude greater than inputs at native or cleared sites (Fig. 3; Tukey's HSD,  $P < 0.05$ ). There were no differences in lateral litter inputs across sites (Tukey's HSD,  $P > 0.05$ ). Saltcedar was the dominant allochthonous input at saltcedar sites (Table 1). Ash litter also represented a significant proportion of inputs at one saltcedar site (Table 1). Ash litter was the dominant allochthonous input at native-upstream sites, while unidentified leaf litter and plant parts constituted the dominant allochthonous input at cleared and native-downstream sites.

Allochthonous inputs across all riparian vegetation types were strongly pulsed in the autumn and early winter. At native and cleared sites, 76–91% of total

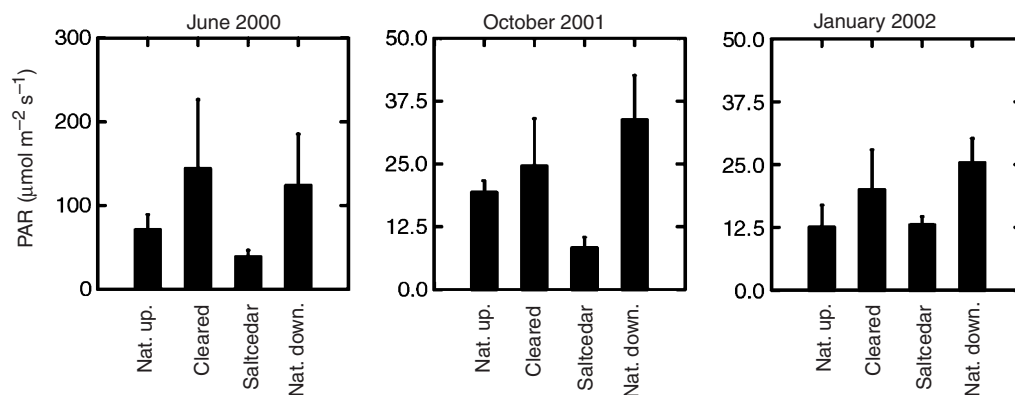


Fig. 2 Photosynthetically Active Radiation (PAR) by riparian vegetation type and time. Data represent the mean 24-h PAR value for each riparian vegetation type plus one standard error. Depth of loggers in the stream ranged from 10 to 50 cm. Note the different y-axis scale for June 2000 compared with October 2001 and January 2002.

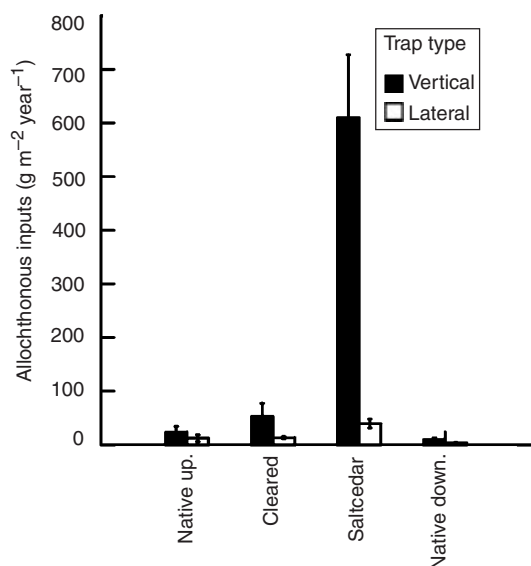


Fig. 3 Allochthonous litter inputs (sum for October 1999 to June 2000: mean + 1 SE) by riparian vegetation type and the type of trap.

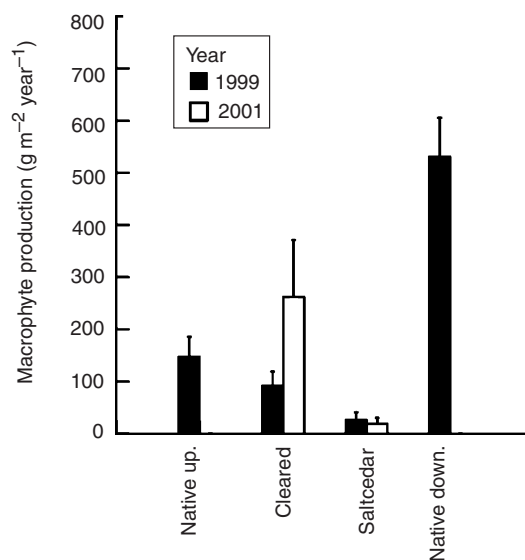


Fig. 4 Macrophyte production (mean + 1 SE) by riparian vegetation type and year. Production at native vegetation sites was only quantified in 1999 while production at cleared and saltcedar sites was quantified in both 1999 and 2001.

allochthonous inputs occurred in the 81 days covered by the first three collections (17 October to 5 January, which represents 33% of the total collection time), while at saltcedar sites 68% of total inputs occurred during this period. Further, the quantity of litter present in the June collection, after 3 months of accumulation, represented only 2% of total litter collected. Given that the riparian trees at Ash Meadows are autumn deciduous, this suggests that the quantity of litter missed during the July to October 2000 period was relatively small.

#### Autochthonous production

Saltcedar invasion also reduced macrophyte production in Jackrabbit Spring (Fig. 4). Macrophyte production was significantly lower at saltcedar sites

compared with all vegetation types during both 1999 and 2001 (Tukey's HSD,  $P > 0.05$ ). In 2001, macrophyte inputs had increased threefold in cleared sites, relative to 1999, while macrophyte inputs at saltcedar sites were essentially unchanged. Bulrush constituted the bulk of macrophyte inputs across all sites (97.6% of total mass), while cattails [*Typha domingensis* (Pers.)], the only other type of macrophyte present at any of our sampling locations, was a minor component of inputs at several sites.

Saltcedar's closed canopy also affected organic matter inputs to the stream by limiting algal production (Fig. 5). Across all time intervals chlorophyll production rates at cleared sites were higher than saltcedar sites. Shortly after clearing, in November 1999 and June 2000, cleared sites showed highly significant, threefold greater algal production relative

Table 1 Allochthonous inputs by category and vegetation type. 'Other' was dominated by grass and forb leaves. Data presented are the oven-dried mass of organic matter in grams  $\pm$  1 SE (per cent of total)

Riparian vegetation type	Organic matter category				Total
	Ash	Saltcedar	Wood	Other	
Native upstream	14.6 $\pm$ 7.4 (59)	0.0 $\pm$ 0.0 (0)	2.0 $\pm$ 2.0 (8)	8.0 $\pm$ 1.7 (33)	24.6 $\pm$ 10.7
Cleared	11.4 $\pm$ 11.4 (27)	3.1 $\pm$ 0.8 (7)	4.5 $\pm$ 1.3 (11)	22.9 $\pm$ 1.4 (55)	42.0 $\pm$ 12.2
Saltcedar	73.4 $\pm$ 72.1 (20)	228.5 $\pm$ 11.3 (61)	17.5 $\pm$ 6.0 (5)	54.3 $\pm$ 7.5 (15)	373.7 $\pm$ 71.2
Native downstream	0.0 $\pm$ 0.0 (0)	0.9 $\pm$ 0.9 (10)	0.0 $\pm$ 0.0 (0)	7.6 $\pm$ 2.0 (90)	8.5 $\pm$ 2.5

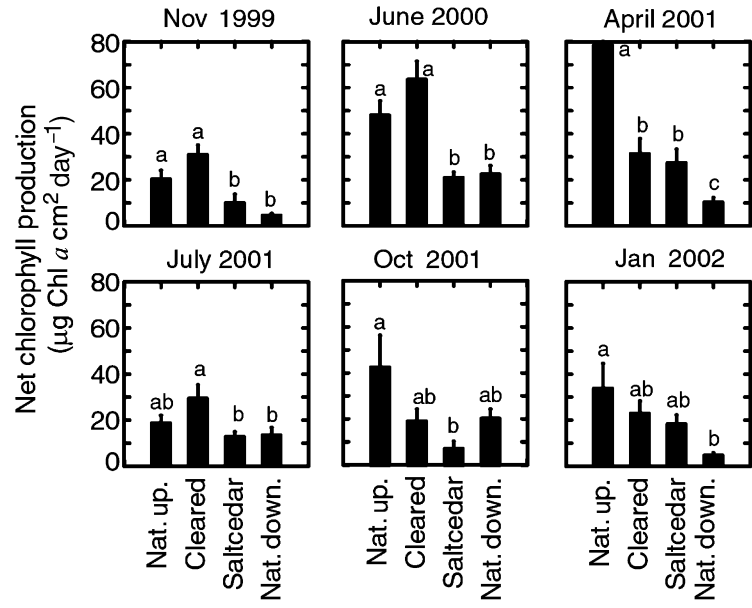


Fig. 5 Net chlorophyll production (mean + 1 SE) by time and riparian vegetation type. Daily chlorophyll *a* production was estimated by determining net chlorophyll *a* accumulation on unglazed clay tiles after 2 weeks. Letters denote significant differences across riparian vegetation types within a given sampling period (ANOVA Tukey's HSD,  $P < 0.05$ ).

to saltcedar sites. Two years later, during the 2001–2002 sampling, cleared sites still had higher algal production rates but this difference was not always significant and the overall magnitude of the difference was smaller. Native-upstream sites, where water temperature is highest, had higher net production than saltcedar sites across all times. In contrast, production rates at cool, native-downstream sites tended to be lower or equal to those at saltcedar sites.

The effects of saltcedar on algal production were even more striking when we adjusted for across-site

differences in water temperature using ANCOVA (Fig. 6). At every time point except the comparison of saltcedar with native-downstream sites in April 2001, saltcedar sites supported the lowest rates of temperature-adjusted chlorophyll production (Fig. 6). The large differences in net chlorophyll production between the warm native-upstream sites and the cooler native-downstream sites disappeared when we adjusted for temperature (except April 2001), but both treatments were nearly always more productive than saltcedar sites.

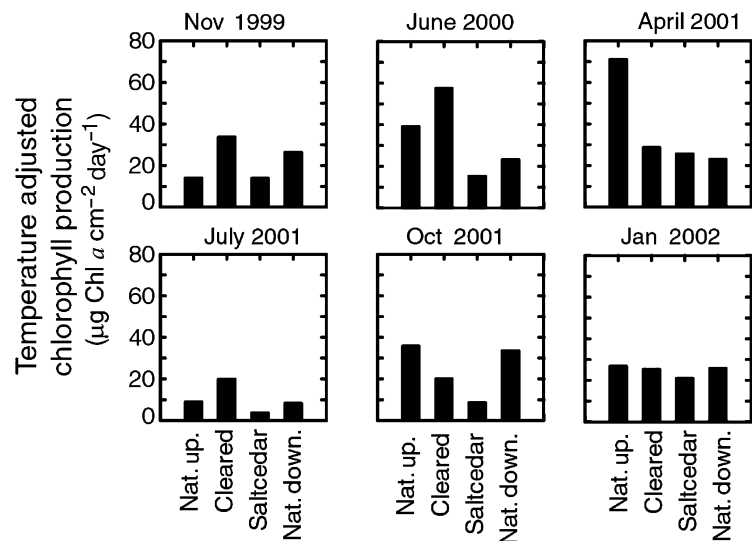


Fig. 6 Temperature-corrected chlorophyll production rates by time and riparian vegetation type. Bars represent the adjusted treatment means from ANCOVA with temperature as the covariate.

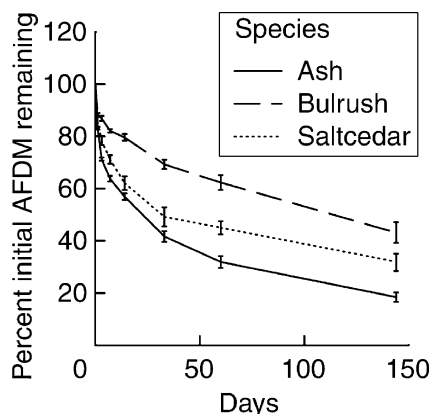


Fig. 7 Per cent initial ash free dry mass remaining for each litter type as a function of time. Data are averaged across all riparian vegetation types  $\pm 1$  SE.

### Leaf breakdown

In addition to changing the quantity and nature of organic matter inputs along Jackrabbit Spring, saltcedar altered the decomposition of organic matter, primarily through its influence on litter quality (Fig. 7) rather than by altering the environment for decomposition (Table 2). Leaf litter at native-upstream sites exhibited faster decay than all other sites (Table 2; Tukey's HSD,  $P < 0.05$ ), but there were no significant differences in decay rate among the other vegetation types. Ash litter decomposed most quickly, followed by saltcedar and then bulrush (Table 2; Tukey's HSD,  $P < 0.05$ ). The two-way interaction of litter type  $\times$  vegetation type was not statistically significant (ANOVA,  $P > 0.05$ ). Litter chemistry analyses suggest that the rapid decay of ash relative to the other litter types resulted from lower tannin concentrations than salt cedar (Stout, 1989) and lower lignin concentrations than bulrush (Melillo, Aber & Muratore, 1982; Table 3).

Table 3 Initial chemistry of the three litter types used in the decomposition experiment. Water soluble (WS) includes amino acids, simple sugars and soluble phenolics, and acid soluble (AS) include cellulose, hemicellulose, starch, polypeptides and nucleic acids

Litter chemistry	Litter type		
	Ash	Bulrush	Saltcedar
Ash (%)	9.03	19.03	17.66
Water soluble (%)	32.82	27.98	55.78
Acid soluble (%)	55.03	52.79	32.54
Lignin (%)	4.08	10.40	4.26
WS polyphenols as tannin (%)	4.34	2.12	10.69
WS polysaccharides as glucose equivalents (%)	11.32	6.21	8.16
AS polysaccharides as glucose equivalents (%)	33.66	46.62	18.57
Silica (%)	0.04	0.25	0.03
Sodium (%)	0.05	0.16	0.72
Magnesium (%)	0.42	0.16	1.25
Carbon (%)	45.2	37.9	43.7
Nitrogen (%)	0.29	0.44	0.55
Carbon : Nitrogen	182	101	93

There were significant riparian vegetation type and litter type differences in the shape of the percent initial nitrogen remaining curves (Fig. 8). However, interpretation of these curves is complicated by highly significant two-way interactions (ANOVA,  $P < 0.001$  for both riparian vegetation type  $\times$  litter type and litter type  $\times$  time). Looking down a given column in Fig. 8 (i.e. across litter types), it is evident that ash litter generally supported the most rapid microbial nitrogen immobilisation. Furthermore, the period of immobilisation for ash was the shortest of all litter types, probably reflecting the relatively rapid breakdown of this species. Saltcedar displayed similar patterns to ash (Fig. 8), with net immobilisation occurring rapidly,

Table 2 Decay constants (per thousand degree days) from a single-exponential decay model and ash free dry mass (AFDM) of litter remaining (per cent of initial) after 144 day in the stream. Decay constants are presented for each litter type in each vegetation type. Final AFDM is presented for each litter type averaged across vegetation type and for each vegetation type averaged across litter type

Litter type	Riparian vegetation type				Final AFDM (%)
	Native upstream	Cleared	Saltcedar	Native downstream	
Ash	1.1019 (0.049)	0.887 (0.052)	0.905 (0.023)	0.894 (0.041)	18.4 (1.8)
Bulrush	0.476 (0.029)	0.395 (0.048)	0.305 (0.018)	0.344 (0.16)	31.7 (3.2)
Saltcedar	0.834 (0.067)	0.635 (0.036)	0.625 (0.30)	0.682 (0.084)	43.1 (3.9)
Final AFDM (%)	15.63 (2.92)	34.0 (3.0)	35.2 (4.3)	39.5 (4.5)	

Data presented are least squares mean (SE). Final AFDM is not temperature corrected.



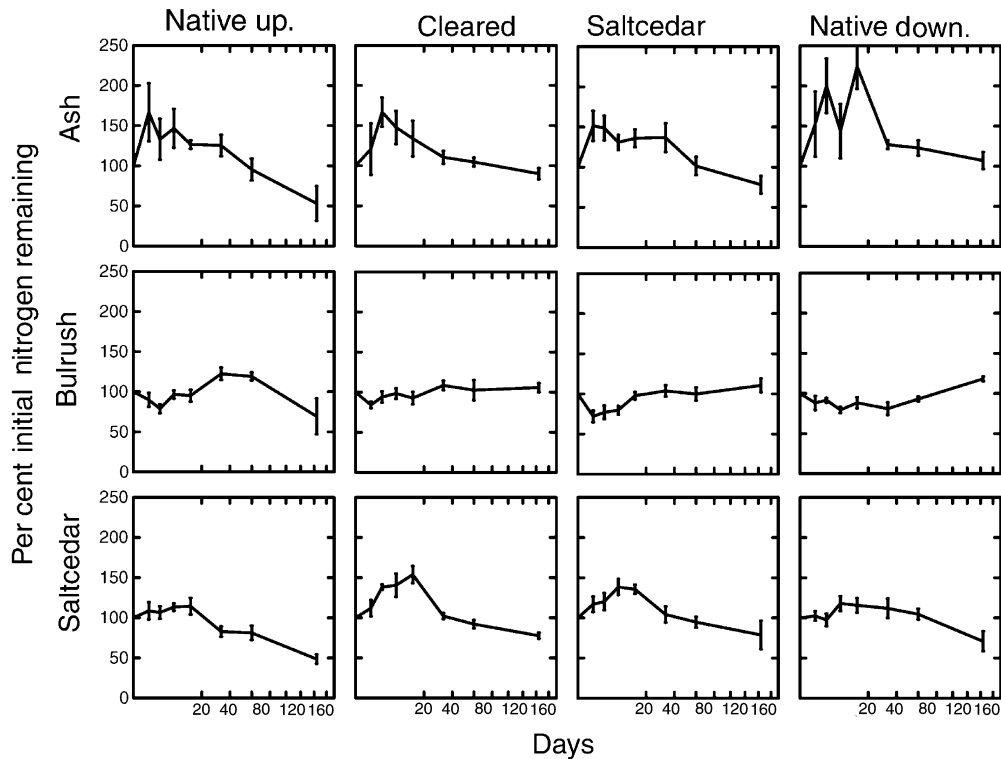


Fig. 8 Per cent initial nitrogen remaining (mean  $\pm$  1 SE) from the litter breakdown experiment by litter type and riparian vegetation type.

but the rate and magnitude of immobilisation were less than that for ash and the period of immobilisation was longer, reflecting a more refractory substrate. Unlike the other litter types, bulrush displayed an initial net loss of nitrogen. With the exception of native-upstream sites, at the end of the experiment bulrush litter exhibited a net immobilisation of nitrogen (i.e. percent initial nitrogen remaining  $>100\%$ ). Furthermore, the rate and magnitude of immobilisation for bulrush were lower than for ash and saltcedar, again reflecting an extremely refractory substrate.

## Discussion

The saltcedar invasion has shifted reaches of Jackrabbit Spring from a system based on autochthonous production to dependence on allochthonous inputs, with saltcedar sites having lower temperature-adjusted chlorophyll and macrophyte production rates and greater allochthonous inputs than virtually all native and cleared sites (Table 4). The effects of saltcedar on macrophyte and algal inputs probably resulted from dense shading, because stream nitrogen and phosphorus concentrations were not affected by the large

Table 4 Summary of total allochthonous and autochthonous inputs by riparian vegetation type, averaged across all sampling times. Allochthonous and macrophyte values were converted to AFDM by multiplication with 0.8, the approximate proportion of AFDM for the three litter types from Table 3. Algal values of chlorophyll production were converted to AFDM with multiplication by 100, a value that falls within the range of published values (Ahlgren, 1983; Taylor, Geider & Gilbert, 1997). Values are mean (SE)

	Native upstream	Cleared	Saltcedar	Native downstream
Allochthonous inputs (g AFDM $m^{-2}$ year $^{-1}$ )	20 (9)	34 (10)	299 (57)	7 (2)
Macrophyte production (g AFDM $m^{-2}$ year $^{-1}$ )	118 (26)	210 (77)	15 (8)	425 (52)
Algal production (g AFDM $m^{-2}$ year $^{-1}$ )	1100 (120)	900 (80)	440 (50)	350 (40)
Algal production-temperature adjusted (g AFDM $m^{-2}$ year $^{-1}$ )	900 (250)	850 (160)	400 (90)	640 (90)

saltcedar stand or by saltcedar removal (Kennedy, 2002). Competition for space was not likely to be responsible for the lower macrophyte production at invaded sites because macrophytes at all sites were most abundant in the stream whereas saltcedar occurred only on the banks.

Changes in algal production because of saltcedar invasion probably influence the community structure of aquatic consumers because algae are a high quality food resource, available year-round for consumption by aquatic invertebrates and fish; algae contain two to six times more tissue nitrogen than senescent saltcedar litter (0.67–0.85% N for saltcedar versus 1.6–4.3% N for filamentous algae) and algae are also more nutritious than even microbially-conditioned leaf litter (Anderson & Sedell, 1979). Furthermore, using chlorophyll production as a proxy for algal production probably underestimates the actual effect of saltcedar on algal production in Jackrabbit Spring. Algae growing in low light environments have more chlorophyll per cell than algae growing in high light environments (Healey, 1985; Wetzel, 2001). Thus, expressing algal production on a chlorophyll basis may partially mask the negative effects of dense saltcedar stands on algal carbon production.

The faster decomposition at native-upstream sites relative to the other vegetation types, even after accounting for across site differences in temperature, may be due to across site differences in the composition of the aquatic community (Anderson & Sedell, 1979); *Gammarus* sp., a shredding invertebrate, were frequently observed at native-upstream sites but were uncommon or absent from other sites (personal observation).

The quality of the dominant vascular plant litter was also altered by saltcedar. Bulrush, the dominant macrophyte across all sites, appears to be a lower quality food resource for aquatic consumers than saltcedar litter, the litter type that effectively replaces bulrush at saltcedar sites. However, both bulrush and saltcedar are likely to be low quality food resources relative to ash, the dominant native allochthonous litter type.

These results concur with two other studies that have compared the litter breakdown rates of saltcedar and native species. Pomeroy, Shannon & Blinn (2000) compared breakdown rates of saltcedar and two native litter types, cottonwood [*Populus fremontii* (S.)] and willow [*Salix exigua* (Nutt.)], in the thermally constant water of the Colorado River below Glen

Canyon Dam. They found that the breakdown of saltcedar was slower than cottonwood but faster than willow. The decay constant for saltcedar calculated by Pomeroy *et al.* (2000) ( $0.005 \text{ day}^{-1}$ ) is somewhat lower than the value we obtained for saltcedar in the cool native-downstream sites ( $0.008 \text{ day}^{-1}$ ). Pomeroy *et al.* (2000) attributed this relatively slow decay, in part, to the absence of shredding invertebrates in their litterbags. However, invertebrates were also virtually absent from litterbags of all litter types at our native-downstream sites. As with our study, Ellis, Crawford & Molles (1998) found no consistent differences in breakdown rates of leaf litter in the riparian zone across sites dominated by either native cottonwood or saltcedar, indicating that the presence of saltcedar in the riparian zone does not alter the environment for decomposition.

Previous research on invertebrate colonisation of litter bags concurs with our conclusion that saltcedar is a poor quality food resource for aquatic consumers (Bailey, Schweitzer & Whitham, 2001). They found that, after 1 week in a small Arizona stream, there were no differences in macroinvertebrate diversity or abundance between litterbags filled with saltcedar or cottonwood leaves, but after 3 weeks cottonwood bags supported a more diverse assemblage of macroinvertebrates and over four times as many individuals as saltcedar litterbags.

Despite a similar overall quantity of inputs, and the fact that saltcedar appears to be a better quality food resource than bulrush, a shift from bulrush to saltcedar alone could negatively affect the aquatic food web in Jackrabbit Spring. Because bulrush is actually rooted in the stream it will support secondary production at that site because it will be processed *in situ*, rather than be transported downstream like saltcedar litter. Furthermore bulrush provides a stable substratum for algae and invertebrates in this soft-bottomed stream and it also increases habitat complexity for the two native fish.

These results indicate that more research is warranted into the potential impacts of saltcedar on aquatic ecosystems. Spring-fed and small streams are common throughout the southwestern United States. Given the strong linkage between streams and their riparian vegetation, it is conceivable that saltcedar is having comparable impacts in other small streams that it has also invaded. Future research on the impacts of saltcedar invasion should investigate whether other

invaded streams become dominated by allochthonous inputs and whether this shift in the nature, quality and timing of inputs affects animal communities.

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