

NOTE

SALT CEDAR NEGATIVELY AFFECTS BIODIVERSITY OF AQUATIC MACROINVERTEBRATES

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Abstract: Salt cedar (*Tamarix ramossissima*), an invasive species, has become a dominant shrub along many streams of the southwestern United States, where it has replaced many native species such as Fremont cottonwood (*Populus fremontii*). We examined whether the successful invasion of this exotic shrub alters stream leaf litter decomposition rates and affects the aquatic macroinvertebrates that are dependent on leaf litter as a food source. With an in-stream leaf pack experiment, we found that faster decomposition of salt cedar litter was associated with a two-fold decrease in macroinvertebrate richness and a four-fold decrease in overall macroinvertebrate abundance, relative to native Fremont cottonwood. Macroinvertebrate communities were also significantly different on the two food sources through time. These studies demonstrate that invasion by salt cedar affects leaf litter quality, which in turn affects stream macroinvertebrates. Such impacts on the primary consumers and food web structure could affect higher trophic levels.

Key Words: *Tamarix*, *Populus*, exotic species, cottonwood, leaf packs, community, riparian ecology, leaf litter decomposition

INTRODUCTION

Riparian forests dominated by cottonwood (*Populus* spp.) are the most threatened forest type in the western United States (Brown 1982, Noss et al. 1995, Stein and Flack 1997) and are declining rapidly. It is estimated that 70–84% of riparian habitat in the U.S. has been destroyed or converted to other uses since European settlement (Noss et al. 1995). Because riparian forests contribute disproportionately to biodiversity in the western United States (Naiman 1993), their conservation is especially important. In addition to threats from river management, cottonwood forests are threatened by invasive species such as the shrub, *Tamarix* spp., which was introduced to the western U.S. in the mid-1800s (Everitt 1998, Gladwin and Roelle 1998). In contrast to the reduction in native riparian habitat, an estimated 526,000 hectares of the western United States are now occupied by salt cedar (Stevens 1985). Because there are tight linkages between riparian forests and stream processes, it is important to investigate the effects of this exotic invasion.

Riparian forests and streams are associated through many processes, such as litter input, nutrient cycling, and evapotranspiration (Gregory et al. 1991). Several studies have shown how the terrestrial biome sur-

rounding a reach of river can affect aquatic macroinvertebrate communities (Vannote et al. 1980, Corkum 1991, Wallace et al. 1997). In small streams, leaf litter input typically is an important food and habitat resource that affects aquatic macroinvertebrate assemblages (Vannote et al. 1980).

The leaves of salt cedar and Fremont cottonwood (*Populus fremontii* L.) differ morphologically and chemically. Fremont cottonwood leaves have low tannin concentrations and are generally regarded as a good food resource for arthropods (Driebe and Whitham 2000). Salt cedar leaves have relatively high concentrations of tannins and are generally regarded as a poor food resource for arthropods (El-Beheiry and El-Kady 1998). In addition to leaf litter as a food resource, Fremont cottonwood leaves are broader than those of salt cedar and may provide better protection for aquatic macroinvertebrates (Dobson 1994).

Despite the potential consequences to aquatic invertebrates, relatively few studies in the U.S. have examined how native and exotic leaf litter differentially affect aquatic macroinvertebrate communities (Boulton et al. 1997, Schulze and Walker 1997). In October 1997, we examined how salt cedar and cottonwood leaf litter affect aquatic macroinvertebrate diversity at Wet Beaver Creek. Because of the reported differences

in the quality and morphology of salt cedar and cottonwood leaf litter, we predicted that taxonomic richness and total abundance of aquatic macroinvertebrates at Wet Beaver Creek would be lowest on salt cedar litter.

METHODS

Study Site

Wet Beaver Creek, Yavapai Co., Arizona, USA (34° Latitude, 111° Longitude) is a perennial, Sonoran Desert creek. It is located in the upper Verde River basin and has a drainage area of 287.5 km². At our study sites, both Fremont cottonwood and salt cedar are common.

Leaf packs have commonly been used to examine decomposition rates of different litter types and to analyze macroinvertebrate assemblages (see review by Boulton and Boon 1991). The use of leaf packs is an experimental method that has the advantage of securing leaf material with very little loss. We used a two-factor (leaf litter * time), in stream, leaf litter decomposition experiment to assess how litter type influences macroinvertebrate community composition over time. Leaf packs (15cm x 15cm) were constructed of 3-mm polyester mesh material. The edges of all packs were taped to ensure structural integrity. The bags allowed most aquatic macroinvertebrates access to the litter and retained most of the leaf material.

Leaves of cottonwood and salt cedar were collected from 10 different trees. Leaves were collected after senescence to represent the natural leaf chemistry of litter entering the creek. The leaves were air-dried for two weeks before placement into the leaf packs. Ten leaf packs were made with each litter type. In late October, during leaf fall, leaf packs containing four grams of leaf material each were attached in five microsites along a single reach of the creek. The sites were chosen for their low velocity and their position opposite the main thalweg. Microsites were spaced approximately 40 m apart and contained naturally accumulated leaf material. In each microsite, two leaf packs of each species were attached to the bottom of the creek with 25 cm tent stakes. Half of the leaf packs were removed from the creek after one week, and the remaining packs were removed after three weeks.

Leaf packs were returned to the lab where the macroinvertebrates were immediately picked from the sample without magnification. Aquatic macroinvertebrates were counted and keyed to family using Merritt and Cummins (1984). Because the data met the assumptions of normality and homogeneity of variance, differences in family richness and abundance of macroinvertebrates on the two litter types at both sample

dates were analyzed by a two-way ANOVA. One-way ANOVAs were performed on all significant two-way ANOVA interactions to determine where significant differences occurred.

We also examined how the composition of the macroinvertebrate community differed through time and by leaf type using the Non-metric Multidimensional Scaling (NMDS) ordination routine within the program DECODA (Minchin 1987a, b). NMDS arranges samples in ordination space based on the similarity between samples (Minchin 1987a, b). In this case, samples were litter packs, and the similarity matrix was based on macroinvertebrate taxonomic richness and abundance. This arranges leaf packs with similar species and abundances closer together in ordination space. Although originally developed for vegetation, it has also been used in analyses of arthropod communities and plant defensive chemistry (e.g., Dungey *et al.* 2000). This method of analysis allowed us to determine whether insect species composition and abundance differed between leaf litter sources and through time. Potential differences between treatments were analyzed using an Analysis of Similarity (ANOSIM) test (Minchin 1987a, b, Oksanen and Minchin 1997). We then used the vector-fitting procedure of DECODA to identify variables that were responsible for separating communities in multidimensional space. Using vectors, it is possible to examine correlations between community and habitat variables and ordination patterns.

After collecting macroinvertebrates, we removed the leaf material from each sample, air-dried it for two weeks, and ashed a sub-sample for 1 hr at 500°C to determine ash-free dry mass (AFDM). Because the data met the assumptions of normality and homogeneity of variance, decomposition was analyzed by a two-way ANOVA. We used decomposition as a vector to explain community composition differences in the NMDS analysis.

RESULTS

In Wet Beaver Creek, the two species had similar litter decomposition rates after one week in the water; Fremont cottonwood leaf litter lost 23% of its mass, and salt cedar lost 28% of its leaf mass (mean leaf mass lost \pm 1SE = 0.23 ± 0.02 and 0.28 ± 0.04 , respectively). However, after three weeks, salt cedar lost a total of 12% more leaf mass than Fremont cottonwood leaves (mean leaf mass lost \pm 1SE = 0.35 ± 0.02 and 0.46 ± 0.03 , respectively; Table 1).

Overall, there were strong differences in macroinvertebrate richness and abundance, on a per-leaf-pack basis among treatment groups. There was also a significant time * leaf type interaction (Table 1), indicat-

Table 1. Mass of leaf packs and associated arthropod species richness and abundance as a function of plant species and time. Mean, standard error, and probability are given for each species and condition. Probabilities are calculated using a two-way ANOVA for variables with a significant species × time interaction (in bold), brackets show the results of significant Post hoc ANOVAs.

Dependent Variable	One Week		Three Weeks		Species	Time	Species × Time
	Cottonwood	Salt Cedar	Cottonwood	Salt Cedar			
Leaf Mass Lost (g)	0.23 ± 0.02	0.28 ± 0.04	0.35 ± 0.02	0.46 ± 0.03	(F = 6.27, p = 0.023*)	(F = 24.81, p < 0.000*)	(F = 0.85, p = 0.371)
Richness (# Macroinvertebrate Families/Leaf Pack)	2.6 ± 0.40	2.8 ± 0.49	6.0 ± 0.55	3.4 ± 0.81	(F = 4.24, p = 0.056)	(F = 11.77, p = 0.003*)	(F = 5.77, p = 0.029*)
Abundance (# Macroinvertebrate/Leaf Pack)	9.8 ± 3.06	8.6 ± 1.69	147.4 ± 14.92	34.60 ± 12.83	(F = 33.43, p < 0.000*)	(F = 70.77, p < 0.000*)	(F = 31.97, p < 0.000*)

d.f. = 1 for all dependent variables for species, time, and species × time effects.
 * Overall significance level <0.05.

ing that there were no differences between leaf litter in initial colonization (1wk) but that, by three weeks, the treatments diverged significantly. In total, fifteen families of macroinvertebrates were represented in the leaf packs (Table 2).

After one week, aquatic macroinvertebrate taxonomic richness did not differ between the two leaf types. However, from week one to week three, the macroinvertebrate richness of cottonwood litter increased ~2.5 times, while no significant increase was detected on salt cedar over the same period. The fact that richness did not continue to increase on salt cedar leaves was surprising because new macroinvertebrate taxa should continue to colonize the leaf material. Most importantly, after three weeks, macroinvertebrate richness on cottonwood litter was twice as high as that on salt cedar (mean richness ± 1SE = 6.0 ± 0.55 vs. 3.4 ± 0.81 species per leaf pack; Table 1).

After one week, there was no difference in macroinvertebrate abundance between cottonwood and salt cedar litter (mean abundance ± 1SE = 9.8 ± 3.06 and 8.6 ± 1.69, respectively; Table 1). Macroinvertebrate abundance in leaf packs with cottonwood leaves was ~15 times greater at three weeks than at one week. Macroinvertebrate abundance on salt cedar was only four times greater at three weeks than at one week. Thus, for both leaf types, macroinvertebrate colonization increased through time. However, macroinvertebrate abundance after three weeks was ~4 times greater on cottonwood leaves than on salt cedar leaves (mean abundance ± 1SE = 147.4 ± 14.92 and 34.6 ± 12.83, respectively; Table 1).

Using ordination techniques that combine both species richness and abundance, we found that overall communities of arthropods occupying cottonwood and salt cedar litter differed significantly. After one week in the stream, there was no significant difference between cottonwood and salt cedar macroinvertebrate community composition. While both types of litter accumulated macroinvertebrates over time, the composition of the aquatic macroinvertebrate community was significantly different between cottonwood and salt cedar leaves after three weeks (Figure 1).

Furthermore, the composition of aquatic macroinvertebrates on salt cedar after three weeks in the stream was different from the composition on salt cedar after one week but not different from the composition on cottonwood after one week. However, the community of aquatic macroinvertebrates on cottonwood leaves after three weeks was significantly different from all other groups, differing in the number of general herbivores (collectors and gatherers) and shredders present.

Vector analysis indicated that decomposition rate was strongly correlated with community composition

Table 2. Macroinvertebrate abundance by family in cottonwood and salt cedar litter after one and three weeks; numbers in columns represent the average number of macroinvertebrates/leaf pack.

Family	One Week		Three Weeks	
	Cottonwood	Salt cedar	Cottonwood	Salt cedar
1. Amphipoda	0	0	0.2	0
2. Baetidae	0	0	0.4	0
3. Chironomidae	8.4	5.0	128	29.6
4. Chrysomelidae	0.2	0.2	0.2	0
5. Coenagrionidae	0	0.2	0.8	0.4
6. Gastropoda	0.4	0	1.6	0.6
7. Heptageneidae	0	0	0.8	0.2
8. Hydropsychidae	0.2	0	0	0.2
9. Hydroptilidae	0	0	0.4	0
10. Philopotamidae	0	0	0	0.4
11. Polymitarcyidae	0	0	0	0.4
12. Psphenidae	0.2	0.6	0.4	0.2
13. Siphonuridae	2.4	2.4	2.8	2.0
14. Tabanidae	0	0	0.4	0
15. Tricorythidae	0	0	0	0.4

($r=0.67$, $p=0.007$, Figure 1). The vector representing slower decomposition rate was in the same direction as increasing macroinvertebrate richness and abundance. Increased richness and abundance on slower decomposing cottonwoods suggest that protracted food and/or habitat availability allows more species to be supported.

DISCUSSION

This study suggests that, in this stream system during a limited period of study, native Fremont cottonwood and exotic salt cedar leaf litter can structure aquatic macroinvertebrate communities differently on a per-unit-substrate basis. Salt cedar leaves can contain up to 15% soluble salts and other easily soluble compounds. Thus, the relatively high proportion of salts in salt cedar, their relative fragility, and their small size may explain why they decompose and leave the leaf packs faster than leaves of Fremont cottonwood. Whether litter from salt cedar is not easily colonized by bacteria and is therefore a poor food resource, or readily fragments in streams and is subsequently a poor habitat resource, is difficult to say without further study. Our data indicate that both food quality and architecture may play a role. In terms of arthropod abundance, per unit of leaf mass, we found four times as many macroinvertebrates on cottonwood leaves as on salt cedar, suggesting that leaf quality is an important factor affecting the macroinvertebrate community. Similarly, there were ~2.5 times as many taxa in leaf packs containing cottonwood leaves. Higher arthropod abundance and richness per unit of leaf mass on cottonwood leaves relative to tamarisk suggests that differences in leaf quality and/or morphology make cottonwood leaves a superior resource for stream arthropods. However, the fact that, over all samples, total richness was similar (cottonwood = 12 taxa, tamarisk = 11 taxa; Table 2), suggests that the lower quality of tamarisk leaves may not result in a diminished com-

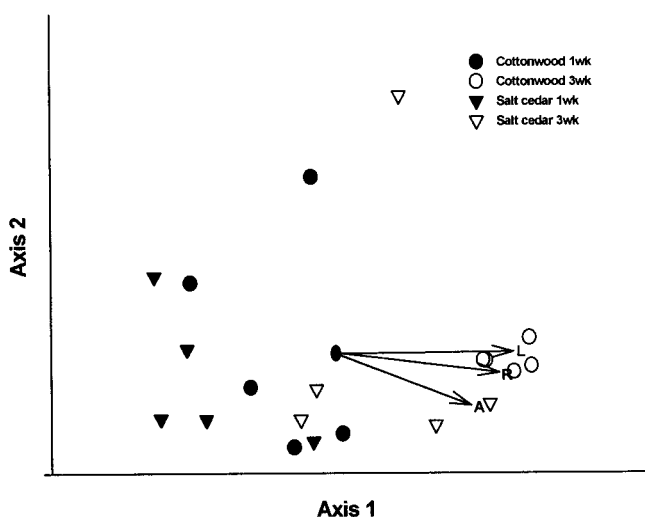


Figure 1. Based on the combined richness and abundance of macroinvertebrates in the leaf packs, results from NMDS indicate that the macroinvertebrate community differed significantly by litter type and time. Vectors indicate increasing leaf mass remaining (Vector L: $r=0.67$, $p=0.007$), increasing taxonomic richness (Vector R: $r=0.57$, $p=0.042$), and increasing total abundance (Vector A: $r=0.85$, $p=0.0001$).

munity at the scale of the entire study reach. Therefore, salt cedar litter negatively affects the alpha-diversity of the macroinvertebrate community but may not affect the beta-diversity of macroinvertebrates at Wet Beaver Creek.

Whether this pattern will occur in other streams or over a longer period of study is unknown. Although our study suggests that cottonwood litter is a better food and habitat resource than salt cedar, the mechanisms behind these patterns are still obscure. However, successful invasions of other aquatic ecosystems by plants and animals have shown similar negative effects of exotic species on aquatic communities. Boulton et al. (1997) found that riparian forests dominated by an exotic species had significantly lower invertebrate fauna in the hyporheic zone than riparian forests dominated by native vegetation. In Australia, Schulze and Walker (1997) reported that native eucalyptus and exotic willow leaves decomposed at different rates and structured macroinvertebrate communities differently.

Because exotic invasions are a global issue (Gillis 1992) and because invasions can alter trophic relationships in aquatic systems, it is important to understand how an invasion will affect a system on multiple levels. The long-term effects of salt cedar invasion on aquatic macroinvertebrate communities and ecosystems are not known. However, it is possible, due to factors such as leaf morphology and leaf chemistry, that the invasion of southwest riparian forests by salt cedar will negatively affect aquatic macroinvertebrate diversity. Furthermore, in stream ecosystems that are structured by leaf litter input (see Schade and Fisher 1997), salt cedar could reduce diversity of higher trophic levels (Naeem et al. 1994) by decreasing the abundance of Chironomid larvae, which make up a large percentage of fish diets (Weller 1981, Batzer et al. 2000).

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LITERATURE CITED

Batzer, D. P., C. R. Pusateri, and R. Vetter. 2000. Impacts of fish predation on marsh invertebrates: direct and indirect effects. *Wetlands* 20:307–312.

- Boulton, A. J. and P. I. Boon. 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? *Australian Journal of Marine Freshwater Research* 42:1–43.
- Boulton, A. J., M. R. Scarsbrook, J. M. Quinn, and G. P. Burrell. 1997. Land use effects on the hyporheic ecology of five small streams near Hamilton, New Zealand. *New Zealand Journal of Marine Freshwater Research* 31:609–622.
- Brown, D. E. 1982. *Biotic Communities of the American Southwest—United States and Mexico*. Desert Plants 4(1–4). University of Arizona Press, Tucson, AZ, USA.
- Corkum, L. D. 1991. Spatial patterns of macroinvertebrate distributions along rivers in eastern deciduous forest and grassland biomes. *Journal of the North American Benthological Society* 10: 358–371.
- Dobson, M. 1994. Microhabitat as a determinant of diversity: stream invertebrates colonizing leaf packs. *Freshwater Biology* 32:565–572.
- Driebe, E. and T. G. Whitham. 2000. Cottonwood hybridization affects tannin and nitrogen content of leaf litter and alters decomposition. *Oecologia* 123:99–107.
- Dungey, H. S., B. M. Potts, T. G. Whitham, and H.-F. Li. 2000. Plant genetics affects arthropod community richness and composition: evidence from a synthetic eucalypt hybrid population. *Evolution* 54:1938–1946.
- El-Beheiry, M. A. H. and H. F. El-Kady. 1998. Nutritive value of two *Tamarix* species in Egypt. *Journal of Arid Environments* 38: 529–539.
- Everitt, B. L. 1998. Chronology of the spread of *Tamarisk* in the central Rio Grande. *Wetlands* 18:658–668.
- Gillis, A. M. 1992. Keeping aliens out of paradise: Government agencies and environmental groups are looking for ways to keep nonnative animal and plant pests out of Hawaii. *Bioscience* 42: 482–485.
- Gregory, S. V., F. J. Swanson, W. A. McKee, and K. W. Cummins. 1991. An ecosystem perspective of riparian zones: focus on links between land and water. *Bioscience* 41:540–551.
- Gladwin, D. N. and J. E. Roelle. 1998. Survival of plains cottonwood (*Populus deltoides* subsp. *Monilifera*) and saltcedar (*Tamarix ramosissima*) seedlings in response to flooding. *Wetlands* 18:669–674.
- Merritt, R. W. and K. W. Cummins. 1984. *An Introduction to the Aquatic Insects of North America*. Second Edition. Kendall/Hunt Publishing, Dubuque, Iowa, USA.
- Minchin, P. R. 1987a. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89–107.
- Minchin, P. R. 1987b. Simulation of multidimensional community patterns: towards a comprehensive model. *Vegetatio* 71:145–156.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecological Applications* 3:209–212.
- Naeem, S., L. J. Thompson, S. P. Lawler, J. H. Lawton and R. M. Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368:734–736.
- Noss, R. F., E. T. LaRoe III, and J. M. Scott. 1995. *Endangered ecosystems of the United States: A preliminary assessment of loss and degradation*. U.S. Department of the Interior, National Biological Service, Washington, DC, USA Biological Report 28.
- Oksanen, J. and P. R. Minchin. 1997. Instability of ordination results under changes in input order: explanations and remedies. *Journal of Vegetation Science* 8:447–454.
- Power, M. E. 1990. Effects of fish in river food webs. *Science* 250: 811–14.
- Schade, J. D. and S. G. Fisher. 1997. Leaf litter in a Sonoran Desert stream ecosystem. *Journal of North American Benthological Society* 16:612–626.
- Schulze, D. J. and K. F. Walker. 1997. Riparian eucalypts and willows and their significance for aquatic invertebrates in the River Murray, South Australia. *Regulated Rivers* 13:557–577.
- Stein, B. A. and S. R. Flack. 1997. Conservation priorities: the state of U.S. plants and animals. *Environment* 39:6–11.
- Stevens, L. 1985. Invertebrate herbivore community dynamics on *Tamarix chinensis* loueiro and *Salix exigua* Nuttall in the Grand

- Canyon, Arizona. Masters Thesis. Northern Arizona University, Flagstaff, AZ, USA.
- Vannote, R. L., W. M. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The River Continuum Concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102–104.
- Weller, M. W. 1981. *Freshwater Marshes*. University of Minnesota Press. Minneapolis, MN, USA.
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