EFFECTS OF THE EXOTIC INVADER, *TAMARIX* SPP., ON

ASPECTS OF THE AQUATIC ECOSYSTEM AT

MCCOMB CREEK, PRESIDIO

COUNTY, TEXAS

by

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ABSTRACT

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The effects of saltcedar, *Tamarix* spp., invasion in riparian zones of the western United States have been well documented. These include, but are not limited to soil salinization, and shifts in hydrology and water use. Comparatively unknown are the effects on the associated aquatic systems and if a significant increase in water salinity accompanies these invasions. Shifts in stream metabolism have been reported, but the impacts of saltcedar invasion on the algal species, which are the dominant primary producers in desert aquatic ecosystems, are unknown. A two year study was conducted in an oligotrophic desert stream, currently experiencing an invasion, to determine the influence of saltcedar on specific environmental factors and their effect on benthic algal assemblages and stream metabolism. Saltcedar presence in this system was expected to increase salinity. A potential increase in phosphorus availability, resulting from this salinity increase, may cause a shift from species-poor

communities of oligotrophic and halosensitive algae to species-rich communities of eutrophic and halotolerant species. The invasion may also influence other aquatic environmental parameters that are fundamental determinants of algal community composition, such as temperature, pH, conductivity and nitrogen. Canopy cover of the stream would also be increased, thereby lowering daily photosynthetically active radiation (PAR) and increasing allochthonous input into the stream in the form of leaf litter. A greater allochthonous input is expected to drive an increase in respiration, effectively counteracting any increase in photosynthesis that may result from increased nutrients in the saltcedar invaded reach. Therefore, no significant difference in stream metabolism between the upstream native and downstream saltcedar reaches was anticipated. Species composition and diversity were assessed across reaches by deploying artificial substrates and performing a series of experiments utilizing nutrient-diffusing substrates (NDS) and transplantation of artificial substrates. Environmental measurements of temperature, pH, conductivity, daily PAR, dissolved oxygen, soluble reactive phosphorus (SRP), nitrate-nitrogen and ammonium-nitrogen were measured to determine if saltcedar presence exerted any effects on these parameters. Leaf litter and chlorophyll a measurements were used to determine allochthonous and autochthonous inputs into the study reaches, respectively. Stream metabolism was assessed as the ratio of photosynthesis to respiration (P:R) using dissolved oxygen data over a 24 hour period.

Species diversity of soft algae and diatoms was significantly higher in the saltcedar reach than in the native reach ($p=0.015$ and $p=0.001$, respectively). This is contrary to previous research indicating that increases in salinity decreases algal diversity. The native communities were dominated by *Achnanthidium minutissimum*, which is the most widespread diatom in the world, characteristically found in oligotrophic systems. Saltcedar communities were dominated by N_2-fixing species of the genera *Rhopalodia* and *Anabaena.* Significantly different

environmental variables that were higher in the saltcedar reach were specific conductance and salinity, while pH was higher in the native reach. Leaf litter mass in the saltcedar reach was significantly higher than that in the native reach, but there was no significant difference in chlorophyll *a* between the sites. Increased allochthonous input was not enough to shift stream metabolism, i.e. the P:R ratio. SRP in the saltcedar reach was significantly increased, indicating a possible relationship between SRP and salinity leading to increased diversity in benthic algal communities. Increased phosphorus availability in the saltcedar reach stimulated proliferation of *Rhopalodia* species with endosymbionts capable of N_2-fixation, thus overcoming the nitrogen limiting conditions. It is shown here that saltcedar invasion along the riparian corridor has shifted a characteristically oligotrophic native system to an ecosystem dominated by a more eutrophic algal community utilizing increased phosphorus. Nutrient enrichment with nitrogen and phosphorus resulted in higher diatom species diversity in experimental treatment samples from the native reach, with community assemblages more closely resembling those communities found in the saltcedar reach. The present results on species diversity of both diatoms and soft algae contradict previous research concluding saltcedar invasion negatively impacts all aspects of both aquatic and terrestrial ecosystems.

TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

CHAPTER 1

INTRODUCTION

1.1 Desert Streams

Streams in arid climates are generally warm, well-lit autotrophic systems with seasonal precipitation and characteristic flow regimes which provide water for only brief periods during the year (Busch and Fisher, 1981; Grimm, 1987). Flooding events, caused by summer monsoons cause mass transport of dissolved nutrients in runoff and eliminate most biota, essentially resetting the system to an early stage of succession post disturbance (Fisher et al., 1982; McLaughlin, 2008). Producer biomass will rapidly return to preflood levels following a fairly predictable successional pattern starting with diatoms, later replaced by green algae, followed by cyanobacteria (Fisher et al., 1982). As time passes, decreases in flow will lead to development of a dense filamentous green algal mat in late spring.

1.1.1 Hydrology

On an annual basis, hydrologic flux in desert streams is extreme. Peak flow during severe flooding events can be several orders of magnitude in excess of base flow rate, carving a wider channel, compared to base flow (Grimm, 1987). Post flood recovery occurs rapidly, often with physical and geomorphic conditions returning to predisturbance parameters within 2 days (Fisher et al., 1982). Valett et al. (1994) suggest that the resilience of these arid land aquatic systems is greatly enhanced by tight hydrologic linkages between surface and hyporheic subsystems. These linkages were physically demonstrated in a Sonoran desert stream where surface water was traced as it flowed into subsurface zones and a significant amount returned back to the surface (Dent et al., 2007).

1

1.1.2 Metabolism and Nutrients

Desert streams generally exhibit high rates of gross primary production (GPP), but are usually nitrogen-limited (Grimm, 1980). In a well studied stream in the Sonoran desert, molar N:P is always very low at <5, while soluble reactive phosphorus (SRP) concentration rarely drops below 200µg/L (Grimm and Fisher, 1986; Grimm, 1987). High concentrations of phosphorus are attributed to southwestern desert soils of recent volcanic origin that are rich in mineral P. Nitrogen concentration is not always low, as summer monsoon events transport N in runoff and groundwater from terrestrial sources maintaining a supply to streamflow. Flooding not only scours the system of biota, but it homogenizes nutrient concentrations by turbulent mixing of sediments and water (Fisher et al., 1982; Grimm 1994; Dent and Grimm, 1999). In hydrologically stable periods, nutrient concentrations steadily decline, leading to spatial heterogeneity and predictable changes as biota return and microbial processes intensify due to reduction in flow (Dent and Grimm, 1999). During late successional stages, N concentrations may increase due to decomposition or N_2-fixation by cyanobacteria (Dent and Grimm, 1999). Fixation of nitrogen can supply 2.7% to 19% of the autotrophic annual demand (Grimm and Petrone, 1997).

Riparian vegetation of desert streams is characteristically sparse and generates very little allochthonous input, therefore algal production in these systems becomes increasingly important. Schade and Fisher (1997) determined that allochthonous input played an insignificant role in the nutrient dynamics and energy flow in a desert stream system, and even a large pulse of litter entering the creek in autumn was not enough to support shredders in the macroinvertebrate assemblage. Maximum input of nitrogen from leaf litter was less than 2% of that demanded by autotrophic production. Grimm (1987) found that benthic algae along with autochthonous detritus provided about 90% of the total nitrogen pool in the same creek in the desert southwest.

Measured as O_2, GPP in a desert stream generally exceeded respiration (Grimm, 1987). Despite these overall high rates of GPP, there is evidence that these streams could be heterotrophic during the late summer months when temperature and solar radiation are highest, because respiration should be at maximum hourly rates for the system, thus offsetting increased photosynthesis at these times (Grimm and Fisher, 1984). A significant flux of water both into and out of deep sediments could potentially shift a highly productive algal-based system to heterotrophy with high rates of deep sediment metabolism. This shift will modify stream ecosystems to extend below the surface sediments when they have permeable substrates. In fact, particulate organic matter (POM) transported during the monsoon season may be a major source of carbon and nitrogen to desert stream ecosystems, potentially fueling heterotrophic activity in sediments and the hyporrheic zone after the season has ended (Brooks et al., 2007). Interactions between zones can heavily influence the distribution and abundance of primary production (Valett et al., 1994).

1.1.3 The River Continuum Concept

Proposed by Vannote et al. (1980), the River Continuum Concept (RCC) is an approach attempting to describe stream and river characteristics based on stream order, riparian vegetation, particulate matter, producer abundance, and benthic macroinvertebrates. It suggests that a stream system will function predictably in a downstream direction and shift from heterotrophic headwaters to autotrophic downstream sections in response to increased solar energy as the stream bed widens and tree canopy separates, providing a decreased allochthonous input. A return to heterotrophy should occur further downstream, as the channel deepens and solar radiation is attenuated due to increased turbidity. This downstream gradient of allochthonous and autochthonous input, will determine the structure and function of the benthic macroinvertebrate community. Relative importance of the major functional groups of shredders, grazers, collectors, and predators gradually changes downstream along with food

supply (Vannote et al., 1980). Any deviation from the expected patterns of RCC could be explained by variations imposed by watershed geology, tributaries, location specific lithologic or geomorphic features, or riparian determinants such as extensive tree cover or open meadow (Minshall et al., 1983).

1.1.3.1 RCC and Desert Streams

There is evidence that the RCC generally applies for small streams and rivers in temperate climates and works best in clean, rocky headwater streams flowing through closed canopy deciduous forests. In desert streams, riparian vegetation is sparse generating little allochthonous input for the stream ecosystem, where algal production becomes increasingly important. Lack of allochthonous input tends to make desert streams exceptions to RCC (Minshall, 1983). Lamberti and Steinman (1997) found patterns consistent with RCC in a broad sampling of rivers, but streams in arid regions demonstrated the highest gross primary production (GPP), most likely due to the fact that photosynthesis was not limited by canopy cover. This led them to conclude that individual streams display unique relationships among hydrology, riparian vegetation, and benthic primary productivity making GPP a complex function of those parameters. The best predictor of GPP, which was highly variable among streams of the same order, was watershed size and this relationship could very well be driven by light, nutrient input, temperature and hydrology (Lamberti and Steinman, 1997).

There are, however, some similarities to the RCC in desert streams where permanent flow occurs. Stream beds are open to direct sunlight and are usually autotrophic with abundant growth of filamentous green algae and macroinvertebrates, dominated by fine particulate organic matter (FPOM) collectors (Cushing and Allan, 2001). In a study by Uehlinger et al. (2002), however, light availability, temperature and nutrient concentrations were enough to support high primary production rates, but absence of rocks and an unstable sandy substrate shifted the system to one dominated by respiration.

4

1.1.4 The Terrestrial-Aquatic Ecotone

The structure and processes of lotic ecosystems are, more than any other system, determined by their interface with the riparian zone and the interaction with the terrestrial ecosystem (Gregory et al., 1991; Naiman and DeCamps, 1997). Diversity and function of stream communities can be tightly linked to the degree of trophic connectivity between land and water (Wallace et al., 1997). Heat and light input are determined by riparian canopy composition and density, while allochthonous food resources directly affect the structure of invertebrate assemblages. In most aquatic systems, stream food webs were influenced by availability of terrestrial arthropods supplied by riparian forest canopies and inputs of particulate organic matter serve as an important energy resource (Nakano, 1999). Wallace et al. (1997) evaluated the impact of terrestrial litter inputs in a forest stream on the abundance, production and biomass of animals and determined that litter exclusion drives major changes in these parameters, demonstrating the importance of the ecotone between the terrestrial and aquatic systems. Therefore, changes in terrestrial community structure will have profound effects on the aquatic ecosystem structure.

Stream nutrient flux is affected by the retention capabilities of riparian vegetation and water quality can be altered by filtering materials that move into the riparian zone either from upland sources, or from the stream itself through subsurface waters (Peterjohn and Correll, 1984; Hill 2000; Fisher et al., 2001). Nutrient retention can occur rapidly at areas of interface with the stream, and only a small portion of inorganic N in groundwater became part of the stream inorganic N pool in a Central Amazon Basin stream margin (McClain et al., 1994; Schade et al., 2001). In Sycamore Creek, groundwater was observed to move to the riparian zone laterally out of the stream in much greater volume than from upland or deeper groundwater sources (Fisher et al. 2001). This movement pattern was in sharp contrast to mesic stream groundwater movement and it possibly results in increased nutrient retention by

riparian plants when compared to mesic system riparian zone hydrology, where labeled groundwater concentration decreases with distance indicating movement back into the stream. Fisher et al. (2001) found high variability but significant hydrologic connections between the riparian zone and the surface stream in terms of processing and retention of materials.

<div align="center">1.2 Salt-affected Streams</div>

Increased salinity of an aquatic freshwater system is strongly correlated with decreased algal and invertebrate biomass and diversity (Blinn and Bailey, 2001; Blinn et al., 2004; Clavero et al., 2000; Potter et al., 2005). Differences in community assemblage between sites can be attributed to magnitude and variability of salinity. Samples from sources with variable salinity supported a larger diversity than samples from sources with constant and relatively high salinity (Clavero et al., 2000; Kirkwood and Henley, 2006). This difference was possibly due to the coexistence of algal species with different halotolerances benefitting from the unstable salinity and exhibiting higher overall diversity. Long term salinity may reduce the sustainability of communities and the ability of r-strategist diatoms to respond to favorable conditions when a flush of fresh water occurs (Nielsen et al., 2003; Kirkwood and Henley, 2006). Species richness values can also be maintained at artificially high numbers because of persistent species that cease growth while waiting for a flush to occur (Kirkwood and Henley, 2006; Potter et al., 2006).

1.2.1 Benthic Community Assemblages

Macroinvertebrate communities can lose species and experience profound compositional changes in response to salinization, altering the trophic structure from scrapers and piercers to domination of filter-feeders and deposit-feeders could directly affect consumption of biofilm and associated stream productivity (Marshall and Bailey, 2004; Piscart et al., 2005). Water salinity is a significant constraint on growth and community assembly in benthic communities and when compared to other algal groups, diatoms are most sensitive to changes in porewater (water filling the spaces between grains of sediment) salinity (Kirkwood

<div align="center">6</div>

and Henley, 2006; Leland et al., 2001). When studied along with water temperature, pH, conductivity, and total dissolved solids, salinity was the most important tested parameter influencing diatom assemblages (Gell, 1997). Potter et al. (2005) observed an inverse relationship between salinity and genus diversity, but indicated that this decline was likely due to dominance by fewer taxa, rather than a loss of richness. It is suggested that if some sensitive species were present prior to any increase in salinity, those species simply persisted in a metabolically inactive state. This conclusion is based on the presence of halosensitive genera, such as *Entomoneis, Nitzschia,* and *Amphora* in found in samples collected from high salinity water (Kirkwood and Henley, 2006; Potter et al., 2005). Other studies determined that loss of diatom diversity attributed to salinity increases was accompanied by a corresponding decrease in species richness (Blinn and Bailey, 2001; Blinn et al., 2004). Variable, or fluctuating conditions may actually promote algal diversity, as it is only necessary that an individual survive through extremes until favorable conditions return. Diatoms can simply survive in salinities above those in which they are able to divide. The highest salinity at which net diatom growth occurred was 15% soluble salts, although 7.5% salinity seems to be a critical physiological point for most species to cease growth (Clavero et al., 2000; Kirkwood and Henley, 2006).

1.2.2 Interactions

Although salinity can explain much of the variability in diatom diversity, there are often other water chemistry parameters that covary with it in salt-impacted streams (Potter et al., 2005). Since the process of salinization likely influences several water quality parameters that interact, it is impossible to attribute all effects of the change in stream community structure to salinity alone. One such interaction, capable of affecting algal and macroinvertebrate communities in this of salinity and phosphorus. Blinn et al. (2004) studied secondary salinization, which is a consequence of human activity, and determined that salinity was not only significantly correlated with diatom community structure, but inhibited macroinvertebrate

assemblage, as well. At lower salinity ($\leq20\mu S/cm$), diatom community structure was defined by the interaction of phosphorus and salinity. At higher salinity, i.e. in hypersaline environments, salinity was the dominant factor (Blinn and Bailey, 2001). This interaction may be due to the decrease in the activity coefficient of phosphate corresponding with increasing salinity, suggesting that phosphate should be more soluble in saline systems than in freshwater (Nielsen et al., 2003). Elevated levels of sulfate, dissolved iron and nitrate have been associated with saline groundwater, and sulfate has been implicated in phosphorus cycling. Anaerobic respiration by sulfate-reducing bacteria results in production of hydrogen sulfide which can play a role in dissolving iron minerals, thus releasing phosphorus previously associated with iron ions leading to the assumption that phosphate should be more soluble in more saline systems (Nielsen et al., 2003). Nitrogen, already low in desert streams, could exhibit the opposite trend as sediment levels have been observed to decrease in availability as salinity increases (Hopkinson et al., 1999).

1.3 Saltcedar Invasion

In terms of species loss, biological invasions are one of the primary threats to earth's ecosystems, second only to physical habitat destruction (Vitousek et al., 1997; Wilcove et al., 1998; Wilson, 1992). Invaders imposing the most severe impacts are those which can engineer existing habitat making it unfavorable for native species. This can be accomplished by creation, destruction, or modification of processes such as productivity, consumption, water fluxes, nutrient cycling, soil fertility, erosion and disturbance regime (Vitousek, 1986; Crooks, 2002). To alter, or engineer these natural ecosystem properties, an invader must have the ability to access available resources in a novel way and then utilize them more efficiently or intensely relative to native species (Vitousek, 1986). Alternative use of resources can enable a species to grow faster, larger or more densely than natives, allowing successful habitat invasion.

8

Saltcedar, *Tamarix* spp., is a halophytic shrub native to China, Mongolia, southern Europe and northern Africa (Baum, 1967). Eight species of *Tamarix* have been introduced to the United States and seven are called saltcedar. This is in reference to its ability to excrete salt through glands in small cedar-like leaves (Frasier and Johnsen, 1991; DiTomaso, 1998). Five of the eight *Tamarix* species are currently present in riparian areas of the desert southwest (DiTomaso, 1998) and have rapidly expanded distribution over the last century (Everitt, 1998).

Compared to most native species, saltcedar exhibits a longer annual reproductive period, flowering twice in a season in many areas (Everitt, 1980; Brotherson and Field, 1987; Gladwin and Roelle, 1998). It is characterized by a rapid seed set, requiring wet areas for germination and early growth. Resources are dedicated to establishment of a tap root down to the water table with very little branching, rendering saltcedar drought-tolerant (Brotherson and Winkle, 1986; Brock, 1994). Once the water table is reached, an extensive root system is developed, enabling the species to sequester soluble salts from deep in the soil profile and to redistribute them to the soil surface (Brotherson and Field, 1987; Kerpez and Smith, 1987). Distinct adaptations of saltcedar for water usage as well as tolerance or interactions with soluble salts in the soil give this species the ability to outcompete natives and cause a shift in riparian community structure from gallery forests dominated by Fremont cottonwood (*Populus fremontii*) and Goodding willow (*Salix gooddingii*) to saltcedar shrub thickets (Busch and Smith, 1995; Dwire and Kaufmann, 2003). These species composition changes can alter fundamental ecosystem patterns, such as flooding, erosion, fire frequency and biodiversity (Busch and Smith, 1995; DiTomaso, 1998). The most noted example of the impact on riparian ecosystems is reduced availability of water in arid and semi-arid areas, where water is already scarce. By further decreasing water availability, saltcedar gains a competitive advantage which will lead to an overall drying of the habitat, desertification of flora and loss of biodiversity along riparian corridors in the southwest (Stromberg et al., 2007) The southwestern region of the United

States has been experiencing drought conditions since 1998 and many riparian areas are no longer able to support shallow-rooted phreatophytes, such as cottonwood, giving a strong competitive advantage to deep-rooted saltcedar (Harms and Hiebert, 2006). Currently, saltcedar has extensively colonized waterways throughout southwestern desert riparian areas; it is estimated to cover 470,000-650,000 hectares and to cost about 127-291 million dollars per year in lost ecosystem services (Zavaleta, 2000).

Once planted for erosion control because of its extensive root system, saltcedar stabilizes bank and traps sediment, thereby increasing hydraulic roughness and water flow. Increased sedimentation leads to channel shallowing and width restriction and as the river is narrowed, saltcedar is able to establish itself further into the channel leading to reduction in streamflow and further channel narrowing (Kerpez and Smith, 1987; DiTomaso, 1998). Research has firmly established saltcedar as a terrestrial habitat modifier and ecosystem engineer in riparian zones.

1.3.1 Salinization of Soil

It has been suggested that saltcedar is allelopathic, due to its ability to excrete salt and tolerate increased salinity (Brock, 1994), but recently it has been demonstrated that litterfall and saline leaf exudates can, in fact, drive an increase in soil phosphorus solubility due to increased polyphenol compounds excreted by salt glands (Lesica and DeLuca, 2004). It is possible that this positive impact on nutrient availability on an infested system would far outweigh the hypothesized allelopathy of saltcedar. Although phosphorus concentrations remain the same between areas dominated by saltcedar and those with native species dominating, it becomes more readily available, giving saltcedar an advantage (Bus and Smith, 1995; Kennedy and Hobbie, 2004). Soil magnesium and calcium were unaffected by saltcedar (Lesica and Deluca, 2004).

1.4 How Saltcedar Alters Desert Streams

As an invasive species becomes a community dominant, it is likely to have environmental effects that are evident over broader areas than it actually occupies. This would be especially apparent with riparian invaders that directly modify terrestrial ecosystem properties and can potentially have cascading effects on aquatic ecosystem function. Introduction and invasion of saltcedar has involved radical changes in instream habitats, as it has affected fluvial geomorphology (Tickner et al., 2001). Saltcedar has a consistently negative effect on instream biotic integrity under mountain and xeric conditions when quantified using macroinvertebrate and vertebrate multimetric indices (Ringold et al., 2008).

Saltcedar impacts on the terrestrial ecosystem are well-documented and not limited to drastic changes in soil chemistry and shifts in hydrology and water use. Evidence of differences in disturbance regimes and phenological impacts are also rampant in invaded communities in the western United States. Comparatively unknown are the aquatic impacts of saltcedar infestation along riparian corridors. Changes in nutrient availability and macroinvertebrate community composition, as well as shifts in productivity are evident, but not as well understood as terrestrial changes (Bailey et al., 2001). Saltcedar is altering properties in these aquatic communities, as there are tight linkages between riparian vegetation and stream processes (Ringold et al., 2008). It is imperative that these shifts are examined to better elucidate the consequences of this invasive species.

1.4.1 Aquatic communities

Saltcedar litter may also have a role in structuring aquatic macroinvertebrate communities because of differences in leaf architecture and litter decomposition rate relative to native plants (Bailey et al., 2001; Going and Dudley, 2008). Saltcedar litter is an acceptable short-term source of nutrition, as larval growth was comparable to that of native litter, but the fragility of the leaves and increased rate of decomposition will lead to lower macroinvertebrate

11

abundances (Going and Dudley, 2008). Bailey et al. (2001) found lower aquatic arthropod abundance and richness per unit leaf mass when compared to cottonwood, leading to the conclusion that cottonwood is a superior resource over time. It remains unclear whether these decreases were due to lower quality of food resource or reduced habitat suitability of saltcedar leaves.

Saltcedar clearing from the riparian zone of Jackrabbit Spring in New Mexico increased densities of native pupfish and decreased density of an exotic crayfish in the same system (Kennedy et al., 2005). This result was most likely due to significant increase in algal production following removal, as reported by Kennedy and Hobbie (2004) because pupfish and screwnail snails are strongly dependent on algal-derived carbon (Kennedy et al., 2005). Changes resulting from saltcedar presence have likely influenced resource availability and habitat complexity affecting macroinvertebrate community structure by causing shifts in favor of exotic consumers over native fish (Bailey et al., 2001; Kennedy and Hobbie, 2004; Kennedy et al., 2005). Ringold et al. (2008) reviewed invasive riparian species in mountain and xeric conditions and showed that saltcedar presence always had a negative impact on instream biotic integrity, quantified with macroinvertebrate and vertebrate indices.

1.4.2 Stream Productivity

An invasion can drive a decrease in net productivity by tying up more nutrients in biomass or undecomposed organic matter. Saltcedar alters the quality of dominant plant litter and provides a poorer quality food resource for decomposers and macroinvertebrates in aquatic systems (Kennedy and Hobbie, 2004). In a study of Jackrabbit Spring in New Mexico, saltcedar presence has shifted reaches of the stream from a system based on autochthonous production to a system dependent on allochthonous inputs (Kennedy and Hobbie, 2004). Saltcedar dominated sites, cleared sites and sites dominated by native riparian species were compared and saltcedar sites had lower temperature-adjusted chlorophyll and macrophyte production and

12

greater allochthonous inputs than almost all native and cleared sites (Kennedy and Hobbie, 2004).

Stream productivity can also be affected by increased shading resulting from saltcedar presence. According to Kennedy and Hobbie (2004), the average photosynthetically active radiation (PAR) values for saltcedar dominated sites were lower than values in native and cleared riparian sites. Removal of saltcedar from experimental sites led to a 60% increase in photosynthetic photon flux (PPF) when it was measured at the mid-canopy level in willow communities (Busch and Smith, 1995).

<div align="center">1.5 Effects of Saltcedar on McComb Creek Ecosystem</div>

The effects of saltcedar invasion on instream algal community assemblages have not been studied. It is important to characterize how saltcedar invasion has affected their colonization, succession and biomass accumulation, as algae are a high quality food resource and particularly important primary producers in these autotrophic systems of the desert southwest. In order to further understand the effects of saltcedar on aspects of the aquatic ecosystem, I located a site in an area unpopulated by humans in Presidio County, Texas, which covers 998,839 hectares. Saltcedar invasion along the Rio Grande is well-documented by Everitt (1998). It is the dominant plant along the river banks on both the United States and Mexican sides of the border, forming monocultural stands for 10 to 20 meters perpendicular to the river edge. McComb Creek is the only permanently flowing tributary to the Rio Grande in the county and saltcedar invasion is currently proceeding in an upstream direction from its confluence with the river. The extent of the invasion, at the time of this study was approximately 1.5km at the lower end of the 9.5km stream.

The invasion in progress provided an opportunity to compare a site on a lower reach of the creek with saltcedar established as the dominant riparian species to an upstream site on the same creek that continues to be dominated by native riparian species. I expected that saltcedar

presence would significantly increase water salinity due to soluble salts being deposited in the stream from dripping leaf glands and leaf litter fall. Water salinity should drive a corresponding increase in algal species richness and diversity due to potentially increased availability of phosphorus along with basic cations. The inclusion of halotolerant species should add to increases in richness and diversity, as well, in this oligotrophic system. Increase in diversity should be especially apparent in diatom assemblages, due to the increased shading of the stream margins by the invasive saltcedar. The presence of saltcedar may be responsible for differences in other water parameters that could affect algal colonization, including pH, conductivity, total nitrate and phosphates, shown to strongly affect diatom communities (Biggs, 1990; Belore et al., 2002). Water temperature differences may not be significant due to proximity of the native and saltcedar dominated reaches.

Increased woody vegetation presence, in the form of saltcedar, will effectively increase allochthonous input to McComb Creek at the lower saltcedar-invaded reach. The abundant, tiny leaves form a thick mat on the ground beneath the trees and along the bed of the stream. Conversely, the vegetation in the native reach is characterized by shrubby growth of seepwillow, *Baccharis* sp., and catclaw acacia, *Acacia greggii*, with a few small leaves. It provides no canopy over the water and leaf litter is sparse along the banks and stream margins. According to the RCC, as a stream increases in order downstream from the headwaters, predicted shifts in primary productivity and allochthonous inputs would occur. McComb Creek remains a first order stream throughout, but there should be a significant shift from autochthonous input in the native reach to allochthonous input in the lower saltcedar dominated reach. The native reach should exhibit characteristics of an oligotrophic system, with low nutrients, leading to low algal biomass, and P:R ≈ 1. The saltcedar reach will have higher nutrients, leading to an increased algal biomass and increased photosynthesis, but the

14

increased litter input would drive increased respiration, resulting in a P:R ≈ 1 in the saltcedar invaded reach, as well.

1.5.1 Hypotheses

Saltcedar invasion on the lower reaches of McComb Creek will significantly shift the aquatic system from a characteristically oligotrophic desert stream ecosystem to a more eutrophic system dominated by halotolerant diatoms.

1.5.1.1 Hypothesis I

The presence of saltcedar may be responsible for differences in water parameters that could affect algal colonization, such as alkalinity and phosphates which are important predictors of species variation in periphyton communities. Water samples will be taken during surveys to determine if there are significant differences between the two reaches.

Saltcedar growth along stream banks will cause an increase in canopy cover of the stream. This increased shading will result in lower daily PAR values and could potentially have an effect on water temperature. Canopy cover will be estimated to test whether significant differences exist between the two study reaches.

1.5.1.2 Hypothesis II

Water salinity increase following saltcedar invasion should drive a corresponding increase in algal species richness due to increased availability of phosphorus. If saltcedar presence does have a positive affect on phosphorus, there will be eutrophic species present in the saltcedar reach but not in the native reach. If this is the case, transplantation of substrates between reaches will demonstrate the loss of these species as they are moved from the saltcedar to the native reach. At the same time, P-enrichment in the native reach will cause an establishment of species characteristic of the saltcedar reach (Figure 1.1). Presence of halotolerant species in the saltcedar reach may also contribute to increased richness, as oligotrophic desert systems are characteristically species poor.

15

1.5.1.3 Hypothesis III

Increased presence of woody deciduous vegetation, in the form of saltcedar, will effectively increase allochthonous inputs in the form of leaf litter to McComb Creek at the lower invaded reach, which will drive an increase in respiration. Any increase in photosynthesis resulting from increased nutrients and salinity will be counteracted and the P:R of McComb Creek, within the confines of my study, will remain ≈ 1. The P:R ratio in the native reach will be ≈ 1 as well because of both low photosynthesis and low Allochthonous inputs, i.e. respiration. Litter will be collected to determine if allochthonous input is significantly greater in the saltcedar reach. A series of dissolved oxygen data will be collected to determine stream metabolism.
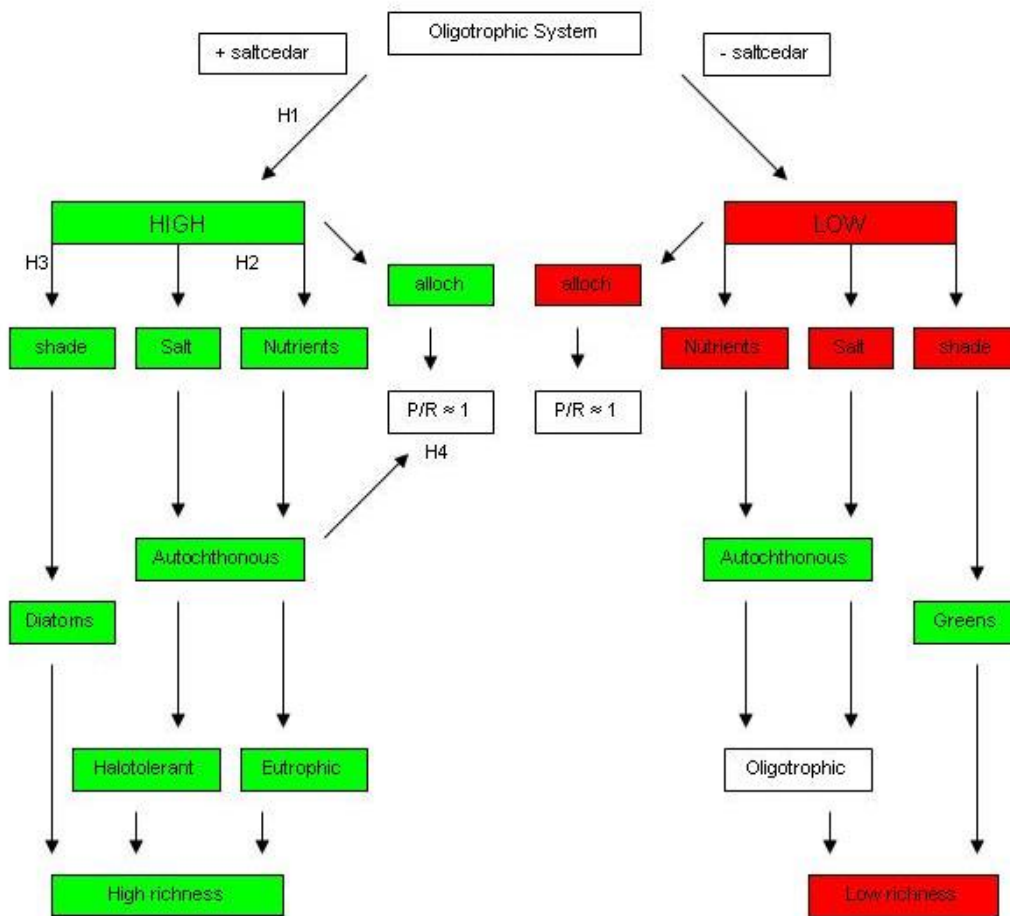
Figure 1.1 Expected effects of saltcedar presence on an oligotrophic aquatic system. Oligotrophic algal species are fewer in number than eutrophic species. Red indicates values that are low, while green indicates high.

CHAPTER 2

METHODS

2.1 Site Description

Sites selected for this study were located along McComb Creek in Presidio County, Texas (Figure 2.1). Presidio County has a subtropical arid climate, with seasonal temperature variations from 0^0C to $+38^0$C. Most precipitation occurs during the summer months and averages 30.5cm/year. Located in the Coldwater Canyon of the Sierra Vieja, McComb Creek is the only permanent stream in the county with continuous flow established in 1964 when the well head on a hot water well was broken (Nelan, pers comm) at the headwaters ($30^0$20'12.24"N $104^0$41'30.23"W). The stream runs down the canyon to a desert floor consisting of quaternary alluvial deposit bedrock covered by gravel, sand and silt. It reaches a confluence with the Rio Grande ($30^0$18'11.00"N $104^0$45'52.85"W) at the border of the United States and Mexico. It covers a total distance of approximately 9.5km and the stream bed ranges in width from 4m to 40m (Figure 2.2).
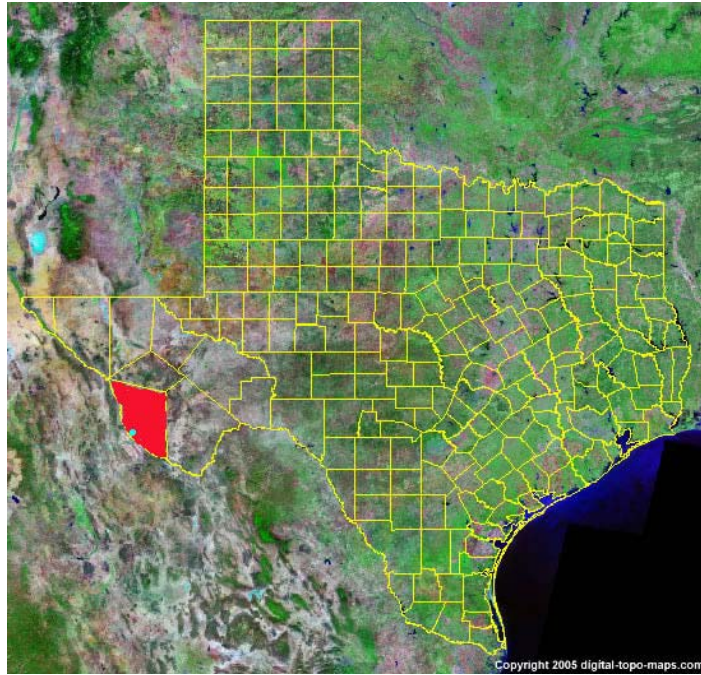
Figure 2.1 Satellite view with Texas counties overlay. Presidio County is indicated in red with a
small blue dot indicating the location of
McComb Creek research site
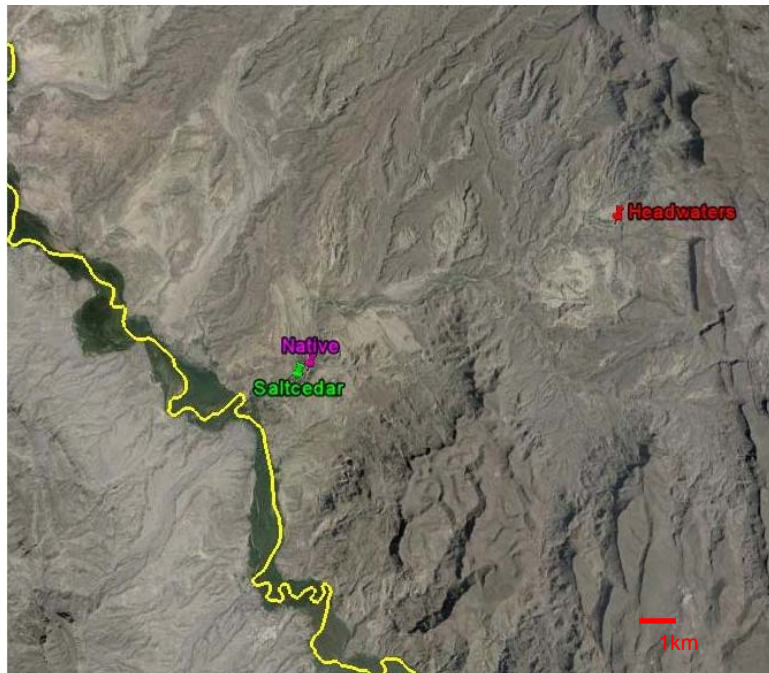
Figure 2.2 Aerial image of McComb Creek identifying the
headwaters and the confluence with the Rio Grande.

19

The spread of saltcedar along the Rio Grande currently covers an extensive area along the banks of the river, both in Presidio County and Mexico. In recent years, saltcedar invasion has proceeded upstream along McComb Creek, from its confluence with the river. The current extent of this invasion stretches approximately 2km and the leading edge of the infestation corresponds with the established saltcedar site for this study ($30^0$18'33.39"N $104^0$45'17.21"W). In this area, McComb Creek supports both invasive saltcedar and native riparian vegetation, providing a reference for determining the impact of saltcedar on aquatic communities (Figure 2.3).
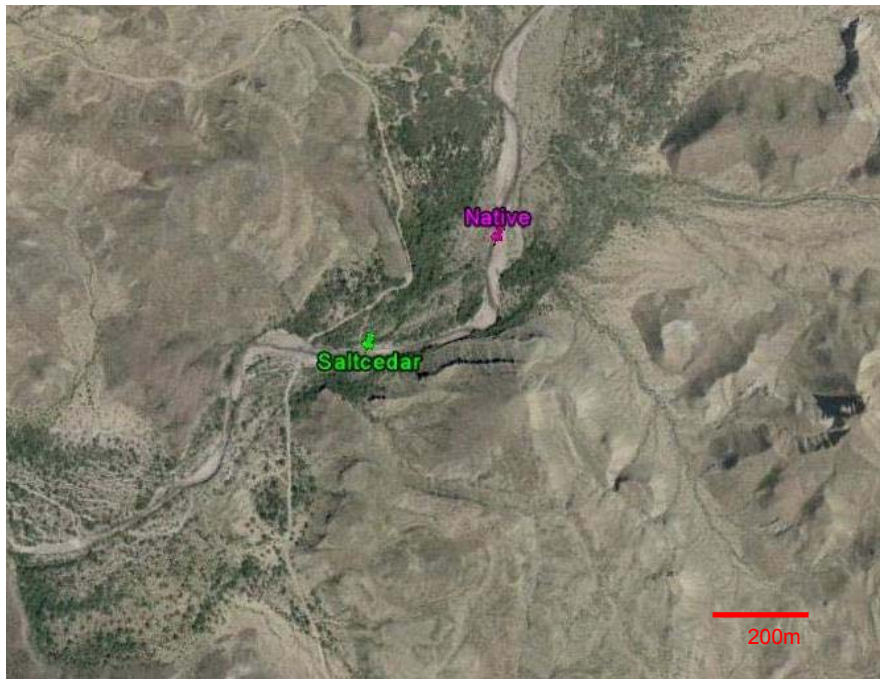
Figure 2.3 Aerial image of lower McComb Creek with the location of the study site identified.

2.1.1 Sampling Area

In October of 2005, aquatic sampling transects were established in the 100m native (Figure 2.4) and saltcedar invaded (Figure 2.5) sites. Beginning at 0m and ending at 100m, these transects were placed at 25m intervals crossing the stream perpendicularly for a total of 5

transects in each reach. Transects were marked, on each side of the creek, outside of the floodplain, with rebar and flagging and were utilized during both sampling seasons to mark sites for substrate deployment and data collection.

Figure 2.4 Image of the native reach of McComb Creek from downstream and facing north in January 2007. Vegetation is primarily *Baccharis* and *Acacia*.

Figure 2.5 Image of the saltcedar dominated reach, photo was taken from the downstream end of the sampling area, facing Northeast in April 2007.

2.2 Vegetation Analysis at McComb Creek

Vegetation analysis was carried out in July of 2005. A line-intercept analysis (Krebs, 2008) was utilized to estimate vegetation composition along the banks of the creek in order to

ensure that one site could accurately be classified as native and the other as saltcedar-invaded. Transects were 100m in length and ran parallel to the stream bank at 0m (edge) and at 10m away from the stream bank. Shrubby and woody species found touching or overlying the line were identified according to Powell (1988) and recorded. The length of the line that each individual intercepted was recorded, as well as the maximum width of the individual perpendicular to the transect line. Using these data, relative abundance of each species was calculated for each reach (Table 2.1 and Table 2.2).

Table 2.1 Native Reach Vegetation

NATIVE REACH	SE 0m	SE 10m	NW 0m	NW 10m
Acacia	27%	13.8%	2%	3%
Baccharis	12.3%	4.8%	12.4%	5.6%
Chilopsis	5.5%	0%	16.6%	0%
Larea	1.7%	4.8%	1%	0%
Prosopis	0%	9.7%	2.9%	10.4%
Salix	4%	0%	0%	0%
Tamarix	1.5%	0%	0.5%	8.2%
Ziziphus	0%	4%	0%	0%

Table 2.2 Saltcedar-invaded Reach Vegetation

SALTCEDAR REACH	N 0m	N 10m	S 0m
Acacia	2.6%	9.9%	0%
Baccharis	0.9%	0%	0%
Chilopsis	3.7%	0%	21.8%
Larea	0%	4%	0%
Prosopis	12.5%	55.7%	28.3%
Salix	0.9%	0%	0%
Tamarix	45%	18%	83.4%
Ziziphus	0%	0%	1.1%

2.2.1 Canopy Cover

Canopy cover was estimated along the margins of the stream by standing in the water at 1m and 3m away from each bank, following the 25m transects established for aquatic sampling. A spherical densiometer (Spherical Densiometer Concave Model C – Forest Densiometers) was used to measure the amount of surface water that was covered by shade

from streamside vegetation. Four densiometer readings were taken from each point while facing

north, south, east and west and percent overstory density was calculated (Table 2.3).

Table 2.3 Percent Canopy Cover in Saltcedar and Native Reaches

Reach	Bank	Canopy Cover at 1m (%)	Canopy Cover at 3m (%)
Saltcedar	West	60	15
Saltcedar	East	83.4	65.1
Native	Southwest	8.3	0
Native	Northeast	1.7	0

Canopy cover and PAR values (see section 2.6) were used to determine whether the

saltcedar site has experienced increased shading and lower overall PAR values compared with

the native site, as in Hypothesis I.

2.3 Algal Colonization

In December of 2005, 10 artificial substrates were deployed in pairs in each site along

the established 25m transects. One of each pair was deployed in the water within 5m of the

bank and the second was deployed in the thalweg of the stream along that transect. Often there

was little difference between the depth at the margin of the creek and the deepest point.

Substrates consisted of an approximately 0.05 X 0.10 X 0.5m piece of wood with 5 unglazed 2.4

x 2.4cm ceramic tiles attached to the top surface, equally spaced using polyurethane glue. On

each end of the wood, a 1.5cm hole was drilled and a 1m length of rebar was threaded through

and driven into the streambed to secure the artificial substrate in place. Bailing wire was

wrapped through the holes in the wood and around the rebar to prevent substrates from floating

to the surface (Figure 2.6).

Figure 2.6 Image of artificial substrate
deployed in McComb Creek in
January 2007.

2.3.1 Sample Collection

Substrates were deployed in this manner beginning December of 2005 and sampled after each period of between 28 and 30 days until April of 2006 (Table 2.4). Following each time interval, substrates were removed from the water and one of the two inner tiles was sampled for algae. A straight razor blade was used to scrape benthic species from the tile surface into a 50ml centrifuge tube and the blade was rinsed using distilled water. Scraping was followed by vigorous brushing with a nylon toothbrush which was then rinsed into the same tube with distilled water. Samples were homogenized and analyzed for chlorophyll content using a HydroLab DataSonde 5 and then preserved using 4% formalin for later microscopic identification in the lab. Substrates were cleaned using distilled water and a scrubbing sponge and then deployed once again. The final sampling of that year was performed in April of 2006. Sampling was not possible during the remainder of the year. Between April and July there was

low flow and overgrowth of a filamentous green algal mat which covered the surface of the water and eliminated light to the benthos. Between July and November there were severe flooding events.

In December of 2006, substrates were once again deployed, in pairs, along the established transects of each site. The samples from the previous year had been examined and algal colonization was sparse. It was determined that substrates should be deployed for longer time periods to allow for algal colonization and substrates would remain in the water for 40 to 45 days. Sampling occurred between December and April, when the substrates were removed from the water permanently.

2.3.2 Transplant Experiment

In January of 2006 and January of 2007, substrates from the algal colonization experiments were utilized to run a concurrent transplantation experiment (Table 2.4). Four artificial substrates were retrieved from each site after 15-20 days of deployment. One tile was marked and sampled from each substrate and the substrate was then transplanted to the other site, these samples were labeled N_{17} for the native samples and S_{17} for the saltcedar reach samples. Substrates retrieved from the saltcedar site were transferred to the native site and those retrieved from the native site were re-deployed in the saltcedar site. At the end of the regular sampling period, 15-20 days later, transplanted substrates were retrieved and samples were taken from the tile scraped in the previous sampling, samples from tiles that had been moved from the native to the saltcedar site were labeled S'_{17} and those transferred from saltcedar to native were labeled N'_{17}. An additional tile, one that had been left untouched prior to the transfer was also sampled and labeled, $N_{17}S'_{17}$ for the sample that spent the first part of the experiment in the native reach and was moved to the saltcedar reach and $S_{17}N'_{17}$ for the corresponding sample that was transferred from the saltcedar to the native reach. Samples that

were collected from tiles that spent the entire duration of the study in one reach were labeled $N_{17}N'_{17}$ for the native reach and $S_{17}S'_{17}$ for the saltcedar reach.

2.3.3 Nutrient Enrichment

In January of 2007, clay pots containing 2% agar and nutrients were prepared according to Fairchild et al. (1985) and deployed in both research site reaches (Figure 2.7). Phosphorus enrichment was in the form of 0.5mol/L concentration K_2HPO_4 and nitrogen as 0.5mol/L concentration $NaNO_3$. Four types of diffusing agar were used; nitrogen, phosphorus, nitrogen and phosphorus and a non-nutrient control pot containing only agar. Two of each type were deployed in both the native and the saltcedar reaches, with the control pot at the top of the reach. Algal samples were scraped from a 2.5 x 2.5 cm area of each pot after 35 days and samples were once again obtained from the same area on the pot after another 35 days. Samples were scraped from the clay pots and preserved in the same manner as those from the artificial substrate tiles.

Figure 2.7 Image of a nutrient-diffusing
Substrate in April 2007

2.3.4 Algal Sample Processing

Following transport to the lab, algal samples were left to settle for a period of greater than 24 hours. Excess fluid was decanted from the top of each tube and then the volume of each tube was brought to 5ml, using 4% formalin. Microscopic identification and enumeration of soft algal species was performed using a Palmer cell at 400X magnification. Multicellular species were measured and recorded in units of 10μmX10μm; unicellular species were given a count of one unit per individual. Diatom numbers were recorded, but individuals were not identified, at this time. Counts on each slide continued until 300 units had been reached, or a maximum of 75 fields had been scanned.

Samples were then processed to exclude organic matter, using sulfuric acid and potassium permanganate, washed with distilled water and then mounted using Naphrax®. Diatoms were identified to species according to Patrick and Reimer (1966) at 1000X

magnification and counted until 300 individuals had been encountered, or the entire slide had been scanned.

Species were identified and quantified in order to characterize algal community assemblage in all of the above experiments. Diatom species were further ecologically classified regarding pH, nutrient, and salinity preferences according to Van Dam (1994). Algal community data were analyzed in order to determine the validity of Hypotheses II, in the previous section.

2.4 Leaf Litter Collection

In November 2006, four 5-gallon buckets were placed along the most densely vegetated bank of each site at 25m intervals. A 1.5cm hole was drilled through the bottom of each bucket to provide drainage for water and a 1m length of rebar was placed through this hole and driven into the ground to anchor the bucket upright (Figure 2.8). Contents of each bucket were removed every 35-40 days at the same time substrate samples were collected. Leaf litter was allowed to air dry on screens for 24 hours and placed in plastic bags and labeled. Once dried, litter was weighed and identified to species. Mass of collected litter will be used to help determine accuracy of Hypothesis III.

(a)

(b)

Figure 2.8 Images of leaf litter collection buckets in
place in November of 2006 in (a) the native reach
and (b) the saltcedar reach

2.5 Water Parameters

A HydroLab DataSonde 5 (Figure 2.9) was utilized to measure salinity, pH, chlorophyll a content, dissolved oxygen, PAR, and water temperature. During the first sampling season, the sonde was deployed once every 28-30 days, corresponding with algal sampling events, for 24 consecutive hours in the lower saltcedar reach and for the following 24 hours in the upper, native reach. Data were recorded each hour. In the following season, the sonde was again utilized according to the algal sampling schedules, so it was deployed for 24 consecutive hours in each site, in the same manner, every 38 to 40 days (Table 2.4). These data were used to determine whether physico-chemistry and algal production were significantly different between sites and could explain differential algal colonization between the two sites, as suggested in Hypothesis I.

Figure 2.9 Image of the HydroLab Datasonde
deployed in March 2007.

Depth and flow measurements were taken at each transect during each sampling event. Depth was measured with a meter stick and flow was measured using a Marsh-McBirney Flow-Mate Model 2000 portable flow meter.

Water samples were also collected from both sites during each of these data collection events. Samples were placed in 1L plastic bottles and frozen within two hours of collection. Samples were transported to the lab on ice and remain frozen until analyzed for ammonium-nitrogen, nitrate-nitrogen and soluble reactive phosphorus (SRP) content.

Water samples were thawed in refrigeration over the course of 12 hours and processed to determine the concentration of PO4 in the dissolved pool. To each 50mL water sample, 2 mL of molybdate antimony tartrate solution and 0.5mL ascorbic acid solution were added. Samples were swirled to develop color and absorbances were read at 720 nm using a 10 cm cuvette in a dual beam spectrophotometer.

Thawed samples were also used to determine nitrate-nitrogen and ammonia nitrogen using LaMotte testing kits, Code 3354 and Model SL-PAN Code 3315, respectively (LaMotte Company, Chestertown Maryland). Nitrogen was recorded in parts per million (ppm) when present in measurable amounts.

Data from this section were used alone and in conjunction with algal community data to determine the validity of Hypotheses I and II.

2.5.1 Dissolved Oxygen

A diel curve for dissolved oxygen was formulated according to Bott (1996). From this curve, gross primary production (GPP), net daily metabolism (NDM) and community respiration over the 24 hour period (CR_{24}) were determined. If the GPP exceeds the CR_{24} for a given 24 hour period, there was a net addition of energy to the system and NDM was a positive number (P>R). If GPP was less than the CR_{24}, NDM was a negative number and P<R (Bott, 1996). Photosynthesis to respiration ratios were determined for each 24 hour deployment of the sonde.

Table 2.4 Schedule of Experiments

EXPERIMENT	NOV 2005	DEC 2005	JAN 2006	FEB 2006	MAR 2006	APR 2006	NOV 2006	DEC 2006	JAN 2007	MAR 2007	APR 2007
Colonization		O	X	X	X	X		O	X	X	X
Transplantation			X						X		
Enrichment										X	X
Leaf Litter							X	X	X	X	
Water Chemistry	X	X	X	X	X	X	X	X	X	X	X
P:R		X	X	X	X	X	X	X	X	X	X
Depth and Flow	X	X	X	X	X	X	X	X	X	X	X

X – indicates when a month in which a particular survey or experiment was conducted
O – indicates a month in which a flash flooding event washed substrates away

32

2.6 Statistical Analyses

2.6.1 Algal Species Composition

Algal species counts for each site were analyzed with all species included and separately, as soft species and then as diatom counts. Soft algal species count data were converted from species units (10µm x 10µm) to organisms per mm^2. Species abundance values were calculated for each species in each sample and Maximum Relative Abundance of each species was determined. Average abundance of each species in each reach over all of the samples was calculated and paired sample t-tests were performed to determine differences in occurrence between saltcedar and native sites in soft species composition. Species richness, Shannon Weiner Index for species diversity and Jaccard's Evenness Index (J') were calculated for all samples and compared between sites by paired sample t-tests to test for any difference.

Relative abundance of each diatom species in each sampling period was determined using diatom counts. Maximum relative abundance for each species was determined, as was average relative abundance for each species in each reach. Paired sample t-tests were used to test for differences between saltcedar and native reaches.

Four multivariate techniques were utilized to examine the possible differences in algal species collected from artificial substrates from the saltcedar and native reaches. These analyses included: 1) analysis of similarities, 2) index of multivariate dispersion, 3) similarity percentages, and 4) nonmetric multidimensional scaling ordinations and were done with ANOSIM, MVDISP, SIMPER, and MDS procedures, respectively in the PRIMER software application (version 6.11; Plymouth Marine Labs, Plymouth UK; Clark and Warwick 2001).

A dissimilarity matrix was constructed for all algal taxa sampled from the artificial substrates by comparing the entire algal species composition of all sample pairs, organized according to reach and year. The intersample compositional similarities were computed with Bray-Curtis coefficient. Matrices were derived from untransformed relative abundance data for

all algal taxa (diatoms and soft species). A one-way ANOSIM was used to compare the average rank similarities of samples between the reaches. ANOSIM calculates a test statistic (R-statistic) which ranges between 0 and 1, indicating complete similarity and dissimilarity, respectively.

Factor value dispersion was calculated for each stream reach to determine within reach variability in benthic algal assemblage. An index of multivariate dispersion (IMD; Clark and Warwick 2001) is a ratio of these values describing the differing dispersion across the groups based on the similarity within groups.

The percent contributions of each species to the overall dissimilarity between the stream reaches was quantified by SIMPER analysis (Clark and Warwick 2001). This procedure also calculates the ratio of the mean dissimilarity for all of the sample pairs between groups to the standard deviation. This ratio indicates how consistently a taxon contributes to mean dissimilarity across all pairs within a group and is a measure of the importance of each taxon in discriminating communities between groups.

The ordination technique of nonmetric multidimensional scaling (NMDS) was utilized to provide a graphical summary of the relationships in the similarity matrices described above (Clark and Warwick 2001). Bubble plots show trends in species abundances in each month that were important in differentiating between stream reaches. Principal Component Analyses were utilized to account for the redundancy in the observed variables and to reduce those variables to a smaller number of Principal Components. The techniques outlined above were carried out on soft algae and diatoms separately to assess their individual behavior.

Eutrophic diatom density and the percent of total density represented by these species was calculated to determine if any differences existed between native and saltcedar reach diatom communities in terms of nutrient preferences.

2.6.2 Nutrient Enrichment Data

Species count data from nutrient diffusing pots were analyzed in three groups (all taxa, soft species only, and diatom species only), as the artificial substrate colonization data from above. Species richness and diversity were determined for all species found on each type of nutrient diffusing substrate (NDS); control pots (C_N and C_S), phosphorus diffusing pots (P_N and P_S), nitrogen diffusing pots (N_N and N_S) and combination pots diffusing nitrogen and phosphorus (NP_N and NP_S). Richness and diversity were also calculated for all NDS in each reach and paired sample t-tests were used to determine if there were any significant differences between sites in these indices.

The same four multivariate techniques as those listed in the previous section were utilized to examine the possible differences in species collected from NDS for; 1) all benthic algal species, 2) soft species only, and 3) diatom species only.

Chlorophyll *a* content in each treatment community was assessed to determine which nutrient, N or P, was limiting in each reach and relationships were analyzed between chlorophyll *a* and diatom density and biomass.

2.6.3 Litter Collection

Relative abundance of each species present was calculated and maximum relative abundance of each species across all samples, both saltcedar and native reaches, was determined. Relative abundance of each species in the native buckets versus relative abundance of the same species from the saltcedar buckets was compared for each month using paired sample t-tests. Relative abundance data was used to determine the overall contribution of each species to litterfall, or allochthonous input. Total mass of litter was calculated for each month and a paired sample t-test was performed to determine if there was a significant increase in allochthonous input at the saltcedar reach. Canopy cover density (%) was

35

also analyzed between reaches with a paired sample t-test to determine if there is increased cover in the saltcedar reach.

2.6.4 Environmental Data

Data obtained from deployment of the HydroLab Datasonde 5 (temperature, pH, specific conductivity, salinity, chlorophyll a, dissolved oxygen, and PAR) along with SRP, depth and flow were analyzed for differences between reaches using paired sample t-tests in SYSTAT, version 11.0. Calculated values for NDM, CR_{24}, GPP and P:R were analyzed using paired sample t-tests. Redundancy Analyses (RDA) was performed in CANOCO (version 4.5 for Windows) on diatom community data with all environmental variables, excluding specific conductance due to high correlation with salinity, to determine the proportion of total variance between saltcedar and native reach diatom community assemblages could be predicted from the environmental variables.

CHAPTER 3

RESULTS

3.1 Environmental Parameters

Organized by sampling date, paired t-tests indicated a significant difference between
the saltcedar reach and the native reach in pH (p=0.000), specific conductance (p=0.000),
salinity (p=0.000), dissolved oxygen (p=0.029), PAR (p=0.001), and SRP (p=0.037). Native
reach values for pH, dissolved oxygen content, and PAR were higher than corresponding
measurements in the saltcedar reach. Specific conductance, salinity and PAR were significantly
greater than in the saltcedar reach. There was no significant difference detected between
saltcedar and native reach in temperature, chlorophyll *a*, depth, or flow. Nitrate-nitrogen was
only present in measurable amounts in samples taken from directly below the NDS in January,
March and April of 2007. There was no measurable ammonia nitrogen at any sampling time.
Descriptive statistics and p-values are recorded in Table 3.1 and relationships between
significant environmental variables are demonstrated in Figure 3.1.

Table 3.1 Environmental variables and paired sample t-test
results for saltcedar versus the native reach

	SALTCEDAR				NATIVE				
	min	max	mean	sd	min	max	mean	sd	p
TEMP (^{o}C)	12.20	22.30	15.64	3.71	7.26	23.39	14.76	5.32	0.209
pH	8.50	8.70	8.58	0.07	8.54	8.88	8.80	0.10	**0.000**
SCON (mS/cm)	2.17	2.29	2.23	0.04	2.08	2.19	2.11	0.03	**0.000**
SAL (ppt)	1.16	1.22	1.19	0.02	1.10	1.17	1.13	0.02	**0.000**
DO2 (mg/L)	0.51	11.20	4.50	3.66	1.19	20.50	8.98	6.31	**0.029**
PAR (E/s/m)	52.13	191.38	109.07	49.76	66.71	419.92	269.83	112.88	**0.001**
CHLa (g/L)	3.60	255.76	91.43	79.53	11.00	236.93	62.25	73.21	0.079
SRP (µM)	0.929	1.600	1.297	0.234	0.465	1.587	0.954	0.413	**0.037**
NH4 (ppm)	0	0	0	0	0	0	0	0	0
NO3 (ppm)	0	0	0	0	0	0	0	0	0
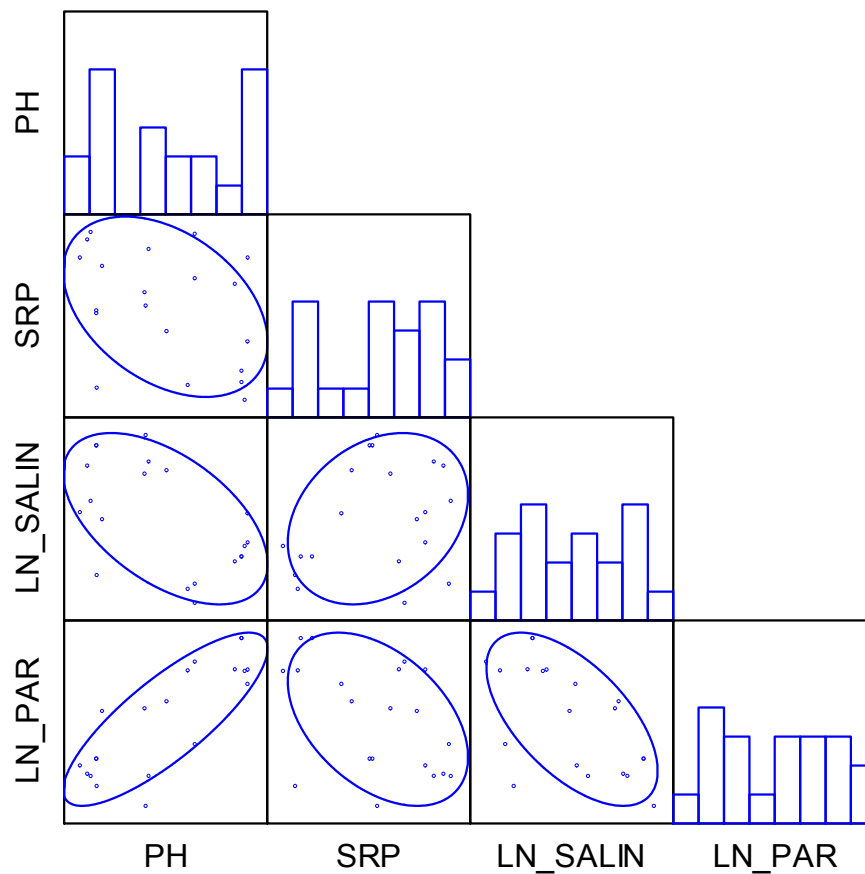
Figure 3.1 Relationships between significant environmental variables
across both sample reaches

Principal Component Analysis, limited to the significantly different environmental variables, indicated that the first two principal components account for 85% of the variance in the data. Water salinity and specific conductance have the highest positive correlation (both 0.47) with the first principal component axis, while PAR is negatively correlated (-0.46). Both DO and SRP had strong negative correlations with the second principal component axis, with -0.58 and -0.632, respectively. An ordination plot indicates a clear separation between the saltcedar (S) and native (N) reach, with salinity and specific conductance more closely correlated with the saltcedar reach and pH and PAR with the native reach (Figure 3.2).
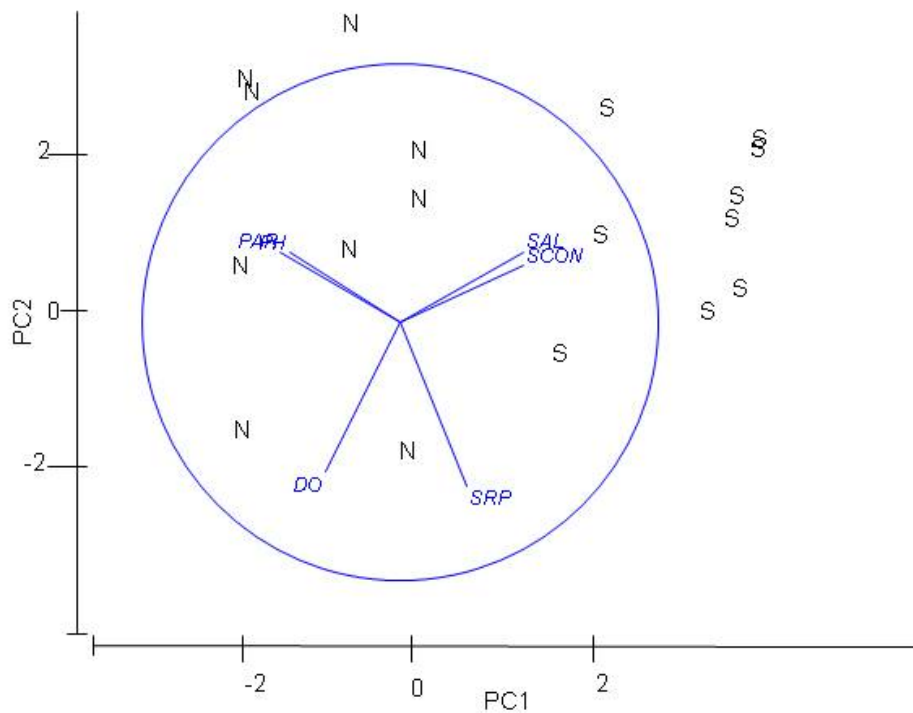
Figure 3.2 PCA ordination of significant environmental variables and
their relationship to sample communities

3.2 Artificial Substrate Colonization

3.2.1 All taxa

Forty-four species of benthic algal colonizers were identified between January of 2006 and April of 2007. Average species richness value for the saltcedar reach was higher than that for the native reach (p=0.03; Figure 3.3) at 21 and 17, respectively. Shannon-Weiner's Diversity Index (H') was not significantly different between the two reaches (p=0.16) nor was Jaccard's (J') Evenness (p=0.14). A paired sample t-test also indicated there was no significant difference between saltcedar and native reaches in green algal species abundance (p=0.531).
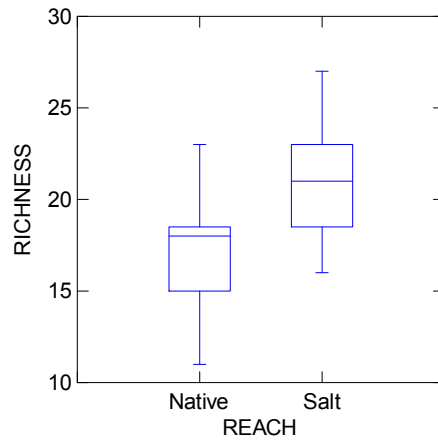
Figure 3.3 Species Richness of Benthic
Algal Assemblage by Reach

Analysis of Similarity (ANOSIM) was used to compare average rank similarities of samples between the reaches and an R-statistic of 0.134 was close enough to zero to indicate very little difference in benthic algal communities as a whole between the saltcedar and the native reaches. Average dissimilarity according to SIMPER dissimilarity within both reaches was 71%. This large temporal dispersion within communities is also reflected in the factor dispersion values obtained from the Multivariate Dispersion function (Native=1.001 and Saltcedar=0.999), which indicates the extent of spread between the communities in multivariate space. The average dissimilarity between the native and saltcedar sites when including all benthic taxa for analysis was 74%, with *Anabaena constricta* and *Achnanthidium minutissimum* each contributing 15% to that dissimilarity. Ordination plots do not indicate a clear separation of stream reaches, based on benthic species composition (Figure 3.4).

40
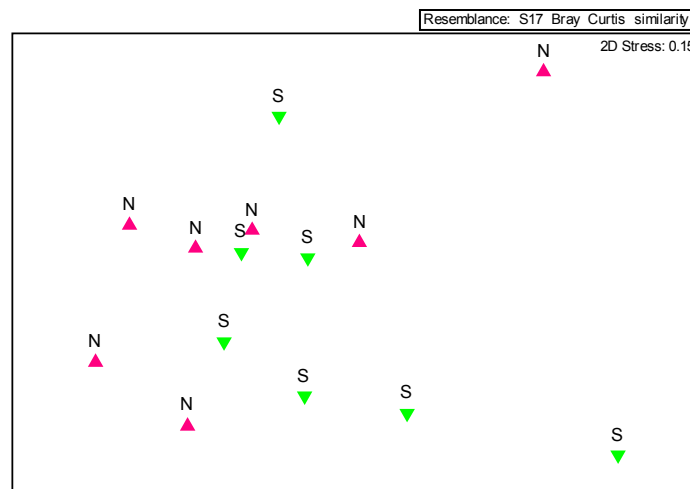
Figure 3.4 MDS ordination of algal relative abundance in
saltcedar (green) and native (pink) reaches.

3.2.2 Soft Algal Species

There were 14 soft algal species identified. The average species richness value was significantly different between the sites (p=0.026; Figure 3.5) and was lower in native site (4.14) than in the saltcedar reach (6.00). Species diversity was also significantly higher in the saltcedar site (p=0.015; Figure 3.5), but evenness was not significantly different between the two reaches (p=0.229). Paired sample t-tests on relative abundances indicated the only statistically significant colonizing soft algae sampled from the artificial substrates were *Ulothrix* spp., present only in the saltcedar reach (p=0.007). *Zygnema* spp. spores were also found in greater abundance in the saltcedar site (p=0.005). Maximum relative abundances of species indicated that some species, such as *Anabaena constricta, A. solitaria, Cladophora* spp. and *Zygnema* spp. were dominant in some samples, excluding all other soft species. Table 3.2 indicates the maximum relative abundance of each species found (RA_{max}) across all samples, the average relative abundance of each species in the native reach (R_{ave_N}), and the average relative abundance of each species in the saltcedar reach (R_{ave_S}).

Table 3.2 Relative abundance of soft algal taxa

Taxon	RA_{max}	$R_{ave\ N}$	$R_{ave\ S}$	p
Anabaena constricta	100	28	31.1	0.340
Anabaena solitaria	100	3.2	0	0.112
Anabaena sphaerica	30.2	3.2	1.4	0.321
Cladophora spp.	100	2.2	4.2	0.301
Closterium spp.	4.2	0	0.2	0.088
Lyngbya gracilis	78.8	3.8	5.3	0.196
Lyngbya maior	47.2	0	3.6	0.069
Merismopedia spp.	8.3	4.4	0.6	0.157
Oscillatoria limnetica	72.6	1.7	6.3	0.066
Spirogyra spp.	95	7.7	2.3	0.273
Spirulina abbreviata	67.8	3.7	2.4	0.451
***Ulothrix* spp.**	**65.9**	**0**	**8.3**	**0.007**
Zygnema spp.	100	24.9	29.1	0.191
***Zygnema* spp. spores**	**100**	**9.5**	**0.3**	**0.005**
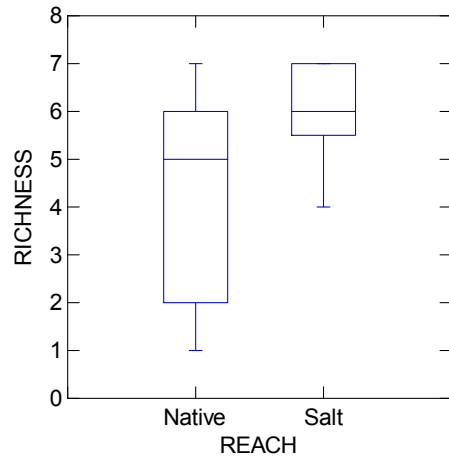
(a)
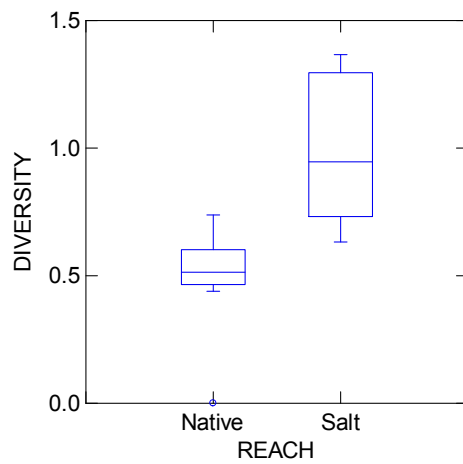
(b)
Figure 3.5 Differences in soft algal species communities
between saltcedar and native reaches shown as
(a) species richness (p=0.026),
and (b) species diversity (p=0.015)

Average dissimilarity in soft species composition within the native reach, according to

SIMPER analysis was 78%, while the average dissimilarity within the saltcedar reach was lower

at 71%. These values indicate the high temporal variability in colonizing soft species in each

reach, reflected as high dispersion in multivariate space with factor dispersion value for the

native reach of 1.143 and for the salt reach of 0.893. Dissimilarity between the reaches was not as high as the within reach values at 73%. Twenty five percent of the dissimilarity between the two sampling reaches was due to the abundance of *A. constricta*, with greater relative abundance in the native reach. Ordination plots demonstrated no clear separation between the reaches (Figure 3.6) and a bubble plot indicates the relative abundance of *A. constricta* to the dissimilarity in soft species community between native and saltcedar reaches in each sample (Figure 3.7).
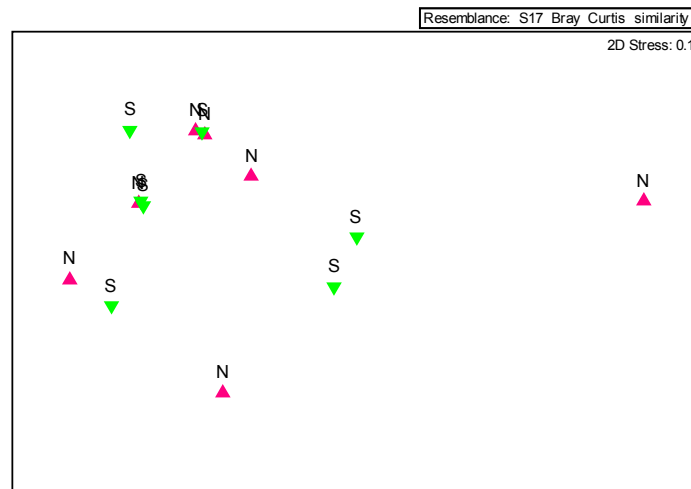
Figure 3.6 MDS ordination of soft algal species abundance.
Saltcedar reach samples are green, native samples are pink.
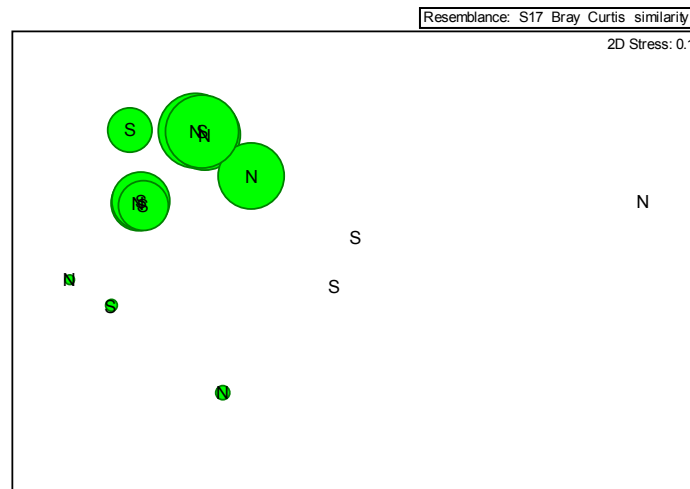
Figure 3.7 Bubble plot indicating relative abundance
of *A. constricta* in saltcedar (S) and native (N) reaches

3.2.3 Diatom Species

Thirty diatom species were identified from the artificial substrate samples. Average diatom species richness was not significantly different between the saltcedar, 14.86 and native reaches, 12.71 (p=0.116), but diatom species diversity was significantly lower for the native reach, H'=1.52 than for the saltcedar reach, H'=2.16 (p=0.001; Figure 3.8). This resulted from a significant difference in evenness between the two reaches (p=0.015; Figure 3.8). Paired sample t-tests indicate that 15 of the 30 species identified were significantly different in relative abundance between the sites. Table 3.3 indicates the maximum relative abundance of each species encountered across reaches (RA_{max}), the average relative abundance of each species in the native reach (RA_{ave_N}), and the average relative abundance of each species found in the saltcedar reach (RA_{ave_S}). Eutrophic classification was based on Van Dam (1994) and Gaiser et al.(2006). A paired sample t-test indicated there was no significant difference in overall diatom density or biovolume between the saltcedar and native reaches (p=0.758 and p=0.821, respectively).

45

Table 3.3 Relative abundances of diatom taxa

Taxon	Eutrophic	RA_{max}	$RA_{ave\ N}$	$RA_{ave\ S}$	P
Achnanthidium affinis		**5.5**	**2.8**	**0**	**0.015**
Achnanthidium exigua		**20.1**	**12.7**	**15.9**	**0.001**
Achnanthidium minutissimum		**96.5**	**96.2**	**22.8**	**0.015**
Amphora veneta	+	45.8	35.3	32.3	0.178
Bacillaria paxillifer	**+**	**19.2**	**.4**	**9.6**	**0.042**
Caloneis bacillum	+	1.6	.8	0	0.161
Caloneis molaris		.8	.4	0	0.164
Craticula ambigua		1.5	.3	.7	0.174
Denticula elegans		20.4	13.1	5.2	0.088
Epithemia adnata	+	25.8	2.2	13.5	0.098
Entomoneis alata		**6.3**	**.3**	**6.1**	**0.000**
Gomphonema clavatum	**+**	**14.8**	**7.4**	**1.3**	**0.004**
Gomphonema gracile		10	5	1.3	0.221
Gomphonema olivaceum		58.8	1	29.4	0.159
Hantzschia amphioxys		**6.5**	**1.3**	**5**	**0.027**
Mastogloia elliptica		10.5	9.7	10.7	0.241
Navicula gracilis	+	9.6	0	4.8	0.002
Navicula trivialis	+	10.8	4.3	5.4	0.002
Nitzschia acicularis	+	0.6	0.3	0	0.021
Nitzschia inconspicua	+	9.2	8.0	4.6	0.149
Nitzschia linearis	**+**	**10.9**	**6.2**	**7.1**	**0.005**
Nitzschia microcephala	**+**	**43.8**	**23.6**	**41.7**	**0.001**
Nitzschia palea	+	8.4	4.2	3.7	0.263
Nitzschia vermicularis		0.6	0	.3	0.164
Pinnularia appendiculata		**4.1**	**2**	**0**	**0.037**
Rhopalodia gibba	**+**	**56.5**	**17.8**	**50.6**	**0.001**
Rhopalodia gibberula	**+**	**62.6**	**24.3**	**46.0**	**0.003**
Sellaphora pupula	+	17.4	10.2	12.0	0.136
Surirella brebissonii	+	30.7	15.7	2.0	0.461
Synedra ulna		34.8	20.3	13.3	0.208

46
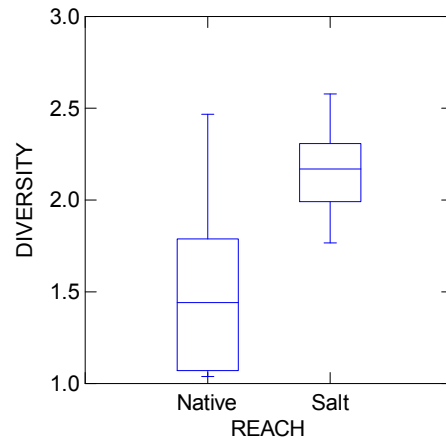
(a)
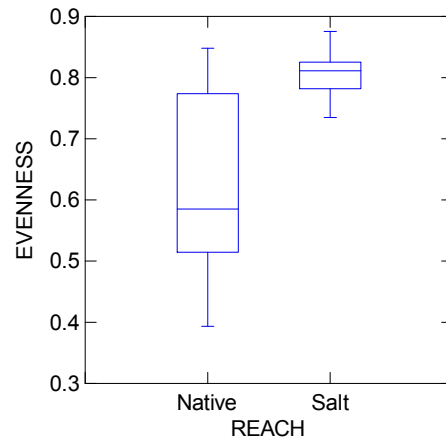
(b)

Figure 3.8 Differences in diatom communities
between native and saltcedar reaches
demonstrated as (a) species diversity (p=0.001),
and (c) evenness (p=0.029)

SIMPER analysis on relative abundance of diatoms resulted in an average dissimilarity within the native reach of 40%, while saltcedar reach dissimilarity between communities was 56%. When the two reaches were compared, average dissimilarity was 64%, with the largest portion of this dissimilarity (35%) due to *A. minutissimum* density. *Rhopalodia gibba* and *N. microcephala* account for another 18% of the dissimilarity. Although multivariate dispersion within each reach was evident (native=0.955, salt=1.045), ordination plots indicated a clear

separation between native and saltcedar reaches (Figure 3.9) and bubble plots demonstrate the density of the more heavily contributing species, *A. minutissimum* (Figure 3.10), *R. gibba* (Figure 3.11), and *N. microcephala* (Figure 3.12).
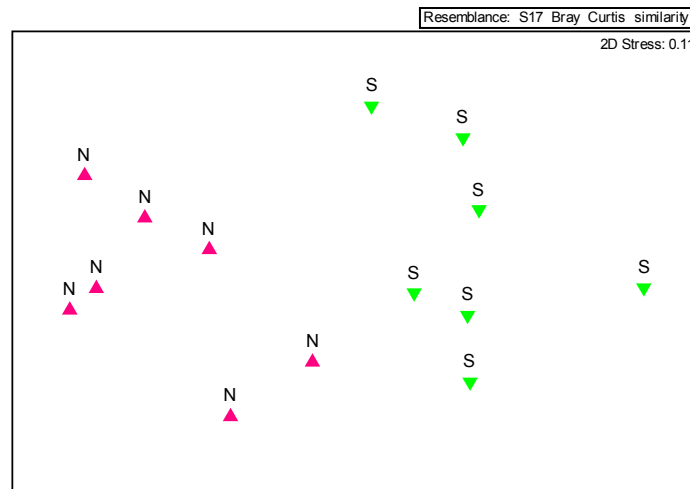
Figure 3.9 MDS ordination for diatom relative abundance between saltcedar and native reaches. Native reach samples are pink, saltcedar samples are green.
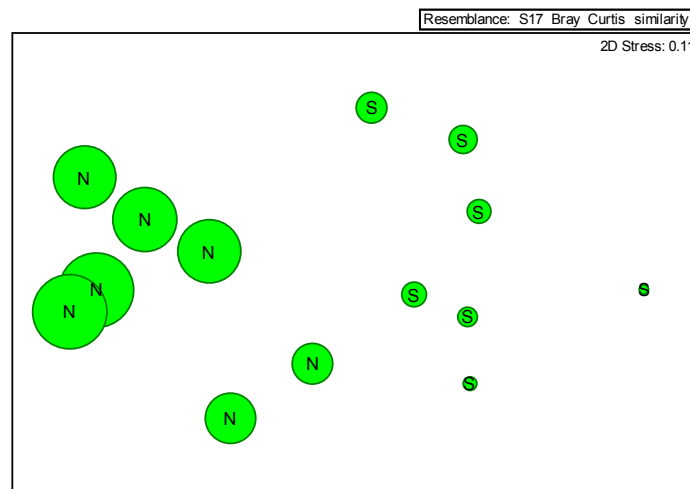
Figure 3.10 Bubble plot representing relative abundance of *A.minutissimum* in each community from the saltcedar (S) and native (N) reaches

2D Stress: 0.11
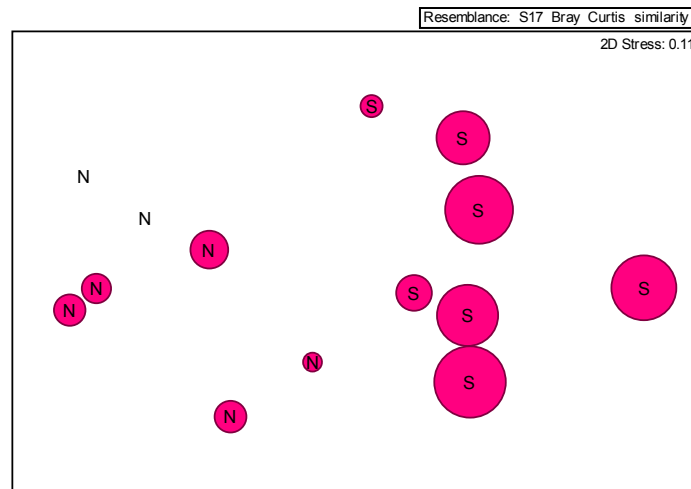
Figure 3.11 Bubble plot representing the relative abundance
of *R. gibba* in each community from the saltcedar (S) and
native (N) reaches

2D Stress: 0.11
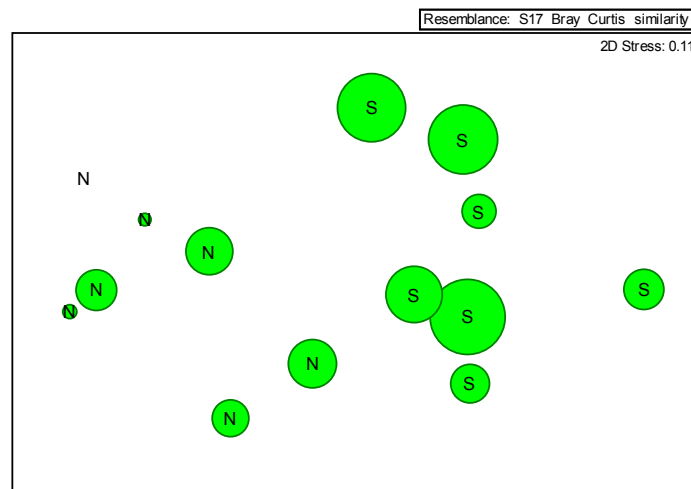
Figure 3.12 Bubble plot representing relative
abundance of *N. microcephala* in each community
from the saltcedar (S) and native (N) samples

Eutrophic diatom species were common in both saltcedar and native reaches, but total

density of these species was significantly higher in the saltcedar reach when analyzed using a

paired sample t-test (p=0.037). Percentage of total diatom density accounted for by eutrophic

species was calculated for each diatom community and it was determined using a paired sample t-test that there was a significant difference between reaches (Figure 3.13; p=0.002) with saltcedar assemblages characteristically consisting of a larger proportion of eutrophic species. Eutrophic species contribute 55% of the total diatom density to saltcedar reach communities and only 27% of the density to native reach assemblages.
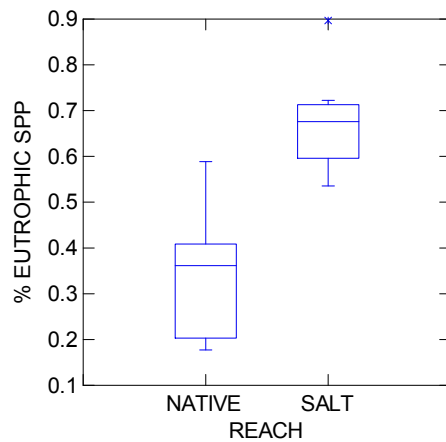
Figure 3.13 Differences in percentage of eutrophic
species between native and saltcedar reaches (p=0.002)

Redundancy Analysis to determine the proportion of diatom communities explained by all of the environmental variables, excluding specific conductance, indicated that the first two axes accounted for 67% of the variance in community assemblages. A biplot indicated the two species of *Rhopalodia*, *R. gibba* and *R. gibberula,* and *Achnanthidium exigua* are highly correlated with salinity and *A. minutissimum* is highly correlated with PAR and pH (Figure 3.14).
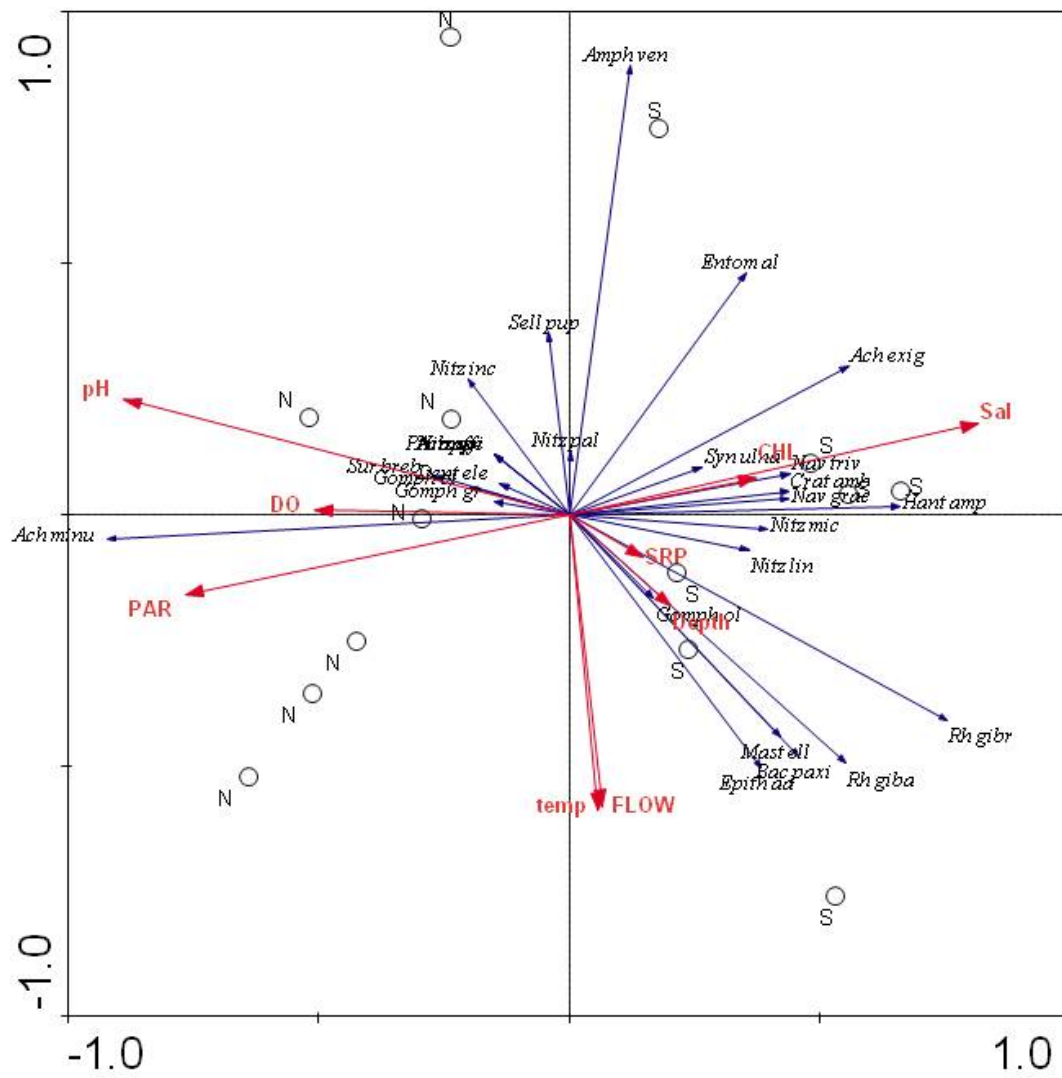
Figure 3.14 RDA ordination plot with environmental and diatom community data.

Proportion of N_2-fixers in total diatom density was higher in the saltcedar reach in all months except for January of 2006 and April of 2007, however paired sample t-tests did not indicate any significant results between reaches in N_2-fixer density (p=0.589) or N_2-fixer proportion of total diatom density (Figure 3.15;p=0.094).
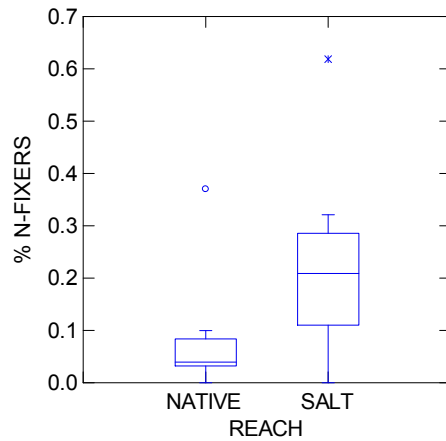
Figure 3.15 Percentage of total diatom
density accounted for by N_2-fixing species
in saltcedar and native reaches.

When sampling year was taken into account, due to the difference in deployment time between the two seasons, pair wise testing by ANOSIM indicated that the significant difference between reaches in diatom assemblage was in the 2006 sampling season ($p=0.029$). The major contributor to that difference across both years was consistently *A. minutissimum,* while other, subdominant species, such as *A. exigua* and the two *Rhopalodia* species fluctuated between months.

3.3 Nutrient Enrichment

3.3.1 Soft Species Communities

SIMPER analysis on soft algal species relative abundance from nutrient-diffusing pots revealed that there was dissimilarity between samples within each reach (Table 3.4). The control sample from the native reach (C_N) was 100% dissimilar to every other sample obtained in this experiment. All dissimilarities were due to species present in the nutrient enriched samples that were absent in the control sample (Table 3.5). The lowest dissimilarity, i.e. 26% was between combination N+P pots from both reaches (NP_N and NP_S). Low average dissimilarity existed between the native nitrogen-diffusing (N_N) pot and the saltcedar

phosphorus-diffusing (P_S) pot at 36%. The saltcedar control pot (C_S) had a range of average dissimilarity from 63% (NP_N) to 100% dissimilarity to the native phosphorus-diffusing (P_N) and P_S. The nitrogen-diffusing pot from the saltcedar reach (N_S) had a high degree of dissimilarity, 95% and above, to every other sampled pot.

Table 3.4 Average dissimilarity (%) between samples

	C_N	P_N	N_N	NP_N	C_S	P_S	N_S
P_N	100						
N_N	100	99					
NP_N	100	100	96				
C_S	100	99	97	63			
P_S	100	100	36	95	100		
N_S	100	100	95	98	98	100	
NP_S	100	100	99	26	69	63	98

Table 3.5 Dissimilarity in Soft Species Between Samples

	Dissimilarity (%)	Contributing Species	Contribution (%)	Reach
C_N X N_N	100	*Spirogyra*	50	Only in N_N
C_N X P_N	100	*Zygnema* spp. *Zygnema* spores	56 43	Only in P_N
C_N X NP_N	100	*Cladophora* spp.	94	Only in NP_N
C_S X N_S	98	*Zygnema* spp. *Zygnema* spores	51 25	Only in N_S Only in C_S
C_S X P_S	100	*Spirogyra* spp. *Oscillatoria limnetica*	38 26	More abundant in P_S Only in P_S
C_S X NP_S	69	*Cladophora* spp. *Oscillatoria limnetica*	43 33	More abundant in NP_S Only in NP_S

An ordination plot of nutrient-enriched soft species relative abundance indicates that the nitrogen containing, both by itself (factor value dispersion=0.4) and along with phosphorus (factor value dispersion=0.8), substrates were closer in species composition between the saltcedar and native reaches than any other grouping within either reach (Figure 3.16).
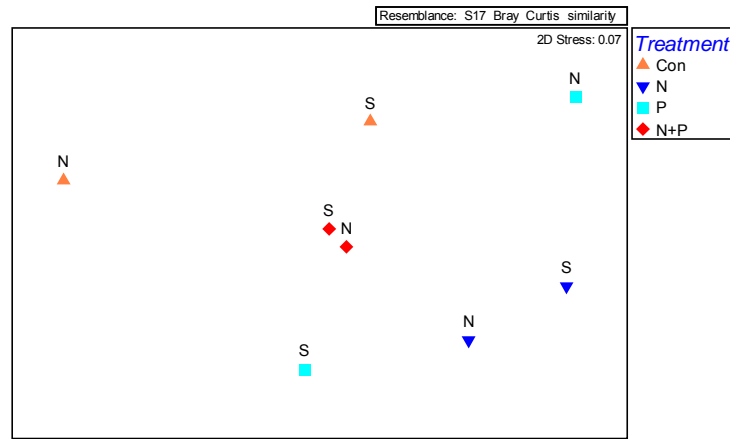
Figure 3.16 MDS ordination plot of soft algal communities on
nutrient-diffusing substrates. Clustering occurs between pots
with the same nutrients, not dependent upon which reach
(native=N; saltcedar=S) they were collected from
in N and N+P.

3.3.2 Diatom Taxa

Nine diatom species in control and treatment communities had relative densities greater
than 10% and were considered dominant in these assemblages (Table 3.6).

Table 3.6 Densities (diatoms/mm^2) of dominant diatom species in nutrient enriched communities

Species	Native				Salt			
	C	N	P	N+P	C	N	P	N+P
A. minutissimum	57.22	255.17	516.03	470.99	57.73	9.39	298.09	136.04
A. veneta	3.76	197.98	624.67	1269.01	490.70	142.70	1397.30	308.71
D. elegans	0.00	263.97	407.39	392.49	245.35	268.50	475.08	88.95
M. elliptica	0.00	237.57	511.51	0.00	158.75	146.46	195.62	41.86
N. microcephala	0.00	101.19	344.02	0.00	158.76	71.35	1201.68	429.05
N. palea	0.00	8.80	167.48	601.82	101.03	73.23	316.72	52.32
R. gibba	0.00	35.20	253.49	0.00	815.43	189.64	568.24	78.49
R. gibberula	0.00	26.40	457.19	0.00	685.54	240.34	1322.10	151.74
S. ulna	2.51	101.19	470.77	91.58	245.35	110.78	1257.57	146.51

According to SIMPER analysis, diatom community assemblage between the saltcedar
and native reaches was an average of 66% dissimilar, compared to 87% dissimilarity in the
artificial substrate diatom community. Average dissimilarity between each of the different

54

treatment pots is recorded in Table 3.7 while heavily contributing species to these dissimilarities are in Table 3.8. The MDS ordination plot reveals that the diatom community that was present in C_N is so different in structure to any of the other treatment pots in the experiment that it is difficult to see any dispersion between the other samples (Figure 3.17). This resulted in an average dissimilarity between the native samples from all of the treatments of 74%, while the average dissimilarity between the salt reach samples was lower at 52%. The control samples, themselves, from the two reaches were 96% in average dissimilarity, higher than that 87% present between the artificial substrate communities, likely due to the fact that the nutrient enrichment community samples were only collected in March and April of 2007.

Table 3.7 Percent dissimilarity between treatments using SIMPER

	C_N	P_N	N_N	NP_N	C_S	P_S	N_S
P_N	97						
N_N	92	52					
NP_N	96	45	63				
C_S	96	39	56	67			
P_S	99	46	74	57	50		
N_S	98	53	40	74	38	70	
NP_S	93	51	50	71	48	67	42

Table 3.8 Average dissimilarities between treatments in native reach and contributing species

	Dissimilarity (%)	Major Contributors	Contribution (%)	Reach
C_N X N_N	92	*D. elegans*	19	Only in N_N
		M. elliptica	17	Only in N_N
C_N X P_N	97	*A. veneta*	14	Higher density in P_N
		M. elliptica	12	Only in P_N
C_N X NP_N	96	*A. veneta*	36	Higher in density NP_N
		N. palea	17	Only in NP_N
C_S X N_S	38	*R. gibba*	34	Higher density in C_S
		R. gibberula	24	Higher density in C_S
C_S X P_S	50	*N. microcephala*	17	Higher density in P_S
		Synedra ulna	17	Higher density in P_S
C_S X NP_S	48	*R. gibba*	30	Higher density in C_S
		R. gibberula	22	Higher density in C_S
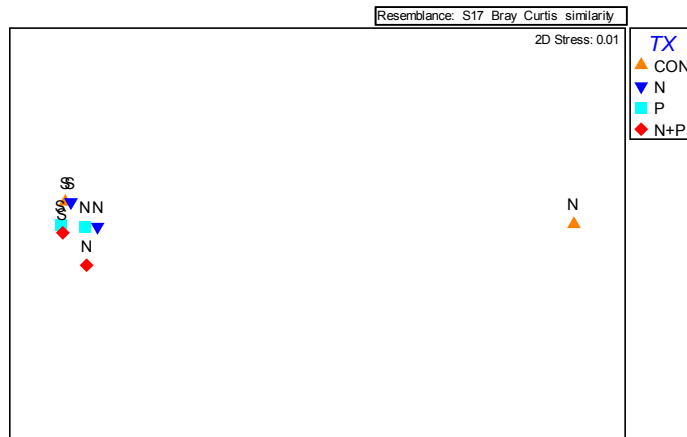
Figure 3.17 MDS ordination plot of diatom communities on
nutrient-diffusing substrates. The native reach control community
has greater difference to all of the other samples than
they have to one another.

The clear separation between C_N and all other samples necessitated the removal of that data from a subsequent analysis to achieve a better picture of the dispersion between the other samples (Figure 3.18). When C_N was excluded from analysis, the average dissimilarity between saltcedar and native reaches was 56%. *A. veneta* density contributed 14% to the dissimilarity, while *R. gibberula* contributed another 12%. A bubble plot based on *R. gibberula* density in each sample demonstrates greater density in the saltcedar reach (Figure 3.19).
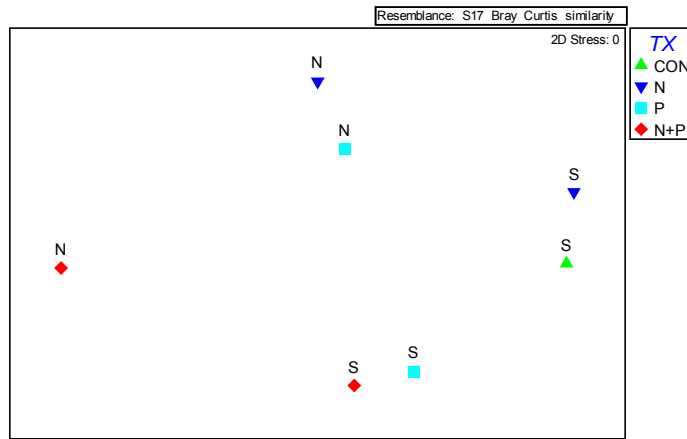
Figure 3.18 Ordination plot of diatom communities on nutrient-diffusing pots with the native control excluded.
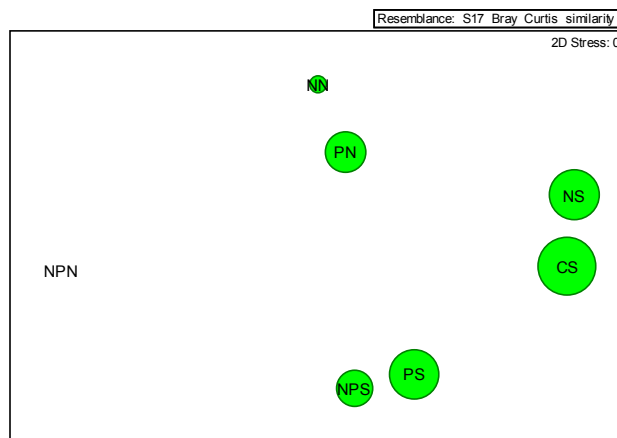
Figure 3.19 Bubble plot of *R. gibberula* density in each sample

Chlorophyll *a* concentrations in the NDS treatment communities demonstrated that in the native reach phosphorus was likely more limiting nutrient, while the saltcedar reach was probably more strongly limited by nitrogen (Figure 3.20). Regressions of chlorophyll *a* against diatom density and biomass did not indicate a significant relationship between these variables.
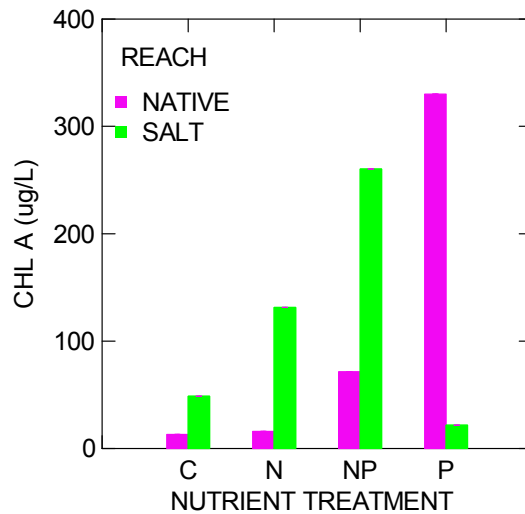
Figure 3.20 Chlorophyll *a* concentration
from each nutrient treatment community

3.4 Transplantation Experiment

Diatom species shifts were apparent when artificial substrates were moved from one reach and placed in the other, this occurred in both directions (Table 3.9). The diatom community present on a substrate that was placed in the native reach for 17 days and then transferred to the saltcedar reach ($N_{17}S'_{17}$) was 82% dissimilar to the community of diatoms on the substrate that remained in the native reach for the entire 34 days ($N_{17}N'_{17}$). This same community was also 85% dissimilar to the assemblage that was present on the substrate allowed to remain in the saltcedar reach for the entire period of 34 days ($S_{17}S'_{17}$). It is important to note that this same community was only 70% dissimilar to the diatom community from the saltcedar reach from the second 17 days of the experiment (S'_{17}) and this S'_{17} community was 91% different from the $S_{17}S'_{17}$.

Table 3.9 Average Dissimilarity Percentages Between Transplant Communities

	N_{17}	N'_{17}	$N_{17}N'_{17}$	$N_{17}S'_{17}$	S_{17}	S'_{17}	$S_{17}S'_{17}$
N'17	80						
$N_{17}N'_{17}$	78	77					
$N_{17}S'_{17}$	83	81	82				
S_{17}	84	74	90	77			
S'_{17}	79	77	89	70	71		
$S_{17}S'_{17}$	91	89	88	85	90	91	
$S_{17}N'_{17}$	80	77	83	77	76	84	79

The diatom community assemblage also experienced a shift when the substrate was transplanted from the saltcedar reach after 17 days to the native reach for the following 17 days ($S_{17}N'_{17}$). When compared to the community obtained after only 17 days in the saltcedar reach (S_{17}), there was 76% dissimilarity. There existed a dissimilarity of 83% between the transplanted community and the community that was allowed to colonize in the native reach for the entire 34 day period ($N_{17}N'_{17}$)and 77% dissimilarity to the native community from the second 17 day period (N'_{17}).

The species that are the strongest contributors to the dissimilarity between communities are recorded in Table 3.10. *Achnanthidium minutissimum* is dominant in the native reach communities, both from N_{17} and $N_{17}N'_{17}$. When the substrate is transplanted to the saltcedar reach, $N_{17}S'_{17}$, *A. minutissimum* density is greater and an increase occurs in the density of *A. veneta*. Two species, *R. gibberula* and *N. palea,* were present in the $N_{17}S'_{17}$ community and absent from the N_{17} community. All other species present in the community exhibited greater densities in the transplanted assemblage when compared to N_{17}. The same taxa were present in communities from $N_{17}S'_{17}$ and S'_{17}, but there was greater density of all except for *A. minutissimum,* which occurred in slightly higher density in S'_{17}. *Amphora veneta* and *R. gibba* were primary contributors to dissimilarity between these two communities, occurring in higher densities in $N_{17}S'_{17}$.

Table 3.10 Community Dissimilarity and Major Contributing Species

	Dissimilarity (%)	Major Contributors	Contribution (%)	Sample
$N_{17}S'_{17}$ X N_{17}	83	*A. minutissimum*	22	Greater in N_{17}
		A. veneta	17	Greater in $N_{17}S'_{17}$
$N_{17}S'_{17}$ X S'_{17}	70	*A. veneta*	20	Greater in $N_{17}S'_{17}$
		R. gibba	15	Greater in $N_{17}S'_{17}$
$N_{17}S'_{17}$ X $S_{17}S'_{17}$	85	*N. microcephala*	21	Greater in $S_{17}S'_{17}$
		A. veneta	14	Greater in $S_{17}S'_{17}$
$N_{17}S'_{17}$ X $N_{17}N'_{17}$	82	*A. minutissimum*	38	Greater in $N_{17}N'_{17}$
		R. gibberula	10	Greater in $N_{17}S'_{17}$
$N_{17}S'_{17}$ X $S_{17}N'_{17}$	77	*N. microcephala*	18	Greater in $N_{17}S'_{17}$
		S. ulna	16	Greater in $N_{17}S'_{17}$
$S_{17}N'_{17}$ X S_{17}	76	*S. ulna*	18	Greater in S_{17}
		R. gibba	14	Greater in S_{17}
$S_{17}N'_{17}$ X N'_{17}	77	*A. minutissimum*	26	Greater in N'_{17}
		N. microcephala	13	Greater in N'_{17}
$S_{17}N'_{17}$ X $N_{17}N'_{17}$	83	*A. minutissimum*	57	Greater in $N_{17}N'_{17}$
$S_{17}N'_{17}$ X $S_{17}S'_{17}$	79	*N. microcephala*	20	Greater in $S_{17}S'_{17}$
		A. veneta	15	Greater in $S_{17}S'_{17}$

3.5 Allochthonous Inputs and Stream Metabolism

Relative abundance based on the mass of each woody species collected were recorded in Table 3.11. Paired-sample t-tests for mass of leaf litter collected while taking litter species composition into account failed to show any significant difference between the two reaches when comparing each sampling date. When the data were analyzed using only mass of leaf litter collected organized by sampling dates, there was a significant difference in litter fall between the native and saltcedar reaches (Figure 3.21, p=0.008) indicating an overall higher allochthonous contribution in the saltcedar reach. Total mass of leaf litter collected in buckets in the native reach was 22.93g, while litter collected from the saltcedar reach totaled 120.01g. The leaf litter collected from the saltcedar reach site consisted of mostly saltcedar leaves with a few leaves of mesquite, while the leaves collected from the native reach were primarily catclaw acacia. Canopy cover was significantly higher over the stream in the saltcedar reach than it was in the native reach (Figure 3.22, p=0.016).

Table 3.11 Relative Abundance of Leaf Litter Species

	NATIVE		SALTCEDAR			
	November	December	November	December	January	March
Acacia	0.367	0.561	0.000	0.000	0.000	0.000
Baccharis	0.309	0.279	0.000	0.000	0.000	0.000
Chilopsis	0.187	0.000	0.147	0.032	0.000	0.000
Prosopis	0.064	0.160	0.513	0.254	0.115	0.000
Salix	0.073	0.000	0.000	0.000	0.000	0.000
Tamarix	0.000	0.000	0.340	0.715	0.885	1.000
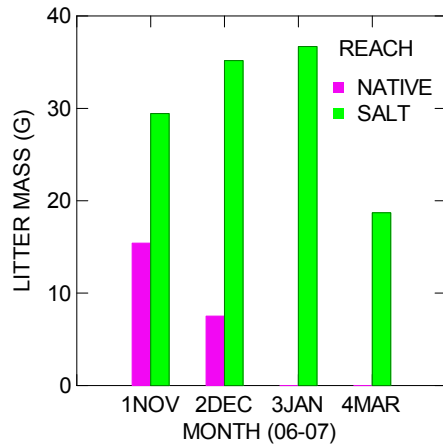
Figure 3.21 Bar graph representing the total mass (g)
of leaf litter collected in saltcedar reach buckets (green)
and native reach buckets (pink) organized by collection month
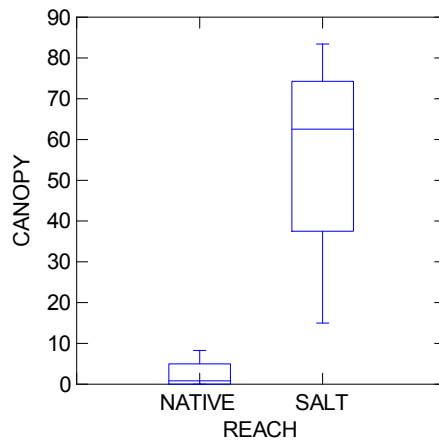
Figure 3.22 Canopy cover over the stream in the saltcedar reach is
significantly greater than cover over the native reach (p=0.016)

61

Paired sample t-test indicated that calculated GPP with a mean of 398.44 mg/cm^2/day in the native site was significantly higher than in the saltcedar reach with a mean of 104.63 mg/cm^2/day (p= 0.004). Mean NDM in the native site was higher at 123.28 mg/cm^2/day, but not significantly different than the mean NDM in the saltcedar reach, which was 30.06 mg/cm^2/day (p=0.078). Community respiration over a 24-hour period (CR24) had a mean of 275.16 mg/cm^2/day in the native reach and was significantly higher than the saltcedar reach, with a mean of 74.58 mg/cm^2/day (p=0.001). The P:R did not significantly differ between the native and saltcedar reaches, with mean values of 1.57 and 1.37, respectively. (p = 0.219). Calculated monthly values for all of the above parameters are reported in Table 3.12.

Table 3.12 Calculated Monthly Metabolism Parameters

	GPP		NDM		CR24		P:R	
	Native	Salt	Native	Salt	Native	Salt	Native	Salt
Dec 05	176.5	40.2	-29.0	0.3	205.5	40.0	0.859	1.006
Jan 06	167.1	66.0	-36.9	7.4	204.0	58.6	0.819	1.127
Jan 06b	435.7	96.5	254.3	32.2	181.4	64.3	2.402	1.501
Feb 06	232.8	102.9	-70.4	17.3	303.2	85.6	0.768	1.203
Mar 06	568.4	99.7	308.6	40.8	259.8	58.9	2.188	1.693
Apr 06	220.5	94.5	-82.4	8.1	302.9	86.4	0.728	1.093
Nov 06	241.8	99.3	-2.5	41.5	244.3	57.8	0.990	1.717
Dec 06	183.2	33.6	92.9	-24.3	90.2	57.9	2.030	0.580
Jan 07	252.6	70.1	177.5	29.2	75.1	40.9	3.363	1.712
Mar 07	1415.9	289.3	738.8	168.2	677.1	121.1	2.091	2.389
Apr 07	488.4	158.7	5.1	9.8	483.3	148.9	1.011	1.066

GPP is Gross Primary Productivity; NDM is Net Daily Metabolism;
CR24 is Community Respiration over 24 hours; P:R is photosynthesis to
respiration ratio.

CHAPTER 4

DISCUSSION

Saltcedar invasion on McComb Creek caused significant shifts in benthic algal communities by changing in environmental parameters with impact on algal composition. This shift included increased diversity of soft algae and diatoms and a transition of dominant species, from common oligotrophic taxa to halophilic N_2-fixers. Native riparian vegetation, which continues to dominate in the upper reaches of the stream, allows a significantly greater amount of PAR to reach the stream, unlike the more heavily shaded lower reaches of the stream, subjected to exotic saltcedar invasion. While nitrogen limitation was consistent between the two stream reaches, phosphorus limitation varied and contributed to differences between the algal communities.

4.1 Aquatic Environment

Saltcedar significantly increased water salinity and specific conductance, consistent with the effects reported for soils. It is likely that salt entered the aquatic system in the same way, by dripping from salt glands in the leaves during spring and summer and in leaf litter in late fall and winter (Ladenburger et al., 2006; Lesica and DeLuca, 2004). Litter input to the saltcedar reach of the stream was significantly higher than to the native reach and consisted largely of saltcedar leaves with very small contributions of honey mesquite and desert willow in the early months of senescence, during November and December. Average water salinity in the native and saltcedar reaches of McComb Creek (1.13 and 1.19ppt, respectively), suggested brackish conditions, which occur at >0.9ppt (Van Dam, 1994). The saltcedar reach supported large populations of brackish diatom species such as *Rhopalodia gibba* and *R. gibberula* (Van Dam,

63

1994), which were either absent or present in very low numbers in the native reach. Considering that the native reach was also saline and supported brackish species such as *Mastogloia elliptica*, *Denticula elegans,* and *Amphora veneta* (Van Dam, 1994), the significant increase in salinity following saltcedar invasion is unlikely to be the primary factor behind the diatom shift in McComb Creek.

Soluble reactive phosphorus was another water chemistry parameter showing a significant increase in the saltcedar reach compared to the native, while pH displayed the opposite trend. Higher concentrations of Na^+ delivered to sandy soils have been shown to cause leaching of phosphorus into the groundwater (Jalali and Merrikhpour, 2008). Therefore, it is possible that the higher SRP in the saltcedar reach was a consequence of Na^+ exchange in the soil and stream sediments. Although it is generally believed that increases in salinity drive a corresponding increase in pH (Blinn and Bailey, 2001; Stevenson et al., 2006), the present results are similar to those found in salinized freshwater systems in Australia where a significant and positive relationship was found between hydrogen ion concentration and Na^+, K^+, Mg^{2+} and Cl^- (Blinn et al., 2004). The expected effect of salinity on the phosphorus cycle was suggested for saline systems (Nielsen et al., 2003); therefore, it is highly likely that the gradient of salinity that exists between the two study reaches was not extensive enough to elucidate this same relationship. In a study of Scottish estuaries, Balls (1992) found that increases in phosphate concentrations occurred at mid salinities, while there was evidence of phosphate removal at lower salinities. The same study showed both nitrate and ammonia concentrations to decrease significantly with increasing salinity, but changes in salinity were of a much higher magnitude than those detected in McComb Creek between the saltcedar and native reaches. It is expected that salinity and SRP continue to increase downstream of the study site because of the longer term and more extensive saltcedar invasion, but this hypothesis has not been tested here.

64

Clearly, however, saltcedar presence has altered water chemistry in my study area, which merits further research on the effects of this invasive plant.

<center>4.2 Benthic Algal Community Assemblages</center>

Species richness of benthic algal communities was significantly higher in the saltcedar reach. Notably, the majority of species were common between the two reaches, but they were more temporally persistent in the saltcedar reach. Only *Ulothrix* spp. and *Nitzschia gracilis* were found exclusively in saltcedar reach assemblages, while *Oscillatoria limnetica* was present in many saltcedar communities over time but only once, in March 2007 in the native reach. All of the diatom species that were consistently present in saltcedar and only seen rarely in the native communities, along with *N. gracilis* are characteristically eutrophic and halophilic species, including *Bacillaria paxillifer, Entomoneis alata,* and *Epithemia adnata* (Van Dam, 1994, Gaiser et al., 2006). Of those species, *E. adnata* is known to possess endosymbionts that fix nitrogen (Prechtl, 2004). *Nitzschia gracilis* is also considered a later successional species in mountain streams (Margalef, 1960). There was very little difference in overall benthic algal community diversity between the saltcedar and native reaches over time. This was likely a result of the rather pronounced nutrient limitation in both reaches, as nitrogen was undetectable as nitrate or ammonia. Soluble reactive phosphorus, with mean concentrations of 0.95 µg/L for the native and 1.30 µg/L for the saltcedar reach, was also limiting considering that dissolved P concentrations of less than 0.011 mg/L are insufficient for growth of eutrophic diatoms (Passy, 2008). Response of benthic diatom assemblages to increases in total phosphorus from 0.10 to 0.30 mg/L was associated with a release from nutrient limitation (Stevenson et al., 2008). Soluble reactive phosphorus concentration in both native and saltcedar reaches of McComb Creek was well below the minimum threshold requirements of orthophosphate reported for diatom species common with stream systems in Victoria, Australia (Blinn and Bailey, 2001).

<center>65</center>

Regardless of the low concentration of phosphorus detected, there is evidence of enrichment in the saltcedar reach.

The most notable compositional difference between the two reaches was the consistently greater relative abundance in the native reach of the oligotrophic, pioneer diatom *Achnanthidium minutissimum* (Van Dam, 1994; Blinn et al., 2004). This species was strongly correlated with the higher pH and PAR experienced by the native reach. Also important, *A. constricta*, a N_2-fixing cyanobacterium found predominantly in the saltcedar reach, was a large contributor to the dissimilarity between reaches. In Douglas Lake, Michigan, *Anabaena* exhibited an extended period rapid growth with P addition (Fairchild and Lowe, 1984). Analyses of soft algal taxa alone did very little to differentiate between benthic communities found in the native and saltcedar reaches. Soft species differences between the reaches were due primarily to the higher relative abundance of *A. constricta* and *Oscillatoria limnetica,* a halophytic species with low light requirements present in high relative abundances in the saltcedar reach samples and in very low abundances, or not at all in native samples. Also of note, *Ulothrix* spp., which tend to occur in rivers of high ionic content (Potapova, 1996), were found occasionally in great abundance in the saltcedar reach, but never in the native reach.

When diatom species were analyzed, temporal variation in the community assemblages was still apparent and average dissimilarity and dispersion values within each reach were still high, but the between reach variation was actually higher than that within each reach. The strongest contributor to the dissimilarity between the two reaches was *A. minutissimum*, which was present in high abundances in the native reach and in lower abundances, if at all, in the saltcedar reach. *Rhopalodia gibba,* a eutrophic alkalibiontic species found in fresh brackish waters like McComb Creek, was present in all of the sampled communities of the saltcedar reach as a dominant or subdominant species. *Nitzschia microcephala,* a eutrophic diatom species, was present in significantly higher densities in the saltcedar site; this species was

66

previously reported to occur at a range of salinity from 7-20 mS/cm (Blinn et al., 2004). In freshwater systems in the Australian wheatbelt, diatoms that were commonly associated with high salinities (>100mS/cm) such as *Hantzschia amphioxys, Achnanthidium exigua* and *E. alata* had significantly higher relative abundances in the saltcedar reach of McComb Creek, consistent with reports of other saline systems, e.g. the Australian wheatbelt, where these diatoms were commonly associated with salinities >100 mS/cm (Blinn et al., 2004).

Nutrient enrichment experiments showed that McComb Creek was nitrogen limited in the native reach and dependent on any cyanobacterial nitrogen fixers present. Salinity increase in the saltcedar reach was associated with greater SRP levels, which supported diatoms with endosymbiotic N_2-fixers, including *R. gibba, R. gibberula* and *E. adnata.* These N_2-fixing species represented 22% of the total diatom density in the saltcedar assemblages while only 7% in the native reach communities. Epithemiaceaen species are not uncommon in desert streams, where nitrogen fixation can account for up to 85% of net flux of nitrogen input (Grimm and Petrone, 1997). *Epithemia adnata* represented a substantial increase in biovolume and *R. gibba* has been shown to exhibit rapid growth on phosphorus-diffusing substrates (Fairchild and Lowe, 1984). Nitrogen-fixation allows these species to circumvent the N-limitation, characteristic in desert streams. Their proliferation in the saltcedar reach is attributed to the combined effect of salinization and mild P enrichment as all of them are eutrophic and halotolerant (Van Dam, 1994).

Although diatom species diversity was significantly different between reaches in McComb Creek, it is preferable to consider variations in assemblage composition when looking at response to environmental changes (Lobo et al., 1995). Ordination revealed that *A. minutissimum,* the dominant diatom in the native reach, contributed 35% to dissimilarity between reaches. Perhaps even more striking in ordination, *R. gibba* densities clearly differentiated saltcedar communities from the native ones, as the species was consistently

67

found in greater abundance in invaded reach assemblages and contributed 9% to dissimilarity. Both species of *Rhopalodia* were highly correlated with the increase in salinity associated with the saltcedar reach communities. Other species, with preferential distribution included *A. veneta* and *N. microcephala*, both found in higher densities in saltcedar communities and contributing 9% and 10%, respectively to dissimilarity. *Nitzschia microcephala* was also highly correlated to the salinity increase in the saltcedar reach. Within reach variation was also apparent, but it can likely be attributed to seasonal variation.

The saltcedar reach communities are composed of significantly higher densities of eutrophic species and the assemblage is significantly higher in eutrophic versus oligotrophic species, indicating the increased ability of eutrophic diatom species to proliferate under conditions altered by saltcedar invasion. This difference in community composition between the two reaches indicates that the small increase in SRP was beneficial to diatoms. There was no measureable nitrogen in either reach of the system so this shift toward eutrophic species must be attributed to SRP increase.

In the wheatbelt region of southern Australia, both diatom species richness and H' diversity showed a strong negative correlation with salinity, which was positively correlated to nitrogen but had no relationship with phosphorus (Blinn et al., 2004). In Kentucky and Michigan streams, nutrient concentrations, measured as total nitrogen (TN) and total phosphorus (TP), were highly correlated with each other, but were not significantly related to alkalinity or canopy cover while increased nutrient concentrations were not accompanied by a significant increase in epilithic diatom biomass (Stevenson et al., 2006). Therefore, the present results on these processes in a desert system fill a gap in the literature and indicate that the affect of salinity on SRP can result in positive effects on diatom communities, thus supporting the hypothesis that saltcedar presence will increase algal species richness in aquatic communities where it invades.

<u>4.3 Nutrient Enrichment</u>

Supplementation with nitrogen and phosphorus had profound effect on the density and composition of soft algae. In both reaches, nutrient-enriched and non-enriched communities were 100% dissimilar. When nitrogen and phosphorus were present, soft species communities from corresponding treatments between reaches were closer in composition to one another than to other nutrient treatments or the control within a reach. For example, enrichment with nitrogen in the native reach resulted in the proliferation of *Spirogyra* spp., which were not present in the control community. In the saltcedar reach, dissimilarity was influenced by *Zygnema* spp. in the N enriched assemblage, but interestingly there was a higher density of *Zygnema* spores in the control community. Algae form spores under unfavorable, nutrient limiting conditions, which can explain the greater density of spores in the control.

Phosphorus enrichment created unique floras in both reaches, diverging not only from the corresponding control within a reach, but also from one another. Thus, phosphorus enrichment in the native reach resulted in both *Zygnema* spp. and spores, not detected in the control, and in the saltcedar reach dissimilarity was the result of increased *Spirogyra* spp. and *Oscillatoria limnetica* relative to the control community.

An interesting convergence between native and saltcedar algal communities was observed in the N+P treatment. Enrichment of the native community with both nitrogen and phosphorus was responsible for a similarity with the control in the saltcedar reach, which was the greatest observed between the two reaches. Increases in density of both *Cladophora* spp. and *Zygnema* spores in the enriched native community were responsible for this observed convergence. The dissimilarity between the control treatments and the nutrient-enriched treatments in each reach was driven by different taxa. Enrichment with N and P resulted in increased *Cladophora* spp. density in the saltcedar reach and allowed the colonization of the

69

same species in the native reach, where they were not observed in control community or in either of the single nutrient enrichment assemblages.

Nutrient enrichment appears to shift native reach diatom communities to more closely resemble saltcedar reach assemblages. All of the nutrient enrichment treatments caused drastic changes in diatom communities from the native reach, diminishing the overall dissimilarity between communities of the two reaches. With the exception of the N+P treatments, alike treatments from each reach supported more similar communities than different treatments from the same reach. In the native reach, nitrogen enrichment resulted in the presence of *Denticula elegans* and *Mastogloia elliptica,* absent from the native control treatment. It is apparent that the addition of nitrogen allowed these species, responsible for a combined 38% of dissimilarity, to dominate relative to the species-poor community from the control. Both are tolerant of high salinity and pH (Blinn et al., 2004) and were encountered in high densities on the nitrogen treatment samples from the saltcedar reach as well, reducing the dissimilarity between N-enriched communities of the two reaches to only 40%. In comparison the controls of the two reaches remained 96% dissimilar.

Nitrogen enrichment in the saltcedar reach resulted in decreased densities of both *R. gibba* and *R. gibberula.* Species of this genus possess unicellular N_2-fixing endosymbionts from the cyanobacterial genus *Cyanothece* (DeYoe et al., 1992; Prechtl et al., 2004). Nitrogen enrichment in this system decreased the density of these species because in conditions of higher nitrogen availability they lose their competitive advantage and become subdominant to species such as *A. minutissimum, D. elegans, A. veneta,* and *Nitzschia linearis. Achnanthidium minutissimum* was also present in consistently higher biovolumes on nitrogen-diffusing substrates relative to phosphorus-diffusing and control substrates in Lake Douglas (Fairchild and Lowe, 1984). *Rhopalodia gibba* and *R. gibberula* contributed a combined 58% of the dissimilarity between control and N-enriched diatom communities in the saltcedar reach and

70

52% of the dissimilarity in the same reach between control and the combined nutrient treatment. A similar decrease in N_2-fixing species has been documented along large scale nitrogen gradients across US streams (Porter et al., 2008).

Phosphorus enrichment in the native reach also resulted in *Mastogloia elliptica* colonization and increased densities of *A. veneta,* a eutrophic species (Van Dam, 1994) common in both reaches all through the study, but in much higher densities in nutrient enriched communities. The phosphorus-enriched community in the saltcedar reach was also dominated by *A. veneta* leading to a dissimilarity with its native counterpart as low as 46%. In the native reach, N+P treatment allowed *Nitzschia palea* to occur in high densities. *Nitzschia palea* is a hypereutrophic species (Van Dam, 1994), and similarly to *A. veneta* is very common in eutrophic and organically-polluted streams (Lange-Bertalot, 1979). Because of its broad salinity tolerance (Blinn et al., 2004; Kwandrans et al., 1998; Tornes et al., 2007), *N. palea* was able to proliferate on nutrient-diffusing substrates in McComb Creek, but was not found in high densities on tiles in either reach. *Rhopalodia gibberula* responded positively with phosphorus enrichment in both the native reach, where it was absent on the control, and saltcedar reaches, with the highest density of this species occurring in the P-enriched community. Similar to Fairchild and Lowe (1984), *R. gibba* responded to P-enrichment in the native reach and occurred in high density, but was notably absent from the control community. Phosphorus enrichment in the saltcedar reach resulted in higher densities of *Nitzschia microcephala,* a common eutrophic species of saltcedar communities, and *Synedra ulna,* which is indifferent to nutrient levels (Van Dam, 1994).

Nutrient treatments, as a whole, did not alter the dominant species in each reach. Both species of *Rhopalodia* and to a lesser extent, *A. minutissimum*, continue to be species that contribute the most to the dissimilarity of diatom communities that persists between the two study reaches. Nutrient enrichment does limit the dominance of *A. minutissimum;* this is

71

consistent with Venaart et al. (2008). *Rhopalodia gibba* and *R. gibberula,* both dominant contributors to un-enriched saltcedar communities are able to utilize P-enriched conditions and persist in high densities in both study reaches. Phosphorus enrichment in the native reach diminished the difference in diatom community assemblage from the saltcedar reach community, which supports the hypothesis that the higher SRP detected in the saltcedar reach is responsible for the differences.

4.4 Transplantation

The native reach substrates transplanted to the saltcedar reach ($N_{17}S'_{17}$) gained diatom species and biomass approximating the community allowed to colonize the saltcedar substrates during the entire time period. All of the species from both communities were common; they were just present in greater densities in the community confined to the saltcedar reach ($S_{17}S'_{17}$). In contrast, the transplanted community was highly dissimilar to the native reach community ($N_{17}N'_{17}$) showing higher densities of common species because of exposure to the P-richer environment of the saltcedar reach. Species that were notably absent from any native community, but present in $N_{17}S'_{17}$ communities were *R. gibba* and *N. palea*, possibly due to increased availability of P in the saltcedar reach as both species are eutrophic. The $N_{17}S'_{17}$ community also, as expected was closer to the saltcedar community from the second half of the experiment (S'_{17}), sharing characteristic saltcedar reach species, e.g. *N. palea, R. gibberula* and *R. gibba.* It should be noted that *A. minutissimum* was present in decreased densities following the transplantation, because it is a less competitive species under eutrophic conditions (Passy et al., 1999).

The saltcedar reach community transplanted to the native reach ($S_{17}N'_{17}$) experienced high dissimilarity to the community that was allowed to colonize for the entire period in the saltcedar reach ($S_{17}S'_{17}$). All colonists from before the transfer were still present, but densities of important species such as *N. microcephala, R. gibba, S. brebissonii,* and *R. gibberula* were

72

greatly reduced in the transplant community compared to the saltcedar community. This loss in density is apparent also when comparing communities from S_{17} to $S_{17}N'_{17}$ community. The high degree of dissimilarity in those communities was also due to lower densities of common species in the transplant assemblage. The $S_{17}N'_{17}$ community experienced even higher dissimilarity when compared to the native diatom community from the entire time period ($N_{17}N'_{17}$). The transplanted community maintained characteristic saltcedar species such as *R. gibba* and *N. palea* in lower densities, but did not experience the high growth rates of *A. minutissimum* observed in the native reach. The probable reason is that *A. minutissimum* is a pioneer species with a distinct preference for unoccupied substrates (Pringle, 1990). These results suggest that the low nutrient availability in the native site maintained algal succession arrested at initial stages. Conversely, the mild P enrichment in the saltcedar site, which was probably a consequence of the higher salt content in this site, stimulated the development of a more mature community with a greater richness and biomass.

4.5 Stream Metabolism

Light is a prominent abiotic factor that limits primary production (Hill et al., 1995). It was significantly lower in the saltcedar reach, due to interception of solar radiation by the shrub canopy. Chlorophyll *a* concentration did not vary significantly between the two study reaches. However, there was a significant increase in biomass of diatoms in the saltcedar reach. In shaded streams, it is possible that light is the primary abiotic constraint on photosynthesis where nutrients are less likely to be limiting at irradiances below photosaturation (Hill et al., 1995; Uehlinger and Brock, 2005). The saltcedar reach of McComb Creek, with an average of 109.07µmol photons/m^2/s was near, but not below the light saturation point of 100µmol photons/m^2/s indicated by Hill et al. (2009) for biovolume accrual. However, photoacclimation by algae under lower irradiances involves the accumulation of photopigments and the chlorophyll *a* molecule requires four nitrogen atoms, while the enzymes necessary for its synthesis have an

73

even greater N requirement (Hill et al., 2009). This could further exacerbate the N-limited conditions in the saltcedar reach, further giving advantage to the N_2-fixing species. Additionally, these lower light conditions could potentially decrease use of phosphorus by benthic algae, due to lower metabolic needs, thus leading to greater diversity based on increased SRP.

Also resulting from the increased canopy cover was a higher overall allochthonous input into the saltcedar reach of McComb Creek in the form of leaf litter from saltcedar, whereas no saltcedar litter was observed in the native reach. Leaf fall occurred between November and January each year and deposited in the stream as small mats. There was a significantly greater mass of leaf litter entering the stream in the saltcedar reach which was expected to increase decomposition and with it, respiration rate. However, community respiration was significantly higher in the native reach, possibly due to higher respiration rates of periphyton under high light which has been shown experimentally (Richardson et al. 1983).

Photosynthesis, measured as GPP, was significantly increased in the native reach. This finding is consistent with increased autochthonous production in native riparian reaches compared to saltcedar invaded reaches of Jackrabbit Springs (Kennedy and Hobbie, 2004). This increased production, coupled with the increased respiration rate in the native reach, is the explanation for the lack of significant increase in NDM when compared to the saltcedar reach. Periphyton from shaded sites was twice as efficient at fixing carbon at low light intensities and attained maximal photosynthetic rates at much lower light intensities in the lab than open site periphyton and this increased efficiency lessened potential differences in primary production at shaded and open sites (Hill et al., 1995). Because of increased respiration in the native reach and a photosynthetic rate response of shade tolerant algae in the saltcedar reach, the P:R did not significantly differ between the two sites. Mean values for both study reaches indicate primary productivity exceeds respiration. Relatively higher rates of community respiration experienced by the native reach are offset by the higher rate of photosynthesis.

Algal community metabolism in the native reach from this study is consistent with previous research in true desert streams (Table 4.1) and supports that autotrophy is prevalent in low order, arid streams (MInshall, 1978). Stream metabolism under saltcedar invasion is shifted and both GPP and respiration are lower than previously reported values.

Table 4.1 Productivity and Respiration Rates in True Desert Streams

	GPP	Respiration	
Sycamore Creek, AZ	2.78	1.67	Busch and Fisher, 1981
Pinto Creek, AZ	1.73	1.41	Lewis and Gerking, 1979
Rattlesnake Springs, WA	7.4	6.2	Cushing and Wolf, 1984
McComb Creek, TX	3.98	2.75	This study
McComb Creek, TX* (saltcedar reach)	1.05	0.75	This study

4.6 Conclusion

McComb Creek, under native riparian vegetation is an oligotrophic system characterized by fresh brackish water, and low algal species diversity. Semi-arid and arid streams typically exhibit increased salinity levels due to high evapotranspiration rates from soils, mineral weathering and brines of geologic origin (Hogan et al., 2007). Saltcedar invasion along the riparian corridor, through direct salt input, has shifted this native aquatic system to an ecosystem dominated by halophilic species capable of N_2-fixation, thus overcoming nitrogen limiting conditions. Native reach assemblages are characteristic of early successional communities with *A. minutissimum* as the consistently dominant species over time indicating that the limited nutrient conditions in this reach are maintaining algal communities at early stages. Increased phosphorus availability, likely driven by increased salinity of the saltcedar reach, allows proliferation of species, such as *Nitzschia gracilis* and *N. palea,* characteristic of mid- to late successional communities. Increased densities of eutrophic diatoms, including *Rhopalodia* and *Epithemia* species, shown to proliferate under phosphorus enrichment indicate that phosphorus increase is important to these diatom communities and is likely the cause of the differences between saltcedar and native reach algal assemblages observed in McComb

Creek. The salinity in the native reach, though significantly lower, was still considered brackish and halophilic species such as *Mastogloia elliptica* and *Denticula elegans* were able to proliferate, indicating the narrow gradient of salinity, although significant is not the primary cause of *Rhopalodia* species colonization in the saltcedar reach. The increase in SRP detected in the saltcedar reach, stimulated colonization and proliferation of *R. gibba* and *R. gibberula* and these species had a competitive advantage in the nitrogen limited conditions. High densities of these *Rhopalodia* species in phosphorus-enriched communities provides further evidence that the increased phosphorus conditions in the saltcedar reach relative to the native reach are the reason for community differences between the two sites. Although SRP concentrations measured in this study are considered extremely low, it is possible that sediments are providing an additional source of P to this system.

Proximity of the two reaches studied along the same creek suggests that the invasion and subsequent domination of the riparian community by saltcedar is the primary cause of observed shifts in aquatic environment to a more eutrophic system. Temporal variation within a reach, although contributing to within reach differences in communities, will tend to be offset by the same conditions experienced by both reaches through time. According to previous research, diatom diversity is negatively correlated with water salinity, conductivity and pH, although gradients in these parameters were not as narrow as those measured in McComb Creek (Gell, 1997; Blinn and Bailey, 2001; Blinn et al., 2004; Kirkwood and Henley, 2006). These parameters were among the significant aquatic environmental parameters between the native and saltcedar reaches in McComb Creek, but increases in salinity and conductivity were positively related to diatom diversity in McComb Creek. Conductivity, closely related to pH, is a major environmental determinant of diatom distribution, closely related to pH (Fritz et al., 1999; Soininen et al., 2004), but these studies found a positive relationship between conductivity and pH. Conditions at McComb Creek were quite the opposite as pH decreased the

76

conductivity/salinity, which was probably due to a positive relationship between hydrogen ion concentration and those of Na^+, K^+, Mg^{2+} and Cl^-, described by Blinn et al. (2004).

Nutrient enrichment with nitrogen and phosphorus resulted in higher diatom species diversity in experimental treatment samples from the native reach, with community assemblages more closely resembling those found in the saltcedar reach, indicating a greater ability of species in the saltcedar reach to utilize nutrients in conditions that are limited in both reaches. According to Fritz et al. (1999), salinity and other lake physicochemical processes that are correlated with it can have a significant impact on nutrient uptake and distribution of diatom taxa can be highly correlated with lake water salinity and those other factors. Nutrient concentration and pH primary factors, along with light levels that influence river diatom distribution and highest pH values were found in the arid regions of the western United States (Potapova and Charles, 2002).

The results presented in this study on species diversity of both diatoms and soft algae contradict previous research concluding that saltcedar invasion negatively impacts all aspects of both aquatic and terrestrial ecosystems. The effects of saltcedar removal have been positive for aquatic organisms such as native pupfish (Kennedy et al., 2005), but more research is necessary to determine the effects of removal on algal community assemblages in stream reaches where saltcedar has invaded.

APPENDIX A

SELECTED MICROSCOPE IMAGES OF
DIATOM SPECIES
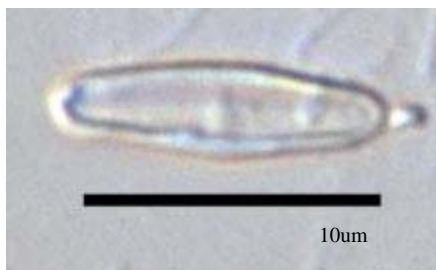
Achnanthidium minutissimum
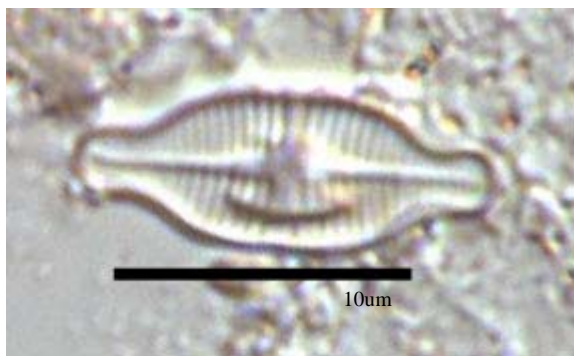
Achnanthidium exigua
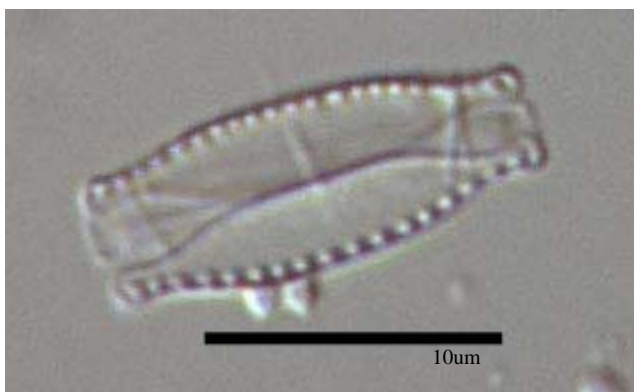
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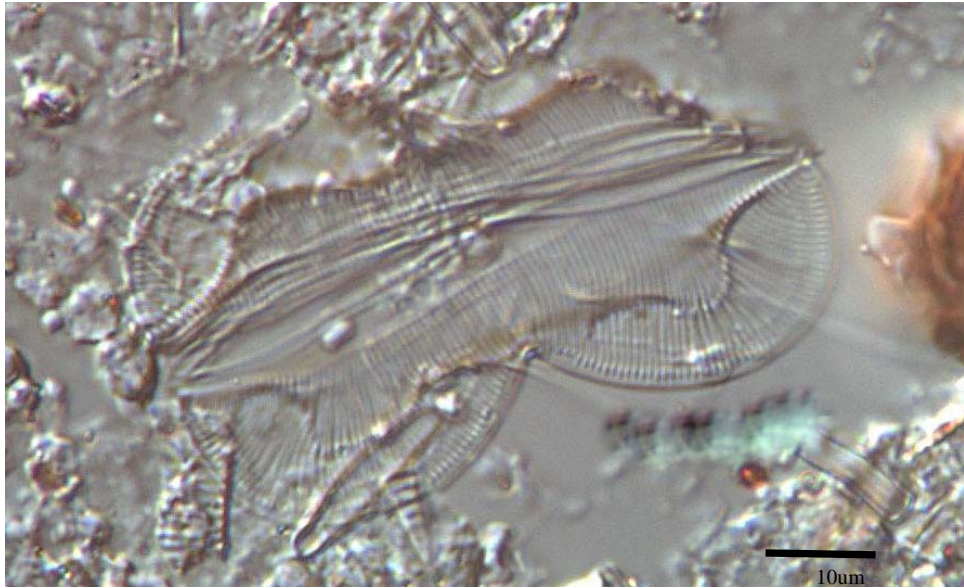
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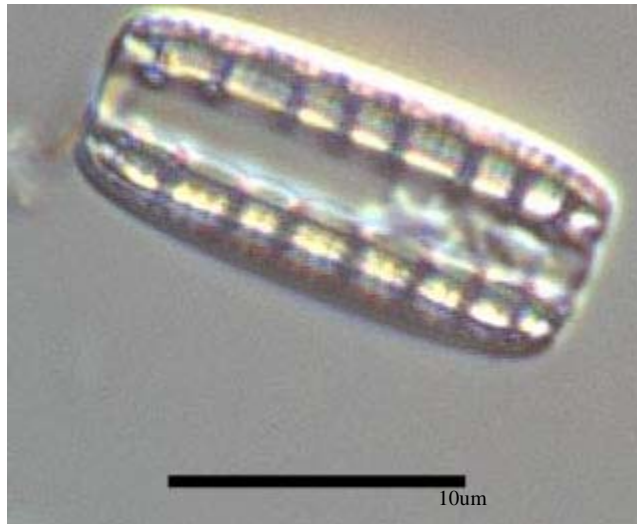
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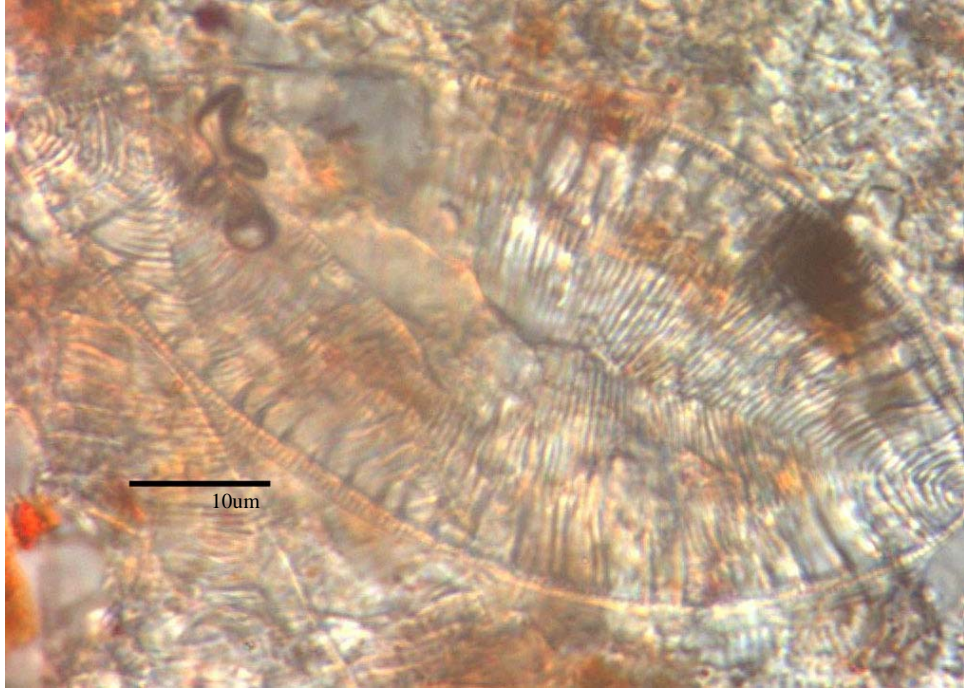
Surirella brebissoni
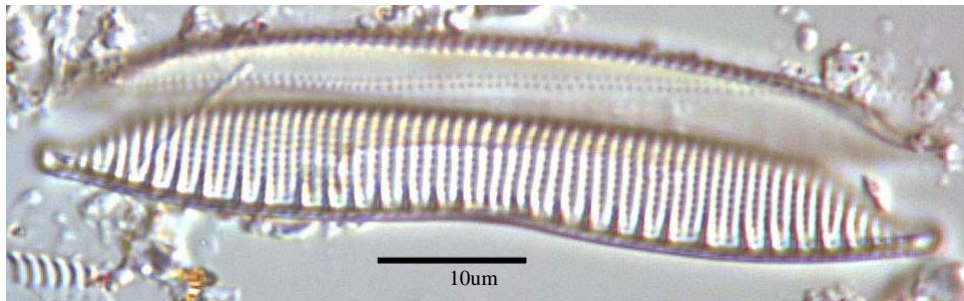
Hantzschia amphioxys
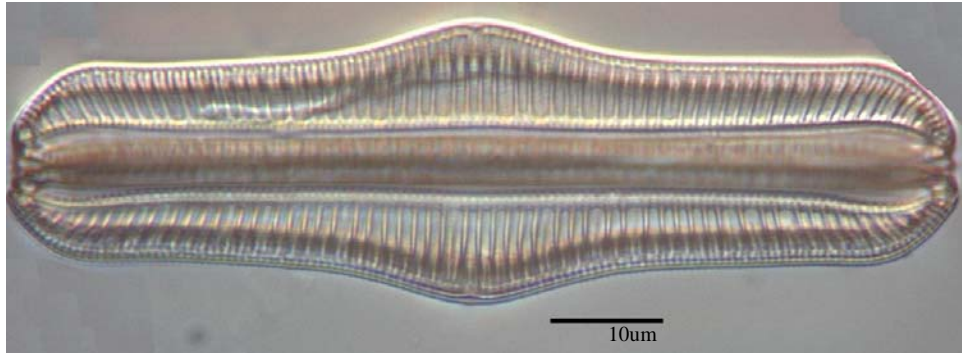
Rhopalodia gibba
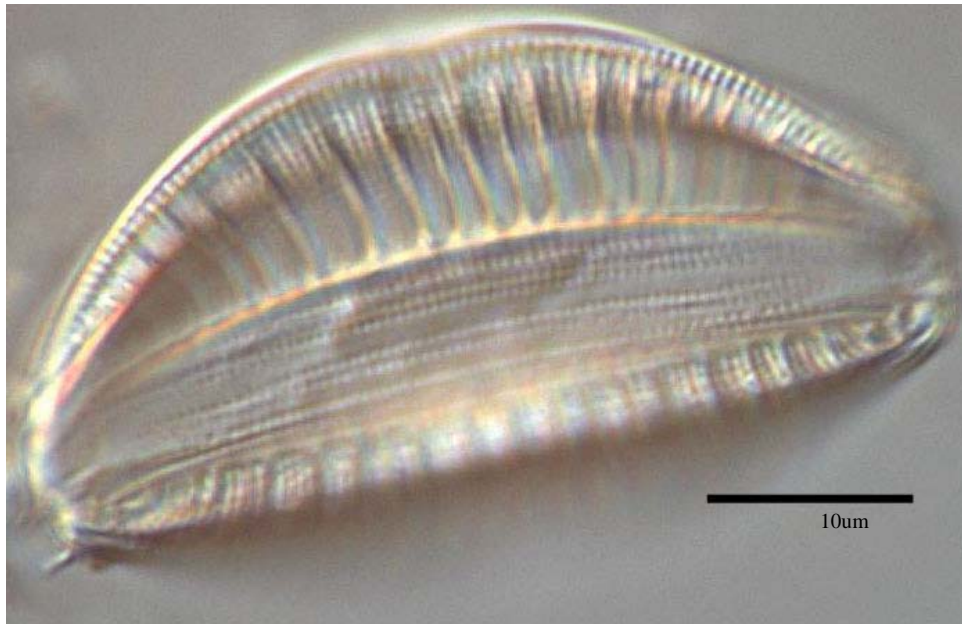
Rhopalodia gibberula
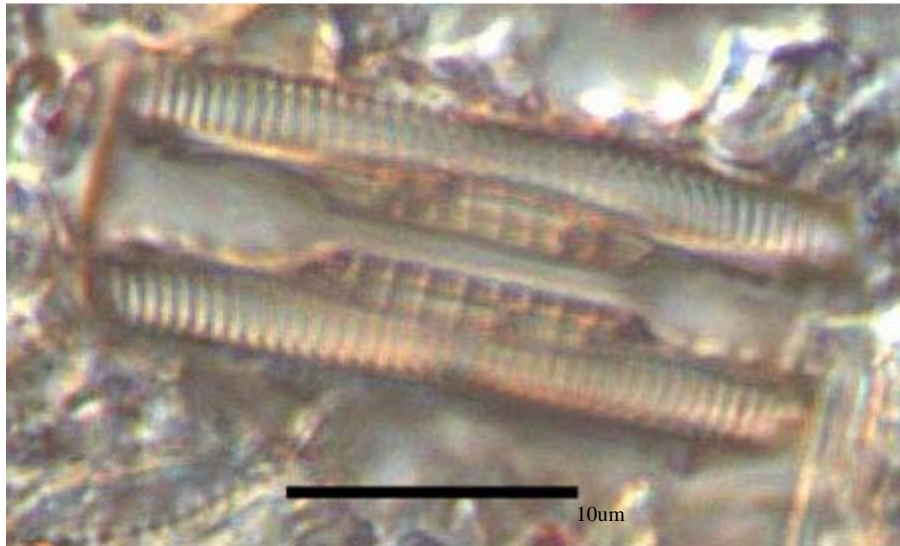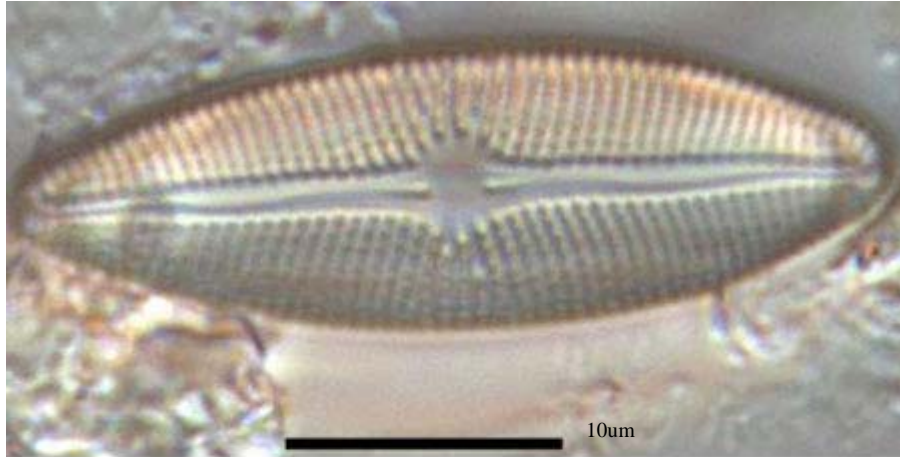
Mastogloia elliptica

APPENDIX B

ENVIRONMENTAL AND RELATIVE ABUNDANCE
DATA

Environmental Data for Each Survey Event in the Native Reach

	Temp (C)	pH	SCON (mS/cm)	SAL (ppt)	DO (mg/L)	PAR (E/s/m)	SRP (ug/L)	CHL (g/L)	Depth (cm)	FLOW (m/sec)
Nat_J06	10.51	8.88	2.19	1.17	9.11	237.42	0.859	22.1	9.11	0.106
Nat_J062	7.26	8.87	2.14	1.14	1.19	278.92	0.465	14.31	9.14	0.111
Nat_F06	12.93	8.88	2.14	1.15	2.14	284.00	1.428	35.6	9.33	0.117
Nat_M06	15.79	8.85	2.12	1.13	7.80	284.92	1.249	18.7	9.42	0.14
Nat_A06	23.39	8.86	2.10	1.14	5.75	419.92	0.661	11	10	0.106
Nat_N06	14.14	8.77	2.11	1.11	8.47	156.45	1.258		10.44	0.099
Nat_D06	14.86	8.54	2.10	1.12	6.44	66.71	0.546		10.72	0.161
Nat_J07	11.48	8.76	2.10	1.12	14.43	112.40	1.587	236.93	10.11	0.101
Nat_F07	11.23	8.74	2.08	1.11	16.72	280.82	0.565	116.86	10.11	0.103
Nat_M07	16.77	8.76	2.08	1.10	20.50	313.29	1.287	47.76	9.4	0.131
Nat_A07	23.39	8.86	2.10	1.14	5.75	419.92	0.585	56.98	6.89	0.095

Environmental Data for Each Survey Event in the Native Reach

	Temp (C)	pH	SCON (mS/cm)	SAL (ppt)	DO (mg/L)	PAR (E/s/m)	SRP (ug/L)	CHL (g/L)	Depth (cm)	FLOW (m/sec)
Nat J06	10.51	8.88	2.19	1.17	9.11	237.42	0.859	22.1	9.11	0.106
Nat J062	7.26	8.87	2.14	1.14	1.19	278.92	0.465	14.31	9.14	0.111
Nat F06	12.93	8.88	2.14	1.15	2.14	284.00	1.428	35.6	9.33	0.117
Nat M06	15.79	8.85	2.12	1.13	7.80	284.92	1.249	18.7	9.42	0.14
Nat A06	23.39	8.86	2.10	1.14	5.75	419.92	0.661	11	10	0.106
Nat N06	14.14	8.77	2.11	1.11	8.47	156.45	1.258		10.44	0.099
Nat D06	14.86	8.54	2.10	1.12	6.44	66.71	0.546		10.72	0.161
Nat J07	11.48	8.76	2.10	1.12	14.43	112.40	1.587	236.93	10.11	0.101
Nat F07	11.23	8.74	2.08	1.11	16.72	280.82	0.565	116.86	10.11	0.103
Nat M07	16.77	8.76	2.08	1.10	20.50	313.29	1.287	47.76	9.4	0.131
Nat A07	23.39	8.86	2.10	1.14	5.75	419.92	0.585	56.98	6.89	0.095

Relative Abundance of Diatom Species in the Native Reach

	NAT_J06	NAT_F06	NAT_M06	NAT_A06	NAT_J07	NAT_M07	NAT_A07
A. affinis	0	0	0	0	0	0	0.020
A. exigua	0	0.004	0.048	0.021	0	0.002	0.036
A. minutissimum	0.52	0.546	0.530	0.738	0.336	0.733	0.219
A. veneta	0.36	0.190	0.181	0.059	0.109	0.059	0.137
B. paxillifer	0	0	0.004	0.003	0	0	0
C. bacillum	0	0	0	0	0	0	0
C. molaris	0	0	0	0	0	0	0
C. ambigua	0	0	0	0	0	0	0.001
D. elegans	0	0.019	0	0.008	0.084	0.004	0.088
E. adnata	0	0.004	0.006	0	0	0.001	0
E. alata	0	0	0	0	0	0	0.004
G. clavatum	0	0	0	0	0.076	0	0.037
G. gracile	0	0	0	0	0.050	0	0.011
G. olivaceodes	0	0	0.004	0	0	0	0
H. amphioxys	0	0	0	0	0	0.001	0.004
M. elliptica	0	0.011	0.006	0.029	0	0.011	0.034
N. gracilis	0	0	0	0	0	0	0
N. trivialis	0	0	0	0	0.025	0	0.033
N. acicularis	0	0	0	0	0	0	0.002
N. inconspicua	0	0.015	0.017	0.002	0	0.001	0.018
N. linearis	0	0	0.011	0	0.034	0.005	0.008
N. microcephala	0	0.008	0.110	0.082	0.067	0.010	0.116
N. palea	0	0	0	0	0	0	0.060
N. vermicularis	0	0	0	0	0	0	0
P. appendiculata	0	0	0	0	0	0	0.007
R. gibba	0	0	0.048	0.029	0.034	0.033	0.012
R. gibberula	0	0.080	0.004	0.011	0	0.066	0.019
S. pupula	0.08	0.008	0.029	0.016	0.017	0.001	0.007
S.brebissoni	0	0.103	0	0	0	0.001	0
S. ulna	0.04	0.011	0.004	0.001	0.168	0.072	0.127

Relative Abundance of Diatoms Species in the Saltcedar Reach

	SAL_J06	SAL_F06	SAL_M06	SAL_A06	SAL_J07	SAL_M07	SAL_A07
A. affinis	0	0	0	0	0	0	0
A. exigua	0.195	0.142	0.083	0.035	0.060	0.048	0.075
A. minutissimum	0.126	0.075	0.105	0.012	0.025	0.050	0.081
A. veneta	0.309	0.251	0.102	0.080	0.164	0.135	0.143
B. paxillifer	0	0.039	0.022	0.083	0	0	0
C. bacillum	0	0	0	0	0	0	0
C. molaris	0	0	0	0	0	0	0
C. ambigua	0	0	0	0	0.008	0	0.001
D. elegans	0	0	0	0	0.009	0.045	0.038
E. adnata	0	0.008	0.005	0.058	0.002	0	0.004
E. alata	0.061	0	0	0	0.015	0.004	0.027
G. clavatum	0	0	0	0	0.008	0	0
G. gracile	0	0	0	0	0	0	0.010
G. olivaceodes	0	0.018	0.249	0	0	0	0
H. amphioxys	0	0.016	0	0.003	0.017	0	0.007
M. elliptica	0.004	0.036	0.019	0.033	0.015	0.015	0.035
N. gracilis	0	0	0	0	0.013	0	0.058
N. trivialis	0	0	0	0	0.062	0	0.068
N. acicularis	0	0	0	0	0	0	0
N. inconspicua	0.016	0	0.003	0	0	0.005	0.013
N. linearis	0	0.013	0	0.002	0.036	0.052	0.023
N. microcephala	0.231	0.057	0.238	0.080	0.074	0.280	0.158
N. palea	0	0	0	0	0.022	0	0
N. vermicularis	0	0	0	0	0	0	0
P. appendiculata	0	0	0	0	0	0	0
R. gibba	0.016	0.153	0.094	0.140	0.170	0.124	0.042
R. gibberula	0.016	0.161	0.063	0.420	0.111	0.085	0.064
S. pupula	0	0.021	0.008	0.025	0.012	0.022	0.019
S.brebissoni	0	0	0	0.008	0.003	0.010	0.004
S. ulna	0.024	0.010	0.008	0.020	0.174	0.125	0.131

Relative Abundances of Soft Algal Species in the Native Reach

	NAT_J06	NAT_F06	NAT_M06	NAT_A06	NAT_J07	NAT_M07	NAT_A07
A. constricta	0.030	0.456	0.835	0.014	0.753	0.653	0
A. solitaria	0	0	0	0	0	0	0
A. sphaerica	0.003	0.004	0.006	0.003	0	0	0
Cladophora	0.062	0	0	0	0.247	0	0
Closterium	0	0.001	0	0	0	0	0
L. gracilis	0.021	0	0	0.009	0	0	0
L. maior	0	0	0	0	0	0	0
Merismopedia	0.001	0.002	0.001	0	0	0	0
O. limnetica	0	0	0	0	0	0.347	0
Spirogyra	0.884	0	0.00	0.087	0	0	0
S.abbreviata	0.001	0	010	0	0	0	0
Ulothrix	0	0	0	0	0	0	0
Zygnema	0	0.536	0.149	0.887	0	0	0
Zygnema spores	0	0	0	0	0	0	1

Relative Abundances of Soft Algal Species in the Saltcedar Reach

	SAL_J06	SAL_F06	SAL_M06	SAL_A06	SAL_J07	SAL_M07	SAL_A07
A. constricta	0.021	0.499	0.370	0.295	0.798	0	0
A. solitaria	0	0	0	0	0	0	0
A. sphaerica	0.002	0.009	0.004	0.012	0.002	0	0
Cladophora	0.615	0	0.093	0	0	0.168	0
Closterium	0	0.002	0	0	0.001	0	0
L. gracilis	0	0	0	0	0	0.020	0.232
L. maior	0.003	0	0	0	0.004	0.018	0.077
Merismopedia	0	0.009	0	0	0	0	0
O. limnetica	0.001	0.008	0.006	0.001	0.067	0.794	0.515
Spirogyra	0	0	0	0.190	0	0	0
S. abbreviata	0	0.029	0	0	0.003	0	0
Ulothrix	0	0	0.176	0.376	0	0	0
Zygnema	0.359	0.444	0.351	0.126	0.125	0	0.136
Zygnema spores	0	0	0	0	0	0	0.039

Density of Diatom Species on Nutrient-Diffusing Substrates

	Nat CON	Salt CON	Nat NIT	Salt NIT	Nat PHOS	Salt PHOS	Nat N+P	Salt N+P
A. affinis	0	0	52.79	0	76.95	0	0	0
A. exigua	0	43.29	21.99	50.69	58.84	102.46	183.16	62.78
A. minutissimum	57.22	57.72	255.17	9.38	516.03	298.09	470.99	136.04
A. veneta	3.76	490.70	197.97	142.7	624.67	1397.30	1269.06	308.70
B. paxillifer	0	0	0	0	0	0	0	0
C. bacillum	0	0	0	0	0	0	0	0
C. molaris	0	0	0	0	0	0	0	0
C. ambigua	0	0	0	0	9.05	0	0	0
D. elegans	0	245.35	263.96	268.50	407.39	475.08	392.49	88.94
E. adnata	0	0	0	0	0	0	0	0
E. alata	0	86.59	26.39	92.00	0	93.15	0	57.55
G. clavatum	0	0	26.39	0	144.85	0	222.41	0
G. gracile	0	0	17.59	0	0	0	0	0
G. olivaceodes	0	0	0	0	0	0	0	0
H. amphioxys	0	50.51	0	13.14	40.73	558.92	52.33	36.62
M. elliptica	0	158.75	237.57	146.45	511.50	195.62	0	41.85
N. gracilis	0	0	0	0	0	0	0	115.11
N. trivialis	0	93.81	30.79	97.63	58.84	698.65	0	99.41
N. acicularis	0	0	8.79	0	9.05	0	0	0
N. inconspicua	0	14.43	30.79	15.02	13.57	46.57	39.24	5.23
N. linearis	0	28.86	17.59	0	126.74	186.30	104.66	10.46
N. microcephala	0	158.76	101.18	71.35	344.02	1201.68	0	429.05
N. palea	0	101.02	8.79	73.22	167.48	316.72	601.82	52.32
N. vermicularis	0	0	0	0	0	0	0	0
P. appendiculata	0	0	21.99	0	81.47	0	104.66	0
R. gibba	0	815.43	35.19	189.64	253.48	568.23	0	78.48
R. gibberula	0	685.54	26.39	240.33	457.18	1332.09	0	151.73
S. pupula	0	14.43	8.79	20.65	54.31	37.26	0	31.39
S. brebissoni	0	0	0	0	18.10	0	0	0
S. ulna	2.51	245.35	101.18	110.78	470.76	1257.57	91.58	146.50

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94

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BIOGRAPHICAL INFORMATION

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