EFFECTS OF FLOOD REGIME AND RIPARIAN PLANT SPECIES ON SOIL NITROGEN CYCLING ALONG THE MIDDLE RIO GRANDE: IMPLICATIONS FOR RESTORATION

by

JENNIFER JO FOLLSTAD SHAH

B.A., Political Science / French, University of Wisconsin-Madison, 1995

DISSERTATION
Submitted in Partial Fulfillment of the Requirements for the Degree of

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BIOLOGY

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Jennifer Jo Follstad Shah
Candidate

Department of Biology

This dissertation is approved, and it is acceptable in quality and form for publication on microfilm:

Approved by the Dissertation Committee:

Clifford N. Dohm, Chairperson
Julie Comod
Jacek Gryf
R. A. Linsdale
Clifford Comfot

Accepted:

Amy B. Wohlet
Dean, Graduate School

JUL 25 2006
Date
DEDICATION

This dissertation is dedicated to
my parents, Judith and George Follstad,
and my husband, Mark Shah,
whose love and support were
always with me along this journey.
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I have been incredibly lucky to be surrounded by many wonderful people, who have been instrumental in helping me to carve out my path in life.

I am indebted to Cliff Dahm for playing an important role as an advisor to me, especially through the early part of my graduate career. Cliff is one of the best scientists that I have met, and I feel very lucky to have had the opportunity to learn from him. Cliff has been particularly instrumental in teaching me about freshwater ecosystems, biogeochemistry, restoration, and how to conduct good, objective science. Cliff also has spent a good deal of time teaching me the art of writing papers for scientific journals. Not only have I gained valuable knowledge and skills from Cliff, but I have also gained a good friend and colleague.

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I am especially appreciative of my husband, Mark Shah. I do not know how I could have completed my work without his enduring love, support, and patience. Mark always knew when to leave me alone with my research or to pull me away from it for a much needed break. He also spent three extra (and rewarding) years in Albuquerque after his medical residency in order for me to complete my dissertation.
I owe many thanks to my parents, Judith and George Follstad, who have been extremely supportive of me and have played an important role in my education. My father has worked hard all his life to provide me with opportunities. He also has offered sage advice pertaining to so many of facets of life. My mother has always encouraged me to pursue my personal interests and provided a sounding board for the discussion of difficulties or decisions.

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ABSTRACT

River and riparian restoration activity has exponentially increased throughout the southwestern U.S. since 1990. I analyzed almost 600 restoration project records from Arizona, Colorado, New Mexico, and Utah (Chapter 2). Riparian management was the most common type of project, followed by water quality management, in-stream habitat improvement, and flow modification. Total restoration costs exceeded $500 million. Monitoring was linked to 28% of projects in the Southwest, as opposed to just 10% nationwide. Restoration efficacy was difficult to ascertain from existing datasets.

The Southwest differed from other regions of the U.S. due to its high proportion flow modification projects. Flow management has reduced the exchange of water, energy, and materials from rivers and floodplains, causing regional declines in native plant populations and the spread of non-natives. Naturalization of flow regime is one form of riparian restoration. I examined the effects of flow regime on soil nitrogen
cycling in riparian forests along the middle Rio Grande of New Mexico that were dominated by native *Populus deltoides* ssp. *wislizenii* and non-native *Tamarix chinensis* (Chapter 3). I also compared the abilities of each species to acquire and allocate nitrogen resources (Chapter 4).

The effects of flow regime varied across plant species. Flood sites had a greater number of nitrogen loss pathways relative to sites that were disconnected from flooding. In addition, sites with high quantities of riparian leaf production maintained greater pools of soil nitrogen, irregardless of flood regime. Patterns of nitrogen acquisition and allocation were similar across species, despite differences in mycorrhizal association. Thus, *T. chinensis* and *P. deltoides* were functionally similar with regards to their effects on soil nitrogen cycling.

Riparian nitrogen resources are, in part, regulated by the timing and duration of floods. Spring floods mobilize nitrogen resources early in the growing season, allowing for maximal nitrogen uptake by riparian plants. Long-term floods promote anoxia in riparian plant roots, resulting in reduced uptake of soil nitrogen and suppressed leaf production. I advocate the continued practice of spring-time naturalized flow within rivers of semi-arid regions, but highlight the need to determine thresholds at which extended flood duration does more harm than good.
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PREFACE

This dissertation comprises five chapters. Chapter one is an introductory chapter that provides the context for the research chapters that follow. The second, third, and fourth chapters represent manuscripts of research that have been or will be submitted individually to scientific journals for publication. Chapter five summarizes the findings and significance of these research chapters, and outlines avenues of future inquiry.

All of the research chapters embodied in this dissertation include co-authors. Chapter two “River and riparian restoration in the Southwest: Results of the National River Restoration Science Synthesis Project” was co-authored by Drs. Clifford N. Dahm (University of New Mexico, Department of Biology), Steven P. Gloss (University of Arizona, U.S. Geological Survey Sonoran Desert Research Station), and Emily S. Bernhardt (Duke University, Department of Biology). This chapter was submitted to
Restoration Ecology in February 2006 for publication in an issue dedicated to the National River Restoration Science Synthesis Project. Chapter two “Soil nitrogen dynamics in stands of *Populus deltoides* ssp. *wislizenii* and *Tamarix chinensis* with differing flood regimes” was co-authored with Dr. Clifford N. Dahm (University of New Mexico, Department of Biology). Chapter three “Similarities in soil nitrogen resource acquisition and allocation by *Populus deltoides* ssp. *wislizenii* and *Tamarix chinensis*” was co-authored by Drs. Clifford N. Dahm, Robert L. Sinsabaugh (University of New Mexico, Department of Biology), and Vanessa B. Beauchamp (U.S. Geological Survey, Fort Collins Science Center). Neither chapters two nor three have yet been submitted for publication.
CHAPTER ONE: INTRODUCTION

Riparian forests are some of the most productive and diverse ecosystems on Earth due to the exchange of water, materials, and nutrients between rivers and their floodplains (Junk et al. 1989, Bayley 1995). Flow regulation has been estimated to control 77% of total water discharge in 139 large river ecosystems in the northern one-third of the world (Dynèsesius and Nilsson 1994), breaking the connectivity between rivers and floodplains. Furthermore, the majority of desert and xeric shrubland catchments worldwide are strongly affected by flow regulation (Nilsson et al. 2005). The effects of flow regulation are pronounced in semi-arid regions where water resources are relatively scarce and flood pulses strongly organize the biotic structure and function of riparian forests (Fisher et al. 1982, Walker et al. 1995, Molles et al. 1998, Jacobson et al. 2000).

Flow regulation has degraded river ecosystems of arid and semi-arid regions of the southwestern U.S. by altering the timing, magnitude and frequency of flood events in most rivers. Cycles of native fish spawning that evolved to be in concert with peak river flows have been offset or interrupted altogether (Allan and Flecker 1993). Populations of non-native fish now thrive as a result of cooler stream temperature and reduced sediment loads resulting from dams (Holden and Stalnaker 1975, Minckley 1991). The altered hydrograph has caused major declines in riparian forests of the Southwest (Christensen et al. 1996) through reduced recruitment of native riparian plants (Rood and Mahoney 1990) and increased invasion by non-natives (Merritt and Cooper 2000, Shafroth et al. 2002, Uowolo et al. 2005). Detrimental effects to river and riparian areas have led to the listing of eleven species native to rivers and riparian areas of the Southwest as threatened
or endangered. Numerous restoration efforts have been conducted or are currently underway to mitigate these effects and to conserve populations of native, threatened, and endangered species. Chapter two of this thesis describes current trends in restoration throughout the Southwest and reveals how perceptions of restoration success compare between restoration practitioners and restoration ecologists.

Two dominant types of restoration in the Southwest pertain to flow and riparian management. Flow management often includes augmentation of base flows or manipulation of hydrographs to mimic flow patterns typical of those that occurred prior to river regulation. This latter type of flow management results in a "naturalized" flow regime (Poff et al. 1997). Common riparian management activities include mechanical or herbicidal control of non-native plants and revegetation with native plants. Removal of non-native plants is sometimes combined with managed flooding to promote the recruitment of native vegetation.

The middle Rio Grande in central New Mexico serves as an optimal system to study riparian forests under regulated flow conditions and invasion by non-native plants. This reach extends 320 km and is delineated by large dams both upstream and downstream. Modern river regulation began in the early 20th century. Elephant Butte Dam, which is located at the southern end of the reach, was completed in 1916 (Bullard and Wells 1992). It was the largest dam in the world at the time of construction and created the second largest man-made water impoundment. Cochiti Dam, completed in 1973, is located at the northern end of the middle Rio Grande. This dam is a rolled earthfill embankment with a crest length of more than 8 km and a crest height of 76 m above the Rio Grande channel bed (Bullard and Wells 1992). Cochiti Dam serves as the
delivery point for releases of water through the middle Rio Grande delivered for human consumption and those designed to preserve ecological integrity. The states of Colorado, New Mexico, and Texas negotiated the Rio Grande Compact in 1923 (Bullard and Wells 1992), which was approved by these states and the U.S. Congress in 1939. The compact prescribes water delivery obligations by upstream states to those downstream. As such, the Rio Grande Compact is the most important document governing the flow of water through the middle Rio Grande. The quantity of water transferred to Texas each water year (October – September) depends on the volume of water that passes through the Otowi stream gauge, which is then stored in either Cochiti Reservoir or Elephante Butte Reservoir. The latter is the delivery point for water delivered from New Mexico to Texas. Water operation managers release water from Cochiti Dam and Elephant Butte Dam to meet delivery requirements of the Rio Grande Compact. Releases from Cochiti Dam can result in overbank flood events within the middle Rio Grande, especially in years of relatively high water supply (e.g., El Niño years; Molles et al. 1992). However, these flows are constrained to roughly 200 m$^3$ s$^{-1}$ through the City of Albuquerque.

The floodplain along the middle Rio Grande, like many other large river systems, was historically a mosaic of ecosystems with differing frequencies and durations of inundation. Flow regulation has resulted in the loss of 50% of wetlands (Crawford et al. 1993) and caused a decline in populations of native riparian plants, such as *Populus deltoides* ssp. *wislizenii* (Rio Grande cottonwood) (Howe and Knopf 1991). *P. deltoides* is an obligate phreatophyte, but cannot thrive in groundwater depths greater than 5 m (Stromberg et al. 1996) due to its susceptibility to drought-induced cavitation (Tyree et al. 1994, Pockman et al. 1995, Leffler et al. 2000). Mature *P. deltoides* ($\geq$ 10 years in
age) set seed in spring, coinciding with flood events historically associated with snowmelt run-off. Germination of *P. deltoides* seedlings requires scoured soils free of shading from larger trees (Scott et al. 1997) and a drawdown of soil moisture under 5 mm d$^{-1}$ over the first 1-2 weeks of establishment (Mahoney and Rood 1998, Taylor et al. 1999). *P. deltoides* mature trees and seedlings can tolerate inundation of 3-4 weeks (Rood and Mahoney 1990). However, extended flood inundation of mature trees promotes root anoxia and reduces leaf production (Smit et al. 1989, Smit et al. 1990).

Today, fewer riparian areas are well-connected to the Rio Grande as a result of reduction in peak flows, incision of channel beds caused by dams and diversions, and bifurcation of floodplains by levees and irrigation canals. These modifications alter the conditions required for *P. deltoides* seedling recruitment and lower water tables in riparian forests (Howe and Knopf 1991, Busch and Smith 1995, Stromberg et al. 1996, Merritt and Cooper 2000).

Non-native plants pose an additional threat to the preservation of native *P. deltoides* forests. *Tamarix chinensis* (salt cedar) and *Elaeagnus angustifolia* (Russian olive) are particularly invasive along the middle Rio Grande. Species of *Tamarix* and *E. angustifolia* were introduced to the U.S. in the late 1800s to create wind breaks, provide shade, and stabilize eroding streambanks (Di Tomaso 1998). They are now the third and fourth most common woody riparian plants throughout the western U.S. (Friedman et al. 2005). Excellent reviews on the taxonomy, biology, and ecology of these species have been provided by Everitt (1980), Brock (1994), Di Tomaso (1998), and Katz and Shafroth (2003). The following text describes a few of the adaptations that allow *T. chinensis* and *E. angustifolia* to compete so well with *P. deltoides*.
Both non-native species are facultative phreatophytes, meaning they utilize soil pore water resources in addition to groundwater resources. *T. chinensis* tolerates groundwater over 5 m deep and has been found where groundwater depths reach 50 m. The rooting system of *E. angustifolia* is much shallower, extending just 1-3 m. *T. chinensis* also has been reported to tolerate inundation for up to 70 days and grows adventitious roots at the water line of riparian inundation. However, flood inundation of one month in duration has induced mortality in *E. angustifolia*. *T. chinensis* close their stomata and drop their leaves during periods of drought, which reduces the chance of drought-induced cavitation. Drought-adapted characteristics of *E. angustifolia* leaves include sunken stomata and pubescence. Seedlings of *T. chinensis* are not shade tolerant, but can establish within light gaps of *P. deltoides* canopies. *E. angustifolia* is tolerant of shade, although it is often found lining the banks of the Rio Grande. *T. chinensis* sets seed throughout the growing season and has been reported to do so as early as its first year of establishment. Like *P. deltoides*, its seeds are dispersed by wind and water and are viable for roughly one month. In contrast, the fruits of *E. angustifolia* are dispersed by animals and its seeds are viable for 1-3 years. *E. angustifolia* and *T. chinensis* are tolerant of soil salinities up to 10 ppt and 36 ppt, respectively, while *P. deltoides* survives in salinities of 1.5 ppt or lower. Thus, these non-natives can establish in riparian areas that have been used for agriculture or where flooding has not occurred for some time. *E. angustifolia* form associations with nitrogen-fixing bacteria of the genus *Frankia*, thereby minimizing its reliance on soil nitrogen resources. Both *T. chinensis* and *P. deltoides* must access groundwater and soil resources to obtain nitrogen required for plant maintenance and growth.
Naturalized flow regimes are regarded as a tool to control non-native plants and promote native plant recruitment (Stromberg 2001, Rood et al. 2003). Return of naturalized flows to disconnected riparian forests also has been shown to stimulate particulate organic matter decomposition, microbial respiration (Molles et al. 1998, Ellis et al. 1999), and retention of dissolved nutrient inputs via floodwaters (Valett et al. 2005). These studies and others (Crawford et al. 1996, Ellis et al. 1998, Ellis 2001) formed the background for a large-scale interdisciplinary study of the role of seasonal flooding in maintaining the ecological integrity of *P. deltoides* riparian forests along the middle Rio Grande. This study was focused on two central questions: 1) How has the isolation of the river from its floodplain affected riparian forest ecosystem structure and function? and 2) What ecological benefits derive from restoration of the flood pulse? Chapters three and four were components of this study. In chapter three, I examined the effects of flood regime (flooding vs. lack of flooding) on soil nitrogen cycling in *P. deltoides* and *T. chinensis* riparian forests along the middle Rio Grande. In chapter four, I compared the abilities of *P. deltoides* and *T. chinensis* to acquire and allocate nitrogen resources to determine whether competition for nitrogen plays a role in riparian invasion by *T. chinensis*. Few studies have examined the role of flood regime on nitrogen cycling in riparian soils of arid to semi-arid regions (e.g., Adair et al. 2004, Heffernan and Sponseller 2004), and little is known about the nitrogen physiology of *T. chinensis* and *P. deltoides*. The studies described in chapters three and four thus fill existing gaps in ecological knowledge and provide additional information with which to guide riparian restoration efforts in arid to semi-arid regions.
CHAPTER TWO: RIVER AND RIPARIAN RESTORATION IN THE SOUTHWEST: RESULTS OF THE NATIONAL RIVER RESTORATION SCIENCE SYNTHESIS PROJECT

Abstract: River and riparian restoration activity has exponentially increased across the U.S. since 1990. Over 37,000 records were compiled into the National River Restoration Science Synthesis database to analyze restoration project trends and effectiveness. I analyzed data from 576 restoration projects in the Southwest. The most common types of restoration were riparian management, water quality management, instream habitat improvement, and flow modification. Estimates of total restoration costs exceeded $500 million. Most restoration dollars have been allocated to flow modification and water quality management. Monitoring was linked to 28% of projects across the Southwest, as opposed to just 10% nationwide. Mean costs were comparable whether or not projects were monitored. Results from 48 telephone interviews provided validation of NRRSS-SW database analyses, but showed that project costs are often under-reported within existing datasets. The majority of interviewees considered their projects to be successful, most often based upon observed improvements to biota or positive public reaction rather than evaluation of field data. The efficacy of restoration is difficult to ascertain given the dearth of information contained within most datasets. There is a great need for regional entities that not only track information on project implementation, but also maintain and analyze monitoring data associated with restoration. Agencies that
fund or regulate restoration should reward projects that emphasize monitoring and evaluation as much as project implementation.

INTRODUCTION

The stress on surface water resources is increasing in concert with societal demands for freshwater (Gleick 2003). Concern over water quality and quantity, biodiversity, and land preservation along rivers has led to a boom in restoration activity across the U.S. at an annual cost of roughly $1 billion (Bernhardt et al. 2005). Trends in river restoration across the U.S. have been described only recently because most projects have been small scale (less than 1 km in length) and datasets on restoration activities have been distributed across numerous locations (Bernhardt et al. 2005). River restoration in the southwestern U.S. has followed national trends to a large degree, but also has been shaped by influences unique to the region.

Restoration activity across the U.S. Southwest has exponentially increased since 1990 in order to counteract the detrimental effects of flow regulation, overgrazing of rangelands, mining and urbanization. Flow regulation has altered the timing, magnitude, duration, and frequency of flood events in most rivers. The altered hydrograph has reduced recruitment of native riparian plants (Rood and Mahoney 1990) and promoted invasion by non-natives (Merritt and Cooper 2000, Shafroth et al. 2002, Uowolo et al. 2005). Riparian forest fire frequency has increased concurrent with fuel load accumulation (Stuever 1997). Increased fuel loads have resulted from the suppression of floods, which remove large woody debris and promote decomposition (Ellis 2001). Cycles of native fish spawning that evolved to be in concert with peak river flows have
been offset or interrupted altogether (Allan and Flecker 1993). Populations of non-native fish now thrive as a result of cooler stream temperature and reduced sediment loads resulting from dams (Holden and Stalnaker 1975, Minckley 1991). Overgrazing adjacent to streams has reduced riparian plant cover and promoted high rates of bank erosion, thus increasing stream temperature and turbidity and reducing the capacity of buffer strips to filter upland run-off (Belsky et al. 1999). Urbanization, agriculture, and mining activities have elevated non-point sources of nutrients, salinity, sediment, and pollutants such as metals and mine tailings. Roughly 14% of assessed river kilometers in the Southwest are impaired as a result of these activities (EPA 2005).

Excessive water withdrawals are a serious problem for southwestern rivers, as they are for other regions of the world (Gleick 2003). Surface freshwater withdrawals in 2000 ranged from 4.4 million m$^3$ d$^{-1}$ (1,170 million gal. d$^{-1}$) in New Mexico to 39 million m$^3$ d$^{-1}$ (10,300 million gal. d$^{-1}$) in Colorado (Hutson et al. 2004). The rate of extraction in Colorado is exceeded only by six other states – California, Texas, Illinois, Idaho, Ohio and South Dakota. Water extraction has dramatically reduced in-stream flows of rivers throughout the world (Nilsson et al. 2005). Today, both the Colorado River and Rio Grande often run dry before reaching the ocean.

Population growth and urban development are partially responsible for high water extraction rates in the Southwest. Population growth ranged from 20% - 40% across Arizona, Colorado, New Mexico, and Utah between 1990 - 2000, while overall growth for the nation was 13% (Perry and Mackun 2001). Arizona, Colorado, and Utah were the three fastest growing states after Nevada during this time period. Domestic water consumption has declined or leveled off since the 1980s, despite continued population
growth (Hutson et al. 2004). Current rates of water consumption, however, are 70% of the renewable water supply in the Rio Grande Watershed, and exceed the renewable water supply in the Lower Colorado Watershed (Anderson and Woosley 2005). Thus, high rates of population increase place an ever greater demand on already limited water resources in the semi-arid to arid Southwest. These demands increasingly tax the biotic structure and function of river ecosystems.

Detrimental effects to river and riparian areas have led to the listing of eleven species native to rivers and riparian areas of the Southwest as threatened or endangered. The listing of these species combined with interests to rehabilitate habitat and improve water management has, in turn, spurred the creation of seven large-scale species recovery or ecosystem adaptive management programs (AMPs; Table 1) including the: Glen Canyon Dam Adaptive Management Program (GCDAMP), Lower Colorado River Multi-Species Conservation Program (LCRMSCP), Middle Rio Grande Endangered Species Collaborative Program (MRGESACP), San Juan River Basin Recovery and Implementation Program (SJRBRIP), Upper Colorado River Endangered Fish Recovery Program (UCREFRP), and the Utah Reclamation, Mitigation, and Conservation Commission’s Restoration of the Provo River (URMCC). The Upper Animas Abandoned Mine Land Program (UAAML) is a pilot program designed to remediate contamination from abandoned hard rock mining operations at the scale of the watershed. These programs are “adaptive” because their work plans are modified as new insights are obtained through monitoring efforts that track population and ecosystem level responses to program actions.
Table 1. Summary of adaptive management programs associated with southwestern rivers.

<table>
<thead>
<tr>
<th>Name of program</th>
<th>Lead agency</th>
<th>State(s)</th>
<th>Years of implementation¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glen Canyon Dam Adaptive Management Program (GCDAMP)¹</td>
<td>Glen Canyon Dam Adaptive Management Work Group⁵</td>
<td>AZ</td>
<td>1997-2005</td>
</tr>
<tr>
<td>Lower Colorado River Multi-Species Conservation Program (LCRMSCP)²</td>
<td>U.S. Bureau of Reclamation</td>
<td>AZ, NV, CA</td>
<td>2004-2055</td>
</tr>
<tr>
<td>Middle Rio Grande Endangered Species Collaborative Program (MRGESACP)³</td>
<td>U.S. Fish and Wildlife Service</td>
<td>NM</td>
<td>2001-2004</td>
</tr>
<tr>
<td>San Juan River Basin Recovery and Implementation Program (SJBRIP)⁴</td>
<td>U.S. Fish and Wildlife Service</td>
<td>CO, NM</td>
<td>1992-2005</td>
</tr>
<tr>
<td>Upper Animas Abandoned Mine Land Program (UAAMLP)⁵</td>
<td>Animas River Stakeholders Group⁶</td>
<td>CO</td>
<td>1994-2005</td>
</tr>
<tr>
<td>Upper Colorado River Endangered Fish Recovery Program (UCREFRP)⁵</td>
<td>U.S. Fish and Wildlife Service</td>
<td>CO, UT, WY</td>
<td>1989-2005</td>
</tr>
<tr>
<td>Utah Reclamation, Mitigation, and Restoration of the Provo River⁶</td>
<td>Utah Reclamation, Mitigation, and Conservation Commission⁸⁸</td>
<td>UT</td>
<td>1992-2005</td>
</tr>
</tbody>
</table>

¹ The Glen Canyon Dam Adaptive Management Workgroup is a Federal Advisory Committee that was established in 1997. It is comprised of federal agencies, states, Native American tribes or nations, federal power purchase contractors, and environmental / recreational interest groups.

² In 1995, the Colorado Water Quality Control Commission empowered the Animas River Stakeholders Group (ARSG) to locate and evaluate sources of metals contamination, determine potential improvements, and prioritize sites for remediation in the Upper Animas River catchment. ARSG is a voluntary consortium of federal and state agencies, municipalities and counties, mining companies, the Southern Ute Tribe, and environmental organizations.

³ The Utah Reclamation Mitigation and Conservation Commission is an Executive branch agency of the federal government. The Commission was authorized under the Central Utah Project Completion Act of 1992.

⁴ Refers to years for which the program has been in existence.

² Murphy 2005; Bureau of Reclamation 2005
³ MRGESACP 2003, 2005; www.fws.gov/mrgesacp
⁴ FWS 2005
⁵ Simon, W., personal communication; http://www.waterinfo.org/arsg/main.html
⁶ Holden, M., personal communication; www.mitigationcommission.gov/prrp/prrp.html

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<table>
<thead>
<tr>
<th>Name of program</th>
<th>River length (km)</th>
<th>Total cost</th>
<th>Estimated cost of restoration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glen Canyon Dam Adaptive Management Program (GCDAMP)</td>
<td>450</td>
<td>$67,520,000</td>
<td>$38,500,000</td>
</tr>
<tr>
<td>Lower Colorado River Multi-Species Conservation Program (LCRMSCP)</td>
<td>640</td>
<td>$626,000,000</td>
<td>$495,000,000</td>
</tr>
<tr>
<td>Middle Rio Grande Endangered Species Collaborative Program (MRGESACP)</td>
<td>320</td>
<td>$30,600,000</td>
<td>$25,600,000</td>
</tr>
<tr>
<td>San Juan River Basin Recovery and Implementation Program (SJRBRIP)</td>
<td>360</td>
<td>$26,700,000</td>
<td>$21,100,000</td>
</tr>
<tr>
<td>Upper Animas Abandoned Mine Land Program (UAAMLP)</td>
<td>60</td>
<td>$34,000,000</td>
<td>$29,000,000</td>
</tr>
<tr>
<td>Upper Colorado River Endangered Fish Recovery Program (UFERFRP)</td>
<td>1600</td>
<td>$150,300,000</td>
<td>$126,200,000</td>
</tr>
<tr>
<td>Utah Reclamation, Mitigation, and Conservation Commission (URMCC) Restoration of the Provo River</td>
<td>16</td>
<td>$41,500,000</td>
<td>$37,000,000</td>
</tr>
</tbody>
</table>

All estimates include costs associated with habitat restoration, non-native fish management, in-stream flow identification/protection, land acquisition and monitoring. Total costs for the LCRMSCP were appropriated in 2005. Therefore, restoration activity costs are unknown but expected to be about 79% of total costs (approximately $495 million). Obligated, proposed, and estimated restoration costs between 2004-2008 equaled $40.8 million, while total costs during this time period were $50.2 million.

2 Murphy 2005; Bureau of Reclamation 2005  
3 MRGESACP 2003, 2005; www.fws.gov/mrgesacp  
4 FWS 2005  
5 Simon, W., personal communication; http://www.waterinfo.org/arsg/main.html  
6 Holden, M., personal communication; www.mitigationcommission.gov/prrp/prrp.html
The proliferation of restoration activity across the region has garnered public attention, raising questions about the number, foci, cost, activities, and effectiveness of restoration projects. Answers to these questions were elusive prior to the compilation of over 37,000 project records into the National River Restoration Science Synthesis (NRRSS) database (Bernhardt et al. 2005), and telephone interviews conducted with restoration project managers for a subset of 315 records (Bernhardt et al. submitted). Here, I report on 576 project records from the NRRSS database for the Southwest (NRRSS-SW), which includes projects conducted or underway within the states of Arizona, Colorado, New Mexico, and Utah. These data represent the most comprehensive summary of restoration efforts in the Southwest to date, synthesizing information from 53 sources (See table of data sources at www.restoringrivers.org). I compared data from the NRRSS-SW database to those obtained by telephone interviews with 48 individuals affiliated with restoration projects across the Southwest and entered into a separate NRRSS-SW interview database. These analyses provide a regional perspective on river restoration, including information on project intents, costs, spatial distribution, and the degree to which project monitoring and evaluation have been conducted. Furthermore, I share suggestions provided by interviewees for improving the science and practice of restoration.

METHODS

Detailed descriptions of database designs and data synthesis efforts are available in the Supplemental Online Material to Bernhardt et al. (2005; www.sciencemag.org/cgi/content/full/308/5722/636/DC1), Bernhardt et al. (submitted), and at the NRRSS
website (www.restoringrivers.org/NRRSS_Process). Here I provide only a brief
description of study methodology.

The NRRSS Database

The goal of the NRRSS project was to understand the current state of river
restoration in the U.S. Researchers affiliated with the NRRSS project collected datasets
that included information on restoration projects from around the country, but our efforts
were focused on seven geographic regions (Bernhardt et al. 2005). We did not limit data
collection to projects that fit our definition of restoration. No judgments were made
regarding the validity of the term "stream restoration" within data records, and there was
no limitation of size or cost unit for projects.

Our working group designed a database in 2002 to consolidate all of the datasets
we had collected. The database contained a) the information fields found within existing
large restoration databases and b) additional fields of interest to our scientific working
group and non-governmental organization partners. This database is now publicly
available at www.nrrss.nbii.gov. Projects were included in the database if they were
conducted for the purpose of improving stream conditions and if the effort could be
evaluated (e.g. some intervention or effort took place in the field). Our decision to
include project records that were not acquired as part of a database specific to stream
restoration was based on whether a) the record contained either a statement of intent or
actions implemented and b) this information indicated an intent of restoring or improving
stream conditions and explicitly mentioned riparian or stream activities. The single
subjective field in the NRRSS database was project intent (i.e., project motivation, goal,
purpose). Our working group identified 13 intent categories under which each project record was classified based upon the project description stated in each record (Supplemental Online Material to Bernhardt et al. 2005). Projects lacking clearly stated project intents or with intents that did not fit into the 13 categories were categorized as "Other". All members of the working group participated in extensive calibration of our classification approach. Duplicate records were identified using a standardized set of criteria (Supplemental Online Material to Bernhardt et al. 2005) and were removed prior to database analysis.

The NRRSS database was intended to be a representative sample of restoration intents and activities throughout the U.S., rather than a comprehensive listing of restoration projects. We sent data summaries (showing the geographic distribution of projects and basic statistics for project costs and intents) to regional “stream restoration experts” in order to validate that the database contained a representative sample of projects. New sources of information suggested by the “expert” reviewers were assessed and added to the database according to established criteria for dataset inclusion or exclusion (Supplemental Online Material to Bernhardt et al. 2005).

Data collection efforts in the Southwest were focused on the Colorado River and Rio Grande Watersheds. The “expert” reviewers of NRRSS-SW data included program coordinators for governmental agencies that either funded restoration or conducted restoration research and managers of conservation activities at the state level. Records within the NRRSS-SW database related to regional AMPs often reflected summaries of programmatic goals, activities, and costs, with the exception of project-specific data for
MRGESACP. Therefore, AMP-related records not associated with MRGESACP were removed from the dataset prior to data analysis.

The NRRSS Interview Database

Projects within the NRRSS database were eligible candidates for a follow-up telephone interview if they a) were implemented or completed between 1996-2002; b) had information about a project contact (e.g. an individual or agency name allowing follow-up); and c) were categorized by at least one of four selected project intents (riparian management, water quality management, in-stream habitat improvement or channel reconfiguration). All projects within each intent category meeting the eligibility requirements above were assigned a random number. Attempts were made to schedule an interview with the listed project contact beginning with the lowest random number in each category. Each project record was removed from the pool of subsequent candidate projects once an interview was completed (i.e., a project that was selected as a riparian management project could not subsequently be selected as a water quality project although both intents might be listed for a single project). A project was “abandoned” if more than five separate attempts to locate or contact the project manager were unsuccessful or if the contact person for a project had previously been interviewed about another project. I abandoned 101 projects in the course of building a database of 48 interviews for projects across the Southwest. Twelve interviews were conducted for each of the four selected intent categories. The final interview format was set in May 2004 and subsequently underwent review by the Institutional Review Board at the University of New Mexico. The official NRRSS interview form is available at
Phone interviews began in September, 2004, and were completed by August, 2005. Agreeable participants were sent, prior to the interview, a one page summary of interview topics along with a confidentiality agreement. Each telephone interview was taped (with the knowledge and permission of the interview subject) to facilitate data entry and quality assurance. Interviews typically lasted between 25 and 60 minutes. All identifying information (e.g., name of interviewee, project name, location of project) was removed from the interview database as required by Institutional Review Board guidelines. Results are discussed only in aggregate form.

Statistics

Most data were analyzed using descriptive statistics. All comparisons of mean costs were conducted using t-tests in SPSS 12.0.1 for Windows (SPSS Inc., Chicago, IL).

RESULTS

NRRSS-SW Database

Data sources, project number, and database validation

The NRRSS-SW database was populated by 53 datasets. The 576 unique project records that comprise the NRRSS-SW database were almost equally obtained from datasets that tracked restoration projects at national (46%) and regional (40%) scales. This distribution differs markedly from trends nationwide, for which <8% of records were acquired from national coverage datasets (Bernhardt et al. 2005). The “experts”
who reviewed the data we had collected for the Southwest considered the NRRSS-SW database to be representative of dominant restoration project intents, costs, and monitoring activity. However, reviewers noted project numbers were low for counties in Colorado located within the Upper Colorado River catchment, where several AMPs are underway.

**Project distribution and size**

The greatest numbers of restoration projects included in the NRRSS-SW database were located in Arizona, followed by New Mexico, Colorado, and Utah, respectively (Table 2). The highest concentration of projects across the region was found in the Lower Colorado River Watershed (Fig 1). The majority of projects across the Southwest (51%) were ≤ 3 km in length, while only 8% of projects were >32 km. The median length of all projects within the NRRSS-SW database was 3.0 km. The median length of projects for each state ranged from 1.6-5.6 km (Table 3). The estimated total length of all projects across the Southwest ranged from 2,900-6,600 km. This estimate was derived by first applying the median and mean project length for each state to project records that lacked information on project length. These values were then summed with those reported for each state within the NRRSS-SW database (Table 3).
Table 2. Statewide distribution and project number and cost by intent category.

<table>
<thead>
<tr>
<th>Project category</th>
<th>Arizona</th>
<th></th>
<th>Colorado</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Project count</td>
<td>Total cost†</td>
<td>Project count</td>
<td>Total cost</td>
</tr>
<tr>
<td>Aesthetics/Recreation/Education</td>
<td>9</td>
<td>30.0</td>
<td>7</td>
<td>0.0</td>
</tr>
<tr>
<td>Bank Stabilization</td>
<td>11</td>
<td>26.9</td>
<td>17</td>
<td>0.3</td>
</tr>
<tr>
<td>Channel Reconfiguration</td>
<td>13</td>
<td>1.7</td>
<td>14</td>
<td>1.6</td>
</tr>
<tr>
<td>Dam Removal/Retrofit</td>
<td>0</td>
<td>0.0</td>
<td>1</td>
<td>0.0</td>
</tr>
<tr>
<td>Fish Passage</td>
<td>4</td>
<td>17.6</td>
<td>1</td>
<td>0.1</td>
</tr>
<tr>
<td>Floodplain Reconnection</td>
<td>1</td>
<td>0.1</td>
<td>3</td>
<td>0.3</td>
</tr>
<tr>
<td>Flow Modification</td>
<td>21</td>
<td>122.1</td>
<td>12</td>
<td>1.0</td>
</tr>
<tr>
<td>In-stream Habitat Improvement</td>
<td>11</td>
<td>4.0</td>
<td>32</td>
<td>1.7</td>
</tr>
<tr>
<td>In-stream Species Management</td>
<td>10</td>
<td>0.5</td>
<td>4</td>
<td>0.0</td>
</tr>
<tr>
<td>Land Acquisition</td>
<td>6</td>
<td>1.2</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Other</td>
<td>12</td>
<td>0.9</td>
<td>10</td>
<td>0.3</td>
</tr>
<tr>
<td>Riparian Management</td>
<td>81</td>
<td>12.6</td>
<td>44</td>
<td>2.3</td>
</tr>
<tr>
<td>Stormwater Management</td>
<td>0</td>
<td>0.0</td>
<td>2</td>
<td>0.0</td>
</tr>
<tr>
<td>Water Quality Management</td>
<td>61</td>
<td>26.8</td>
<td>35</td>
<td>2.8</td>
</tr>
<tr>
<td>Not specified</td>
<td>10</td>
<td>1.8</td>
<td>4</td>
<td>0.7</td>
</tr>
<tr>
<td><strong>Totals†</strong></td>
<td>193</td>
<td>186.7</td>
<td>112</td>
<td>7.5</td>
</tr>
</tbody>
</table>

† Total costs are in millions of dollars.
‡ Total costs were $130,000 for aesthetics/recreation/education, $922,000 for bank stabilization, and $4.2 million for flow modification, after exclusion of high cost outliers in Arizona.
§ About one-third of project records cited two or more categories as main project goals, so the sum of projects across project intents is greater than the total number of projects for each state. Nine projects span more than one state, so the sum of projects across states does not equal the total number of projects in the NRRSS-SW database (n = 576).
Table 2 (cont). Statewide distribution and project number and cost by intent category.

<table>
<thead>
<tr>
<th>Project category</th>
<th>New Mexico</th>
<th></th>
<th>Utah</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Project</td>
<td>Total cost(^1)</td>
<td>Project</td>
<td>Total cost(^1)</td>
</tr>
<tr>
<td></td>
<td>count</td>
<td></td>
<td>count</td>
<td></td>
</tr>
<tr>
<td>Aesthetics/Recreation/Education</td>
<td>11</td>
<td>0.7</td>
<td>6</td>
<td>1.1</td>
</tr>
<tr>
<td>Bank Stabilization</td>
<td>12</td>
<td>0.9</td>
<td>8</td>
<td>2.3</td>
</tr>
<tr>
<td>Channel Reconfiguration</td>
<td>11</td>
<td>3.2</td>
<td>5</td>
<td>0.1</td>
</tr>
<tr>
<td>Dam Removal/Retrofit</td>
<td>0</td>
<td>0.0</td>
<td>1</td>
<td>0.0</td>
</tr>
<tr>
<td>Fish Passage</td>
<td>0</td>
<td>0.0</td>
<td>1</td>
<td>0.0</td>
</tr>
<tr>
<td>Floodplain Reconnection</td>
<td>8</td>
<td>4.6</td>
<td>0</td>
<td>0.0</td>
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<tr>
<td>Flow Modification</td>
<td>18</td>
<td>60.7</td>
<td>5</td>
<td>0.0</td>
</tr>
<tr>
<td>In-stream Habitat Improvement</td>
<td>23</td>
<td>4.8</td>
<td>12</td>
<td>0.8</td>
</tr>
<tr>
<td>In-stream Species Management</td>
<td>7</td>
<td>0.6</td>
<td>15</td>
<td>1.8</td>
</tr>
<tr>
<td>Land Acquisition</td>
<td>1</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Other</td>
<td>32</td>
<td>30.4</td>
<td>1</td>
<td>0.0</td>
</tr>
<tr>
<td>Riparian Management</td>
<td>94</td>
<td>10.1</td>
<td>64</td>
<td>4.3</td>
</tr>
<tr>
<td>Stormwater Management</td>
<td>2</td>
<td>0.0</td>
<td>0</td>
<td>0.0</td>
</tr>
<tr>
<td>Water Quality Management</td>
<td>50</td>
<td>36.1</td>
<td>20</td>
<td>5.1</td>
</tr>
<tr>
<td>Not specified</td>
<td>3</td>
<td>0.3</td>
<td>4</td>
<td>0.6</td>
</tr>
<tr>
<td><strong>Totals(^3)</strong></td>
<td><strong>179</strong></td>
<td><strong>108.8</strong></td>
<td><strong>101</strong></td>
<td><strong>8.5</strong></td>
</tr>
</tbody>
</table>

\(^1\) Total costs are in millions of dollars.
\(^*\) Total costs were $7.4 million for flow modification, after exclusion of a high cost outlier in New Mexico.
\(^3\) About one-third of project records cited two or more categories as main project goals, so the sum of projects across project intents is greater than the total number of projects for each state. Nine projects span more than one state, so the sum of projects across states does not equal the total number of projects in the NRRSS-SW database (n = 576).
Figure 1. The distribution of river and riparian restoration projects in the NRRSS-SW database by county. Data collection focused on the Upper and Lower Colorado River and Rio Grande watersheds, whose borders are delineated in orange, red, and brown, respectively.
Table 3. Recorded and estimated project lengths by state.

<table>
<thead>
<tr>
<th>State</th>
<th>Records recording length (%)</th>
<th>Total recorded length (km)</th>
<th>Median project length (km)</th>
<th>Estimated total # of river km with restoration activity†</th>
<th>State total # of river km‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>AZ</td>
<td>20</td>
<td>488</td>
<td>4.8</td>
<td>1,200 - 2,400</td>
<td>145,400</td>
</tr>
<tr>
<td>CO</td>
<td>23</td>
<td>105</td>
<td>1.8</td>
<td>250 - 440</td>
<td>172,800</td>
</tr>
<tr>
<td>NM</td>
<td>24</td>
<td>560</td>
<td>1.6</td>
<td>780 - 2,350</td>
<td>178,200</td>
</tr>
<tr>
<td>UT</td>
<td>9</td>
<td>134</td>
<td>5.6</td>
<td>660 - 1,440</td>
<td>138,300</td>
</tr>
</tbody>
</table>

† Estimated values represent ranges, based on the median and mean project lengths across project records.
‡ Data from the U.S. Environmental Protection Agency 2002 National Assessment Database for Water Quality (www.epa.gov/waters/305b).

Restoration project goals and activities

The majority of project records within the NRRSS-SW database (64%) were associated with just one project intent, while the remainder of records cited two or more project intent categories. The four categories of restoration most commonly cited as main project intents across the Southwest were riparian management, water quality management, in-stream habitat improvement, and flow modification (Figs. 2 and 3, Table 4). Riparian management and water quality management projects far exceeded other types of restoration projects across the Southwest, as well as within each state. Neither dam removal/retrofit nor stormwater management project intent categories were well represented within the NRRSS-SW database. Arizona was characterized by a higher number of projects focused on water quality, flow modification, land acquisition, and fish passage relative to other states (Table 2). Colorado was distinguished by the highest number of bank stabilization and in-stream habitat improvement projects in the Southwest. More riparian management and floodplain reconnection projects were conducted in New Mexico than in other states. New Mexico also was characterized by a
high number of miscellaneous projects such as riparian fuels reduction (i.e., removal of downed wood and invasive vegetation), endangered species recovery, and unspecified habitat restoration. The highest number of in-stream species management projects was found in Utah, which also was unique for having the fewest number of channel reconfiguration projects in the Southwest. No more than ten projects in any given state lacked information regarding project intent.

**Figure 2.** The distribution and cumulative costs of restoration projects by intent category. The numbers in parentheses represent the number of projects per category. About one-third of project records cited two or more categories as main project goals, so the sum of project records across categories exceeds 576. Cumulative costs per category are derived from the project records with cost information, which totaled 74% of records within the NRRSS-SW database.
Figure 3. Examples of the most common types of restoration in the Southwest. Non-native, weedy vegetation (a) was cleared (b) from the understory of a riparian forest in Albuquerque, New Mexico to reduce the possibility of canopy fire during an ongoing drought. Willow stakes were planted (c) at a ranch near Nutrioso, Arizona to prevent erosion, thereby improving water quality. A “high test flow” of 1,160 m$^3$ s$^{-1}$ was released (d) from Glen Canyon Dam on November 2, 2004 to distribute sediment downstream. A fish barrier was constructed (e) on a headwater stream in the Santa Fe National Forest of New Mexico to exclude non-native fish from habitat supporting native populations of Rio Grande cutthroat trout (*Oncorhynchus clarki virginalis*). Photo credits: (a) D. McDonnell; (b) J. Follstad Shah; (c) J. Crosswhite; (d) D. Blank; (e) Trout Unlimited.
### Table 4. Number of restoration projects, their costs, and the percent of project records that cited project cost and monitoring activities by intent category.

<table>
<thead>
<tr>
<th>Project category†</th>
<th>Project count‡</th>
<th>Total cost§</th>
<th>Median project cost*</th>
<th>Records citing cost (%)</th>
<th>Records citing monitoring (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aesthetics/Recreation/Education</td>
<td>32</td>
<td>31.8</td>
<td>37</td>
<td>63</td>
<td>16</td>
</tr>
<tr>
<td>Bank Stabilization</td>
<td>47</td>
<td>30.4</td>
<td>103</td>
<td>64</td>
<td>43</td>
</tr>
<tr>
<td>Channel Reconfiguration</td>
<td>43</td>
<td>6.6</td>
<td>143</td>
<td>56</td>
<td>44</td>
</tr>
<tr>
<td>Dam Removal/Retrofit</td>
<td>2</td>
<td>0.0</td>
<td>0</td>
<td>0</td>
<td>100</td>
</tr>
<tr>
<td>Fish Passage</td>
<td>6</td>
<td>17.6</td>
<td>65</td>
<td>50</td>
<td>33</td>
</tr>
<tr>
<td>Floodplain Reconnection</td>
<td>12</td>
<td>5.0</td>
<td>293</td>
<td>75</td>
<td>25</td>
</tr>
<tr>
<td>Flow Modification</td>
<td>55</td>
<td>183.9</td>
<td>310</td>
<td>45</td>
<td>47</td>
</tr>
<tr>
<td>In-stream Habitat Improvement</td>
<td>77</td>
<td>11.3</td>
<td>96</td>
<td>56</td>
<td>48</td>
</tr>
<tr>
<td>In-stream Species Management</td>
<td>36</td>
<td>3.0</td>
<td>54</td>
<td>72</td>
<td>19</td>
</tr>
<tr>
<td>Land Acquisition</td>
<td>7</td>
<td>1.2</td>
<td>336</td>
<td>57</td>
<td>29</td>
</tr>
<tr>
<td>Other</td>
<td>54</td>
<td>31.6</td>
<td>50</td>
<td>78</td>
<td>33</td>
</tr>
<tr>
<td>Riparian Management</td>
<td>277</td>
<td>29.4</td>
<td>46</td>
<td>77</td>
<td>26</td>
</tr>
<tr>
<td>Stormwater Management</td>
<td>4</td>
<td>0.0</td>
<td>0</td>
<td>0</td>
<td>25</td>
</tr>
<tr>
<td>Water Quality Management</td>
<td>166</td>
<td>70.9</td>
<td>124</td>
<td>86</td>
<td>28</td>
</tr>
</tbody>
</table>

† See Bernhardt et al. (2005) for definitions and examples of each project category.
‡ About one-third of project records cited two or more categories as main project goals, so the sum of project records across categories exceeds the total number of projects in the NRRSS-SW database (n = 576).
§ Total costs are in millions of dollars.
* Total costs are in thousands of dollars.

The most common types of restoration activities in the Southwest were well matched to riparian management and water quality management. All forms of revegetation exceeded, by over two-fold, other types of activities (Fig. 4). Fencing to protect riparian vegetation and to curb streambank erosion was the second most common restoration activity, followed closely by eradication of weeds or non-native plants. Four of the twenty most common activities were those associated with ranching or agricultural
practices to improve streams (i.e., fencing, livestock exclusion, unspecified agricultural best management practices [BMPs], off-channel watering of livestock), while three addressed management of water availability (i.e., flow regime enhancement, maintaining hydraulic connections, increased irrigation efficiency). Other common activities were associated with projects focused on in-stream habitat improvement or channel reconfiguration (i.e., bank or channel reshaping, addition of boulders, creation of pools). Educational activities, ranked fifth, were often linked to restoration efforts in the Southwest, as were many types of project monitoring.

![Graph showing the twenty most common restoration activities cited within the NRRSS-SW database. The x-axis refers to the number of project records that listed each activity.]

**Figure 4.** The twenty most common restoration activities cited within the NRRSS-SW database. The x-axis refers to the number of project records that listed each activity.
Project costs

The cost of restoration in the Southwest for 1990-2003 totaled $192 million, according to NRRSS-SW project records. The median project cost for this time period was $60,000. This value exceeded the national estimate of median project cost, which equaled $45,000 (Bernhardt et al. 2005). I assumed an additional $8-67 million has been allocated to restoration by applying mean and median project costs to records for projects implemented from 1990-2003 that lacked cost data. I did not include costs incurred by AMPs during 1989–2005, but estimated that these programs have allocated 79% of total costs, or $277 million, to restoration activities (Table 1). Thus, the sum of restoration costs in the Southwest from 1989–2005 ranges from $477 - $536 million, as estimated from NRRSS-SW database records and available information on AMPs. The projected cost of restoration activities associated with the LCRMSCP through 2055 is estimated to be $495 million. This program alone will roughly double previous expenditures on river and riparian restoration in the Southwest.

Almost 87% of project costs in the Southwest were solely funded by federal sources. Most restoration dollars have been allocated to flow modification, exceeding costs for other project categories by over $100 million (Fig. 2, Table 4). Over 85% of cumulative flow modification costs in New Mexico and Arizona were driven by just one or two projects. Water quality management was the most expensive type of project in the Southwest once outliers associated with high cost flow modification projects were removed from the analysis (Table 2). Riparian management projects were ranked sixth in terms of cumulative costs, despite being the most common restoration project type across
the Southwest (Fig. 2, Table 4). The median project cost for riparian management projects was $46,000, which was inexpensive relative to costs for other project intents.

**Project monitoring**

NRRSS-SW database records showed that some type of monitoring occurred in conjunction with 28% of restoration projects across the Southwest. This proportion is almost triple that of the nation, where only 10% of project records indicated monitoring activities had occurred (Bernhardt et al. 2005). One-quarter of project records associated with riparian and water quality management included monitoring information (Table 4). In contrast, monitoring was conducted for more than 40% of projects focused on instream habitat improvement, flow modification, channel reconfiguration, or bank stabilization. Only projects focused on dam removal/retrofitting had a better record of monitoring, although the NRRSS-SW database included just two of these types of projects. The mean cost of monitored projects that were implemented from 1990–2003 was $187,517 (n = 70), while the mean cost of projects lacking monitoring information was $539,376 (n = 350). The difference between these costs was not significant (t = -0.582, p = 0.561), suggesting that the inclusion of monitoring activities as part of the restoration process does not necessarily drive up project costs.
NRRSS-SW Interview Database

Interviewees

The individuals I interviewed represented diverse backgrounds. Some 33% of interviewees were federal employees, 19% represented non-profit organizations, 17% were state employees, and 10% represented regional agencies (e.g., conservation districts). The remaining interviewees were academics, consultants, local government agents, or private landowners.

Comparison of project costs across databases

Data obtained through telephone interviews with restoration practitioners largely provided corroboration of analyses of data within the NRRSS-SW database. However, restoration costs reported during interviews showed that costs were under-reported by records for each respective project within the NRRSS-SW database. Restoration costs obtained from the 48 interviewees totaled more than $379 million, which included $45 million worth of in-kind donations. Partial or total costs associated with four AMPs were obtained through the interview process and significantly elevated the mean project cost for the interview database as compared to the NRRSS-SW database. Exclusion of AMP records from the interview dataset resulted in similar mean project costs across both databases (t = -1.389, p = 0.172).
Insights about project planning, monitoring, and evaluation

The individuals I interviewed generally indicated that the planning perspective for most projects was large-scale and ecologically-focused, although project size was typically small. Just over half of the projects were reported to have been influenced by a local watershed assessment and/or a watershed management plan. Interviewee responses suggested that project intents matched those of watershed management plans in 60% of cases, and were established for 44% of projects to address causes of river degradation. One-quarter of interviewees reported that restoration sites were chosen due to localized ecological concerns, while 2% of sites were identified in watershed plans. Over 83% of interviewees stated that their associated projects were designed with knowledge of other projects in the vicinity. Another quarter of interviewees noted that their projects transcended boundaries of land ownership. These statistics suggest coordination across projects and communication amongst project partners were essential components of project implementation.

Almost all interviewees reported that monitoring was linked to their project, which suggested that project monitoring has been more prevalent than NRRSS-SW database records have indicated. Pre-project monitoring activity was reported by 79% of interviewees, while 88% reported post-project monitoring activity. Less than one-third of interviewees indicated reference sites were a part of pre- or post-project monitoring programs. Physical factors (e.g., river cross sections and stream flow) were reported to have been measured prior to project implementation more often than other forms of monitoring. Photography was cited by one-quarter of interviewees as their means of post-project monitoring, while tracking of biological (e.g., surveys of vegetation, fish,
and macroinvertebrates) and physical factors were reported by slightly fewer interviewees. Post-project data collection of water or soil chemistry was less commonly reported (14% of interviewees). Over two-thirds of interviewees stated that monitoring programs collected data on two or more variables, often for 2-5 years or longer, and that 41% of monitored variables indicated positive trends. Results of monitoring efforts were synthesized and sent to the program manager(s) of funding agencies or shared with advisory committee members for only 25% of projects for which interviewees reported monitoring had been conducted.

The majority of interviewees considered their project was partially (42%) or totally (46%) successful. Just over one-half of interviewees stated that explicit success criteria (e.g., improvements to fish or plant communities) had been established prior to project implementation; however, only 8% of interviewees based their evaluation of project success on the fulfillment of these criteria or on measurable improvements of ecological indicators. Invasion by weeds, inadequate project design, and unexpected response of the ecosystem to restoration were most commonly cited as limitations to project success. Ongoing maintenance was reported to have been needed for 75% of projects in our interview database, and almost half of these projects required maintenance on an annual basis. About 52% of interviewees stated that monitoring data were used to evaluate project success. Other evaluation tools cited by interviewees included photography or site visits, reactions of participants or the public to project outcomes, and independent review by consultants.
Lessons learned

Most interviewees, in hindsight, would have made some changes to the way restoration projects were conducted. The most common types of changes related to project monitoring (Fig. 5). Approximately 54% of interviewees stated that constraints to monitoring existed due to limited funds or staff availability. Ongoing drought throughout the Southwest limited the monitoring of water quality or changes in geomorphology due to reduced stream flow. Improved collaboration and communication between project partners was cited by 12% of interviewees as a means to improve project management, a subset of which related to contract preparation or the flow of money between agencies. Another 8% of interviewees cited the need for a project manager who is both well-organized and present throughout the duration of the project, and who establishes clear roles for project participants. Interviewees also called for more streamlined processes for permit application and project reporting to funding agencies. Changes to the design process suggested by interviewees included increased public involvement, incorporation of a broader geographic context and experimental framework to test implementation techniques, and scientific review of design plans. Adaptability was cited as a key characteristic to effective project implementation, especially in the face of changes in project design or environmental conditions (e.g., drought). Improvements to project evaluation suggested by interviewees included the development of success criteria prior to project implementation, more rigorous analysis of monitoring data, and the establishment of a formal evaluation program that includes independent review.
**Figure 5.** The distribution of suggested changes to improve restoration projects, as cited by 48 interviewees. The majority of interviewees cited multiple changes for a single restoration project.

**DISCUSSION**

*A good record of project monitoring in the Southwest*

Restoration project monitoring in the Southwest appears to be more common than in any other part of the country, based on the percentage of records reporting monitoring activities in regional NRRSS databases (Supplementary Online Material, Bernhardt et al. 2005). NRRSS-SW database records indicated that monitoring activities have been implemented for 25% or more of projects in each southwestern state, except Utah for which 16% of records cited project monitoring. The only other states with a comparable percentage of project monitoring include Iowa, North Carolina, and South Carolina.
(Supplementary Online Material, Bernhardt et al. 2005). Why do restoration projects in the Southwest have a better track record of monitoring as compared to projects in other regions? First, many restoration practitioners I interviewed noted a personal commitment to learning from the projects they implement and cited monitoring as the most objective way to determine which methods work best. Second, ongoing monitoring programs (e.g., water quality) conducted by state and regional agencies facilitated aspects of monitoring for about 42% of the projects in the NRRSS-SW interview database. Finally, some of the most data rich sources of information for the Southwest came from agencies that require a monitoring plan in order for a project to be awarded funding.

It was encouraging that the majority of the individuals I interviewed reported that project monitoring had been conducted both before and after project construction, and that monitoring data often had been used to evaluate project success. Another positive trend proved to be that monitoring efforts usually tracked multiple variables over somewhat longer time scales. Monitored projects at the national scale typically were more expensive than projects that lacked monitoring information (Bernhardt et al. 2005). In contrast, the inclusion of monitoring activities for projects in the Southwest did not elevate mean project costs. This finding implies monitoring programs can be incorporated into projects without significantly increasing project budgets. I found that interviewees less frequently reported the monitoring of water chemistry as compared to biological and physical factors. This result is surprising given the large number of water quality management projects in the Southwest, and highlights the need to better tie monitoring activities to project intents. I reiterate Palmer et al. (2005) who recognized that every single restoration project need not be monitored, but who encouraged entities
that fund and regulate restoration projects to ensure that an appropriate number of
different types of projects include broad ecological monitoring and evaluation.

*The role of adaptive management programs in the Southwest*

The recognition of ecological degradation and threats to species at broad scales
has been responsible for a great deal of restoration across the country. Nearly 88% of
projects within the NRRSS database are located in the Pacific Northwest, Chesapeake
Bay, or California nodes (Bernhardt et al. 2005). Over 23,000 restoration projects were
located in the Pacific Northwest alone (Katz et al. submitted). The high degree of
restoration activity in the Pacific Northwest has been driven by the designation of more
than twenty “evolutionarily significant units” of salmon and steelhead as endangered or
threatened under the Endangered Species Act (Jenkinson et al. 2006). Some 400
restoration projects have been conducted in California as part of the California Bay-Delta
Program, which is a 30-year program to restore regional ecological health, protect fifteen
at-risk native species, and improve water management (C ALFED 2004). Congressional
funding aimed at improved water quality of the Chesapeake Bay has spurred thousands of
restoration projects in Maryland, Virginia, and Pennsylvania (Hassett et al. 2005).
Similarly, large-scale AMPs in the Southwest have implemented restoration projects,
with an estimated value of $277 million, as part of their efforts to conserve populations of
threatened and endangered species, improve water quality, and provide adequate water
resources for both human consumption and ecological services. Incorporation of AMP-
related project information into the NRRSS-SW database would certainly increase the
total number of projects in the Southwest, while augmenting the number of projects
associated with flow modification, in-stream species management, fish passage, water quality management, and land acquisition. Yet the number of projects in the Southwest would likely still rank lower than other regions simply due to the scarcity of flowing water relative to more mesic systems like the Pacific Northwest, Chesapeake Bay, and northern California.

**Restoration challenges for the Southwest**

Has restoration across the Southwest ameliorated degradation to river systems resulting from flow regulation, overgrazing, mining, and urbanization? Are populations of threatened and endangered species more robust due to restoration efforts? These questions are difficult to answer because existing datasets do not provide enough information (e.g., success criteria, monitoring actions and duration, data on baseline conditions and effects of restoration) to make assessments. It is good news that the four dominant project intents (riparian management, water quality management, in-stream habitat improvement, and flow modification) and the most common restoration activities in the Southwest address the primary drivers of river and riparian decline, but much more work is required to gauge which types of restoration are truly effective. Studies of the two most common restoration activities, riparian revegetation and fencing, provide a good case in point. Fencing to exclude livestock or wildlife from riparian areas has been demonstrated to increase the height and vigor of vegetation (Sarr 2002). Yet, the degree to which plant communities return to pre-grazing conditions is difficult to assess because trajectories of ecosystem recovery are non-linear and hard to decipher without adequate datasets of long-term monitoring (Sarr 2002). Furthermore, the management of invasive
plants continues to be an issue after livestock removal or the completion of revegetation efforts in semi-arid environments (Jansen and Robertson 2001), but non-native invasive plant encroachment is less of a problem where overbank flood regimes actively favor native vs. non-native plant recruitment (Taylor and McDaniel 2004, Shafroth et al. 2005). Some revegetation projects have been successful at reducing nutrient levels in agricultural streams (Hill 1996). Yet, the width and continuity of buffer strips are important factors regulating the magnitude of filtration capacity (Weller et al. 1998, Sweeney et al. 2004, Parkyn et al. 2005) that need to be considered during project design. Reviews by Sarr (2002) and Roni et al. (2005) found that reports of fish population response to riparian plantings or fencing were inconclusive, and very few studies have examined other aquatic biota. Mixed results of studies on revegetation and fencing projects illustrate that restoration activities are not universally effective. Restoration practitioners in the Southwest have done a reasonably good job of pre- and post-project monitoring and using monitoring data to evaluate project success, but more effort needs to go towards making monitoring data accessible to other practitioners and scientists for making better decisions about where and how to implement different types of restoration.

Water scarcity is another challenge for restoration practitioners of the Southwest. This is one reason why flow modification is a common restoration project intent for the region, but not nationwide. Flow modification has been used as a tool to conserve populations of threatened or endangered fish and to induce floods that promote recruitment of native riparian plants. The most renowned flow modification projects in the Southwest are the experimental flows released from the Glen Canyon Dam (Patten et al. 2001, Schmidt et al. 2001). The results of these experimental flows, which have been
studied in great detail, highlight the difficulty in determining whether flow modification has a beneficial effect on fish species of concern. For example, Gloss and Coggins (2005) reported that recruitment of humpback chub (*Gila cypha*), which has been in decline within the Grand Canyon ecosystem since the 1980s, has not been stimulated by the implementation of the “modified low fluctuating flow” (MLFF) regime for the Colorado River. The data, however, are unclear as to whether the MLFF has had either a negative effect on humpback chub recruitment or no influence at all. Cessation of groundwater pumping is another form of flow modification that has been reported to increase in-stream flows. Fleckenstein et al. (2004) point out that cessation of groundwater pumping in some cases must be combined with other forms of flow augmentation to meet the needs of aquatic organisms. These studies accentuate the complexity of river restoration in regions of water scarcity and point to the need for a greater degree of research on flow modification as a restoration tool.

Some within the restoration community have recommended coordination of projects at the watershed scale in order to improve the overall ecological success of restoration (Bohn and Kershner 2002, Roni et al. 2002, Palmer et al. 2005). A watershed approach provides a broader context for identifying the factors that degrade river systems and allows practitioners to prioritize where and when restoration activities ought to occur. AMPs of the Southwest are authorized to carry out their missions across large catchments, and thus coordinate restoration activities at the watershed scale.

Interviewees also reported that implementation of smaller projects is often guided by a watershed plan or assessment. Yet, most restoration projects in the Southwest are ≤ 3 km in length. Numerous small, disparate projects create a challenge for estimating the
cumulative effects of restoration activity unless significant efforts are made to track
project implementation and monitoring data. This challenge is highlighted by the fact
that I spent roughly 350 hours identifying and acquiring datasets of restoration projects
across the Southwest because just three of the 53 datasets I compiled as part of the
NRRSS-SW database were from regional sources that provided ≥ 45 project records
each. Two of these sources, the Arizona Water Protection Fund and Middle Rio Grande
Bosque Initiative, were good examples of internet-accessible datasets that provided
project information organized by catchment. These datasets can be found at
www.awpf.state.az.us/funded.htm and www.fws.gov/southwest/mrgbi. There is a need
for other state and regional agencies that fund or implement restoration to a) create
similar websites or relational databases that can queried by the public, and b) maintain
the monitoring data associated with restoration.

*Are we making a difference?*

The Southwest is comprised of roughly 634,000 km of river, of which 20,000 km
have been designated as impaired (EPA 2005). I estimated from NRRSS-SW database
records that restoration activities have occurred on 2,900-6,600 km of river. It is possible
that restoration projects have been implemented on 15% - 33% of impaired river
kilometers in the Southwest, if all activity has taken place within impaired river reaches.
This rough estimate suggests that progress has been made towards improving river
systems of the Southwest, but more resources urgently need to be allocated to additional
projects and the evaluation of project success.
Palmer et al. (2005) provided five standards for judging the ecological success of restoration. I used these standards to ascertain whether the perceived project success reported by the vast majority of individuals I interviewed and ecological success based on responses to selected interview questions were correlated. The first standard is the establishment of a guiding image for restoration towards the least degraded most ecologically dynamic state possible. The interview responses suggested that project goals and restoration sites have been selected more commonly to stem ecological degradation as opposed to other motivations. Yet, few interviewees provided objective statements that described a dynamic system post-restoration. The second standard is the measurable improvement of river and riparian ecological condition based upon success criteria established prior to project implementation. The majority of individuals I interviewed reported that success criteria had indeed been established at the outset of the project, but few based project success on the fulfillment of stated success criteria or on measurable improvements of ecological indicators. The third standard is the promotion of system resilience and self-sustainability so that little or no project maintenance is required. The high percentage of interviewees that reported the need for annual project maintenance indicated that restoration efforts are not crafting resilient, sustainable systems. The fourth standard is the avoidance of lasting harm inflicted upon the ecosystem during project construction. The determination of whether lasting harm has been inflicted downstream of restoration sites is difficult to assess because the cumulative effects of multiple restoration projects within a single watershed are rarely quantified. However, more than three-quarters of interviewees stated that efforts had been made during project implementation to minimize the impact of construction. The final standard is the
completion of both pre- and post-project assessment, with data made publicly available. The majority of interviewees stated that monitoring had been conducted both before and after project construction and more than half used monitoring data during the evaluation process. Yet, monitoring data were often unreported to agencies that can synthesize and disseminate the results of restoration for many projects. This does not mean that data on project monitoring is not available to the public, but it is clearly difficult to obtain.

The evaluation of survey results with respect to the standards purported by Palmer et al. (2005) reveals that restoration practitioners in the Southwest can improve the likelihood of ecological success by (1) articulating success criteria in quantifiable terms prior to project implementation and describing a range of desired conditions; (2) reducing the amount of project maintenance a) by prioritizing sites in areas with intact biological or physical processes needed to sustain restoration, or b) through innovation of restoration design and materials; (3) engaging in studies that measure the cumulative effects of multiple restoration projects within a given region; (4) evaluating project success based upon reviews of pre- and post-project monitoring data in relation to stated success criteria; and (5) reporting monitoring data to funding agencies or agencies that compile restoration information within publicly available databases.

CONCLUSIONS

I have attempted to capture trends pertaining to river and riparian restoration efforts in the Southwest. The NRRSS-SW database represents the most comprehensive dataset of restoration projects in the Southwest to date. The database was created because none existed from which the ecological efficacy of restoration practices could be
assessed. Efficacy was still difficult to ascertain given the dearth of information contained within most datasets I compiled into the NRRSS-SW database. This fact, together with existing NRRSS-SW database deficiencies resulting from omissions of AMP datasets, underscores the great need for the creation and maintenance of relational databases to store information about restoration projects and associated monitoring data at regional or national scales. Efficacy, especially in ecological terms, also will be easier to assess as practitioners better utilize suggested standards of success as guidelines during all phases of the restoration process.

Monitoring and post-project evaluation prove to be the greatest challenge, as well as the greatest opportunity, for learning from restoration successes and failures. The primary impediment to making improvements towards better project monitoring, reporting, and tracking has been inadequate funding. Therefore, more funding must be secured for river and riparian restoration. Meanwhile, agencies that fund or regulate restoration should reward projects that emphasize monitoring and evaluation as well as project implementation.
CHAPTER 3: SOIL NITROGEN DYNAMICS IN STANDS OF

*Populus deltoides ssp. wislizenii* and *Tamarix chinensis*

WITH DIFFERING FLOOD REGIMES

*Abstract:* The biotic structure and function of semi-arid riparian forests around the world are strongly organized by flood pulses. Flow management has reduced the exchange of water, energy, and materials from rivers and floodplains, caused declines in native plant populations, and advanced the spread of non-native plants. Naturalized flow regimes are regarded as a means to restore degraded riparian areas around the world. I examined the effects of flood regime on litter production and soil nitrogen dynamics in riparian forests along the middle Rio Grande of New Mexico dominated by native *Populus deltoides ssp. wislizenii* and non-native *Tamarix chinensis*. Feedbacks between litter production and soil inorganic nitrogen determined the degree of nitrogen accumulation within all riparian study sites. *P. deltoides* and *T. chinensis* flood sites had consistently lower potential net nitrogen mineralization rates than their respective non-flood sites. Flood regime also promoted differences in riparian soil nitrogen concentrations within stands dominated by each species, but flood effects contrasted across species. *P. deltoides* flood sites had low soil nitrogen concentrations, likely due to increased nitrogen uptake by plant and microbial communities, denitrification, and nitrogen export to surface and ground water that are associated with flooding. Litter production was suppressed at *P. deltoides* flood sites relative to *P. deltoides* non-flood sites, although roots from *P. deltoides* flood sites showed a greater capacity to take up
inorganic nitrogen. *P. deltoides* non-flood sites had higher soil nitrogen concentrations compared to *P. deltoides* flood sites due to elevated nitrogen inputs associated with increased litterfall and the lack of transport associated with flooding. In contrast, *T. chinensis* flood sites were characterized by greater litter production, nitrogen inputs via litterfall, and concentrations of soil inorganic nitrogen relative to *T. chinensis* non-flood sites. *T. chinensis* has the ability to produce adventitious roots at the elevation of floodwaters, an adaptation that may help to support leaf production during inundation. In addition, litter production at *T. chinensis* non-flood sites was potentially limited by increased competition for nitrogen between plants and microbes, as inferred from soil C:N molar ratios much greater than 25:1. The practice of spring-time naturalized flows within the rivers of semi-arid regions ought to continue when adequate water supplies permit. Flood events associated with these flows promote increased recruitment of native plant seedlings, as well as increased mobilization of nutrients at a time most conducive to plant growth. However, flood inundation may be less important for the preservation of mature forests dominated by *P. deltoides* than the maintenance of shallow groundwater tables that have been shown to support high leaf production. Flood inundation, particularly if long in duration, also promotes increased losses of soil nitrogen and reduces leaf and litter production within stands of *P. deltoides*. Additional research is required to determine the thresholds at which extended flood duration does more harm than good for the conservation of *P. deltoides* along rivers of the U.S.
INTRODUCTION

Riparian forests are some of the most productive and diverse ecosystems on Earth due to the exchange of water, materials, and nutrients between rivers and their floodplains (Junk et al. 1989, Bayley 1995). The biotic structure and function of semi-arid riparian forests around the world are strongly organized by flood pulses due to the relative scarcity of water resources in these regions (Fisher et al. 1982, Walker et al. 1995, Molles et al. 1998, Jacobson et al. 2000). However, flow regulation has been estimated to control 77% of total water discharge in 139 large river ecosystems in the northern one-third of the world (Dynesius and Nilsson 1994) and has reduced river-floodplain connectivity (Ward and Stanford 1995). In addition, roughly 82% of desert and xeric shrubland catchments worldwide are strongly affected by flow regulation (Nilsson et al. 2005).

Fifty years of flow regulation along the middle Rio Grande of New Mexico has resulted in the loss of 50% of wetlands (Crawford et al. 1993) and spurred a decline in populations of native riparian plants (Howe and Knopf 1991). Riparian forest fire frequency has increased along the Rio Grande concurrent with fuel load accumulation, which has resulted from the suppression of floods (Ellis et al. 1998, Ellis et al. 1999). Flow regulation across the western and southwestern U.S. has reduced the recruitment of native riparian plants (Rood and Mahoney 1990) and promoted invasion by non-natives (Merritt and Cooper 2000, Shafroth et al. 2002, Uowolo et al. 2005). Degradation of riparian areas due to river regulation has spurred hundreds of restoration projects in the southwestern U.S. that are focused on riparian management, flow modification, and floodplain reconnection, with costs totaling over $200 million since 1990 (Chapter 1).
The floodplain along the middle Rio Grande, like many other large river systems, has historically represented a mosaic of ecosystems perpetuated by differing frequencies and durations of inundation. Today, fewer riparian areas are well-connected to the river as a result of reduction in peak flows, incision of channel beds in response to dams and diversions, and bifurcation of floodplains by levees and irrigation canals. Flood pulses still occur within the middle Rio Grande, particularly during wet El Niño years (Molles et al. 1992), when adequate stores of water are available to be released downstream of dams as “naturalized” flows (sensu Poff et al. 1997) or when monsoonal precipitation induces spates from tributaries. Return of naturalized flows to disconnected riparian forests has been shown to stimulate particulate organic matter decomposition and microbial respiration (Molles et al. 1995, Ellis et al. 1999) and promote recruitment of native riparian vegetation (C.S. Crawford, pers. comm.). Connected forests also prove effective at retaining inputs of dissolved nutrients via floodwaters (Valett et al. 2005).

Nitrogen (N) enters riparian areas through biological nitrogen fixation, atmospheric deposition, surface run-off and ground water from upland areas, hyporheic flow of surface water to ground water, and overbank flood events. Floodwaters are a major source of N to riparian areas of semi-arid to arid regions that are typically characterized by N-poor alluvial soils (Adair et al. 2004, Jacobson et al. 2000). Floods also flush N, in the form of organic debris and dissolved solutes, from riparian ecosystems. Nitrogen, in addition to water, has been shown to limit the growth of Populus species native to riparian areas of the western and southwestern U.S. (Marler et al. 2001, Adair and Binkley 2002, Harner 2006). Many studies have shown that flow regulation alters riparian plant species diversity, composition, and productivity (Busch
and Smith 1995, Tremolières et al. 1998, Merritt and Cooper 2000, Stromberg 2001, Beauchamp 2004). Flow regulation also reduces the bidirectional flow of nutrients between surface waters and their floodplains (Busch and Smith 1995, Molles et al. 1998, Ellis et al. 1999), but few studies have examined the effects of flow regulation on riparian soil nutrient availability and cycling (e.g., Adair et al. 2004). Since water and nitrogen co-limit many riparian ecosystems of the western and southwestern U.S., anthropogenic changes in patterns of riparian N availability and subsequent changes in riparian plant community composition and productivity are concerns for natural resource managers.

The objective of this study was to investigate how pools of soil inorganic N and potential rates of net N mineralization are influenced by the occurrence or absence of frequent floods within riparian forests. Flood effects on soil nitrogen cycling were assessed within stands along the middle Rio Grande in New Mexico dominated by either native Populus deltoides ssp. wislizenii Eckenwalder (Rio Grande cottonwood) or non-native Tamarix chinensis Lour. (salt cedar) because the distribution of both species within the study area is similar. Patterns of soil N acquisition and allocation by P. deltoides and T. chinensis also were studied to assess species-level effects on soil nutrient cycling. These patterns are not discussed herein, but rather are the focus of Chapter 4.

METHODS

Study site description and history

The middle Rio Grande of New Mexico extends from the Otowi gauge in the north to the Elephant Butte gauge in the south (Fig. 1). It is approximately 320 km in
length, beginning at an altitude of 1672.9 m and ending at an altitude of 1262.2 m. The drainage area included within this reach of river is roughly 39,200 km².

![Map of study sites along the middle Rio Grande of New Mexico.](image)

**Figure 1.** Map of study sites along the middle Rio Grande of New Mexico. Circles indicate study sites dominated by *P. deltoides*, while triangles indicate study sites dominated by *T. chinensis*. Solid and hollow symbols represent flood and non-flood sites, respectively.

The middle Rio Grande is slightly sinuous with straight, meandering, and braided reaches that traverse three major biotic communities: Great Basin grassland, semi-desert grassland, and Chihuahan Desert scrub (Brown and Lowe 1980). The floodplain varies in width from less than 1.5 km to about 10 km. Levees or natural bluffs generally limit the extent of the riparian forest, with the greatest widths reaching 4-5 km in the south.
Floodplain soils are Typic Ustifluvents of the Gila-Vinton-Brazito association with 0-2% slope. These soils are stratified sandy clay loam over sandy, mixed calcareous alluvium.

Three diversion dams regulate river flow throughout the middle Rio Grande. The flow in most of the reaches is perennial, although some of the reaches at or below the town of Bernardo cease to flow in years of drought. Peak flows occurred historically at the end of May to early June, concurrent with snowmelt from headwater sources in the San Juan Mountains of Colorado. Flooding has been less frequent since the installation of dams on the Rio Grande, but intense summer thunderstorms and dissipating tropical storms in fall still induce peaks that sometimes result in overbank flood events (Bullard and Wells 1992, Vivoni et al. 2006). These events occur primarily in the south below the confluences of the Rio Puerco and Rio Salado with the Rio Grande. The climate of the region is classified as arid to the south and semi-arid to the north (Tuan et al. 1973). Mean annual precipitation ranges from 31 cm in the north to 20 cm in the south. Mean monthly air temperatures in July range from 21-24 °C, while minimum monthly air temperatures are about 4 °C throughout the valley (Table 1). Roughly 50% of annual precipitation is supplied by summer monsoonal storm events, although the proportion can vary considerably from year to year (Table 1).

Plant communities of riparian forests of the middle Rio Grande were historically dominated by *P. deltoides* interspersed with native understory species, such as *Salix exigua* Nutt (coyote willow), *Baccharis glutinosa* Pers. (seep willow), *Amorpha fruticosa* L. (false indigo bush), and *Forestiera neomexicana* A. Gray (New Mexico olive) (Crawford et al. 1993). Introduction of non-native species since the early 20th century has altered the riparian community composition. Invasion by *Elaeagnus angustifolia* L.
(Russian olive) prevails in the north, while *T. chinensis* is prevalent in the south. *E. angustifolia* typically lines the banks of the Rio Grande, but also is found in the understory of stands dominated by *P. deltoides*. *T. chinensis* is present in the understory of some *P. deltoides* stands in the north, but forms monocultures in the south.

I selected eight study sites located as far north as the city of Albuquerque (35° 05’ N, 106° 40’ W) and as far south as Bosque del Apache National Wildlife Refuge (NWR; 33° 46’ N, 106° 52’ W; Figure 1). Four of these sites were dominated by *P. deltoides*, which ranged in age from roughly 35-61 years at the start of the study (P. Jacobson, pers. comm.). The other four sites were dominated by *T. chinensis*, which ranged in age from roughly 16-26 years at the start of the study (V. Beauchamp, pers. comm.). Two *P. deltoides* and two *T. chinensis* sites were designated as flood sites based on their elevation about the stream channel and their history of flooding. These sites experienced at least one and up to three flood events during the period of study. The remainder of the study sites were designated as non-flood sites and never flooded during the period of study. Non-native vegetation (i.e., *E. angustifolia* and *T. chinensis*) was present in the understory of the Central Albuquerque and South Valley Albuquerque study sites throughout most of the study, but was mechanically cleared from these sites in winter 2003 and spring 2004. *P. deltoides* sites in the south either had an understory that included native and non-native vegetation (i.e., *S. exigua*, *B. glutinosa*, *E. angustifolia*, and *T. chinensis*) or lacked an understory community. Non-flood *T. chinensis* sites were mixed communities that included *Distichlis spicata* (salt grass), *Prosopis pubescens* (screwbean mesquite), *Atriplex* spp. (four-wing saltbush), and *Lycium* spp. (wolfberry). Monocultures characterized periodically flooded *T. chinensis* sites in the south.
Table 1. Climate characteristics during the period of study.

<table>
<thead>
<tr>
<th>Year</th>
<th>Season</th>
<th>Climate description‡</th>
<th>Mean PDZI‡</th>
<th>Cumulative precipitation (cm)</th>
<th>Mean air temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>2001</td>
<td>Spring</td>
<td>mild to moderate wetness</td>
<td>1.63</td>
<td>3.2</td>
<td>13.9</td>
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<tr>
<td></td>
<td>Summer</td>
<td>near normal</td>
<td>0.60</td>
<td>9.8</td>
<td>24.1</td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>mild to moderate drought</td>
<td>-1.31</td>
<td>3.8</td>
<td>14.8</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>near normal</td>
<td>0.94</td>
<td>5.0</td>
<td>3.0</td>
</tr>
<tr>
<td>2002</td>
<td>Spring</td>
<td>mild to moderate drought</td>
<td>-1.66</td>
<td>1.1</td>
<td>14.3</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>near normal</td>
<td>-1.19</td>
<td>8.3</td>
<td>24.7</td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>near normal</td>
<td>0.93</td>
<td>9.0</td>
<td>13.0</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>near normal</td>
<td>0.16</td>
<td>3.6</td>
<td>3.0</td>
</tr>
<tr>
<td>2003</td>
<td>Spring</td>
<td>near normal</td>
<td>-0.42</td>
<td>2.2</td>
<td>13.5</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>extreme drought</td>
<td>-3.05</td>
<td>4.3</td>
<td>24.9</td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>near normal</td>
<td>-0.27</td>
<td>6.8</td>
<td>14.7</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>near normal</td>
<td>-0.59</td>
<td>2.5</td>
<td>4.4</td>
</tr>
<tr>
<td>2004</td>
<td>Spring</td>
<td>mild to moderate wetness</td>
<td>2.37</td>
<td>8.9</td>
<td>14.3</td>
</tr>
<tr>
<td></td>
<td>Summer</td>
<td>near normal</td>
<td>-0.24</td>
<td>9.7</td>
<td>23.4</td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>mild to moderate wetness</td>
<td>1.26</td>
<td>9.8</td>
<td>13.1</td>
</tr>
<tr>
<td></td>
<td>Winter</td>
<td>near normal</td>
<td>0.46</td>
<td>4.3</td>
<td>2.7</td>
</tr>
</tbody>
</table>

‡The climate description refers to the qualitative assessment associated with ranges of PDZI values, as designated by the U.S. National Oceanic and Atmospheric Administration (NOAA).

‡PDZI refers to the Palmer Drought “Z” index. Values were obtained from the NOAA National Climate Data Center, [http://www.ncdc.noaa.gov oa/ climate/research/ monitoring.html](http://www.ncdc.noaa.gov/oa/climate/research/monitoring.html). The following are Z value ranges for each climate description: 1.00, 2.49 (mild to moderate wetness); -1.24, 0.99 (near normal); -1.25, -1.99 (mild to moderate drought); > -2.75 (extreme drought).

The climatic regime varied throughout the period of study (Table 1). Spring 2001 was a normal to wet spring, which allowed water operation managers to release a pulse of river flow that resulted in a flood event and subsequent riparian inundation lasting one
week in May. A normal to weak monsoon season marked late summer to early fall 2001. Spring 2002 was relatively dry and was followed by a weak monsoon season, although mean values of the Palmer Drought “Z” Index (PDZI) were near normal. The PDZI is a monthly measure of the departure from the normal moisture climate (NOAA 2006). This index can respond to a month of above-normal precipitation, even during a long-term drought. Precipitation events in October 2002 led to inundation for approximately one week at only the *P. deltoides* flood site within the Bosque del Apache NWR. Spring 2003 was normal to dry and was followed by extreme drought in the summer. However, a few intense precipitation events occurred in fall 2003, resulting in high tributary flows and riparian inundation at all sites within the Bosque del Apache NWR for roughly 10 days. The climate of 2004 was similar to that of 2001, but more precipitation fell in spring and fall of 2004 relative to these seasons in 2001. Two flood events occurred in April and May 2004 at the Bosque del Apache NWR as a result of spring precipitation. These floods inundated riparian study sites for a total of about 45 days.

*Ground water sampling and analysis*

An 80 m x 80 m study plot was delineated at each study site, with groundwater wells located in each corner and at the center of the plot. Groundwater wells were constructed of 5 cm inner diameter polyvinyl chloride (PVC) pipe with approximately 100 cm screen lengths capped at the bottom. Each shallow groundwater well was hand-driven to one meter below the winter water table. At least three wells at each site were equipped with pressure transducers (EEI Model 2.0 Submersible Sensor, EEI Technologies, Las Cruces, NM, U.S.A. in 2001-2003; Model 3001 Mini LT Levelogger,
Solinst Canada Ltd., Georgetown, Ontario, Canada in 2003-2004) that logged depth to groundwater every 30 minutes. Depth to groundwater was corrected regularly with data collected using a Model 101 water level meter (Solinst Canada Ltd., Georgetown, Ontario, Canada). Data on depth to groundwater table was collected at *P. deltoides* sites from January 2001 through December 2003 and at *T. chinensis* sites from January 2002 through December 2004. Mean depth to groundwater was compared at flood and non-flood sites using a Friedman test. Separate tests were run for sites dominated by either *P. deltoides* or *T. chinensis*.

Samples of groundwater were collected from wells at each site in June of 2003 and 2004 for chemical analyses. Each well was bailed and allowed to recharge before using a 30 ml polypropylene syringe attached to three meters of flexible tubing to collect samples. Samples were filtered through a pre-rinsed 0.7 μm glass fiber filter and stored at 4 °C for chemical analyses within 24-48 hours after sample collection. Groundwater NH$_4^+$-N and NO$_3^-$-N concentrations were measured on a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, New York, U.S.A.) using Technicon Industrial Methods 98-70W and 100-70W. Mean concentrations of groundwater NH$_4^+$-N and NO$_3^-$-N for June of 2003 and 2004 were compared across treatments (species plus flood regime) using repeated measures ANOVA.

*Soil sampling and analysis*

Four transects ran from the center groundwater well to wells in each corner of the plot. Three soil sampling points were established at 10 m intervals along each transect. Soils were collected seasonally (April 2001-July 2004 for *P. deltoides* sites; November
2002-July 2004 for *T. chinensis* sites) using a 2.2 x 30 cm stainless steel soil probe (AMS Inc., American Falls, ID, U.S.A.) fitted with a butyrate plastic liner that was discarded after sampling along each transect. Soils collected along each transect were pooled and homogenized within polyethylene bags. Samples were stored at 4 °C until further processing could be conducted.

In the laboratory, samples were sieved (2 mm) to remove roots and organic debris. Gravimetric field water content was measured by drying 10-20 g sub-samples of soil for 24 hours at 100 °C and subtracting the sample dry weight from its initial weight. The proportion of soil comprised of organic matter was determined by mass loss-on-ignition at 500 °C. Another set of pre-weighed soil sub-samples was saturated with deionized water, drained for 30 minutes, and dried for 24 hours at 100 °C. Water holding capacity was calculated by subtracting the dry weight from the wet weight of each sample and dividing the remainder by the dry weight. Two more sets of soil sub-samples, weighing 10 g by dry mass, were used to measure soil concentrations of NO$_3^-$-N and NH$_4^+$-N and potential rates of net N mineralization. Sub-samples used to measure soil N concentrations were immediately extracted with 100 ml of 2M KCl. Net N mineralization sub-samples were brought to 50% water holding capacity with deionized water on a weekly basis and incubated at 20 °C for ten weeks. Nitrogen within the samples was extracted with 100 ml of 2M KCl at the end of the incubation. KCl extractions were analyzed for NH$_4^+$-N and NO$_3^-$-N on a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, New York, U.S.A.) using Technicon Industrial Methods 98-70W and 100-70W. Net N mineralization was calculated as the sum of the final concentration of NO$_3^-$-N and NH$_4^+$-N minus the initial concentration.
Soil pH was measured electrometrically using a 1:1 suspension of soil sample to 0.01 mol l⁻¹ CaCl₂ solution. Electrical conductivity was measured on a Accumet Model 50 conductivity meter (Fisher Scientific International Inc., Hampton, NH, U.S.A.) using a slurry of 2:1 parts deionized water to soil sample. Bulk density of samples was determined as oven-dry mass per volume (based on core volume). Soil texture for each study site was determined using the hydrometer method for particle size analysis (Gee and Bauder 1986). Each of these measures was performed for a single set of soil samples.

Percent nitrogen (% N) and percent carbon (% C) of 50-100 mg sub-samples of soil were determined via high temperature combustion using a ThermoQuest CE Instruments NC2100 Elemental Analyzer (ThermoQuest Italia, S.p.A., Rodano, Italy). Total phosphorus (P) content of soils was measured by combusting 10 g samples at 500 °C for one hour, adding 100 ml of 1N HCl to each sample, and incubating them for 30 minutes at 80 °C (Stelzer and Lamberti 2001). Dilution aliquots of extracts were analyzed for PO₄³⁻-P on a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, New York, U.S.A.) using Technicon Industrial Methods 94-70W. The % N, C, or P of soil samples were transformed to molar concentrations, which were used to compare C:N, C:P, and N:P ratios.

Comparisons of gravimetric soil moisture, concentrations of soil inorganic N, and potential rates of net N mineralization at flood and non-flood sites were conducted using repeated measures ANOVA, with time as the repeated measure. Data were transformed (arcsine-square root for soil moisture; log [x + 1] for soil N) as needed to meet test assumptions. These analyses were conducted separately for sites dominated by P.
*deltoides* or *T. chinensis* to isolate the effect of flooding from species and because the number of sampling dates was uneven across species. Data on physical characteristics of soil were transformed (log \(x + 1\) for electrical conductivity and bulk density of soils; arcsine-square root for % sand, silt, clay) before conducting comparisons across treatments using one-way ANOVA and *a posteriori* tests (Tukey’s HSD for data with equal variance; Tamahane’s T2 for data with unequal variance). Data on % organic matter were transformed (arcsine-square root) and compared across treatments using repeated measures ANOVA. Soil stoichiometry data (%N, %P, %C, C:N, C:P, N:P) were compared across treatments for each year of data using a multivariate general linear model (GLM) and Tukey’s HSD or Tamahane’s T2 *a posteriori* tests. Monthly site means of soil % C, % organic matter, % gravimetric soil moisture, depth to groundwater table, PDZI, and precipitation were entered into step-wise linear regressions to predict the major control(s) on total inorganic N concentrations at flood and non-flood sites. Total soil inorganic N concentrations were transformed (log \(x + 1\)) prior to analysis to ensure a normal distribution of regression residuals.

**Root biomass and rates of N uptake measurement and analysis**

Soil samples were collected in April 2005 to determine the biomass of roots at three study trees within each site. Three soil cores were collected within 1 m of the base of each study tree using an 8 x 14 cm stainless steel soil corer (AMS Inc., American Falls, ID, U.S.A.). Roots were removed from soils, rinsed with deionized water, and separated into categories based on size (< 2 mm diameter, > 2 mm diameter) and activity (live or dead). Samples were dried at 60 °C for 48 hours and weighed. Fine root (< 2
mm) biomass data were transformed (log [x + 1]) and compared across treatments using one-way ANOVA with a posteriori Tukey’s HSD tests.

Rates of inorganic N uptake by *P. deltoides* and *T. chinensis* roots were estimated using the methodology described in Treseder and Vitousek (2001). Freshly excised roots were incubated in a control solution (no N addition) and 100 µM solutions of $^{15}$N-labeled KNO$_3$ and NH$_4$Cl. Concentrations of $^{15}$N labeled solutions were comparable to maximum measured concentrations of extractable soil NO$_3^-$-N and NH$_4^+$-N (142 µM and 107 µM, respectively). Assay samples were collected in the same manner as samples collected to measure root biomass. Assays were conducted in early September 2005 within 48 hours of root sample collection from five study trees per site. Roots were dried at 60 °C for 48 hours post-incubation, weighed, and ground to a homogenous powder. Stable isotope analysis was conducted at the University of California-Davis Stable Isotope Laboratory.

Growing season inorganic N uptake by roots was estimated from measures of hourly uptake per gram root and measures of root biomass for each site. Growing season net N mineralization was estimated from measures of daily rates of net N mineralization for 2003-2004 and the bulk density of soil samples. Linear regression was used to determine the relationship between growing season estimates of net N mineralization and root inorganic N uptake. Growing season N uptake rates were transformed (log [x + 1]) before testing for flood regime differences across species using one-way ANOVA.

*Leaf and litter production measurement and analysis*

Leaf area index (LAI) was measured each month throughout the growing season in 2001-2003 using a LAI-2000 sensor (Li-Cor Inc., Lincoln, NB, U.S.A.). The sensor
was placed at the ground surface for all below-canopy measurements. Above canopy measurements were made either from a ladder at sites equipped with micrometeorological towers or from levee roads adjacent to study sites. LAI data were collected from five locations at each study site. Because of rapidly changing light conditions before dawn and after sunset, above-canopy measurements were taken both before and after the associated below-canopy measurements. In addition, the first plot measured post-dawn or pre-sunset was repeated at the end of the sequence. The leaf area at *P. deltoides* sites was calculated to be twice the measured LAI. The morphology of *T. chinensis* causes a large proportion of stems to be included in measures of LAI. Thus, stem area index (SAI) was measured at *T. chinensis* sites after defoliation in winter of each year to measure the contribution of SAI to LAI at these sites. SAI was subtracted from LAI for *T. chinensis* sites. The resulting value was multiplied by π to reflect the cylindrical geometry of *T. chinensis* leaves and represented the leaf area of *T. chinensis* sites. Monthly site means of soil inorganic N and depth to groundwater were entered into a step-wise linear regression to characterize the correlations between these variables and mean values of LAI for June of 2001–2003. Repeated measures ANOVA was used to test within species differences across flood regime in values of LAI for June of 2001 and 2002.

Litterfall was collected from early 2001 through summer 2003 in 0.10 m² plastic tubs placed under 5 study trees at each *P. deltoides* site. Litterfall was collected from fall 2004 through spring 2005 in 0.17 m² mesh traps placed under 3-5 study trees at both *P. deltoides* and *T. chinensis* sites. The mass of litterfall production was recorded for individual species of vegetation at each site. Litter samples were dried at 60 °C for 48
hours and stored in a desiccator until processed for chemical analysis. Litter C:N:P ratios of 10 mg sub-samples were determined using the same methods to determine the stoichiometric ratios of soil samples. Standing stock of litter was determined in February 2004 by collecting all organic matter within a 0.06 m$^2$ quadrat placed adjacent to each soil sampling point. Litter samples were dried at 60°C for 48 hours and weighed.

Data on litter production and total N inputs via litter from *P. deltoides* sites for 2000-2002 were compared using Mann-Whitney U tests. Kruskal-Wallis H tests and Mann-Whitney pair-wise comparisons were used to compare litter production and total N inputs across treatments in 2004-2005. A multivariate GLM was used to test differences in litter stoichiometry across treatments. Post-hoc tests (Tukeys HSD or Tamahane’s T2) were required only for litter data collected in 2004. Data on litter standing stock were transformed (log $[x + 1]$) before conducting comparisons across treatments using one-way ANOVA and *a posteriori* Tamahane’s T2 tests. Non-linear regression was used to determine the relationship between N inputs via litterfall at *P. deltoides* sites in 2001-2003 and mean annual concentrations of soil inorganic N for each consecutive year. All statistical analyses in this study were performed using SPSS 12.0.1 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

*Depth to ground water and groundwater chemistry*

Mean depth to ground water fluctuated seasonally and varied across treatments (Fig. 2). Groundwater tables were most shallow at *P. deltoides* flood sites and deepest at *T. chinensis* flood sites, ranging from 1.2-2.9 m across years, respectively. Data from
flood sites depicted greater variability in depth to ground water as compared to non-flood sites. Flood sites also showed greater response to peaks in river flow, particularly during flood events in May 2001 and April 2004. Mean depth to ground water was usually deeper within *P. deltoides* non-flood sites relative to *P. deltoides* flood sites (2001-2003: $X^2 = 537$, df = 1, $p < 0.001$). In contrast to *P. deltoides* sites, mean depth to ground water was typically deeper within *T. chinensis* flood sites relative to *T. chinensis* non-flood sites (2002-2003: $X^2 = 730$, df = 1, $p < 0.001$). Ongoing drought in 2002-2003 caused groundwater tables to drop below 2 m and 3 m at *T. chinensis* non-flood and flood sites, respectively.

![Graph showing depth to ground water over time](image.png)

**Figure 2.** Rio Grande hydrograph at USGS gauge 08330000 in Albuquerque and mean daily depth to ground water by species and flood regime. Data for ground water depth at *P. deltoides* sites were available from January 2001 through December 2003, while data for *T. chinensis* sites were available from January 2002 through December 2004. Each trend line represents the mean daily depth to ground water for two study sites.
Mean concentrations of ground water NH$_4^+$-N ranged from 0.17-0.33 mg l$^{-1}$ across treatments, while mean NO$_3^-$-N concentrations ranged from 0.02-0.05 mg l$^{-1}$ (Table 2). Groundwater concentrations of both solutes were comparable across sampling dates (RMANOVA, df = 2, $F = 2.57$, $p = 0.09$). Differences between treatments for both solutes were insignificant (RMANOVA, df = 6, $F = 1.21$, $p = 0.31$), despite the fact that one study site (South Valley Albuquerque) was situated just downstream of a wastewater treatment plant.

Physical characteristics of soils

Most physical characteristics of soils were similar across species and flood regime, with a few exceptions. *T. chinensis* non-flood sites had higher electrical conductivity and reduced soil organic matter ($p < 0.05$; Table 2) relative to other sites. Flood sites generally had less sand (30-60%) and more clay (30-70%) than non-flood sites (Table 2).

Gravimetric soil moisture significantly fluctuated over time within both *P. deltoides* and *T. chinensis* sites (RMANOVA, *P. deltoides*: df = 2, $F = 33.14$, $p = 0.03$; *T. chinensis*: df = 8, $F = 70.61$, $p < 0.001$; Fig. 3), ranging from 13-34% across flood sites and 7-24% across non-flood sites. Soil moisture was generally higher in fall and winter than in spring and summer, due to the onset of the monsoon and cessation of the growing season. Flood sites within stands of both *P. deltoides* and *T. chinensis* were wetter, on average, than non-flood sites (RMANOVA, *P. deltoides*: df = 1, $F = 6.35$, $p = 0.03$; *T. chinensis*: df = 1, $F = 4.63$, $p = 0.05$). This trend was most prominent post-flooding in fall 2003 and spring 2004 (Fig. 3).
Table 2. Soil pH, electrical conductivity, bulk density, soil texture, % organic matter, standing stock of litter, root biomass, and groundwater nitrate and ammonium concentrations by species and flood regime.

<table>
<thead>
<tr>
<th>Factor</th>
<th>P. deltoides</th>
<th>T. chinensis</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>Flood</td>
<td>Non-flood</td>
</tr>
<tr>
<td>pH</td>
<td>7.55 ± 0.11&lt;sup&gt;a&lt;/sup&gt;</td>
<td>7.41 ± 0.09&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>EC&lt;sup&gt;+&lt;/sup&gt; (mS cm&lt;sup&gt;-1&lt;/sup&gt;)</td>
<td>0.23 ± 0.07&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.28 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>Bulk density (g cm&lt;sup&gt;-3&lt;/sup&gt;)</td>
<td>1.10 ± 0.12&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.10 ± 0.03&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>% sand&lt;sup&gt;f&lt;/sup&gt;</td>
<td>14.69 ± 6.64&lt;sup&gt;a&lt;/sup&gt;</td>
<td>25.13 ± 6.35&lt;sup&gt;a,b&lt;/sup&gt;</td>
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<tr>
<td>% silt&lt;sup&gt;f&lt;/sup&gt;</td>
<td>39.57 ± 2.14&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>% clay&lt;sup&gt;f&lt;/sup&gt;</td>
<td>46.10 ± 6.77&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>33.33 ± 4.04&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>% organic matter&lt;sup&gt;§&lt;/sup&gt;</td>
<td>4.54 ± 0.12&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Litter (kg m&lt;sup&gt;-2&lt;/sup&gt;)&lt;sup&gt;f&lt;/sup&gt;</td>
<td>4.27 ± 1.53&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>3.71 ± 0.32&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>Root biomass (g m&lt;sup&gt;-2&lt;/sup&gt;)&lt;sup&gt;f&lt;/sup&gt;</td>
<td>0.82 ± 0.07&lt;sup&gt;a&lt;/sup&gt;</td>
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<tr>
<td>NO&lt;sub&gt;3&lt;/sub&gt;-N (mg L&lt;sup&gt;-1&lt;/sup&gt;)&lt;sup&gt;+&lt;/sup&gt;</td>
<td>0.03 ± 0.02&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.05 ± 0.02&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td>NH&lt;sub&gt;4&lt;/sub&gt;+-N (mg L&lt;sup&gt;-1&lt;/sup&gt;)&lt;sup&gt;+&lt;/sup&gt;</td>
<td>0.33 ± 0.15&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.17 ± 0.09&lt;sup&gt;a&lt;/sup&gt;</td>
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</tbody>
</table>

<sup>f</sup> Data represent means ± 1 SE for an individual sampling date, n = 8 for all but root biomass for which n = 6. Entries sharing common letter superscripts denote between-treatment statistical difference at p ≥ 0.05.

<sup>§</sup> Electrical conductivity.

<sup>§</sup> Data represent means ± 1 SE of samples collected seasonally from November 2002 through July 2004, n = 64. Entries sharing common letter superscripts denote between-treatment statistical difference at p ≥ 0.05.

<sup>+</sup> Data represent means ± 1 SE of samples collected in June of 2003, n = 10. Solute concentrations were statistically similar across 2003 and 2004 sampling dates. Entries sharing common letter superscripts denote between-treatment statistical difference at p ≥ 0.05.
Figure 3. Mean gravimetric soil moisture (%) at flood (solid symbols) and non-flood (hollow symbols) study sites dominated by (a) *P. deltoides* or (b) *T. chinensis*. Error bars represent ± 1 SE of the mean gravimetric soil moisture on each date. Soils were sampled at *P. deltoides* study sites from April 2001 through July 2004, and from November 2002 through July 2004 for *T. chinensis* study sites. Blue arrows denote the occurrence of overbank flood events at some or all flood sites. Blue squares indicate climatic periods of mild to moderate wetness, brown squares indicate periods of mild to moderate drought, and red squares indicate periods of extreme drought.

Soil inorganic N and potential rates of net N mineralization

Concentrations of NO$_3^-$-N and NH$_4^+$-N within soils showed variation over time across species and flood regime (Fig. 4 and Table 3). Mean NO$_3^-$-N concentrations ranged from 1.1-12.8 µg g$^{-1}$ soil at *P. deltoides* sites and 1.5-7.2 µg g$^{-1}$ soil at *T. chinensis* sites, while mean NH$_4^+$-N concentrations ranged from 1.1-8.8 µg g$^{-1}$ soil and 0.5-3.0 µg g$^{-1}$ soil at *P. deltoides* and *T. chinensis* sites, respectively. Patterns of fluctuation for both flood and non-flood sites were similar across treatments, with the exception of a pulse in NO$_3^-$-N availability at *T. chinensis* flood sites relative to non-flood sites in winter 2003.
induced by the flood event of fall 2003 (Fig. 4c). Seasonal effects were most evident for extractable soil NO$_3^-$-N at P. deltoides sites (Fig. 4a), which exhibited peak values in late winter to early spring of each year followed by reduced concentrations during the growing season.

![Graphs showing mean soil NO$_3^-$-N and NH$_4^+$-N concentrations](image)

**Figure 4.** Mean field available NO$_3^-$-N (a, c) and NH$_4^+$-N (b, d) concentration at flood (solid symbols) and non-flood (hollow symbols) study sites dominated by P. deltoides (a, b) or T. chinensis (c, d). Error bars represent ±1 SE of the mean NO$_3^-$-N or NH$_4^+$-N concentration on each date. Soils were sampled at P. deltoides study sites from April 2001 through July 2004, and from November 2002 through July 2004 for T. chinensis study sites. Blue arrows denote the occurrence of overbank flood events at some or all flood sites. Blue squares indicate climatic periods of mild to moderate wetness, brown squares indicate periods of mild to moderate drought, and red squares indicate periods of extreme drought.
Extractable soil NO$_3^-$-N at *P. deltoides* sites was consistently and significantly greater over time in the absence of flooding (Table 3). In contrast, *T. chinensis* flood and non-flood sites had similar concentrations of soil NO$_3^-$-N over the period of study, despite the flood-related pulse of NO$_3^-$-N in fall 2003. Flood regime influenced the concentration of soil NH$_4^+$-N at both *P. deltoides* and *T. chinensis* sites, but had contrary effects within stands of each species. *P. deltoides* non-flood sites generally had greater concentrations of soil NH$_4^+$-N relative to flood-sites (Fig. 4b and Table 3). Conversely, NH$_4^+$-N concentrations were elevated at *T. chinensis* flood sites compared to non-flood sites (Fig. 4d and Table 3). Pulses in soil NH$_4^+$-N were evident across treatments in spring 2004 due to increases in soil moisture resulting from monsoonal precipitation throughout the middle Rio Grande valley that also induced flooding within the Bosque del Apache NWR.

Mean potential rates of net N mineralization ranged from 0.00-0.44 µg g$^{-1}$ soil d$^{-1}$ at *P. deltoides* sites and from 0.00-0.14 µg g$^{-1}$ soil d$^{-1}$ at *T. chinensis* sites (Fig. 5). Mean rates of net nitrification were 78% of net N mineralization rates. However, nitrification rates frequently accounted for over 100% of net N mineralization due to immobilization of soil ammonium that was not associated with nitrification. Non-flood sites across species generally had higher potential rates of net N mineralization (RMANOVA, *P. deltoides*: df = 1, $F = 15.39$, $p < 0.01$; *T. chinensis*: df = 1, $F = 5.92$, $p = 0.03$), but rates were inconsistent over time (RMANOVA, *P. deltoides*: df = 4, $F = 11.42$, $p = 0.02$; *T. chinensis*: df = 7, $F = 12.56$, $p = 0.001$). Peak rates at *P. deltoides* sites occurred in November 2001 and continued to decline until May 2004, when both flood and non-flood *P. deltoides* sites were marked by net N immobilization. A similar decline over time
**Table 3.** Degrees of freedom (df), *F*-statistic, and significance for repeated measures analysis of variance for transformed (log \([x + 1]\)) field available soil nitrate and ammonium at sites dominated by *P. deltoides* or *T. chinensis*. Site was not included as a variable in analyses due to a limitation in degrees of freedom.

### *P. deltoides: NO₃⁻-N*

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### *P. deltoides: NH₄⁺-N*

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† Analyses were performed for fourteen sampling dates, *n* = 8.

### *T. chinensis: NO₃⁻-N*

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### *T. chinensis: NH₄⁺-N*

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‡ Analyses were performed for eight sampling dates, *n* = 8.

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characterized rates of net N mineralization at *T. chinensis* sites, but peak rates at *T. chinensis* non-flood sites occurred in May 2004 concurrent with net N immobilization at *T. chinensis* flood sites.

**Stoichiometry of soils**

N:P ratios of soils ranged from roughly 2-5, indicating that soils were likely N limited. N limitation was more severe at *T. chinensis* non-flood sites relative to other types of sites (p < 0.05 for both 2003 and 2004; Table 4). These sites also were
characterized by high soil C:N ratios, with means of 40:1 in 2003 and 130:1 in 2004. Soil C:N ratios at other sites ranged from 22:1-30:1 over the same time period. Soil C ranged from roughly 1.3-2.2% across species and flood regime, while soil N ranged from 0.03-0.12%. Percentages of both C and N were consistently and significantly lower at T. chinensis non-flood sites relative to other treatments.

Results of a step-wise linear regression indicated that soil % C explained 65% of the variation in NO$_3^-$-N + NH$_4^+$-N concentrations at non-flood sites ($y = 0.32 + 0.28 \times x$, $n = 32$, $R^2_a = 0.65$, $p < 0.001$; Fig. 6 and Table 5). In contrast, gravimetric soil moisture, but not soil % C (Fig. 6), was a predictor of soil inorganic N concentrations at flood sites. However, this regression explained just 10% of the variation ($y = 0.60 + 0.80 \times x$, $n = 32$, $R^2_a = 0.10$, $p = 0.04$; Table 5). No other factors entered into either model were included as significant predictor variables of soil inorganic N at flood or non-flood sites.
Table 4. Soil and litter stoichiometry. Soil data represent annual means ± 1 SE, n = 32. Entries sharing common letter superscripts denote between-treatment statistical difference at p ≥ 0.05. Litter data represent means ± 1 SE for samples collected in December of 2001 (n = 30) and 2002 (n = 10) and October of 2004 (n = 6).

<table>
<thead>
<tr>
<th></th>
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<th>P. deltoides</th>
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<th>T. chinensis</th>
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<tr>
<td></td>
<td>Year</td>
<td>Factor</td>
<td>Flood</td>
<td>Non-flood</td>
<td>Flood</td>
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<td>Soils</td>
<td>2003</td>
<td>%C</td>
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<td>2.21 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>1.76 ± 0.05&lt;sup&gt;b&lt;/sup&gt;</td>
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<tr>
<td></td>
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<td>%N</td>
<td>0.11 ± 0.01&lt;sup&gt;a,b&lt;/sup&gt;</td>
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<td>0.09 ± 0.00&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>%P</td>
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<td>0.08 ± 0.01&lt;sup&gt;a,b&lt;/sup&gt;</td>
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<tr>
<td></td>
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<td>C:N</td>
<td>24.4 ± 0.6&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>N:P</td>
<td>3.72 ± 0.36&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>4.19 ± 0.33&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>2004</td>
<td>%C</td>
<td>2.15 ± 0.08&lt;sup&gt;a&lt;/sup&gt;</td>
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<td>%N</td>
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<td>%P</td>
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<td>C:N</td>
<td>29.9 ± 1.6&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>N:P</td>
<td>4.19 ± 0.33&lt;sup&gt;a,b&lt;/sup&gt;</td>
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<td>0.41 ± 0.01&lt;sup&gt;b&lt;/sup&gt;</td>
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<td>2001</td>
<td>%C</td>
<td>45.7 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45.6 ± 0.2&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%N</td>
<td>0.28 ± 0.01&lt;sup&gt;b&lt;/sup&gt;</td>
<td>0.52 ± 0.05&lt;sup&gt;a&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C:N</td>
<td>196.0 ± 8.8&lt;sup&gt;a&lt;/sup&gt;</td>
<td>139.5 ± 21.6&lt;sup&gt;b&lt;/sup&gt;</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>2004</td>
<td>%C</td>
<td>42.4 ± 0.5&lt;sup&gt;b&lt;/sup&gt;</td>
<td>42.6 ± 0.3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>44.7 ± 0.9&lt;sup&gt;ab&lt;/sup&gt;</td>
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<tr>
<td></td>
<td></td>
<td>%N</td>
<td>0.42 ± 0.04&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.53 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.67 ± 0.06&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>%P</td>
<td>0.03 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.04 ± 0.01&lt;sup&gt;a&lt;/sup&gt;</td>
<td>0.05 ± 0.00&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C:N</td>
<td>123.6 ± 9.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>100.2 ± 12.0&lt;sup&gt;a,b&lt;/sup&gt;</td>
<td>80.3 ± 6.3&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>C:P</td>
<td>3620 ± 292&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2943 ± 339&lt;sup&gt;a&lt;/sup&gt;</td>
<td>2468 ± 172&lt;sup&gt;a&lt;/sup&gt;</td>
</tr>
<tr>
<td></td>
<td></td>
<td>N:P</td>
<td>29.3 ± 0.4&lt;sup&gt;b&lt;/sup&gt;</td>
<td>29.4 ± 0.2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>30.9 ± 0.6&lt;sup&gt;ab&lt;/sup&gt;</td>
</tr>
</tbody>
</table>
Figure 6. Relationship between percent soil carbon and transformed (log [x + 1]) soil inorganic nitrogen concentration across species and flood regime. Data represent means for samples collected from 2001-2004 at flood (solid symbols and solid regression line; y = 0.46 + 0.16 x, n = 32, r² = 0.04, p = 0.14) and non-flood (hollow symbols and dotted regression line; y = 0.29 + 0.39 x, n = 32, r² = 0.70, p < 0.001) P. deltoides (circles) and T. chinensis (triangles) sites. The equations listed above represent the results of simple linear regression.

Table 5. Coefficients and significance for a step-wise multiple linear regression for prediction of mean inorganic N concentrations within soils. Values of mean inorganic N concentration were transformed (log [x + 1]) prior to analysis.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Flood†</th>
<th>Non-flood‡</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Coefficient</td>
<td>p</td>
</tr>
<tr>
<td>Soil carbon (%)</td>
<td>1.32</td>
<td>0.20</td>
</tr>
<tr>
<td>Soil organic matter (%)</td>
<td>-0.89</td>
<td>0.38</td>
</tr>
<tr>
<td>Gravimetric soil moisture (%)</td>
<td>2.14</td>
<td>0.04</td>
</tr>
<tr>
<td>Depth to groundwater table (cm)</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>PDZI§</td>
<td>0.20</td>
<td>0.85</td>
</tr>
<tr>
<td>Precipitation (cm)</td>
<td>-0.97</td>
<td>0.34</td>
</tr>
</tbody>
</table>

§ Palmer Drought "Z" Index. See Table 2 for additional explanation.
† Model R₂ = 0.10, F = 4.57, p = 0.04.
‡ Model R₂ = 0.65, F = 45.40, p < 0.001.
Root biomass and rates of N uptake

Mean root biomass within the upper 20 cm of soils was similar across treatments (Table 2). Estimated potential rates of net N mineralization throughout the growing season explained 24% of the variation in estimated inorganic N uptake by roots ($y = 118.97 - 0.84 x$, $n = 8$, $r^2 = 0.24$, $p < 0.01$; Fig. 7). This trend was driven by flood sites, where N uptake was significantly greater relative to non-flood sites (ANOVA: $df = 1$, $F = 10.04$, $p < 0.01$).

![Graph showing Relationship between growing season estimates of net N mineralization and root inorganic N uptake.](image)

**Figure 7.** Relationship between growing season estimates of net N mineralization and root inorganic N uptake. Data represent means (net N mineralization: 2003-2004; root uptake: 2005) for *P. deltoides* (circles) and *T. chinensis* (triangles) flood (solid symbols) and non-flood (hollow symbols) sites. Error bars represent means ± 1 SE.

Leaf and litter production, litter stoichiometry, and N inputs to soils via litter

Results of step-wise linear regression indicated that mean soil inorganic N concentrations ($x_1$) and mean depth to ground water ($x_2$) together explained 60% of the variation in LAI measured in June of 2001-2003 ($y = 5.77 + 0.24 x_1 - 0.02 x_2$, $n = 15$, $R^2_a$)
= 0.60, p = 0.01; Fig. 8a and 8b). Mean growing season LAI values ranged from 3.2-6.8 and 0.8-6.6 for P. deltoides and T. chinensis sites, respectively. LAI values in June of 2001 and 2002 for each species were similar across flood regime (RMANOVA, P. deltoides: df = 1, F = 0.24, p = 0.66; T. chinensis: df = 1, F = 3.10, p = 0.10). However, litterfall production significantly differed across study treatments ($X^2 = 16.92, df = 3, p = 0.001; Fig. 9a). Mann-Whitney pair-wise comparisons showed that T. chinensis flood sites had significantly more litterfall than T. chinensis non-flood sites in 2004-2005 (U$_{3,0}$, p = 0.02). P. deltoides flood and non-flood sites had comparable quantities of litterfall in 2004-2005, but litterfall was significantly greater at non-flood sites relative to flood sites from 2000-2002 (2000-2001: U$_{83,0}$, p < 0.01; 2001-2002: U$_{15,0}$, p < 0.001). The standing stock of litter did not differ across flood regime within P. deltoides and T. chinensis study sites (Table 2), despite flood-related differences in annual litterfall production.

Litter at P. deltoides non-flood sites had significantly higher % N and lower C:N ratios than P. deltoides flood sites throughout 2000-2001 (p < 0.05; Table 4), but % N and C:N ratios did not differ across P. deltoides sites in 2004. N inputs via litterfall were defined as the total quantity of N present in litter collected from October-February in 2004-2005. Differences in litter production and litter % N across P. deltoides sites throughout 2001-2003 led to significantly more N inputs via litterfall at P. deltoides non-flood sites relative to flood sites (2000-2001: U$_{55,0}$, p < 0.001; 2001-2002: U$_{4,5}$, p < 0.001; Fig. 9b), but inputs were comparable across P. deltoides sites in 2004-2005 due to similarities in litter production. The total quantity of N inputs from P. deltoides litter in 2000-2002 explained 50% of the variation in mean annual concentrations of soil inorganic N for the years following those inputs ($y = 19.85 x / 1.98 + x, n = 12, r^2 = 50$,
p < 0.01; Fig. 10). Although litter % N and C:N ratios did not differ across T. chinensis sites (Table 4), differences in litter production at flood and non-flood T. chinensis sites led to significantly more N inputs via litterfall at T. chinensis flood vs. non-flood sites in 2004-2005 (U3,0, p = 0.02; Fig. 9b). Data was not available to assess the relationship between litter-derived N inputs and mean annual concentrations of soil inorganic N at T. chinensis sites.

**Figure 8.** Relationships between (a) soil inorganic nitrogen and (b) depth to ground water and growing season leaf area index (LAI). Data represent means for samples collected from 2001-2003 at flood (solid symbols) and non-flood (hollow symbols) P. deltoides (circles) and T. chinensis (triangles) sites. The regressions in (a) and (b) represent correlations across treatments.
Figure 9. Differences across species and flood regime in (a) litter production and (b) nitrogen inputs via litterfall. Data in (a) represent total litterfall for October-February of each year. Data in (b) represent the product of total litterfall and the mean percentage of nitrogen in litter for each treatment. Error bars in (a) and (b) represent ± 1 SE of the mean. Differing letter superscripts denote between-treatment statistical difference at p < 0.05.

Figure 10. Relationship between nitrogen inputs via litterfall and annual soil inorganic nitrogen for flood (solid circles) and non-flood (hollow circles) stands of P. deltoides. Data represent means for samples collected from 2001-2003. The regression refers to the correlation across flood regime.
DISCUSSION

Intermittently flooded *P. deltoides* sites in this study represented "open" systems, with multiple pathways of N input and loss (Fig. 11a), and were characterized by reduced pools of soil inorganic N relative to *P. deltoides* non-flood sites (Fig 4a and 4c). In contrast, non-flooded *P. deltoides* sites represented "closed" systems, with strong internal recycling of N resources (Fig. 11b) that augmented pools of soil inorganic N. Litter production and its associated inputs of N to soils enhanced differences in soil inorganic N concentrations at *P. deltoides* flood and non-flood sites. *T. chinensis* sites included in this study did not conform to "open" and "closed" system models as well as *P. deltoides* study sites. Rather, differences in litter production at *T. chinensis* sites controlled soil N concentrations to a greater degree than differences in flood regime.

Intermittently flooded riparian areas as open systems

Floodwaters are sources of N to riparian systems either through direct inputs (Valett et al. 2005) or via re-mobilization of nutrients from riparian soils (Heffernan and Sponseller 2004). Riparian soils and litter can retain significant fractions of total inorganic N inputs from flooding (Brunet et al. 1994, Andersen et al. 2003, Valett et al. 2005). However, N uptake by microbes and plants or gaseous losses of N to the atmosphere through denitrification can result in a net loss of N from soils (Vought et al. 1994, Pinay et al. 1995, Holmes et al. 1996, Baldwin and Mitchell 2000, Forshay and Stanley 2005). Potential denitrification rates for semi-arid floodplain soils (i.e., anaerobic conditions plus C and N amendments) have been reported to be between 60-80 ng N g⁻¹ soil h⁻¹ (Holmes et al. 1996). These rates accounted for only 25% of declines in

75
NO$_3^-$-N observed during an artificial re-wetting experiment using soils from the same location for which the denitrification measures were conducted (Heffernan and Sponseller 2004). The remainder of NO$_3^-$-N decline was attributed to microbial immobilization, although not directly measured. Periodic inundation of riparian forests along the middle Rio Grande has been observed to increase microbial and fungal growth (Molles et al. 1998), likely fueled by flood-related increases of dissolved organic carbon (DOC) (Valett et al. 2005). This mechanism of N retention is partially supported by evidence that mats of *P. deltoides* litter can immobilize floodwater-N before it reaches riparian soils (Andersen et al. 2003). Uptake by plants is another significant source of N loss from riparian soils. Roots from trees located within our flood sites had greater estimated rates of inorganic N uptake over the growing season relative to non-flood sites (Fig. 7). All of the mechanisms listed above are active within non-flood as well as flood sites, but activity rates of these mechanisms are often lower in areas of reduced soil moisture. Thus, non-flood sites represent relatively more “closed” systems in contrast to flood sites.
Figure 11. Generalized models of ecosystem dynamics at (a) flood and (b) non-flood study sites along the middle Rio Grande of New Mexico.
Suppression of leaf production by flood inundation

Flooding has been shown to increase plant productivity in some systems (Tremolières et al. 1998). *Populus* species are generally regarded as being tolerant of excessive moisture relative to other species of woody plants (Harrington 1987). Yet, flooding can induce anoxic conditions surrounding plant roots, which has been shown to slow root growth and reduce nutrient uptake in *P. deltoides* (Harrington 1987, Liu and Dickmann 1992). Flooding also promotes the closure of stomata in *P. deltoides* leaves, which can suppress leaf growth over the long-term (Smit et al. 1989, Smit et al. 1990), thereby reducing canopy leaf area (i.e., LAI) and subsequent litterfall. Physiological responses of *P. deltoides* to flooding support the findings of this study and those of Ellis et al. (1998) that litter production at *P. deltoides* flood sites was reduced relative to non-flood sites (Fig. 9a).

In contrast to *P. deltoides* sites, litter production at *T. chinensis* flood sites was elevated in comparison to litter production at *T. chinensis* non-flood sites (Fig. 9a). Flood inundation has been shown to reduce biomass production of *T. chinensis* saplings relative to native riparian plants (e.g., Vandersande et al. 2001), but growth effects of flooding on mature *T. chinensis* have not been studied in detail. Brotherson and Field (1987) reported that *T. chinensis* can survive inundation of up to 70 days, which is almost half the reported flood tolerance of *P. deltoides* (120 days; Rood and Mahoney 1990). Mature *T. chinensis* trees respond to flood inundation by growing adventitious roots at the surface of floodwaters (Everitt 1980). This adaptation, which was observed within flooded stands of *T. chinensis* along the middle Rio Grande, may allow *T. chinensis* to maintain leaf growth during periods of inundation.
The relatively high quantity of litter production at *T. chinensis* flood sites could also be attributed to the averaging of values from *T. chinensis* non-flood sites. The LAI values at one of these sites (Bernardo) ranged from 4.1-5.9, which were similar to or higher than the mean value of LAI (4.4) across all sites and sampling dates. In contrast, LAI values at the other *T. chinensis* non-flood site (Sevilleta) ranged from 0.8-2.0, and were the lowest values across all sites. Leaf production at Sevilleta was potentially limited by low soil moisture (Fig. 2), mean depth to ground water > 2 m (Fig. 8b), and increased competition for nitrogen between plants and microbes, as inferred from soil C:N molar ratios much greater than 25:1 (Table 4). High values of LAI at Bernardo were supported by moderate concentrations of soil N and depth to ground water (Fig. 8a and 8b). These values also suggested that leaf production at both *P. deltoides* and *T. chinensis* flood sites may be suppressed by flood inundation.

*Feedbacks between riparian soil N concentrations and litter production*

Feedbacks between litter production and soil inorganic N determined the degree of nitrogen accumulation within all riparian study sites. Study sites with greater concentrations of soil N and shallow water tables supported greater LAI (Fig. 8a and 8b). A canopy with greater LAI should produce greater amounts of litter. LAI values were statistically similar within each species, but quantities of litter significantly differed for each species by flood regime. *P. deltoides* litterfall was generally greater at non-flood vs. flood sites (Fig. 9a). In contrast, *T. chinensis* litterfall was greater at flood vs. non-flood sites (Fig. 9a). Sites with elevated litter production obtained greater N inputs via litterfall and vice-versa (Fig. 9b). Data from *P. deltoides* sites demonstrated that pools of soil N
were well correlated with N inputs via litter (Fig. 10), but the relationship was best
described by a saturation function. This trend may have resulted from a shift in control of
soil N concentration by annual litter inputs to a regime of more shared control by
multiple sources, such as N fixation by non-native understory shrubs, accumulation of
litter standing stock, and increased N deposition associated with urban influences.
Evidence for control over soil N concentrations by N-fixation within our study sites
exists. *E. angustifolia* leaf % N was reported by Tibbets and Molles (2005) to be three
times greater than that of *P. deltoides*. Also, annual litterfall by understory *E.
angustifolia* within *P. deltoides* sites explained 83% of the variation in annual soil
inorganic N concentrations for 2002 (p < 0.01; Tibbets 2005).

The feedbacks between riparian soil N and litter production determine the rate of
soil N accumulation, particularly in the absence of flooding (i.e., in “closed” systems).
Soil inorganic N at non-flood sites was positively correlated with soil % C (Fig. 6), which
is largely derived from the decomposition of litter in many systems. Soil % C was
greatest at *P. deltoides* non-flood sites and lowest at *T. chinensis* non-flood sites. These
sites represent the ends of the spectrum in litter production across the sites included in
this study. In turn, sites with greater pools of soil inorganic N produced greater quantities
of litter.

*Soil inorganic N dynamics within T. chinensis study sites*

Contrary to patterns at *P. deltoides* sites, soil inorganic N concentrations were
greater at *T. chinensis* flood sites relative to *T. chinensis* non-flood sites. This difference
was driven primarily by greater concentrations of soil NH₄⁺-N. Greater soil NH₄⁺-N
concentrations in flood vs. non-flood sites have been observed in other riparian systems (Pinay et al. 2000). Riparian inundation can increase decomposition of forest floor detritus (Ellis et al. 1998, 1999), thereby introducing substantial amounts of NH$_4^+$-N to soils. Inundation and high soil moisture also can lead to anoxic conditions within soils that promote increased cation exchange of NH$_4^+$-N within sediments and cessation of nitrification (Paul and Clark 1996). These processes may have been the dominant drivers of elevated soil NH$_4^+$-N concentrations at _T. chinensis_ flood vs. non-flood sites (Fig. 4d), since flood events did not stimulate increased rates of net N mineralization within _T. chinensis_ sites (Fig. 5b). The pulse of NO$_3^-$-N at _T. chinensis_ flood sites post-flooding (Fig. 4c) was likely caused by nitrification of NH$_4^+$-N mobilized from sediments during inundation (Qiu and McComb 1996). In contrast to all other study sites, soils at _T. chinensis_ non-flood sites were extremely N limited (C:N ratios between 40-130:1; Table 4). N-limitation ought to have induced chronic net N immobilization by microbial communities, but net N mineralization was predominant in soils of _T. chinensis_ non-flood sites throughout mineralization assays (Fig. 5b). However, these assays were conducted under optimal soil moisture conditions that likely promoted rates greater than rates in situ. Low concentrations of soil inorganic N at _T. chinensis_ non-flood sites were attributed to low soil moisture (Fig. 3) and the low quantity and quality of organic matter (Table 4) resulting from reduced litter production (Fig. 9a), all of which support slower rates of in situ microbial decomposition and mineralization.
Possible effects of drought and stand age on soil inorganic N

The climate regime throughout the study was characterized by periods of mild to moderate wetness interspersed with periods of mild to extreme drought. Drought has been correlated to increases in soil mineralization potential within grasslands of semi-arid regions (White et al. 2004). Initial declines in soil moisture within low-land riparian soils of Australia were associated with declines of soil inorganic N, but complete desiccation elevated pools of soil inorganic N (Baldwin and Mitchell 2000). Soil desiccation leads to mortality of microbes and decomposition of osmoregulatory molecules (Fierer and Schimel 2003), which promotes increased nutrient availability upon rewetting (Heffernan and Sponseller 2004). I observed initial decreases in soil NO$_3^-$-N concentrations (Fig. 4a) that coincided with declines in soil moisture (Fig. 3) concurrent with the onset of drought. Soil NO$_3^-$-N concentrations increased as the drought continued. However, soil moisture also increased and coincided with the end of the growing season, suggesting that oscillations in pools of soil inorganic N were driven more by season than by drought. Similar seasonal fluctuations in soil inorganic N have been observed by Nadelhoffer et al. (1984) and Pinay et al. (2000).

Soil N is known to accumulate with increasing stand age (Klingensmith and Van Cleve 1993, Kaye et al. 2003, Adair et al. 2004). The *P. deltoides* stands included in this study were 9-45 years older than the *T. chinensis* study sites. Thus, processes associated with aging (e.g., increased aboveground biomass, accumulation of organic matter and stable pools of soil N; Van Cleve et al. 1983, Kaye et al. 2003) may have contributed to differences in soil N across vegetation types.
Soil N availability as compared to other riparian ecosystems

Soil inorganic N concentrations within our study sites (<1-17 μg g\(^{-1}\) soil) were similar to values reported for Sycamore Creek in Arizona (<1-11 μg g\(^{-1}\) soil; Heffernan and Sponseller 2004), but lower than concentrations (403-462 μg g\(^{-1}\) soil) along the Green River and Yampa River in Colorado (Adair et al. 2004). Sycamore Creek and the Yampa River are free-flowing systems, while the flow of the Green River is regulated. These data point out that concentrations of soil inorganic N not only differ across flood regimes within a single river system, but also are highly variable across riparian ecosystems of the southwestern U.S. with differing flood regimes.

Potential rates of net N mineralization in this study (<0-0.5 μg g\(^{-1}\) soil d\(^{-1}\)) were similar to in situ mineralization rates reported for the Tanana River floodplain in Alaska (<1-3 μg g\(^{-1}\) soil d\(^{-1}\); Klingensmith and Van Cleve 1993), Sycamore Creek riparian soils (<0-0.06 μg g\(^{-1}\) soil d\(^{-1}\); Schade et al. 2002), and temperate deciduous forests (<1-4 μg g\(^{-1}\) soil d\(^{-1}\); Nadelhoffer et al. 1984, Raison et al. 1987). Thus, in situ rates of net N mineralization in soils along the middle Rio Grande are potentially much lower than rates within these other riparian ecosystems, which are characterized by greater quantities of mean annual precipitation.

Naturalized flows and riparian management

Water operation managers throughout the U.S. have begun to implement naturalized flow regimes (e.g., Sparks et al. 1998, Schmidt et al. 2001), in part to assist natural resource managers and restoration practitioners to promote recruitment of native vegetation and to control the spread of non-native vegetation. The May 2001 flood along
the middle Rio Grande resulted from naturalized flows released for ecological reasons (Robert 2005). The pulse from this release lasted just a few days, but riparian inundation persisted for about a week. However, the timing and duration of flow releases are often influenced by delivery requirements governed by interstate compact agreements. Such releases can extend for up to three months during periods of increased water availability, which occurred along the middle Rio Grande in spring 2005 (USGS 2006). Long-duration floods have caused mortality of bottomwood hardwood forests (Harms et al. 1980). Naturalized flow in semi-arid regions thus poses a potential irony: releases of water concurrent with snowmelt run-off in the spring help to promote *P. deltoides* recruitment (Mahoney and Rood 1998), but releases of long duration can be detrimental to mature populations of *P. deltoides* located in flood-prone areas. The relationship between shallow water tables and leaf area production illustrated in this study (Fig. 8b) highlights the importance of base flow regulation to maintain *P. deltoides* productivity. Portions of the middle Rio Grande have gone dry during periods of drought. Drying of the river spurred precipitous drops in groundwater table elevation at some of the sites included in this study (e.g., *T. chinensis* flood sites, Fig. 2). Thus, management of minimum base flows, as well as peak flows, is critical to the long-term conservation and regeneration of *P. deltoides* gallery forests of the southwestern U.S.

**CONCLUSIONS**

Riparian soils of semi-arid regions are N limited, resulting in a high biological demand for N resources. This study demonstrates that floods promote both gains and losses of inorganic N within riparian soils, depending on the timing of floods, the
duration of inundation, and the quantity of leaf production. Precipitation and floods promote nutrient availability via increased decomposition and N mineralization, particularly if these events follow dry conditions (Ellis et al. 2002). Winter or spring precipitation and floods mobilize nutrients that can be accessed by vegetation throughout the growing season, while vegetation has less time to assimilate nutrients liberated by monsoon-related events (Gosselink et al. 1981, Ellis et al. 2002). Late summer and fall flood events also promote the recruitment of *T. chinensis* since its seeding phenology extends throughout the growing season (Di Tomaso 1998). Long-duration inundation results in greater N losses via denitrification and greater stress to riparian vegetation due to root anoxia. Thus, short-duration inundation may have greater benefit to native riparian vegetation. Working definitions of “long” vs. “short” duration may vary from system to system depending on geomorphic variability and differences in soil texture. This study also demonstrates that riparian sites with greater productivity will support greater inputs of organic matter to be mineralized by microbial communities during periods of increased moisture and provide increased inputs of N to riparian soils.

The natural flow regime concept of Poff et al. (1997) emphasizes that managed flows ought to mimic the variability in historic river hydrographs. The timing and duration of precipitation-induced floods are variable along the middle Rio Grande, as well as within other rivers in semi-arid regions with major tributaries between dams. In contrast, the timing and duration of spring floods are controlled more often by the needs to meet compact delivery requirements than to provide ecologically beneficial flows. The practice of spring-time naturalized flow within the rivers of semi-arid regions ought to continue, particularly when adequate quantities of water are available. These flows are
required for the regeneration of *P. deltoides* gallery forests of the western and southwestern U.S. More research needs to be conducted to determine the thresholds at which extended flood duration does more harm than good for mature stands of *P. deltoides* and to better quantify the effects of flooding on the physiology of mature *T. chinensis*. Finally, natural resource managers and restoration practitioners need to consider modification of base flows or elevation of channel form for maintaining shallow groundwater tables in riparian areas dominated by *P. deltoides* or in areas slated for riparian restoration.
CHAPTER 4: SIMILARITIES IN SOIL NITROGEN RESOURCE ACQUISITION AND ALLOCATION BY *Populus deltoides* ssp. *wislizenii* AND *Tamarix chinensis*

*Abstract:* Riparian forests are prone to biotic invasion by non-native plants. Non-native plants can alter ecosystem-level nutrient dynamics by differing from native species in key physical or physiological traits. Few studies have examined the effects of non-native species on nutrient cycling in riparian zones. This study compared the influence of native *Populus deltoides* ssp. *wislizenii* (cottonwood) and non-native *Tamarix chinensis* (salt cedar) on soil nitrogen cycling in riparian forests along the middle Rio Grande of New Mexico. This study demonstrated, perhaps for the first time, that native and non-native riparian plants of semi-arid regions consume organic forms of N, in addition to mineral forms. In addition, *T. chinensis* and *P. deltoides* were similar with respect to nitrogen preferences, rates of nitrogen uptake, root surface enzyme activity, and leaf stoichiometry, despite differences in mycorrhizal associations. Greater retranslocation of nutrients prior to leaf senescence by *P. deltoides* resulted in lower quality litter relative to *T. chinensis*. However, higher litter production within stands of *P. deltoides* provided increased nitrogen inputs to soils and thus supported greater pools of soil nitrogen as compared to stands of *T. chinensis*. Potential rates of net nitrogen mineralization were similar across species. Functional similarities in nitrogen acquisition and allocation between *T. chinensis* and *P. deltoides* indicate that *T. chinensis* invasion does not substantially alter ecosystem nitrogen recycling or retention.
INTRODUCTION

Riparian forests are productive, species-rich ecosystems (Gregory et al. 1991). They provide linkages for dispersal of plant seeds and animals between aquatic and terrestrial habitats (Naiman et al. 1993, Naiman and Décamp 1997), experience frequent disturbance via flooding that promotes optimal conditions for the recruitment of riparian plants (Junk et al. 1989, Mahoney and Rood 1998), and typically have elevated groundwater tables relative to upland areas. Effective seed dispersal, frequency of soil disturbance, and consistent water supply are characteristics of riparian ecosystems which not only support numerous native plant species, but also lend themselves to invasion of by non-native riparian plants (Planty-Tabacchi et al. 1996, Levine 2000, Tickner et al. 2001). Non-native plants are known to alter ecosystem-level nutrient dynamics by differing from native species in terms of biomass and productivity, tissue chemistry, plant morphology, and phenology (Ehrenfeld 2003). Despite numerous studies examining the influence of non-native species on ecosystem-nutrient cycling (see reviews by Ehrenfeld 2003, D'Antonio and Hobbie 2005), few have studied non-native riparian plants.

Improved understanding of plant species effects on nitrogen (N) cycling is of importance in N-limited systems, such as riparian forests of semi-arid regions (Adair and Binkley 2002). N-fixation by non-natives is the trait most commonly cited as the major driver of ecosystem change, particularly if a system had been void of N-fixers prior to invasion (e.g., Myrica faya in Hawaiian forests; Vitousek et al. 1987). However, the rapidity of change caused by many fast-spreading non-natives that do not fix N offers the opportunity to evaluate more subtle species effects on N cycling (D'Antonio and Hobbie 2005).
Riparian forests in the western and southwestern U.S., once dominated by native
*Populus* (cottonwood) species, are under invasion by non-native *Tamarix* (salt cedar)
species and *Elaeagnus angustifolia* L. (Russian olive). These non-natives are currently
the third and fourth most frequently occurring woody riparian plants in the region,
following native *Populus* and *Salix* (willow) species (Friedman et al. 2005). Zavaleta
(2000) estimated that comprehensive eradication and restoration of *Tamarix* dominated
areas costs $700,000 km\(^{-2}\) (in 1998 $US). In fiscal years 2004-2005 alone, the U.S.
interagency federal budget allocated almost $11 million to *Tamarix* control (Simberloff et
al. 2005). Clearly, the management of non-native plants in the western and southwestern
U.S. poses significant economic considerations.

There is much debate in the literature regarding which species traits or ecosystem
processes are most important for allowing invasions to occur (see review by Cronk and
Fuller 1995) and multiple traits or processes may interact to promote invasion (D'Antonio
and Hobbie 2005). Characteristics that favor *Tamarix* species over native species include
greater tolerance of drought and deeper groundwater table elevation (Brock 1994, Horton
et al. 2001a, 2001c, 2001b), the ability to use either surface water or groundwater
resources (Di Tomaso 1998), tolerance of salinity (Everitt 1980, Di Tomaso 1998), and
longer duration of seeding phenology (Everitt 1980, Busch and Smith 1995, Di Tomaso
1998). Unlike *E. angustifolia*, *Tamarix* species do not fix N, and therefore rely on access
to ground water and soils for N acquisition.

Marler et al. (2001) provided evidence of competition for mineral nutrients
between *Tamarix ramosissima* (salt cedar), *Populus fremontii* (Fremont cottonwood), and
*Salix gooddingii* (Goodding’s willow) seedlings. Seeds of all three species were sown
together and treated with uniformly increasing concentrations of solution containing 
NH$_4^+$-N, NO$_3^-$-N, and PO$_4^{3-}$-P. The results of the experiment showed that only *T.
ramossisima* significantly increased stem number and total biomass at the highest level of 
fertility (556 mmol m$^{-3}$ NH$_4^+$-N, 556 mmol m$^{-3}$ NO$_3^-$-N, and 323 mmol m$^{-3}$ PO$_4^{3-}$-P). 
However, *P. fremontii* was significantly taller, produced more leaves, and had greater 
biomass production than either *T. ramosissima* or *S. gooddingii* at all nutrient 
concentrations. Sher et al. (2002) found that *Populus deltoides* ssp. *wislizenii* (Rio 
Grande cottonwood) seedlings also grew taller and faster than neighboring seedlings of 
*Tamarix ramosissima* in stands that established concurrently. Furthermore, *T.
ramossisima* growth was negatively correlated with neighbor densities of *P. deltoides* and 
*Salix exigua* (Sher et al. 2002). Sher et al. (2000) also found that increasing densities of 
*P. deltoides* seedlings has been shown to reduce concentrations of N in leaf tissues of co-
eexisting *P. deltoides* and *T. ramosissima* seedlings. The results of these experiments 
indicate that (1) interspecific competition between *Tamarix* and *Populus* species exists, 
(2) *Populus* seedlings have a competitive advantage over *Tamarix* seedlings that establish 
during the same recruitment event, and (3) *Tamarix* seedlings are more N-demanding 
than *Populus* seedlings.

No studies have assessed the relative abilities of mature *Populus* and *Tamarix*
trees to consume and allocate N resources. It also is unknown whether key physiological 
traits of these species differ to a degree that could alter ecosystem-level nitrogen cycling. 
The first objective of this study was to determine whether differences in soil N 
concentration and net N mineralization existed between mature stands of *Tamarix 
chinensis* (salt cedar) and *Populus deltoides* ssp. *wislizenii* (Rio Grande cottonwood)
located along the middle Rio Grande of New Mexico. This study did not address competition for nitrogen resources directly; since study sites were dominated either by *P. deltoides* or *T. chinensis* instead of being mixed stands of both species. However, further information about the relative consumption and use of nitrogen by these species would help to determine whether competition for nitrogen may be another factor facilitating the spread of *T. chinensis*. Secondary study objectives were to compare plant tissue production and species-specific patterns of N acquisition and allocation to discern mechanisms contributing to potential differences in soil N resources. Effects of flood regime on soil N cycling also were studied because four of the eight sites included in this study experienced periodic flooding during the study period. These patterns are not discussed herein, but rather are the focus of Chapter 3.

METHODS

*Study site description and history*

The middle Rio Grande of New Mexico extends from the Otowi gauge in the north to the Elephant Butte gauge in the south (Fig. 1). It is approximately 320 km in length, beginning at an altitude of 1672.9 m and ending at an altitude of 1262.2 m. The drainage area included within this reach of river is roughly 39,200 km².

The middle Rio Grande is slightly sinuous with straight, meandering, and braided reaches that traverse three major biotic communities: Great Basin grassland, semi-desert grassland, and Chihuahan Desert scrub (Brown and Lowe 1980). The floodplain varies in width from less than 1.5 km to about 10 km. Levees or natural bluffs generally limit
the extent of the riparian forest, with the greatest widths reaching 4-5 km in the south.

Floodplain soils are Typic Ustifluvents of the Gila-Vinton-Brazito association with 0-2% slope. These soils are stratified sandy clay loam over sandy, mixed calcareous alluvium.

**Figure 1.** Map of study sites along the middle Rio Grande of New Mexico. Circles indicate study sites dominated by *P. deltoides*, while triangles indicate study sites dominated by *T. chinensis*. Solid and hollow symbols represent flood and non-flood sites, respectively.

Three diversion dams regulate river flow throughout the middle Rio Grande. The flow in most reaches is perennial, although some reaches at or below the town of Bernardo cease to flow in years of drought. Peak flows occurred historically at the end of May to early June, concurrent with snowmelt from headwater sources in the San Juan
Mountains of Colorado. Flooding has been less frequent since the installation of dams on the Rio Grande, but intense summer thunderstorms and dissipating tropical storms in fall still induce peaks that sometimes result in overbank flood events (Bullard and Wells 1992). These events occur primarily in the south below the confluences of the Rio Puerco and Rio Salado with the Rio Grande. The climate of the region is classified as arid to the south and semiarid to the north (Tuan et al. 1973). Mean annual precipitation ranges from 31 cm in the north to 20 cm in the south. Mean monthly air temperatures in July range from 21-24 °C, while minimum monthly air temperatures are about 4 °C throughout the valley. Roughly 50% of annual precipitation is supplied by summer monsoonal storm events, although the proportion can vary considerably from year to year.

Plant communities of riparian forests of the middle Rio Grande were historically dominated by native *Populus deltoides* ssp. wislizenii Eckenwalder (Rio Grande cottonwood) interspersed with native understory species, such as *Salix exigua* Nutt (coyote willow), *Baccharis glutinosa* Pers. (seep willow), *Amorpha fruticosa* L. (false indigo bush), and *Forestiera neomexicana* A. Gray (New Mexico olive) (Crawford et al. 1993). Introduction of non-native species since the early 20th century has altered the riparian community composition. Invasion by *Elaeagnus angustifolia* L. (Russian olive) along the middle Rio Grande prevails in the north, while *Tamarix chinensis* Lour. (salt cedar) is prevalent in the south. *E. angustifolia* typically lines the banks of the Rio Grande, but also is found in the understory of stands dominated by *P. deltoides*. *T. chinensis*, in addition to *E. angustifolia*, is present in the understory of some *P. deltoides* stands in the north, but forms monocultures in the south. *E. angustifolia* is occasionally
cultivated in far southern New Mexico and Arizona but is generally not abundant along the Rio Grande below ca.175 km south of Albuquerque, New Mexico and is not widely naturalized south of the Mogollon Rim, Arizona (as reviewed by Katz and Shafroth 2003). In contrast, *Tamarix* species are continuing to spread northward to Montana and Canada and southward into northwestern Mexico (as reviewed by Di Tomaso 1998).

I selected eight study sites located as far north as the city of Albuquerque (35° 05’ N, 106° 40’ W) and as far south as the Bosque del Apache National Wildlife Refuge (NWR; 33° 46’ N, 106° 52’ W; Figure 1). Four of these sites were dominated by *P. deltoides*, which ranged in age from roughly 35-61 years at the start of the study (P. Jacobson, pers. comm.; Table 1). The other four sites were dominated by *T. chinensis*, which ranged in age from roughly 16-26 years at the start of the study (V. Beauchamp, pers. comm.; Table 1). Two of the *P. deltoides* sites and two of the *T. chinensis* sites experienced one to three flood events during the period of study. All flood sites were inundated in spring 2001. Flood sites at the Bosque del Apache NWR were inundated in fall 2003 and spring 2004. Flood inundation varied across events, ranging from 1-4 weeks in duration. Flooding never occurred at non-flood study sites. Non-native vegetation (i.e., *E. angustifolia* and *T. chinensis*) was present in the understory of *P. deltoides* study sites located in Albuquerque (Cental Albuquerque and South Valley Albuquerque) throughout most of the study, but were mechanically cleared from these sites in winter 2003 and spring 2004. *P. deltoides* sites in the south either had an understory that included native and non-native vegetation (i.e., *S. exigua*, *B. glutinosa*, *E. angustifolia*, and *T. chinensis*) or lacked an understory community. Non-flood *T. chinensis* sites were mixed communities that included *Distichlis spicata* (salt grass),
Prosopis pubescens (screwbean mesquite), Atriplex spp. (four-wing saltbush), and Lycium spp. (wolfberry). Monocultures characterized periodically flooded T. chinensis sites in the south.

Table 1. Study site plant community characteristics.

<table>
<thead>
<tr>
<th>Site</th>
<th>Dominant Vegetation</th>
<th>Understory Vegetation†</th>
<th>Year of Stand Recruitment‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Central Albuquerque</td>
<td><em>P. deltoides</em> ssp. witsizenii</td>
<td><em>T. chinensis, Elaeagnus angustifolia</em></td>
<td>1966</td>
</tr>
<tr>
<td>South Valley Albuquerque</td>
<td><em>P. deltoides</em> ssp. witsizenii</td>
<td><em>T. chinensis, E. angustifolia</em></td>
<td>1952</td>
</tr>
<tr>
<td>Belen</td>
<td><em>P. deltoides</em> ssp. witsizenii</td>
<td><em>E. angustifolia</em></td>
<td>1952</td>
</tr>
<tr>
<td>Bernardo</td>
<td><em>T. chinensis</em></td>
<td><em>Lycium spp., Distichlis spicata, Chrysothamnus spp.</em></td>
<td>1985</td>
</tr>
<tr>
<td>Sevilleta NWR</td>
<td><em>T. chinensis</em></td>
<td><em>D. spicata, Prosopis pubescens, Atriplex spp.</em></td>
<td>1975</td>
</tr>
<tr>
<td>Bosque del Apache NWR 1</td>
<td><em>P. deltoides</em> ssp. witsizenii</td>
<td><em>Salix exigua, E. angustifolia</em></td>
<td>1940</td>
</tr>
<tr>
<td>Bosque del Apache NWR 2</td>
<td><em>T. chinensis</em></td>
<td>None</td>
<td>1980</td>
</tr>
<tr>
<td>Bosque del Apache NWR 3</td>
<td><em>T. chinensis</em></td>
<td>None</td>
<td>1980</td>
</tr>
</tbody>
</table>

† Understory vegetation at Central and South Valley Albuquerque study sites were cleared in Spring 2004 and Winter 2003, respectively.
‡ Year of stand recruitment was estimated from tree ring samples (n = 3-7) for each site that were measured by P. Jacobsen or V. Beauchamp (unpub. data).
Inorganic and organic soil nitrogen

An 80 m x 80 m study plot was delineated at each study site. Four transects ran from the center of each plot to a corner in each of the cardinal directions. Three soil sampling points were established at 10 m intervals along each transect. Soils were collected seasonally from November 2002 through July 2004 using a 2.2 x 30 cm stainless steel soil probe (AMS Inc., American Falls, ID, U.S.A.) fitted with a butyrate plastic liner that was discarded after sampling along each transect. Soils collected along each transect were pooled and homogenized within polyethylene bags. Samples were stored at 4 °C until further processing could be conducted.

In the laboratory, samples were sieved (2 mm) to remove roots and organic debris. Gravimetric field water content was measured by drying 10-20 g sub-samples of soil for 24 hours at 100 °C and subtracting the sample dry weight from its initial weight. Another set of pre-weighed soil sub-samples was saturated with deionized water, drained for 30 minutes, and dried for 24 hours at 100 °C. Water holding capacity was calculated by subtracting the dry weight from the wet weight of each sample and dividing the remainder by the dry weight. Two more sets of soil sub-samples, weighing 10 g by dry mass, were used to measure soil concentrations of NO$_3^-$-N and NH$_4^+$-N and potential rates of net N mineralization. Sub-samples used to measure soil N concentrations were immediately extracted with 100 ml of 2M KCl. Net N mineralization sub-samples were brought to 50% water holding capacity with deionized water on a weekly basis and incubated at 20 °C for ten weeks. Nitrogen within the samples was extracted with 100 ml of 2M KCl at the end of the incubation. KCl extractions were analyzed for NH$_4^+$-N and NO$_3^-$-N on a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, New
York, U.S.A.) using Technicon Industrial Methods 98-70W and 100-70W. Net N mineralization was calculated as the sum of the final concentration of NO$_3^-$-N and NH$_4^+$-N minus the initial concentration. Repeated measures ANOVA was used to compare soil inorganic N concentrations and potential rates of net N mineralization across species and flood regime.

Soil samples were collected in September 2005 to determine the concentration of soil proteins and amino acids, as well as rates of proteolysis. Three samples were collected within 1 m from the base of three study trees at each site using a 2.2 x 30 cm stainless steel soil probe (AMS Inc., American Falls, ID, U.S.A.). Samples from each tree were homogenized and stored at 4 °C until further processing could be conducted within 24 hours of sample collection. In the laboratory, samples were sieved (2 mm) to remove roots and organic debris. Protein and amino acid concentrations were determined from modified protease and ninhydrin assays based upon the methods described in Watanabe and Hayano (1996) and Rosen (1957). Three replicates of 3 g sub-samples were amended with 1.5 ml of 1% bovine serum albumin solution and 4.5 ml of 50 mM sodium bicarbonate buffer. These samples were used to determine potential rates of proteolysis. Control replicates received 6 ml of sodium bicarbonate buffer. Samples were vortexed for 2 minutes and then centrifuged for 5 minutes at 3500 rpm. A 1.5 ml aliquot was immediately removed from the supernatant and centrifuged at 10,000 G for 5 minutes. Aliquots were then placed on ice to stop any further reaction until analysis for initial concentrations ($T_0$) of soluble proteins, amino acids, and ammonium. Control and amended replicates were incubated for 1-1.5 hrs at 20 °C, during which time samples were mixed using an orbital shaker set to 30 rpm. Exact incubation times for all
replicates were recorded. These replicates (T₁) were processed after incubation in the same manner described for T₀ replicates. The difference in the concentrations of proteins, amino acids, and ammonium between T₁ and T₀ control and amended replicates were used to calculate rates of proteolysis. Protein concentrations were measured by adding 50 µl of protein reagent (500-0006, BioRad Laboratories Inc., Hercules, CA, U.S.A.) to 200 µl of standards, blanks, and T₀ and T₁ aliquots within a 96-well microplate. Absorbance of samples was read at 595 nm on a microplate reader (VersaMax Model, Molecular Devices Corporation, Milpitas, CA, U.S.A.) and compared to a standard curve. Ammonium concentrations were determined by adding 40 µl of ammonia salicylate reagent (1:5 reagent to deionized water solution; 23953-66, Hach Europe, Düsseldorf, Germany) and 40 µl of ammonia cyanurate reagent (1:5 reagent to deionized water solution; 23955-66, Hach Europe, Düsseldorf, Germany) to 200 µl of standards, blanks, and T₀ and T₁ aliquots within a 96-well microplate. Sample absorbance was read at 610 nm and compared to NH₄Cl standards made from a 1 mM stock solution. Further processing of supernatant from control and amended samples was required to determine amino acid concentration. A 0.5 ml aliquot of supernatant was placed into a 1.5 ml microcentrifuge tube, to which 0.25 ml of 1 M acetate-cyanide buffer and 0.25 ml of 3% ninhydrin solution were added. Samples were capped and placed in an 80 °C water bath for 10 minutes. Three replicates of 100 µl aliquots were extracted from each microcentrifuge tube and placed on a 96-well microplate. Amino acid concentration was measured by reading sample absorbance at 570 nm, which was compared to leucine standards made from 0.4 mM stock solution. Initial concentrations of soluble proteins and amino acids in control replicates were averaged for each study tree and compared.
across species and flood regime using repeated measures ANOVA, with time as the repeated measure. Proteolytic rates were averaged for each study tree and compared using a univariate general linear model (GLM), with treatment (i.e., control vs. amended samples) and species as fixed factors.

Root biomass, rates of root N uptake, and root surface enzyme activity

Soil samples were collected in April 2005 to determine the biomass of roots at three study trees within each site. Three soil cores were collected within 1 m of the base of each tree using an 8 x 14 cm stainless steel soil corer (AMS Inc., American Falls, ID, U.S.A.). Roots were removed from soils, rinsed with deionized water, and separated into categories based on size (< 2 mm diameter, > 2 mm diameter) and activity (live or dead). Samples were dried at 60 °C for 48 hours and weighed. Fine root (< 2 mm) biomass data were transformed (log [x + 1]) and compared across species and flood regime using a univariate GLM.

Rates of organic and inorganic N uptake by P. deltoides and T. chinensis roots were estimated using the methodology described in Treseder and Vitousek (2001). Freshly excised roots were incubated in a control solution (no N addition) and 100 μM solutions of $^{15}$N-labeled KNO$_3$, NH$_4$Cl, and glycine. Concentrations of $^{15}$N labeled solutions were comparable to maximum measured concentrations of extractable soil NO$_3^-$-N and NH$_4^+$-N (142 μM and 107 μM, respectively). Assay samples were collected in the same manner as samples collected to measure root biomass. Assays were conducted in early September of 2004 and 2005 within 48 hours of root sample collection. Roots were collected from three study trees in 2004 and five study trees in 2005. Roots were dried at
60 °C for 48 hours post-incubation, weighed, and ground to a homogenous powder. Stable isotope analysis was conducted at the University of California-Davis Stable Isotope Laboratory. Root N uptake rates in excess of control samples were compared across species and flood regime using a multivariate GLM, with year as a random factor. Data for NO$_3^-$-N and NH$_4^+$-N uptake were transformed (log $[x + 1]$) prior to analysis. Separate multivariate GLM models were run to isolate the effects of species and flood regime across nutrient parameters for each year of data. Repeated measures ANOVA was not utilized due to unequal sample sizes across years. Uptake ratios of NH$_4^+$-N: glycine, NH$_4^+$-N:NO$_3^-$-N, and glycine:NO$_3^-$-N for September 2005 were calculated, transformed (log $[x+1]$), and compared using a multivariate GLM with species and flood regime as fixed factors. Growing season inorganic N uptake by roots was estimated from September 2005 measures of hourly uptake and root biomass for each site. Data from 2004 were not included in growing season estimates, since fewer replicates per site were assayed. Growing season net N mineralization was estimated from measures of daily rates of net N mineralization for 2003-2004 and the bulk density of soil samples. Linear regression was used to determine the relationship between growing season estimates of net N mineralization and root inorganic N uptake.

Root extracellular enzyme activities of L-leucine aminopeptidase and alkaline phosphatase were measured in September 2005 following the methodology of Sinsabaugh et al. (2003). For each assay, three replicate sub-samples of fine roots (20-30 mg) from three study trees were placed within nine wells of a 12-well microplate. Roots were covered with 800 µl of 50 mM bicarbonate buffer, pH 8, and 200 µl of substrate solution (10 µM of 4-MUB-phosphate or L-leucine-7-amino-4-methylcoumarin). The
remaining three wells served as a negative control (roots plus 1 ml of buffer), a quenched standard (roots plus 1 ml of substrate solution), and a reference standard (800 μl of buffer plus 200 μl of substrate solution). Roots were incubated at 20 °C for 30 minutes on a shaker table set to 80 rpm. Aliquots of 200 μl were withdrawn from each well and placed into a 96-well microplate. Fluorescence was measured using a microplate fluorometer (UV-1601, Shimadzu Corporation, Kyoto, Japan) with 355 nm excitation and 460 nm emission filters. Root material from each well was dried and weighed. Activity rates for L-leucine aminopeptidase and phosphatase were averaged for each study tree, transformed (log [x+1]), and compared using a multivariate GLM with species and flood regime as fixed factors. Ratios of L-leucine aminopeptidase:phosphatase activities also were included as dependent variables within the model.

Leaf and litter production

Leaf area index (LAI) was measured each month throughout the growing season in 2001-2003 using a LAI-2000 sensor (Li-Cor Inc., Lincoln, NB, U.S.A.). The sensor was placed at the ground surface for all below-canopy measurements. Above canopy measurements were made either from a ladder at sites equipped with micrometeorological towers or from levee roads adjacent to study sites. LAI data were collected from five locations at each study site. Because of rapidly changing light conditions before dawn and after sunset, above-canopy measurements were taken both before and after the associated below-canopy measurements. In addition, the first plot measured at post-dawn or pre-sunset was repeated at the end of the sequence. Stem area index (SAI) was measured at T. chinensis sites after defoliation in winter of each year to
measure the contribution of SAI to LAI at these sites. The leaf area at *P. deltoides* sites was calculated to be twice the measured LAI. SAI was subtracted from LAI for *T. chinensis* sites. The resulting value was multiplied by \( \pi \) to reflect the cylindrical geometry of *T. chinensis* leaves and represented the leaf area of *T. chinensis* sites. Repeated measures ANOVA was used to compare mean values of LAI for June and August of 2001 and 2002 across species and flood regime, with time as the repeated measure. Linear regression was used to determine the relationship between mean rates of root NO\(_3^–\)-N uptake for 2004-2005 and mean values of LAI for 2001-2003.

Litterfall was collected from fall 2004 through spring 2005 in 0.17 m\(^2\) mesh traps placed under 3-5 study trees at both *P. deltoides* and *T. chinensis* sites. Litter samples were dried at 60 °C for 48 hours, after which time the mass of litter production was recorded for individual species of vegetation at each site. Data on litter production of *P. deltoides* and *T. chinensis* was transformed (log \( [x + 1] \)) and compared using a univariate GLM, with species and flood regime as fixed factors.

*Stoichiometry of roots, leaves, and litter*

Leaves exposed to full sunlight were collected in May, July, and September 2004 from the upper canopy of three study trees at each site. A slingshot and a lead weight tied to fishing line were used to sample leaves at *P. deltoides* sites, while leaves at *T. chinensis* sites were collected with a telescoping tree pruner. Fine roots were collected in April and September 2005 using the same procedures previously described for root sampling. Sub-samples of litter collected for production measurements also were used to quantify carbon (C), nitrogen (N), and phosphorus (P) content. All plant tissue samples
were dried at 60 °C for 48 hours, ground to a homogenous powder, and stored in a desiccator until analyzed for C, N, and P content. Sub-samples were analyzed for C and N content via high temperature combustion using a ThermoQuest CE Instruments NC2100 Elemental Analyzer (ThermoQuest Italia, S.p.A., Rodano, Italy). Total P content of plant tissues was measured by combusting sub-samples at 500 °C for one hour, adding 100 ml of 1N HCl to each sample, and incubating samples for 30 minutes at 80 °C (Stelzer and Lamberti 2001). Dilution aliquots of extracts were analyzed for PO₄⁻³-P on a Technicon AutoAnalyzer II (Technicon Industrial Systems, Tarrytown, New York, U.S.A.) using Technicon Industrial Methods 94-70W. The % N, C, or P of soil samples were transformed to molar concentrations, which were used to compared C:N, C:P, and N:P ratios. Data on leaf and root stoichiometry were lumped across sampling dates. Differences in root stoichiometry were compared across species and flood regime using Kruskal-Wallis H tests. Leaf and litter stoichiometry were compared using a multivariate GLM, with species and flood regime as fixed factors. Mean values of litter % N were multiplied by the sum of litterfall for each study site to determine the cumulative N inputs to soils via litterfall and the N use efficiency ratio (i.e., biomass:N content ratio of litter) of each species. Nitrogen inputs to soils from *P. deltoides* and *T. chinensis* litterfall was transformed (log [x + 1]) and compared using a univariate GLM, with species and flood as fixed factors. The N use efficiency ratio of *P. deltoides* and *T. chinensis* was compared using a Mann-Whitney U test.
Mycorrhizal colonization of roots

Roots were collected in February 2005 within 1 m of the base of five study trees using procedures previously described for root sampling. Samples were collected as far away from other species of herbaceous and woody plants or at greater depths (~ 50 cm) where grasses were present. Fine roots were cleaned of soil particles and preserved in a 70% ethanol solution. Samples were processed at the U.S. Geological Survey, Fort Collins Science Center to determine the extent of root colonization by arbuscular (AM) and ectomycorrhizal (EM) fungi. Roots were cleared in 5% KOH and stained in trypan blue and sudan IV (Koske and Gemma 1989). Root colonization by AM and EM fungi was assessed using the gridline intersect method (Jacobson 2004). Percentages of root colonization were transformed (arcsine-square root) and compared across species and flood regime using a multivariate GLM. All statistical analyses in this study were performed using SPSS 12.0.1 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

Inorganic and organic soil nitrogen

Soils from *P. deltoides* sites had significantly greater concentrations of inorganic N as compared to *T. chinensis* sites (RMANOVA, NO$_3^-$-N: df = 1, $F = 4.74$, $p = 0.04$, Fig. 2a; NH$_4^+$-N: df = 1, $F = 128.67$, $p < 0.001$, Fig. 2b), despite fluctuations in soil inorganic N at both sites over time (RMANOVA, NO$_3^-$-N: df = 7, $F = 24.48$, $p < 0.001$; NH$_4^+$-N: df = 7, $F = 38.86$, $p < 0.001$). Mean NO$_3^-$-N and NH$_4^+$-N concentrations at *P. deltoides* sites ranged from 2.4-7.9 µg g$^{-1}$ soil and 2.0-7.3 µg g$^{-1}$ soil, respectively. Mean NO$_3^-$-N and NH$_4^+$-N concentrations at *T. chinensis* sites ranged from 1.6-5.2 µg g$^{-1}$ soil.
and 0.7-2.8 3 μg g⁻¹ soil, respectively. Potential rates of net N mineralization also varied through time (RMANOVA, df = 7, F = 20.84, p < 0.001; Fig. 2c). However, potential rates of net N mineralization across species were statistically similar (RMANOVA, df = 1, F = 3.93, p = 0.06), and ranged from -0.01-0.12 μg g⁻¹ soil d⁻¹ at P. deltoides sites and 0.03-0.13 μg g⁻¹ soil d⁻¹ at T. chinensis sites.

Concentrations of soil proteins did not differ across species, but amino acid concentrations were significantly greater at P. deltoides sites relative to T. chinensis sites (RMANOVA, proteins: df = 1, F = 0.001, p = 0.97, Fig. 3a; amino acids: df = 1, F = 23.92, p < 0.001, Fig. 3b). Soil protein concentrations were significantly greater in September vs. February (RMANOVA, df = 1, F = 223.25, p < 0.001), while concentrations of amino acids were similar across sampling dates.

Rates of proteolysis, amino acid deamination, and ammonium production for control samples were similar across species (Fig. 4). However, potential rates of proteolysis and amino acid deamination were greater for amended samples compared to control samples (multivariate GLM, proteins: df = 1, F = 105.08, p < 0.001; amino acids: df = 1, F = 151.82, p < 0.001), suggesting that the in situ proteolytic capacity of soils at P. deltoides and T. chinensis sites was substrate limited. Mean potential rates of proteolysis were 755 μg g⁻¹ soil hr⁻¹ for soils from P. deltoides and T. chinensis sites, while potential rates of amino acid deamination were 925 nmol g⁻¹ soil hr⁻¹.
**Figure 2.** Mean soil (a) NO$_3^-$-N and (b) NH$_4^+$-N concentration and (c) mean rates of net nitrogen mineralization at study sites dominated by *P. deltoides* (circles) or *T. chinensis* (triangles). Error bars represent ± 1 SE of the mean NO$_3^-$-N or NH$_4^+$-N concentration on each date; n = 16.
Figure 3. Mean water extractable soil (a) protein and (b) amino acid concentration for February and September 2005 at study sites dominated by *P. deltoides* (white bars) or *T. chinensis* (grey bars). Error bars represent ± 1 SE of the mean protein or amino acid concentration; n = 12. An asterisk above a set of bars represents a significant difference (p < 0.05) between species on each date.
**Figure 4.** Mean proteolytic rates, ammonium deamination rates, and ammonium production for September 2005 at study sites dominated by *P. deltoides* or *T. chinensis*. Error bars represent ± 1 SE of the mean rate; n = 12. Common letter superscripts denote statistical difference at p ≥ 0.05.

*Root biomass, rates of root N uptake, and root surface enzyme activity*

Stands of *P. deltoides* and *T. chinensis* had similar quantities of root biomass within the upper 20 cm of soils (Table 2). Root surface activities of L-leucine aminopeptidase and phosphatase enzymes also were similar across species (Table 2). Phosphatase activities were over 75% greater than L-leucine aminopeptidase activities across species, resulting in L-leucine aminopeptidase:phosphatase activity ratios ≤ 0.25 (Table 2).
Table 2. Production of roots, litter, and leaves, litterfall N inputs to soils, root nutrient preference ratios, and root surface enzyme activities at *P. deltoides* and *T. chinensis* sites. Data represent means ± 1 SE. Nitrogen uptake ratios (n = 20) and root surface enzyme activity and ratios (n = 12) represent data from September 2005. LAI values represent data collected from 2001-2003 (n = 20). Litter production data represent the cumulative quantity of litter collected from October to February of 2004-2005 (*P. deltoides*, n = 20; *T. chinensis*, n = 12). Litterfall production values were multiplied by mean values of % N per gram leaf to obtain litterfall N inputs to soils (*P. deltoides*, n = 20; *T. chinensis*, n = 12). Root biomass values represent data from April 2005 (n = 12). Entries sharing common letter superscripts denote between-species statistical difference at p ≥ 0.05.

<table>
<thead>
<tr>
<th>Factor</th>
<th><em>P. deltoides</em></th>
<th><em>T. chinensis</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>NH₄⁺-N:Glycine</td>
<td>3.25 ± 0.49ᵃ</td>
<td>3.74 ± 0.35ᵃ</td>
</tr>
<tr>
<td>NH₄⁺-N:NO₃⁻-N</td>
<td>49.67 ± 9.87ᵇ</td>
<td>23.39 ± 4.58ᵇ</td>
</tr>
<tr>
<td>Glycine:NO₃⁻-N</td>
<td>21.17 ± 5.10ᵇ</td>
<td>6.02 ± 0.76ᵃ</td>
</tr>
<tr>
<td>LAP† (µmol g⁻¹ root hr⁻¹)</td>
<td>0.60 ± 0.14ᵃ</td>
<td>0.51 ± 0.12ᵃ</td>
</tr>
<tr>
<td>PHOS† (µmol g⁻¹ root hr⁻¹)</td>
<td>2.40 ± 0.37ᵃ</td>
<td>3.25 ± 0.50ᵃ</td>
</tr>
<tr>
<td>LAP:PHOS</td>
<td>0.25 ± 0.05ᵃ</td>
<td>0.16 ± 0.03ᵃ</td>
</tr>
<tr>
<td>LAI‡</td>
<td>5.09 ± 0.13ᵃ</td>
<td>3.66 ± 0.20ᵇ</td>
</tr>
<tr>
<td>Litter production (g m⁻²)</td>
<td>384 ± 53ᵃ</td>
<td>156 ± 24ᵇ</td>
</tr>
<tr>
<td>Litterfall N inputs (g m⁻²)</td>
<td>1.80 ± 0.23ᵃ</td>
<td>1.06 ± 0.19ᵇ</td>
</tr>
<tr>
<td>Root biomass (g m⁻²)</td>
<td>5.33 ± 0.85ᵃ</td>
<td>6.63 ± 0.96ᵃ</td>
</tr>
</tbody>
</table>

†LAP and PHOS stand for leucine amino peptidase and phosphotase, respectively.
‡Leaf area index.

Assays of potential¹⁵N uptake by roots indicated that *P. deltoides* and *T. chinensis* both prefer NH₄⁺-N over other forms of N (Fig. 5). Assays conducted in 2005 showed that NH₄⁺-N was taken up more rapidly than glycine by a factor of 3 (Table 2). Ammonium also was taken up 23-50 times faster than NO₃⁻-N, depending on species (Table 2). *T. chinensis* and *P. deltoides* root uptake of glycine was 6 and 21 times greater than uptake of NO₃⁻-N, respectively (Table 2). The magnitude of NH₄⁺-N uptake differed considerably by year (multivariate GLM: df = 1, F = 9.89, p < 0.01), while uptake rates
of glycine and NO$_3^-$-N were generally consistent. Roots of *P. deltoides* took up more NH$_4^+$-N than roots of *T. chinensis* in 2004 (multivariate GLM: df = 1, $F = 6.33$, p = 0.02; Fig. 5a), but NH$_4^+$-N uptake was similar across species in 2005. In contrast, roots of *T. chinensis* took up more NO$_3^-$-N than roots of *P. deltoides* in 2005 (multivariate GLM: df = 1, $F = 14.78$, p < 0.001; Fig. 5b), but NO$_3^-$-N uptake was similar across species in 2004.

**Figure 5.** Mean uptake rates of $^{15}$NO$_3^-$-N, $^{15}$NH$_4^+$-N, and $^{15}$N-glycine by excised *P. deltoides* (white bars) and *T. chinensis* (grey bars) roots in September (a) 2004 (n = 12) and (b) 2005 (n = 20 for *P. deltoides*; n = 18 for *T. chinensis*). Error bars represent ± 1 SE of the mean uptake rate for each form of nitrogen. Asterisks above a set of bars represent a significant between-species difference (* p < 0.05, *** p < 0.001).
Estimated potential rates of net N mineralization throughout the growing season were inversely correlated with estimated inorganic N uptake by roots \( y = 118.97 - 0.84x \), \( n = 8, r^2 = 0.24, p = 0.007; \) Fig. 6). The contribution of net N mineralization to riparian plant nitrogen requirement was calculated by quantifying and comparing the annual net quantity of inorganic N made available through N mineralization and the annual consumption of inorganic N by stands of *P. deltoides* and *T. chinensis*. These estimates showed that N mineralization provided, on average, 91 and 131% of the estimated N taken up at sites dominated by *P. deltoides* and *T. chinensis*, respectively. Estimated N mineralization supported less than 50% of plant N uptake only at the *P. deltoides* site within the Bosque del Apache NWR.

![Graph](image)

**Figure 6.** Relationship between growing season estimates of net N mineralization and root inorganic N uptake. Data represent means (2003-2004 for net N mineralization; 2005 for root uptake) for *P. deltoides* (circles) and *T. chinensis* (triangles) flood (solid symbols) and non-flood (hollow symbols) sites. Error bars represent ± 1 SE of the mean rate of net N mineralization and root inorganic N uptake.
Leaf and litter production

LAI values at *P. deltoides* sites were significantly greater than at *T. chinensis* sites (RMANOVA: df = 1, \( F = 11.01, p < 0.01 \); Table 2). LAI values were higher for both species in 2001 vs. 2002, the latter of which was characterized by drought (RMANOVA: df = 3, \( F = 23.20, p < 0.001 \)). LAI was inversely correlated with site-based growing season estimates of root NO\(_3\)\(^-\)-N uptake (\( y = 5.78 - 0.05 x, n = 8, r^2 = 0.52, p < 0.001 \); Fig. 7), but showed no relationship with root uptake of other forms of N. Litter production also was significantly greater at *P. deltoides* sites relative to *T. chinensis* sites (univariate GLM: df = 1, \( F = 30.25, p < 0.001 \); Table 2).

**Figure 7.** Relationship between rates of root NO\(_3\)\(^-\)-N uptake over a growing season and leaf area index (LAI). Data represent site means (2001-2003 for LAI; 2004-2005 for NO\(_3\)\(^-\)-N uptake) for stands of *P. deltoides* (solid circles) and *T. chinensis* (hollow circles).
Stoichiometry of roots, leaves, and litter

*P. deltoides* had greater % C and % P in root tissues relative to *T. chinensis*, but lower % N (Kruskal-Wallis H, C: df = 1, $X^2 = 4.937$, $p = 0.026$; N: df = 1, $X^2 = 7.714$, $p = 0.005$; P: df = 1, $X^2 = 6.923$, $p = 0.009$; Table 3). Differences in C, N, and P content resulted in higher C:N and lower N:P ratios in *P. deltoides* roots compared to *T. chinensis* roots (Kruskal-Wallis H, C:N: df = 1, $X^2 = 17.970$, $p < 0.001$; N:P: df = 1, $X^2 = 10.914$, $p = 0.001$; Table 3). Leaf stoichiometry was similar across species (Table 3). Percentages of C, N, and P were all significantly greater in litter at *T. chinensis* sites relative to litter at *P. deltoides* sites (multivariate GLM, C: df = 1, $F = 16.84$, $p = 0.001$; N: df = 1, $F = 8.36$, $p = 0.01$; P: df = 1, $F = 5.77$, $p = 0.03$; Table 3). *T. chinensis* litter thus had lower C:N and C:P ratios than *P. deltoides* litter, but higher N:P ratios (multivariate GLM, C:N: df = 1, $F = 7.38$, $p = 0.01$; C:P: df = 1, $F = 5.34$, $p = 0.03$; Table 3).

The N use efficiency ratio of *P. deltoides* litter was significantly greater than that of *T. chinensis* litter (Mann-Whitney, $U_{45,000} = 0.004$), with means of 216 ± 7 and 160 ± 11, respectively. Nitrogen inputs to soils via litterfall also were greater at *P. deltoides* vs. *T. chinensis* sites (univariate GLM: df = 1, $F = 7.46$, $p = 0.01$; Table 2). Greater litterfall at *P. deltoides* sites supported greater N inputs to soils by compensating for the effect of a lower %N in *P. deltoides* litter relative to that of *T. chinensis*. 

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Table 3. Stoichiometry of root, leaf, and litter tissues. Data represent mean values for each factor ± 1 SE. Data for roots represent means across two sampling dates during the growing season of 2005 (n = 12). Data for leaves represent means across three sampling dates during the growing season of 2004 (n = 12). Data for litter represent means for samples collected in October 2004 (P. deltoides, n = 20; T. chinensis, n = 12). Entries sharing common letter superscripts denote between-species statistical difference at p ≥ 0.05.

<table>
<thead>
<tr>
<th>Factor</th>
<th>P. deltoides</th>
<th>T. chinensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Roots</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% C</td>
<td>38.55 ± 1.32a</td>
<td>34.59 ± 1.76b</td>
</tr>
<tr>
<td>% N</td>
<td>0.95 ± 0.03b</td>
<td>1.21 ± 0.07a</td>
</tr>
<tr>
<td>% P</td>
<td>0.14 ± 0.01a</td>
<td>0.10 ± 0.00b</td>
</tr>
<tr>
<td>C:N</td>
<td>48.72 ± 1.58a</td>
<td>34.74 ± 1.75b</td>
</tr>
<tr>
<td>C:P</td>
<td>834.91 ± 85.38a</td>
<td>909.47 ± 56.11a</td>
</tr>
<tr>
<td>N:P</td>
<td>17.38 ± 1.67b</td>
<td>27.26 ± 1.81a</td>
</tr>
<tr>
<td>Leaves</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% C</td>
<td>44.15 ± 0.14a</td>
<td>44.29 ± 0.42a</td>
</tr>
<tr>
<td>% N</td>
<td>1.27 ± 0.04a</td>
<td>1.39 ± 0.06a</td>
</tr>
<tr>
<td>% P</td>
<td>0.11 ± 0.01a</td>
<td>0.11 ± 0.01a</td>
</tr>
<tr>
<td>C:N</td>
<td>41.12 ± 1.16a</td>
<td>39.04 ± 1.87a</td>
</tr>
<tr>
<td>C:P</td>
<td>1138.20 ± 62.57a</td>
<td>1170.03 ± 55.81a</td>
</tr>
<tr>
<td>N:P</td>
<td>27.83 ± 1.36a</td>
<td>29.85 ± 0.91a</td>
</tr>
<tr>
<td>Litter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% C</td>
<td>42.47 ± 0.30b</td>
<td>44.78 ± 0.45a</td>
</tr>
<tr>
<td>% N</td>
<td>0.47 ± 0.04b</td>
<td>0.66 ± 0.05a</td>
</tr>
<tr>
<td>% P</td>
<td>0.04 ± 0.00b</td>
<td>0.05 ± 0.00a</td>
</tr>
<tr>
<td>C:N</td>
<td>111.93 ± 8.19b</td>
<td>84.22 ± 6.44a</td>
</tr>
<tr>
<td>C:P</td>
<td>3281.57 ± 236.32a</td>
<td>2595.97 ± 189.88b</td>
</tr>
<tr>
<td>N:P</td>
<td>29.34 ± 0.20b</td>
<td>30.93 ± 0.31a</td>
</tr>
</tbody>
</table>
Mycorrhizal colonization of roots

Percentages of AM and EM root colonization were significantly greater in *P. deltoides* roots compared to *T. chinensis* roots, since 94.6 ± 1.9% of *T. chinensis* roots were uncolonized (multivariate GLM, AM: df = 1, $F = 26.58$, $p < 0.001$; EM: df = 1, $F = 72.01$, $p < 0.001$; uncolonized: df = 1, $F = 175.88$, $p < 0.001$; Fig. 8). A significantly lower percentage (30.9 ± 5.2%) of *P. deltoides* roots was uncolonized. Mean AM and EM colonization of *P. deltoides* roots were 24.2 ± 4.8% and 48.3 ± 9.0%, respectively. Mean AM colonization of *T. chinensis* roots was 5.6 ± 2.0%. EM colonization was absent from *T. chinensis* roots.

![Graph showing fungal colonization](image)

**Figure 8.** Colonization by arbuscular (AM) and ectomycorrhizal (EM) fungi in roots of *P. deltoides* (white bars) and *T. chinensis* (grey bars). Error bars represent ± 1 SE of the mean percent root colonization for each species; n = 12. Asterisks above each set of bars represent a significance difference (*** $p < 0.001$) between species.
DISCUSSION

All of the variables included in this study collectively suggested that *T. chinensis* and *P. deltoides* were equally capable of acquiring and allocating N resources, but *P. deltoides* had an increased ability for biomass production per unit N. These findings supported the results of competition studies conducted on seedlings of *P. deltoides* and *T. chinensis* (Sher et al. 2000, Marler et al. 2001, Sher et al. 2002). The discussion that follows expands upon these findings in greater detail.

*Reasons for differences in pools of soil nitrogen*

Soil organic and inorganic N concentrations were significantly greater at *P. deltoides* sites relative to *T. chinensis* sites. Potential uptake rates of N by *P. deltoides* and *T. chinensis* roots were similar (Fig. 7), suggesting differences in soil N concentrations were not due to differences in nutrient uptake by plants. Two other factors influenced the differences in pools of soil nitrogen at *P. deltoides* vs. *T. chinensis* sites. First, higher quantities of litter production at *P. deltoides* sites supported greater inputs of N to riparian soils, despite lower % N in *P. deltoides* litter relative to that of *T. chinensis* (Table 2). In turn, pools of soil inorganic N were well correlated with N inputs via litter (see Chapter 3, Fig. 10). Second, *E. angustifolia* was present in the understory of most *P. deltoides* study sites. Tibbets (2005) showed that litterfall by *E. angustifolia* within stands of *P. deltoides* has been shown to explain 83% of the variation in annual soil inorganic N concentrations in some years.
Fluxes of soil N meet riparian plant demand for N

Net N mineralization is a good proxy for plant availability in N-limited systems if rates are positive throughout the growing season and provide most if not all of N required to support plant maintenance and growth (Schimel and Bennett 2004). Estimates of N mineralization, under optimal conditions, provided at least half of the N taken up within stands of P. deltoides and T. chinensis included in this study (Fig. 6). Potential rates of net N mineralization were similar across species and positive in all but one instance (Fig. 2c). These results indicated that (1) net N mineralization provided a good index of plant availability, and (2) inorganic N resources were equally available across the sites included in this study.

Concentrations of proteins and amino acids were comparable to those of mineral N (Fig. 3). Potential rates of proteolysis within soils at P. deltoides and T. chinensis sites were similar to potential rates in arctic tundra soils (0.5-3 uM g⁻¹ soil hr⁻¹, Weintraub and Schimel 2005; Fig. 4), where plants are known to take up amino acids at rates that equal or exceed those for inorganic N (Chapin et al. 1993, Kielland 1994, Raab et al. 1996, Nashölrm et al. 1998, Raab et al. 1999, Nordin et al. 2001). Therefore, amino acid supply was substantial enough to potentially provide a significant portion of N required by P. deltoides and T. chinensis that was not met by mineral N resources.

Evidence for similarities in N acquisition and allocation

Assays of root ¹⁵N uptake showed that both P. deltoides and T. chinensis indeed utilized amino acids in addition to mineral N (Fig. 5). The lack of ¹³C labeling of glycine in the uptake experiments prevented the demonstration of direct uptake of glycine by
plant roots. Potential rates of amino acid hydrolysis were high within soils derived from both *P. deltoides* and *T. chinensis* sites (Fig. 4). Thus, these species could have consumed the ammonium liberated through amino acid hydrolysis. Nonetheless, data from $^{15}$N uptake assays showed that amino acids provided a greater N resource to plants than nitrate, whether taken up directly or first hydrolyzed to ammonium. These assays also provided evidence for equal rates of organic and inorganic N uptake by roots of *P. deltoides* and *T. chinensis* (Fig. 5). Rates of root surface enzyme activity (Table 2), foliar % N, and foliar N:P ratios (Table 3) also were similar across species. These data indicated that *P. deltoides* and *T. chinensis* have comparable competitive abilities to acquire N resources.

Differences in C:N:P ratios between litter and foliage reflect the resorption of nutrients during leaf senescence, a mechanism thought to have evolved to conserve nutrients in environments with limited nutrient supply (Chapin and Kedrowski 1983, Aerts 1996, Killingbeck 1996). In addition, resorption of N and P from senescing leaves can be as important to plant nutrition as direct N and P uptake from soils (Chapin and Kedrowski 1983, Aerts 1996, Killingbeck 1996, Franklin and Ägren 2002). *P. deltoides*, on average, resorbed 37% of N and 36% of P prior to leaf senescence. The mean percentage of N (47%) and P (45%) resorption by *T. chinensis* was slightly higher than that of *P. deltoides*. However, *P. deltoides* litter had higher ratios of N use efficiency, C:N, and C:P as compared to *T. chinensis* litter. Nitrogen use efficiency is generally considered to be an indicator of the capacity of a plant to produce biomass per unit N assimilated into tissue, and is usually greater in systems that are N limited (Vitousek 1982). Although soils from *P. deltoides* sites had greater pools of soil N relative to *T.
*chinensis*, greater N use efficiency by *P. deltoides* may reflect its evolutionary history within N-limited soils.

**Nitrogen preferences by roots of *P. deltoides* and *T. chinensis***

Many species prefer ammonium, and sometimes amino acids, over nitrate when all forms are equally available (Chapin et al. 2002). These forms of nitrogen differ in terms of their carbon cost of incorporation into biomass (Chapin et al. 2002). Nitrate must first be reduced to ammonium, which in turn must be attached to a carbon skeleton for plant assimilation. The carbon cost to plants for amino acid incorporation is minimal. Species frequently show a propensity for taking up the form of N in greatest abundance (e.g., Nordin et al. 2001), despite differences in costs associated with assimilation. The results of this study showed that the preferences of N for both *P. deltoides* and *T. chinensis* followed the same progression: ammonium > glycine > nitrate (Fig. 5, Table 2).

In contrast, nitrate was most abundant within soils, followed almost equally by ammonium and amino acids (Figs. 2 and 3). Preference ratios of NH$_4^+$-N:NO$_3^-$-N were slightly higher than those reported for boreal trees (19.3 ± 5.8, as reviewed in Chapin et al. 2002). Both arctic and boreal trees, however, have lower NH$_4^+$-N:glycine preference ratios (~0.2-0.8) than those found for *P. deltoides* and *T. chinensis* (~3.0-4.0, Table 2).

Few studies have assessed the nitrogen preference ratios of *P. deltoides* and *T. chinensis*. Woolfolk and Friend (2003) examined the growth response of *P. deltoides* roots supplied with 2 mM N solution with varied NH$_4^+$-N:NO$_3^-$-N ratios (0:100, 20:80, 40:60, 60:40, 80:20, and 100:0) and found that the 20:80 NH$_4^+$-N:NO$_3^-$-N treatment promoted the greatest total root length, specific root length, and root N concentration.
Estimates of NH$_4^+$-N:NO$_3^-$-N preference ratios for roots of *P. deltoides* and *T. chinensis* from this study (Table 2) were two orders of magnitude greater than that of Woolfolk and Friend (2003). Preference ratios reported by Woolfolk and Friend (2003) may have been much lower than the ratios reported by this study because of the difference in N solution within which roots from each study were incubated (2000 μM vs. 100 μM). Results from this study showed that the greatest rate of root uptake of inorganic N occurred at the sites with the lowest rates of net N mineralization (or N availability; Fig. 6).

Leaf production across *P. deltoides* and *T. chinensis* sites was inversely correlated with nitrate uptake (Fig. 7). Nitrate was the least preferred form of N by the roots of both species, likely due to its high energetic cost of acquisition relative to ammonium and amino acids. *T. chinensis* sites that had high nitrate uptake rates also had lower concentrations of inorganic soil N and high soil C:N ratios (Chapter 2). N limitation was thus more severe at these sites, which was a factor contributing to lower leaf production.

**Mycorrhizal colonization of roots**

Plants form associations with mycorrhizal fungi as an adaptation to nutrient limitation. Mycorrhizal fungi augment the capacity for plants to acquire water and nutrients in exchange for carbon fixed through photosynthesis (Smith and Read 1997). The trade-off for increased water and nutrient acquisition is roughly 4-20% of carbon gain (Lambers et al. 1996). Several studies have shown that *Populus* species form associations with both AM and EM fungi (Vozzo and Hacskaylo 1974, Lodge 1989, Beauchamp 2004, Jacobson 2004). Jacobson (2004) found that AM colonization in stands of *P. deltoides* along the middle Rio Grande ranged from 15-45% of root intersections
surveyed, while EM colonization ranged from 47-80%. Pratt (1997) conducted a study of AM colonization within roots of *P. deltoides* and *T. chinensis* at the Bosque del Apache NWR and found similar percentages of colonization across species (~45%). However, studies in the Mojave Desert (Titus et al. 2002) and along the Verde River (Beauchamp 2004) have reported that *T. chinensis* roots were non-mycorrhizal. *P. deltoides* roots we examined were colonized by AM and EM to degrees similar to those reported by Jacobson (2004; Fig. 7). We also found low colonization by AM fungi in *T. chinensis* roots, and no colonization by EM fungi, contradicting the findings of Pratt (1997). The stand from which samples were collected by Pratt (1997) contained both *P. deltoides* and *T. chinensis*. In addition, root samples were collected from both species, situated 2 m apart, along the same transects. Therefore, it is possible that the *T. chinensis* root samples collected by Pratt (1997) also contained roots of *P. deltoides*.

Differences in mycorrhizal association between *P. deltoides* and *T. chinensis* may have promoted the differences in root stoichiometry observed across species. *P. deltoides* roots had significantly lower % N, but higher % C and % P content compared to *T. chinensis* (Table 3). These differences resulted in a lower N:P ratio within *P. deltoides* roots relative to that of *T. chinensis* roots (Table 3). AM fungi assist plants in the acquisition of P (Read 1991). Greater root colonization by AM fungi in *P. deltoides* roots (Fig. 8) may be one explanation for higher P content in *P. deltoides* vs. *T. chinensis* roots. Potential mycorrhizal effects on plant tissue nutrient content were not consistent in all cases. EM fungi have proteases and other enzymes that break down organic N compounds that can be transferred from fungus to plant (Read 1991). *T. chinensis* roots
had higher % N content than *P. deltoides* roots, but were void of colonization by EM fungi (Fig. 8).

Elevated root phosphatase activities relative to L-leucine aminopeptidase activities typically indicate P limitation (Treseder and Vitousek 2001). Phosphatases hydrolyze the ester-phosphate bonds in soil organic P, which releases the phosphate into soil solution for uptake by nearby roots or microbes. Aminopeptidases are proteases that hydrolyze the peptide bonds of proteins, releasing C and N-rich amino acids to the environment. One would expect activity rates of phosphatase and aminopeptidase to be greater in the presence of AM and EM fungi, but activity rates for both enzymes were similar for roots of *P. deltoides* and *T. chinensis* (Table 3). This fact, taken with the fact that *T. chinensis* roots had greater % N in the absence of EM fungi, suggested that mycorrhizal fungi may be more important to *P. deltoides* for the acquisition of water rather than nutrients.

**CONCLUSIONS**

This study demonstrated, perhaps for the first time, that native and non-native riparian plants of semi-arid regions can take up organic forms of N, in addition to mineral forms. *T. chinensis* and *P. deltoides* were similar with respect to N preferences and rates of N consumption, root surface enzyme activity, and leaf stochiometry, despite differences in mycorrhizal associations. However, *T. chinensis* and *P. deltoides* differed with regards to leaf production and retranslocation of nutrients prior to leaf senescence. Ratios of N use efficiency were greater in *P. deltoides* and suggested that *P. deltoides* efficiently recycles ecosystem N resources. Differences in leaf production and N inputs
to soils resulted in greater pools of soil N at *P. deltoides* sites relative to *T. chinensis* sites. However, soil N availability, as assessed via potential rates of net N mineralization and proteolysis, was similar across stands dominated by either species. Chapin et al. (1996) suggested that plant invasion induces substantial change in ecosystem processes only if non-native species are discretely different from native species in key traits. Thus, overall functional similarities between *T. chinensis* and *P. deltoides* indicated that *T. chinensis* invasion does not substantially alter ecosystem nitrogen recycling or retention.
CHAPTER 5: CONCLUSIONS AND FUTURE PROSPECTS

Riparian forests are complex systems within which biota, hydrology, and biogeochemical processes interact. This complexity creates a challenge for scientists trying to understand general mechanisms driving ecological patterns and for restoration practitioners trying to rehabilitate ecosystem structure and function. One generality often purported by scientists and restoration practitioners is the need to periodically flood riparian forests of large river systems within arid and semi-arid regions (Howe and Knopf 1991, Crawford et al. 1996, Molles et al. 1998, Ellis et al. 2002). Flooding facilitate the exchange of water, materials, and energy between rivers and their floodplains (Junk et al. 1989, Bayley 1995) that stimulates microbial respiration (Molles et al. 1998), decomposition (Ellis et al. 1999, Ellis et al. 2002), nutrient cycling (Brunet et al. 1994, Valett et al. 2005), and, in some cases, leaf production (Tremolières et al. 1998). However, the timing, duration, frequency, and magnitude of flooding are important factors that affect the response of riparian ecosystems to flood events. In terms of timing, winter or spring precipitation and floods mobilize nutrients that can be accessed by vegetation throughout the growing season, while vegetation has less time to assimilate nutrients liberated by monsoon-related events (Gosselink et al. 1981, Ellis et al. 2002). Late summer and fall flood events also promote the recruitment of *T. chinensis*, because its seeding phenology extends throughout the growing season (Di Tomaso 1998). Long-duration inundation results in greater stress to riparian vegetation due to root anoxia, thereby reducing leaf production (Smit et al. 1989, Chapter 3, Smit et al. 1990) and litterfall. Greater quantities of litterfall provide greater inputs of nitrogen to riparian
soils. In turn, greater soil nitrogen concentrations plus shallow water tables support
greater leaf production in subsequent growing seasons (Chapter 3). The practice of
spring-time naturalized flow within the rivers of semi-arid regions ought to continue
when adequate quantities of water are available, but additional research is needed to
determine the thresholds at which extended flood duration does more harm than good for
mature stands of native vegetation. More research also is needed to assess the
physiological effects of long-term flooding on mature stands of non-native vegetation.

Minimum base flows are as important to the conservation of native riparian
vegetation as peak flows that are required for native vegetation regeneration. Greater leaf
production of native *P. deltoides* ssp. *wislizenii* (Rio Grande cottonwood) occurs under
conditions of high soil inorganic nitrogen concentrations plus shallow groundwater tables
(Chapter 3). The regulation of base flows or the elevation of channel form, ideally
through system-wide alterations in sediment transport, ought to be considered by natural
resource managers and restoration practitioners as means to elevate groundwater tables in
areas dominated by *P. deltoides* or in areas slated for riparian restoration.

Another generality resulting from these studies (Chapter 4) is the functional
similarity between *T. chinensis* and *P. deltoides* regarding nitrogen acquisition and
allocation. This conclusion parallels that of Stromberg (1998), who was the first to
recognize that traits of *T. chinensis* stands in Arizona (% organic matter, soil texture,
electrical conductivity, stem density, herbaceous species richness and density, native herb
% cover) and their effects on soil nitrate concentrations were similar to those of *Populus
fremontii* (Fremont cottonwood). The spread of *T. chinensis* is considered to be
deleterious to riparian communities because it can salinize soils to levels intolerable by
native species (Busch and Smith 1995), promote increased frequency and magnitude of
riparian forest fires (Ellis 2001), provide lower quality bird habitat than native forests
(Hunter et al. 1988), and transpire more water than native species of plants (Di Tomaso
1998). Stromberg (1998) noted that the effects of *T. chinensis* are context-specific and
variable among sites. This point is supported by findings that (1) many species of birds
use *T. chinensis*, particularly when native riparian vegetation is absent (Hunter et al.
1988), (2) rodent and ground-dwelling arthropod population composition and density
have been reported to be similar within stands of *T. chinensis* and native-dominated
forests (Ellis et al. 1997, Ellis et al. 2000), and (3) *T. chinensis* transpires similar or lower
amounts of water compared to native plants, depending on local conditions (Devitt et al.
Thus, caution is advised before undertaking widespread measures to control *T. chinensis*
in all cases. These plants serve an ecologically important functional role, particularly
under physical and chemical conditions that no longer support native plant species.

N-fixation by non-natives is a major driver of ecosystem change, particularly if a
system has been void of nitrogen-fixers prior to invasion (Vitousek et al. 1987). Thus,
soil nutrient dynamics in riparian forests of the western and southwestern U.S. are more
likely to be altered by *E. angustifolia* than by *T. chinensis*. The nitrogen-fixing capacity
of *Frankia* within root nodules of *E. angustifolia* supports a foliar nitrogen content in *E.
angustifolia* three times greater than that of *P. deltoides* (Tibbets and Molles 2005).
Higher foliar nitrogen content has resulted in mean litterfall nitrogen inputs of $7.3 \pm 2.4$ g
m$^{-2}$ at a study site dominated by *E. angustifolia* (Follstad Shah unpub. data) compared to
mean litterfall nitrogen inputs of $1.8 \pm 0.2$ g m$^{-2}$ and $1.5 \pm 0.3$ g m$^{-2}$ at *P. deltoides* and *T.*
*chinensis* sites, respectively (Chapter 3). *E. angustifolia* litter production has been well-correlated to the concentration of soil inorganic nitrogen within stands of *P. deltoides*, although its quantity was an order of magnitude less than *P. deltoides* (Tibbets 2005). The effects of elevated nitrogen availability on the structure and function of historically nitrogen-limited riparian forests of arid and semi-arid regions are less well studied than their counterparts in temperate regions. It is unlikely that *E. angustifolia* will widely out-compete *T. chinensis* and *P. deltoides* due to its inability to tap into deep groundwater tables and to survive extended inundation. However, the possibility exists that the spread of *E. angustifolia* can lead to nitrogen saturation relative to the capacity of arid and semi-arid ecosystems to retain and process nitrogen, particularly in areas that already experience high anthropogenic inputs of nitrogen. Thus, additional research is needed to predict the effects of *E. angustifolia* on riparian soil biogeochemical cycling.

Further research also is required to determine whether river and riparian restoration projects are ecologically effective. The NRRSS-SW database represents the most comprehensive dataset of restoration projects in the southwestern U.S. to date (Chapter 2). The database was created because none existed from which the ecological efficacy of restoration practices could be assessed. Efficacy was still difficult to ascertain given the dearth of information contained within most datasets we compiled into the NRRSS-SW database. The creation and maintenance of relational databases at regional or national scales to store information about restoration projects, including associated monitoring data, will be instrumental in determining restoration efficacy over the long-term. In the meantime, more studies comparing the effects of restoration actions to pre-
restoration conditions ought to be conducted, as well as communicated to the scientific and restoration communities.
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