Managing Invasive Plants during Wetland Restoration: The Role of Disturbance, Plant Strategies, and Environmental Filters

by

Michael J. Osland

Department of Ecology
Duke University

Date:_______________________
Approved:

____
Curtis Richardson, Supervisor

____
Justin Wright

____
Dean Urban

____
Daniel Richter

Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Ecology in the Graduate School
of Duke University

2009

ABSTRACT

Managing Invasive Plants during Wetland Restoration: The Role of Disturbance, Plant Strategies, and Environmental Filters

by

Michael J. Osland

Department of Ecology
Duke University

Date:_______________________
Approved:

____
Curtis Richardson, Supervisor

____
Justin Wright

____
Dean Urban

____
Daniel Richter

An abstract of a dissertation submitted in partial
fulfillment of the requirements for the degree
of Doctor in the Department of
Ecology in the Graduate School
of Duke University

2009

Abstract

Since wetlands provide many important ecosystem services, there is much interest in protecting existing wetlands and restoring degraded wetlands. Yet, degraded wetlands and restoration sites are often vulnerable to plant invasions that can hinder restoration success. Invasive plants typically reduce biodiversity and alter important ecosystem functions and services. This dissertation examines the ecological impact and management of invasive plant species during wetland restoration with a focus on three important drivers of plant community change in wetland ecosystems: disturbance, plant strategies, and environmental filters.

The investigations included in this research were conducted in a tropical dry wetland (Palo Verde Marsh, Palo Verde National Park, Costa Rica) and a temperate piedmont riparian forest (Sandy Creek, Duke Forest Stream and Wetland Assessment and Management Park, Durham, North Carolina). In these experiments, the primary species of interest are *Typha domingensis* Pers. (cattail; Typhaceae), *Ligustrum sinense* Lour. (Chinese privet; Oleaceae), *Arundinaria gigantea* (Walter) Muhl. (giant cane; Poaceae), and *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass; Poaceae).

The expansion of *Typha* into wetlands historically not dominated by cattail typically occurs in response to natural and anthropogenic perturbations. Management approaches that reduce *Typha* dominance, increase diversity, and restore or maintain

wetland ecosystem services are of interest worldwide. The objective of the first phase of the research was to investigate a unique *Typha* removal method that is used in one of the most dynamic and ecologically important wetlands in Central America (Palo Verde Marsh, Palo Verde National Park, Costa Rica; a Ramsar Wetland of International Importance). Palo Verde Marsh is a tropical dry wetland with distinct and extreme wet and dry seasons; it is flooded during the wet season and has no standing water for much of the dry season. Palo Verde Marsh has historically provided important habitat for very large populations of migratory birds. However, a cattail (*T. domingensis*) expansion in the 1980s greatly altered the plant community and reduced avian habitat. Since then, *Typha* has been managed using fangueo (a Spanish word, pronounced as "fahn-gay-yo" in English). During fangueo, *Typha* is crushed and locally removed by a tractor with metal paddle wheels. I applied a *Typha* removal treatment at three levels (control, fangueo, and fangueo with fencing to exclude cattle grazing) at Palo Verde Marsh. Fangueo was applied at the beginning of the dry season resulting in a large reduction in *Typha* dominance (decreased aboveground biomass, ramet density, ramet height), an increase in open areas with no vegetation, and a 98 and 5-fold increase in avian density and richness, respectively. Importantly, fangueo had no apparent long-term impact on any of the soil properties measured (including bulk density). Interestingly, low soil and foliar N:P values indicate that Palo Verde Marsh and other wetlands in the region may be nitrogen limited. The fangueo process is an effective method for restricting *Typha* expansion and increasing plant and avian diversity. I present a model that illustrates the impact of *Typha* management and seasonal flooding on the plant and avian community. The technique might be adopted or modified for the restoration and management of *Typha* and other invasive emergent plants in other wetlands.

The second objective of this research was to better quantify the impact of the distinct and extreme anaerobic/aerobic annual cycle on the plant community in Palo Verde Marsh. Since the impact of seasonal flooding on the plant community in seasonal wetlands is often most evident after disturbance, I created gaps in the wetland vegetation via the mechanical removal of emergent vegetation and then measured plant community change using surveys of the wet and dry season standing vegetation, the seed bank, and *in situ* seedling recruitment. As expected, seasonal flooding acted as an environmental filter and resulted in distinct dry and wet season assemblages. The dominant plant life forms present after vegetation removal differed between seasons with emergents dominating during the dry season and floating-rooted, free-floating, and submerged species more dominant during the wet season. I identified common species that are characteristic of both seasonal assemblages and used indicator species analyses to identify species that are only likely to be found during the wet season. I also characterized the seed bank at this site; like most seasonal wetlands, plant species' resilience in this wetland were dependent upon a large and diverse seed bank which allowed many species to revegetate after disturbance and the extreme wet/dry conditions which acted like environmental filters.

In addition to the experiments conducted in Palo Verde Marsh, this dissertation also presents the results from an experiment in a temperate riparian restoration site in the North Carolina Piedmont (Sandy Creek, Duke Forest Stream and Wetland Assessment and Management Park, Durham, NC). Since riparian restoration efforts in the southeastern U.S. are often hindered by invasive non-native plants, there is much interest in approaches that can be used to reduce the impact of invasive non-native plant populations at the local level (e.g., a restoration site). In addition to the impact of non-native species-specific removal efforts, there is also much interest in the identification and assessment of native competitive-dominant plant species that can be used during riparian restoration to support important ecosystem functions and reduce non-native invasibility. *Ligustrum sinense* (Chinese privet) is a very common invasive non-native shrub in the region. *Arundinaria gigantea* (giant cane) is a native bamboo species that used to be very abundant in riparian and wetland ecosystems in the region. The objectives of this phase of the research were to: (1) measure the plant community response to removal of mature *L. sinense* individuals; and (2) quantify planted *A. gigantea* clonal expansion in the presence of other plants, particularly common non-native invasive species. Due to its potential for rapid growth and expansion, it was hypothesized that *A. gigantea* would be able to compete with common non-native species and reduce non-native invasibility. In a three-year split-plot experimental design, I applied a Privet-Presence treatment at two levels (Privet Present, Privet Removed) and a Cane-Planting treatment also at two levels (Cane, No Cane). The privet removal treatment resulted in 100% mortality of mature privet individuals. After privet removal, *L. sinense* seedlings recruited into these plots but growth has been very slow and these *L. sinense* individuals are not yet dominant. The privet canopy allows minimal understory plant recruitment and growth and privet removal resulted in an increase in species richness and diversity in the first year. However, in these Privet-Removed plots, a non-native invasive annual grass (*Microstegium vimineum*) invaded, became the most dominant species, and reduced species richness and diversity. In Privet-Removed plots, *A. gigantea* clonal expansion (i.e., ramet density, genet area, ramet diameter, and ramet height) was small in the first year but increased in the second and third years. Importantly, in Privet-Removed plots where *A. gigantea* was planted, *M. vimineum* cover was lower and species richness and diversity were greater; planting *A. gigantea* appears to have facilitated the establishment of other species and, in the process, increased diversity.

Our results emphasize several general conclusions that are applicable to other restoration efforts in other ecosystems with other plant species. First, during ecological restoration, invasive non-native plant removal alone will typically not restore native plant communities. Non-native invasive plant populations are typically very resilient to removal. Hence, long-term reductions in non-native invasibility will often require additional management efforts. For example, in the tropics my research showed the effectiveness of Fangueo for reducing *Typha* monocultures and increasing native plant and bird diversity. Another approach for improving ecosystems functions and reducing non-native invasibility after invasive plant removal is to carefully select and plant native species with competitive-dominant traits that will be able to compete with invading non-native species and resist invasion. Although this seemingly simple approach is often used by restoration practitioners, the results are rarely monitored and surprisingly few studies are designed to explicitly identify and investigate the performance of these important native competitive-dominant species.

Contents

List of Tables

List of Figures

Acknowledgements

I would first like to thank my advisor, Curt Richardson, for his guidance, encouragement, sense of humor, and support throughout my graduate studies. I also would like to thank my committee members (Justin Wright, Dean Urban, and Dan Richter) for their insightful comments and suggestions. I am grateful to Eugenio González who provided me with valuable advice and support during the Costa Rica portion of this project. This research would not have been possible without the help of the incredible folks at the Duke University Wetland Center (Wes Willis, Paul Heine, Mengchi Ho, Randy Neighbarger, Jim Pahl, Neal Flanagan, Amani McHugh, Arianna Sutton-Grier, Jen Morse, Wyatt Hartman, Julie Demeester, Greg Bruland) and also at the Organization for Tropical Studies' Palo Verde Biological Station (Gilberto Murillo, Juan Serrano, Davi González, Maria Aléman, Maritza López, Salomón Bermudez, Rodolpho Mora, Romelio Campos, Alberth Rojas, Mario Gómez). Thanks very much!

My graduate studies were made possible by the tremendous support of the Duke Graduate School, the Nicholas School of the Environment, the University Program in Ecology, and the Duke Wetland Center. I am very appreciative.

For the research conducted in Costa Rica (Chapters Two and Three), I am extremely grateful to Anna Osland, Amani McHugh, Alexander Blanco Sibaja, and Davi González for their assistance in the field and in the lab. Gilberto Murillo provided valuable logistical assistance. The soil and vegetation analyses were greatly improved by the help of Wes Willis, Paul Heine, and Mengchi Ho. The hydrology and climate data were obtained from OTS records with the assistance of Juan Serrano and Wagner Lopez. I appreciate the tremendous logistical support provided by the OTS staff at the Palo Verde Biological Station and also in the San Jose and Durham offices. I also thank MINAE and the PVNP Rangers for their assistance and permission to conduct this research. Nolber González and his son provided the tractor and assistance needed to implement the fangueo treatments. Joe Sexton, Amy Daniels, and Steven Hall provided valuable comments on a previous draft of Chapter Two. The research in these two chapters was conducted with the support of a Fulbright Fellowship, an NSF IRES Grant, an OTS Research Fellowship, a Duke Graduate School Pre-Dissertation Research Travel Award, a Duke Provost's Pre-Dissertation International Field Research Grant, and the Duke Wetland Center Case Studies Endowment.

The following people helped establish the research conducted in the temperate portion of this research (Chapters Four and Five): Erin Brosnan, Judd Edeburn, Doug Gorecki, Amy Hammontree, Menghci Ho, Lauren Kinsman, Amani McHugh, Randy Neighbarger, Anna Osland, Jim Pahl, Arianna Sutton-Grier, Jocelyn Tutak, and Wes Willis. I am grateful to Jim Pahl for his help with the experimental design, the privet removal, and the text in Chapter Four. Menghci Ho provided valuable comments, plant identification support, and plant survey assistance. Roger Hansard, Robert Merriam, Barbara Doll, and Mark Feily helped identify potential donor stands. I also thank the USACE for permission to collect from the donor stand, Jimmy Triplett for taxonomic guidance, and Scott Franklin for organizing the 2008 ASB *Arundinaria* symposium. The text in Chapter Four was greatly improved by the comments provided by two anonymous reviewers. The research in both of these chapters was funded by a grant from the USDA-NRCS to the Duke University Wetland Center (DUWC) as well as DUWC Case Studies Endowment Funding.

Finally, a special thanks to my family for their continued encouragement and support. Thanks to my parents (Joyce and Asbjorn) and sisters (Jessica and Katrina) for cheering me on from day one. Thanks also to my mother, father, and brother in law (Barb, Ross, and Mike, respectively) for their support. Most importantly, thanks to my wife Anna and son Jacob. In addition to her encouragement and good cheer, Anna has helped this research in many ways. She has helped me in the field, provided feedback on the research and writing, and was even adventurous enough to drive to Costa Rica from North Carolina (seven countries in eight days and then back again a year later). Jacob, who recently turned one, provided hours of entertainment during the final year of this research. Thank you!

1. Introduction

Wetlands provide many important ecosystem services (e.g., biodiversity and wildlife habitat, flood abatement and water storage, sediment and nutrient retention/transformation). As a result, there is much interest in protecting existing wetlands and restoring degraded wetlands. Yet, degraded wetlands and restoration sites are often vulnerable to plant invasions that can hinder restoration success (Zedler and Kercher 2004). Invasive plants reduce biodiversity and typically alter important ecosystem functions and services (Vitousek et al. 1996). A common objective of ecological restoration is to constrain non-native plant invasions and restore native plant communities. Yet, most established invasive non-native plant populations are very resilient and the disturbances associated with restoration efforts sometimes make restoration sites even more susceptible to plant invasions (D'Antonio and Chambers 2006). This research examines the ecological impact and management of invasive plant species during wetland restoration with a focus on the role of disturbances, environmental filters, and plant strategies.

Disturbances, environmental filters, and plant strategies are very important drivers of plant community change in wetland ecosystems. Wetlands are often located in parts of the landscape that receive and store very large and dynamic inputs (e.g., water, nutrients, sediment, propagules) from more elevated parts of the watershed. As a result, disturbances in "upstream" parts of the watershed will typically lead to disturbances in "downstream" wetlands (Zedler and Kercher 2004). Some examples of typical disturbances in wetlands include flooding, scouring, and sediment/debris deposition. Disturbances are often more frequent in wetland ecosystems than in their terrestrial counterparts. As a result, wetland plant species often have growth strategies and life history traits that enable them to be resilient to disturbances. During restoration, disturbances can sometimes be used to manage invasive plant populations and favor the establishment and growth of native species. In this research, the specific disturbances examined include invasive plant removal and herbivory.

In addition to disturbances, wetland plant communities are defined by environmental filters. An environmental filter constrains the number of species that will be able to survive and become dominant in a given area. The most important environmental filter in wetlands is the oxygen limitation associated with flooding. A classic example of how environmental filters define wetland plant communities is the Environmental Sieve model developed by van der Valk (1981). The Environmental Sieve was developed to predict the plant community response to flooding and drawdown cycles in prairie pothole wetlands. Flooding is a potent physiological stress for plants and greatly impacts survival, growth, and reproduction. Hence, van der Valk demonstrated that specific plant traits (e.g., life-span, propagule longevity, and establishment requirements) were important for predicting which species would be present during the aerobic or anaerobic conditions associated with extreme hydrologic fluctuations. For example, annual species with high propagule longevity that cannot germinate during flooded conditions are likely to be found during drawdown but be locally extinct during flooding. In contrast, almost all floating and submerged species can only become established during flooded conditions. Hence, these species will not be present during extensive drawdown and their reappearance during flooding will be dependent upon propagule longevity.

Although the Environmental Sieve was developed for prairie pothole wetlands, the conceptual pieces included in van der Valk's model can be modified and applied to various wetland (e.g., Weiher and Keddy 1995, Middleton 1999, Finlayson 2005) and terrestrial (e.g., George and Bazzaz 1999, Diaz et al. 2003) ecosystems in order to interpret the plant community response to diverse combinations of disturbance, environmental filters, and plant strategies. In this research, the specific filters examined include flooding/drawdown and light limitation induced by invasive plant presence. The specific plant strategies assessed include species' life form, growth, dispersal, seed banking, and seedling establishment requirements.

These investigations were conducted in a tropical dry wetland (Palo Verde Marsh, Palo Verde National Park, Costa Rica) and a temperate piedmont riparian forest (Sandy Creek, Duke Forest Stream and Wetland Assessment and Management Park, Durham, North Carolina). In these experiments, the primary species of interest are *Typha domingensis* Pers. (cattail; Typhaceae), *Ligustrum sinense* Lour. (Chinese privet;

Oleaceae), *Arundinaria gigantea* (Walter) Muhl. (giant cane; Poaceae), and *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass; Poaceae).

The tropical portion of this research is presented in the second and third chapters. The second chapter is entitled "Plant and avian community response to cattail (*Typha* spp.) removal via fangueo in a tropical dry wetland: implications for restoration and invasive plant management." Cattail (*Typha* spp.) are among the most ubiquitous and competitive wetland plants in the world. *Typha* invasions are particularly common in degraded wetlands resulting in reduced biodiversity and the loss of important ecosystem services. Sustainable management techniques that reduce *Typha* dominance, increase diversity, and restore or maintain wetland ecosystem services are needed. In this chapter, we investigated a unique *Typha* removal technique (called fangueo in Costa Rica which is a Spanish word, pronounced as "fahn-gay-yo" in English) that is used in one of the most dynamic and ecologically important wetlands in Central America (Palo Verde Marsh). We measured the impact of this technique upon soil properties, the seed bank, plant community change (e.g., composition, diversity, recruitment), avian visitation, and *Typha* dominance. We then used these data to develop a management model that illustrates plant community change and we finish this chapter by discussing the application of this technique in other *Typha*-dominated wetlands.

The third chapter is entitled "Tropical dry wetland plant community response to seasonal flooding: the role of the seed bank, plant life forms, and environmental filters."

This chapter examines the impact of seasonal flooding on the plant community in Palo Verde Marsh. Tropical dry wetlands are flooded during the wet season and have no standing water for much of the dry season. This anaerobic/aerobic annual cycle drives ecosystem functions (e.g., decomposition, productivity) and greatly dictates community composition. In this study, we measured the post-disturbance plant community response to seasonal flooding in Palo Verde Marsh via surveys of the wet and dry season standing vegetation, a seed bank experiment, and *in situ* seedling recruitment.

The results of the temperate portion of this research are presented in chapters four and five. The fourth chapter is entitled: "Native bamboo (*Arundinaria gigantea* (Walter) Muhl., Poaceae) establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): implications for restoration." Giant cane (*A. gigantea*) is a native bamboo species that was once abundant in wetlands and riparian areas throughout the southeastern United States. As part of an effort to identify competitive-dominant native species that can be utilized to maximize the restoration of riparian ecosystem functions/services and reduce non-native community invasibility, we transplanted cane clump divisions into areas either dominated by or recently cleared of Chinese privet (*L. sinense*), an invasive non-native shrub. This chapter quantifies cane survival and growth in the first two years of this experiment and discusses the practical implications of transplantation via clump division for riparian and canebrake restoration.

The fifth chapter is entitled "Plant community response to removing an invasive non-native shrub and planting a native bamboo." We use three years of data to: (1) measure the plant community response to removal of mature *L. sinense* individuals; and (2) quantify planted *A. gigantea* clonal expansion in the presence of other plants, particularly common non-native invasive species. The Privet-Removed plots in this experiment were quickly invaded by a common invasive non-native annual grass (*Microstegium vimineum*) which enabled us to also assess the impact of *M. vimineum* dominance on plant diversity. *M. vimineum* cover was negatively related to both species richness and diversity. Importantly, in Privet-Removed plots where we planted *A. gigantea*, *M. vimineum* cover was lower and species richness and diversity were greater; planting *A. gigantea* appears to have facilitated the establishment of other species and, in the process, inceased diversity. Our results emphasize several general conclusions that are applicable to other restoration efforts in other ecosystems with other plant species. First, during ecological restoration, invasive non-native plant removal alone will typically not restore native plant communities; non-native invasive plant populations are typically very resilient. Hence, long-term reductions in non-native invasibility will often require additional efforts. One of the most straightforward approaches for improving ecosystems functions and reducing non-native invasibility after invasive plant removal is to carefully select and plant native species with competitive-dominant traits that will be able to compete with invading non-native species and resist invasion.

Although this seemingly simple approach is often used by restoration practitioners, the results are rarely monitored and surprisingly few studies are designed to explicitly identify and investigate the performance of these important native competitive-dominant species.

2. Plant and avian community response to cattail (*Typha* spp.) removal via fangueo in a tropical dry wetland: implications for restoration and invasive plant management

Abstract

Cattail (*Typha* spp.) are among the most ubiquitous and competitive emergent wetland plants in the world. The expansion of *Typha* into wetlands historically not dominated by cattail typically occurs in response to natural and anthropogenic perturbations. Management approaches that reduce *Typha* dominance, increase diversity, and restore or maintain wetland ecosystem services are of interest. We investigated a unique *Typha* removal method that is used in one of the most dynamic and ecologically important wetlands in Central America (Palo Verde Marsh, Palo Verde National Park, Costa Rica). Palo Verde Marsh has historically provided important habitat for very large populations of migratory birds. However, a cattail (*T. domingensis*) expansion in the 1980s greatly altered the plant community and reduced avian habitat. Since then, *Typha* has been managed using fangueo (a Spanish word, pronounced as "fahn-gay-yo" in English). During fangueo, *Typha* is crushed and locally removed by a tractor with metal paddle wheels. We applied a *Typha* removal treatment at three levels (control, fangueo, and fangueo with fencing to exclude cattle grazing) at Palo Verde Marsh, a seasonal wetland with distinct and extreme wet and dry seasons. Fangueo was applied at the beginning of the dry season resulting in a large reduction in *Typha* dominance (decreased aboveground biomass, ramet density, ramet height), an increase

in open areas with no vegetation, and a 98 and 5-fold increase in avian density and richness, respectively. As in most seasonally flooded wetlands, the seed bank at this site is large and fangueo resulted in a more diverse plant community that was strongly dictated by seasonal processes (distinct wet/dry season assemblages). Importantly, fangueo had no apparent long-term impact on any of the soil properties we measured (including bulk density). Interestingly, low soil and foliar N:P values indicate that Palo Verde Marsh and other wetlands in the region may be nitrogen limited. The fangueo process is an effective method for restricting *Typha* expansion and maintaining plant and avian diversity. We present a model that illustrates the impact of *Typha* management and seasonal flooding on the plant and avian community. The technique might be adopted or modified for the restoration and management of invasive plants in other wetlands.

Keywords: *Typha domingensis*; Palo Verde National Park; seasonal wetlands; tropical wetlands; monsoonal floodplain wetlands; invasive plant resilience; wetland restoration; restoration ecology; plant succession; seed bank.

2.1 Introduction

Globally, cattail (*Typha* spp.; Typhaceae) are among the most ubiquitous and competitive emergent plants in freshwater wetland ecosystems. The expansion of *Typha* into wetlands historically not dominated by cattail often occurs in response to natural and anthropogenic perturbations (e.g., vegetation removal, nutrient enrichment, altered hydroperiod, reduced salinity, altered sedimentation rates, non-native genotype introductions) (Galatowitsch et al. 1999, Zedler and Kercher 2004, Richardson 2008a). Due to *Typha*'s potential for rapid dispersal, establishment, and clonal growth, *Typha* expansion typically results in monotypic plant communities and greatly alters important ecosystem functions and services (Richardson 2008a). Restoration objectives in such wetlands often include the removal of *Typha* in order to restore biodiversity and/or specific services.

In this study, we investigated the effectiveness of *Typha* management via a vegetation removal method called fangueo (a Spanish word, pronounced as "fahn-gay-yo" in English). Fangueo is a technique used locally in NW Costa Rica during rice farming to control weeds and also reduce water infiltration via increased soil compaction. See McCoy and Rodriguez (1994) for a discussion of how the fangueo method was first used to restrict *Typha* expansion in PVNP wetlands. In the context of this study, we use the term fangueo to refer to the use of a tractor with metal paddle wheels to crush and locally remove *Typha* in standing water (see photos in Figure 2.1abc). During the first pass of a fangueo tractor, *Typha* ramets are crushed and crimped which limits oxygen transport (McCoy and Rodriguez 1994). During subsequent passes, the *Typha* ramets and parts of the rhizome are typically pulled up,

Figure 2.1: Photos from Palo Verde Marsh, Palo Verde National Park, Costa Rica depicting: (a, b) a tractor with metal paddle wheels that is used to remove *Typha* via a process called fangueo; (c) the edge of a plot where *Typha* was removed via fangueo, and (d) migratory birds utilizing and flying away from a plot where *Typha* was removed via fangueo. Most of the individuals in this photo are Black-bellied Whistling Ducks (photos taken by M.J. Osland).

temporarily dragged behind the tractor, and locally removed. After fangueo treatment, stresses associated with a lack of moisture availability during the dry season and lack of oxygen due to flooding will typically lead to *Typha* mortality.

Two previous studies have investigated *Typha* control using crushing methods that are somewhat similar to fangueo (Nelson and Dietz 1966, Beule 1979). The method used by Beule (1979) is slightly different in that various cylindrical containers without cleats were pulled behind a tractor. Nelson and Dietz (1966) pulled a 55-gallon drum with attached angle-iron cleats behind a tractor, a method that is more similar to fangueo. In addition to crushing, Nelson and Dietz (1966) informally compared various other *Typha* control methods. Based upon their visual observations (little data were presented), they found crushing to be the most cost effective and second most rapid technique to control *Typha* (herbicide application was the most rapid).

The impact of fangueo on avian visitation and the creation of desirable avian habitat in PVNP is dramatic and extremely effective in the short term (McCoy and Rodriguez 1994, Trama 2005). However, as in most other *Typha* removal efforts, the impact of fangueo on the plant community and other ecosystem properties has not been extensively investigated and the long-term effectiveness of fangueo for *Typha* removal has not been quantified. Previous studies discussed the use of fangueo at PVNP for avian habitat restoration (McCoy and Rodriguez 1994) and examined aggregate changes in wetland cover and avian populations using aerial surveys (Trama 2005). Another study (Burnidge 2000) provides additional discussion of the history and policy implications of *Typha* management at Palo Verde National Park. Burnidge (2000) conducted a small field study designed to coarsely assess the impact of fangueo and grazing on the plant community and avian habitat; however, the results from this study were partly inconclusive due to drought-related complications and a small sample size (Burnidge 2000).

The objective of our study was to better quantify the impact of fangueo on soil properties, the plant community, and avian visitation via well-replicated ground-based field surveys. We investigated whether the physical disturbance and potential compaction associated with tractor use has any detrimental impact on soil properties and seedling emergence. In the process, we characterized several important soil physical and chemical properties at the site. In addition, we quantified the impact of *Typha* removal on the plant community with an emphasis on the impact of seasonal flooding/drawdown and measurements that relate to *Typha* dominance and resilience (i.e., *Typha* germination from the seed bank, *in situ* recruitment, vertical growth, and clonal expansion). These *Typha* population biology and growth measurements were used to investigate the effectiveness of *Typha* removal efforts via fangueo. Since *Typha* removal at PVNP has historically had a very dramatic and immediate impact on avian populations, we also measured the impact of fangueo on avian visitation and diversity.

2.2 Methods

2.2.1 Study site

This study was conducted in Palo Verde Marsh, within PVNP. PVNP is located in the Province of Guanacaste (NW Costa Rica; Figure 2.2) in the lowlands of the Tempisque River Watershed. The climate in this part of Costa Rica is tropical and very seasonal. The wetlands of PVNP are collectively designated a RAMSAR Wetland of International Importance and cover an estimated 9880 ha of the total 18,800 ha area included in the park (J. Serrano, personal communication). These wetlands are some of the most dynamic, ecologically important, and diverse wetlands in Central America. The Organization for Tropical Studies (OTS) manages the Palo Verde Biological Station which is within the park and immediately adjacent to Palo Verde Marsh.

Ecosystem processes in the region's freshwater wetlands are defined by seasonal flooding and drawdown associated with wet and dry seasons. Palo Verde Marsh (~1250 ha; 10^{o}20'35" N, 85^{o}20'25" W), fills with water during the wet season (~May-November) to a typical maximum depth of about 1.5 m (Figure 2.3abc). Most of these hydrologic inputs are due to surface water runoff from the adjacent forest during the wet season. However, in some years, tropical storm activity at the end of the wet season (typically in September or October) will produce water levels in excess of 1.5 m at the site as the Tempisque River rises higher than the natural levees and causes widespread flooding. During the dry season (~December-May), the water level gradually recedes due to high

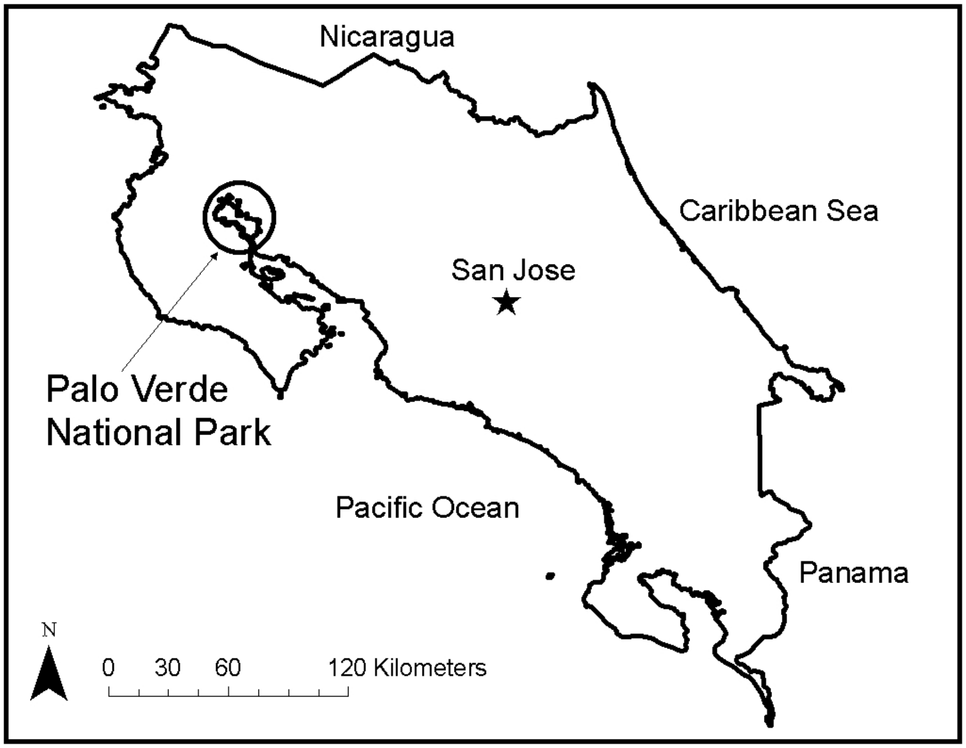

Figure 2.2: Map of Costa Rica identifying the location of Palo Verde National Park.

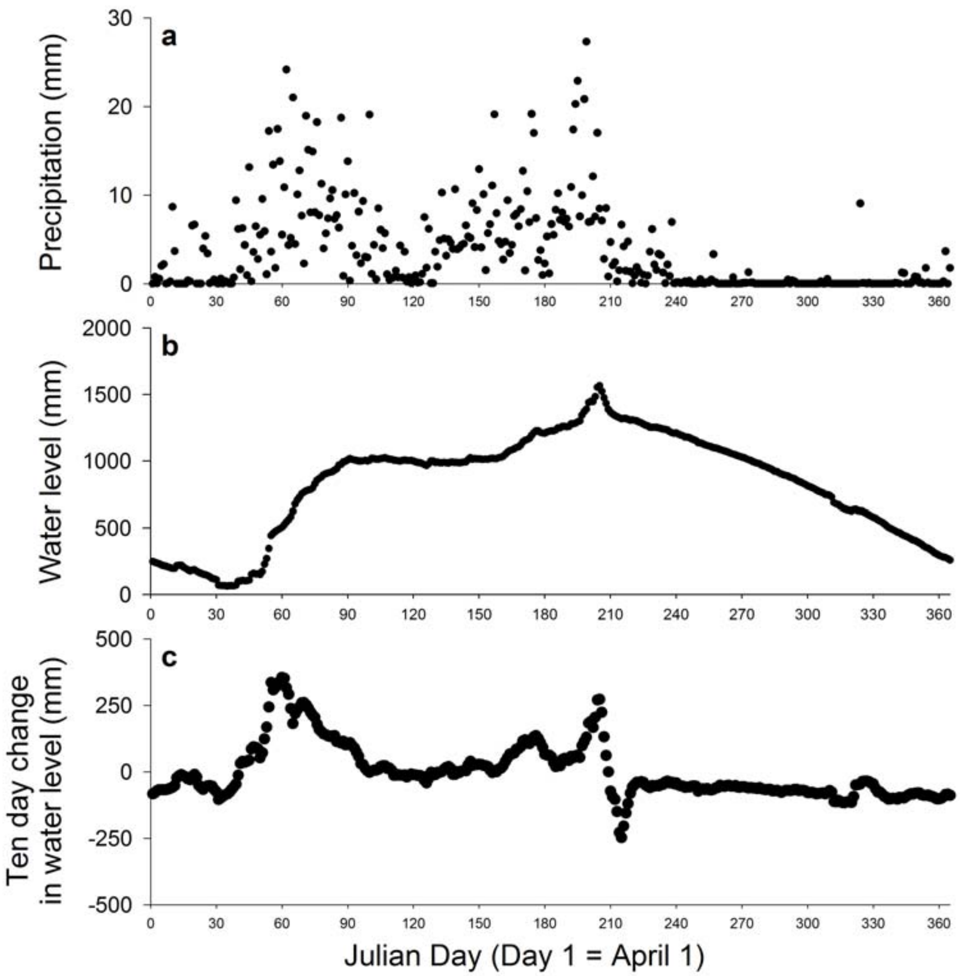

Figure 2.3: Mean daily precipitation (a), water level (b), and ten day change in water level (c) at Palo Verde Marsh for a five year period (2003-2008). These figures illustrate the distinct wet and dry seasons and also the rapid changes in water level that occur in May/June and September/October due to intense rainfall. Note that these data were collected from a relatively deep part of the marsh. Parts of the marsh that are less deep can be without standing water for an additional one to three months.

evapotranspiration rates that exceed the rainfall. At the end of the dry season, much of the marsh has no standing water. However, small precipitation events during the last few months of the dry season (March-April) in some years will delay and sometimes prevent complete drawdown in the wetlands. The soils in most of the wetlands within and adjacent to PVNP (including Palo Verde Marsh) are Vertisols (Loaiciga and Robinson 1995) which expand in the wet season and contract during the dry season forming a relatively uniform and deep A horizon. Extensive cracking during the dry season (especially in areas without vegetation) promote the mixing of this layer as pieces from the surface fall into cracks. The shrink-swell qualities of Vertisols typically enable them to recover from compaction (Sarmah et al. 1996). Sadly, the soil properties at the site are not well documented in the literature.

The range in total annual precipitation at the site is large. Between 1997-2007, the mean ± SE, minimum, and maximum annual cumulative precipitation for a hydrologic year (April-March) were 1271 ± 131, 717, and 2201 mm respectively (data obtained from on-site OTS records). For a longer time period (1921-1999), the mean precipitation for the entire Tempisque River Watershed was estimated to be 1817 mm (Mateo-Vega 2001). The mean ± SE annual temperature at the site between 1997-2007 was 28.1 ± 0.3 ^{o}C. The coldest months (defined as months with the lowest average temperatures) were at the end of the wet season (September and October) with a mean ± SE temperature of 26.8 ± 0.2 ^{o}C. The warmest months (defined as months with the highest average temperatures) were at the end of the dry season (March and April) with a mean ± SE temperature of 29.7 ± 0.2 ^{o}C.

2.2.2 Cause(s) and consequences of Typha expansion at the study site

Determining the cause of the cattail expansion in Palo Verde Marsh is not the goal of this study. However, we must discuss the land-use history of PVNP wetlands and the potential causes for *Typha* expansion in order to clarify the management history that led to the use of fangueo to restrict *Typha* expansion. In many wetlands, *Typha* expansion is caused by changes in land use (Zedler and Kercher 2004). However, the definitive cause of the *Typha* expansion in Palo Verde Marsh has not been conclusively determined and warrants more attention. The PVNP *Typha* expansion and removal efforts have been accompanied by considerable land-use change within the park (Burnidge 2000, Trama 2005) and also throughout the Tempisque River Watershed (see Daniels and Cumming 2008 for a discussion of wetland conservation and conversion in the watershed). These wetlands have a grazing-intensive land-use history that is common to seasonal wetlands in the wet-dry tropics where, during the dry season, wetlands are the only areas with water in an otherwise very dry landscape (Middleton 1999). Prior to becoming a protected area, these wetlands were utilized for cattle grazing for at least a century and potentially since the 16th or 17th century (Peters 2001). In 1975, the ranch that contained Palo Verde Marsh was expropriated by the Costa Rican government and later deemed a wildlife refuge in order to protect the tropical dry forest and also the wetlands which support very large populations of resident and migratory birds. The area was designated a national park in 1990.

The historical intensity of cattle grazing in Palo Verde Marsh before it received protective status has been debated and estimates of the total head of cattle in the wetland range from 500 to 18,000 (see discussion in Burnidge 2000 and Trama 2005). In association with the protective status, these cattle were removed from the wetlands by 1980 (McCoy and Rodriguez 1994). During the same time period, *Typha domingensis* Pers., which is actually native to the region (Horn and Kennedy 2006), began to expand and form dense monotypic stands throughout Palo Verde Marsh and other adjacent marshes. The cause of the very sudden and dramatic *Typha* expansion has most often been attributed to the reduction in cattle grazing (i.e., the cattle actually eat young *Typha* shoots and trample vegetation; thus, it is hypothesized that cattle grazing prevented competitive exclusion) (McCoy and Rodriguez 1994, Burnidge 2000). Although this is a plausible explanation and similar results have been observed in several other seasonally flooded and historically grazed tropical wetlands (Middleton 1999), rigorous tests of this hypothesis at Palo Verde Marsh have never been implemented and debates regarding the grazing intensity continue.

Furthermore, historic abiotic conditions throughout the watershed were also greatly altered during this period and other potential causal factors that have been mentioned but not conclusively tested include altered hydroperiod (González 2002, Jiménez et al. 2003), reduced salinity, increased nutrient inputs, altered fire regimes, and *Typha* hybridization. The proximity of Palo Verde Marsh to sea level and a tidally influence river indicates that the role of salinity may be important. Yet, the impact of increased salinity on *Typha* germination and expansion at PVNP has not been tested. Another abiotic factor that has changed dramatically in the Tempisque River Watershed is the timing, quality, and quantity of freshwater inputs (see Daniels In press for a discussion of land use change and the growth of irrigation-supported agriculture in the Tempisque River Watershed). Agricultural crops in the region (primarily rice, sugarcane, and cantaloupe) require irrigation during the dry season. Much of the water used for irrigation on the western side of Tempisque River is pumped from the Tempisque River or an underground aquifer. On the eastern side of the Tempisque River, a large portion of the irrigation water is made available from an adjacent watershed via the Proyecto Riego Arenal Tempisque (PRAT). PRAT water is derived from a large reservoir (Laguna Arenal) that was constructed to support the largest hydroelectric plant in Costa Rica. Water from the reservoir is then made available to farmers via an extensive network of PRAT canals. González (2002) and Jimenez et al. (2003) rightfully argue that more attention should be directed to the impact of PRAT and other land use changes in the Tempisque Watershed on the wetlands' hydroperiod, particularly the timing and intensity of flooding at the beginning of the dry season. However, the long-term hydrologic records needed to assess such changes in hydroperiod are lacking. As a result, the impact of such hydrologic changes on the *Typha* expansion and ecological processes in Palo Verde Marsh have not been investigated.

The cause(s) of the *Typha* expansion at Palo Verde Marsh remain unknown and warrant more attention. What is known is that the PVNP cattail expansion resulted in a regime shift from areas of open water, bare sediment, and higher plant diversity to a nearly monotypic *Typha* state (McCoy and Rodriguez 1994, Burnidge 2000, Trama 2005). As a result, resident and migratory bird populations decreased due to the lack of adequate habitat (McCoy and Rodriguez 1994, Trama 2005). Management efforts in the last 20 years have been directed towards controlling the *Typha* expansion and restoring plant diversity and avian habitat heterogeneity. After 20 years of management, *Typha* growth in small sections of Palo Verde Marsh is currently restricted via a combination of repeated physical disturbance (fangueo) and flooding. Cattle have also been reintroduced to these sections of the wetland and consume some of the post-*Typha* removal vegetation. The result has been an increase in plant and avian diversity in these managed sections of the marsh.

2.2.3 Experimental design

Since the hydrologic and edaphic spatial variability at the site was unknown when we began the study and potentially heterogeneous, we selected a randomized complete block design for this investigation. Within fifteen blocks, a *Typha* removal treatment was applied at three levels [Control (C), *Typha* removed via fangueo (F), and *Typha* removed via fangueo and plot fenced (F&F) to exclude cattle grazing; Figure 2.4]. Whereas the cattail in the C plots was not removed, the cattail in the F and F&F plots was removed via fangueo. The F&F plots were also enclosed by a barbed wire fence in order to restrict cattle access and assess the additional impact of grazing after fangueo on the vegetation. The lack of a fence in the F plots allowed cattle to graze in those plots. *Typha* removal via fangueo was conducted in early February 2007. With each block, the three treatment levels were each randomly assigned to 20-m^2 plots with at least 5-m buffers on all sides (total # of 20-m^2 plots = 45). Within each 20-m^2 plot, three nested 1-m^2 permanent quadrats were randomly established for vegetation surveys (total # of 1-m^2 quadrats = 135). The relative water depth of each plot was determined during the wet season surveys.

In order to facilitate long-term monitoring, the coordinates of each plot were recorded with a handheld GPS unit and each plot was marked with a pvc pipe placed over rebar that was pounded roughly 0.5 m into the soil. This section of rebar proved to be an important addition to the plot markers as several of the pvc portions were broken off by cattle and, potentially, white-faced capuchin monkeys looking for potable water in plots closest to the forest and the park camping facilities. Along the border of each C and F plot, a 10-m permanent transect was established to monitor and measure cattail horizontal clonal expansion.

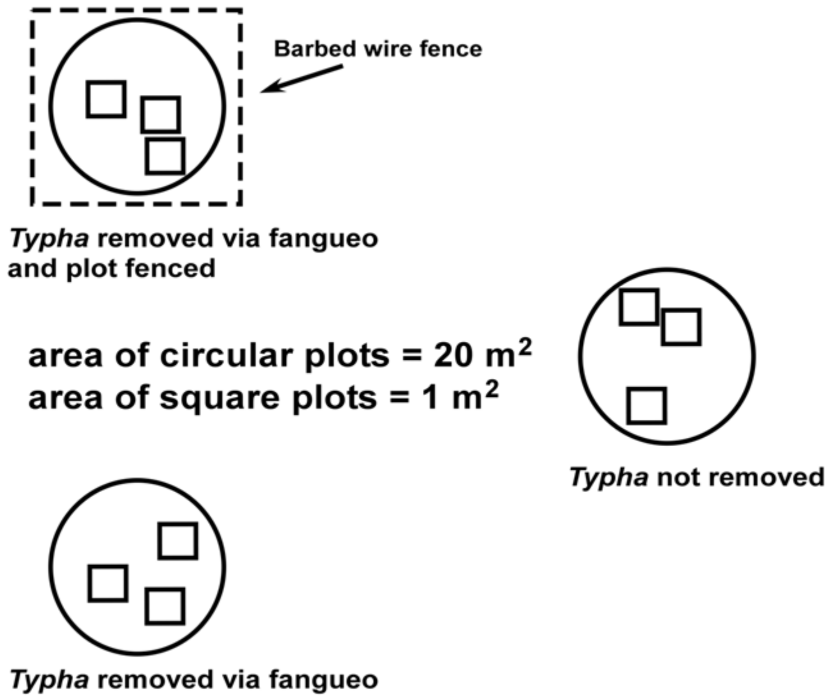

Figure 2.4: Illustration of the experimental design used in this study.

2.2.4 Soil

Within each of the C & F 20-m^2 plots, two soil samples to 10-cm depth were collected during the first month after fangueo. Whereas one of the samples was used to determine bulk density (BD) and soil organic matter (SOM), the other sample was used for total nitrogen (TN), total carbon (TC), and total phosphorus (TP) analyses. To minimize compaction, soil samples were collected by gently pounding a lightweight stainless steel piston core liner with a sharpened tip into the soil using a 680-g dead blow hammer. After collection, samples were stored at 4 ^{o}C in sealed plastic bags at the OTS Palo Verde Biological Station until transport to the Duke University Wetland Center for analysis. Samples to be analyzed for TN, TP, and TC were dried, homogenized into fine powder via a mixer mill, and passed through a 2-mm sieve. SOM was determined using the loss on ignition method (Karam 1993). TN and TC were measured via dry combustion using a Carlos Erba CHN autoanalyzer (McGill and Figueiredo 1993, Tiessen and Moir 1993). TP was measured after nitric-perchloric acid digestion (Sommers et al. 1970) using an automated ascorbic acid method (Murphy and Riley 1962) on a Lachat autoanalyzer (O'Halloran 1993). Soil and plant tissue N:P ratios on a mass basis were calculated to gauge nutrient limitation (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Bedford et al. 1999). We measured the soil pH of a subset of five samples in dilute salt solution (0.01 M $CaCl_2$).

2.2.5 Seed bank

A seedling emergence study was used to: (1) examine the seed bank in Palo Verde Marsh; and (2) gauge the short-term impact of physical disturbance via fangueo upon the seed bank. A seedling emergence experiment was established with the following factors: *Typha* removal via fangueo (using the C and F plots) and water level (drawdown, flooded). Two sets of duplicate composite cores were collected from each of the C and F treatment plots. Each composite contained 11 cores (5-cm depth, 4.6-cm diameter each; total pre-composite cores = 660; total volume and area for each composite sample was 914 cm^3 and 183 cm^2 respectively). Each composite was mixed and placed in a 2-cm layer on top of a 5-cm layer of sterilized potting soil in flats with the following dimensions: 25-cm long x 20-cm wide x 10-cm deep. Each duplicate was assigned to one of two water level treatments: flooded or drawdown. Whereas the water level in the flooded flats was maintained 3 cm above the soil surface, the water level in the drawdown flats was kept moist but not flooded. This study was conducted in a lathe house at the OTS' Palo Verde Biological Station. In order to account for contaminant seeds, eight control trays were included in the experimental design (four drawdown and four flooded). However, we lost two controls due to an iguana that repeatedly defecated from the lathehouse roof above these trays preventing any potential germination. Emerging seedlings were identified and counted on seven dates between May and September, 2007.

2.2.6 Plant community

Vegetation surveys and measurements were conducted within each 1-m^2 quadrat. We established these three smaller nested quadrats within each 20-m^2 plot because determining percent cover and measuring *Typha* biomass growth was not feasible across the entire 20-m^2 plot. For statistical analyses, we used the means from the three nested and randomly assigned 1-m^2 quadrats to represent the community found in the larger 20-m^2 plots. During the first dry season, percent cover was determined on roughly a monthly basis (March, April, and May 2007). Thereafter, percent cover was measured twice during the first wet season (June and September, 2007) and once during the second dry season (April 2008). In order to quantify the post-disturbance *Typha* recruitment potential, the number of *Typha* seedlings present in each 1-m^2 quadrat was recorded during these vegetation surveys. The cover data was used to calculate species richness and diversity (using the Shannon-Wiener index with the use of the relative percent cover of species i to represent p_i in the calculations). In order to gauge species dominance, we used the percent cover values to calculate importance values (I.V.), calculated as: I.V. = (mean % cover * Frequency)/100. We also calculated indicator values for the standing vegetation via indicator species analysis (INSPAN) (Dufrene and Legendre 1997) using PC-ORD Version 4 (MjM Software, Gleneden Beach, OR, USA; McCune and Medford 1999). Indictor values represent the percent of perfect indication for a given group.

Typha ramet density, basal diameter [in two directions: a long diameter (d_1) and a short diameter (d_2)], and height were measured within each 1-m^2 quadrat in April 2007 and 2008. A ramet is an individual culm or shoot in a clonal plant and the product of asexual vegetative propagation. Ramets that are connected to each other via rhizomes are genetically identical and collectively called a genet. Since destructive sampling to determine cattail biomass would increase light availability and bias future vegetation surveys, an allometric relationship for aboveground cattail biomass was developed (*sensu* Miao et al. 2008) using biomass, leaf height, and basal area measurements from 148 ramets. Basal area was calculated *sensu* Miao et al. (2008) as the area of an ellipse [i.e., area = $\pi * (d_1/2) * (d_2/2)$] using two perpendicular basal diameter measurements (d_1 and d_2) for each ramet. These measurements produced the following equation ($r^2 = 0.97$) which was used to calculate *Typha* aboveground biomass within each plot:

$$\ln\text{(Aboveground Biomass)} = -5.729 + 0.420 * \ln\text{(Basal Area)} + 1.281 * \ln\text{(Height)}$$

In order to quantify annual cattail horizontal rhizome growth, fifteen 10-m permanent transects were established on the edges between the C and F plots. The distance from the edges to the furthest cattail ramet was measured at 2-m intervals during the 2007 and 2008 dry season. However, on two of these transects, cattail recruitment and growth was so extensive that we could not determine the limit of vegetative expansion. Hence, these two transects were not measured and the results from the remaining 13 transects are presented here.

2.2.7 Birds

We conducted avian surveys to determine the number of individuals and species that visited the C and F treatments. Due to obstructed visibility in most plots and the need to survey from afar, only three blocks were available for the avian surveys. On two consecutive days (17 and 18 February, 2007), avian surveys were conducted at each plot once in the morning and once in the afternoon (total of two morning surveys and two afternoon surveys for each plot). A survey consisted of scanning the treatment area including the plot buffer with binoculars for 15 minutes in order to identify the number of individuals of each species present.

2.2.8 Data analyses

To assess the impact of *Typha* removal on the measured avian, soil, and seed bank dependent variables, we used univariate mixed factor analyses of variance (ANOVA) models with block as a random effect and *Typha* removal as a fixed effect. For the seed bank analyses, water level was also added to the model as a fixed effect. For the analyses, avian density, seed density and soil TP, TN, TC, and SOM were log-transformed to improve normality. The avian, soil, and seed bank response variables were only measured for two levels of the *Typha* removal treatment (C and F) and, hence, means were compared using Student's t-tests.

To compare *Typha* stand characteristic (*Typha* ramet density, height, and aboveground biomass) differences in response to *Typha* removal, we used repeated measures mixed factor effects ANOVA models with the following independent variables: block (random effect), year (fixed effect), *Typha* removal (fixed effect), and the interaction between year and *Typha* removal. *Typha* data was collected from all three *Typha* removal treatment levels for this analysis. So, comparisons of means between treatments within years and between years within treatments were conducted using Tukey's Studentized Range (HSD) tests and repeated measures t-tests respectively.

To test for differences in plant diversity and richness, we also used repeated measures mixed factor effects ANOVA models but with the following independent variables: block (random effect), date (fixed effect), *Typha* removal (fixed effect), and the interaction between date and *Typha* removal. Data for this analysis was also collected from all three *Typha* removal treatment levels. Comparisons of means between treatments within dates and between dates within treatments were conducted using Tukey HSD tests and repeated measures t-tests respectively. All ANOVA analyses were conducted using SAS Version 9.1.3 (SAS Institute, Cary, NC, U.S.A.).

To illustrate changes in plant community composition due to the *Typha*-removal treatments, a nonmetric multidimensional scaling (NMS) analysis (Kruskal 1964, Mather 1976, McCune and Grace 2002) was performed using PC-ORD (McCune and Medford 1999). Prior to analysis, we relativized the species cover data by species maxima and removed rare species which were defined as species present in less than 5 % of the plots. We also removed one plot survey that had zero plants present. The resultant matrix contained 20 species and 251 plots. Bray-Curtis dissimilarity coefficients were used to quantify plant species compositional distance (Bray and Curtis 1957). In order to determine the appropriate number of dimensions to include in the analysis, we used a stepdown procedure to compare the number of dimensions with the corresponding change in final ordination stress. We initially evaluated 6 axes using 100 runs with real data, a stability criterion of 0.00001, a maximum of 400 iterations, and a Monte Carlo test with 300 randomizations to determine whether the resultant axes were stronger than those identified by chance (McCune and Grace 2002). Based upon this procedure, a three dimensional analysis was deemed optimal and resulted in a final stress of 17.1, a P value of 0.001, and a final instability of 0.00001 after 219 iterations. Multi-response permutation procedures (MRPP) were then used to compare the treatment effect on plant community composition within and between dates. For all MRPP analyses, we used Bray-Curtis dissimilarity as the distance measure and n/(sum n) to weight groups.

2.3 Results

2.3.1 Soil

There was no significant impact of fangueo on bulk density or any of the soil properties we measured (Table 2.1). Of the soil properties measured, the blocking factor was only significant for TP ($F_{14,14} = 4.3$, $P < 0.01$) which had a wide range in values; the median, minimum, and maximum TP were 473, 357, and 1114 mg/kg respectively. The soil N:P at Palo Verde Marsh is low and there was no significant relationship between

Table 2.1: Effect of *Typha* removal via fangueo on mean ± SE soil properties at the site. There was no significant short-term impact of fangueo on any of the properties measured.

	***Typha* not removed**	***Typha* removed via fangueo**
BD (g/cm^3)	1.02 ± 0.03	0.95 ± 0.06
SOM (g/kg)	99 ± 7	108 ± 14
TC (g/kg)	39.4 ± 3.8	48.1 ± 8.3
TN (g/kg)	3.5 ± 0.3	3.9 ± 0.6
TP (mg/kg)	529 ± 53	545 ± 36
C:N [mass]	11.4 ± 0.5	12.0 ± 0.6
N:P [mass]	6.8 ± 0.5	7.0 ± 0.9

soil TP and *Typha* aboveground biomass, ramet density, or ramet height. The mean ± SE soil pH (in 0.01 M $CaCl_2$) was 6.5 ± 0.1.

2.3.2 Seed bank

As in most wetlands, seed bank germinant density and richness under drawdown conditions was higher than under flooded conditions (Figure 2.5ab; $F_{1,41}$ = 75.3, P < 0.0001; $F_{1,41}$ = 51.9, P < 0.0001 respectively). The seed bank in Palo Verde Marsh is both dense and rich (Figure 2.5ab). There was no apparent impact of physical disturbance via fangueo on seed bank germinant density or richness (Figure 2.5ab). *T. domingensis* is one of the most common species in the seed bank at the site; for the drawdown treatment, the mean ± SE *T. domingensis* seed bank germinant density was 456 ± 61 germinants/m^2.

2.3.3 Typha biomass, ramet architecture, recruitment, and clonal expansion

As expected, *Typha* removal via fangueo resulted in a dramatic decrease in *Typha* aboveground biomass (ABG), ramet height, and ramet density during the first year (Figure 2.6abc; $F_{2,28}$ = 229.1, P < 0.0001; $F_{2,28}$ = 704.4, P < 0.0001; $F_{2,28}$ = 227.5, P < 0.0001 respectively). However, post-removal *Typha* recruitment and growth at the site was high (Figure 2.6abc) and resulted in significant increases in *Typha* ABG, height, and density in the *Typha*-Removed plots (F and FF treatment levels) in the second year (Figure 2.6abc; $F_{1,42}$ = 13.9, P < 0.001; $F_{1,42}$ = 21.5, P < 0.0001; $F_{1,42}$ = 14.7, P < 0.001 respectively). Despite this increase, *Typha* ABG, height, and density in the Typha-

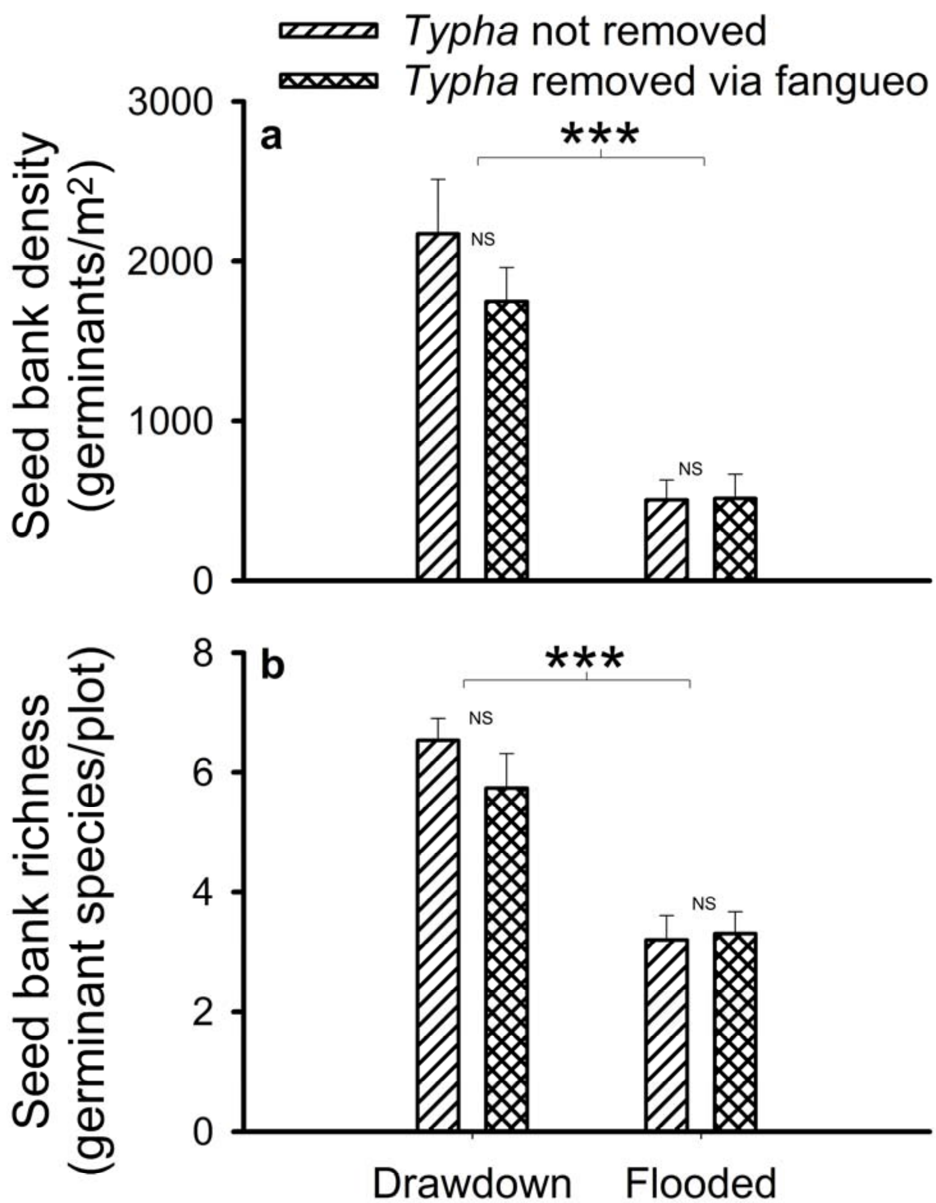

Figure 2.5: Impact of *Typha* removal via fangueo and waterlevel on seed bank (a) density and (b) richness (mean + SE). *** $P < 0.001$

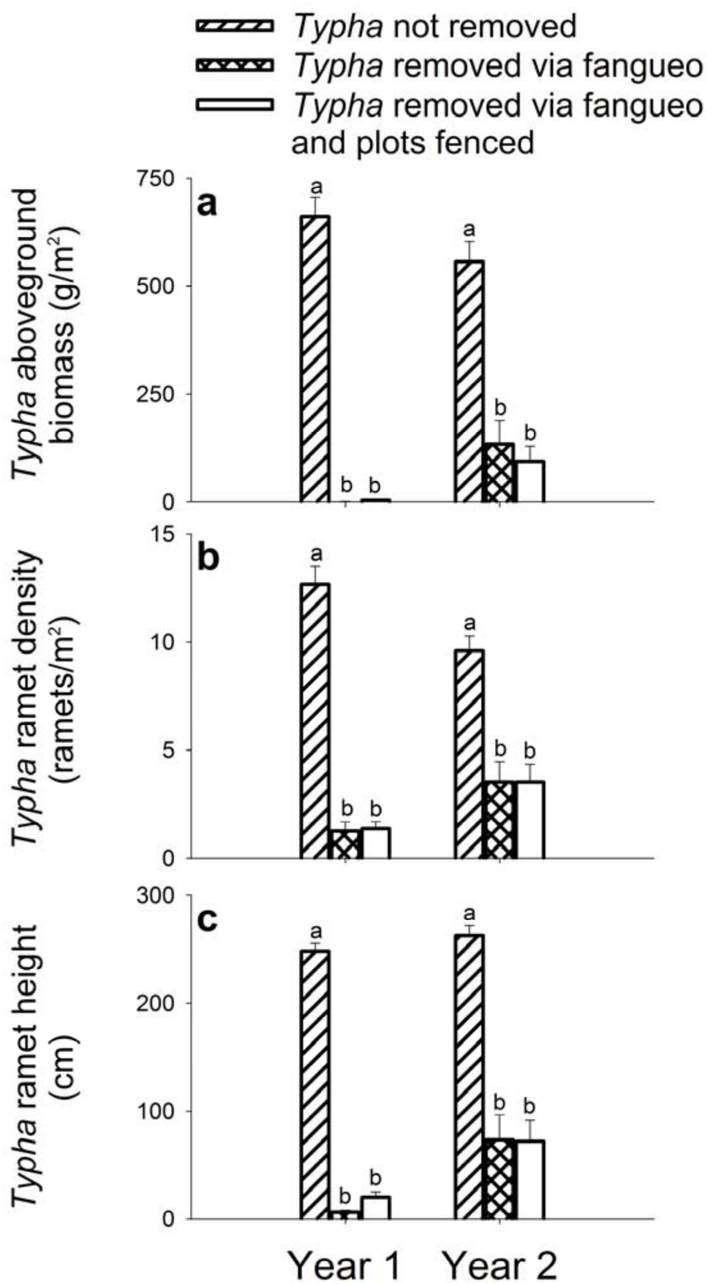

Figure 2.6: Impact of *Typha* removal via fangueo and fenced plots on *Typha* (a) aboveground biomass, (b) ramet density, and (c) ramet height (mean + SE). Letters refer to comparisons between treatments within each year.

Removed plots in the second year were still much lower than in the control plots (Figure 2.6abc; $F_{2,28} = 43.3$, $P > 0.0001$, $F_{2,28} = 76.9$, $P < 0.0001$; $F_{2,28} = 24.5$, $P < 0.0001$ respectively). Throughout the study, there was no significant difference between the two *Typha*-Removed treatment levels (F and FF) in *Typha* ABG, height, or density (Figure 2.6abc).

Recently germinated *Typha* seedlings were observed in the *Typha*-Removed plots during the March and April 2007 vegetation surveys. *Typha* recruitment in these plots was highest in April 2007 with a mean ± SE and maximum of 84 ± 20 and 368 individuals/m^2 respectively. *Typha* horizontal rhizome expansion in the second year along the edge between control and fangueo plots was also high with a mean ± SE and maximum expansion of 247 ± 41 and 571 cm/year respectively.

2.3.4 Plant community

Typha removal via fangueo resulted in higher plant species diversity (Shannon H') and richness (Figure 2.7ab; $F_{2,221} = 162.3$, $P < 0.0001$; $F_{2,221} = 54.6$, $P < 0.0001$ respectively). Both diversity and richness were higher during the wet season surveys than the dry season surveys (Figure 2.7ab; $F_{5,221} = 21.0$, $P < 0.0001$; $F_{5,221} = 74.0$, $P < 0.0001$ respectively). Throughout the study, there was no difference in plant species diversity between the two *Typha*-Removed treatment levels (F and FF; Figure 2.7a). However, the fenced plots (FF) had a slightly higher plant richness than the unfenced plots (F) (Figure 2.7b; $F_{1,138} = 10.1$, $P = 0.002$) and this difference was greatest during the months of May and June (Figure 2.7b; $F_{4,138} = 3.2$, $P = 0.016$).

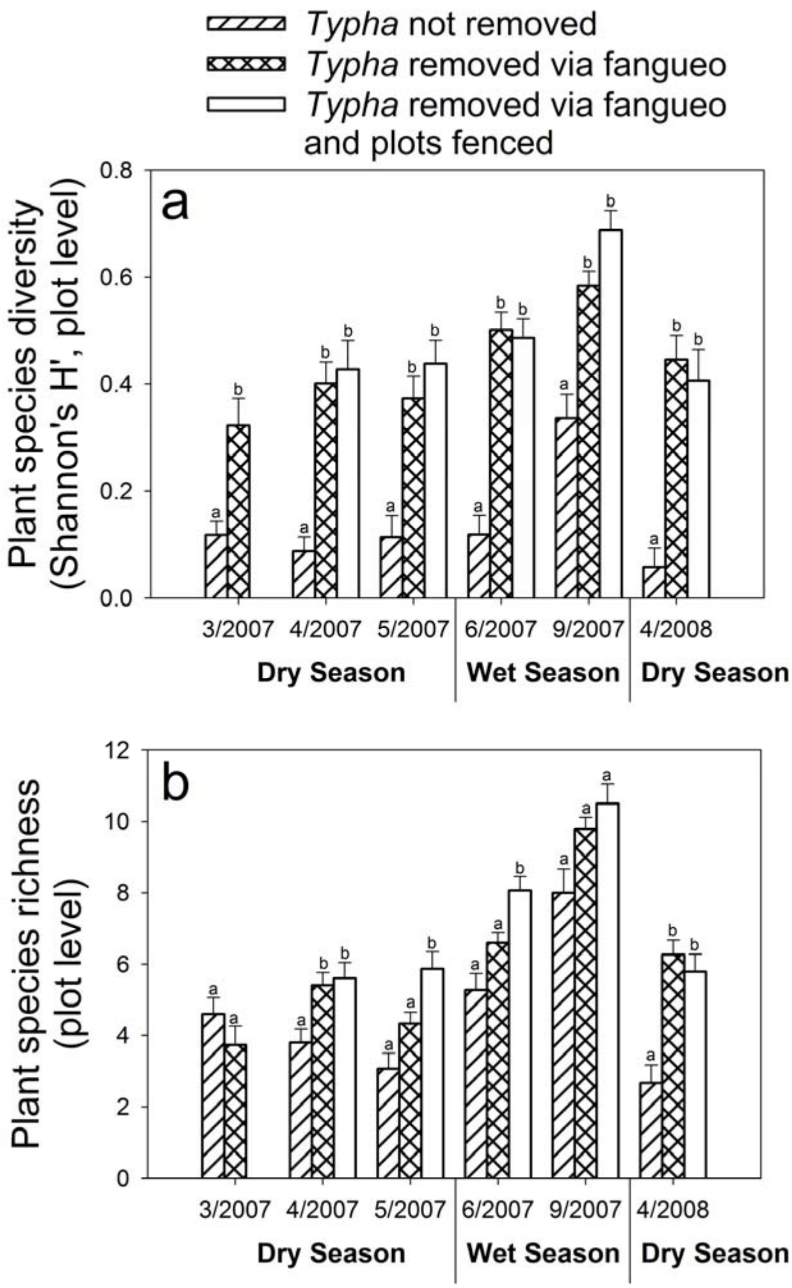

Figure 2.7: Impact of *Typha* removal via fangueo and fenced plots on plant species (a) diversity and (b) richness (mean + SE). Letters refer to comparisons between treatments within each sampling period.

The first NMS ordination (Figure 2.8) depicts changes in plant community composition after *Typha* removal via fangueo throughout the study. There was no significant difference between the plant community in the *Typha*-removed treatments (F and FF) at any single date in the study (MRPP, $A < 0.02$ and insignificant P for all tests); hence, these two treatments are illustrated as one group (*Typha* removed via fangueo) in the NMS ordination. These surveys were conducted in both the wet and dry season and the ordination depicts the change in composition in response to seasonal flooding. The proportion of the compositional variance represented by the three axes included in the analysis was 0.619 (Axis 1: 0.167, Axis 2: 0.265, and Axis 3: 0.187). Although we tested various environmental variables (i.e., soil properties, elevation, bare ground, litter cover, water depth), water depth was the only variable we measured that was strongly correlated to the biplot axes. Water depth was most strongly correlated to the vertical biplot axis ($r^2 = 0.370$, $\tau = 0.476$).

As expected, the plant community in the *Typha* removed via fangueo plots (F) was significantly different than in the control plots (C) immediately after fangueo (MRPP, March 2007, $A = 0.28$, $p < 0.0000001$) and throughout the course of this study (MRPP, April 2007, $A = 0.29$; May 2007, $A = 0.30$; June 2007, $A = 0.27$; September 2007, $A = 0.26$; April 2008, $A = 0.33$; $P < 0.000001$ for all tests). However, there was considerable temporal change in the composition found in both *Typha* removed via fangueo treatments (F and FF) particularly in response to seasonal flooding; there was a

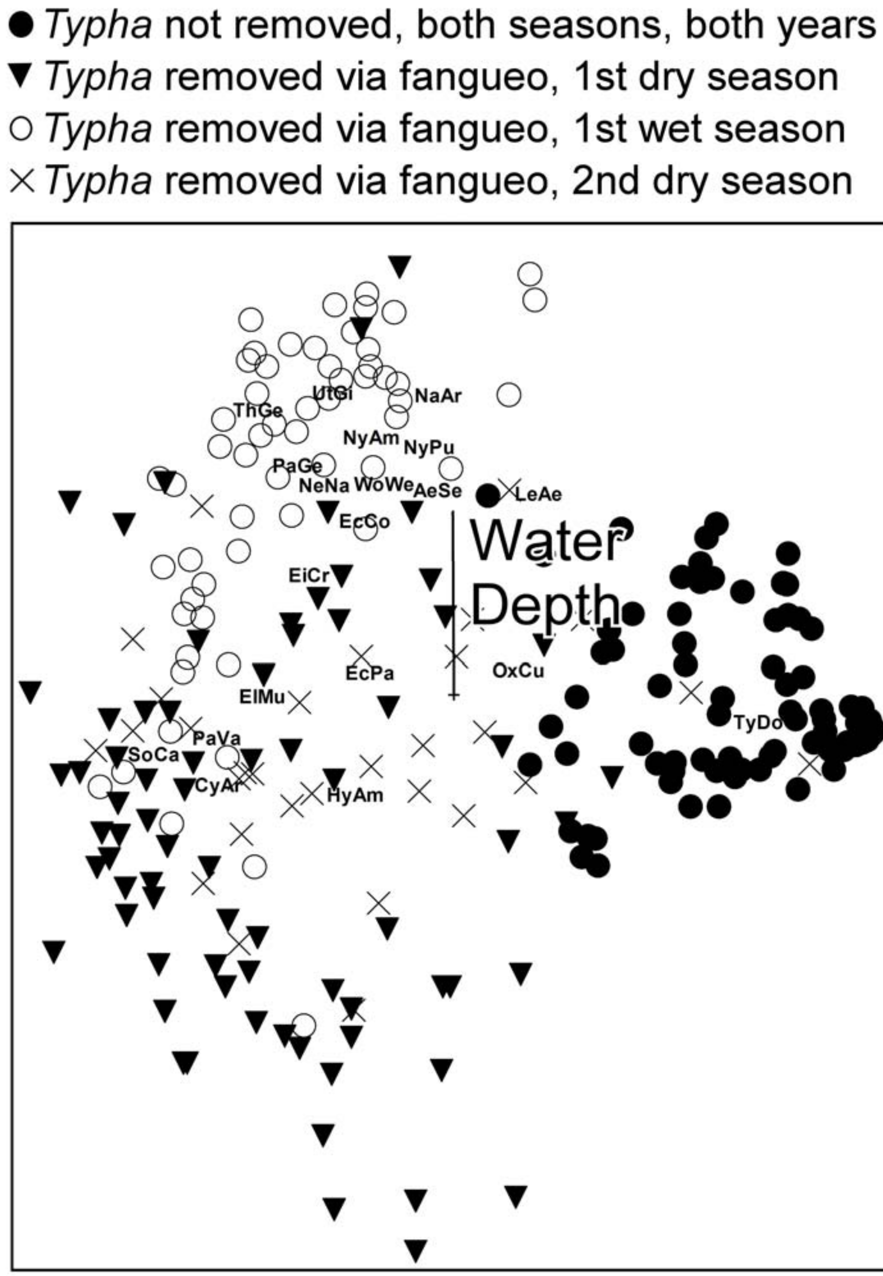

Figure 2.8: Impact of *Typha* removal via fangueo and seasonality on plant community composition. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four letter species codes that can be interpreted with Table 2.3. Water depth (the only environmental variable we measured with a strong correlation to ordination space) was most strongly correlated to the vertical axis.

significant difference between the wet and dry season communities (MRPP, dry 2007 vs. wet 2007, $A = 0.06$, $P < 0.00001$; wet 2007 vs. dry 2008, 0.05, $P < 0.00001$) that can also be seen in Figure 2.8. In the second dry season, the composition in these plots (F and FF) showed more variation than in the first year; whereas some of the plots were dominated by *Hymenachne amplexicaulis*, *Cyperus articulatus*, and *Paspalum vaginatum*, others were dominated by *Typha* (compare the locations of the X symbols in Figure 2.8 with the species centroids). In Figure 2.9AB, we show plot-level trajectories for six paired plots. This figure highlights the impact of seasonal flooding (note the parallel trajectories that connect the wet and dry season communities). These trajectories also show that *Typha* dominance has increased in some of the managed plots. Whereas Figure 2.9A shows plots that were not dominated by *Typha* by the end of the second dry season, Figure 2.9B shows plots that increased in *Typha* dominance by the end of the second dry season.

The species present in the groups denoted in the NMS ordinations with the highest importance values (i.e., the most frequent and abundant species) are shown in Table 2.2. Note that both the importance values and the indicator values for these species are shown in this table. As expected, the *Typha*-Control plots were strongly dominated by *Typha* and very few other species were present in abundance in these plots. After *Typha* removal, plots retained little vegetation cover until the wet season when the floating and floating rooted species *Neptunia natans* and *Nymphaea amazonum* became the dominant plants. During the second dry season in these *Typha*-removed

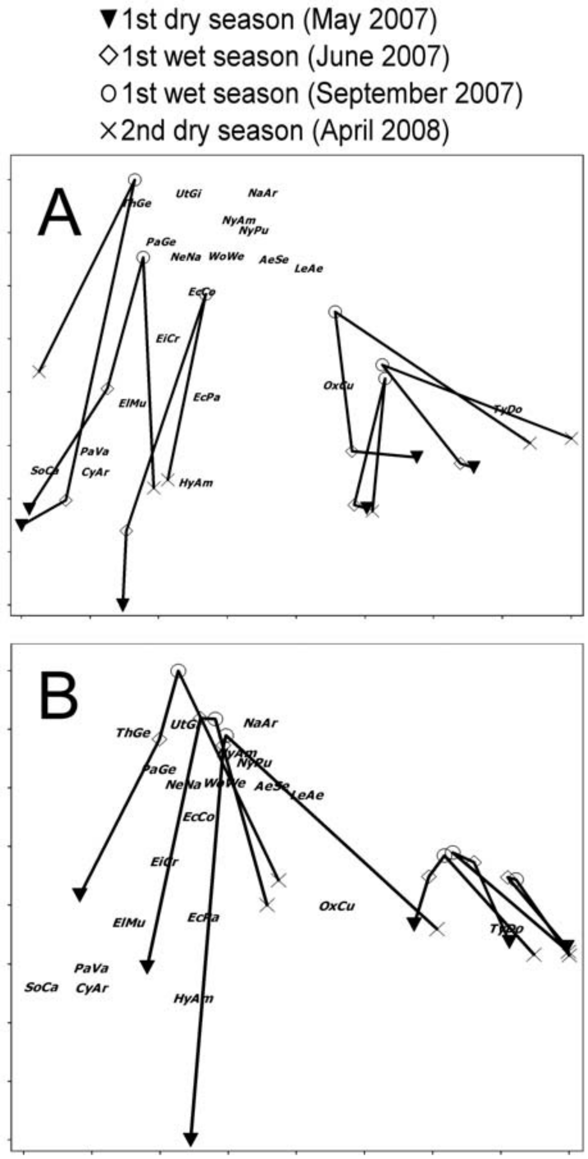

Figure 2.9: Plot-level plant community compositional trajectories. Whereas the trajectories on the left show plots where *Typha* was removed via fangueo, the trajectories on the right show plots where *Typha* was not removed. Although many *Typha*-removed plots were not dominated by *Typha* at the end of the second dry season (A), *Typha* has become established and is becoming more dominant in some *Typha*-removed plots (B). Note the pronounced impact of seasonal flooding/drawdown on the plant community that is reflected by the close to parallel lines that connect the seasonal assemblages.

Table 2.2: Common plant species in the control and *Typha* removed via fangueo plots during the dry and wet seasons. The five plant species with the highest importance values are shown for each of the four groups illustrated in the nonmetric multidimensional scaling (NMS) analysis. Species are listed in descending rank order of importance value. The values in parentheses represent the importance value (mean % cover * Frequency)/100) and indictor value (% of perfect indication for that group; calculated using indicator species analysis, INPAN) for each species respectively. Significant indicator values are denoted by an asterisk.

***Typha* not removed, Both Seasons Both Years**	***Typha* removed via fangueo, Dry Season 2007**	***Typha* removed via fangueo, Wet Season 2007**	***Typha* removed via fangueo, Dry Season 2008**
Typha domingensis (82, 89*)	*Paspalum vaginatum* (2, 12)	*Neptunia natans* (20, 65*)	*Hymenachne amplexicaulis* (13, 44*)
Hymenachne amplexicaulis (1, 6)	*Hymenachne amplexicaulis* (2, 8)	*Nymphaea amazonum* (11, 72*)	*Neptunia natans* (6, 21)
Neptunia natans (1, 3)	*Solanum campechiense* (1, 46*)	*Utricularia gibba* (3, 44*)	*Typha domingensis* (6, 7)
Nymphaea amazonum (1, 4)	*Neptunia natans* (1, 4)	*Hymenachne amplexicaulis* (3, 14)	*Paspalum vaginatum* (4, 18*)
Echinodorus paniculatus (0, 5)	*Cyperus articulatus* (1, 13)	*Paspalum vaginatum* (2, 12)	*Eichhornia crassipes* (3, 21*)

Table 2.3: Common plant species observed in Palo Verde Marsh during the course of this study. Each species is accompanied by a four letter code that can be used to interpret the species centroids in the NMS ordination. Common species were defined as those present in greater than 5% of the plots.

Species	Code	Species	Code
Aeschynomene sensitiva	AeSe	*Nymphaea amazonum*	NyAm
Cyperus articulatus	CyAr	*Nymphaea pulchella*	NyPu
Echinochloa colona	EcCo	*Oxycaryum cubense*	OxCu
Echinodorus paniculatus	EcPa	*Paspalum vaginatum*	PaVa
Eichhornia crassipes	EiCr	*Paspalidium geminatum*	PaGe
Eleocharis mutata	ElMu	*Solanum campechiense*	SoCa
Hymenachne amplexicaulis	HyAm	*Thalia geniculata*	ThGe
Lemna aequinoctialis	LeAe	*Typha domingensis*	TyDo
Najas arguta	NaAr	*Utricularia gibba*	UtGi
Neptunia natans	NeNa	*Wolffiella welwitschii*	WoWe

plots, several grass species (*Hymenachne amplexicaulis* and *Paspalum vaginatum*) and *Typha* all increased in importance (i.e., their importance values increased).

2.3.5 Birds

Typha removal via fangueo resulted in higher avian density and richness (Figure 2.10ab; $F_{1,2} = 19.3$, $P = 0.048$; $F_{1,2} = 18.1$, $P = 0.051$ respectively; Table 2.4). Whereas eleven species were observed in the F plots, only four species were observed in the C plots. Only the Northern Jacana (*Jacana spinosa*) was observed in both treatments. In plots where *Typha* was removed, Black-bellied Whistling Ducks (*Dendrocygna autumnalis*), Blue-winged Teal (*Anas discors*), and Northern Jacana (*Jacana spinosa*) had the highest densities (Table 2.4). The density of Black-bellied whistling ducks was especially large in these F plots (mean ± SE: 1798 ± 396 individuals/ha). In contrast, the intact *Typha* stands had fewer individuals and different species. The Groovebilled Ani (*Crotophaga sulcirostris*) was the most common species in the C plots (Table 2.4).

2.4 Discussion

Cattail invasions are common in degraded wetlands throughout the world and these invasions typically result in the loss of biodiversity and important ecosystem services. Hence, there is much interest in sustainable techniques that can be used to restrict the extent of cattail expansion and restore or maintain previously-present services. The most common way to manage invasive cattail stands is with aerial herbicidal applications. Yet, aerial herbicidal applications can be expensive and the

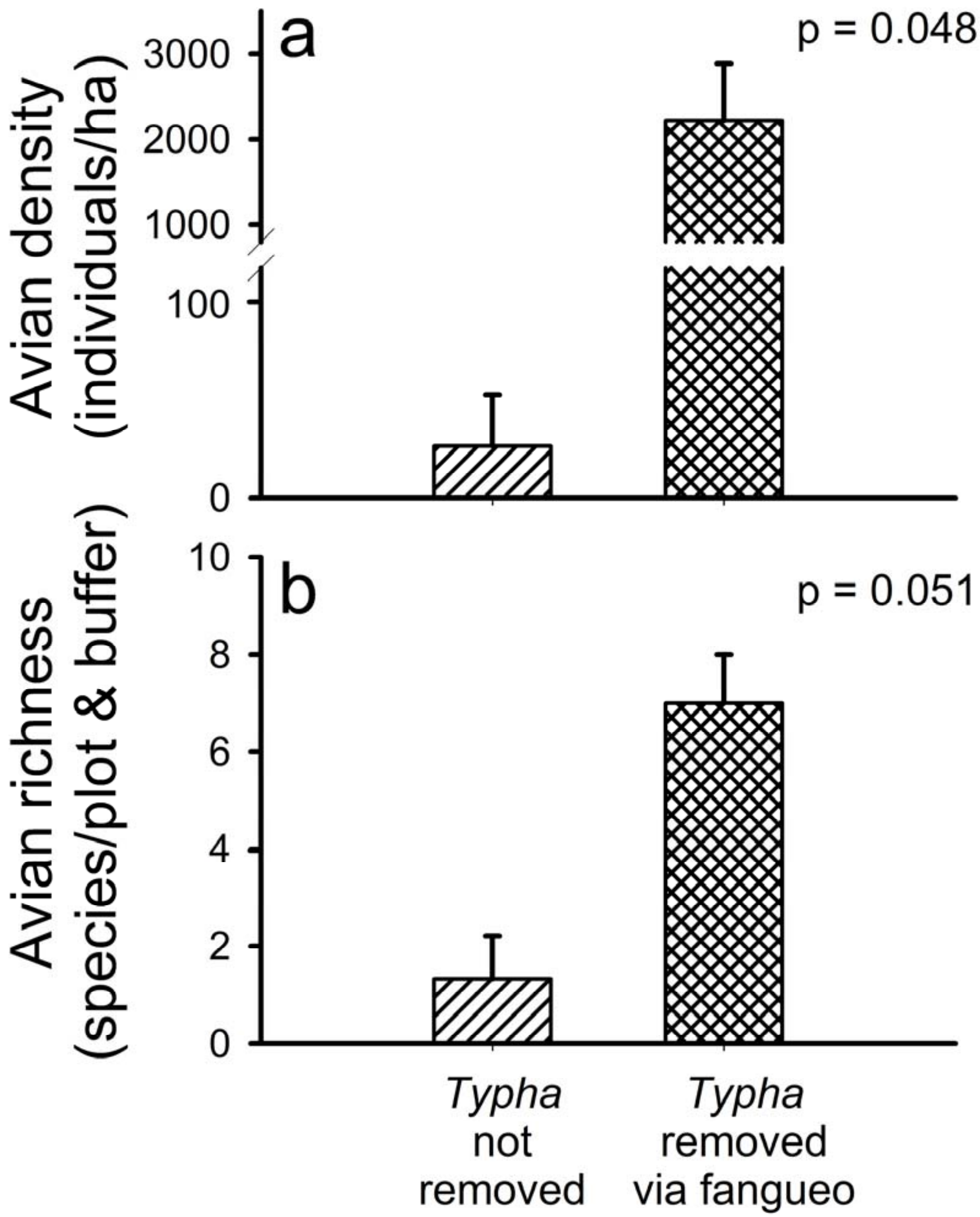

Figure 2.10: Impact of *Typha* removal via fangueo on avian (a) density and (b) richness (mean + SE).

Table 2.4: Effect of *Typha* removal via fangueo on mean ± SE avian density (number of individuals per ha).

	***Typha* not removed**	***Typha* removed via fangueo**
Groovebilled Ani (*Crotophaga sulcirostris*)	19 ± 19	0
Sora (*Porzana carolina*)	1 ± 1	0
Purple Gallinule (*Porphyrula martinica*)Sora	<1	0
Northern Jacana (*Jacana spinosa*)	2 ± 2	57 ± 33
Black-bellied Whistling Duck (*Dendrocygna autumnalis*)	0	1798 ± 396
Blue-winged Teal (*Anas discors*)	0	345 ± 297
Limpkin (*Aramus guarauna*)	0	12 ± 5
Fulvous Whistling Duck (*Dendrocygna bicolor*)	0	3 ± 3
Snowy Egret (*Egretta thula*)	0	2 ± 2
Muscovy Duck (*Cairina moschata*)	0	1 ± 1
Great Egret (*Andrea alba*)	0	1 ± 1
Tricolored Heron (*Egretta tricolor*)	0	1 ± 1
White Ibis (*Eudocimus albus*)	0	1 ± 1
Snail Kite (*Rostrhamus sociabilis*)	0	1 ± 1

impacts on aquatic ecosystems are somewhat unknown and potentially very large (Pratt et al. 1997, Relyea 2005, Kolpin et al. 2006, Pérez et al. 2007, Rinella et al. 2009). Hence, alternative and more sustainable cattail management methods are of great interest to wetland ecologists and practitioners.

This is the first study to quantify the effectiveness of a unique cattail management technique that has been used successfully in one of the most ecologically important wetland complexes in Central America. This method, fangueo, is relatively cheap ($40 per ha in this site), rapid (one tractor can remove 10-16 ha of *Typha* per day), and has been used for almost two decades to restrict cattail expansion, create habitat heterogeneity, and increase both plant and avian diversity. Thousands of tourists visiting Palo Verde Marsh have observed the very large increase in avian visitation that results from cattail management. The concentrations of wetland birds in the managed sections of Palo Verde Marsh are so dramatic that one of our plant surveys was briefly interrupted by the arrival of the president of Costa Rica who flew to the marsh in a helicopter in order to film a conservation-focused video with the wetland birds in the background. Despite such public attention, a replicated field-based experiment designed to measure and document the impact of fangueo had not been conducted until this study. Hence, the potential application of this technique for cattail management in other degraded wetlands had not been adequately investigated and communicated.

2.4.1 Impact of fangueo on soil properties and the seed bank

During rice farming in NW Costa Rica, fangueo is used to control weeds and also decrease water loss due to infiltration via an increase in soil compaction. Many wetland soils are characterized by low bulk densities and the compaction associated with tractor usage in most wetlands could result in long-lasting change. We hypothesized that areas of PVNP where the fangueo treatment was used to control *Typha* would be more compacted (i.e., have higher soil bulk densities) relative to areas where the fangueo treatment was not used. We also expected that the mechanical disturbance associated with fangueo might have an impact on the seed bank and alter the pool of plant species that would germinate from the seed bank. However, we found no apparent long-term impact of fangueo on soil bulk density or seed bank germinant composition. Importantly, fangueo had no impact on any of the soil properties we measured (Table 2.1). We must note that we were not able to measure plant available inorganic nitrogen which is often elevated after disturbances that remove plant biomass (Richardson 2008b). The soil bulk density in this wetland is relatively high compared to many other wetlands, particularly wetlands with organic soils and very low soil bulk densities. Tractor use in wetlands with low soil bulk densities is not advised because it would likely result in long-lasting change and also probably be risky for tractor operators due to high soil instability. The relatively compact clays at Palo Verde Marsh are stable enough to support a tractor. They also expand and contract due to seasonal flooding and drying cycles, a process that has been shown to somewhat lessen the impact of soil compaction in Vertisols (Sarmah et al. 1996).

This study is among the first to report soil nutrient concentrations for Palo Verde Marsh. Although the main focus of this study is not on soil nutrient dynamics, *Typha* dominance is unlikely in wetlands with low phosphorus availability and high N:P ratios. Although N:P stoichiometry in aquatic ecosystems cannot be used as a definitive indicator of nutrient limitation, it is a useful tool that can be used to initially gauge nutrient limitation and identify interesting patterns in nutrient availability. N:P ratios have been used successfully to identify nutrient limitation in lacustrine (Downing and McCauley 1992), marine (Redfield 1958, Downing 1997), and wetland ecosystems (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Bedford et al. 1999). In wetlands, soil and macrophyte mass N:P ratios greater than 16 are sometimes indicative of P-limitation, whereas wetlands with soils and macrophyte mass N:P ratios less than 14 are sometimes indicative of N-limitation (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Bedford et al. 1999). Most published biogeochemical investigations in Central American wetlands have been conducted in the uniquely oligotrophic, calcareous, and P-limited wetlands of the Yucatan Peninsula (Rejmánková et al. 1996, Rejmánková 2001) and a P-limited coastal mire in Panama (Troxler 2007). The results from these studies and from the Everglades (Davis 1994, Richardson et al. 1999, Noe et al. 2001) are sometimes extrapolated to all wetlands in the region and seem to imply that most Central American wetlands may be P-limited. However, the low soil N:P (mean ± SE = 6.9 ± 0.5) in Palo Verde Marsh indicates that this wetland and others in the region may be N-limited. *Typha* foliar N:P measurements from another marsh in Palo Verde National Park (La Bocana Marsh) were also indicative of nitrogen limitation (mean ± SE = 7.6 ± 0.2). Note also that these N:P values and the other soil property values measured at Palo Verde Marsh are consistent with values reported for mineral soils in many temperate freshwater wetlands (Bedford et al. 1999).

The high soil phosphorus at PVNP relates to the potential for *T. domingensis* dominance since this species is not competitive in wetlands with low phosphorus concentrations (Richardson et al. 1999). *T. domingensis* is a competitive-dominant species (*sensu* Grime 1979) that is only able to form dense monocultures in area of low stress and high resource availability. *Typha* is less adapted to low resource environments where it is outcompeted by stress-tolerant species (*sensu* Grime 1979). In many tropical and subtropical wetlands, phosphorus availability has been linked to *T. domingensis* invasion (Craft and Richardson 1997, Vaithiyanathan and Richardson 1999, Chiang et al. 2000, Noe et al. 2001, Johnson and Rejmánková 2005). In the Everglades, soil phosphorus concentrations are correlated to *T. domingensis* dominance and a potential invasion threshold of about 500 mg P/kg (mass-basis) has been identified (Richardson et al. 1999, Debusk et al. 2001, Craft and Richardson 2008). Unenriched areas of the Everglades with little *Typha* typically have soil phosphorus values below this threshold. At Palo

Verde Marsh, the mean ± SE soil phosphorus is just above this threshold on a mass-basis (537 ± 31 mg P/kg). However, the mineral soils at Palo Verde Marsh have a higher bulk density than the organic soil of the Everglades Water Conservation Areas where this threshold was determined [mean ± SE: 0.98 ± 0.03 g/cm^3 versus roughly 0.1 ± 0.01 μg/cm^3 (Craft and Richardson 2008), respectively]. Hence, on a volume-basis, the mean soil phosphorus concentration at Palo Verde Marsh (528 μg P/cm^3) is far above the identified threshold in the Everglades (~50 μg P/cm^3 using the bulk density and mass-basis estimates cited above) and may help explain the potential for *Typha* dominance in wetlands in and around PVNP.

2.4.2 Impact of fangueo on *Typha* dominance and the plant community

As in most wetlands that are dominated by *Typha*, there are very few plant species in Palo Verde Marsh that can survive and compete with the very dense, tall, rapidly expanding, and interconnected *Typha* ramets (Table 2.2; Figure 2.8). *Typha* utilizes a "guerilla" clonal growth strategy (*sensu* Lovett Doust and Lovett Doust 1982) to access new resource patches, monopolize nutrients, and produce enough ramets to limit the light available to other species. As a result, *Typha* marshes are among the most productive ecosystems in the world (Richardson 1979) and the control and removal of mature *Typha* stand biomass is typically very difficult. At PVNP, there are some marsh sections (e.g., La Bocana Marsh) that have *Typha* stands with ramets that are over 5-m tall. Most of the mature *Typha* stands in our study area, Palo Verde Marsh, are between 2 and 4-m tall with ramet densities typically in the 9-14 ramets/m^2 range.

As a result of this large amount of biomass and the tremendous potential for *Typha* clonal regrowth, the removal of mature *Typha* stands initially challenged natural resources managers at PVNP who experimented with many techniques before successfully using fangueo (McCoy and Rodriguez 1994). In this experiment, the fangueo treatment resulted in a very large reduction in *Typha* aboveground biomass, ramet density, and ramet height (Figure 2.6abc). Fangueo has proven to be a very effective technique for short-term control of PVNP *Typha* stands. However, like all *Typha* control efforts, fangueo is most likely to be effective when combined with an abiotic physiological stressor (e.g., anaerobic conditions due to flooding or low water availability due to drought). Also, the importance of *Typha* phenology and physiology is a critical component to *Typha* control. *Typha* store large carbohydrate energy reserves in rhizomes which are used to produce new ramets and recover from disturbances. Linde et al. (1976) demonstrated the importance of planning control efforts for periods when these energy reserves are at their minimum (e.g., for *T. latifolia*, when the fruiting head is being produced, immediately after the pistillate spathe leaf is shed). In this study, the removal via fangueo was implemented roughly one month prior to the production of fruiting heads.

After *Typha* removal in this study, seasonal flooding played an important role in determining plant community development and resulted in a distinct dry and wet season community (Figure 2.8; Figure 2.9; Table 2.2). During the wet season, floating and floating-rooted species like *Neptunia natans*, *Nymphaea amazonum*, and *Utricularia gibba* greatly increased in abundance. Many of these floating and floating-rooted species were not able to survive the dry season. Some emergent grass species like *Hymenachne amplexicaulis* and *Paspalum vaginatum* were able to grow in both seasons and became more dominant in the second dry season. Interestingly, the wet season plant community was more diverse than the dry season community (Figure 2.7ab). Whereas many of the wetland plant species are adapted to the anaerobic conditions present during flooding in the wet season, a smaller number of species are adapted to the intense water limitation present during the drought-like conditions of the dry season.

Like many other seasonal wetlands, the seed bank in Palo Verde Marsh is relatively diverse and seedling germination during drawdown conditions was much greater than during flooded conditions (Figure 2.5ab). Seasonal wetland plant communities typically rely on a well-developed seed bank for plant community development after disturbances and seedling germination is typically greatest during drawdown conditions because there is higher light and oxygen availability which will improve the growth and survival of most species' seedlings (van der Valk 1981, Middleton 1999).

2.4.3 Typha resilience via dispersal, seed bank, recruitment, and clonal expansion

Established *Typha* stands are very resilient to disturbances. The long-term removal of *Typha* is complicated by *Typha*'s capability for tremendous clonal expansion, seed production, and dispersal (Richardson 2008a). McNaughton noted and compared this combination of *r*- and *K*- type strategies that enable *Typha* to be such a dominant, ubiquitous, and resilient genus (1966, 1975). Although the seed bank in Palo Verde Marsh is relatively diverse, *Typha* is one of the most ubiquitous and abundant species in the seed bank. The portion of the marsh in which *Typha* is actively managed is extremely small relative to the areas that are dominated by *Typha*. As a result, *Typha* seeds are readily dispersed via wind throughout the entire wetland. During April 2008, *Typha* dispersal was so widespread that the soil was coated in a white layer of *Typha* fruit. *Typha* germination from seeds *in situ* and in the lathehouse were both very high in this study and *Typha* had recruited into most of the *Typha*-Removed plots during the two years of our study. Given the short duration of this study, the *Typha* biomass, height, and density in most of these plots was still small at the end of this study relative to the plots covered in mature *Typha* stands (Figure 2.6abc). However, we expect that *Typha* would eventually dominate these plots without additional management. In addition to the high potential for *Typha* recruitment in Palo Verde Marsh, *Typha* clonal expansion is also rapid; the average rate of vegetative expansion along our fangueo edges was about 2.5 m/year. So, once a *Typha* ramet has recruited into an area, it is very likely that without additional management the area will be dominated by *Typha* in the future due to clonal expansion and resource monopolization. We discuss potential management schedules in the implications for restoration and invasive plant management section of the discussion.

2.4.4 Impact of fangueo on avian visitation

As in many freshwater marshes, the *Typha* control efforts at PVNP were initiated to improve avian habitat via the restoration of a hemi-marsh state. Hemi-marsh is a term often used by waterfowl managers to describe marshes that have a roughly 50:50 mix of interspersed open water and emergent vegetation. This combination of open water and vegetation has been shown to maximize the habitat available for large and diverse avian assemblages (Weller and Spatcher 1965, Kaminski and Prince 1981, Weller 1981). Although wetland bird species' habitat needs and life histories are spatially and temporally diverse, many species preferentially select marshes with greater habitat heterogeneity. Hence, the marsh vegetation and hydroperiod at many wetland wildlife refuges is actively managed to establish habitat heterogeneity (i.e., a hemi-marsh state) and maximize avian visitation.

The avian surveys in this investigation provide data to support previous observations and aerial surveys that note an increase in open water, avian density, and avian diversity following *Typha* removal via fangueo at PVNP (McCoy and Rodriguez 1994, Burnidge 2000, Trama 2005). As expected, plots that received the fangueo treatment showed an immediate and dramatic increase in avian density and richness (Figure 2.10ab; Table 2.4). Black-bellied Whistling Ducks were especially abundant in these plots. One noteworthy species at PVNP that utilizes managed marsh areas with open water is the Jabiru Stork (*Jabiru mycteria*), an endangered species in the region which can reach heights of 1.5 m and is a charismatic symbol for conservation in NW Costa Rica (Villareal Orias 2000). Our avian surveys characterize the immediate impact of fangueo over a short time interval. Our findings are similar to the results of a two-year study that used aerial surveys to characterize the species-specific seasonal differences in avian use of open (i.e., *Typha* removed) and vegetated areas (i.e., *Typha* present) (Trama 2005). During her study, Trama observed a total of 62 wetland bird species in Palo Verde Marsh and emphasized the importance of habitat heterogeneity; although the majority of species and individuals use the open areas of the marsh, a few species actually rely primarily on the *Typha* stands and/or the adjacent dry forest (Trama 2005).

Many other studies have shown that the dramatic avian response to marsh management is often accompanied by distinct shifts in the invertebrate community (Kaminski and Prince 1981, Murkin et al. 1982, Davis and Bidwell 2008). Wetland birds consume invertebrates; hence, wetland avian communities are dependent on wetland invertebrate communities (Batzer and Wissinger 1996). Since marsh management can have a large impact on invertebrate resource availability and predator-prey relationships

(Batzer and Wissinger 1996), additional research in Palo Verde Marsh is needed to assess the impact of seasonal hydrologic change, *Typha* management via fangueo, and cattle grazing on the invertebrate community as well as the other prominent organisms that are directly or indirectly dependent on the invertebrate community (e.g., amphibians, fish, microbes, and reptiles including turtles and crocodiles).

2.4.5 Implications for restoration and invasive plant management

Fangueo is an effective tool for restricting *Typha* expansion. In Palo Verde Marsh, fangueo has been successfully used to restrict *Typha* expansion, increase plant diversity, and dramatically increase the habitat available for the large concentrations of migratory and resident birds that utilize the marsh. In many degraded wetlands that have been invaded by *Typha* or other invasive emergent clonal plant species, the restoration of historic abiotic conditions is often not feasible or too costly. Biomass removal may be the most sustainable way to restrict the expansion of competitive dominant plants, increase diversity, and maintain previously-present ecosystem services (e.g., avian habitat). In grasslands and cultural landscapes throughout the world, mowing and grazing are often used to simulate historic herbivory rates, reduce the biomass of competitive dominant tall plants, and increase plant diversity (Collins et al. 1998, Bakker and Berendse 1999, Maron and Jefferies 2001). Annual mowing is also effectively used to remove plant biomass and increase plant diversity in many European floodplains (Grootjans et al. 2002, Gerard et al. 2008). In Central Mexican wetlands, *T.*

domingensis is repeatedly harvested for weaving, fodder, and fertilizer, a sustainable process that results in higher plant diversity and a source of income for local communities (Hall et al. 2008).

At PVNP, *Typha* removal via fangeuo is currently repeated annually and has resulted in a dramatic increase in plant and avian diversity. A successional management model for *Typha* removal in Palo Verde Marsh is shown in Figure 2.11. This model illustrates the impact of seasonal flooding and *Typha* removal via fangueo on the plant and avian community. The model is modified from the general successional models for temperate and tropical seasonal marshes developed by van der Valk 1981, and Middleton 1999, respectively. In Palo Verde Marsh, seasonal flooding dictates the plant community with distinct dry and wet season plant assemblages. High seedling germination from the relatively large and diverse seed bank occurs with the first rainfall events of the wet season. During the wet season, floating and floating-rooted species become more dominant. During the dry season, most of the wet season species die and only a few emergent species persist. At the beginning of the dry season, there are extensive open areas without vegetation that provide excellent avian habitat and support large and diverse bird assemblages. Currently, *Typha* is removed via fangueo at the beginning of the dry season which enables this cycle to occur. *Typha* mortality is increased due to the abiotic stresses associated with drought conditions during the dry season and then the anaerobic conditions associated with rapid flooding at the onset of

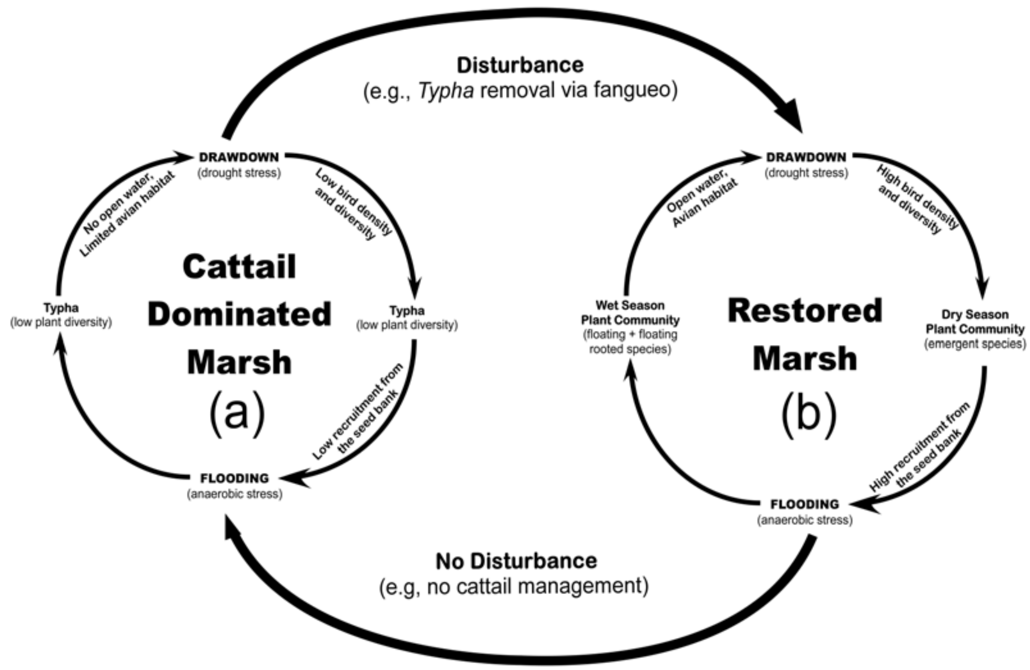

Figure 2.11: Plant successional model illustrating the impact of Typha removal via fangueo and seasonal flooding in Palo Verde Marsh ***(adapted from the general successional models for temperate and tropical seasonal marshes developed by van der Valk 1981, and Middleton 1999, respectively)*****. The first portion of the model (a) depicts the Typha-dominated plant community. The second portion of the model (b) depicts the restored plant community after cattail management using a Typha removal technique called fangueo.**

the wet season. Prior to fangueo, this area of the wetland was dominated by *Typha* throughout the entire year as depicted in Figure 2.11a. Fangueo is used to remove *Typha* and reestablish avian habitat and a seasonal plant community as illustrated in Figure 2.11b.

In other tropical seasonally flooded wetlands around the world (e.g., India, Australia, Zambia), the cessation of grazing has resulted in plant invasions, a reduction of open water, and a decrease in plant diversity. Although the cause of the *Typha* invasion at PVNP has not been conclusively attributed to the removal of cattle, the success of fangueo shows how the technique might be used in other tropical and temperate seasonal wetlands to simulate the historic and important role of herbivores during wetland succession (see van der Valk 1981, McCoy and Rodriguez 1994, Middleton 1999)

Typha invasion is currently common in many degraded wetlands throughout the world including the Everglades and Great Lakes marshes of the United States. Wetland scientists and managers seek alternative methods to restrict the expansion of *Typha*. Biomass removal is a potential option in many degraded wetlands for maintaining biodiversity and important ecosystem services. The fangueo process used at PVNP is an effective means for biomass removal and is an alternative to the aerial herbicidal applications which are frequently used to control *Typha* and other invasive emergent wetland plants. Based upon our measurements of *Typha* recruitment, vertical growth, and clonal expansion, we expect that fangueo does not need to be applied every year for *Typha* management; a 2-4 year cycle would probably be sufficient to limit *Typha* dominance. However, if the goal is to restore open areas with no vegetation for avian habitat (i.e., a hemi-marsh state), an annual or biennial application is probably needed. We must stress that the application of fangueo with a tractor is probably only appropriate in wetlands with relatively compact mineral soils. In wetlands with organic soils (i.e., the Everglades), the use of a tractor would likely be dangerous and detrimental unless a modified drum chopper system can be devised which can operate on peat soils. The mechanical disturbance that enables fangueo to be effective might be replicated and implemented in wetlands like the Everglades with an airboat instead of a tractor (Richardson 2008).

2.4.6 Summary

Typha removal via fangueo in Palo Verde Marsh has been an effective way to restrict *Typha* expansion and restore the habitat needed by the very large and diverse populations of birds in the wetland. As in most seasonal wetlands, the seed bank in Palo Verde Marsh is large and fangueo results in a more diverse plant community that is strongly dictated by seasonal processes (distinct wet/dry season assemblages). Importantly, the fangueo technique has had no apparent long-term impact on any of the soil properties we measured including bulk density. For avian habitat management, we expect that fangueo should probably be repeated annually or biennially. For *Typha* management, we expect that a 2-4 year cycle would probably be sufficient. The fangueo method is especially appropriate for tropical and temperate seasonally flooded wetlands where the historic successional role of herbivores has been altered. However, the method is very effective and can also be adopted or modified for restoration or invasive plant management in various other types of degraded wetlands.

3. Tropical dry wetland plant community response to seasonal flooding: the role of the seed bank, plant life forms, and environmental filters

Abstract

Tropical dry wetlands in Central America are flooded during the wet season and have no standing water for much of the dry season. The objective of this research was to better quantify the impact of these distinct and extreme anaerobic/aerobic annual cycles on the plant community in a large and ecologically important tropical dry wetland in northwestern Costa Rica (Palo Verde Marsh, Palo Verde National Park; a RAMSAR Wetland of International Importance). Since the impact of seasonal flooding on the plant community in seasonal wetlands is often most evident after disturbance, we created gaps in the wetland vegetation via the mechanical removal of emergent vegetation. We then measured plant community change using surveys of the wet and dry season standing vegetation, the seed bank, and *in situ* seedling recruitment. As expected, seasonal flooding acted as an environmental filter and resulted in distinct dry and wet season assemblages. The dominant plant life forms present after vegetation removal differed between seasons with emergents dominating during the dry season and floating-rooted, free-floating, and submerged species more dominant during the wet season. We identified common species that are characteristic of both seasonal assemblages and used indicator species analyses to identify species that are only likely to be found during the wet season. We also characterize the seed bank at this site; like

most seasonal wetlands, plant species' resilience in this wetland is dependent upon a large and diverse seed bank which allows many species to revegate after the frequent disturbances and extreme wet/dry environmental filters.

3.1 Introduction

Tropical dry wetlands are located in tropical portions of the world that have distinct and extreme wet and dry seasons. These dynamic wetlands fill during the first major precipitation event of the wet season and typically remain flooded for the remainder of the wet season. Then, during the dry season, standing water is gradually lost via evapotranspiration until, by the end of the dry season, there is no standing water. In seasonal wetlands at all latitudes, these extreme anaerobic/aerobic cycles drive ecosystem functions (e.g., productivity, decomposition, nutrient cycling) and greatly dictate community composition (Mitsch and Gosselink 2007).

Much like the prairie pothole wetlands of the Midwestern U.S. (e.g., van der Valk 1981), the plant community present in tropical dry wetlands is regulated by the environmental filters associated with flooding and drawdown cycles (Finlayson et al. 1990, Middleton 1999, Finlayson 2005). These environmental filters create a very dynamic plant community, particularly when these filters are combined with the diverse and frequent disturbances that are common in these ecosystems (e.g., herbivory, fire, hurricanes). As a result, most of the plant species found in tropical dry wetland plant communities are very resilient; they have adaptations and life history traits that enable them to rapidly revegetate after disturbances and also tolerate or avoid the pronounced and fluctuating aerobic/anaerobic environmental filters. Like most seasonally flooded wetlands, tropical dry wetlands also typically have a large seed bank. The majority of plant species in these wetlands germinate during drawdown conditions and most of the post-disturbance plant community recruitment occurs during the dry season (Middleton 1999). Well-studied tropical dry wetlands around the world include those in Kakadu National Park- Australia (Finlayson and Woodroffe 1996, Finlayson 2005), Keoladeo National Park- India (van der Valk et al. 1993, Middleton 1999), and the Kafue Flats- Zambia (Howard 1985).

The tropical dry wetlands in and around Palo Verde National Park (PVNP; Northwestern Costa Rica; see Figure 3.1 for location) are among the most dynamic, ecologically important, and diverse wetlands in Central America. PVNP wetlands have been collectively designated a RAMSAR Wetland of International Importance and cover an estimated 9880 ha of the total 18,800 ha area included in the park (J. Serrano, personal communication). Of the wetlands within PVNP, Palo Verde Marsh is the most accessible and is visited by recreational and educational tourists from around the world. However, only a few studies have attempted to characterize the plant community in Palo Verde Marsh or any of the other wetlands within PVNP (Hernández Esquivel 1990, Crow 2002).

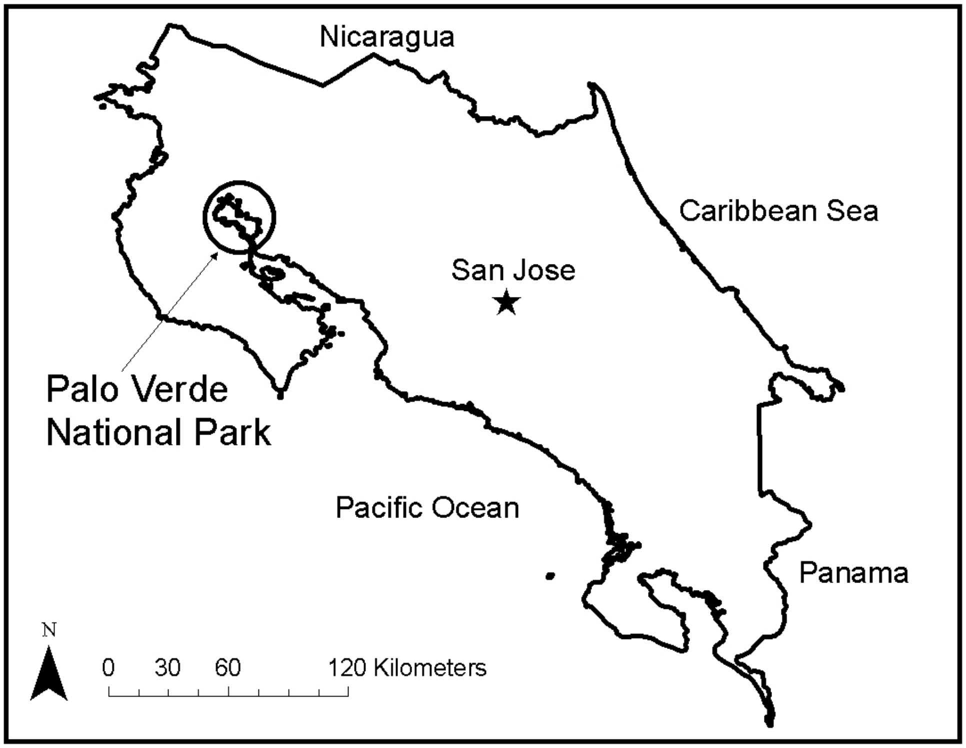

Figure 3.1: Map of Costa Rica identifying the location of Palo Verde National Park.

The objective of this study was to examine the plant community response to seasonal flooding in Palo Verde Marsh via surveys of the wet and dry season standing vegetation, the seed bank, and *in situ* seedling recruitment. Since the impact of seasonal flooding on the plant community in seasonal wetlands is often most evident after disturbance, we created gaps in the wetland vegetation via the mechanical removal of emergent vegetation and monitored the subsequent changes in the plant community. Our hypotheses included the following: (1) Due to the multiple and diverse disturbances that impact Palo Verde Marsh (e.g., herbivory, fire, scouring, deposition), the plant community would have a large and diverse seed bank; (2) For most species, germination from the seed bank would occur primarily during the dry season (drawdown conditions); (3) The intense environmental filters associated with drawdown and flooding would greatly define the post-disturbance community with aquatic life forms dominating during the wet season and species with emergent life forms dominating during the dry season; and (4) Some species would only be present during one of the two seasons (dry versus wet) due to their inability to persist during the anaerobic conditions found during the wet season or the intense water-limitation found during the dry season.

3.2 Methods

3.2.1 Study site

This study was conducted in Palo Verde Marsh, within PVNP. PVNP is located in the Province of Guanacaste (NW Costa Rica; Figure 3.1; see photos in Figure 3.2) in the lowlands of the Tempisque River Watershed. The climate in this part of Costa Rica is tropical and very seasonal. Importantly, the Organization for Tropical Studies (OTS) manages a field station (Palo Verde Biological Station) that is within the park and immediately adjacent to Palo Verde Marsh.

Ecosystem processes in the region's freshwater wetlands are visibly defined by seasonal flooding and drawdown associated with wet and dry seasons. Palo Verde Marsh (~1250 ha; $10^{o}20'35''$ N, $85^{o}20'25''$ W), fills with water during the wet season (~May-November) to a typical maximum depth of about 1.5 m (Figure 3.3abc). Most of these hydrologic inputs are due to surface water runoff from the adjacent forest during the wet season. However, in some years, tropical storm activity at the end of the wet season (typically in September or October) will produce water levels in excess of 1.5 m at the site as the Tempisque River rises higher than the natural levees and causes widespread flooding. During the dry season (~December-May), the water level gradually recedes due to high evapotranspiration rates that exceed the rainfall. At the end of the dry season, much of the marsh has no standing water. However, small precipitation events during the last few months of the dry season (March-April) in some

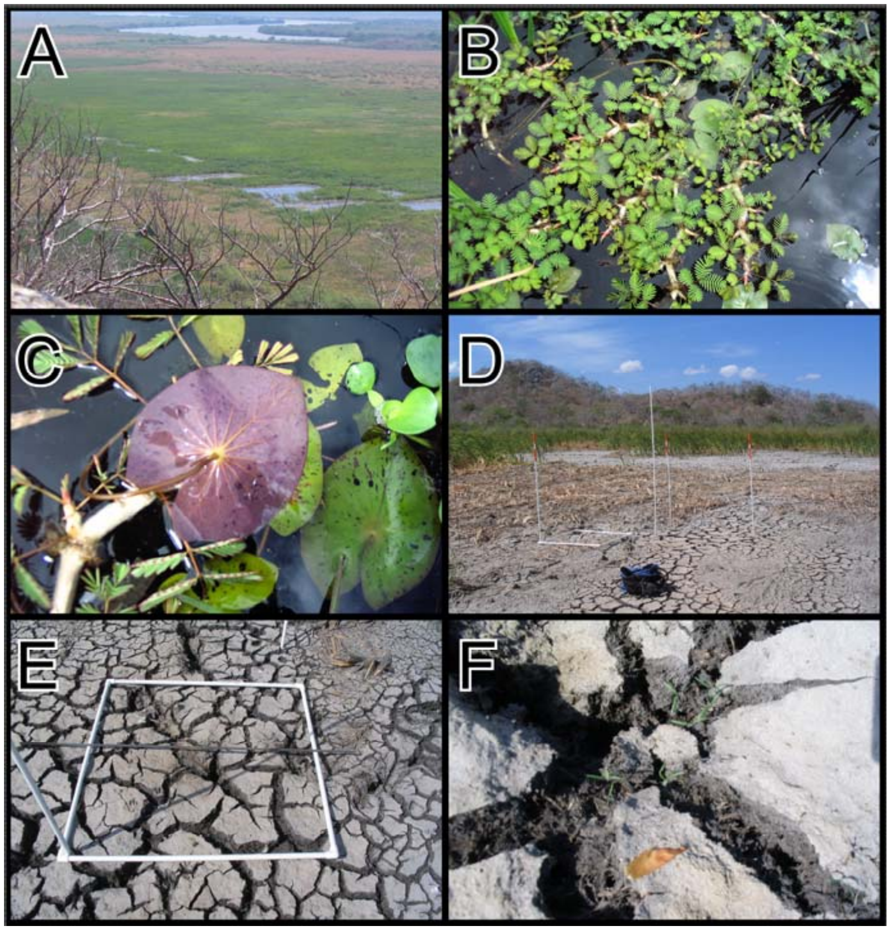

Figure 3.2: Photos of: (A) Palo Verde Marsh and the Tempisque River; (B) and (C) wet season plant communities highlighting the free-floating and floating-rooted species *Neptunia natans* and *Nympaea* spp., respectively; (D), (E) and (F) dry season photos showing soil contraction and little vegetation. In (F), small seedlings are germinating in cracks but not on the soil surface which is a common occurrence during the intense dry season.

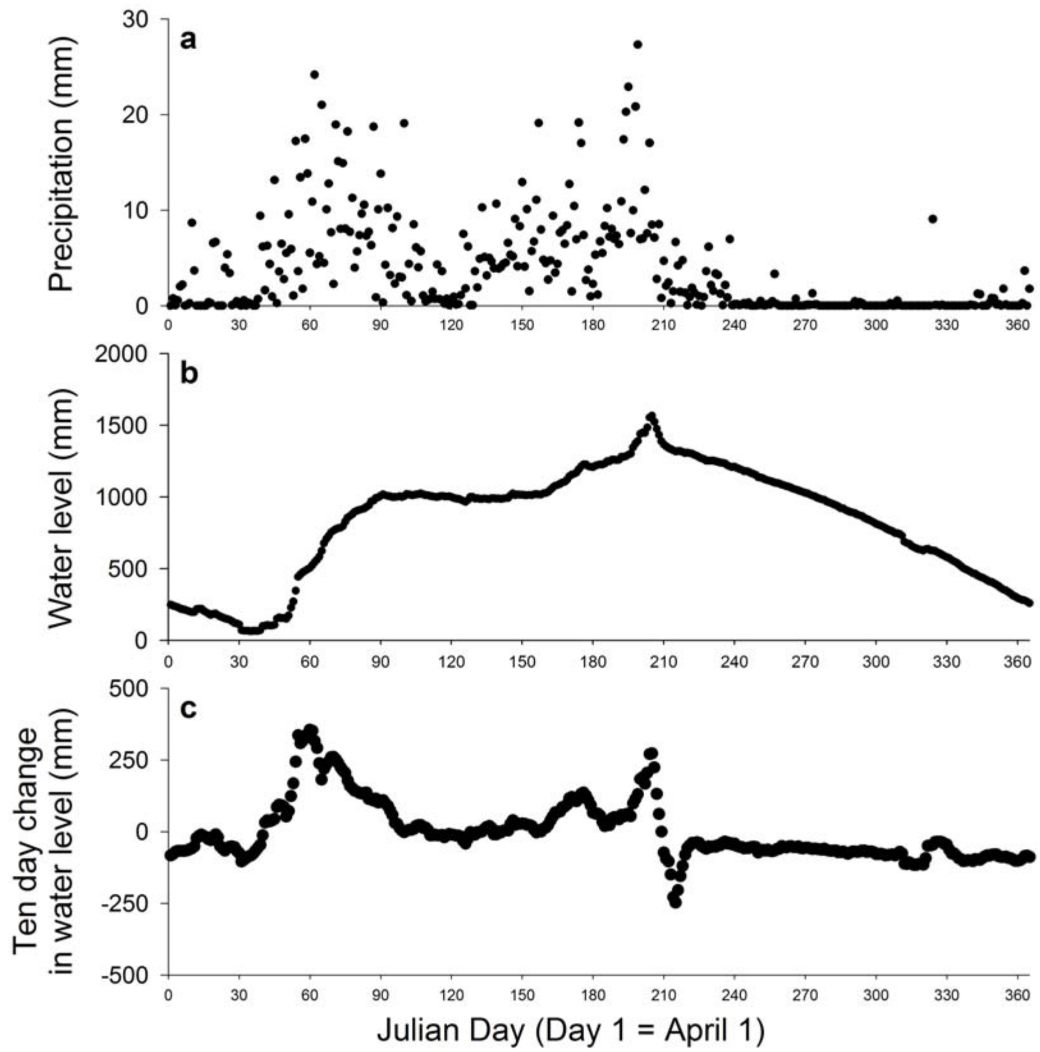

Figure 3.3: Mean daily precipitation (a), water level (b), and ten day change in water level (c) at Palo Verde Marsh for a five year period (2003-2008). These figures illustrate the distinct wet and dry seasons and also the rapid changes in water level that occur in May/June and September/October due to intense rainfall. Note that these data were collected from a relatively deep part of the marsh. Parts of the marsh that are less deep can be without standing water for an additional one to three months.

years will delay and sometimes prevent complete drawdown in the wetlands. The soils in most of the wetlands within and adjacent to PVNP (including Palo Verde Marsh) are Vertisols (Loaiciga and Robinson 1995) which expand in the wet season and contract during the dry season forming a relatively uniform and deep A horizon. Extensive cracking during the dry season (especially in areas without vegetation) promote the mixing of this layer as pieces from the surface fall into cracks.

The range in total annual precipitation at the site is large. Between 1997-2007, the mean ± SE, minimum, and maximum annual cumulative precipitation for a hydrologic year (April-March) were 1271 ± 131, 717, and 2201 mm respectively (data obtained from on-site OTS records). For a longer time period (1921-1999), the mean precipitation for the entire Tempisque River Watershed was estimated to be 1817 mm (Mateo-Vega 2001). The mean ± SE annual temperature at the site between 1997-2007 was 28.1 ± 0.3 ^{o}C. The coldest months were at the end of the wet season (September and October) with a mean ± SE temperature of 26.8 ± 0.2 ^{o}C. The warmest month were at the end of the dry season (March and April) with a mean ± SE temperature of 29.7 ± 0.2 ^{o}C.

3.2.2 Experimental design

The data used in these analyses are part of the larger study described in Chapter 2 of this dissertation; for this chapter (Chapter 3), a subset of the treatments and surveys described in Chapter 2 are presented and examined in more detail. Since the hydrologic and edaphic spatial variability at the site was unknown when we began the study and potentially heterogeneous, we selected a randomized complete block design for this investigation. Within fifteen blocks (all areas dominated by cattail, *Typha domingensis*), a *Typha* removal treatment was applied at three levels [Control (C), *Typha* removed via fangueo (F), and *Typha* removed via fangueo and plot fenced (F&F) to exclude cattle grazing; Figure 2.4]. Fangueo is a technique used locally in NW Costa Rica during rice farming to control weeds and also reduce water infiltration via increased soil compaction. See McCoy and Rodriguez (1994) for a discussion of how the fangueo method was first used to restrict *Typha* expansion in PVNP wetlands. In the context of this study, we use the term fangueo to refer to the use of a tractor with metal paddle wheels to crush and locally remove *Typha* in standing water. Fangueo is the disturbance used to remove emergent vegetation in this study.

Whereas the cattail in the C plots was not removed, the cattail in the F and F&F plots was removed via fangueo. The F&F plots were also enclosed by a barbed wire fence in order to restrict cattle access and assess the additional impact of grazing after fangueo on the vegetation. The lack of a fence in the F plots allowed cattle to graze in those plots. Comparisons of the plant communities present in the F and FF plots indicated no significant difference (presumably due to low stocking rates and/or herbivory by other organisms; see results section in Chapter 2; MRPP comparison between the F and FF groups at any single date was not significant, $A < 0.02$ and insignificant P for all tests). Hence, these two groups were treated as one group (a post-disturbance group where *Typha* removal via fangueo is the disturbance) for the plant survey analyses in this study.

Typha removal via fangueo was conducted in early February 2007. Within each block, the three treatment levels were each randomly assigned to 20-m^2 plots with at least 5-m buffers on all sides (total # of 20-m^2 plots = 45). Within each 20-m^2 plot, three nested 1-m^2 permanent quadrats were randomly established for vegetation surveys (total # of 1-m^2 quadrats = 135). The relative water depth of each plot was determined during the wet season surveys.

3.2.3 Seed bank and seedling recruitment

A seedling emergence study was used to examine the seed bank in Palo Verde Marsh. Two sets of duplicate composite cores were collected from the F and C plots. Each composite contained 11 cores (5-cm depth, 4.6-cm diameter each; total pre-composite cores = 660; total volume and area for each composite sample was 914 cm^3 and 183 cm^2 respectively). Each composite was mixed and placed in a 2-cm layer on top of a 5-cm layer of sterilized potting soil in flats with the following dimensions: 25-cm long x 20-cm wide x 10-cm deep. Each duplicate was assigned to one of two water level treatments: flooded or drawdown. Whereas the water level in the flooded flats was maintained 3 cm above the soil surface, the water level in the drawdown flats was kept moist but not flooded. This study was conducted in a lathe house at the OTS' Palo Verde Biological Station. In order to account for contaminant seeds, eight control trays were included in the experimental design (four drawdown and four flooded). However, we lost two controls due to an iguana that repeatedly defecated from the lathehouse roof above these trays preventing any potential germination. Emerging seedlings were identified and counted on seven dates between May and September, 2007.

In addition to quantifying seedling emergence in the lathehouse, we also measured *in situ* seedling recruitment during the dry season (March and April 2007); we identified and counted the number of seedlings that germinated in our field plots.

3.2.4 Plant community composition

Vegetation surveys and measurements were conducted within each 1-m^2 quadrat. We established these three smaller nested quadrats within each 20-m^2 plot because determining percent cover was not feasible across the entire 20-m^2 plot. For statistical analyses, we used the means from the three nested and randomly assigned 1-m^2 quadrats to represent the community found in the larger 20-m^2 plots. We compared percent cover data from the first wet season (June and September, 2007) and the second dry season (April 2008). The cover data was classified according to the common life forms present in the wetland (i.e., emergent, free-floating, floating-rooted, and submerged) and also used to calculate species richness and diversity (using the Shannon-Wiener index with the use of the relative percent cover of species i to represent p_i in the calculations).

3.2.5 Data analyses

To compare wet and dry season plant community characteristics, we used mixed factor analyses of variance (ANOVA) models with block as a random effect and season (wet or dry) as a fixed effect. Our response variables were life form (i.e., emergent, free-floating, floating-rooted, and submerged) relative abundance and species richness. These analyses were conducted using PROC MIXED in SAS Version 9.1.3 (SAS Institute, Cary, NC, U.S.A.).

To illustrate differences in plant community composition between the dry and wet seasons, a nonmetric multidimensional scaling (NMS) analysis (Kruskal 1964, Mather 1976, McCune and Grace 2002) was performed using PC-ORD (McCune and Medford 1999). Prior to analysis, we relativized the species cover data by species maxima and removed rare species which were defined as species present in less than 5% of the plots. The resultant matrix contained 22 species and 82 plots. Bray-Curtis dissimilarity coefficients were used to quantify plant species compositional distance (Bray and Curtis 1957). In order to determine the appropriate number of dimensions to include in the analysis, we used a stepdown procedure to compare the number of dimensions with the corresponding change in final ordination stress. We initially evaluated 6 axes using 100 runs with real data, a stability criterion of 0.00001, a maximum of 400 iterations, and a Monte Carlo test with 150 randomizations to determine whether the resultant axes were stronger than those identified by chance

(McCune and Grace 2002). Based upon this procedure, a three dimensional analysis was deemed optimal and resulted in a final stress of 18.0, a P value of 0.007, and a final instability of 0.00001 after 112 iterations. This ordination was rotated 30 degrees to load the strongest secondary matrix variables (water depth and emergent vegetation cover) on the horizontal axis. To compare the wet and dry season plant communities, we used Multi-Response Permutation Procedure (MRPP) with Bray-Curtis dissimilarity as the distance measure and n/(sum n) to weight groups. We also calculated indicator values for the 22 common species for each season via indicator species analysis (INSPAN) (Dufrene and Legendre 1997) using PC-ORD Version 4 (MjM Software, Gleneden Beach, OR, USA; McCune and Medford 1999). Indictor values represent the percent of perfect indication for a given group.

3.3 Results and discussion

3.3.1 Seed bank and seedling recruitment

Like most seasonal wetlands, the seed bank at Palo Verde is large and most species germinated better during drawdown conditions (Figure 3.4A; Figure 3.5ABC). The number of seedlings that emerged from the drawdown treatment was greater than in the flooded treatment (mean ± SE was 1960 ± 201 and 510 ± 95 individuals/m^2 for the drawdown and flooded treatments, respectively; t = 6.5, $P < 0.0001$). The site-level seed bank species richness was 24 and 11 species for the drawdown and flooded treatments, respectively (Figure 3.5C). Common species that emerged during drawdown conditions

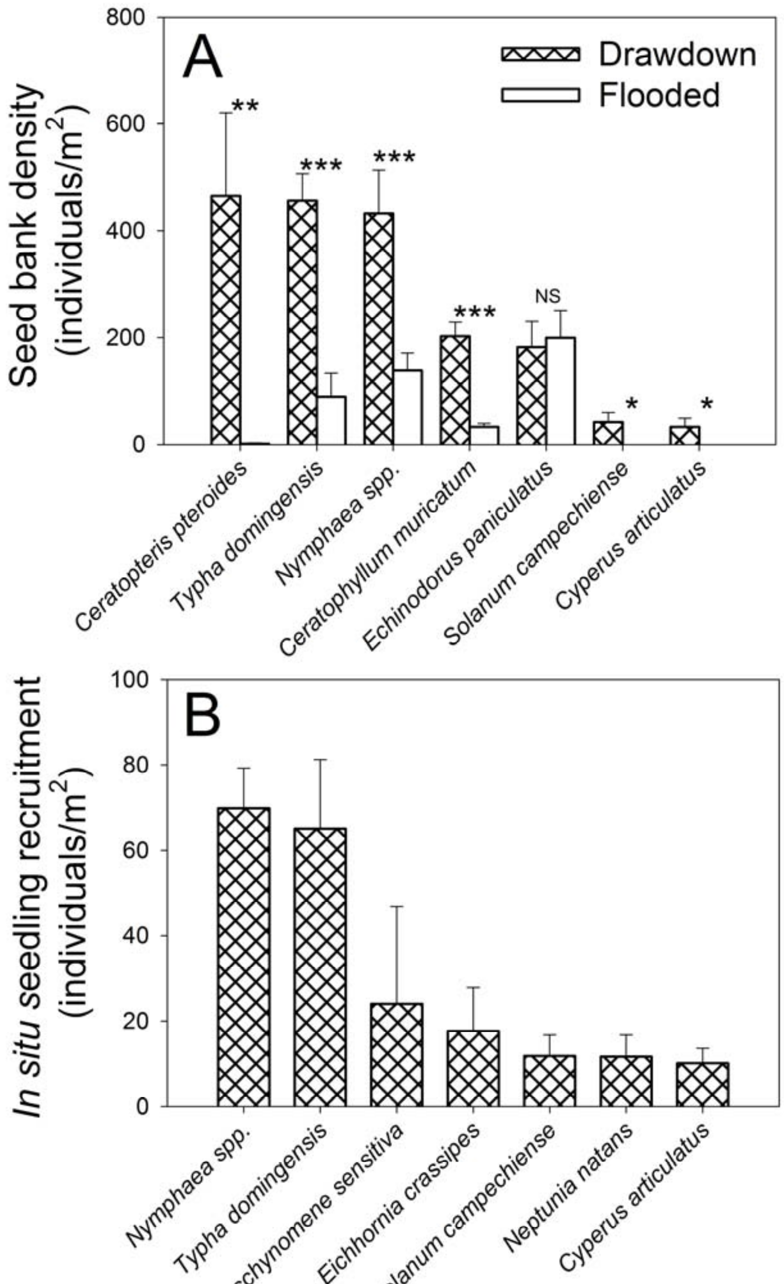

Figure 3.4: The most common species measured during (A) a seed bank seedling emergence study and (B) field-based seedling recruitment surveys at the end of the dry season. Note that the seed bank study has two treatments (drawdown and flooded).

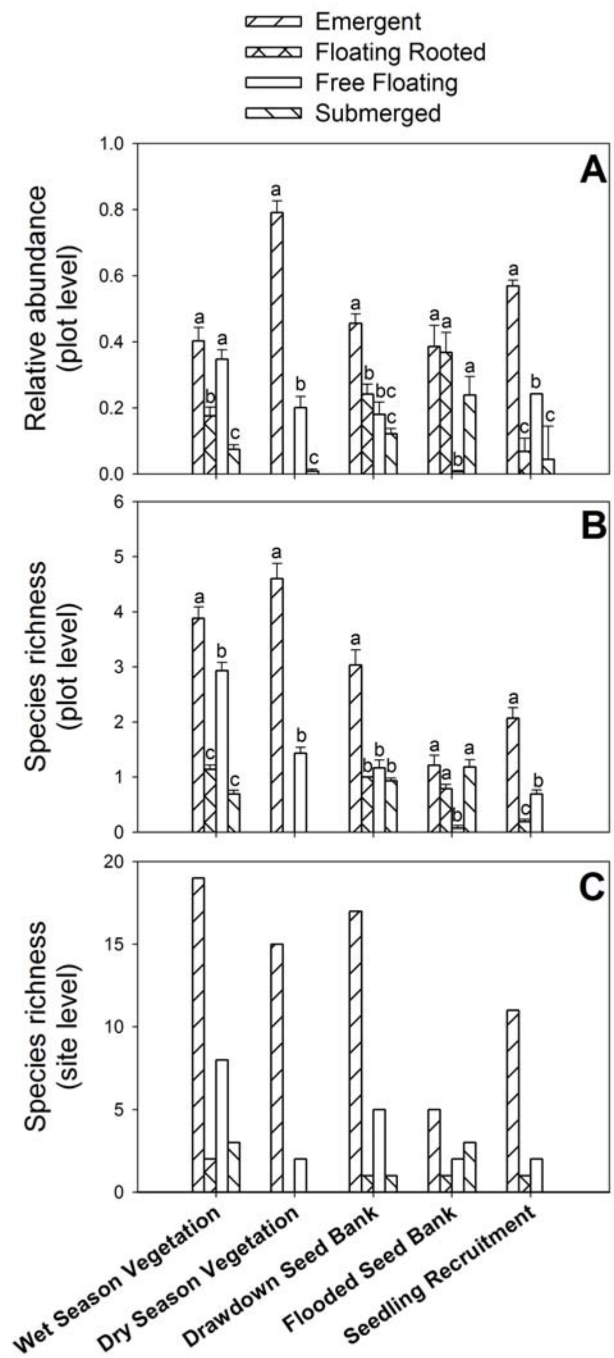

Figure 3.5: A comparison of four plant life forms found in various components of the plant community using measures of (A) relative abundance at the plot level, (B) species richness at the plot level, and (C) species richness at the site level.

include *Ceratopteris pteridoides* (note this is an aquatic fern with reproduction from spores), *T. domingensis*, *Nymphaea* spp., *Ceratophyllum muricatum*, *Echinodorus paniculatus*, *Solanum campechiense*, and *Cyperus articulatus* (Figure 3.4A). Common species that were able to germinate during flooded conditions include *Najas arguta* and *E. paniculatus* (Figure 3.4A). A greater number of species and individuals with emergent life forms germinated from the seed bank during drawdown conditions (Figure 3.5ABC; [t = 5.5, P> 0.0001] and [t = 4.5, P <0.0001], for species richness and seed bank density, respectively).

The most common species that germinated during our field-based seedling recruitment surveys at the end of the dry season were *Nymphaea* spp., *T. domingensis*, *Aeschynomene sensitiva*, *Eichhornia crassipes*, *S. campechiense*, *Neptunia natans*, and *C. articulatus* (Figure 3.4B). Interestingly, most of the seedlings that germinated in the field during the dry season, germinated in cracks formed by soil contraction (Osland, personal observation), presumably due to higher moisture availability in these microsites. The site level species richness from these *in situ* seedling recruitment measurements was 14 species (Figure 3.5C). The majority of the species and individuals that were observed in these seedling surveys were classified in the emergent life form (Figure 3.5ABC).

3.3.2 Plant community composition

As expected, the wet and dry season plant communities were significantly different (Figure 3.6; Figure 3.7; Table 3.1; Table 3.2; MRPP, wet vs. dry, A = 0.05, P

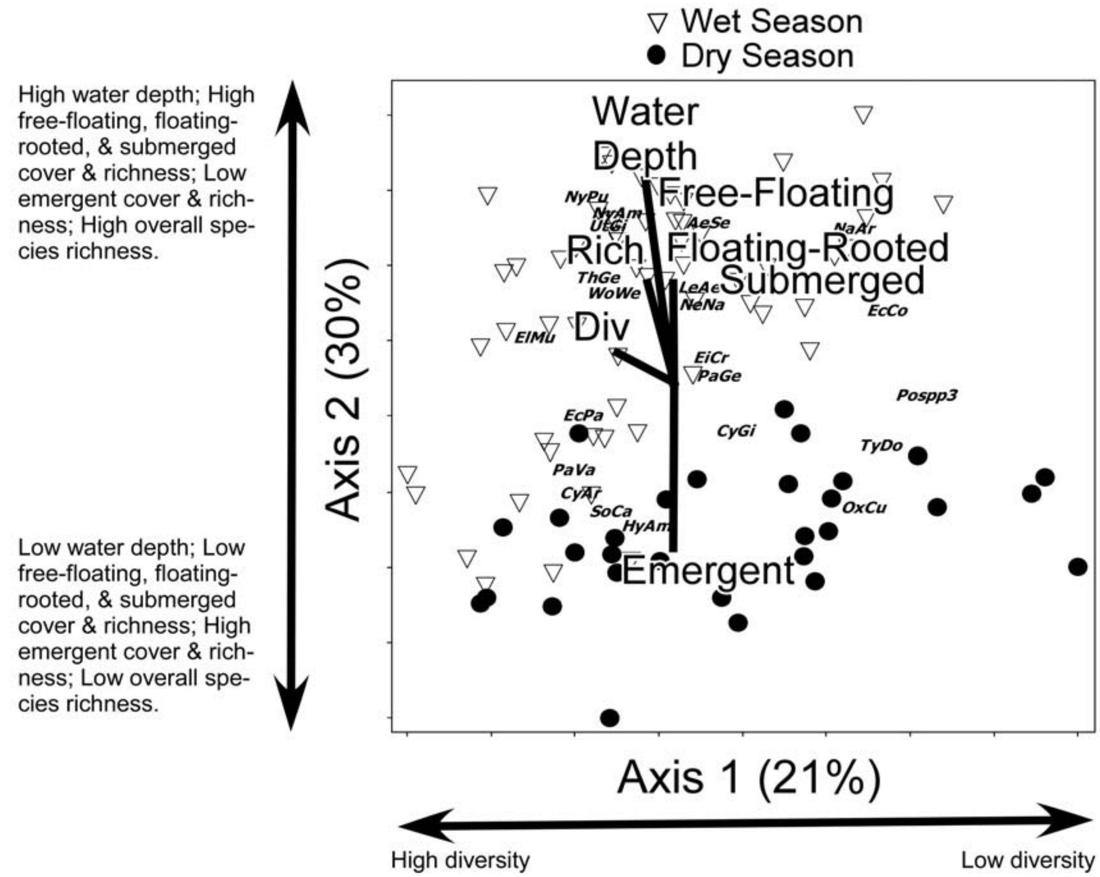

Figure 3.6: A comparison of plant community composition during the wet and dry season. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four letter species codes that can be interpreted with Table 3.1.

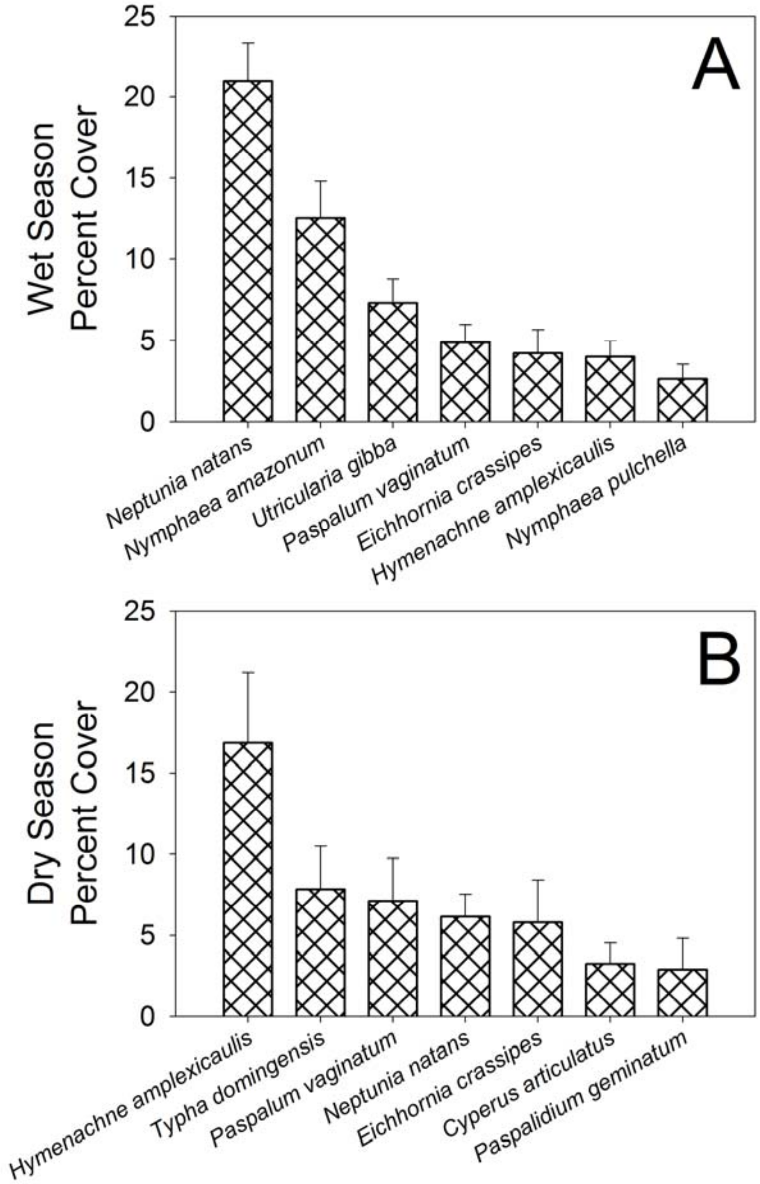

Figure 3.7: Plant species with the highest percent cover measurements during the (A) wet season and (B) dry season.

Table 3.1: The results of an indicator analysis (INSPAN) of the 22 common species present in the plant community surveys. The indicator value represents the percent of perfect indication for either the wet or dry season plant community. A Monte Carlo test was conducted to identify significant indicator values. The * denotes *P* values that were not significant after a Bonferroni correction. Due to the order of our analyses (wet then dry), *P* values are only shown for the wet season species. The species codes can be used to interpret the NMS ordination in Figure 3.6. The life form abbreviations represent the following: E = emergent, FF = free floating, FR = floating rooted, S = submerged.

			Indicator Value		
Species	Code	Life Form	Wet Season	Dry Season	Wet Season *P*
Aeschynomene sensitiva	AeSe	E	14	0	NS
Cyperus articulatus	CyAr	E	12	20	NS
Cyperus gigantea	CyGi	E	1	8	NS
Echinochloa colona	EcCo	E	8	23	NS
Echinodorus paniculatus	EcPa	E	26	20	NS
Eichhornia crassipes	EiCr	FF	11	27	NS
Eleocharis mutata	ElMu	E	17	0	0.04*
Hymenachne amplexicaulis	HyAm	E	14	65	NS
Lemna aequinoctialis	LeAe	FF	78	0	≤0.0001
Najas arguta	NaAr	S	19	0	0.02*
Neptunia natans	NeNa	FF	73	22	≤0.0001
Nymphaea amazonum	NyAm	FR	88	0	≤0.0001
Nymphaea pulchella	NyPu	FR	26	0	0.007*
Oxycarium cubense	OxCu	E	0	40	NS
Paspalidium geminatum	PaGe	E	20	7	NS
Paspalum vaginatum	PaVa	E	18	30	NS
Poaceae spp.	Pospp3	E	2	13	NS
Solanum campechiense	SoCa	E	0	33	NS
Thalia geniculata	ThGe	E	15	0	NS
Typha domingensis	TyDo	E	7	64	NS
Utricularia gibba	UtGi	S	47	0	≤0.0001
Wolffiella welwitschii	WoWe	FF	81	0	≤0.0001

Table 3.2: Comparison of life form relative abundance and species richness (plot level) between the wet season and dry season plant communities. Significant *F* values are denoted by asterisks (* $P < 0.001$, ** $P < 0.01$, * $P < 0.5$).**

Source	$F_{1,72}$
Emergent relative abundance	41.9***
Emergent species richness	7.3**
Floating-rooted relative abundance	20.4***
Floating-rooted species richness	105.4***
Free-floating relative abundance	7.1**
Free-floating species richness	46.6***
Submerged relative abundance	15.3***
Submerged species richness	50.0***

<0.00001). The NMS ordination in Figure 3.6 illustrates the compositional differences associated with seasonal flooding. Common species present during the wet season include *N. natans*, *Nymphaea amazonum*, *Utricularia gibba*, *Paspalum vaginatum*, *E. crassipes*, *Hymenchme amplexicaulis, and Nymphaea pulchella* (Figure 3.7). Common species present during the dry season include *H. amplexicaulis*, *T. domingensis*, *P. vaginatum*, *N. natans*, *E. crassipes*, *C. articulatus*, and *Paspalidium geminatum* (Figure 3.7). Interestingly, species richness and diversity were higher during the wet season (Figure 3.6; Figure 3.7).

Whereas emergent species relative abundance and richness were higher during the dry season, the relative abundance and richness of free-floating, floating-rooted, and submerged species were higher during the wet season (Figure 3.5ABC; Figure 3.6; Table 3.2). We examined relationships between compositional space and the following variables: water depth, species diversity (Shannon H'), species richness, and also the percent cover and species richness of plants with the four life forms of interest (i.e., emergent, free-floating, floating-rooted, or submerged). The proportion of the compositional variance represented by the three axes included in the analysis was 66% (Axis 1: 21%, Axis 2: 30%, and Axis 3: 15%). Water depth, species richness, and the percent cover and richness of free-floating, floating-rooted, and submerged life forms were all positively correlated with Axis 2 (using the notation of variable followed by [r^2, τ]: water depth [0.66, 0.61], species richness [0.33,0.40], free-floating richness [0.30, 0.43], free-floating cover [0.12,0.24], floating-rooted richness [0.25,0.40], floating-rooted cover

[0.14,0.46], submerged richness [0.33,0.47], and submerged cover [0.07,0.37]. In contrast, emergent richness and cover were negatively correlated with Axis 2 (using the notation of variable followed by [r^2, τ]: emergent richness [0.16, -0.31] and emergent cover [0.53,-0.55]. Species diversity was the only variable that was correlated to Axis 1 (using the notation of variable followed by [r^2, τ]: species diversity [0.18, -0.26]).

In seasonal wetlands like Palo Verde, seasonal flooding typically acts as an environmental filter constraining the number of species that are present during flooded conditions and drawdown conditions (van der Valk 1981, Middleton 1999). We used an indicator species analysis to identify species that were significant indicators of the wet season. The results from this analysis are presented in Table 3.1. Eight species that were present during the wet season were not observed during the dry season (see indicator values of zero in the dry season column in Table 3.1). In contrast, only two species that were present during the dry season were not observed during the wet season (see indicator values of zero in the wet season column in Table 3.1). The following five species were significant indicators of the wet season plant community: *Lemna aequinoctialis*, *N. natans*, *N. amazonum*, *U. gibba*, and *Wolffiella welwitschii* (see significant wet season *P* values in Table 3.1). Although the order of our surveys (wet followed by dry) prevents us from making strong conclusions regarding species that are only present during the dry season, our previous observations (which are supported by the indicator values) indicate that *S. campechiense* is an annual drawdown species that is not present during the wet season. In other words, *S. campechiense* individuals germinate during the dry season and are relatively common in the marsh during drawdown. However, this species is not present during the wet season. Surprisingly, this is the only species for which we can make this conclusion. Almost all of the species that we observed in these surveys are species that are able to persist during the wet season. There are very few "upland" species that recruit into the site during the dry season. We expect that the reason for this is that the intense dry season conditions (i.e., high temperatures and very low water availability) are too stressful for successful recruitment.

3.3.3 Conclusions

The wetlands of PVNP are collectively designated a Ramsar Wetland of International Importance and are among the most dynamic, diverse, and ecological important wetlands in Central America. Of the wetlands within PVNP, Palo Verde Marsh is the most accessible and is visited by recreational and educational tourists from around the world. The primary objective of this research was to better characterize the wetland plant community response to hydrologic fluctuations associated with the distinct and extreme wet and dry seasons present in Palo Verde Marsh (i.e., flooding during the wet season and drawdown conditions during the dry season). Our results are generally consistent with previous successional research in seasonally flooded wetlands [e.g., (van der Valk 1981, Middleton 1999)]; seasonal flooding in Palo Verde Marsh acts as an environmental filter and results in distinct dry and wet season assemblages. After a gap-opening disturbance, the dominant plant life forms differ between seasons with emergent species dominating during the dry season and floating-rooted, free-floating, and submerged species more dominant during the wet season. A previous study examining *Typha* dominance indicated that without gap-creating disturbances (e.g., herbivory, fire, hurricanes, anthropogenic management) emergent species would probably become dominant during both the wet and dry seasons and result in more similar wet and dry season assemblages (see discussion in Chapter 2).

We identified common species that are characteristic of both seasons and used indicator species analyses to identify species that are only likely to be found during the wet season. We also characterized the seed bank at this site; like most seasonal wetlands, the majority of plant species in these wetlands germinated during drawdown conditions and most of the plant community recruitment occurred during the dry season. Our results indicate that many of the plant species found in Palo Verde Marsh are very resilient with adaptations and life history traits that enable them to rapidly revegetate after disturbances and also tolerate or avoid the pronounced and fluctuating environmental filters that define these ecosystems.

4. Native bamboo (*Arundinaria gigantea* (Walter) Muhl., Poaceae) establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): implications for restoration

Abstract

Giant cane (*Arundinaria gigantea*) is a native bamboo species that was once abundant in wetlands and riparian areas throughout the southeastern United States. As part of an effort to identify competitive-dominant native species that can be utilized to maximize the restoration of riparian ecosystem functions/services and reduce non-native community invasibility, we transplanted cane clump divisions into areas either dominated by or recently cleared of Chinese privet (*Ligustrum sinense*), an invasive non-native shrub. We quantified cane survival and growth in the presence of privet and other plants including several common invasive non-natives. Removal of mature privet via a cut and paint application of glyphosate herbicide resulted in 100% mortality. Cane survival was high in both the high and low-light conditions provided by the contrasting privet treatments. During the first year, there was little cane growth or expansion in either privet treatment. In the second year, cane growth and expansion in the Privet-Present treatment was also very low. However, during the second year in the Privet-Removed treatment, cane genets produced more ramets, increased in genet area, and developed ramets that were taller and wider. Despite very high recruitment and cover of Japanese stilt grass (*Microstegium vimineum*) and other common invasive non-natives

in the Privet-Removed treatment, transplanted cane genets continue to grow and expand. Our future research will continue to monitor the rate of cane growth as we investigate whether cane can compete with the common non-native invasive species that are dominant at this site and at other riparian ecosystems throughout the region.

4.1 Introduction

Riparian restoration efforts have historically focused more on abiotic conditions (e.g., hydrology, topography) and less on the biotic community. In the southeastern United States, the outcome of such efforts is often plant communities dominated by invasive non-native species such as Chinese privet (*Ligustrum sinense Lour.*), Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), and Japanese honeysuckle (*Lonicera japonica* Thunb.). These three species are especially common in the region and have the potential to impede the restoration of ecosystem structure, functions, and services (Ehrenfeld et al. 2001, Morris et al. 2002, Schierenbeck 2004). Restricting the spread of invasive non-native species at the regional level is very unlikely. However, at the local level (e.g., a specific restoration site), ecologists should be able to use an understanding of ecological competition theory related to invasive species plant biology to limit non-native invasions and improve efforts to restore ecosystem structure and functions.

Since interspecific competition is recognized as one of the primary mechanisms controlling plant community composition (Harper 1977, Grime 1979, Tilman 1982), identifying and utilizing native competitive-dominant plant species is a reasonable starting point for restoration efforts. Competitive-dominant species typically determine ecosystem functions (Grime 1998, Walker et al. 1999, Cardinale et al. 2006) and dictate community invasibility (Crawley et al. 1999, Smith et al. 2004, Emery and Gross 2007). However, surprisingly little research has focused on identifying and utilizing native competitive-dominant species for riparian restoration purposes in the Southeast. We ask the following question: which native competitive-dominant plant species can be used during riparian restoration to maximize ecosystem functions/services and also reduce non-native community invasibility? We define non-native community invasibility as the extent to which a plant community or restored area is susceptible to recruitment, growth, and eventual dominance of non-native species.

Giant cane (*Arundinaria gigantea* (Walter) Muhl.) is a competitive-dominant woody grass (i.e., a bamboo) that was once very abundant in riparian and wetland ecosystems throughout the southeastern United States (Bartram 1791, Platt and Brantley 1997, Stewart 2007). European settlers in the region found vast expanses of monotypic cane stands and often referred to them as canebrakes. There are three native bamboo species in the United States: giant cane (*A. gigantea*), switch cane (*A. tecta* (Walter) Muhl.), and hill cane (*A. appalachiana* Tripplett, Weakley, and L.G. Clark) (Triplett et al. 2006). This research examines giant cane and any future mention of "cane" in the text will refer exclusively to *A. gigantea*.

Giant cane is a perennial woody grass with dense mats of underground rhizomes, dense ramets, and evergreen foliage leaves. Although giant cane has the potential to expand aggressively through vegetative reproduction, cane dispersal is relatively infrequent and not well studied (Gagnon and Platt 2008b). Riparian cane buffers have been shown to reduce sediment load, groundwater nitrate, groundwater phosphate, and surface runoff nutrients (specifically nitrate, ammonium, and orthophosphate) to adjacent aquatic ecosystems (Schoonover and Williard 2003, Blattel et al. 2005, Schoonover et al. 2005, 2006). In addition to these potential water quality-related ecosystem services, canebrakes also provide habitat for a wide range of unique and obligate wildlife species (Brantley and Platt 2001).

Despite cane's historical presence in the region and its tremendous potential for vegetative expansion via clonal growth, few studies have investigated the utility of cane for floodplain restoration. Insufficient information is available regarding the transplantation, establishment, growth, and competitive ability of this species. Many bamboo species can be effectively propagated via clump division, a method that refers to the transplantation of a clump of culms and rhizomes collected from a donor bamboo stand (McClure 1966). However, previous investigations of the effectiveness of giant cane propagation via clump division have shown mixed results (Feedback and Luken 1992, Platt and Brantley 1993, Dattilo and Rhoades 2005). Furthermore, these studies typically have focused solely on cane survival and growth and have ignored or even avoided the impact of competition from other species.

Although the focus of this experiment is primarily on giant cane survival, growth, and expansion, the experimental design specifically manipulates the presence of Chinese privet and we also investigate the effectiveness of Chinese privet removal. In riparian forests of the southeastern United States, Chinese privet is one of the most common invasive non-native shrubs (Miller 2003, Webster et al. 2006). In this study, future mention of "privet" in the text will refer exclusively to *Ligustrum sinense*. Privet is a native of China, Laos, and Vietnam, that was introduced to the United States in the 19th century for ornamental purposes (Urbatsch 2000). It is a shade-tolerant evergreen shrub of the olive family (Oleaceae). When trained, it serves as an effective fence-like barrier due to its rapid growth and ability to reproduce vegetatively. Privet produces large quantities of fruit whose seeds are dispersed primarily by birds. Once germinated, privet can outcompete most native shrubs and limit understory succession due to its ability to acquire and block light (Merriam and Feil 2002, Morris et al. 2002). Mature privet stands often reach heights of 6 to 7 meters or more (Brown and Pezeshki 2000, Miller and Albritton 2004). As a result, this species has successfully invaded both urban and rural riparian forests in the region. Although privet's distribution in the United States is large, it appears to be most invasive in the Southeast. Privet appears to tolerate a wide range of conditions ranging from sunny and dry to shaded and flooded.

However, privet thrives in riparian areas where it often forms dense monospecific stands (Merriam 2003, Burton et al. 2005, Loewenstein and Loewenstein 2005). Privet growth is much greater under elevated CO_2 concentrations and this species is expected to become more invasive with future increases in atmospheric CO_2 (Smith et al. 2008).

The broad purpose of this investigation is to clarify the potential for using giant cane for floodplain and canebrake restoration. We specifically were interested in determining whether giant cane can compete with and ultimately replace widespread invasive non-native species like Chinese privet and Japanese stilt-grass. Our research questions were the following: (1) Giant cane establishment and growth. How effective is giant cane transplantation via clump division and will transplanted giant cane genets be able to grow and expand despite competition from invasive non-native species?; (2) Chinese privet control. How effective is the cut and paint method for removing mature stands of Chinese privet?; and (3) Recruitment and growth of other species. Which species will recruit and be dominant after privet removal? What portion of these species will be invasive non-natives and what will be the impact of giant cane upon post-transplantation non-native dominance and community invasibility?

4.2 Methods

4.2.1 Study site

This research was conducted within the Duke University Wetland Center's Stream Wetland Assessment and Management Park (SWAMP) in Durham County, North Carolina (lat 35°59'27", long 78°56'28"; U.S.A.). The site is located within the floodplain of Upper Sandy Creek, a headwater piedmont stream within the Cape Fear River Basin. This section of Upper Sandy Creek has a drainage area of approximately 480 ha that includes much of Duke University's West Campus. The climate at the site includes a growing season of roughly 200 days. The thirty-year mean annual temperature and precipitation near the site was 15.3°C and 1190 cm, respectively [based on data from 1970-2001 (NOAA 2008); measured at the Raleigh-Durham International Airport which is 19 km away]. However, 2006 and 2007 were relatively abnormal years with annual precipitation values of 1360 and 910 cm, respectively.

Soil series at the site include Cartecay (coarse-loamy, mixed, nonacid, thermic Aquic Udifluvents) and Chewacla (fine-loamy, mixed, thermic Fluvaquentic Dystrochrepts). Adjacent soil series that drain into the site include Mayodan (clayey, kaolinitic, thermic Typic Hapludults) and White Store (fine, mixed, thermic Vertic Hapludalfs) (Kirby 1976). The riparian forest canopy in the Upper Sandy Creek floodplain is dominated by *Acer rubrum* L., *Liriodendron tulipifera* L., *Liquidambar styraciflua* L., and *Ulmus americana* L. (Watts 2000). The specific portion of the floodplain where this experiment was conducted is also dominated by *Acer negundo* L. The understory shrub layer is dominated by dense stands of *Ligustrum sinense*.

4.2.2 Experimental design

Since quantifying the impact of privet removal cannot be accomplished in small areas and requires a treatment buffer to provide relatively homogenous light conditions, a randomized split-plot experimental design was established with two factors: Privet-Presence and Cane-Planting. Privet-Presence treatments (two levels: Privet-Present and Privet-Removed) were applied as the whole-plot factor to 40-m^2 plots. The Cane-Planting treatments (two levels: No Cane and Cane) were applied as the subplot factor to 4-m^2 subplots (for an illustration of the experimental design, see Figure 4.1). Since the understory in a portion of the research area contains extensive coverage of the ground cover *Hedera helix* L., two blocks were established to account for potential confounding effects associated with *H. helix* presence (Block 1: *H. helix* not present, Block 2: *H. helix* present); whereas six replicates were randomly established in Block 1, three replicates were randomly established in Block 2. In total, the experimental design includes 18 whole-plots and 36 subplots. In order to minimize light variation due to edge effects, whole-plot treatments were also applied to a 1.5-m buffer around each subplot. Whole-plots and subplots were randomly assigned treatments. To facilitate sampling, paired subplots within whole-plots were separated by at least 50 cm.

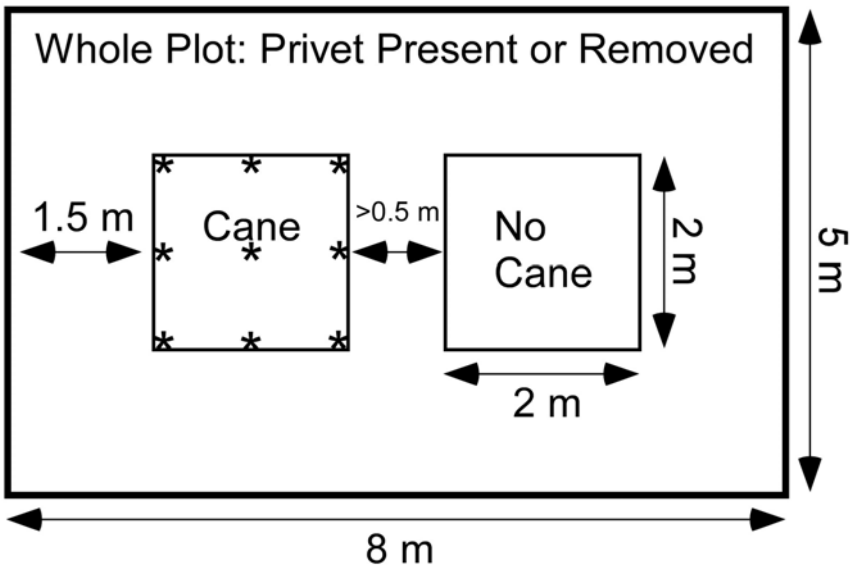

Figure 4.1: An illustration of the experimental design. The Privet treatment (Privet-Present or Privet-Removed) was applied to 40-m² whole plots. The Cane transplantation treatment (Cane or No Cane) was applied to 4-m² subplots. In the Cane subplot treatment, nine *Arundinaria gigantea* clump divisions were transplanted as depicted by the asterisks in the illustration.

4.2.3 Privet removal

In the Privet-Removed treatment, privet stems were cut 3-5 cm above the ground in March 2006 and exposed stumps were immediately painted with undiluted 50.2% glyphosate (Roundup® Weed & Grass Killer Super Concentrate, Monsanto Company, St. Louis, MO, U.S.A.). We refer to this removal method as "cut and paint" (as discussed in Miller and Albritton 2004). Since this stand was close to monotypically privet, very few species remained in the plots after privet removal. This privet removal method resulted in 100% mortality; none of the privet treated in this manner resprouted. In the Privet-Present treatment, the privet stands were left intact.

4.2.4 Cane planting via clump division

The cane treatments were applied at the subplot level in late April 2006. Whereas the No Cane treatments received no cane transplants, nine clump divisions were transplanted within each Cane Planted treatment plot (planting arrangement resulted in a density of 2.25 clump divisions/m^2 with clumps planted in three rows, 1 m apart). The 162 clump divisions were obtained from a donor cane stand along the floodplains of New Hope Creek within the Jordan Game Lands, Durham, NC. This donor cane stand is about 7 km downstream of the study area and is one of few remnant cane stands within Durham city limits. The topography, hydrologic regime, and forest composition of the donor stand are similar to the conditions at the research site. Clump divisions were approximately 30 cm in diameter, 15 cm deep, and contained 1-5 ramets (mean # of ramets ± SE = 1.8 ± 0.1). In order to prevent desiccation and maximize transplantation survival, the clump divisions were buried in a bed of saturated peat moss during transport and planted the same day. To reduce transpiration, the number of leaves on each transplant was reduced by pruning each ramet at the lowest branching node, typically the third or fourth node. During transplanting, we dug a hole, inserted the clump division, and used the soil from the hole to cover the transplanted clump. We lightly compacted this soil with our hands to minimize evaporation and desiccation. Transplants were watered via precipitation or manually almost every day for the first two weeks after transplantation. The number of ramets and the diameter of these ramets were recorded for each clump division. Transplantation survival was determined by the number of genets alive at the end of the first and second growing seasons. Once a clump division survived transplantation, we refer to the group of rhizomes and culms as a genet. Each individual culm or shoot is referred to as a ramet.

4.2.5 Light measurements

In order to compare canopy transmittance between treatments, we measured Photosynthetically Active Radiation (PAR) within each subplot using a linear PAR ceptometer (AccuPAR, Decagon Devices, Pullman, WA). AccuPAR instantaneously averages PAR measurements at 80 independent photodiode sensors spaced at 1-cm intervals. In order to account for daily fluctuations in PAR due to changes in the angle of the sun, we measured PAR within each subplot once each hour for seven consecutive hours on two different days. For each time period and within each subplot, we took twelve measurements during cloudless periods (three in each of the four cardinal directions for a total of 960 photodiode measurements per time period). Each subplot estimate represents the mean of 14 time-period estimates where each is the mean of 960 photodiode measurements. During analysis of the whole plot treatment effect, we used the mean of the two subplot estimates from each whole plot.

4.2.6 Vegetation measurements: growth, expansion, and recruitment

The height and diameter of each new giant cane ramet was measured at the end of each of the first two growing seasons. Since destructive sampling for belowground biomass was not possible, total genet area was used as a substitute and determined as the product of the greatest distance between two ramets and the distance between two ramets that were perpendicular to that axis (*sensu* Datillo and Rhoades 2005). Understory species presence and percent cover were measured in each plot at the end of both growing seasons. Percent cover was quantified as the estimated percent cover and not via the use of cover classes. In order to gauge species dominance, we used the percent cover values to calculate frequency and importance values (I.V.), calculated as: I.V. = (Mean Cover * Frequency) / 100.

4.2.7 Statistical analyses

To assess the impact of privet removal and time on cane growth and expansion, we conducted a univariate repeated measures analysis of variance (ANOVA) for cane genet area, number of ramets per genet, ramet diameter, and ramet height data using SAS Version 9.1.3 (SAS Institute, Cary, NC, U.S.A.). To avoid pseudoreplication, we used the mean of all nine cane genets present in a subplot for all analyses and figures. Our model was structured with Block, Privet (Privet-Presence treatment), Year, and the Privet*Year interaction. To improve normality and better meet the assumptions of ANOVA, genet area and the number of ramets per genet were log-transformed prior to analyses. Block was treated as a random effect and there was no significant block effect for any of the cane growth and expansion models. Comparisons of means between treatments within years and between years within treatments were conducted using Student's t-tests and repeated measures t-tests, respectively. Survival analyses were conducted using Pearson chi-square tests to compare clump division survival between Privet-Presence treatments.

To assess the impact of privet removal, time, and cane transplanting on the abundance of native and non-native plants, we conducted a univariate repeated measures split-plot analysis of percent cover of bare ground, non-native plant species, and native plants species. The model was structured with Privet, Cane (presence or absence), Year, and the two and three-way interactions. In order to avoid the confounding impact of pre-existing and extensive *H. helix* coverage in Block 2 on recruitment after privet removal, this model was developed with Block 1 data. Comparisons of means between treatments within years and between years within treatments were conducted using Student's t-tests and repeated measures t-tests, respectively. Statistical significance was assigned at $\alpha < 0.05$.

4.3 Results

4.3.1 Chinese privet removal, Chinese privet recruitment, and light availability

The use of the cut and paint method to remove mature privet individuals resulted in 100% mortality. However, privet recruitment following removal of mature individuals was high but spatially patchy; for Year 1, the mean ± 1SE was 26.0 ± 9.7 seedlings/m^2 and the range was 0 - 157 seedlings/m^2. As expected, privet removal resulted in greater light availability; the mean PAR ± 1SE for the Privet-Present and Privet-Removed plots was 52.1 ± 2.9 and 211.2 ± 29.6 μmol/m^2/s, respectively ($t = 5.4$, $p < 0.001$).

4.3.2 Cane survival

After two years, cane survival for all clump divisions was 91%. Of the 162 total clump divisions transplanted, 11 died during the first growing season (Table 4.1). During the second growing season, only three additional clump divisions died. There were no significant differences in cane survival between the Privet-Present and Privet-Removed treatments in either Years 1 or 2 (Table 4.1).

4.3.3 Cane growth and expansion

At the end of Year 1, there were no significant differences in cane genet area, total number of ramets per genet, ramet height, or ramet diameter between the Privet-

Table 4.1: ***Arundinaria gigantea*** **clump survival after transplantation via clump division. Data shown are the total number of individuals in each category. Data in parentheses represent the survival and mortality percentages at the end of the growing season relative to the number that were alive at the start of the growing season. There were no significant differences in cane survival between the Privet Present and Privet Removed treatments in either Years 1 or 2 (Year 1: $\chi^2 = 2.4$, $p = 0.12$; Year 2: $\chi^2 = 2.8$, $p = 0.09$).**

	Privet Present	Privet Removed
Year 1		
Live- start of growing season	81	81
Live- end of growing season	73 (90%)	78 (96%)
Dead- end of growing season	8 (10%)	3 (4%)
Year 2		
Live- start of growing season	73	78
Live- end of growing season	71 (97%)	77 (99%)
Dead- end of growing season	2 (3%)	1 (1%)

Present and Privet-Removed treatments (compare Year 1 black and grey bars in Figures 2 and 3). However, by the end of Year 2, all measurements of cane growth (ramet height and diameter) and expansion (genet area and number of ramets per genet) were greater in the Privet-Removed plots (compare Year 2 black and grey bars in Figures 2 and 3; t = 6.0, 6.0, 5.0, and 4.1, respectively; $p \leq 0.0001$, 0.0001, 0.001, and 0.002, respectively). Although there were no significant differences in either cane growth or expansion for the Privet-Present plots during the two-year time frame of the experiment (compare black bars for both years in Figures 2 and 3), there was significant growth (ramet height and diameter) and expansion (genet area and number of ramets per genet) in the Privet-Removed plots (compare grey bars for both years in Figures 2 and 3; t = 12.4, 4.9, 5.0, and 5.8, respectively; $p \leq 0.0001$, 0.002, 0.001, and 0.001, respectively).

4.3.4 Plant percent cover, frequency, and importance values after privet removal

Privet-Present plots had very little vegetation beneath the dense privet canopy in either year. Hence, we focus on the change in cover in the Privet-Removed plots in these analyses. As expected, the percent cover of bare ground after privet removal decreased from Year 1 to Year 2 in both the Cane and No Cane plots (compare black bars for both years and grey bars for both years in Figure 4.4a; t = 4.0 and 3.9, respectively; $p = 0.01$ and 0.01, respectively). At the end of the second growing season, Privet-Removed plots were dominated primarily by non-native species (Table 4.2) and there was no significant difference in non-native cover in the plots with or without Cane (compare Year 2 black

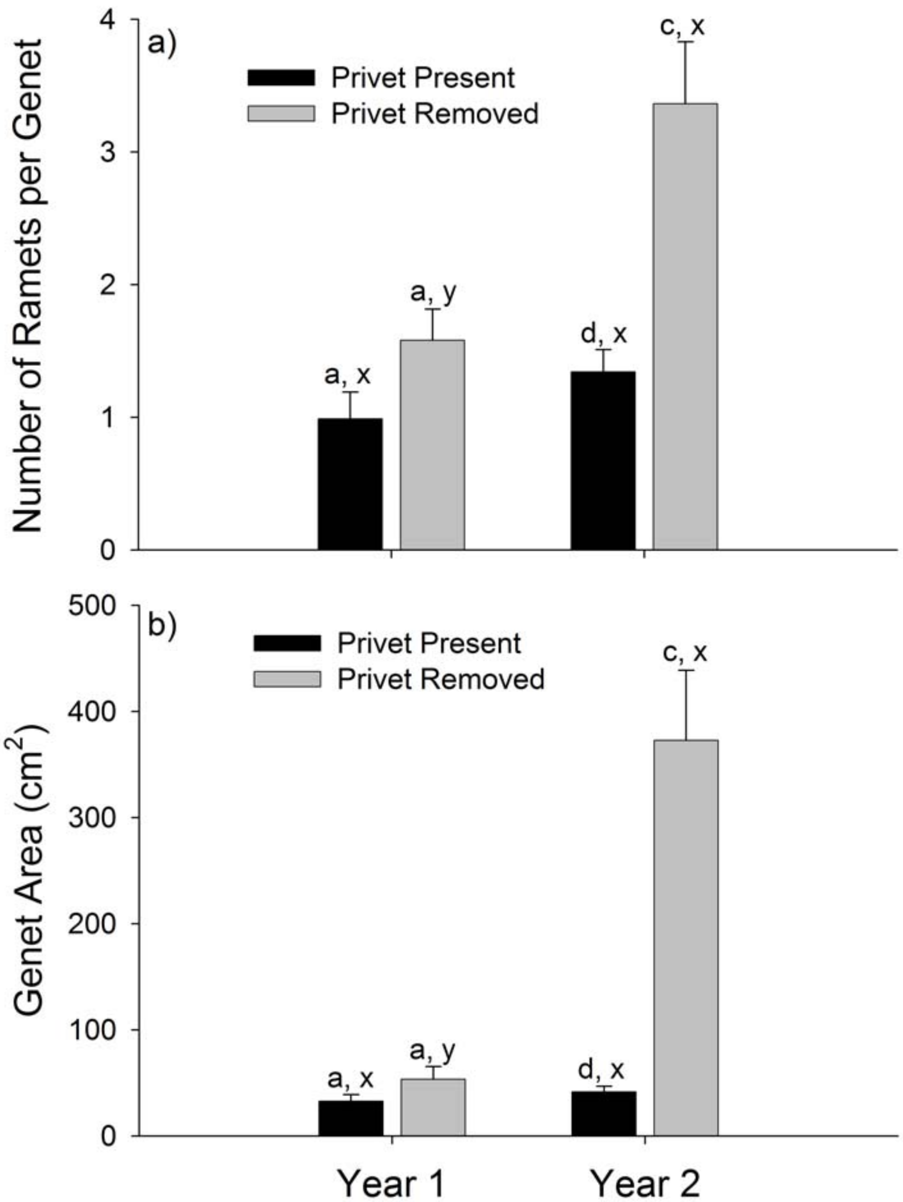

Figure 4.2: Effect of Privet-Presence and Year on: a) mean # of ramets per *A. gigantea* genet; and b) mean *A. gigantea* genet area. Error bars depict +1SE. Columns not connected by the same letter are significantly different (α <0.05). Whereas the first letter (a or b for year 1; c or d for year 2) refers to comparisons between treatments within each year, the second letter (x or y) refers to comparisons between years within each treatment.

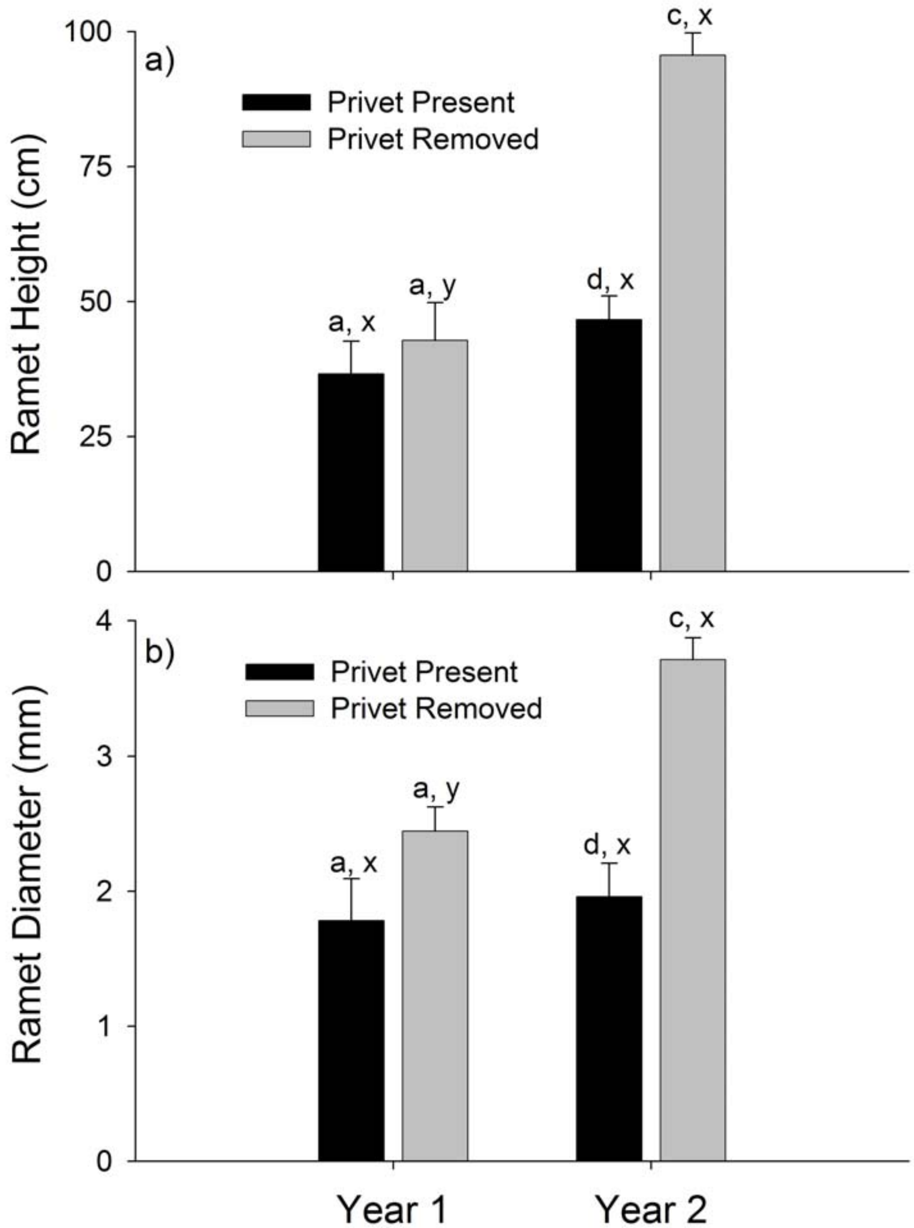

Figure 4.3: Effect of Privet-Presence and Year on: a) mean *A. gigantea* ramet height; and b) mean *A. gigantea* ramet diameter. Error bars depict +1SE. Columns not connected by the same letter are significantly different (α <0.05). Whereas the first letter (a or b for year 1; c or d for year 2) refers to comparisons between treatments within each year, the second letter (x or y) refers to comparisons between years within each treatment.

Table 4.2: Mean Cover, Frequency (Freq.), and Importance Value (I.V.) of the most common plant species in the Privet Removed Plots with and without Cane transplants (Cane and No Cane respectively) at the end of the second growing season. Only the five most common species in the Cane and No Cane treatment are presented. I.V. was calculated as: I.V. = Mean Cover * Frequency. The letters in parentheses following species names denote whether the species is non-native (nn) or native (N).

	No Cane				Cane		
Species	Mean Cover (%)	Freq.	I.V.	Species	Mean Cover (%)	Freq.	I.V.
Microstegium vimineum (nn)	55.4	77.8	43.1	*Microstegium vimineum* (nn)	41.1	100.0	41.1
Phytolacca americana (N)	9.1	55.6	5.1	*Arundinaria gigantea* (N)	26.7	100.0	26.7
Hedera helix (nn)	6.7	44.4	3.0	*Phytolacca americana* (N)	8.0	88.9	7.1
Lonicera japonica (nn)	3.2	77.8	2.5	*Lonicera japonica* (nn)	2.7	77.8	2.1
Ligustrum sinense (nn)	2.4	100.0	2.4	*Ligustrum sinense* (nn)	2.1	88.9	1.8

and grey bars in Figure 4.4b). In Privet-Removed plots with No Cane transplants, there was a large increase in non-native cover (compare black bars for both years in Figure 4.4b; $t = 3.1$, $p = 0.03$) and an insignificant increase in native cover during the second year (compare black bars for both years in Figure 4.4c). In Privet-Removed plots with Cane transplants, there was an insignificant increase in non-native cover during the second year (compare grey bars for both years in Figure 4.4b), and a large increase in native cover (compare grey bars for both years in Figure 4.4c; $t = 4.4$, $p < 0.01$). The majority of the native cover in these Privet-Removed plots with Cane consists of one species, the transplanted cane (Table 4.2). The only other native species in these plots with an importance value that ranked in the top five was *Phytolacca americana* L. which was frequently present but with a relatively small mean cover (Table 4.2).

4.4 Discussion

Moisture availability during transplantation appears to play an important role in determining the survival of giant cane clump divisions (Platt and Brantley 1993, Dattilo and Rhoades 2005); transplantation is more likely to be successful when implemented early in the growing season and in conditions that will minimize desiccation. In this study, cane transplantation via clump division was very successful. However, we must note that we were very careful to insure high moisture availability during clump transport and also during the first two weeks post-transplantation. Successful use of this species by the restoration community will likely require a similar level of initial

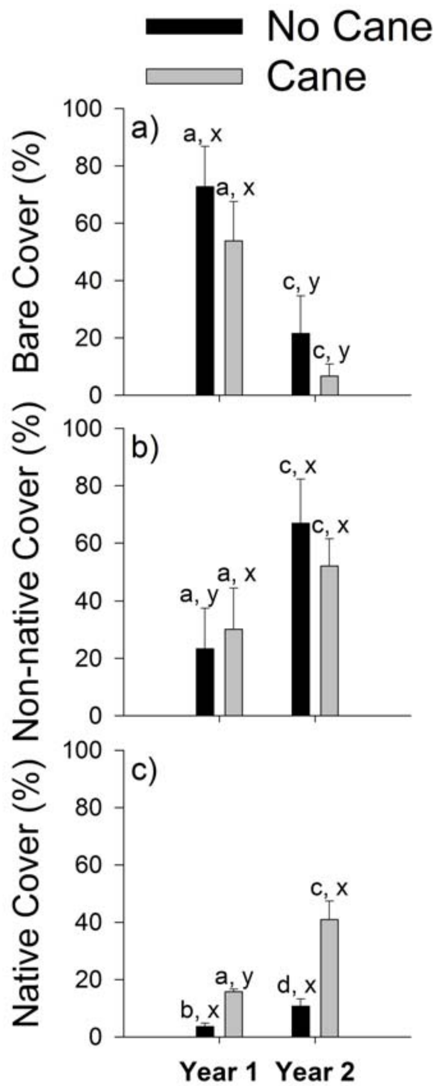

Figure 4.4: The effect of *A. gigantea* transplantation via clump division and time on (a) mean bare, (b) mean native plant, and (c) mean non-native plant percent cover in plots where privet was removed. Error bars depict +1SE. Columns not connected by the same letter are significantly different (α <0.05). Whereas the first letter (a or b for year 1; c or d for year 2) refers to comparisons between treatments within each year, the second letter (x or y) refers to comparisons between years within each treatment. Bare refers to the area not covered by vegetation. This figure only depicts the change in cover after privet removal. Plots with privet had very little vegetation beneath the dense privet canopy throughout the study and are not included in this figure.

transplant care to ensure comparable transplant survivability. Once established, cane transplants appear to be very drought-resilient; despite an extraordinary drought in the second growing season of this study (2007), cane survival was very high. In an experiment with cane seedlings, Cirtain et al. found similar results; cane seedling survival was high despite periodic drought conditions (2004). However, they also found the cane seedling growth was reduced during drought conditions (Cirtain et al. 2004)

With regards to light availability, cane survival was high in both the low and high-light conditions provided by the privet treatments indicating that cane transplants can tolerate diverse light conditions in at least the first several years. This finding is supported by Gagnon et al. (2007) who found that cane is able to persist sparsely in low-light environments. Despite high survival, cane growth and expansion during the first year of this study was minimal and not different in the contrasting light conditions provided by the privet treatments. Datillo and Rhoades (2005) also observed minimal growth and expansion during the first year post-transplantation. In the second year of our investigation, the genets not beneath a privet canopy (i.e., higher light availability and potentially greater availability of other resources such as moisture and nutrients) produced more ramets, expanded in genet area, and grew taller and thicker. Fire and gap opening disturbances have been shown to stimulate cane growth and canebrake formation (Gagnon 2006, Gagnon et al. 2007, Gagnon and Platt 2008a), and we expect that in future years the difference in cane growth and expansion between privet treatments will be even more dramatic as the cane genets in the Privet-Removed treatment continue to grow and expand more rapidly.

Cane restoration via clump division is an effective but somewhat labor intensive process. However, cane is not readily available commercially and other techniques for propagation are not yet widespread. In the next decade, it is likely that more efficient and commercially viable techniques for cane propagation and canebrake restoration will be available (Sexton et al. 2003, Brendecke and Zaczek 2008). In the meantime, clump division appears to be a relatively simple and effective way to transplant cane into a site. Even if cane propagules become more available commercially in the future, restoration via clump division may continue to be a valuable technique for cane transplantation, particularly in sites where restoration objectives stipulate the use of local genotypes.

One of our tangential objectives was to assess the cut and paint method for removal of mature privet individuals. This method resulted in 100% mortality in this study and appears to be an effective means for removing mature stands of privet (Miller and Albritton 2004). As expected, privet removal resulted in rapid recruitment and growth of other plant species. To our knowledge, this is the first study to assess cane growth in the presence of other plant species in a restoration context, particularly common invasive non-native species. Invasive non-native plants are common in southeastern United States floodplain ecosystems/restoration sites and we were especially interested in monitoring cane growth in the presence of the following invasive non-native species: *M. vimineum*, *Ligustrum sinense*, and *Lonicera japonica.* In these initial years, *M. vimineum* has clearly become the most dominant species at the site. However, giant cane genets continue to grow and expand despite the presence of this non-native grass. We will monitor whether cane will be able to compete with *M. vimineum* in the future and prevent it from continuing as the dominant understory species. In addition to the interaction with *M. vimineum*, we will also closely monitor the competitive interaction between cane and the very dense privet seedlings which have recruited in parts of the site. Although these privet seedlings have grown very slowly in these first two years, we plan to monitor growth in the subsequent years and determine whether these individuals will negatively impact future cane growth.

The cane transplantation process we utilized presents several potentially confounding factors to plant community composition comparisons that are not directly controlled in the experimental design and should be addressed. These factors include possible additions or withdrawals from the seed bank and the physical soil disturbance associated with transplanting clump divisions. Within each cane plot, the area potentially impacted by the transplantation process is fairly large, roughly 20% of the overall plot area. Hence, the disturbance associated with transplantation could potentially have a considerable impact on the plant community. When designing the experiment, we expected that the cane in the Privet-Removed plots would quickly fill in this disturbed area and continue to expand into the undisturbed portions of the plot.

In these first two years, the mean cane genet area has increased sevenfold after privet removal and much of this rhizome expansion has occurred in areas well beyond the immediate area impacted by the transplantation process. The maximum and mean ± 1SE genet length (an indicator or rhizome expansion) in Privet-Removed plots after the second year was 100 cm and 25.8 ± 2.6 cm, respectively. Although these expansion values are not extremely large by leptomorphic bamboo standards, they do help demonstrate that much of the cane expansion is occurring beyond the area potentially impacted by the transplantation process.

After these first two years, plots with cane had greater native cover relative to plots without cane. However, we must be clear that the increase in native cover is not due to a facilitative process; most of native cover in these plots consists of one species, cane, and the increase in native cover is due to the fact that we planted cane in these plots and this cane has begun to expand. Another critical point is that in addition to increasing the overall native cover, the transplantation process simultaneously decreased the non-native cover since *M. vimineum* or one of the other common non-native species would likely have recruited into and dominated these areas if cane was not planted there. The results from these first two years indicate that the cane in Privet-Removed plots will likely be able to compete with the other species present in this study. However, we only have two years of data and are hesitant to make strong conclusions regarding long-term future trajectories. Our future research will continue to measure the rate of cane growth and expansion and monitor changes in plant community composition. In the process, we will continue to investigate whether giant cane is a suitable native competitive-dominant species that can be targeted during floodplain restoration efforts for its ability to reduce non-native community invasibility and also restore important ecosystem functions and services.

5. Plant community response to removing an invasive non-native shrub and planting a native bamboo

Abstract

Since riparian restoration efforts in the southeastern U.S. are often hindered by invasive non-native plants, there is much interest in approaches that can be used to reduce the impact of invasive non-native plant populations at the local level (e.g., a restoration site). In addition to the impact of non-native species-specific removal efforts, there is also much interest in the identification and assessment of native competitive-dominant plant species that can be used during riparian restoration to support important ecosystem functions and reduce non-native invasibility. *Ligustrum sinense* (Chinese privet) is a very common invasive non-native shrub in the region. *Arundinaria gigantea* (giant cane) is a native bamboo species that used to be very abundant in riparian and wetland ecosystems in the region. The objectives of this study were to: (1) measure the plant community response to removal of mature *L. sinense* individuals; and (2) quantify planted *A. gigantea* clonal expansion in the presence of other plants, particularly common non-native invasive species. Due to its potential for rapid growth and expansion, we hypothesized that *A. gigantea* would be able to compete with common non-native species and reduce non-native invasibility. In a three-year split-plot experimental design, we applied a Privet-Presence treatment at two levels (Privet Present, Privet Removed) and a Cane-Planting treatment also at two levels (Cane, No

Cane). The privet removal treatment resulted in 100% mortality of mature privet individuals. After privet removal, *L. sinense* seedlings recruited into these plots but growth has been very slow and these *L. sinense* individuals are not yet dominant. The privet canopy allows minimal understory plant recruitment and growth and privet removal resulted in an increase in species richness and diversity in the first year. However, in these Privet-Removed plots, a non-native invasive annual grass (*Microstegium vimineum*) invaded, became the most dominant species, and reduced species richness and diversity. In Privet-Removed plots, *A. gigantea* clonal expansion (i.e., ramet density, genet area, ramet diameter, and ramet height) was small in the first year but increased in the second and third years. Importantly, in Privet-Removed plots where we planted *A. gigantea*, *M. vimineum* cover was lower and species richness and diversity were greater; planting *A. gigantea* appears to have facilitated the establishment of other species and, in the process, inceased diversity.

Keywords: *Arundinaria gigantea*; *Ligustrum sinense*; *Microstegium vimineum*; bamboo; giant cane; canebrake restoration; plant community restoration; clonal expansion; invasive plant management; community invasibility.

5.1 Introduction

Invasive non-native plant species typically reduce native biodiversity and alter important ecosystem functions and services (Vitousek et al. 1996). A common objective of ecological restoration is to constrain non-native plant invasions, restore native plant communities, and restore important ecosystem functions and services. However, most established invasive non-native plant populations are very resilient to removal efforts and the disturbances associated with restoration efforts often make restoration sites more susceptible to plant invasions (D'Antonio and Chambers 2006). Successful restoration of native plant communities is often dependent upon the presence of native competitive-dominant species that will be able to occupy and become dominant in niches that would be utilized by invasive non-native species (Funk et al. 2008). Interspecific competition is recognized as one of the primary mechanisms controlling plant community composition (Harper 1977, Grime 1979, Tilman 1982). Competitive-dominant species typically determine ecosystem functions (Grime 1998, Walker et al. 1999, Cardinale et al. 2006) and dictate community invasibility (Crawley et al. 1999, Smith et al. 2004, Emery and Gross 2007). There is a need for research that identifies and evaluates native plant species with competitive-dominant traits that can be targeted during restoration efforts for their ability to resist non-native invasions and restore important ecosystem functions.

In southeastern U.S. riparian ecosystems, invasive plant species introduced from Asia are very common. For example, *Ligustrum sinense* (Chinese privet), *Lonicera japonica* (Japanese honeysuckle), and *Microstegium vimineum* (Japanese stiltgrass) are three practically ubiquitous species that limit understory plant recruitment and prevent native riparian plant community development (Ehrenfeld et al. 2001, Morris et al. 2002, Schierenbeck 2004). There is much interest in techniques that can be used to constrain the expansion and dominance of these species at the local level (e.g., a restoration site) and restore native plant communities. Due to its potential for rapid growth and expansion, we hypothesized that a native competitive woody grass (i.e., a bamboo; *Arundinaria gigantea*; giant cane) would be able to compete with these species and reduce their invasibility. *A. gigantea* used to be one of the most common and competitive plants in riparian and wetland ecosystems in the southeastern U.S. but is less common today presumably due to agricultural conversion, overgrazing, and changes in disturbance regimes (Bartram 1791, West 1934, Platt and Brantley 1997, Stewart 2007, Gagnon and Platt 2008a). *A. gigantea* is a clonal plant that spreads rapidly via leptomorhic rhizome expansion forming a dense network of interconnected ramets. This species is a dominant competitor (*sensu* Grime 1979) and can form extensive monotypic areas which are often called canebrakes. There is much interest in restoring canebrakes and using *A. gigantea* for riparian restoration (Brantley and Platt 2001, Dattilo and Rhoades 2005, Brendecke and Zaczek 2008). Previous research has shown that canebrakes provide important wildlife habitat (Brantley and Platt 2001) and support various water-quality related ecosystem services (Schoonover and Williard 2003, Blattel et al. 2005, Schoonover et al. 2005, 2006). Several studies have examined techniques for cane transplantation and propagation (Feedback and Luken 1992, Platt and Brantley 1993, Sexton et al. 2003, Dattilo and Rhoades 2005, Brendecke and Zaczek 2008, Osland et al. *in press*). However, we have not seen any studies that have assessed *A. gigantea*'s ability to compete with other plants, particularly non-native invasive species (other than the preliminary results reported in Osland et al. *in press*).

In this study, we quantified the plant community response to removing an invasive non-native shrub (*L. sinense*) and planting a native competitive-dominant bamboo (*A. gigantea*). The objectives of this study were to: (1) measure the effectiveness and plant community response to removing an invasive non-native shrub (mature individuals of *L. sinense*); and (2) quantify planted *A. gigantea* clonal expansion in the presence of other plants, particularly common non-native invasive species. We expected that removing *L. sinense* would result in an increase in plant recruitment and diversity. However, due to the large number of non-native species present at the site, we expected that non-native species would quickly become dominant in plots where we did not plant *A. gigantea.* Due to its potential for rapid clonal expansion and vertical growth, we expected that, where planted, *A. gigantea* would become dominant, compete with common invasive non-native species, and reduce invasibility.

5.2 Methods

5.2.1 Study site

This research was conducted within the Duke University Wetland Center's Stream Wetland Assessment and Management Park (SWAMP) in Durham County, North Carolina (lat 35°59'27", long 78°56'28"; U.S.A.). The site is located within the floodplain of Upper Sandy Creek, a headwater piedmont stream within the Cape Fear River Basin. This section of Upper Sandy Creek has a drainage area of approximately 480 ha that includes much of Duke University's West Campus. The climate at the site includes a growing season of roughly 200 days. The thirty-year mean annual temperature and precipitation near the site was 15.3^{o}C and 1190 cm, respectively [based on data from 1970-2001 (NOAA 2008); measured at the Raleigh-Durham International Airport which is 19 km away]. However, 2006 and 2007 were relatively abnormal years with annual precipitation values of 1360 and 910 cm, respectively.

Soil series at the site include Cartecay (coarse-loamy, mixed, nonacid, thermic Aquic Udifluvents) and Chewacla (fine-loamy, mixed, thermic Fluvaquentic Dystrochrepts). Adjacent soil series that drain into the site include Mayodan (clayey, kaolinitic, thermic Typic Hapludults) and White Store (fine, mixed, thermic Vertic Hapludalfs) (Kirby 1976). The riparian forest canopy in the Upper Sandy Creek floodplain is dominated by *Acer rubrum* L., *Liriodendron tulipifera* L., *Liquidambar styraciflua* L., and *Ulmus americana* L. (Watts 2000). The specific portion of the floodplain where this experiment was conducted is also dominated by *Acer negundo* L. The understory shrub layer is dominated by dense stands of *L. sinense*. Additional information on the soils, vegetation, and hydrologic functioning of the SWAMP restoration site are available in Richardson et al. (2006), Kazezyilmaz-Alhan et al. (2007), and Sutton-Grier (2008).

5.2.2 Experimental design

In a randomized split-plot experimental design, we applied a Privet-Presence treatment at two levels (Privet Present, Privet Removed) and a Cane-Planting treatment also at two levels (Cane, No Cane) (see Figures 5.1 and 5.2BDE for an illustration and photos of the experimental design). Whereas the Privet-Presence treatment levels were applied to 40-m^2 whole-plots, the Cane-Planting treatment levels were applied to 4-m^2 subplots. Two additional blocks were established to account for potential confounding effects associated with *Hedera helix* presence (Block 1: *H. helix* not present, Block 2: *H. helix* present); whereas six replicates were randomly established in Block 1, three replicates were randomly established in Block 2. In total, the experimental design includes 18 whole-plots and 36 subplots.

In the Privet-Removed treatment level, privet stems were cut 3-5 cm above the ground in March 2006 and exposed stumps were immediately painted with undiluted 50.2% glyphosate (Roundup® Weed & Grass Killer Super Concentrate, Monsanto Company, St. Louis, MO, U.S.A.). We refer to this removal method as "cut and paint" (as discussed in Miller and Albritton 2004). The cut and paint method resulted in 100% mortality; none of the privet treated in this manner resprouted. Since this stand was nearly monotypically privet, very few species remained in the plots after privet removal. In the Privet-Present treatment, the privet stands were left intact. As expected, privet removal resulted in greater light availability; the mean Photosynthetically Active

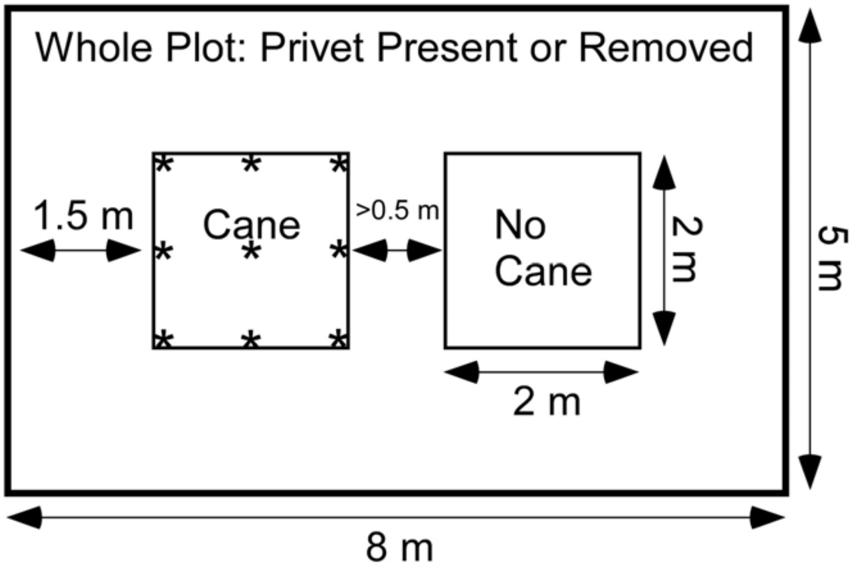

Figure 5.1: An illustration of the experimental design. The Privet treatment (Privet-Present or Privet-Removed) was applied to 40-m^2 whole plots. The Cane transplantation treatment (Cane or No Cane) was applied to 4-m^2 subplots. In the Cane subplot treatment, nine *Arundinaria gigantea* clump divisions were transplanted as depicted by the asterisks in the illustration.

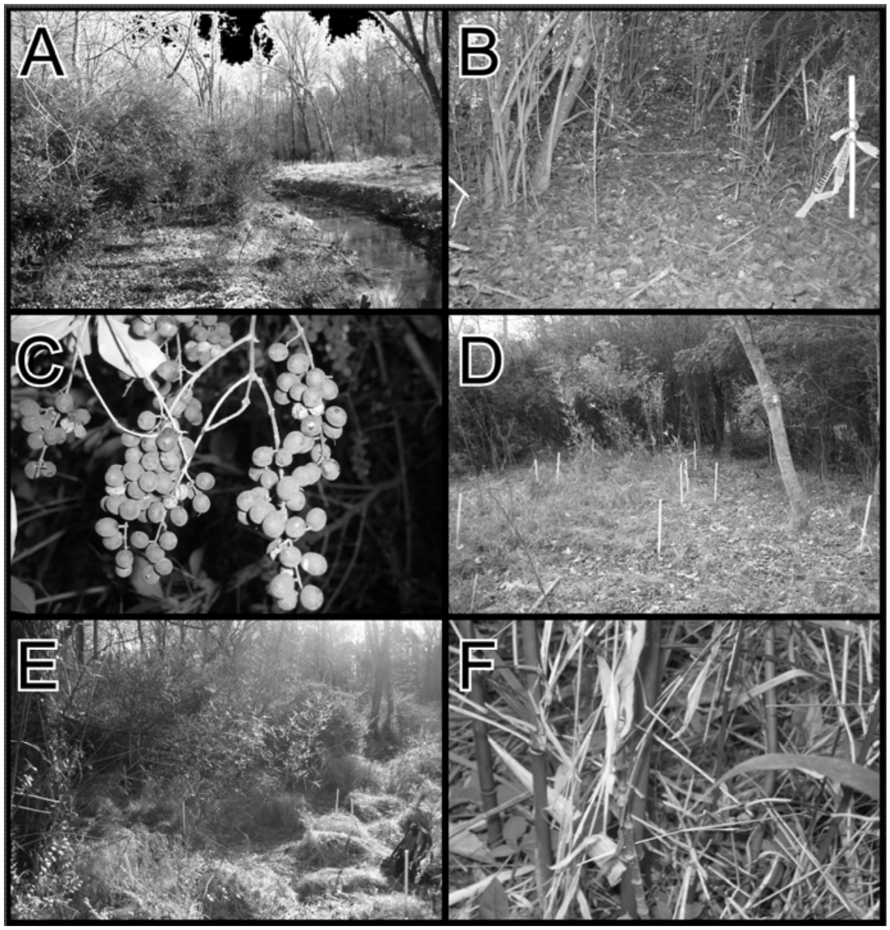

Figure 5.2: Photos of: (A) Sandy Creek with stands of mature *Ligustrum sinense* on the left bank and *Microstegium vimineum* on the right bank; (B) the understory beneath mature *L. sinense*, note that there is very little recruitment and growth beneath the *L. sinense* canopy; (C) *L. sinense* drupes which are easily dispersed by birds; (D) a Privet-Removed whole plot in the second year of the study with No Cane and Cane subplots, note the mature *L. sinense* behind this plot; (E) a Privet-Removed plots with cane planted, this photo was taken in the third year, note the dense *M. vimineum* litter; and (F) *Arundinaria gigantea* ramets in a Privet-Removed plot.

Radiation (PAR) ± 1SE for the Privet-Present and Privet-Removed plots (measured in late June/early July of the first year) was 52.1 ± 2.9 and 211.2 ± 29.6 μmol/m²/s, respectively ($t = 5.4$, $p < 0.001$) (Osland et al. *in press*).

The Cane-Planting treatment levels were applied at the subplot level in late April 2006. Whereas the No Cane treatment plots received no cane transplants, nine clump divisions were transplanted within each Cane treatment plot (planting arrangement resulted in a density of 2.25 clump divisions/m² with clumps planted in three rows, 1 m apart). The 162 clump divisions were obtained from a donor cane stand along the floodplains of New Hope Creek within the Jordan Game Lands, Durham, NC (roughly 7 km downstream of the study site).

5.2.3 Plant community measurements including cane growth and expansion

Understory species presence and percent cover were measured in each subplot at the end of each of three growing seasons. The cover data was used to calculate species richness and diversity (using the Shannon-Wiener index with the use of the relative percent cover of species i to represent p_i in the calculations). In order to gauge species dominance, we used the percent cover values to calculate importance values (I.V.), calculated as: I.V. = (mean % cover * Frequency)/100. We also measured cane ramet density, ramet height, ramet diameter, and genet area at the end of each growing season. We refer to a group of interconnected rhizomes and culms as a genet and each individual culm or shoot as a ramet. Genet area was determined as the product of the greatest distances between two ramets along two perpendicular axes (*sensu* Datillo and Rhoades 2005).

5.2.4 Data analyses

To compare the impact of privet removal and time on cane growth and expansion (i.e., cane genet area, ramet height, ramet diameter, and ramet density), we used repeated measures mixed factor effects analyses of variance (ANOVA) models with the following independent variables: block (random effect), Privet (Privet-Presence treatment; fixed effect), Year (fixed effect), and the interaction between Privet and Year. To avoid pseudoreplication, we used the mean of all nine cane genets present in a subplot for all analyses and figures. To improve normality and better meet the assumptions of ANOVA, genet area and the number of ramets per genet were log-transformed prior to analyses. Comparisons of means between treatments within years and between years within treatments were conducted using Student's t-tests and repeated measures t-tests, respectively.

To test the impact of privet removal, time, and cane transplanting on plant community measures (plant species richness, plant species diversity, *A. gigantea* cover, and *M. vimineum* cover) we used mixed factor effects ANOVA models with the following independent variables: block (random effect), Privet (Privet-Presence treatment; fixed effect), Year (fixed effect), Cane (Cane-Planting treatment; fixed effect) and the two and three-way interactions between the fixed effects. Comparisons of means between treatments within years and between years within treatments were conducted using Tukey HSD tests and repeated measures t-tests respectively. All ANOVA analyses were conducted using PROC MIXED in SAS Version 9.1.3 (SAS Institute, Cary, NC, U.S.A.).

To illustrate changes in plant community composition due to Privet-Presence treatment levels and Cane-Planting treatment levels for all three years of the study, a nonmetric multidimensional scaling (NMS) analysis (Kruskal 1964, Mather 1976, McCune and Grace 2002) was performed using PC-ORD (McCune and Medford 1999). Prior to analysis, we relativized the species cover data by species maxima and removed rare species which were defined as species present in less than 5 % of the plots. The resultant matrix contained 29 species and 102 plots. Bray-Curtis dissimilarity coefficients were used to quantify plant species compositional distance (Bray and Curtis 1957). In order to determine the appropriate number of dimensions to include in the analysis, we used a stepdown procedure to compare the number of dimensions with the corresponding change in final ordination stress. We initially evaluated 6 axes using 100 runs with real data, a stability criterion of 0.00001, a maximum of 400 iterations, and a Monte Carlo test with 150 randomizations to determine whether the resultant axes were stronger than those identified by chance (McCune and Grace 2002). Based upon this procedure, a three dimensional analysis was deemed optimal and resulted in a final stress of 16.9, a P value of 0.007, and a final instability of 0.00001 after 163 iterations.

To illustrate and highlight the changes in plant community composition due to Cane-Planting treatment levels after privet removal in the third year, an additional NMS was performed using just the third year data from the Privet-Removed plots. We used an identical stepdown procedure as the one used in the initial NMS and based upon this procedure, a three dimensional analyses was deemed optimal and resulted in a final stress of 10.0, a *P* value of 0.007, and a final instability of 0.00001 after 172 iterations.

5.3 Results

5.3.1 Cane growth and expansion

During the first year, there was no difference in cane growth and expansion (i.e., change in ramet height, ramet diameter, ramet density, and genet area) between the Privet-Present and Privet-Removed plots (Figure 5.3ABCD). However in the second and third year, the increase in cane ramet height, ramet diameter, ramet density, and genet area was significantly greater in the Privet-Removed plots (Figure 5.3ABCD). After three years, the maximum individual values for ramet height, ramet diameter, ramet density, and genet area were 335 cm, 12 mm, 18 ramets / genet, and 1.8 m^2, respectively (all of these maximum values were measure in Privet-Removed plots).

5.3.2 Plant community composition

In the three years of this study, we observed 80 different plant species, 51 of which were deemed rare (i.e., present in less than 5% of the plots; common species are shown in Table 5.1). Importantly, throughout the three years of this study, 79 species

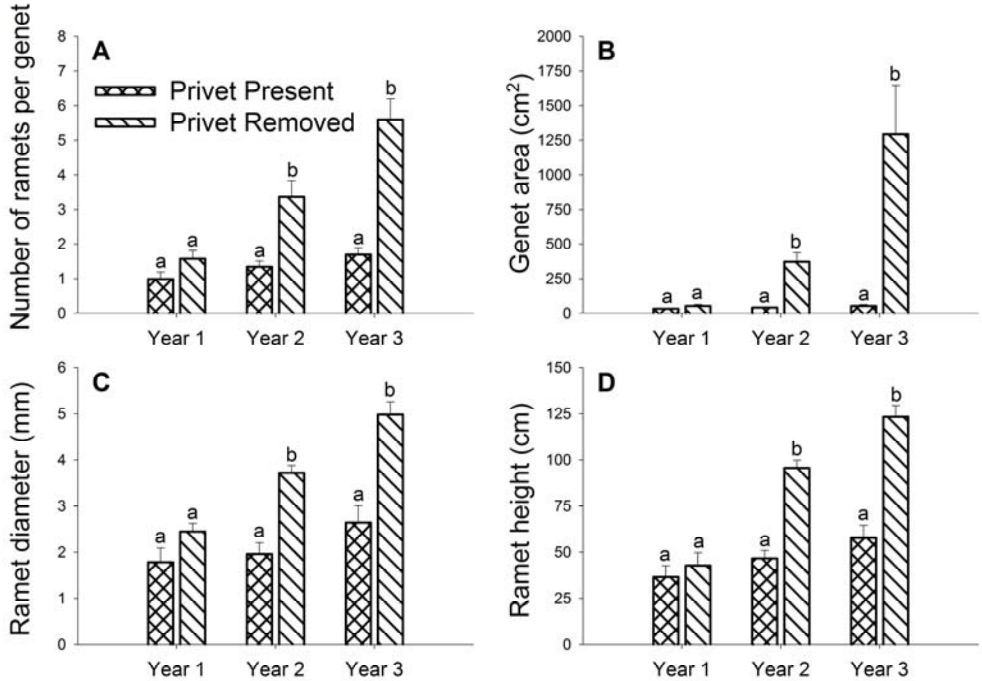

Figure 5.3: Impact of privet presence on cane (A) ramet density, (B) genet area, (C) ramet diameter, and (D) ramet height (mean + SE). Letters refer to comparisons between treatments within years.

Table 5.1: Importance values for common species in the Privet-Presence and Cane-Planting treatment combinations for the three years of the study. The 29 common species included in this table were defined as those species present in greater than 5% of the plots. The treatment codes are as follows: PP = Privet Present, PR = Privet Removed, C = Cane Planted, and NC = Cane Not Planted. The form and nativity codes are as follows: G = graminoid, F = Forb, S = Shrub, V = Vine, SS = Subshrub, N = Native, and nn = Non-native. The species codes can be used to interpret the ordinations in Figures 5.7 and 5.8. Importance values (IV) were calculated as: IV = (mean cover * frequency)/100.

			Year 1				Year 2				Year 3			
Species	**Code**	**Form, Nativity**	**PP, C**	**PP, NC**	**PR, C**	**PR, NC**	**PP, C**	**PP, NC**	**PR, C**	**PR, NC**	**PP, C**	**PP, NC**	**PR, C**	**PR, NC**
Microstegium vimineum	MiVi	G, nn	0.19	0.00	19.28	10.50	0.10	0.19	41.06	43.11	0.09	0.31	39.07	69.50
Arundinaria gigantea	ArGi	G, N	7.83	0.00	11.28	0.00	15.17	0.00	26.67	0.00	11.00	0.00	30.33	0.00
Phytolacca americana	PhAm	F, N	0.00	0.00	1.51	1.99	0.00	0.00	7.11	5.06	0.05	0.07	4.89	2.04
Ligustrum sinense	LiSi	S, nn	11.17	6.94	3.22	4.64	14.39	9.68	1.83	2.40	10.43	13.07	4.79	8.56
Lonicera japonica	LoJa	V, nn	0.45	0.34	0.39	0.52	0.56	1.40	2.12	2.48	1.17	1.94	1.50	1.90
Hedera helix	HeHe	V, nn	8.04	8.44	2.82	7.73	12.56	18.69	1.56	2.99	16.80	20.95	1.34	0.84
Toxicodendron radicans	ToRa	V, N	0.00	0.00	0.23	0.32	0.00	0.10	0.92	1.10	0.01	0.01	0.88	0.22
Rubus argutus	RuAr	SS, N	0.00	0.00	0.01	0.04	0.00	0.00	0.59	0.22	0.00	0.00	0.74	0.67
Bignonia capreolata	BiCa	V, N	0.02	0.00	0.03	0.00	0.12	0.00	0.42	0.00	0.06	0.00	0.34	0.02
Vitis cinerea	ViCi	V, N	0.00	0.00	0.09	0.07	0.00	0.00	1.27	0.52	0.00	0.04	0.31	0.45
Vitis rotundifolia	ViRo	V, N	0.00	0.00	0.19	0.14	0.00	0.00	0.13	0.01	0.00	0.00	0.20	0.00
Eupatorium serotinum	EuSe	F, N	0.00	0.00	0.26	0.00	0.00	0.00	0.26	0.07	0.00	0.00	0.19	0.49
Carex spp.	CaSpp	G, N/A	0.01	0.01	0.03	0.00	0.00	0.02	0.14	0.00	0.00	0.00	0.13	0.00
Smilax rotundifolia	SmRo	V, N	0.00	0.00	0.00	0.00	0.04	0.00	0.06	0.00	0.02	0.00	0.05	0.01
Acer negundo	AcNe	T, N	0.00	0.01	0.05	0.07	0.00	0.09	0.11	0.16	0.00	0.03	0.05	0.30
Celastrus orbiculatus	CeOr	V, nn	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.03	0.01
Fraxinus americana	FrAm	T, N	0.00	0.00	0.00	0.00	0.00	0.04	0.04	0.06	0.00	0.04	0.02	0.00
Albizia julibrissin	AlJu	T, nn	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.01
Polygonum cespitosum	PoCa	F, N	0.00	0.00	1.05	0.02	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.02
Euonymus fortunei	EuFo	V, nn	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.00
Oxalis stricta	OxSt	F, N	0.00	0.00	0.09	0.01	0.00	0.00	0.01	0.03	0.00	0.00	0.00	0.00
Parthenocissus quinquefolia	PaQu	V, N	0.00	0.00	0.02	0.01	0.00	0.05	0.10	0.30	0.00	0.03	0.00	0.00
Digitaria spp.	DigSpp	G, N/A	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.06	0.00	0.00	0.00	0.00
Dioscorea oppositifolia	DiOp	V, nn	0.00	0.00	0.00	0.00	0.11	0.03	0.11	0.03	0.00	0.00	0.00	0.00
Erechtites hieraciifolia	ErHi	F, N	0.00	0.00	0.14	0.62	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Solanum nigrum	SoNi	F, nn	0.00	0.00	0.27	0.19	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Quercus phellos	QuPh	T, N	0.00	0.01	0.00	0.01	0.01	0.00	0.01	0.00	0.02	0.00	0.00	0.03
Liriodendron tulipifera	LiTu	T, N	0.00	0.00	0.02	0.07	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.06
Morus rubra	MoRu	T, N	0.00	0.00	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.06

were observed in the Privet-Removed plots, while only 24 species were observed in the Privet-Present plots. During the first year, species richness at the plot level was greater in the Privet-Removed plots than in the Privet-Present plots (Figure 5.4CD: Table 5.2; $t = 8.2$, $P < 0.0001$). Nine of the 29 common species observed during the study were non-native species and four of the six species with the highest importance values at the end of the third year were non-native species (Table 5.1). Throughout the study, the species with the highest annual importance value in the Privet-Removed plots was *M. vimineum*. *M. vimineum*'s importance value increased seven fold between the first and the third year (Table 5.1).

As expected, *A. gigantea* cover in the third year was significantly greater in the Privet-Removed plots than in the Privet-Present plots (Figure 5.4A; Table 5.2; $t = 6.2$, $P < 0.001$). Despite *M. vimineum*'s rapid dominance of all of the Privet-Removed plots, *M. vimineum* cover in the third year was significantly lower in the Privet-Removed plots where we planted cane (Figure 5.4B; Table 5.2; $t = 3.0$, $P < 0.01$). Both species richness and diversity were greater in Privet-Removed plots where we planted cane than Privet-Removed plots with no cane (Figure 5.4CD: Table 5.2; [$t = 2.2$, $P = 0.02$] and [$t = 2.7$, $P < 0.01$] for richness and diversity, respectively). While there was a significant negative relationship between *M. vimineum* percent cover and both species richness and diversity (Figure 5.5AB; Table 5.3), there was a positive relationship between *A. gigantea* cover and both species richness and diversity (Figure 5.5CD: Table 5.3). There was a significant

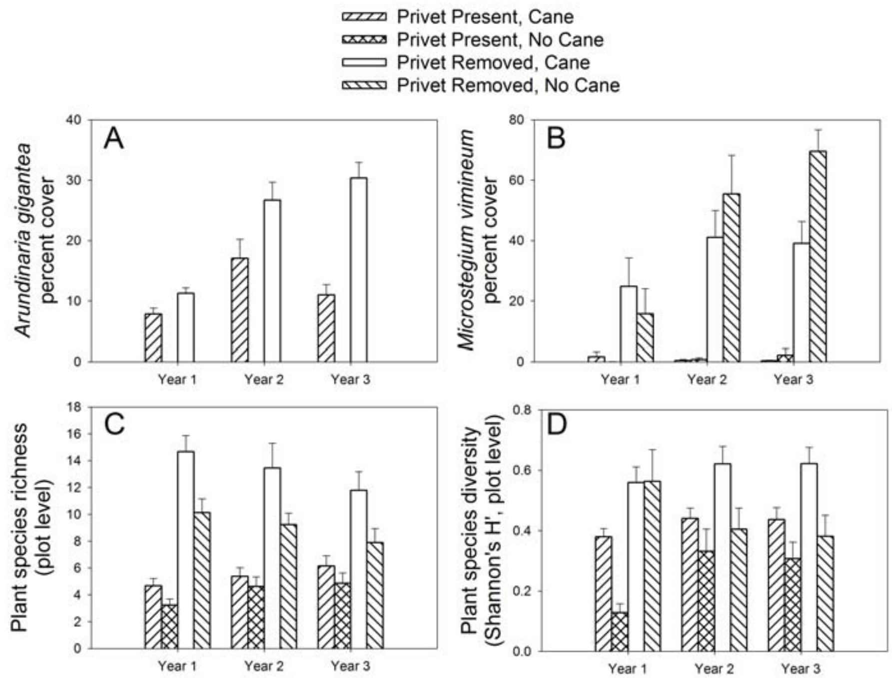

Figure 5.4: Impact of privet presence and cane planting on (A) *Arundinaria gigantea* (cane) percent cover, (B) *Microstegium vimineum* percent cover, (C) plant species richness, and (D) plant species diversity (mean + SE).

Table 5.2: Impact of privet presence and year on cane growth and expansion measurements.

Source	*df*	*Ramet density*	*Genet area*	*Ramet diameter*	*Ramet height*
Year	2, 44	54.9***	55.6***	26.4***	71.7***
Privet	2, 44	6.2*	48.5***	41.5***	41.9***
Privet x Year	2, 44	10.1***	31.2***	7.1**	27.0***

Notes: Data shown are F statistics from ANOVA analyses. Significant F values are denoted by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.5$).

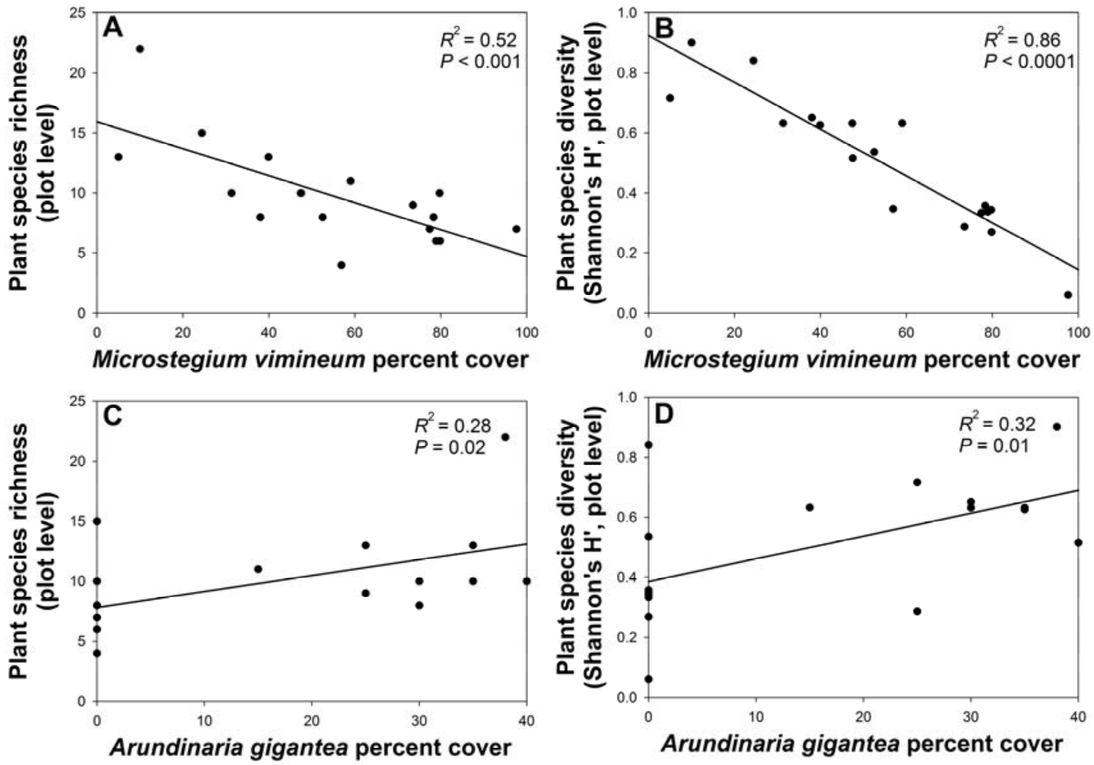

Figure 5.5: Linear regression of (A) *Microstegium vimeneum* percent cover vs. plant species richness, (B) *M. vimeneum* percent cover vs. plant species diversity, (C) *Arundinaria gigantea* percent cover vs. plant species richness, and (D) *A. gigantea* percent cover vs. plant species diversity. These plots depict data from Privet-Removed plots for the third year of the study.

Table 5.3: Impact of privet presence, cane planting and year on species richness, species diversity (H′), *Arundinaria gigantea* cover, and *Microstegium vimineum* cover.

Source	*df* [a]	*Species richness*	*Species Diversity (H')*	*Arundinaria gigantea cover*	*Microstegium vimineum cover*
Year	2, ~76	0.4	0.7	21.5***	13.7***
Privet	1, ~15	37.1***	10.8**	20.5***	30.1***
Cane	1, ~74	37.1***	30.0***	410.3***	4.5*
Year x Privet	2, ~76	7.2**	4.5*	6.9**	13.1***
Year x Cane	2, ~74	0.1	0.4	21.7***	4.8*
Privet x Cane	1, ~74	12.0***	0.0	39.6***	4.2*
Year x Privet x Cane	2, ~74	0.1	4.6*	7.2**	3.4*

Notes: Data shown are F statistics from ANOVA analyses. Significant F values are denoted by asterisks (*** $P < 0.001$, ** $P < 0.01$, * $P < 0.5$).

[a] Since we used a Satterthwaite procedure during these analyses, the denominator degrees of freedom are approximate (±1)

negative relationship between *M. vimineum* percent cover and *A. gigantea* ramet density, ramet diameter, ramet height, and percent cover (Figure 5.6ABCD).

The NMS ordination in Figure 5.7 depicts plant community compositional differences between all of the treatment plots over the three years of the study. The proportion of the compositional variance represented by the three axes included in the analysis was 73% (Axis 1: 30%, Axis 2: 21%, and Axis 3: 22%). We tested relationships between compositional space and the following variables: light availability, species richness, species diversity, privet presence, and cane planting. Light, species richness, species diversity, and privet presence were all most strongly correlated to Axis 1 (using the notation of variable [r^2, τ]: light [0.33, 0.53], species richness [0.42, 0.53], species diversity [0.20, 0.30], privet presence [0.57, -0.63]). Cane planting was most strongly correlated to Axis 2 (r^2 and τ: 0.59 and -0.65, respectively).

The NMS ordination in Figure 5.8 depicts plant community compositional differences for just the third year in just the Privet-Removed plots. The objective of this analysis was to highlight to impact of *M. vimineum* cover and *A. gigantea* expansion on species richness and diversity. We tested relationships between compositional space and the following variables: light availability, species richness, species diversity, cane planting, *A. gigantea* ramet density, *A. gigantea* ramet height, *A. gigantea* genet area, *A. gigantea* ramet diameter, *A. gigantea* cover, and *M. vimineum* cover. This ordination was rotated 48 degrees to load the strongest secondary matrix variable (*M. vimineum* cover).

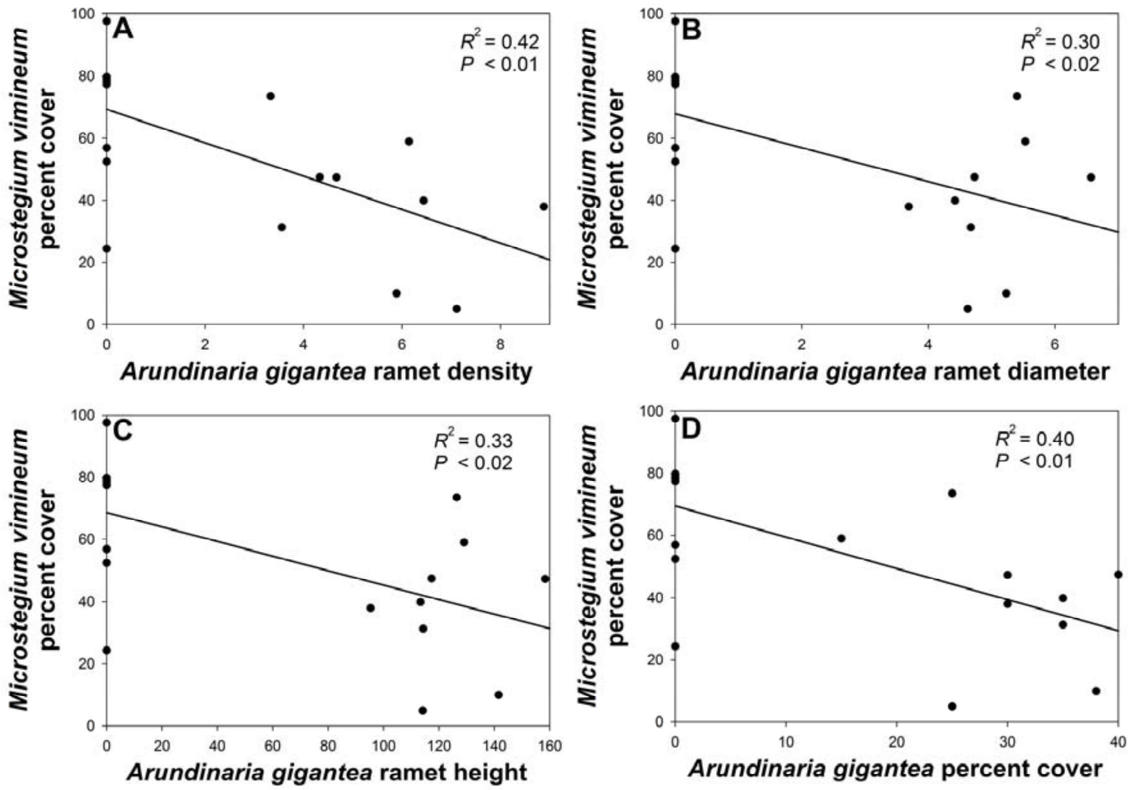

Figure 5.6: Linear regression of (A) ***Arundinaria gigantea*** **ramet density vs.** ***Microstegium vimeneum*** **percent cover, (B)** ***A. gigantea*** **ramet diameter vs.** ***M. vimeneum*** **percent cover, (C)** ***A. gigantea*** **ramet height vs.** ***M. vimeneum*** **percent cover , and (D)** ***A. gigantea*** **percent cover vs.** ***M. vimeneum*** **percent cover. These plots depict data from Privet-Removed plots for the third year of the study.**

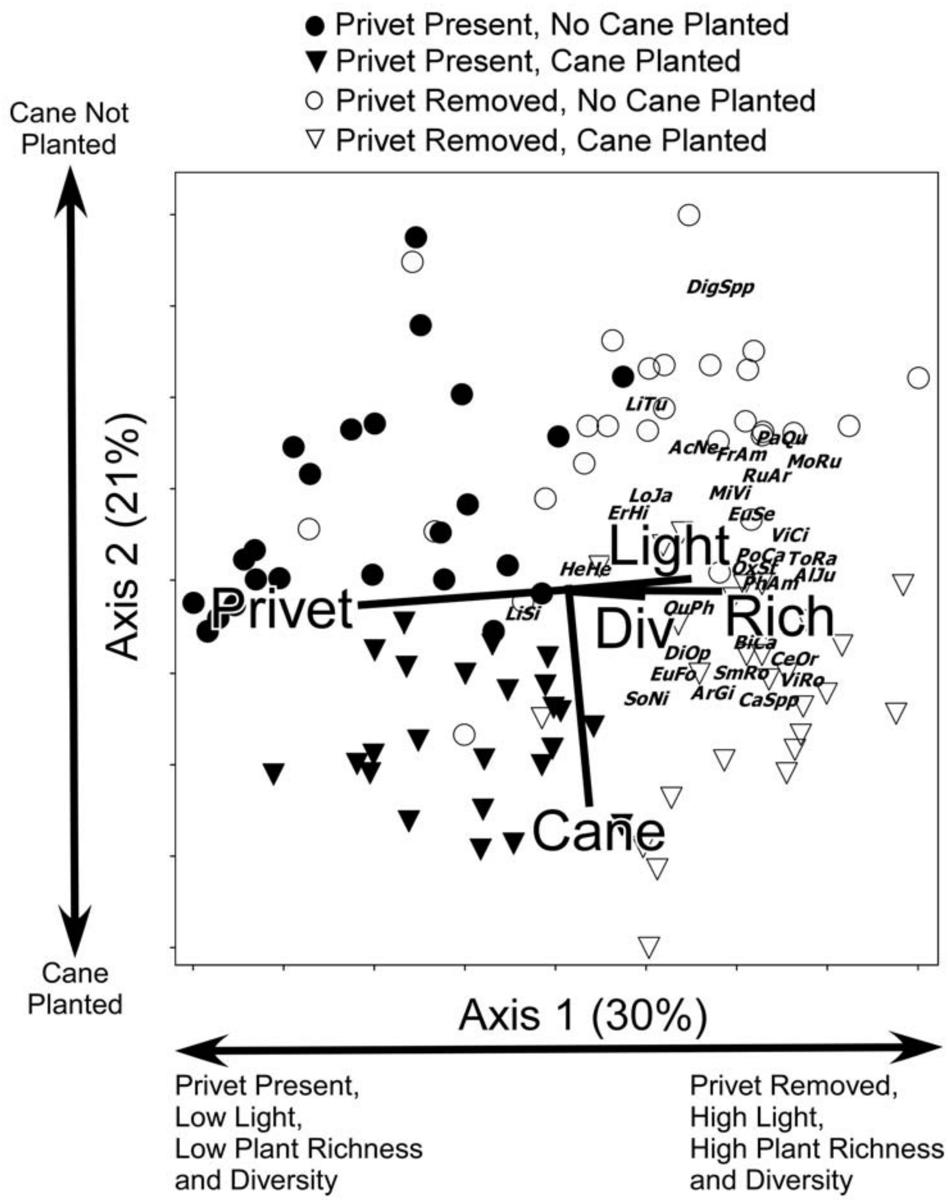

Figure 5.7: Impact of privet presence and cane planting on plant community composition in all plots for all three years of this study. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four letter species codes that can be interpreted with Table 5.1. The vectors reflect the direction and magnitude of significant correlations between variables of interest and ordination space.

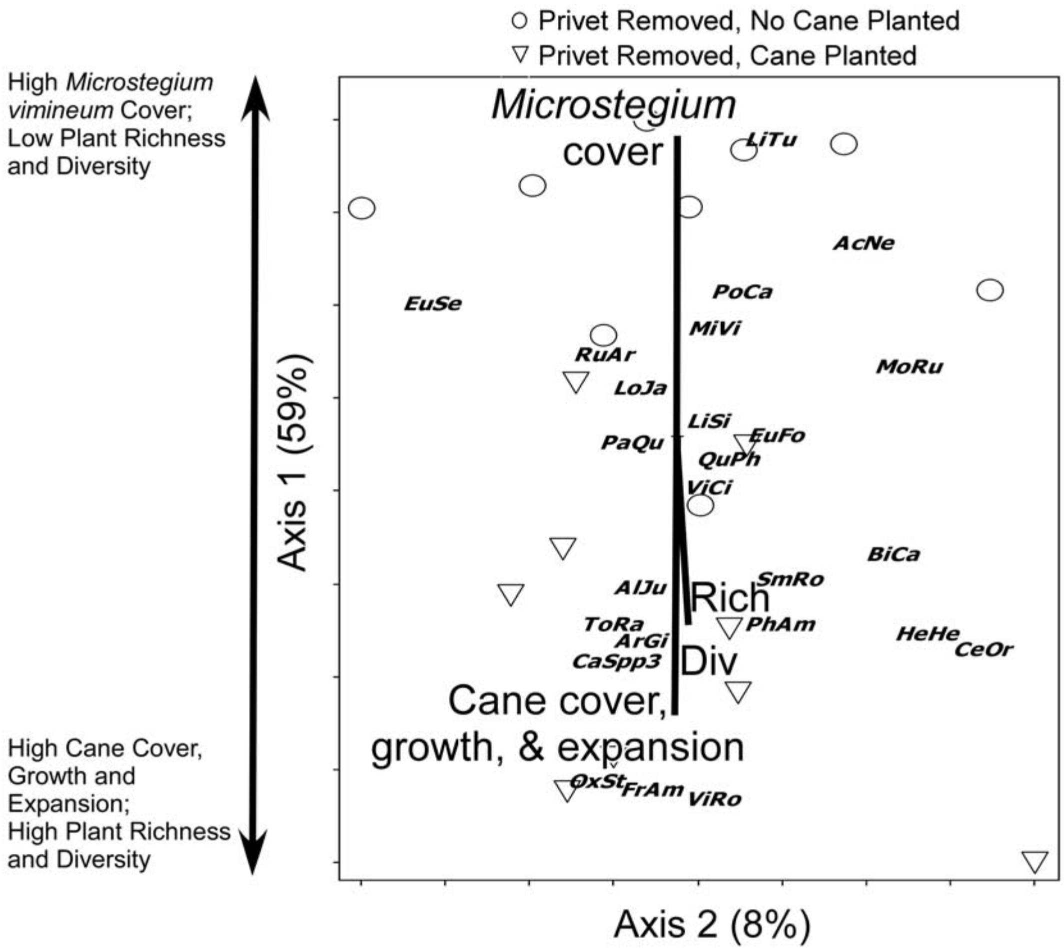

Figure 5.8: Impact of cane planting on plant community composition in Privet-Removed plots in the third year of this study. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four letter species codes that can be interpreted with Table 5.1. The vectors reflect the direction and magnitude of significant correlations between variables of interest and ordination space.

The proportion of the compositional variance represented by the three axes included in the analysis was 89% (Axis 1: 59%, Axis 2: 8%, and Axis 3: 22%). Species richness, species diversity, cane planting, *A. gigantea* ramet density, *A. gigantea* ramet height, *A. gigantea* genet area, *A. gigantea* ramet diameter, *A. gigantea* cover, and *M. vimineum* cover were all most strongly correlated to Axis 1 (using the notation of variable [r^2, τ]: Species richness [0.51, -0.58], species diversity [0.65, -0.62], cane planting [0.69, -0.69], *A. gigantea* ramet density [0.63, -0.63], *A. gigantea* ramet height [0.63, -0.52], *A. gigantea* genet area [0.15, -0.50], *A. gigantea* ramet diameter [0.60, -0.49], *A. gigantea* cover [0.75, -0.70], and *M. vimineum* cover [0.81, 0.75]). This ordination indicates that plots with higher *M. vimineum* cover had lower species richness and diversity. In contrast, plots that were planted with *A. gigantea* had higher species richness and diversity.

5.4 Discussion

5.4.1 Cane growth and expansion

To our knowledge this is the first study to quantify planted *A. gigantea* growth and expansion in the presence of other plants, particularly dominant non-native invasive species. For both the Privet-Present and Privet-Removed plots, cane growth and expansion was minimal in the first year. For cane planted via clump division, this first year appears to be an establishment year and significant growth was not visible above the soil surface until the second year. Beneath a mature privet canopy, *A. gigantea* growth and expansion was minimal throughout the three years of this study. This result is consistent with other studies; although *A. gigantea* can persist in dense shade, its growth is limited in low-light environments but will typically increase in response to disturbances that increase light-availability (Gagnon et al. 2007, Gagnon and Platt 2008a). We expect that if the mature privet individuals in these plots where removed, the *A. gigantea* individuals would respond with vigorous growth and expansion.

In areas where we removed privet prior to planting and increased the amount of light available (i.e., the Privet-Removed plots), *A. gigantea* growth and expansion increased in both the second and third years despite high recruitment and growth of many other species including a very common invasive non-native annual grass, *M. vimineum*. *A. gigantea* mean and maximum ramet height and diameter have steadily increased in these plots over the three years of this study. Future measurements will determine how much longer this increase will continue and also identify the maximum attainable height and diameter for *A. gigantea* ramets at this site. In addition to expanding vertically, *A. gigantea* genets in the Privet-Removed plots have steadily expanded horizontally; *A. gigantea* genet area and ramet density in these plots have steadily increased throughout the three years of this study. To date, the increase in genet area has been nearly linear and we are curious whether this rate will continue at the same pace in the future. The individual genets are now beginning to merge and expand outside of our 4-m^2 plots. At some point, these genets will likely reach the physical transition between the Privet-Removed and Privet-Present plots and it will be interesting to see whether the genet expansion continues into areas with a dense *L. sinense* canopy.

5.4.2 Plant community composition

Beneath the dense canopy of Privet-Present plots, very few species were able to recruit and grow; plant percent cover, species richness, and species diversity were all significantly lower in these plots. The privet canopy is an effective filter which prevents understory plant community development. The few species that could persist beneath the mature privet canopy and had the highest importance values in these plots include *L. sinense*, *A. gigantea* (note that this species was planted), *L. japonica, and H. helix.*

After privet removal, plant richness and diversity increased. However, four of the five most common species for all three years in these Privet-Removed plots were non-native species (*M. vimineum*, *L. sinense, L. japonica*, and *H. helix*). Aside from the planted *A. gigantea,* the only common native species in Privet-Removed plots was *Phytolacca americana* which was locally very abundant/dominant but not as ubiquitous as *M. vimineum, L. japonica*, or *L. sinense*.

In Privet-Removed plots, the most dominant species in all three years was the invasive non-native annual grass, *M. vimineum*. The rapid invasion of *M. vimineum* resulted in reduced species richness and diversity. Despite the dominance of *M. vimineum* in all of the Privet-Removed plots, planted *A. gigantea* was able to grow and expand. In Privet-Removed plots where *A. gigantea* was planted, *M. vimineum* dominance was lower and species richness and diversity were higher. *A. gigantea* appears to be a species that can be planted during riparian restoration to compete with common non-native invasive species like *M. vimineum* and, in the process, reduce non-native invisibility and increase diversity.

Although *L. sinense* individuals have recruited into the Privet-Removed plots, these individuals are not as dominant as *M. vimineum* or *A. gigantea*. Even though these *L. sinense* seedlings have grown very slowly in these first three years, it is possible that they have been investing in belowground resources prior to initiating extensive aboveground growth. In other words, it is possible that *L. sinense* dominance may increase at some point in the future.

5.4.3 Plant restoration guidelines

L. sinense is an invasive non-native shrub that prevents understory plant community development in riparian ecosystems. Local short-term removal of mature *L. sinense* individuals is possible via the cut and paint method used in this study. Long-term removal of *L. sinense* would likely require some type of additional effort to remove seedlings during the first year (e.g., an herbicidal application or removal by hand; although mature *L. sinense* individuals cannot be removed by hand, seedlings with their roots are easily pulled out by hand). *L. sinense* seedlings did recruit into the site after the removal of mature individuals. Yet, *L. sinense* seedling growth was minimal during the three years of this study. We must stress that cutting mature *L. sinense* individuals without the herbicidal portion of the cut and paint removal treatment is not effective and will result in vigorous resprouting. Due to this vigorous vegetative growth and efficient dispersal, *L. sinense* is a highly invasive species and we consider it to be a species that should not be available commercially.

M. vimineum is a shade-tolerant C_4 species that dominates many disturbed riparian and upland forest ecosystems in the region via rapid growth rates, a large/persistent seed bank, and the development of a thick litter layer (Barden 1987, Gibson et al. 2002, Leicht et al. 2005). Invasive stands of *M. vimineum* typically limit understory succession (Oswalt et al. 2007, Adams and Engelhardt 2009, Flory and Clay 2009) and the shallow rooting depth of this species may contribute to poor bank stability at riparian restorations sites. Hence, there is much interest in techniques that can be used to constrain *M. vimineum* dominance and restore native plant communities (Judge 2006, Flory and Clay 2009). Although various removal methods have been assessed (Judge et al. 2005, Judge 2006, Vidra et al. 2007, Flory and Clay 2009), *M. vimineum*'s persistent seed bank makes long-term removal unlikely without follow-up removal efforts. In this study, the planted *A. gigantea* was able to compete with *M. vimineum*. One way to manage *M. vimineum* in a restoration setting is to plant tall native competitive-dominant species (i.e., tall herbaceous species, shrubs, or trees) that will be able to compete with *M. vimineum* for light. In this study, *A. gigantea* ramets were able to grow taller than *M. vimineum* and we conjecture that they were able to successfully compete with *M. vimineum* for light resources.

Our approach for limiting the dominance of non-native invasive species was simple: we planted a native competitive-dominant species (*A. gigantea*) that we thought would be able to help provide important ecosystem functions and also compete with the common non-native invasive species at the site. Studies of established canebrakes indicate that *A. gigantea* is capable of rapid clonal growth and expansion, especially in response to disturbances (Gagnon et al. 2007, Gagnon and Platt 2008a). This study indicates that such growth can also occur from planted *A. gigantea* genets during riparian restoration and in the presence of competitive species. In addition to canebrakes' cultural and historical significance in the southeastern U.S., these bamboo-dominated ecosystems provide several important services including the support of unique wildlife habitat (Brantley and Platt 2001) and ground and surface water quality improvements via nutrient and sediment reductions (Schoonover and Williard 2003, Blattel et al. 2005, Schoonover et al. 2005, 2006). As a result, there is much interest in restoring canebrakes and using *A. gigantea* for riparian restoration. However, we still know surprisingly little about the competitive ability, environmental requirements, and sexual reproduction of this unique plant species (Platt and Brantley 1997, Dattilo and Rhoades 2005, Gagnon 2006, Gagnon and Platt 2008b).

Our results emphasize several general conclusions that are applicable to other restoration efforts in other ecosystems with other plant species. First, during ecological restoration, invasive non-native plant removal alone will typically not restore native plant communities (D'Antonio and Chambers 2006, Vidra et al. 2007). Non-native invasive plant populations are typically very resilient to removal. The disturbance often associated with restoration and invasive non-native plant removal efforts will often result in reinvasion (either by the previously dominant species or by other species present in the area). Hence, sustainable reductions in non-native invasibility will often require additional efforts. One of the most straightforward approaches for improving ecosystems functions and reducing non-native invasibility after invasive plant removal is to carefully select and plant native species with competitive-dominant traits that will be able to compete with invading non-native species and resist invasion. Although this seemingly simple approach is often used by restoration practitioners, the results are rarely monitored and surprisingly few studies are designed to explicitly identify and investigate the performance of these important native competitive-dominant species.

References

Adams, S. N., and K. A. M. Engelhardt. 2009. Diversity declines in *Microstegium vimineum* (Japanese stiltgrass) patches. Biological Conservation **142**:1003-1010.

Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. Trends in Ecology & Evolution **14**:63-68.

Barden, L. S. 1987. Invasion of *Microstegium vimineum* (Poaceae), an exotic, annual, shade-tolerant, C_4 grass, into a North Carolina floodplain. American Midland Naturalist **118**:40-45.

Bartram, W. 1791. Travels through North & South Carolina, Georgia, East & West Florida. *in* M. van Doren, editor. 1928. The travels of William Bartram. Dover Publications, New York, New York.

Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in nontidal wetlands. Annual Reviews of Entomology **41**:75-100.

Bedford, B. L., M. R. Walbridge, and A. Aldous. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology **80**:2151-2169.

Beule, J. D. 1979. Control and management of cattails in southeastern Wisconsin wetlands. Wisconsin Department of Natural Resources Technical Bulletin 112, Madison, Wisconsin.

Blattel, C. R., K. W. J. Williard, S. G. Baer, and J. J. Zaczek. 2005. Abatement of ground water phosphate in giant cane and forest riparian buffers. Journal of the American Water Resources Association **41**:301-307.

Brantley, C. G., and S. G. Platt. 2001. Canebrake conservation in the southeastern United States. Wildlife Society Bulletin **29**:1175-1181.

Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of Southern Wisconsin. Ecological Monographs **27**:325-349.

Brendecke, W. W., and J. J. Zaczek. 2008. Greenhouse and field performance of giant cane propagules from natural and planted stands. Pages 8-19 *in* D. F. Jacobs and C. H. Michler. Proceedings of the 16th Central Hardwoods Forest Conference.

Gen. Tech. Rep. NRS-P-24. USDA, Forest Service, Northern Research Station, Lafayette, Indiana.

Brown, C. E., and S. R. Pezeshki. 2000. A study on waterlogging as a potential tool to control *Ligustrum sinense* populations in western Tennessee. Wetlands **20**:429-437.

Burnidge, W. S. 2000. Cattle and the management of freshwater neotropical wetlands in Palo Verde National Park, Costa Rica. M.S. Thesis. University of Michigan, Ann Arbor, Michigan.

Burton, M. L., L. J. Samuelson, and S. Pan. 2005. Riparian woody plant diversity and forest structure along an urban-rural gradient. Urban Ecosystems **8**:93-106.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature **443**:989-992.

Chiang, C., C. B. Craft, D. W. Rogers, and C. J. Richardson. 2000. Effects of 4 years of nitrogen and phosphorus additions on Everglades plant communities. Aquatic Botany **68**:61-78.

Cirtain, M. C., S. B. Franklin, and S. R. Pezeshki. 2004. Effects of nitrogen and moisture regimes on *Arundinaria gigantea* (Walt.) Muhl. seedling growth. Natural Areas Journal **24**:251-257.

Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. Science **280**:745-747.

Craft, C. B., and C. J. Richardson. 1997. Relationships between soil nutrients and plant species composition in Everglades peatlands. Journal of Environmental Quality **26**:224-232.

Craft, C. B., and C. J. Richardson. 2008. Soil characteristics of the Everglades peatland. Pages 59-72 *in* C. J. Richardson. The Everglades Experiments: Lessons for Ecosystem Restoration. Springer-Verlag, New York, New York.

Crawley, M. J., S. L. Brown, M. S. Heard, and G. R. Edwards. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? Ecology Letters **2**:140-148.

Crow, G. E. 2002. Aquatic plants of Palo Verde National Park and the Tempisque River Valley. National Biodiversity Institute, Santo Domingo de Heredia, Costa Rica.

D'Antonio, C. M., and J. C. Chambers. 2006. Using ecological theory to manage or restore ecosystems affected by invasive plant species. Pages 260-279 *in* D. A. Falk, M. A. Palmer, and J. B. Zedler, editors. Foundations of restoration ecology. Island Press, Washington D.C., U.S.A.

Daniels, A. E. *In press*. Forest expansion in northwest Costa Rica: conjuncture of the global market, land-use intensification and forest protection. *in* H. Nagendra and J. Southworth, editors. Reforesting Landscapes: Linking Pattern and Process. Springer, New York, New York, USA.

Daniels, A. E., and G. S. Cumming. 2008. Conversion or conservation? Understanding wetland change in northwest Costa Rica. Ecological Applications **18**:49-63.

Dattilo, A. J., and C. C. Rhoades. 2005. Establishment of the woody grass *Arundinaria gigantea* for riparian restoration. Restoration Ecology **13**:616-622.

Davis, C. A., and J. R. Bidwell. 2008. Response of aquatic invertebrates to vegetation management and agriculture. Wetlands **28**:793-805.

Davis, S. M. 1994. Phosphorus inputs and vegetation sensitivity. Pages 357-378 *in* S. M. Davis and J. C. Ogden, editors. Everglades: The Ecosystem and Its Restoration. St. Lucie Press, Delray Beach, Florida.

Debusk, W. F., S. Newman, and K. R. Reddy. 2001. Spatio-temporal patterns of soil phosphorus enrichment in Everglades Water Conservation Area 2A. Journal of Environmental Quality **30**:1438-1446.

Diaz, S., A. J. Symstad, F. S. Chapin, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. Trends in Ecology & Evolution **18**:140-146.

Downing, J. A. 1997. Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. Biogeochemistry **37**:237-252.

Downing, J. A., and E. McCauley. 1992. The nitrogen:phosphorus relationship in lakes. Limnology and Oceanography **37**:936-945.

Dufrene, M., and P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs **67**:345-366.

Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. Ecological Applications **11**:1287-1300.

Emery, S. M., and K. L. Gross. 2007. Dominant species identity, not community evenness, regulates invasion in experimental grassland plant communities. Ecology **88**:954-964.

Feedback, D., and J. O. Luken. 1992. Proper transplanting method critical in restoration of canebrakes (Kentucky). Restoration and Management Notes **10**:195.

Finlayson, C. M. 2005. Plant ecology of Australia's tropical floodplain wetlands: A review. Annals of Botany **96**:541-555.

Finlayson, C. M., I. D. Cowie, and B. J. Bailey. 1990. Sediment seedbanks in grassland on the Magela Creek floodplain, northern Australia. Aquatic Botany **38**:163-176.

Finlayson, C. M., and C. D. Woodroffe. 1996. Wetland vegetation. Pages 81-112 *in* C. M. Finlayson and I. Von Oertzen, editors. Landscape and Vegetative Ecology of the Kakadu Region, Northern Australia. Kluwer Academic, Dordrecht, Netherlands.

Flory, S. L., and K. Clay. 2009. Invasive plant removal method determines native plant community responses. Journal of Applied Ecology **46**:434-442.

Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. Trends in Ecology & Evolution **23**:695-703.

Gagnon, P. R. 2006. Population biology and disturbance ecology of a native North American bamboo (*Arundinaria gigantea*). Louisiana State University, Baton Rouge, Louisiana.

Gagnon, P. R., and W. J. Platt. 2008a. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. Ecology **89**:612-618.

Gagnon, P. R., and W. J. Platt. 2008b. Reproductive and seedling ecology of a semelparous native bamboo (*Arundinaria gigantea*, Poaceae). Journal of the Torrey Botanical Society **135**:309-316.

Gagnon, P. R., W. J. Platt, and E. B. Moser. 2007. Response of a native bamboo [*Arundinaria gigantea* (Walt.) Muhl.] in a wind-disturbed forest. Forest Ecology and Management **241**:288-294.

Galatowitsch, S. M., N. O. Anderson, and P. D. Ascher. 1999. Invasiveness in wetland plants in temperate North America. Wetlands **19**:733-755.

George, L. O., and F. A. Bazzaz. 1999. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. Ecology **80**:833-845.

Gerard, M., M. El Kahloun, J. Rymen, O. Beauchard, and P. Meire. 2008. Importance of mowing and flood frequency in promoting species richness in restored floodplains. Journal of Applied Ecology **45**:1780-1789.

Gibson, D. J., G. Spyreas, and J. Benedict. 2002. Life history of *Microstegium vimineum* (Poaceae), an invasive grass in southern Illinois. Journal of the Torrey Botanical Society **129**:207-219.

González, E. 2002. Restauración y manejo del Humedal Palo Verde, un Sitio Ramsar en el Registro de Montreux de humedales en peligro. Organization for Tropical Studies, San Pedro, Costa Rica.

Grime, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, Chichester, United Kingdom.

Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. Journal of Ecology **86**:902-910.

Grootjans, A. P., J. P. Bakker, A. J. M. Jansen, and R. H. Kemmers. 2002. Restoration of brook valley meadows in the Netherlands. Hydrobiologia **478**:149-170.

Hall, S. J., R. Lindig-Cisneros, and J. B. Zedler. 2008. Does harvesting sustain plant diversity in Central Mexican wetlands? Wetlands **28**:776-792.

Harper, J. L. 1977. Population biology of plants. Academic Press, London.

Hernández Esquivel, D. A. 1990. Flora acuática y sus cambios anuales en un humedal estacional de Costa Rica. M.S. Thesis. Universidad Nacional, Heredia, Costa Rica.

Horn, S. P., and L. M. Kennedy. 2006. Pollen evidence of the prehistoric presence of cattail (*Typha*: Typhaceae) in Palo Verde National Park, Costa Rica. Brenesia:85-87.

Howard, G. W. 1985. The Kafue Flats of Zambia: a wetland ecosystem comparable with floodplain areas of northern Australia. Proceedings of the Ecological Society of Australia **13**:293-306.

Jiménez, J. A., E. González, and J. Calvo. 2003. Recomendaciones técnicas para la restauración hidrológica del Parque Nacional Palo Verde. Organization for Tropical Studies, San Jose, Costa Rica.

Johnson, S., and E. Rejmánková. 2005. Impacts of land use on nutrient distribution and vegetation composition of freshwater wetlands in northern Belize. Wetlands **25**:89-100.

Judge, C. A. 2006. Japanese stiltgrass (*Microstegium vimineum*): Population dynamics and management for restoration of native plant communities. Ph.D. Dissertation. North Carolina State University, Raleigh, NC.

Judge, C. A., J. C. Neal, and J. F. Derr. 2005. Response of Japanese stiltgrass (*Microstegium vimineum*) to application timing, rate, and frequency of postemergence herbicides. Weed Technology **19**:912-917.

Kaminski, R. M., and H. H. Prince. 1981. Dabbling duck and aquatic macroinvertebrate responses to manipulated wetland habitat. Journal of Wildlife Management **45**:1-15.

Karam, A. 1993. Chemical properties of organic soils. Pages 459-471 *in* M. R. Carter, for Canadian Society of Soil Science, editor. Soil sampling and methods of analysis. Lewis Publishers, London.

Kazezyilmaz-Alhan, C. V., M. A. Medina Jr., and C. J. Richardson. 2007. A wetland hydrology and water quality model incorporating surface water/groundwater interactions. Water Resources Research **43**:1-16.

Kirby, R. M. 1976. Soil Survey of Durham County, North Carolina. USDA, Soil Conservation Service in cooperation with the North Carolina Agricultural Experiment Station, Washington, D.C.

Koerselman, W., and A. F. M. Meuleman. 1996. The vegetation N:P ratio: A new tool to detect the nature of nutrient limitation. Journal of Applied Ecology **33**:1441-1450.

Kolpin, D. W., E. M. Thurman, E. A. Lee, M. T. Meyer, E. T. Furlong, and S. T. Glassmeyer. 2006. Urban contributions of glyphosate and its degradate AMPA to streams in the United States. Science of the Total Environment **354**:191-197.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29**:1-27.

Leicht, S. A., J. A. Silander Jr, and K. Greenwood. 2005. Assessing the competitive ability of Japanese stilt grass, *Microstegium vimineum* (Trin.) A. Camus. The Journal of the Torrey Botanical Society **132**:573-580.

Linde, A. F., T. Janisch, and D. Smith. 1976. Cattail: the significance of its growth, phenology and carbohydrate storage to its control and management. Wisconsin Department of Natural Resources Technical Bulletin 94, Madison, Wisconsin.

Loaiciga, H. A., and T. H. Robinson. 1995. Sampling of agrochemicals for environmental assessment in rice paddies: dry tropical wetlands, Costa Rica. Ground Water Monitoring & Remediation **15**:107-118.

Loewenstein, N. J., and E. F. Loewenstein. 2005. Non-native plants in the understory of riparian forests across a land use gradient in the Southeast. Urban Ecosystems **8**:79-91.

Lovett Doust, L., and J. Lovett Doust. 1982. The battle strategies of plants. New Scientist **95**:81-84.

Maron, J. L., and R. L. Jefferies. 2001. Restoring enriched grasslands: effects of mowing on species richness, productivity, and nitrogen retention. Ecological Applications **11**:1088-1100.

Mateo-Vega, J. 2001. Características generales de la cuenca del Río Tempisque. Pages 32-72 *in* J. A. Jiménez and E. González, editors. La cuenca del Río Tempisque: perspectivas para un manejo integrado. Organization for Tropical Studies, San Jose, Costa Rica.

Mather, P. M. 1976. Computational methods of multivariate analysis in physical geography. John Wiley & Sons, London.

McClure, F. A. 1966. The bamboos: a fresh perspective. Harvard University Press, Cambridge, Massachusetts.

McCoy, M. B., and J. M. Rodriguez. 1994. Cattail (*Typha domingensis*) eradication methods in the restoration of a tropical, seasonal, freshwater marsh. Pages 469-482 *in* W. J. Mitsch, editor. Global Wetlands: Old World and New. Elsevier Science, Amsterdam, Netherlands.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B., and M. J. Medford. 1999. PC-ORD. Multivariate Analysis of Ecological Data, Version 4. MjM Software Design, Gleneden Beach, Oregon, USA.

McGill, W. B., and C. T. Figueiredo. 1993. Total nitrogen. Pages 201-211 *in* M. R. Carter, for Canadian Society of Soil Science, editor. Soil sampling and methods of analysis. Lewis Publishers, London.

McNaughton, S. J. 1966. Ecotype function in the *Typha* community-type. Ecological Monographs **36**:298-325.

McNaughton, S. J. 1975. *r*-and *K*-selection in Typha. The American Naturalist **109**:251-261.

Merriam, R. W. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. Journal of the Torrey Botanical Society **130**:283-291.

Merriam, R. W., and E. Feil. 2002. The potential impact of an introduced shrub on native plant diversity and forest regeneration. Biological Invasions **4**:369-373.

Miao, S. L., E. Sindhoj, and C. Edelstein. 2008. Allometric relationships of field populations of two clonal species with contrasting life histories, *Cladium jamaicense* and *Typha domingensis*. Aquatic Botany **88**:1-9.

Middleton, B. A. 1999. Succession and herbivory in monsoonal wetlands. Wetlands Ecology and Management **6**:189-202.

Miller, J. H. 2003. Nonnative invasive plants of southern forests: a field guide for identification and control.   SRS-62. USDA, Forest Service, Southern Research Station, Asheville, NC.

Miller, J. H., and T. Albritton. 2004. Privet is a plague: you can help stop it. Alabama Treasure Forests **23**:20-21, 26.

Mitsch, W. J., and J. G. Gosselink. 2007. Wetlands. John Wiley & Sons, New York, New York.

Morris, L. L., J. L. Walck, and S. N. Hidayati. 2002. Growth and reproduction of the invasive *Ligustrum sinense* and native *Forestiera ligustrina* (Oleaceae): implications for the invasion and persistence of a nonnative shrub. International Journal of Plant Sciences **163**:1001-1010.

Murkin, H. R., R. M. Kaminski, and R. D. Titman. 1982. Responses by dabbling ducks and aquatic invertebrates to an experimentally manipulated cattail marsh. Canadian Journal of Zoology **60**:2324-2332.

Murphy, J., and J. P. Riley. 1962. A modified single solution method for the determination of phosphate in natural waters. Analytica Chimica Acta **27**:31-36.

Nelson, N. F., and R. H. Dietz. 1966. Cattail Control Methods in Utah. Utah Department of Fish and Game Publication **66**:1-31.

NOAA. 2008. NOAA Online Weather Data. Raleigh (RDU) Monthly Climate Averages. *in* Raleigh Weather Forecast Office. National Weather Service, Raleigh, NC 27606 USA.

Noe, G. B., D. L. Childers, and R. D. Jones. 2001. Phosphorus biogeochemistry and the impact of phosphorus enrichment: Why is the Everglades so unique? Ecosystems **4**:603-624.

O'Halloran, I. P. 1993. Total and organic Phosphorus. Pages 213-229 *in* M. R. Carter, for Canadian Society of Soil Science, editor. Soil sampling and methods of analysis. Lewis Publishers, London.

Osland, M. J., J. W. Pahl, and C. J. Richardson. *in press*. Native bamboo (*Arundinaria gigantea* (Walter) Muhl., Poaceae) establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): implications for restoration. Castanea.

Oswalt, C. M., S. N. Oswalt, and W. K. Clatterbuck. 2007. Effects of *Microstegium vimineum* (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. Forest Ecology and Management **242**:727-732.

Pérez, G. L., A. Torremorell, H. Mugni, P. Rodríguez, M. Solange Vera, M. do Nascimento, L. Allende, J. Bustingorry, R. Escaray, M. Ferraro, I. Izaguirre, H. Pizarro, C. Bonetto, D. P. Morris, and H. Zagarese. 2007. Effects of the herbicide Roundup on freshwater microbial communities: a mesocosm study. Ecological Applications **17**:2310-2322.

Peters, G. 2001. La cuenca del Tempisque: una perspectiva historica. Pages 1-21 *in* J. A. Jiménez and E. González, editors. La Cuenca del Río Tempisque: perspectivas para un manejo integrado. Organization for Tropical Studies, San Jose, Costa Rica.

Platt, S. G., and C. G. Brantley. 1993. Switchcane: propagation and establishment in the Southeastern United States. Restoration and Management Notes **11**:134-137.

Platt, S. G., and C. G. Brantley. 1997. Canebrakes: an ecological and historical perspective. Castanea **62**:8-21.

Pratt, J. R., A. E. Melendez, R. Barreiro, and N. J. Bowers. 1997. Predicting the ecological effects of herbicides. Ecological Applications **7**:1117-1124.

Redfield, A. C. 1958. The biological control of chemical factors in the environment. American Scientist **46**:205-221.

Rejmánková, E. 2001. Effect of experimental phosphorus enrichment on oligotrophic tropical marshes in Belize, Central America. Plant and Soil **236**:33-53.

Rejmánková, E., K. O. Pope, R. Post, and E. Maltby. 1996. Herbaceous wetlands of the Yucatan Peninsula: communities at extreme ends of environmental gradients. Internationale Revue der gesamten Hydrobiologie und Hydrographie **81**:223-252.

Relyea, R. A. 2005. The impact of insecticides and herbicides on the biodiversity and productivity of aquatic communities. Ecological Applications **15**:618-627.

Richardson, C. J. 1979. Primary productivity values in fresh water wetlands. Pages 131-145 *in* P. E. Greeson, J. R. Clark, and J. E. Clark, editors. Wetland functions and values: the state of our understanding. Proceedings of the National Symposium on Wetlands. American Water Resources Association, Minneapolis, Minnesota

Richardson, C. J. 2008a. An ecological approach for the restoration of the Everglades fen. Pages 621-642 *in* C. J. Richardson. The Everglades Experiments: Lessons for Ecosystem Restoration. Springer-Verlag, New York, New York.

Richardson, C. J. 2008b. The Everglades Experiments: Lessons for Ecosystem Restoration. Springer-Verlag, New York, New York.

Richardson, C. J., R. Elting, J. Pahl, and G. Katul. 2006. Restoration of hydrologic and biogeochemical functions in bottomland hardwoods. *in* D. Amayta. International Conference on Hydrology and Management in Forested Wetlands. American Society of Agricultural and Biological Engineers. April 12-16, 2006., New Bern, North Carolina.

Richardson, C. J., G. M. Ferrell, and P. Vaithiyanathan. 1999. Nutrient effects on stand structure, resorption efficiency, and secondary compounds in Everglades sawgrass. Ecology **80**:2182-2192.

Rinella, M. J., B. D. Maxwell, P. K. Fay, T. Weaver, and R. L. Sheley. 2009. Control effort exacerbates invasive-species problem. Ecological Applications **19**:155-162.

Sarmah, A. K., U. Pillai-McGarry, and D. McGarry. 1996. Repair of the structure of a compacted Vertisol via wet/dry cycles. Soil & Tillage Research **38**:17-33.

Schierenbeck, K. A. 2004. Japanese honeysuckle (*Lonicera japonica*) as an invasive species; history, ecology, and context. Critical Reviews in Plant Sciences **23**:391-400.

Schoonover, J. E., and K. W. J. Williard. 2003. Ground water nitrate reduction in giant cane and forest riparian buffer zones. Journal of the American Water Resources Association **39**:347-354.

Schoonover, J. E., K. W. J. Williard, J. J. Zaczek, J. C. Mangun, and A. D. Carver. 2005. Nutrient attenuation in agricultural surface runoff by riparian buffer zones in southern Illinois, USA. Agroforestry Systems **64**:169-180.

Schoonover, J. E., K. W. J. Williard, J. J. Zaczek, J. C. Mangun, and A. D. Carver. 2006. Agricultural sediment reduction by giant cane and forest riparian buffers. Water, Air, and Soil Pollution **169**:303-315.

Sexton, R. L., J. J. Zaczek, and J. W. Groninger. 2003. Giant cane propagation techniques for use in restoration of riparian forest ecosystems. *in* J. W. Van Sambeek, J. O. Dawson, F. Ponder, Jr., E. F. Loewenstein, and J. S. Fralish. Proceedings, 13th Central Hardwoods Forest Conference. Gen. Tech. Rep. NC-234. USDA, Forest Service, North Central Research Station, St. Paul, Minnesota.

Smith, K. E., G. B. Rumon, S. A. Prior, A. J. Price, H. H. Rogers, and H. A. Torbert. 2008. Chinese privet (*Ligustrum sinense*) in an elevated CO_2 environment. Botany Research Journal **1**:43-48.

Smith, M. D., J. C. Wilcox, T. Kelly, and A. K. Knapp. 2004. Dominance not richness determines invasibility of tallgrass prairie. Oikos **106**:253-262.

Sommers, L. E., R. F. Harris, J. D. H. Williams, D. E. Armstrong, and J. K. Syers. 1970. Determination of total organic phosphorus in lake sediments. Limnology and Oceanography **15**:301-304.

Stewart, M. A. 2007. From king cane to king cotton: razing cane in the old south. Environmental History **12**:59-79.

Sutton-Grier, A. E. 2008. The role of plant functional diversity and soil amendments in regulating plant biomass and soil biogeochemistry in restored wetland ecosystems in the North Carolina Piedmont. Ph.D. Dissertation. Duke University, Durham, NC.

Tiessen, H., and J. O. Moir. 1993. Total and organic carbon. Pages 187-199 *in* M. R. Carter, for Canadian Society of Soil Science, editor. Soil Sampling and Methods of Analysis. Lewis Publishers, London.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey.

Trama, F. A. 2005. Manejo activo y restauración del Humedal Palo Verde: cambios en las coberturas de vegetación y respuesta de las aves acuáticas. M.S. Thesis. Universidad Nacional de Costa Rica, Heredia, Costa Rica.

Triplett, J. K., A. S. Weakley, and L. G. Clark. 2006. Hill cane (*Arundinaria appalachiana*), a new species of bamboo (Poaceae: Bambusoideae) from the southern Appalachian Mountains. Sida **22**:79-95.

Troxler, T. G. 2007. Patterns of phosphorus, nitrogen and $\delta^{15}N$ along a peat development gradient in a coastal mire, Panama. Journal of Tropical Ecology **23**:683-691.

Urbatsch, L. E. 2000. Plant guide: exotic weed species. Chinese privet *Ligustrum sinense* Lour. USDA, NRCS, National Plant Data Center, Baton Rouge, Louisiana.

Vaithiyanathan, P., and C. J. Richardson. 1999. Macrophyte species changes in the Everglades: Examination along a eutrophication gradient. Journal of Environmental Quality **28**:1347-1358.

van der Valk, A. G. 1981. Succession in wetlands: a Gleasonian approach. Ecology **62**:688-696.

van der Valk, A. G., B. A. Middleton, R. L. Williams, D. H. Mason, and C. B. Davis. 1993. The biomass of an Indian monsoonal wetland before and after being overgrown with *Paspalum distichum* L. Vegetatio **109**:81-90.

Verhoeven, J. T. A., W. Koerselman, and A. F. M. Meuleman. 1996. Nitrogen- or phosphorus-limited growth in herbaceous, wet vegetation: Relations with atmospheric inputs and management regimes. Trends in Ecology & Evolution **11**:494-497.

Vidra, R. L., T. H. Shear, and J. M. Stucky. 2007. Effects of vegetation removal on native understory recovery in an exotic-rich urban forest. The Journal of the Torrey Botanical Society **134**:410-419.

Villareal Orias, J. A. 2000. Tamaño poblacional, reproducción y habitat del Jabirú (*Jabiru mycteria*) en el Area de Conservación Tempisque, Costa Rica. Ministerio del Ambiente y Energía (Area de Conservación Tempisque), Instituto Nacional de Biodiversidad, Organización para Estudios Tropicales y American Bird Conservancy, San Jose, Costa Rica.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist **84**:468-478.

Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. Ecosystems **2**:95-113.

Watts, S. C. 2000. The effects of reduced flooding frequency on species composition in a bottomland hardwood stand in the piedmont of North Carolina. M.E.M. Thesis. Duke University, Durham, North Carolina.

Webster, C. R., M. A. Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. Journal of Forestry **104**:366-374.

Weiher, E., and P. A. Keddy. 1995. The assembly of experimental wetland plant communities. Oikos:323-335.

Weller, M. W. 1981. Freshwater marshes: ecology and wildlife management. University of Minnesota Press, Minneapolis, MN.

Weller, M. W., and C. S. Spatcher. 1965. Role of habitat in the distribution and abundance of marsh birds. Agricultural and Home Economic Experiment Station Special Report 43, Iowa State University, Ames, Iowa.

West, E. M. 1934. Canebrakes of the southeastern United States. Ph.D. Dissertation. Ohio State University, Columbus, Ohio.

Zedler, J. B., and S. Kercher. 2004. Causes and consequences of invasive plants in wetlands: opportunities, opportunists, and outcomes. Critical Reviews in Plant Sciences **23**:431-452.

Biography

Place and date of birth:

Atlanta, Georgia; December 22, 1977

Education:

Duke University: Ph.D. Candidate (expected May 2009), Ecology

Willamette University: B.A. (2000), Biology, *Cum Laude* with Biology Dept. Honors

Publications:

Osland, M. J., J. W. Pahl, and C. J. Richardson. *in press*. Native bamboo (*Arundinaria gigantea* (Walter) Muhl., Poaceae) establishment and growth after the removal of an invasive non-native shrub (*Ligustrum sinense* Lour., Oleaceae): implications for restoration. Castanea.

Grants, Fellowships, & Awards:

Organization for Tropical Studies (OTS) Research Fellowship (2007)

OTS-NSF International Research Experience for Graduate Students Grant (2007)

Fulbright Fellowship, U.S. Dept. of State, Institute of International Education (2006-2007)

Duke Graduate School Pre-Dissertation Research Travel Award (2005)

Duke Provost's Pre-Dissertation International Field Research Grant (2004 & 2005)

Tinker Field Research Grant (Duke Center for Latin Amer. & Caribbean Studies (2004)

Duke Program in Ecology Graduate Teaching Assistantship (2003-2006, 2007-2009)